

Nitty-Gritty into the Plant Microbiomes: **13** Understanding Microbial Niche Associations and Dynamics in Various Plant Parts

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Abstract

The plant microbiome, which can be found in every accessible tissue of healthy plants, is made up of a diverse collection of microorganisms that are classified according to their taxonomy. Plants with plant-associated microbiomes have improved growth, nutrient uptake, stress tolerance, and disease resistance, among other characteristics. Microbes associated with plants show several genetic, biochemical, physical, and metabolic links, all of which have implications for plant health. Beyond identifying information gaps and potential initiatives, we are investigating how a plant's microbiome can be influenced by these interactions, which can then alter the plant's ability to absorb nutrients and stay healthy.

Keywords

Plant microbiomes · Microbiota · Abiotic · Agriculture

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13.1 Introduction

The composition of the plant microbiome is bacteria, fungus, protists, nematode worms, and viruses. In their natural habitats, these bacteria create complex connections with plants, increasing plant productivity and health. Some argue that plants and bacteria constitute a "holobiont," with plant and bacterial evolution symbiotic. This is yet to be confirmed. The bulk of species in complex plant microbiological communities has deep branching lines and poor phylogenetic resolution. High-throughput sequencing allows us to better understand plant and environmental microbes. The phrase "core microbiota" refers to a set of bacteria that are constantly found around a single host in varying conditions (Lemanceau et al. 2017). Plant-associated microorganisms include archaea, algae, and nematodes, as well as bacteria and fungi. Plant-associated microbiome genes have aided our understanding of bacterial adaptation to plants. Many questions remain unresolved about how plants and microorganisms interact in communities.

The microbiome of a plant contains beneficial, neutral, and even harmful microbes. Plant development, nutrient uptake, and disease resistance have all been linked to microbial populations (Gouda et al. 2018). Microbial communities related to plants have beneficial features, but these benefits cannot be anticipated from individual member traits. Many elements are at play here, including the dynamics of pathogen populations and their interactions with the plant microbiome environments (Trivedi et al. 2017).

Microbes can assist their host plants in several ways, including nitrogen fixation, water conservation, disease protection, antibiosis, and hydrolytic enzyme production. However, improving a plant's resistance responses gives an indirect benefit. Researchers believe that plant-associated microbe interactions are a way of producing new phenotypes that can survive in a variety of situations (Trivedi et al. 2020). This is because the microbiome of plants influences several plant properties. It is possible to create synthetic communities (SynComs) of microorganisms that assist plant growth in greenhouse or field conditions. A brief overview of plant microbiomes is provided in this chapter, as well as information on microbiome types appropriate for each plant part and also on cultivational, abiotic stress factors on the molecular structures of plant microbiomes.

13.2 The Microbiome Composition of Plants

The microorganisms in microbiota are found in tissues that are intimately linked to plants. In terms of mineral and nutrient uptake, tolerance to stress, immunological regulation, and resistance to disease, plant microbiomes promote the genetic and metabolic performance of the host plant (Liu et al. 2020). Algae, bacteria, fungi, oomycetes, and archaea are important plant microbiomes. The majority of research data is accessible on bacteria (bacteriome) and to a lesser extent on fungi (mycobiome). Plant-microbiome interaction offers both merits and disadvantages. Some microbiomes promote plant growth, whereas others are harmful and neutral

(Glick 2020). The plant microbiota comprises a diverse range of species that are transported horizontally and vertically through the soil environment and seeds, respectively (Trivedi et al. 2020). Plant productivity enhancement mediated by microbiomes is a superb platform for a modern green revolution.

Plant species have a vast range of microbiome compositions (Chaparro et al. 2014), genotypes (Bressan et al. 2009), and even in highly similar plants with minor genetic changes, such as transgenics (Badri et al. 2009). An organism's microbiome can be significantly altered by abiotic stress (drought, salinity, temperature, and UV radiation, among other things) (Lin et al. 2016).

13.3 Diverse Microbial Niches in Various Plant Parts

Plants are connected to the majority of microbes in the indigenous ecosystem, and they interact with a wide variety of systems. The highly varied plant system seems to have a better degree of microbial diversity (Mahnert et al. 2015). Decomposition of leaves and branches, as well as the discharge of root exudates, can affect microbial diversity (Millard and Singh 2010). Plants regulate multiple processes in this environment to attract or deter microorganisms from the bulk soil microbiome. The microbiological diversity of the bulk soil is directly related to the effectiveness of these selective mechanisms. The differences in properties of plant-microbe interactions in natural and agricultural ecosystems are depicted in Fig. 13.1.

Plant diversity represents varied root systems and exudate composition along with high microbial diversity. In a natural ecosystem, plants rely on microbiomes for nutritional supplements and protection. The agricultural field, on the contrary, has a low diversity of species of plants and a monotonous exhibition of roots and exudates. This lowers the microbiological diversity. A greater number of investigations are there on the microbiomes of plants found in forest ecosystems of extreme environments (Jorquera et al. 2016), in normal forest trees (Bonito et al. 2014), or in plants with different strengths such as *Arabidopsis thaliana* (Zolla et al. 2013) and medicinal plants. Recent data indicate that some core phytomicrobiome species are present in the majority of samples of a specified plant species, despite geographical and environmental situations (Hamonts et al. 2018). Plants are highly focused on

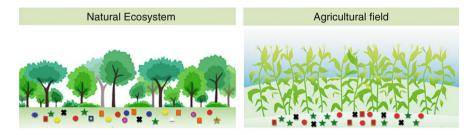


Fig. 13.1 Differences in plant and microbe traits and microbial interactions in natural ecosystems and agricultural fields

selecting the microbiota from the atmosphere (flower environment), the troposphere (external environment of fruits), and the phyllosphere (external environment of aerial plant parts and germinated seeds (Hardoim 2015). *Actinobacteria, Firmicutes, Bacteroidetes,* and *Proteobacteria* appear to predominate in aboveground portions (branch, leaf, flower, and seed) (Steven et al. 2018). The largest reservoir of microbial habitats is the rhizosphere microbiome. *Planctomycetes, Verrucomicrobia, Acetobacteria,* and *Gemmatimonadetes* are the dominant bacteria in the root microbiome, according to previous research.

13.4 Microbiomes of Plant Parts in the Rhizosphere

13.4.1 The Microbiome of the Roots

Root-associated microbiomes have an important function in providing nutrition, immunity, and long-term viability in a tough environment (Fitzpatrick et al. 2018). Root microbiomes are thought to serve a similar and broad function in plant health and fitness as gut microbiomes do in humans, including the supply of nutrients, defense from pests and diseases, and adaptability to stress (Singh et al. 2018). The plant primarily selects the root microbiomes by structural reforms and by secretion of carbohydrates, amino, and organic acids through the root exudation. The rhizobiome serves as a magnet for soil bacteria, attracting or repelling them to the plant. The relationship between soil bacteria and roots is regulated by root exudates. Monosaccharides (fructose, mannose, and glucose), disaccharides (maltose), five carbon (arabinose), and oligosaccharides are among the sugar molecules found in root exudates. Microbes, on the other hand, select plants based on their expandability and capability for resources, as well as their potential to offer tolerance to abiotic and biotic challenges (Trivedi et al. 2020). The amino acids; organic acids such as benzoic, ferulic, and ascorbic acids; and some tannins, flavonoids, steroids, terpenes, etc. are found in exudates of roots and play an imperative role in microbiome selection and recruitment.

Because of their role as a microbial seed bank for plants and interactions with soil, root-associated microbiomes (e.g., endosphere) are extraordinarily diverse (e.g., endosphere). In-plant roots, *Actinobacteria*, *Proteobacteria*, and *Bacteroidetes*, are prominent microbial components (Hacquard et al. 2015). Several studies of root microbiomes have confirmed the enrichment reports mentioned above and the reduction reports on plant root microbial taxa including maize, *Arabidopsis*, lettuce, barley, sugarcane, and rice (Cordero et al. 2020). The schematic representation of communities of microbe fluctuation within plant root and different parts of soil is shown in Fig. 13.2 (Glick and Gamalero 2021).

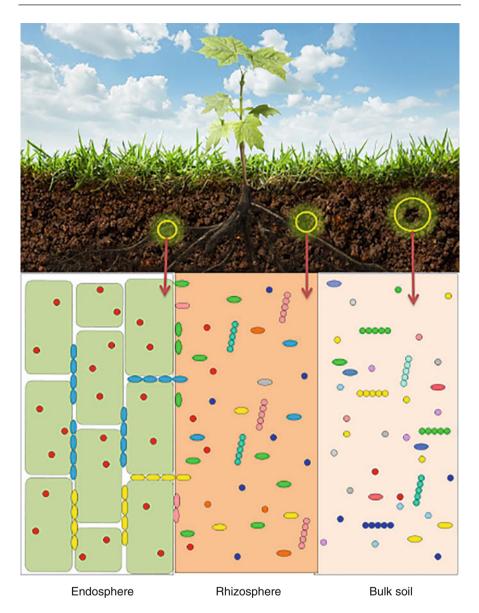


Fig. 13.2 A schematic representation of several microorganisms found in the endosphere, rhizo-sphere, and bulk soil of plants (Glick and Gamalero 2021)

13.4.2 The Microbiomes of Aboveground Plant Components

The phyllosphere of plants has diverse microorganisms. This diversity depends on the exudation of trichomes, wax layers, and secondary metabolites of the plant (Remus-Emsermann and Schlechter 2018). The exterior portion of the leaf, flower,

stem, and their endosphere makes up the microbial habitats. The nectar microbiomes, which interact with pollinators, are shown to impact pollinator behavior and health and are thus gaining more study interest (Liu et al. 2019). Surface phyllosphere microbiome cultivar-dependent selection can be affected by abiotic variables such as humidity, increasing radiation levels, temperature fluctuations, nutrient accessibility, and genetic composition of plants in both direct and indirect ways (Singh et al. 2019). Enzymes, phytohormones, biocontrol agents, and other metabolic products generated by seed-borne endophytes enhance the productivity and efficiency of a plant under stressful circumstances (Mukherjee et al. 2020b). The restoring seed microbiome results in the improvement of plant growth (Mukherjee et al. 2020a).

13.4.3 Can Seed Microbiomes Influence Plant Health?

Seeds are the most important products in most farmed crops, beneficial for human consumption as well as for crop cultivation. The seed microbiome contains a vast range of microbial species that can influence plant health through symbiosis, interspecific cooperation, commensalism, and harmful interactions (Links et al. 2014). Individual plant species have particular microbial species on a surface within the seed that act as a microbiome pool for the plant's endophytic microbiome. The predominant phyla of microbial groups mentioned above can colonize seeds. Seed microbiomes vary in richness of microbes and composition based on numerous environmental factors, including abiotic and biotic factors (Klaedtke et al. 2016).

Phyla Actinobacteria, Proteobacteria, Bacteroidetes, and Firmicutes evolved a vast spectrum of microbial taxa from their original seeds (Johnston-Monje et al. 2016). Alfalfa and *Cucurbita pepo* seed microbiomes are dominated by *Proteobacteria*, Actinobacteria, and Firmicutes, according to other studies (Adam et al. 2018). Plant species, soil, and environmental conditions all influence seed microbiome formation (Nelson 2018). Endophytic mycobiota for germinating seeds is derived from seed fungal endophytes, which are dominated by *Ascomycota* (Raj et al. 2019). According to Vujanovic et al. (2019), seed microbiome components can be transferred to direction perpendicular from one generation to the next, but the mechanism of seed microbiome congregation and the ecological process of seed microbiome remain a mystery.

Enzymes, phytohormones, biological controls, and other byproducts generated by seed-borne endophytes improve plant productivity and effectiveness under stressful environments. Previous research has shown that restoring seed microorganisms in plants with different plant growth-promoting treatments can boost the plant development in chickpeas (Mukherjee et al. 2020a). A great deal of potential exists in the use of seed microbiome to manage abiotic or biotic challenges and, as a result, boost crop output. According to a recent discovery, flower inoculation is a well-developed method for testing scientific questions and in the future also for exploiting microbiomes of seed for long-term agriculture (Mitter et al. 2017).

13.4.4 Flower Microbiomes in Plant Reproductive Success

The environment of flower microbiomes has a critical role in the persistent viability of essential ecosystem facilities, as well as with reproductive potential of plant and communication with useful insects. Flower-associated microbial communities, on the other hand, are far less linked to the microbiome of the phyllosphere (Massoni et al. 2020). The flower microbiome's heterogeneity and diversity are far lower than that of the phyllosphere microbiome. Owing to the nutrient-rich and excessive osmotic potential of the nectar present in the flower, *Bacteroidetes, Proteobacteria*, and *Firmicutes* are the most common taxa detected in floral microbiomes, which differ from root and leaf microbiomes. Aside from that, the flower has an open habitat that allows microorganisms, both pathogenic and plant probiotics, to spread through insects and other animals (Kim et al. 2019).

Floral microbiomes also provide insight into the overall ecology of microbial community which can be used as models to study microbiological construction and survivorship. Finally, knowing the repercussions of flower microbial communities throughout the plant's entire lifecycle, from inflorescence to fruit to endosperm and thereafter to a normal adult, will help researchers determine whether vertical flower microbiota transmission is feasible and prevalent, as well as which floral communities behave as native reservoirs for microbiota of plant in general.

13.4.5 Leaf Microbiome Modulates the Host Plant Immune System

The microbiome found in the leaf is an important element of the plant that regulates transpiration and photosynthesis which inturn on plant development and expansion. As a result, the microbiome on the leaf can modify the plant's functional qualities to protect it from changing surroundings and weather patterns. Toju et al. (2019) discovered that Alphaproteobacteria (Sphingomonas and Methylobacterium) exhibited more controlling leaf-associated bacterial associations in the tomato plant, while Bai et al. (2015) discovered that Gammaproteobacteria (Pseudomonas sp.) proved more controlling bacterial leaf associations in non-cultivating and cultivating plants. In most leaf microbiomes, the phylum Proteobacteria has been found. Leaf microbiomes of rice plants are identified as Burkholderia, Pseudomonas, Xanthomonas, and Mycoplasma (Roman-Reyna et al. 2020). Epicoccum was discovered to be the most abundant genus among ancient plants. In the microbiome of tomato leaves, ascomycete and basidiomycete fungi were shown to be more colonized. Similarly, the fungus taxa Moesziomyces, Hannaella, Cladosporium, and *Dioszegia* were found in abundance in the tomato leaf microbiome (Toju et al. 2019). Leaf microbes are resistant to abiotic stress factors (Crombie et al. 2018). However, the overstressed and degraded state of the leaf renders these environments selective to specific bacteria. Colonization development may be dependent on a range of microbial activities, including the ability to take nutrients and creation of biofilm from the environment (Streletskii et al. 2019). Plant fitness is influenced by leaf microorganisms under abiotic stress circumstances such as harmful UV

radiation, oxidative stress, and dehydration, and they can use vitamins on the surface of leaves (Yoshida et al. 2019). The aboveground tissue plant growth and immune system of the host plant are modulated by leaf microbial communities (Stone et al. 2018).

13.5 Root-Shoot Circuit Microbiota Promotes Plant Stress Resistance

Endophytic bacteria have been found in the shoot material of several plants, according to research. Communities of Sphingomonas, Methylobacterium, and Curtobacterium are more limited in sugarcane stalks, according to Hamonts et al. (2018). The biomass of Sedum alfredii shoots increased twofold after vertical transmission in irradiated soil, according to Luo et al. (2019). Sedum alfredii shoot biomass is significantly connected to a dominant set of microbial linkages from Streptomycetaceae, Nocardioidaceae, and Nocardioidaceae. To spread vertically, these endophytes can grow primarily in the shoot meristem of newly generated shoot tissue (Shahzad et al. 2018). Bidirectional microbiota-root-shoot interactions are expected to play a substantial impact on plant health because plant root microbiota governs the host development and immunological systems (Hacquard et al. 2015). Researchers (Stassen et al. 2021) predict that by year 2020, there will be a prominent enhancement in the number of people with autism spectrum disorder (ASD). Rootshoot microbiota circuit helps plants cope with stress to get a better grasp of how signals from microbes in the soil and the environment aboveground interact to influence plant behavior.

13.6 Plant and Microbe: Molecular Interactions

There are both living and nonliving elements in bulk soil that interact frequently to preserve ecosystem equilibrium. Rhizosphere shows interactions between two plants or two microbes and between a plant and microbe (Richardson and Simpson 2011). Decomposition of organic debris, recycling of nutrients, toxicity removal, suppression of pathogens, and noxious species are all facilitated by the soil microbiome (Singh 2015a, b). A symbiotic and defensive link between plants and bacteria is commonly regarded as a result of molecular signaling. Both plant- and microbederived signaling molecules are implicated in plant-microbe interactions. As a result, the signaling molecule consists of both primary and secondary metabolites (e.g., carbohydrates, proteins, and organic acids). Bacteria and fungi release substances like auxins and cytokines that affect cell proliferation and root system architecture, resulting in increased water absorption and lateral root hair growth (Ortíz-Castro et al. 2009). Acyl-acetoin and 2,3-butanediol are the bacterial volatile chemicals that act as the signaling molecules for plant-microbial communication and hence stimulate plant growth promoters (Ortíz-Castro et al. 2009). Bacterial exudates emit citrate, oxalate, and malate, which work as detoxifiers in the rhizosphere to remove aluminum toxicity. The plant's ability to endure aluminum toxicity is enhanced by the organic acids produced by the bacterial community (Ma et al. 2001). Lipopolysaccharides are produced by the plant as a result of the release of flavonoids, which communicate with the rhizobia-legume signal transduction pathway (2010). *Fusarium oxysporum*, a soil-dwelling plant pathogen, grows in the roots of the tomato host plant when class III peroxidases are active, as shown by Turrà et al. (*Solanum lycopersicum*). There are a wide variety of signaling molecules and their specific roles in microbial communities, which enhances the communication between plants and microorganisms.

13.7 Impact of Plant Microbiomes on Biological and Non-Biological Variables

13.7.1 Pathogens

Plant phytoconstituents reduce plant infections, acting as antibiotics that inhibit the diseases' growth and reproduction. Many bacterial and fungal diseases, larvae, and insects are vulnerable to phytohormones and phytoconstituents in recent times. By reactivating dormant microbiota and producing phytohormones, these plant microbiomes are involved in offering protection against infections and biotic stress (Figuerola et al. 2015). Resistance to the fungus *Gaeumannomyces graminis* was established by inoculating barley with *Pseudomonas* species, which function as antagonists and protect the plant from infections (Rodriguez et al. 2019). *Rhizophagus irregularis*, an AM fungus, increased *Medicago truncatula*'s resistance to *Xanthomonas campestris*, and rhizobia enhanced its resistance to *Erysiphe pisi* (Smigielski et al. 2019).

13.7.2 Abiotic Stress

Microbial communities subjected to natural environmental conditions affect the evolution of microbiomes in varied forms (Tripathi et al. 2017). There were distinct microbial communities in the rhizospheres of plants grown in different climates. Arid ecosystems, on the other hand, lack diversity in taxonomic and functional variety. The microbiota of the rhizosphere differs significantly among soil types and nations, and these differences in taxonomic richness and structure were found to be exacerbated by the effects of environmental alterations on diverse microbiomes. The pH of the soil was found to be a significant factor in taxonomic diversity and structure (Simonin et al. 2020). Abiotic factors that affect microorganisms, such as drought, are critical. As a result of soil osmotic stress, nutrients are unable to move freely, and oxygen cannot get to the soil. *Actinobacteria* and *Chloroflexi* are among the microbes that are more prevalent in the rhizospheres of drought-resistant plants, but *Acetobacteria* and *Deltaproteobacteria* are less prevalent. A rise in the number of *Acetobacteria* was seen in the root microbiome when drought circumstances

prevailed (Fitzpatrick et al. 2018). In part, it is due to a decrease in the affluence of antagonistic microbes such as *Streptomycetes*, *Micrococcaceae*, and *Mycobacteriaceae*, which change their microbe community and reduce their disease suppression rate. The bacterial community in the microbiome is profoundly affected by temperature variations, which aids in disease suppression (van der Voort et al. 2016). Radiation changes leaf bacterial populations by damaging the DNA of microbes. Some bacteria can withstand high levels of ultraviolet radiation due to the existence of pigments and mucopolysaccharides and the production of spores (Kumar et al. 2019).

13.8 Sustainable Agricultural Practices for Enhanced Productivity

Plant microbiomes are constantly changing as a result of regular agricultural practices. Changes in soil properties are to blame for this phenomenon. Directly stimulating or inhibiting the microbiota's activity, depending on dietary preferences, is one way it can influence it while trying to interfere with the way plants select microorganisms is another (Cai et al. 2016). The protection of microbial flora is becoming increasingly important as sustainable technology gains traction around the world. Plant microbial communities need to be studied extensively to understand their importance and influence on their structure. The bacterial microbiome of Yebra mate is altered by the use of agroforestry and the application of the green manure system, whereas monoculture cultivation results in an abundance of fungal microbiome development (Bergottini et al. 2017). Plant microbiomes are frequently altered as a result of routine agricultural practices. Soil characteristics change as a result of this effect. Depending on the diet, it can either stimulate or impede the microbiota's activity, or it can interfere with the way plants select microorganisms indirectly (Cai et al. 2016). There is a pressing need to protect microbial flora as sustainable technology takes the root in agriculture around the world. Plant microbial community structure must be studied extensively to understand its importance and influence. While the Yebra mate bacterial microbiome grows in abundance when grown in a monoculture, the agroforestry systems and green manure usage change the bacterial microbiome structures (Bergottini et al. 2017).

In comparison to the usual cultivation system, the use of organic compost and rotational cultivation for crops enhances the phylogenic, microbial, and bacterial diversity of the soil. *Fusarium* pathogens are inhibited by the use of mulch in the potato's rhizosphere, which increases fungal diversity (Qin et al. 2017). Nitrogen fertilizer application is a common practice in agriculture, and understanding the microbiome's response to nitrogen fertilizer application is critical. *Bacillales*, *Rhodocyclales*, and *Nitrosomonadales*, all of which play a role in nitrogen cycling, are impacted by nitrogen fertilizer use (Zhu et al. 2016). For more than a decade, long-term monoculture alters the structure of soil microbiomes. A decline in *Firmicutes* in non-rhizospheric soil was observed in studies on black pepper conducted over a four-decade period that showed monoculture increased bacterial

phyla levels in the rhizosphere (Li et al. 2016). Beneficial bacterial population reduction is depicted to have increased rhizosphere *Fusarium* population. Crop rotation between black pepper and banana has been shown to reduce *Fusarium oxysporum* pathogens while increasing the microbiome structure composed of *Gemmatimonas, Sphingobium, Sphingomonas, Penicillium,* and *Chaetomium.* Seed microbiomes alfalfa (Lopez et al. 2017) and *Cucurbita pepo* (Adam et al. 2018) were found to be predominated by *Proteobacteria, Actinobacteria,* and *Firmicutes* in other studies (Fig. 13.2). Soil, environmental conditions, and plant species all influence the seed microbiome's composition (Nelson 2018). Sugar beets have a very limited microbial genetic diversity, whereas wild plants have a much more diverse bacterial community (Zachow et al. 2014).

13.9 Future Perspectives and Conclusions

We can boost a plant's productivity by inoculating the soil with a microbial community that we know everything about, thanks to our detailed knowledge of its microbiome. Cultivating a variety of plant species in the same location is one traditional method of increasing microbial diversity. The microbiota of plants is essential for their survival in addition to the basic nutritional needs of plants. When cultivating and harvesting plants, the plant mycobiome is one of the most important aspects to consider. Under both living and nonliving stress conditions, the plant's microbial community provides protection. To better understand and help plants, more research into the microbiome interactions is required. Plants need microbiota in addition to their basic nutritional and other needs to thrive. Cultivated and wild plants alike must consider the plant mycobiome. Plant defenses are assisted by the microbiome in both biotic and abiotic stress situations. To better understand and improve the lives of plants, researchers need to study the interactions between plant microbiomes in greater detail.

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