



(REVIEW ARTICLE)



Phytomicrobiome systems affect plant health and crop production

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Abstract

The sustainability of plant life is intimately connected to its evolution with microbial life. Based on experimental evidence, microbial assemblages benefit plants on molecular, cellular, and ecological levels. The plant microbiome or phytomicrobiome are the microbes closely associated with a particular plant species. Distinct plant microbial ecosystems are in the phyllosphere, rhizosphere, soil, and endosphere. Plant-associated microbes affect plants in numerous ways and participate in various physiological functions essential for the plant, including nutrient recycling, the breakdown and synthesis of critical molecules, and other phytoprotective functions. While studying plant-microbe interactions is not new, recent developments in metagenomic sequencing and high-throughput pathway identification techniques have allowed scientists to explore unculturable microbes associated with plants. This review primarily focuses on the significant role of the phytomicrobiome and describes the prevalent taxonomic units found in association with plants. Plants are suitable tractable model systems to study plant-microbe interactions and can be grown under different experimental conditions to examine other characteristics of the phytomicrobiome. This article also provides a systematic review of the current research on the phytomicrobiome. It explores the extent to which the phytomicrobiome participates in an essential process that promotes plant fitness and sustainability and reviews research that focuses on microbiome community shifts in response to abiotic and biotic stress. Genetic engineering of plant-associated microbes to enhance plant growth and protection is addressed. The use of nanofertilizers and phytomicrobiome transplantation to restore plant health and improve the success of agriculturally beneficial crops is also discussed.

Keywords: Holobiont; Phytomicrobiome; Metagenomics; Earth Microbiome Project

1. Introduction

The phytomicrobiome refers to all the microorganisms internally or externally associated with the plant [1]. The phytomicrobiome represents the amalgam of different and distinct microbiomes that impact plant viability. A staggering number of symbiotic microbial species are evolutionarily linked with varying components of the plant. Microbes and plant cells engage in synergistic and reciprocal processes to benefit plants and the environment in numerous ways. Data suggest that plants determine the specificity of their microbial populations regardless of growth conditions. The biological details by which plants mediate microbial specificity need more investigation. While the complete role of the phytomicrobiome is still being unraveled, evidence has shed light on its role in plant growth, health, signaling, and crop productivity.

Over the last ten years, an increasing number of experimental investigations have attempted to understand the taxonomic organization of plant-microbe interactions. While it is widely known and intuitive that pathogenic microorganisms (e.g., viruses, bacteria, fungi) play a role in plant health and function, it is becoming evident that symbiotic microbes also play a role in plant health, maintenance, physiology, and sustainability. Like humans, evidence suggests that plant health depends on the intricate balance of plant-associated microbes. Understanding the nature of

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beneficial holobionts will allow scientists opportunities to develop microbial restoration and remediation strategies to improve plant fitness and crop stability [2]. Determining the optimal distribution of microorganisms for crop success may yield more productive crops and address food insecurity. That is, if crop output is dependent on the types of microorganisms in close association with the crops, it may be possible to transplant specific microbial communities to crops and make them more resistant to pests and drought. Examining existing phytomicrobiome data using meta-analysis will reveal new information about the complex ways bacterial communities communicate to promote plant health.

These studies will also indicate the nature of the microbiome on different parts of the plant and how one microbial community in one region affects the microbial community in another. Moreover, carefully designed experiments can interrogate the role of the phytomicrobiome during natural disasters and soil erosion and examine the effects climate change, air pollution, and oil spills have on plant microbial signatures and function. The unique microbial signature linked to a particular plant is based on many factors, including the plant's genetic disposition, environment, and anatomy. The phytomicrobiome, like the human microbiome, is subject to change over time during the organism's life, and that change often is correlated with the health of the plant.

Following the completion of the Human Microbiome Project in 2016 [3], a broad front of research has elucidated the importance of the phytomicrobiome. While there are significant methodological and knowledge gaps in phytomicrobiome research, positive correlational studies indicate that the phytomicrobiome plays a role in the processing and assimilation of chemicals and other nutrients in organisms and environmental sectors, including oceans, soil, and the atmosphere. As reviewed by Arif et al. [4], utilization of targeted plant-linked bacterial communities or plant microbiome engineering can enhance crop productivity and confer protective characteristics to plants. They argue that both indirect (e.g., soil enhancements, microfertilizers, plant probiotics) and direct (e.g., microbiome transplantation) agricultural strategies should be considered to positively augment plant qualities. Current experimental investigations are beginning to provide underlying molecular details regarding how plant-associated microbiomes influence plant cells and biological processes. Moreover, exploring how microbial genomes and proteins affect plant physiology is presently lacking in the literature. A combination of shotgun metagenomics, metabolomics, and metaproteomics will answer fundamental questions regarding how the endogenous phytomicrobiome and artificial phytomicrobiome contribute to plant growth, disease, and protection from environmental factors [5]. Identification of transformative bacterial genes coupled with biotechnology approaches may lead to the development of future commercial plant-associated microbiomes that enhance specific plant properties.

Averill et al. [6] employed meta-analysis from eighty different studies to demonstrate that enriching the soil with advantageous microbes can dramatically increase the size of plants. Moreover, nanofertilizers have been discussed to alter soil conditions and microbiome stability to enhance plant productivity [7-8]. Nanofertilizers catalyze a prolonged and highly efficient transfer of nutrients from nanomaterials to the biological organism. Accumulating data suggests that nanofertilizers impact plant characteristics (e.g., crop yield) and microbiome structure stability. More work must be completed to address critical bottlenecks and limitations associated with nanofertilizers.

A summary of the evidence of microbes associated with the phyllosphere, rhizosphere, soil, and endosphere forms the basis of this review article. Future research and review articles will focus on each distinct region and examine the microbe-plant interface. Future research studies that elaborate the precise mechanisms that determine phytomicrobiome specificity and resolve plant-mediated signaling strategies to recruit bacteria and other microbes during threat detection are necessary to advance phytomicrobiome science. Moreover, a molecular comprehension of the microbial metabolic programs that facilitate plant growth is paramount for developing the discipline. It may lead to conceptualizing sustainable microbial-based methods to address global food production and insecurity problems.

2. Phyllosphere Microbiome

The phyllosphere region on a plant represents the structures located above ground (e.g., above the soil). The phyllosphere is in clear contrast to the rhizosphere, which is located below ground. The interaction between the phyllosphere, air, pollutants, climate patterns, and biological organisms affects the microbial community structure of the phyllosphere microbiome [9]. It is generally believed that the phytomicrobiome displays targeted plasticity and can enlist various taxonomic groups to protect the plant from infection from harmful microorganisms and other abiotic complications. A more thorough understanding of phyllosphere and rhizosphere microbiome communication strategies will provide elusive details into the complex events involved in microbiota-dependent defense and health promotion mechanisms from above ground and below ground microorganisms. Identifying bacteria specific to the phyllosphere may expand our understanding of its function.

The phyllosphere microbiome was recently shown to undergo antifungal modifications in response to *Diaporthe citri* [10]. Following infection with the fungal pathogen, infected citrus leaves, compared to uninfected leaves, demonstrated a dramatic increase in microbes with purported antimicrobial activities to target *D. citri* and to mitigate the impact of infection on plant health. Isolation and characterization of recruited microorganisms, such as *Pantoea* and *Methylobacterium*, may identify novel strategies to fight plant-based infections to reduce our global dependence on potentially dangerous chemicals for which the long-term effects on human and environmental health remain unclear. Reducing antibiotic resistance genes in the phyllosphere is a significant problem for critical crops. The phyllosphere harbors deleterious antibiotic resistance genes that may increase the presence of antibiotic resistant organisms. Deng, Li, and Zhu [11] demonstrated that film mulching was adequate and sufficient to block the transfer of antibiotic resistance genes from the soil to the phyllosphere. Attenuation of the dispersal of antibiotic resistance genes and confinement of these problematic genes may help lessen the burden antibiotic resistance genes may cause on humans.

3. Rhizosphere Microbiome

The rhizosphere represents the microbial communities nearest the plant root system [12]. The rhizosphere plays a significant role in maintaining the chemical environment of the soil and stimulating the growth of rhizosphere microbial populations. It also plays a role in the gene expression and secretion of critical microbial factors vital to environmental biogeochemical cycles, inhibition of macroscopic and microscopic organisms, and plant growth. Plant microbiome research studies have demonstrated the importance of rhizosphere-associated microbes to plant health and immunity. Specifically, much work has been done to explore plant growth-promoting rhizobacteria (PGPR). Rhizobacteria perform several functions, including modifying lateral and primary root development and root hair extension [13]. As with all microbiomes, the relationship between the host and microbe can be beneficial or harmful. Healthy and productive plants and crops result from proper nutrients, abiotic factors, and supportive root exudates that create a healthy balance of the holobiont. A greater comprehension of the genomic structure of commensal microbes in the rhizosphere will aid our knowledge of root signaling mechanisms in the rhizosphere. To better understand the impact of rhizosphere-associated microbiomes on disease resistance to bacterial pathogens, researchers compared two types of tomato plants, a resistant tomato plant (Hawaii 7996) and a tomato plant (Moneymaker) susceptible to *Ralstonia solanacearum*, a common soil-dwelling disease-causing bacterium [14]. They found critical differences in the rhizosphere microbiome populations of the two tomato plants suggesting that distinct microbial species may play unique roles in counteracting the pathogenic effects of *Ralstonia solanacearum*.

Transplantation of the rhizosphere microbiome from the resistant Hawaii 7996 plants to Moneymaker plants was sufficient to reduce disease progression in the susceptible tomato plants. Moreover, genomic analysis led to the discovery of a single flavobacterium, TRM1, shown to block *Ralstonia solanacearum* through unknown mechanisms. Enhanced information regarding the structure and activity of the rhizosphere from diverse environments and in response to environmental stressors may yield promising rhizosphere engineering strategies to address global crop productivity and sustainability issues [15].

4. Soil Microbiome

Many research studies have investigated the soil microbiome and its impact on plant properties and components. Recently, researchers utilized soil microbiome disruption (SMD) techniques to determine how disrupted soils would affect the microbiota composition of corn, beet, lettuce, and tomato crops. [16]. Following SMD using heat sterilization, crops were planted to observe microbial population distribution. Microbiome analysis revealed decreases in many bacterial symbionts and increases in beneficial bacteria such as *Dyadobacter* and *Luteoliobacter* in all four crops. *Dyadobacter* was shown to play a positive role in the bioremediation of contaminated soil [17]. The results suggest that following deleterious ecological events in the soil, such as soil microbiome disruption, certain plants can direct proficuous bacterial occupation in the soil and rhizosphere to maintain and enhance plant growth. The route of bacterial dispersal affects microbiome constituency and function. Experiments demonstrated that above ground and nearby ground dispersal patterns were sufficient to alter soil microbial assemblage [18].

The question of whether the use of soil tilling practices could modify the structure of microbial communities was addressed by Kraut-Cohen et al. [19]. Soil tillage was shown to alter microbial abundance but did not significantly affect the microbial diversity or the ability of soil to maintain and grow crops. Additionally, Ossowicki et al. [20] reviewed studies attempting to assess the impact of soil stress conditions (e.g., heat, biocides) on microbial community structure. Not surprisingly, the accumulation of data suggests that microbial abundance and diversity of the soil microbiome are affected by prolonged exposure to harmful environmental conditions. The understanding that a particular soil microbiome may hold promise to enhance vegetation production and isolation of potential probiotic microbes has led

to the establishment of soil storage and preservation strategies to serve as biological-based vital assets [21]. We may learn that specific microbial populations are particularly suited to improve plant and crop production for unique climates, crops and environments. Enriching the soil with beneficial microbes can enhance agricultural practices and outcomes. Complete documentation of specific taxonomic units of the soil microbiome affected by various soil disturbances and the ecosystem's reduced or abnormal functional consequences would allow for the development of potential therapeutic strategies.

5. Endosphere Microbiome

Our discussion of the phytomicrobiome has primarily focused on the microorganisms outside of plant tissues and microorganisms found in the soil. The endosphere microbiome is a plant region in which microbes penetrate and inhabit the interior of plant tissues. These microbes have been classified as symbionts and opportunistic pathogens threatening plant health. A vast communication system exists between internal microbes, plant tissues, and cell components. The endosphere microbiome protects plants from pathogens and plant disease progression. Liu et al. [22] analyzed the banana endosphere microbiome and revealed that members of Enterobacteriaceae were important for wilt resistance. Genetic engineering of *Enterobacter* sp. and *Kosakonia* sp. and subsequent inoculation with engineered strains (E5P and S1P) enhanced wilt resistance in bananas. While most of the research on the phytomicrobiome has centered on interactions between microbial community alterations impacted by biotic stress (e.g., pathogens), an emerging sector of research focuses on changes to the normal phytomicrobiome caused by abiotic stress (e.g., drought, climate change, pH, air pollution). Zhang et al. [23] performed a 16s ribosomal RNA gene sequencing experiment to determine the relative abundance of microorganisms in the root endosphere of *Alhagi sparsifolia*, a desert plant found in Asian countries. They found a high abundance of *Pseudomonas* sp. and ultimately isolated LTGT-11-2Z a pseudomonas strain using culture isolation techniques. Following sequencing approaches, several genes were identified that corresponded to biofilm formation.

Biofilms are a compact, highly efficient network of microbes living together on a substrate. Cellular biofilm inhabitants produce extracellular molecules that protect microbes from the environment. Bacterial endophytes capable of forming biofilms could presumably confer anti-drought characteristics for the plant during periods of water deficiency. The identification of abiotic tolerant and abiotic resistant bacteria and essential associated microbial genes is crucial and may transform pre-treatment and post-treatment strategies before and after abiotic exposure to indispensable crops [24]. The potential use of bacterial endophytes is an active area of research with many biotechnological applications. Bacterial endophytes isolated from ginseng demonstrated the ability to perform catabolic reactions on ginsenosides to produce molecules important to the pharmaceutical and food industries [25].

6. Conclusion

Based on the success of the Earth Microbiome Project, it seems reasonable that documenting the microbiome of many plant species may prove a worthwhile endeavor [26]. Moreover, comparing the microbial populations from each plant species' phyllosphere, rhizosphere, soil, and endosphere may provide unique evidence of how microbiomes promote the health, protection, and sustainability of plants on earth and point the way to the development of microbiome engineering strategies to increase crop yields. Since plant-based microbiomes provide functional growth molecules, their isolation, purification, and agricultural application could reduce the dependence on chemical fertilizers that have negative impacts and unpredictable outcomes on the environment. Signaling mechanisms between plant cells and microorganisms will reveal exciting cell-cell unresolved communication mechanisms. Moreover, molecular mechanisms by which plant-growth-promoting microbes suppress the growth of phytopathogenic bacteria and viruses may yield essential molecules that can be used to promote plant and crop sustainability and potentially serve as human therapeutics. Uncovering more information about symbiotic microbes may shed additional light on how plants respond to UV light, infestation, drought, and climate change. Future phytomicrobiome-derived insights on crucial biological processes and molecular mediators will lead to novel biotechnological, agricultural, and pharmaceutical discoveries.

Compliance with ethical standards

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