

PHYTOMICROBIOME UNVEILED: A REVIEW OF PLANT-ASSOCIATED
MICROORGANISMS AND THEIR FUNCTIONAL POTENTIALAbhijeet S. Bairagi^{1*}, Nirmala V. Shinde², Sachin K. Bhosale³, Rani D. Navale⁴^{1,2,3,4}Department Pharmaceutical Chemistry, SMBT College of Pharmacy, Nandi-Hills Dhamangaon, Nashik -422403.

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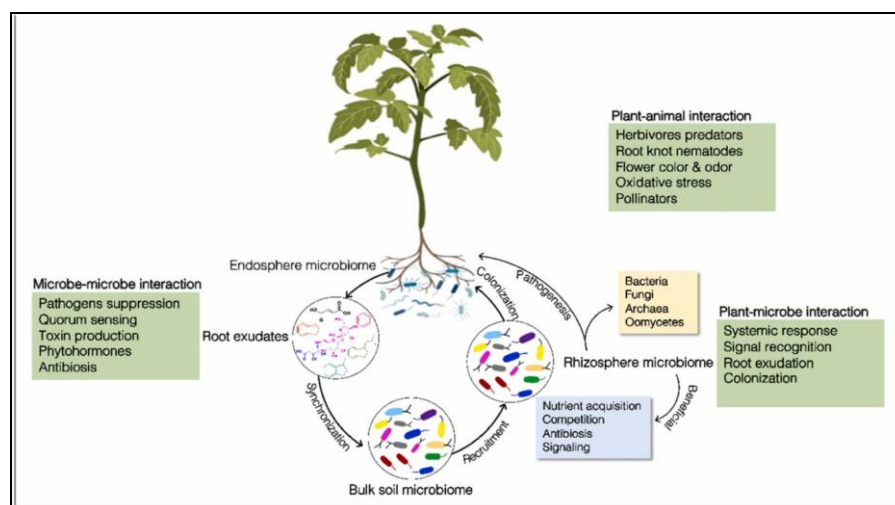
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ABSTRACT

The complex and dynamic assemblage of bacteria, fungi, viruses, archaea, and protozoa that co-exist with plants is referred to as the phytomicrobiome. These microorganisms inhabit different environments of plants such as the phyllosphere (leaf surface), endosphere (internal tissues), rhizosphere (soil surrounding roots), and spermosphere (seed environment). Advances in high-throughput sequencing, metagenomics, and molecular biology have significantly improved our understanding of the phytomicrobiome and its importance in plant production, health, and sustainability. environmental management, this review aims to explore the diversity, composition, and functional potential of these organisms. Plant-associated microbes have interactions with their host plants, which can be commensal, beneficial, or sometimes harmful to the plants. By various mechanisms like biological nitrogen fixation, phosphate solubilization, phytohormone production (auxins, gibberellins, and cytokinins), and siderophore production for enhanced iron bioavailability, beneficial microbes help in plant growth.

KEYWORDS: Phytomicrobiome, Plant–Microbe Interactions, Rhizosphere Microbiota, Endophytic Microorganisms, Plant Growth-Promoting Microorganisms (PGPM).

[2] INTRODUCTION

The interactions between microorganisms, plant parts, and soil in the vicinity of plant roots are collectively known as the phytomicrobiome or plant microbiome. Plant productivity, growth, health, and disease are all affected by the phytomicrobiome.^[1] A better understanding of host-microbe interactions and microbiological ecology could be achieved by a better understanding of the phytomicrobiome and the microbial reaction to undesirable plant modifications due to physical, chemical, and biological principles (Laurence o flower)^[2]

There has been immense interest from both academia and industry in the use of bacteria and microbiomes, and the agricultural microbiome is one of the fastest-growing markets in the world, with a growth rate of 17% per annum.^[3] The agricultural microbiome market is growing because of factors such as the increasing demand from the general public for foods with lower chemical residues, government regulations (such as the EU Green Deal, which aims to reduce chemical pesticide use by 50% by 2030).^[4]

Plants show modifications in their physiological and biochemical interactions based on external environmental cues. Microbes have been associated with plants at all stages of their life cycle.^[5] Hence, even the slightest modification in metabolism or development affects them. In the terrestrial ecosystem, microorganisms act as the silent wheel that sustains plant development, stress responses, and interactions. The diversity, type, and microstructure of microorganisms depend on the associated plant interactions and environmental systems.^[6]

Due to its high metabolic potential, the plant microbiome offers the host an abiotic stress protection mechanism by increasing the plants' capacity to uptake nutrients and develop stress tolerance.^[7]

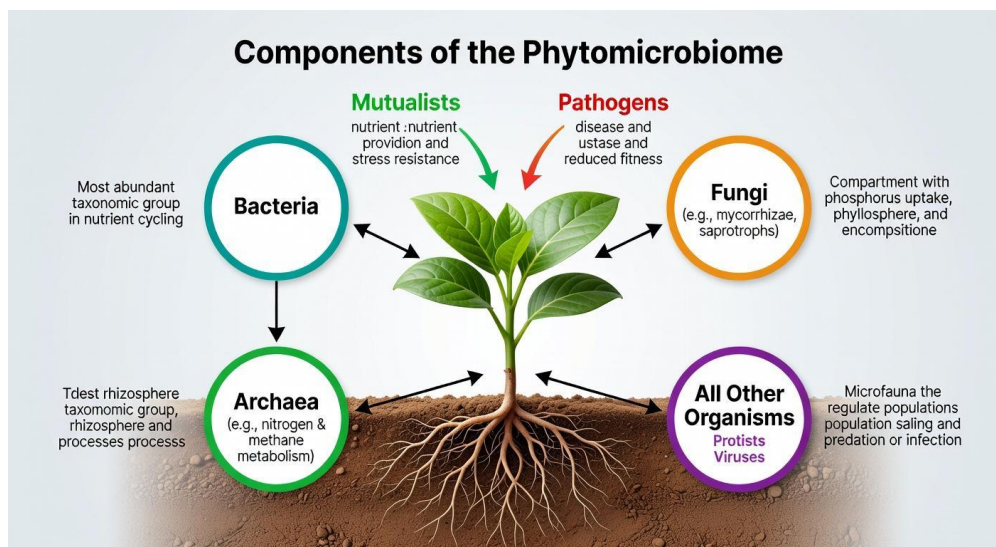
The extent and duration of abiotic stress determine the structure of the dynamic phyto-microbiome. For mutual survival and growth, the plant and the microbiome associated with it respond to abiotic stress in a synergistic way.^[8]

Apart from the rhizospheric region, the phyllosphere, which harbors a variety of living organisms such as bacteria, fungus, yeasts, algae, nematodes, and so on, is the region where the microbial population comes into contact with the plant.^[9]

It influences overall development and phytophysiology. The composition of the microbiome in the phyllosphere is influenced by both biotic and abiotic factors^[10] inside and between tissues. Because a huge diversity of microorganisms is linked to plant roots, they can be harnessed to alter the defense, physiological, and metabolic processes of the host.^[11] This consequently leads to a huge increase in the plants' vigor, growth, productivity, and efficiency in the absorption of nutrients and stress resistance.^[12]

In addition to parasitic and commensal microorganisms, the phytomicrobiome also includes mutualists, or beneficial microorganisms, such as plant growth-promoting bacteria (PGPB) and mycorrhizal fungi (MF), which enable plant holobionts to thrive in different environments. Beneficial microorganisms help plant holobionts adapt to changes in their environment and their responses to biotic and abiotic stresses.^[13]

The phytomicrobiome could hold the secret to pesticide degradation in a sustainable future, offering a way forward for climate-resilient agricultural practices that can safeguard our irreplaceable soils. In order to unlock the full potential of the phytomicrobiome in efficient pesticide degradation, however, an important challenge is yet to be overcome, namely the divide between basic and applied research.^[14]



[3] Component of phytomicrobiome

complex, multi-kingdom microbial community that is intricately associated with plants is referred to as the phytomicrobiome. These microorganisms form a structured community within the ecological niches of rhizosphere, rhizoplane, endosphere, and phyllosphere after colonizing the internal and external plant tissues.^[15] The phytomicrobiome's composition and functional activities are influenced by environmental conditions, soil characteristics, plant genotype, and growth stage. These microbial communities interact with each other to regulate immunity, stress responses, plant development, and nutrient acquisition.^[16] Below is a discussion of the phytomicrobiome's key components-

[3.1] Rhizobacteria

[3.2] Endophytic bacteria

[3.3] Actinomycetes

[3.4] Arachea

[3.5] Viruses

[3.6] Protists

[3.7] Algae and Cynobacteria^[17]

[3.1] Rhizobacteria

flavonoids, is where rhizobacteria are found. These exudates play a role in the development of microbial communities as they act as signaling molecules and carbon sources.^[18]

Plant Growth-Promoting Rhizobacteria (PGPR) are important among rhizobacteria. They enhance plant growth using both direct and indirect mechanisms. Biological nitrogen fixation, phosphate solubilization, potassium mobilization, siderophore-mediated iron acquisition, and the production of phytohormones such as cytokinins gibberellins, and indole-3-acetic acid (IAA) are some examples of direct mechanisms. Additionally, the production of ACC deaminase helps in the enhancement of root growth by reducing stress-induced ethylene production during unfavorable conditions. The production of antibiotics, the secretion of lytic enzymes (such as proteases and chitinases), competition for habitat, and the induction of systemic resistance (ISR) in plants are examples of indirect mechanisms that inhibit phytopathogens.^[19]

[3.2] Endophytic bacteria

Internal plant tissues are inhabited by endophytic bacteria, which do not cause harm. Usually, wounds, natural openings, or root hairs provide entry, followed by systemic colonization. Enhanced nutrient uptake, production of antimicrobial agents, regulation of plant hormone signaling pathways, and resistance to abiotic stress such as salt, drought, and heavy metals are all made possible by endophytes. Endophytes often display stable associations with the host plant due to their protected internal environment.^[20]

[3.3] Actinomycetes

Gram-positive, filamentous bacteria known as actinomycetes are often observed in soil and

environments associated with roots. By decomposing complex polymers such as cellulose, lignin, and chitin, they play vital roles in the decomposition of organic matter.^[21] Moreover, actinomycetes are rich sources of bioactive secondary compounds that can be used to decrease soil-borne diseases, such as antibiotics. In addition, their abundance increases the fertility and porosity of the soil.^[22]

[3.5] Arachea

Archaea are gradually gaining recognition as important components of the phytomicrobiome, albeit as less abundant entities than bacteria and fungi.^[23] In soil microbiota, ammonia-oxidizing archaea have an important role in nitrogen cycle and nitrification. In soil microbiota, ammonia-oxidizing archaea have an important role in nitrogen cycle and nitrification. Due to their versatile nature, they can survive in extreme conditions, which helps in maintaining ecological balance and nutrient cycling.^[24]

[3.6] Viruses

In plant-associated microbiomes, viruses are considered integral but often overlooked components. Plant viruses can interact with their host's immune signaling pathways, besides being pathogens.^[25] Bacteriophages, which infect their bacterial hosts, regulate the balance of bacterial populations and facilitate horizontal gene transfer. The role of viruses in the evolutionary mechanisms of the phytomicrobiome is fulfilled by these pathways.^[26]

[3.7] Protists

Protists, which are single-celled eukaryotes, are also present in rhizosphere and soil environments. Protists regulate bacterial mass and populations, primarily through bacterivory. Bacterivory or grazing by protists enhances nutrient mineralization, leading to an increase in the availability of phosphate and nitrogen to plants.^[27]

[3.8] Algae and Cyanobacteria

The phytomicrobiome also comprises photosynthetic microorganisms such as cyanobacteria and algae, particularly in aquatic and agricultural systems. Cyanobacteria possess the ability to improve soil aggregation, increase soil organic matter, and fix nitrogen from the atmosphere. Such organisms play a crucial role in desert ecosystems and paddy fields, as they increase soil fertility and improve soil stability.^[28]

[4] Spatial organization of phytomicrobiome

The phytomicrobiome is a very organized and spatially structured ecosystem rather than a scattered microbial community. Plant morphology, physiology, age, environmental conditions, and microbe interactions are factors that influence its organization.^[29] Various plant-associated environments, like the bulk soil, rhizosphere, rhizoplane, endosphere, and phyllosphere, harbor microorganisms. The composition and role of the microbial community are shaped by the unique physicochemical properties, resource gradients, and host-

associated signals present in each of these environments. Understanding plant-microbe interactions and developing microbiome-driven agricultural solutions demand knowledge of the spatial organization of the phytomicrobiome.^[30]

[4.1] The soil plant continuum

The bulk soil, the primary microbial reservoir, is where the spatial organization of the phytomicrobiome begins. By surface communication and root exudation, plants selectively favor some microbes from the reservoir to come closer.^[10] As this hierarchical organization approaches plant tissues, more specialized microbial communities are established. The soil-plant continuum can be conceptualized as a gradient: Endosphere → Rhizoplane → Rhizosphere → Bulk Soil.^[31]

Microbial diversity typically decreases and functional specialization increases as one moves along this gradient of increasing distance from the plant. By biochemical communication, plants exert a selective pressure that favors beneficial microbes.^[32]

[4.2] Rhizosphere: The microbial hotspot

The region of soil influenced by root exudates and microbial activity is referred to as the rhizosphere. The rhizosphere is one of the most densely populated microbial zones on the planet. Sugars, amino acids, organic acids, phenolics, fatty acids, flavonoids, and secondary metabolites are all present in root exudates, which create nutrient-rich microzones that attract and support diverse microbial populations.^[33] 4.2.1 Rhizosphere Microbial Diversity Microfauna, viruses, protists, fungi, bacteria, and archaea coexist in the rhizosphere. Bacterial populations, however, usually dominate. The following factors have a great influence on rhizospheric community structure

Genotype of plants pH and type of soil Climate conditions Agricultural practices.^[34]

[4.2.1] Functional Zonation

There is micro-level variation in the rhizosphere. The geographical distances are small, and hence the differences in water content, nutrient availability, pH variation, and oxygen concentration.^[35] The micro-niches created by these variations support specialized microbial populations. The rhizosphere functional properties are: Nitrogen fixation, nitrification, and denitrification are examples of nutrient cycling. The solubilization of phosphorus Siderophore-mediated iron acquisition suppression of pathogens found in soil Microbiological communication mediated by quorum The rhizosphere is often termed a "biological battlefield," where cooperation and competition coexist, due to the intense microbial interactions that take place.^[36]

[4.3] Rhizoplane: The root surface interface

The root surface is called the rhizoplane. It acts as a very important interface between plant tissues and microorganisms in the soil. Some properties, such as biofilm production, motility, and chemotaxis to root exudates, are often observed in microorganisms that can successfully attach to plant root surfaces.^[33]

[4.3.1] Biofilm formation

Biofilms, which are microbial communities organized in a structured manner and embedded in extracellular polymeric substances (EPS), are produced by a large number of bacteria associated with the rhizoplane.^[37] Biofilm formation enhances: Persistence of microorganisms Adaptability to environmental stress Effective exchange of nutrients Defense against antimicrobial substances.^[38]

[4.3.2] Selective filtering mechanism

However, only certain microorganisms have the ability to further colonize the root tissues because of the biological filtering process that occurs in the rhizoplane. Certain microorganisms may be able to bypass the plant defenses and switch from being surface colonizers to endophytes.^[39]

[4.4] Endosphere

the internal microbe habitat: Microorganisms that live inside plant tissues, such as roots, stems, leaves, flowers, and seeds, are referred to as the endosphere. Compared to the rhizosphere, this niche has a relatively lower variety of microorganisms and is quite selective.^[40]

[4.4.1] Entry and colonization

The endosphere is accessed by microorganisms via: Hairs on the roots Sites of lateral root emergence The stomata Injuries For microorganisms to establish sustained colonization once inside, they must avoid plant defense responses.

[4.5] Phyllosphere

The aerial microbial habitat All above-ground plant surfaces, especially leaves, are regarded as the phyllosphere. It is a specific biological habitat that is exposed to a variety of environmental conditions, such as desiccation, temperature variations, ultraviolet irradiation, and the absence of nutrients.^{[41][41]}

[4.5.1] Limitation in the environment

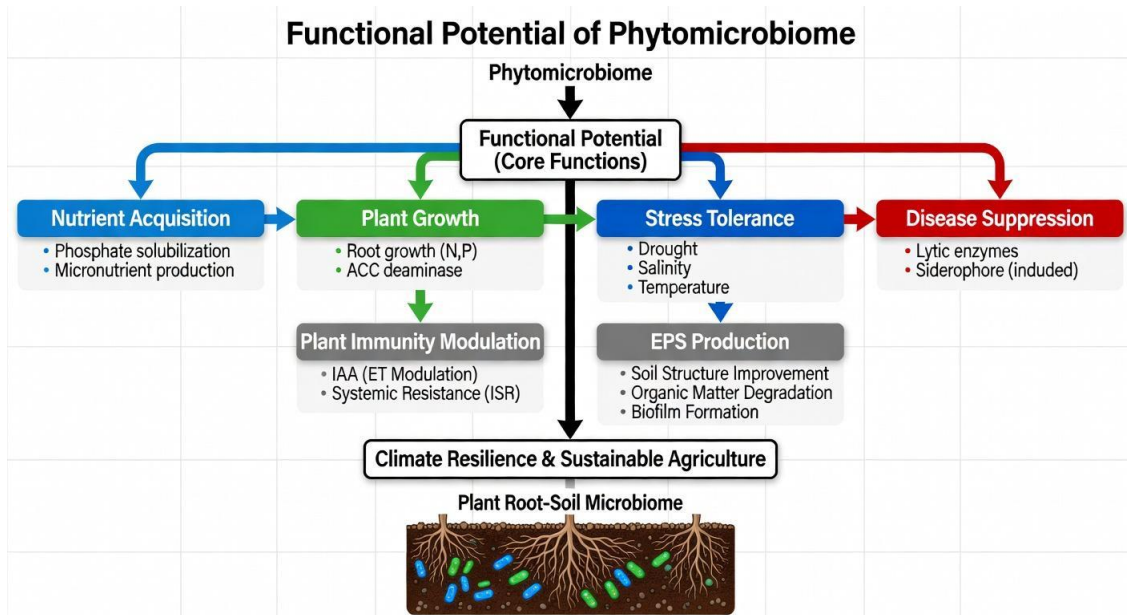
The phyllosphere is a more extreme and relatively less nutrient-rich environment than the rhizosphere. Colonization by microorganisms is limited by the following factors: Tolerance to ultraviolet light Desiccation resistance Utilization of limited carbon sources.^[42]

[4.5.2] The role of microbes

Phyllosphere bacteria assist in the following functions despite the harsh conditions: Resistance to foliar infections Production of antimicrobial compounds

Production of immunomodulatory compounds in plants
Alterations in atmospheric nutrients
Certain phyllosphere

microorganisms possess the ability to colonize internal
plant tissues and establish endophytic populations.^[43]



[5] Functional potential of phytomicrobiome

The phytomicrobiome represents a highly dynamic and multifunctional microbial consortium that significantly influences plant growth, development, health, and productivity. Beyond its taxonomic diversity, the true importance of the phytomicrobiome lies in its functional potential—the collective metabolic, biochemical, ecological, and molecular capabilities that contribute to plant fitness and ecosystem sustainability. These functions are mediated through intricate plant–microbe and microbe–microbe interactions occurring across various plant compartments, including the rhizosphere, rhizoplane, endosphere, and phyllosphere.^[44]

The functional potential of the phytomicrobiome can be broadly categorized into nutrient acquisition and cycling, plant growth promotion, stress tolerance, disease suppression, modulation of plant immunity, soil structure improvement, and ecological resilience.^[45] Advances in metagenomics, transcriptomics, proteomics, and metabolomics have greatly enhanced our understanding of these functions at molecular and systems levels. As the rhizosphere, rhizoplane, endosphere, and phyllosphere, mediate these processes. Nutrient acquisition and cycling, plant growth promotion, stress tolerance, disease suppression, plant immunity modulation, soil structure enhancement, and ecological resilience are the major categories into which the phytomicrobiome's functional potential can be divided. Developments in proteomics, metabolomics, transcriptomics, and metagenomics have significantly improved our comprehension of these roles at the molecular and systemic levels.^[46]

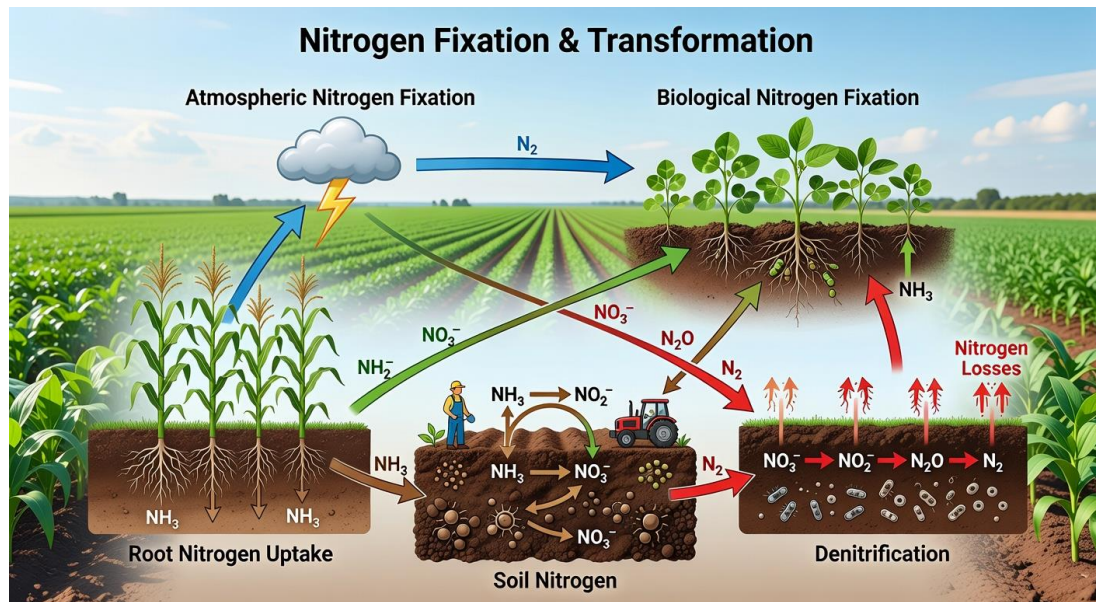
[5.1] Nitrogen fixation and transformation

Nutrient mobilization and transformation is one of the most fundamental functions of the phytomicrobiome. For

the plants to get essential nutrients that are not available or are poorly soluble in soil, they rely on microbes.^[47]

5.1.1 Fixation and Transformation of Nitrogen

Nitrogen is one of the macronutrients required by plants for the synthesis of proteins, nucleic acids, and chlorophyll. Although nitrogen in the atmosphere is abundant, plants cannot utilize it.^[48] Nitrogen-fixing bacteria convert atmospheric nitrogen into ammonia using the enzyme nitrogenase. Legume plants have a symbiotic nitrogen fixation process via rhizobial interactions, where nitrogen transformation is aided by root nodules. The availability of nitrogen in non-legume crops is also largely affected by free-living and associative nitrogen-fixing bacteria in the rhizosphere. Apart from nitrogen fixation, the phytomicrobiome regulates nitrogen movement within the soil-plant ecosystem by participating in nitrification, denitrification, ammonification, and nitrogen mineralization processes.^[49]



[5.2] Phosphorus solubilization and mineralization

Insoluble phosphorus compounds bound to calcium, iron, or aluminum complexes are often observed in soil. The phosphatase enzymes and organic acids produced by phosphate-solubilizing bacteria result in the liberation of soluble phosphate ions. The solubilization process reduces the use of chemical fertilizers and enhances phosphorus uptake by roots. Mycorrhizal fungi increase the extent of hyphal growth beyond the root depletion zone, thus further enhancing phosphorus uptake.^[50]

[5.3] Mobilization and micronutrients

Moreover, the phytomicrobiome helps in the mobilization of micronutrients such as iron, zinc, manganese, and copper. Under limiting conditions, bacteria that produce siderophores secrete iron-chelating compounds with high affinity for iron, thus increasing iron availability. Apart from benefiting plants, siderophores limit the availability of iron to diseases.^[51]

[6] Stress tolerance

Plants are constantly under the influence of various abiotic stresses like drought, salinity, high and low temperatures, flooding, and toxic heavy metals, which greatly hamper agricultural productivity. Besides abiotic stress, plants are also under biotic stress, which is caused by pathogens and insects. The phytomicrobiome is an important component that greatly helps in improving stress resistance in plants by various physiological, biochemical, and molecular processes. These beneficial microbes are considered to be an extended functional genome of the plant, which greatly helps in improving adaptability under adverse environmental conditions.^[52]

[6.1] Drought stress condition

Water deficit, oxidative stress, reduced cell turgor, and impaired photosynthesis are effects of drought. Drought tolerance can be increased by the presence of phytomicrobiome-associated bacteria and fungus in several ways. Exopolysaccharides (EPS), which are

produced by many rhizobacteria, increase soil aggregation and water-holding capacity in the root zone. By producing indole-3-acetic acid (IAA), some microorganisms increase root system development, leading to an increase in the root length and root surface area for water absorption.^[53] Additionally, microbial inoculation increases the production of osmoprotectants, which help in maintaining cellular osmotic balance, such as proline, glycine betaine, and trehalose. To reduce oxidative stress, some microorganisms regulate the expression of aquaporin and activate antioxidant enzymes such as catalase, peroxidase, and superoxide dismutase.^[54]

[6.2] Salinity stress tolerance

Osmotic stress occurs in plants due to the disturbance in ion balance caused by high salinity in the soil. Plant growth-promoting rhizobacteria (PGPR) with ACC deaminase activity reduce the concentration of ethylene, thus preventing growth inhibition caused by stress. Mycorrhizal fungi enhance the uptake of nutrients and prevent the accumulation of excess salt in plant cells. Osmotic adjustment is also increased by the production of compatible solutes by microorganisms, and antioxidant systems protect plants from reactive oxygen species generated in a saline environment.^[55]

[6.3] Temperature stress

Enzyme activity and membrane stability are affected by high temperatures. Through the production of heat shock proteins and stress genes, some endophytic bacteria and fungi have shown enhanced heat tolerance. To enhance cellular stability at low temperatures, cold-tolerant bacteria can alter the lipid composition of their membranes and enhance the production of antifreeze proteins.^[56]

[6.4] Heavy metal stress

The plants are poisoned by heavy metals such as cadmium, lead, and arsenic. The phytomicrobiome has

biosorption, bioaccumulation, and enzymatic detoxification mechanisms that help in heavy metal tolerance.^[57] Some microorganisms prevent the plant from absorbing heavy metals by immobilizing them in the rhizosphere. Others produce antioxidants and metal chelating agents that protect the cell from damage.^[58]

[6.5] Induced systemic stress

Beneficial microbes induce systemic tolerance (IST), which is a primed physiological state that enhances plant responsiveness to stress, aside from specific stress responses. This involves the regulation of hormonal signaling pathways, particularly those related to ethylene, jasmonic acid, and abscisic acid.^[59]

[7] Application of phytomicrobiome in sustainable agriculture

Due to its diverse functional capabilities that enhance plant productivity while reducing environmental effects, the phytomicrobiome has emerged as a powerful tool in sustainable agriculture. Plant-associated microbial communities offer environmentally friendly alternatives to chemical-reliant agricultural practices, and sustainable agriculture is a strategy that seeks to meet the global demand for food without consuming natural resources. The primary application of the phytomicrobiome is in nutrient management by biofertilizers, where siderophore-producing microbes enhance iron and micronutrient acquisition, phosphate-solubilizing microorganisms release insoluble phosphorus by the production of organic acids, and nitrogen-fixing bacteria convert atmospheric nitrogen into plant-available forms.^[60]

In addition to mobilizing nutrients, the phytomicrobiome plays a critical role in biological control and integrated pest management as it inhibits pathogens by the production of antibiotics, lytic enzymes, competition, and induced systemic resistance in plants. This reduces ecological toxicity and the use of chemical pesticides.^[61] Abiotic stress tolerance is also significantly enhanced by the phytomicrobiome, which can protect crops against drought, salinity, temperature stress, and heavy metal stress. For example, ACC deaminase production decreases stress-induced ethylene, mycorrhizal fungi enhance water and nutrient absorption under saline stress, some microbes can immobilize or detoxify heavy metals, and microbial production of exopolysaccharides enhances soil aggregation and water-holding capacity.^[62]

Moreover, through the decomposition of organic residues to humus, increasing soil organic carbon, improving soil aggregation by extracellular polymeric substances and fungal hyphae, and managing carbon cycling processes, which contribute to the mitigation of climate change by carbon sequestration, plant-associated microbes contribute to the rehabilitation of healthy soil. Through the reduction of chemical use, microbiome-based approaches enhance ecological balance and biodiversity by decreasing water pollution, soil acidification, and

harmful impacts on beneficial organisms. Through the development of synthetic microbial consortia that are appropriate for specific crops and environmental conditions, microbiome research has enhanced precision agriculture and sustainable crop intensification without the need for an expansion of agricultural land.^[63] The uses of the seed microbiome, such as microbial seed coatings, ensure rapid root establishment, enhanced seedling growth, and better stress tolerance. Moreover, with the replacement of biological compounds with synthetic ones, microbiome-based agriculture helps to support organic and low-input agricultural practices, which are in line with environmentally friendly and climate-resilient agricultural practices. The integration of phytomicrobiome approaches into agricultural practices has vast possibilities for enhancing crop productivity, improving soil fertility, and achieving agricultural sustainability: despite the existing challenges such as variability in microbial performance in agricultural fields and environmental factors affecting microbial survival.^{[64][65]}

In addition, through the substitution of biological materials for synthetic materials, microbiome-based agriculture assists in organic and low-input agricultural practices, which align with environmentally benign and climate-resilient agricultural practices.^{[66][67]} The integration of phytomicrobiome approaches in agricultural practices has vast potential for enhancing crop productivity, improving soil fertility, increasing stress resistance, and achieving agricultural sustainability in the context of global climate change and increasing demands for food security,^{[69][70]} despite the existing challenges such as variability in microbial survival and field performance.

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