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The Role of Plant Microbiome in Enhancing Environmental Stress Tolerance: A Review

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I. Abstract

The plant microbiome represents a complex and integrated biological system that plays a fundamental role in supporting plant growth and enhancing plant adaptability to a wide range of environmental stresses, including both biotic and abiotic factors. Plant-associated microorganisms significantly contribute to improving nutrient acquisition from the soil through processes such as nitrogen fixation, phosphate solubilization, and increased availability of essential mineral elements, thereby promoting plant growth and improving overall physiological performance.

Moreover, the plant microbiome plays a crucial role in regulating plant hormonal balance through the production of growth-promoting compounds such as auxins, cytokinins, and gibberellins, which positively influence root development and overall biomass accumulation. In addition, it contributes to reducing oxidative stress induced by harsh environmental conditions by activating antioxidant defense systems and minimizing reactive oxygen species accumulation, thereby maintaining cellular integrity.

Furthermore, the plant microbiome enhances plant tolerance to drought, salinity, and temperature extremes by improving water use efficiency, maintaining ionic homeostasis, and protecting cellular proteins and membranes from damage. It also strengthens plant immune responses against pathogens through mechanisms such as induced systemic resistance (ISR), biological competition, and the production of antimicrobial compounds.

Based on the findings presented, the utilization of the plant microbiome represents a promising strategy for advancing sustainable agriculture. It contributes to reducing dependence on chemical fertilizers and pesticides, improving crop productivity, and strengthening global food security in the face of increasing climate change and environmental challenges.

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II. Introduction

The plant microbiome refers to the complex community of microorganisms, including bacteria, fungi, archaea, and viruses, that are closely associated with plants in different ecological niches such as the rhizosphere, phyllosphere, and endosphere[1] . These microorganisms constitute an essential component of the plant holobiont, playing critical roles in plant growth, nutrient acquisition, protection against pathogens, and enhancement of plant adaptation to diverse environmental conditions[2] .

The interaction between plants and microorganisms is based on intricate symbiotic relationships that contribute significantly to maintaining plant physiological and ecological balance[3] . Plant growth-promoting microorganisms (PGPM) enhance nutrient uptake, synthesize phytohormones, stimulate systemic resistance mechanisms, and improve water and mineral utilization efficiency. Consequently, the plant microbiome is increasingly recognized as the “second genome” of plants due to its profound influence on plant health, productivity, and environmental adaptability[4] .

Plants are continuously exposed to various environmental stresses that adversely affect their growth and agricultural productivity. These stresses are generally classified into abiotic stresses, such as drought, salinity, extreme temperatures, and heavy metal toxicity, and biotic stresses, including infections caused by pathogens and insect infestations[5] . Such stress conditions induce numerous physiological and biochemical disturbances within plants, including excessive production of reactive oxygen species (ROS), impairment of photosynthetic efficiency, and disruption of water and nutrient balance[6] .

In recent years, considerable scientific attention has been directed toward the study of the plant microbiome as a sustainable biological strategy for enhancing plant tolerance to environmental stresses while reducing dependence on chemical fertilizers and pesticides[7] . Emerging studies have demonstrated that beneficial microorganisms can improve plant stress resilience through multiple mechanisms, including regulation of gene expression, stimulation of antioxidant defense systems, production of osmolytes, and enhancement of nutrient acquisition[8] . Therefore, the application of plant microbiome-based approaches represents a promising direction in modern agriculture for achieving sustainable crop production and food security under the increasing challenges posed by global climate change[9] .

This review aims to highlight the vital role of the plant microbiome in enhancing plant tolerance to various environmental stresses, including abiotic stresses such as drought, salinity, high temperatures, and heavy metal toxicity, as well as biotic stresses caused by pathogens and pests. It also seeks to clarify the nature of the interactions between plants and beneficial microorganisms, in addition to explaining the physiological and molecular mechanisms through which these microorganisms improve plant growth and increase resistance to adverse environmental conditions.

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2. Plant Microbiome

2.1 Definition of the Plant Microbiome

The term *microbiome* refers to the entire community of microorganisms inhabiting a specific environment, together with their genetic material, metabolic products, and interactions with the surrounding ecosystem[10] . In plants, the microbiome includes diverse groups of microorganisms such as bacteria, fungi, archaea, viruses, and protozoa that colonize different plant-associated niches including the rhizosphere, phyllosphere, and endosphere. These microbial communities play fundamental roles in maintaining plant health, growth, nutrient cycling, and environmental adaptation[11] .

Although the terms *microbiota* and *microbiome* are often used interchangeably, they differ scientifically in meaning[12] . The term *microbiota* specifically refers to the collection of living microorganisms present within a defined habitat, whereas *microbiome* encompasses not only the microorganisms themselves but also their collective genomes, functional genes, metabolites, and ecological interactions[13] . Therefore, the microbiome represents a broader and more comprehensive concept that includes both the microbial community and its functional potential within the plant environment[14] .

The plant microbiome is increasingly recognized as an integral component of plant biology due to its significant influence on physiological processes, stress tolerance, disease resistance, and overall agricultural productivity[15] . Recent advances in molecular biology and metagenomic technologies have greatly enhanced the understanding of plant–microbe interactions and the functional diversity of microbial communities associated with plants[16] .

2.2 Types of Plant-Associated Microorganisms

Plants are associated with a highly diverse community of microorganisms that inhabit different plant compartments and contribute significantly to plant growth, nutrient acquisition, and stress tolerance. These microorganisms include bacteria, fungi, actinomycetes, algae, and several other microscopic organisms that establish complex ecological interactions with their host plants[17] .

Bacteria

Bacteria are among the most abundant and extensively studied components of the plant microbiome. They colonize the rhizosphere, phyllosphere, and internal plant tissues[18] , where they perform essential biological functions. Plant growth-promoting bacteria (PGPB) enhance plant development through nitrogen fixation, phosphate solubilization, siderophore production, phytohormone synthesis, and induction of systemic resistance against pathogens[19] . Genera such as *Pseudomonas*, *Bacillus*, *Azospirillum*, and *Rhizobium* are widely recognized for their beneficial effects on plant growth and environmental stress tolerance[20] .

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Fungi

Fungi constitute another major group of plant-associated microorganisms and are involved in numerous symbiotic interactions with plants. Mycorrhizal fungi establish mutualistic associations with plant roots, improving water absorption and nutrient uptake, particularly phosphorus and micronutrients[21] . In addition, certain endophytic fungi enhance plant resistance to drought, salinity, and pathogenic infections by producing bioactive metabolites and stimulating plant defense mechanisms. However, some fungal species may also act as plant pathogens under favorable conditions[22] .

Actinomycetes

Actinomycetes are filamentous Gram-positive bacteria commonly found in soil and root-associated environments. They are known for their ability to produce a wide range of secondary metabolites, including antibiotics, enzymes, and growth-promoting compounds[23] . Members of the genus *Streptomyces* play important roles in suppressing plant pathogens and enhancing soil fertility. Actinomycetes also contribute to organic matter decomposition and nutrient cycling, thereby improving soil health and plant productivity[24] .

Algae and Other Microorganisms

Certain algae, particularly cyanobacteria, contribute to plant growth through nitrogen fixation, production of bioactive compounds, and improvement of soil structure and fertility[25] . In aquatic and semi-arid environments, these microorganisms play essential ecological roles in maintaining nutrient balance and enhancing soil stability[26] . Other plant-associated microorganisms, including archaea, protozoa, and viruses, also influence plant health and microbial community dynamics. Although their functions are less extensively studied, emerging research suggests that these organisms participate in nutrient transformation, microbial regulation, and plant stress adaptation[27] .

2.3 Locations of the Plant Microbiome

The plant microbiome is not randomly distributed, but rather occupies specific ecological niches on and within plant tissues. These habitats provide distinct physical and chemical environments that shape microbial composition, diversity, and function[28] .

Rhizosphere (Root Zone)

The rhizosphere refers to the narrow region of soil directly influenced by plant roots[29] . It is considered one of the most microbiologically active zones due to the continuous release of root exudates, including sugars, amino acids, organic acids, and secondary metabolites[30] . These compounds serve as energy sources that attract and support dense microbial populations. The rhizosphere microbiome plays a crucial

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role in nutrient cycling, particularly nitrogen and phosphorus availability, suppression of soil-borne pathogens, and enhancement of plant growth and stress tolerance[31] .

Endophytes (Internal Plant Tissues)

Endophytes are microorganisms that colonize internal plant tissues without causing visible disease symptoms. They can inhabit roots, stems, leaves, and even seeds[32] . These microorganisms live in a protected environment within the plant, where they establish mutualistic relationships with their host. Endophytic bacteria and fungi contribute to plant health by producing phytohormones, enhancing nutrient uptake, inducing systemic resistance, and improving tolerance to abiotic stresses such as drought, salinity, and temperature extremes[33] .

Phyllosphere (Leaf Surface)

The phyllosphere refers to the above-ground surfaces of plants, particularly leaves, which are exposed to fluctuating environmental conditions such as ultraviolet radiation, temperature variation, and limited nutrient availability[34] . Despite these harsh conditions, a diverse microbial community exists on leaf surfaces[35]. Phyllosphere microorganisms contribute to plant health by protecting against foliar pathogens, modulating leaf physiology, and participating in nutrient exchange. Some also produce antimicrobial compounds that inhibit pathogen colonization[36] .

3. Environmental Stresses Affecting Plants

3.1 Biotic Stress

Biotic stress refers to the harmful effects imposed on plants by living organisms that interfere with their normal growth, development, and productivity[37] . These stresses result from continuous ecological interactions between plants and a wide range of biological agents present in their environment, and they represent a major limiting factor in agricultural systems worldwide[38] .

One of the primary sources of biotic stress is plant pathogens, which include bacteria, fungi, viruses, and nematodes. These pathogens infect different plant tissues and disrupt essential physiological and biochemical processes. The infection process often leads to symptoms such as leaf spots, wilting, root rot, vascular dysfunction, and tissue necrosis[39] . As a consequence, the transport of water and nutrients is impaired, photosynthetic efficiency is reduced, and the plant activates complex defense responses. In severe cases, pathogen infection can result in substantial yield losses and a decline in crop quality[40] .

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In addition to microbial pathogens, insects and parasitic organisms also constitute significant biotic stress factors[41] . Herbivorous insects damage plants through direct feeding on leaves, stems, roots, or reproductive structures, leading to tissue destruction, reduced biomass, and weakened plant vigor[42] . Moreover, many insect species act as vectors for plant pathogens, thereby facilitating the spread of infectious diseases. Parasitic plants further intensify this stress by extracting water and nutrients directly from host plants, which ultimately results in growth suppression and developmental abnormalities[43] .

3.2 Abiotic Stress

Abiotic stress refers to the adverse effects on plants caused by non-living environmental factors that disrupt normal physiological, biochemical, and molecular processes[44] . These stresses represent major constraints on plant growth and agricultural productivity worldwide, particularly under changing climatic conditions[45] .

One of the most significant abiotic stresses is drought, which leads to water deficiency in plant tissues, resulting in reduced cell turgor, impaired photosynthesis, and inhibition of growth and development[46] . Prolonged water scarcity also triggers oxidative stress due to the overproduction of reactive oxygen species (ROS), which can damage cellular structures if not properly regulated[47] .

Salinity stress is another critical factor affecting plant performance, particularly in irrigated and arid regions[48] . High salt concentrations in the soil cause osmotic stress, reducing the plant's ability to absorb water, and ionic stress due to the toxic accumulation of sodium (Na^+) and chloride (Cl^-) ions. These conditions negatively affect enzyme activity, nutrient balance, and overall metabolic functions[49] .

Temperature extremes, both high and low, also impose severe stress on plants. High temperatures can denature proteins, disrupt membrane stability, and accelerate water loss through transpiration[50] , while low temperatures may lead to membrane rigidity, reduced enzymatic activity, and inhibition of metabolic reactions. Both conditions ultimately impair plant growth and productivity[51] .

Heavy metal stress arises from the accumulation of toxic metals such as cadmium, lead, and mercury in the soil[52] . These metals interfere with essential physiological processes, inhibit enzyme function, and induce oxidative damage, leading to growth retardation and potential plant toxicity[53] .

Nutrient deficiency is another important abiotic stress factor that affects plant development. Insufficient availability of essential macro- and micronutrients such as nitrogen, phosphorus, potassium, iron, and zinc limits metabolic activities, reduces chlorophyll synthesis, and impairs overall plant vigor[54] .

4. Mechanisms of the Microbiome in Enhancing Environmental Stress Tolerance

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The plant microbiome enhances plant tolerance to environmental stresses through multiple integrated physiological, biochemical, and molecular mechanisms. These interactions collectively improve plant growth, resilience, and survival under adverse conditions[55] .

4.1 Enhancement of Nutrient Uptake

Plant-associated microorganisms significantly improve nutrient availability and uptake. One of the most important mechanisms is biological nitrogen fixation, in which diazotrophic bacteria convert atmospheric nitrogen (N_2) into ammonia, a form usable by plants[56] . In addition, many microbes contribute to phosphate solubilization by releasing organic acids and phosphatases that convert insoluble phosphorus into plant-available forms[57] . Furthermore, microbial activity enhances the uptake of essential mineral nutrients such as iron, zinc, and potassium by increasing their solubility and mobility in the soil[58] .

4.2 Production of Plant Growth-Promoting Compounds

Beneficial microorganisms synthesize a wide range of phytohormones that directly stimulate plant growth and development[59] . These include auxins, which promote root elongation and branching; cytokinins, which regulate cell division and delay senescence; and gibberellins, which enhance seed germination, stem elongation, and overall biomass production[60] . The production of these compounds enables plants to maintain better growth performance under stressful environmental conditions[61] .

4.3 Reduction of Oxidative Stress

Under environmental stress, plants often accumulate reactive oxygen species (ROS), which can damage proteins, lipids, and nucleic acids[62] . Plant-associated microorganisms help mitigate oxidative stress by activating the plant's antioxidant defense system[63] . This includes the stimulation of key antioxidant enzymes such as catalase, superoxide dismutase, and peroxidase, which detoxify ROS and protect cellular structures from oxidative damage[64] .

4.4 Regulation of Plant Hormones

Microbial communities play a crucial role in modulating plant hormonal balance, particularly under stress conditions. A key mechanism involves the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase[65] , which reduces ethylene levels in plants. Since ethylene is a stress hormone that accumulates under adverse conditions and inhibits plant growth, its regulation by microorganisms helps alleviate stress-induced growth inhibition and promotes better plant development[66] .

4.5 Enhancement of Plant Immune System

The plant microbiome also strengthens plant defense mechanisms through the induction of systemic resistance. This process, known as induced systemic resistance (ISR)[67] , primes the plant's immune system to respond more rapidly and effectively to pathogen attack. Beneficial microorganisms activate signaling

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pathways that enhance the production of defensive enzymes, antimicrobial compounds, and structural barriers, thereby improving resistance against a wide range of biotic stresses[68] .

5. Role of the Microbiome in Tolerance to Different Types of Stress

The plant microbiome contributes significantly to improving plant tolerance to a wide range of environmental stresses through physiological and biochemical modulation that enhances plant adaptation and survival[69] .

5.1 Drought Tolerance

Under drought conditions, plant-associated microorganisms improve plant performance by enhancing water use efficiency and maintaining cellular hydration. Many beneficial microbes stimulate root system development, leading to increased root length, density, and surface area, which allows plants to access water from deeper soil layers. In addition, some microorganisms induce the accumulation of osmoprotectants that help maintain cellular turgor under water-limited conditions[70] .

5.2 Salinity Tolerance

In saline environments, the plant microbiome plays a crucial role in reducing sodium toxicity and maintaining ionic balance within plant tissues. Beneficial microorganisms can limit sodium (Na^+) uptake or promote its compartmentalization, thereby preventing its toxic accumulation in sensitive cellular compartments. Moreover, they enhance the uptake of essential nutrients such as potassium (K^+), contributing to ion homeostasis and improved metabolic stability under salt stress[71] .

5.3 Heat and Cold Tolerance

Microorganisms associated with plants also improve tolerance to temperature extremes. Under heat stress, they help stabilize cellular membranes and reduce protein denaturation by enhancing antioxidant activity and protective metabolite production. Under cold stress, they contribute to maintaining membrane fluidity and supporting enzymatic activity, thereby reducing the damaging effects of low temperatures on cellular metabolism[72] .

5.4 Resistance to Plant Pathogens

The plant microbiome enhances resistance to pathogenic organisms through multiple mechanisms. One of the most important is competitive exclusion, where beneficial microorganisms outcompete pathogens for space and nutrients. Additionally, many microbes produce antimicrobial compounds such as antibiotics, enzymes, and secondary metabolites that directly inhibit pathogen growth and infection. These processes collectively reduce disease incidence and severity in plants[73] .

6. Agricultural Applications of the Plant Microbiome

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The functional properties of the plant microbiome have been widely exploited in modern agriculture to improve crop productivity and sustainability[74].

One of the most important applications is the development of biofertilizers, which contain beneficial microorganisms that enhance nutrient availability and promote plant growth. These biofertilizers reduce the need for chemical fertilizers and improve soil fertility in an environmentally friendly manner[75] .

Another major application is the use of biocontrol agents, which are microbial organisms capable of suppressing plant pathogens through antagonistic interactions, competition, and the production of antimicrobial substances. These agents provide an eco-friendly alternative to chemical pesticides[76] .

The plant microbiome also plays a central role in sustainable agriculture by improving soil health, enhancing stress tolerance, and supporting long-term productivity without degrading environmental resources. As a result, it contributes to the development of resilient agricultural systems under changing climatic conditions[77] .

In recent years, there has been a growing interest in studying the plant microbiome and its role in enhancing plant tolerance to various environmental stresses, particularly in the context of climate change and the degradation of natural resources. Numerous recent studies have demonstrated that plant-associated microorganisms possess a remarkable capacity to improve plant growth and increase resistance to drought, salinity, extreme temperatures, and other stress conditions [78-79]

A recent study indicated that plant growth-promoting bacteria (PGPR) significantly contribute to improving drought tolerance by enhancing water use efficiency, stimulating root growth, regulating plant hormonal balance, activating antioxidant defense mechanisms, and reducing oxidative stress induced by water deficiency [80] Other studies have further shown that these microorganisms enhance nutrient uptake, modify root architecture, and increase the production of osmoprotectants, which enable plants to adapt more effectively to severe drought conditions [81] .

Regarding salinity stress, recent scientific reviews have highlighted that the plant microbiome plays a crucial role in mitigating sodium toxicity by regulating ionic homeostasis within plant cells, enhancing potassium uptake, and stimulating the production of protective compounds that maintain metabolic stability [82] In addition, these microorganisms contribute to strengthening antioxidant enzymatic activity and reducing cellular membrane damage caused by salt stress [83]

In the case of biotic stress, studies have demonstrated that the plant microbiome enhances plant resistance to pathogens through multiple mechanisms, including competition for resources, production of antimicrobial compounds, and induction of induced systemic resistance (ISR). These mechanisms collectively reduce disease severity and improve overall plant health [84-85].

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Conclusion

The plant microbiome plays a key role in supporting plant growth and improving tolerance to both abiotic and biotic stresses through enhancing nutrient uptake, regulating hormones, reducing oxidative stress, and strengthening plant defense systems. These functions collectively improve plant health and productivity. Utilizing the plant microbiome represents a sustainable strategy to enhance agricultural production and support global food security by reducing dependence on chemical fertilizers and pesticides.

Future research should focus on better understanding plant–microbe interactions and developing efficient microbial applications that can be used effectively under field conditions to promote sustainable agriculture.

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