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Drought Tolerance in Plants: Plant- Microbe Interactions, Mechanisms and Management Strategies

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Drought is a major abiotic stress that severely constrains global agricultural productivity by disrupting plant water status, nutrient balance, and hormonal homeostasis. It is characterized by prolonged water deficiency in the atmosphere, soil, or hydrological reserves, leading to significant physiological and metabolic disturbances in crops. Drought stress reduces germination rates, restricts photosynthesis through stomatal closure, impairs nutrient uptake, and ultimately diminishes flowering, fruit set, and yield. Plants respond to water deficit through complex hydraulic and chemical signaling pathways; however, these adaptive mechanisms are often insufficient under prolonged stress conditions. Recent research highlights the critical role of the plant microbiome—often referred to as the plant's “second genome”—in enhancing drought tolerance. Drought significantly reshapes microbial community composition across plant compartments, frequently enriching drought-adapted taxa such as *Actinobacteria* and specific fungal groups while reducing overall microbial diversity in certain niches. These shifts are influenced by plant genotype, developmental stage, soil legacy effects, and alterations in root exudation patterns. Under water-limited conditions, plants modify rhizodeposition and metabolite profiles, selectively recruiting beneficial microorganisms, including plant growth-promoting rhizobacteria (PGPR), that enhance nutrient acquisition, hormone regulation, osmotic adjustment, and stress resilience. Understanding the dynamic interactions between plants and their associated microbiomes under drought stress offers promising opportunities for sustainable crop improvement. Strategies such as rhizosphere enrichment, microbiome engineering, improved water management, and genome editing hold potential for mitigating drought impacts. However, further research is required to elucidate the molecular mechanisms governing plant–microbe interactions and to validate these approaches under field conditions. Integrating microbiome-based solutions with climate-smart agricultural practices will be essential for ensuring long-term food security in the face of increasing water scarcity.

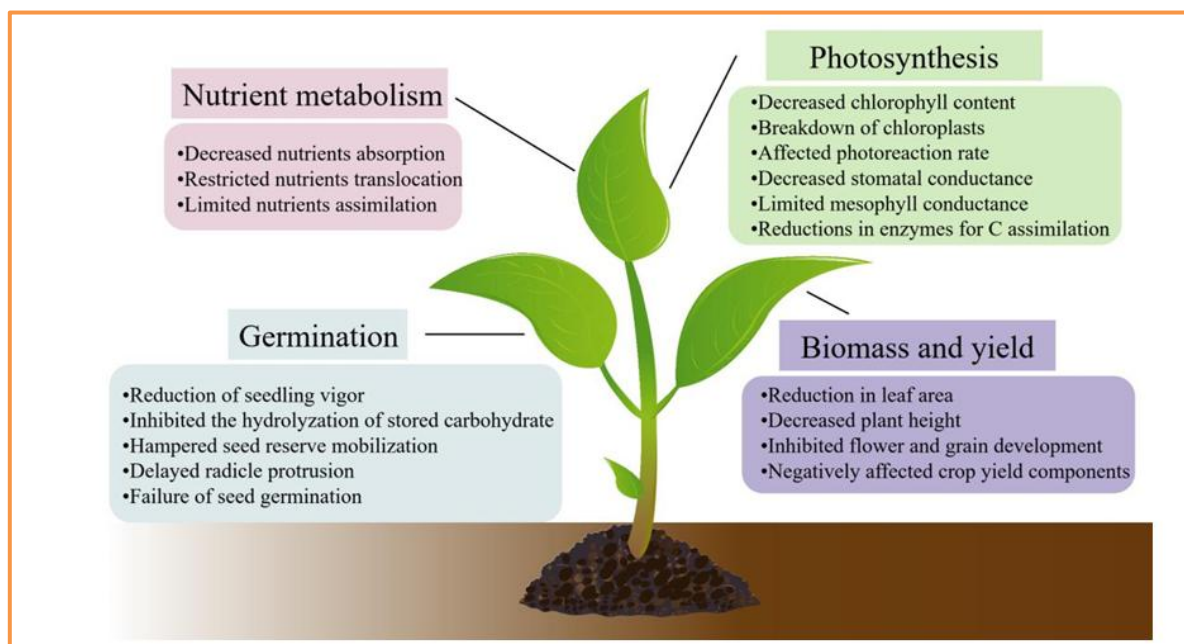
Introduction

Drought is characterized by prolonged water shortages, whether in the atmosphere (below-average precipitation), surface water, or groundwater. Meteorologists describe it as an extended period of below-average rainfall. Agriculture drought arises when insufficient rainfall limits water availability for crop growth and development, thereby affecting plant physiology [1] and disrupting normal biological functions. Hydrological drought occurs when water reserves fall below locally significant thresholds. As drought persists, its impacts on ecosystems and human populations intensify. Plants respond to drought through various signaling mechanisms, which are generally categorized as hydraulic or chemical signals. Both types of signals can be triggered by elevated vapor pressure deficits in the shoots [2]. Hydraulic signals involve changes in water status that are transmitted between plant organs,

such as from roots to leaves, whereas chemical signals rely on hormones and their transport throughout the plant. While metabolic and hormonal responses share similarities across different stress conditions, ion transport mechanisms often differ depending on the specific stress encountered [3].

Adverse Impacts of Drought Stress on Crop Growth

- Low germination Rate [4,5]
- Reduces growth and photosynthesis due to stomatal closure [6]
- Causes wilting, leaf rolling and early leaf dropping [7]
- Reduce flowering, fruit set and over all yield [8]
- Decreases nutrient and water uptake affecting plant metabolism [9]



Plant Microbiome Response to Drought Stress

The plant microbiome, often referred to as the plant's second genome, plays an essential role in supporting growth and survival under adverse environmental conditions. Among abiotic stresses, drought has been widely shown to reshape crop-associated fungal communities. In castor bean, for instance, drought induces pronounced alterations in root-associated fungal assemblages, with *Fusarium*, *Chytridiomycota*, *Ascomycota*, and *Basidiomycota* becoming predominant in the rhizosphere and surrounding soil [10]. In grapevine, the root endosphere exhibits the most substantial compositional shifts under severe water limitation, and both Chao1 richness and Shannon diversity indices significantly decline compared with well-watered conditions. Additionally, drought leads to marked enrichment of the arbuscular mycorrhizal fungus *Funneliformis* within roots, likely driven by reduced phosphorus availability in dry soils [11,12].

In wheat, drought-specific fungal taxa have been reported, such as *Trichoderma longibrachiatum* and *T. velutinum*, whereas species including *Zopfiella* sp., *M. hedericola*, *A. verrucaria*, *G. radicola*, and *A. salicis* are predominantly detected in irrigated treatments [13]. Similarly, drought alters the root fungal community structure in rice, often accompanied by increased fungal diversity, with most operational taxonomic units belonging to the Pezizomycotina subphylum [14]. In tomato phyllospheres, water deficit enhances community evenness and increases the Shannon diversity index, while reducing the relative abundance of dominant fungal groups [15]. Collectively, these findings demonstrate that drought stress exerts strong compartment-specific effects on fungal communities. Studies using sorghum further reveal that stochastic processes dominate fungal community assembly under drought, with host compartment exerting the strongest influence, followed by developmental stage and plant genotype [16]. Moreover, the impact of water stress on fungal diversity appears to be

modulated by both plant genotype and soil legacy effects, as increased rhizosphere fungal diversity has been observed in wheat grown in soils with prior drought history, whereas no significant changes occur in soils without such history [17].

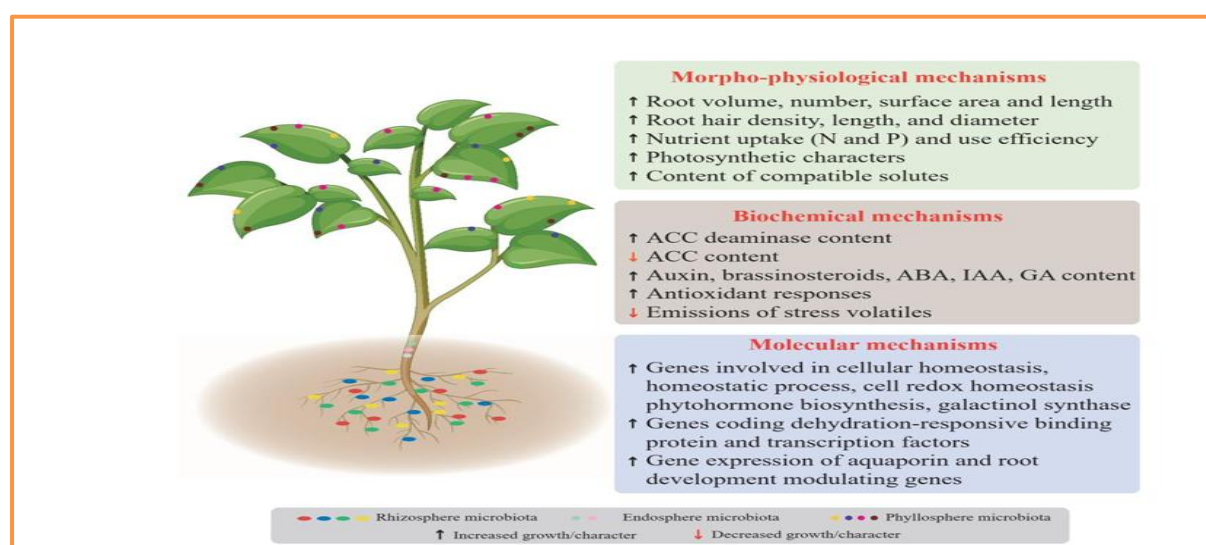
Wheat cultivated under water-limited conditions tends to host a greater abundance of fungi but a reduced bacterial population [18]. In addition, drought stress has been shown to decrease bacterial diversity in bulk soil while increasing diversity within the root endosphere [19]. In rice, drought appears to exert minimal influence on the alpha diversity of rhizosphere bacterial communities; however, it significantly shifts community composition by enriching Actinobacteria and reducing Firmicutes [20]. Consistently, drought-driven alterations in rice microbiomes include enrichment of Actinobacteria and Chloroflexi in both endosphere and rhizosphere compartments, accompanied by declines in Acidobacteria and Deltaproteobacteria. Stage-specific responses have also been observed in peanut, where drought increases the relative abundance of Actinobacteria and Acidobacteria during the seedling and podding stages, while Cyanobacteria and Gemmatimonadetes become more abundant during flowering [21]. In millet, the degree of drought stress positively correlates with the level of Actinobacterial enrichment, indicating that drought intensity is a key determinant of bacterial community shifts [22]. Overall, the consistent enrichment of Actinobacteria across diverse plant species suggests a conserved microbial response to drought. Moreover, drought frequently leads to reductions in Proteobacteria and Verrucomicrobia, along with an increased ratio of Gram-positive to Gram-negative bacteria [20]. In sorghum, early-stage drought markedly reshapes root microbiome structure and function, coinciding with enhanced abundance and metabolic activity of monoderm (Gram-positive) bacteria [23]. Notably, bacterial responses in the phyllosphere differ substantially from those in soil and root compartments. In tomato leaves, water deficit decreases bacterial richness and Shannon diversity while promoting certain Proteobacteria and Bacteroidetes families and suppressing several Actinobacteria families [24].

Plant-Microbe Interactions under Drought Stress

Drought-induced modifications in plant morphology and metabolic activity profoundly shape the composition and functionality of associated microbial communities [25]. Under water-limited conditions, plants often develop more extensive and deeper root systems, resulting in an elevated root-to-shoot ratio. Such architectural adjustments alter the spatial organization and diversity of rhizosphere microbiota, while microorganisms concurrently modulate plant adaptive responses to drought. Water deficit commonly triggers stomatal closure, leading to reduced photosynthesis and substantial reprogramming of plant metabolic pathways. For instance, marked changes in metabolite profiles have been documented in soybean roots exposed to drought stress [26]. Plants further influence their surrounding soil environment by adjusting root exudation patterns, thereby selectively promoting beneficial microbes and improving stress resilience [27]. Compounds released through root exudation-including soluble sugars, amino acids, and organic acids-generally increase with drought severity and act as key determinants of rhizosphere microbial assembly [28]. Alterations in carbon allocation via rhizodeposition can significantly affect soil microbial activity and restructure root-associated microbial communities [29]. Nevertheless, drought-driven changes in rhizodeposition vary considerably among plant species, leading to distinct microbial responses across different cropping systems. Certain metabolites are especially influential; for example, glycerol-3-phosphate-an intermediate of glycolysis and a precursor for bacterial peptidoglycan and cell wall synthesis-accumulates in sorghum during drought conditions [30], potentially shaping microbial recruitment. Strong linkages between root exudates and rhizosphere bacterial communities have also been identified in drought-stressed rice. In this context, *Streptomyces* exhibits a positive correlation with abscisic acid (ABA) but a negative association with jasmonic acid. Moreover, several Actinobacterial genera-including *Conexibacter*, *Gaiella*, *Marmoricola*, and *Nocardioides*-show positive correlations with amino acids such as L-threonine, L-valine, and L-tryptophan [31], suggesting metabolite-mediated microbial selection under water-deficit conditions.

In addition, plant genotype is a key determinant of plant-microbe interactions under drought stress, primarily by regulating genotype-specific root exudation profiles. The rhizosphere, enriched with metabolites released by both plant roots and associated microorganisms, serves as the core interface sustaining these dynamic interactions [32]. In sugarcane, drought-tolerant cultivars display significantly greater operational taxonomic unit (OTU) richness and a higher abundance of saprotrophic microorganisms in both the rhizoplane and rhizosphere compared with drought-sensitive cultivars. This enhanced microbial recruitment is associated with improved drought resilience, partly mediated through alterations in abscisic acid (ABA) signaling pathways and subsequent shifts in root exudation patterns [33]. Likewise, drought-tolerant rice genotypes exhibit a higher relative abundance of *Bacillus*, which has been correlated with increased secretion of specific amino acids, suggesting that genotype-driven metabolic adjustments actively shape rhizosphere microbial assembly under water-deficit conditions [31]

Mechanisms Underlying the Mitigation Effect of Microbes on Crop Drought Stress



Management strategies to improve drought tolerance

- Rhizosphere Enrichment [34]
- Effective water management [35]
- Plant modification using genome editing tools [36]
- Rhizosphere Engineering with Plant growth-promoting rhizobacteria (PGPR) [37]

Conclusion

Water scarcity will continue to threaten global agricultural productivity under the ongoing pressures of climate change. Implementing climate-smart agricultural strategies is therefore essential to sustain crop yields and ensure food security for the rapidly growing global population. This article outlines how drought stress impairs plant growth and productivity by disturbing nutritional balance and hormonal homeostasis. Although numerous approaches are currently employed to enhance drought tolerance in plants, the molecular mechanisms governing plant-microbiome interactions remain insufficiently understood. The plant microbiome, often described as the plant's "second genome," plays a pivotal role in maintaining plant health and stress resilience. Recent research in plant-microbe interactions has demonstrated that plants actively influence the composition of their rhizosphere microbiome, as different plant species recruit distinct microbial communities even when cultivated in identical soils. A deeper understanding of the factors that underpin beneficial plant growth-promoting rhizobacteria (PGPR) associations will provide valuable insights for effectively harnessing microbial resources to improve plant performance under drought conditions. This article highlights a holistic framework for integrated drought stress

management in crops. Depending on soil characteristics, drought severity, and climatic conditions, tailored strategies may involve manipulating the rhizosphere microbiome, enriching soils with organic matter and nutrients, applying phytohormones, incorporating liquid nanoclay or nanoparticles, and adopting improved water management practices to maintain productivity without yield penalties. Advanced genome-editing technologies also offer promising avenues for developing drought-resilient cultivars; however, most of these approaches are still in preliminary stages and require extensive validation under field conditions.

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