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# Plant-microbiome interactions under drought—insights from the molecular machinist's toolbox

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Plants face numerous challenges in novel and harsh environments, including altered precipitation regimes, salinity, extreme temperatures, increased atmospheric CO<sub>2</sub>, nutrient deficiency, heavy metals, and oxygen. Drought remains a major constraint to crop productivity and meeting food demand, with the frequency, intensity, and duration of drought expected to raise in the coming century. The “cry for help” hypothesis proposes that timely recruiting of the microbiome by plants may confer benefits in stress alleviation, plant growth, fitness, and health. The root-associated microbiome harbors 10–100 times more functional genes than the host, which can significantly stimulate the metabolic and genetic potential of plant–microbiome assembly. However, cross-talk among drought and the root-associated microbes, and among the root-associated microbiome and the host-plant, is less well understood. Understanding the molecular aspect of multiple mechanisms by which microbes associate with plants during drought stress is of fundamental importance in plant biology and agriculture. In this review, we examine the progress in research on the response of plant and its microbiome assemblages and interactions to drought stress, including the impact of drought and root exudates on host resilience. We delve into the potential of ‘omics’ technologies to unravel the signaling networks underlying these interactions and the multiway interactions that occur among the host and its associated microbiome. We then discuss the shortfalls, challenges, and future research directions in this field. Overall, we argue that harnessing/manipulating the crop microbiome presents a promising strategy for improving agricultural systems in the face of global climate change.

## KEYWORDS

plant-associated microbiome, biostimulants, plant resilience, ‘omics’, signaling networks, water deficit, root exudates, multiway interactions

## 1 Drought-tolerant microbiome: a growing field of scientific interest

Plants are continuously exposed to harsh environmental conditions, including water scarcity, salinity, heat waves, elevated CO<sub>2</sub> levels, heavy metals accumulation, and soil poverty, which challenge their adaptability and resilience (Shen et al., 2020). Drought remains a serious impediment to crop productivity and food security, especially with the increase in its frequency,

duration, and intensity under global climate change (Canarini et al., 2021; Anli et al., 2022). It disrupts plant metabolism, reduces photosynthetic activity, and induces electrolyte disturbances and reactive oxygen species (ROS) accumulation, causing cell apoptosis and plant death (Boutasknit et al., 2021; Benaffari et al., 2022; Toubali et al., 2022).

Drought stress affects plant functioning, which in turn alters plant metabolism and root exudates, influencing the plant rhizosphere microbiome. Plant exudates, such as sugars, vitamins, organic acids, amino acids, fatty acids, flavonoids, carboxylic acids, benzoxazinoids, and ethylene (ET), play a crucial role in selectively recruiting rhizospheric microbial communities (Vives-Peris et al., 2020). Phytohormones, such as jasmonic acid (JA) and salicylic acid (SA), and their signaling pathways significantly impact plant microbiome structure (French et al., 2019). Drought may also impact plant microbiome association, putting selective pressure on its components to endure stressful conditions. Inducing glycerol-3-phosphate (G3P) synthesis during drought, for example, favors Actinobacteria in the rhizosphere, which promotes plant fitness and health under water deficit (Xu et al., 2018b). Drought also induces a decline in SA production, which significantly impacts the formation of both exo- and endogen microbiome (Lebeis et al., 2015). Many investigations have revealed that during drought stress, plants promote monoderm bacteria (or gram-positive) over diderm bacteria (or gram-negative) in the rhizosphere (Naylor et al., 2017; Naylor and Coleman-Derr, 2018). Drought reduces iron and phytosiderophore availability in the rhizosphere, favoring Actinobacteria that may thrive in such environment and promote plant performances (Xu et al., 2021). A recent study by Santos-Medellin et al. (2021) revealed that drought can have long-lasting impact on the rhizospheric microbiome. They discovered that the rice root-associated microbiome structure was severely altered during a short period of water deficit but retrieved to its predrought state after recovery. However, extended water stress had serious and long-term impact on the endosphere community, which were not completely recovered even after rewatering. According to the same study, the abundance of Actinobacteria recorded a significant increase after prolonged drought, accounting for >80% of the bacterial community after the drought period. In the same vein, water shortage intervals the establishment of sorghum root microbial communities during the early development and plays a role in restructuring the root microbiome by increasing enrichment in monoderm bacteria and their activity (Xu et al., 2018b). Various studies have demonstrated that drought has a substantial impact on the activity and composition of plant root-associated bacteria in a manner that is remarkably preserved regardless of host species and sites (Karlowsky et al., 2018; De Vries et al., 2019; Williams and De Vries, 2020). The analysis of co-cited references in Figure 1 identified emerging trends and research hotspots in the field. Nine clusters were identified, with each cluster corresponding to a specific line of research. All clusters, except for “Cluster #1: Antibiotic resistance genes,” were closely related to the topic of plant-microbe interactions under drought. “Cluster #0: Water deficit” contained the majority of the nodes and has been widely reported. “Cluster #1: Antibiotic resistance genes” and “Cluster #2: Abiotic stress tolerance” were the most active areas of research. Recent research has focused on plant tolerance to water stress and their associated microorganisms, as seen in “Cluster #0: Water deficit,” “Cluster #2: Abiotic stress tolerance,” “Cluster #4: Microbial communities,” “Cluster #5: Plant responses,” and “Cluster #7: Crop

resiliency.” These results emphasize the significance of understanding the role of plant-microbe interactions for mitigating the effects of drought and enhancing plant resilience. The evolving trends and research priorities in this field underscore the important role performed by plant-associated microorganisms.

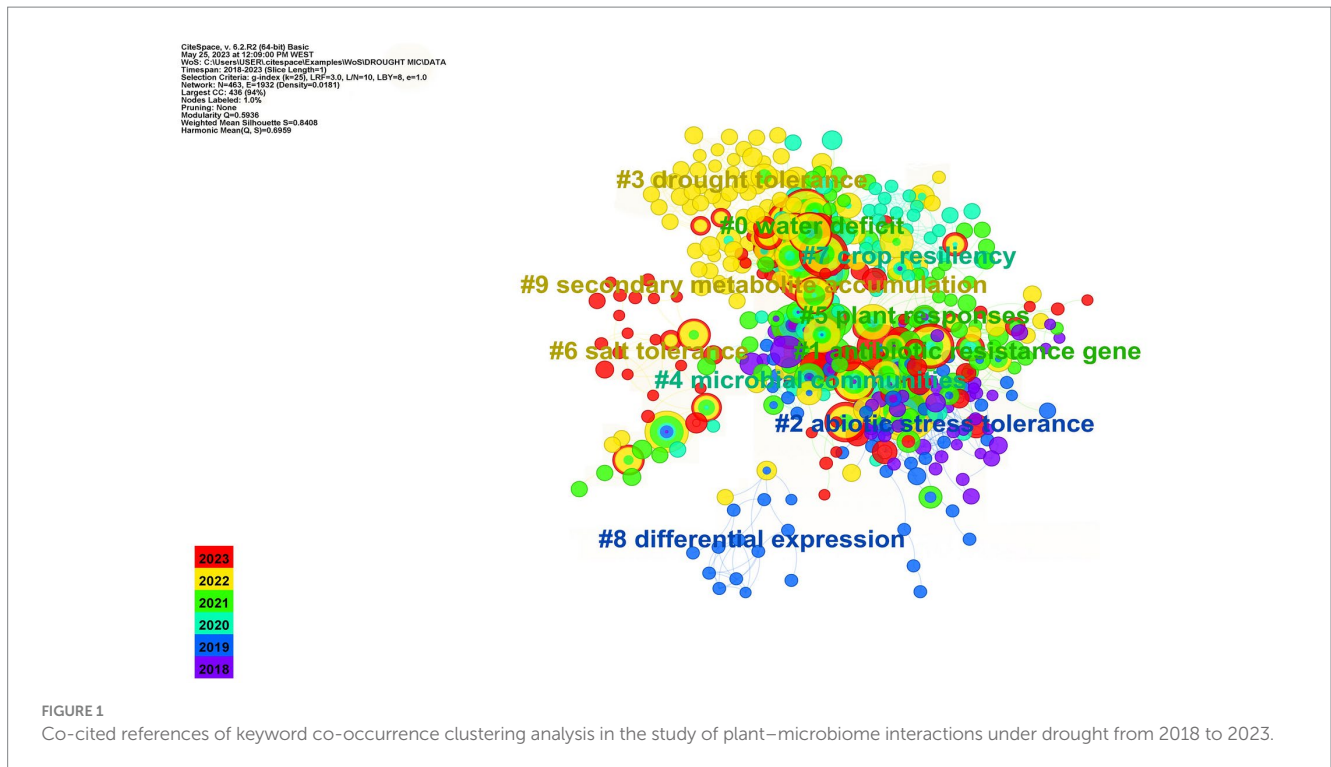
The root-associated microbiome, including plant growth-promoting fungi (PGPF) and plant growth-promoting bacteria (PGPB), may promote plants’ resistance and adaptation to water deficiency (Xu and Coleman-Derr, 2019; Table 1). Plant tolerance to drought is increased either directly by members of the root microbial community or indirectly via microbe-microbe interactions (Hartman and Tringe, 2019; Abbott et al., 2021). Microbiome may help host resist water deficit by activating transcriptional reprogramming of multiple genes and transcription factors (TFs) regulating plant defense. Microbes, for instance, have recently been shown to induce various genes expression under drought stress.

Although the composition of the plant-associated microbial communities has been studied in a great number of plant species, less interest has been paid to the effect of water shortage on the root-associated microbiota. There is a lack of understanding of the ‘cross-talk’ among drought, the root-associated microbiome, as well as between the root-associated microbial communities and the host-plant. Understanding the molecular patterns that orchestrate the assemblage of microbial communities with plants under drought stress is critical for the plant survival and fitness. Thus, knowledge of plant-microbe-drought regulation will be necessary for the design of environmentally-friendly crop management strategies and sustainable agriculture under changing environments. This review summarizes the research advances on the shaping of plant microbiome under water deficit conditions and the mechanisms by which microbiome could alleviate the adverse impact of drought on plants. Finally, we highlight the gaps, challenges, and perspectives of future research in this ‘ménage à trois’ that could help harnessing the microbiota to improve drought outcomes.

## 2 Plant-mediated changes in microbiota during drought trends

### 2.1 Plant-microbiome communication under drought trends: host plant churn out valuable chemicals for regulating microbial functions

Plants continuously release exudates into their surroundings, in the form of liquid, solid, or gaseous compounds, through their leaves, shoots, or roots. Plants exuded c. 11% of the net fixed C or 27% of the C assigned to roots to the rhizosphere. The amount of these compounds varies depending on multiple factors, such as plant age, species, and nutritional performance (Bais et al., 2006; Jones et al., 2009; Nakayama and Tatenno, 2018). Root exudates contain various substances, including primary and secondary metabolites and phytohormones, such as ET, JA, SA, indole 3-acetic acid (IAA), abscisic acid (ABA), gibberellic acid (GA), and cytokinins (CKs). Primary metabolites consist of sugars, amino acids, and organic acids, while secondary metabolites include flavonoids, glucosinolates, phytoalexins, triterpenes, and benzoxazinoids (Badri et al., 2008; Pang et al., 2021). For instance, tomato plants exude a mixture of



metabolites, including organic acids, steroidal glycoalkaloids, acylsugars, and hydroxycinnamic acid derivatives, into the rhizosphere (Korenblum et al., 2020).

Microbes diverge in their functioning and metabolism, and their sensitivity to water availability varies. Thus, drought can directly impact the assembly of plant microbiome. Plant surface microbiome, i.e., phyllosphere, is likely to be significantly altered by drought since environmental conditions vary more rapidly than those inside plant tissue (i.e., endosphere), which is more stable (Trivedi et al., 2020). Most of the microbes from the bulk soil (a source of potential microbes to colonize plant roots) are directly influenced by external climatic factors, including drought. On the other hand, rhizosphere microbiome are directly altered by these factors and indirectly by plant responses, such as changes in host morphology, physiology, immune system, and root exudation (Figure 2). Previous studies suggest a consistent response of the host-associated microbiome to water deficiency (Vescio et al., 2021; Wipf et al., 2021; Aslam et al., 2022; Tebele et al., 2023). Under water limitation, several plant species recruit monoderm bacteria that are resistant to dryness owing to their thicker cell walls and reduce diderm bacteria in the roots and rhizosphere (Naylor et al., 2017; Naylor and Coleman-Derr, 2018).

Understanding how drought stress affects plant-microbiome assemblage is still a challenging task owing to the multilayers and complex interconnections that orchestrate this 'triangle' interaction. Chemical signals exchange heavily influences plant-microbiome communication under water scarcity (Figure 2). For example, under stressful environments, plants have evolved a 'cry for help' mediated exudation, resulting in the recruitment of stress-mitigating microbes (Liu et al., 2020). Plants have a complex microbial recruiting system to select the most beneficial microorganisms to incorporate into plant tissues, discriminating between friendly and beneficial or hostile and harmful interactions (Hacquard et al., 2017; Teixeira et al., 2019;

Zhang et al., 2023). The host plant possesses protective mechanisms to perform this selection: (i) pattern recognition receptors (PRRs), the initial mechanism of defense to identify microbe-associated molecular patterns (MAMPs), such as fungal chitin or bacterial flagellin, leading to MAMP-triggered immunity (MTI) and (ii) nucleotide-binding leucine-rich repeat (NLR) proteins as a second defense mechanism to identify pathogen effectors, inducing effector-triggered immunity (ETI). Changes in plant immunity caused by drought could structure the plant-microbiome assembly, especially inside host plant tissues. Suppression of ETI may interfere with host-mediated management of microbe colonization and may result in microbial dysbiosis inside plant tissues. The suppression of ETI can also be a new pattern used by plants to lessen their defense mechanisms, allowing beneficial microbes to colonize roots and promote stress mitigation-related gene transcripts.

The mutual communication involving the plant defense system and the microbiome structures the plant-microbiome assemblage. Plants control immune response in rapidly changing environmental conditions using active but tightly controlled modifications in different hormone pathways (i.e., ET, SA, ABA, and JA; Li et al., 2021; Ait-El-Mokhtar et al., 2022). Lebeis et al. (2015) reported that drought reduces SA production, which is involved in the assembly of both endophytic and epiphytic microbiome. SA can promote or inhibit microbial community growth directly on microbiome members or through established signaling pathways based on hormonal cross-talk. For instance, ABA-induced production under water scarcity interferes with the SA-mediated immune pathway. Drought-mediated alterations in plant hormones may differ depending on the plant developmental stage and tissue type. For example, maize grown under water limitation boosts benzoxazinoid defense system in plant aboveground part while stimulating terpenoid phytoalexins in the belowground tissues (Vaughan et al., 2018). Alterations in the

TABLE 1 Role of microbiome in drought tolerance: summary of reported studies.

Microbe inoculation	Plant	Inoculation method	Tolerance strategy	Ref.
<i>Bacillus thuringiensis</i> AZP2	Wheat	Drenching	Induced the production of VCs.	Timmusk et al. (2014)
<i>Pantoea alhagi</i>	Wheat	Drenching	Enhanced the production of siderophores, EPS, IAA, soluble sugars, ammonia, and protease and decreased chlorophyll degradation.	Chen et al. (2017)
<i>Bacillus licheformis</i> K11	Pepper	“watered in” via irrigation	Upregulated stress-related genes ( <i>Cadh1</i> , <i>VA</i> , <i>sHSP</i> and <i>CaPR-10</i> ) and proteins.	Lim and Kim (2013)
<i>Sphingomonas</i>	Soybean	“watered in” via irrigation	Enhanced biomass, proline, glycine, glutathione, glutamine, ABA, and JA content.	Khan et al. (2014) and Asaf et al. (2017)
<i>B. amyloliquefaciens</i> FZB42	Arabidopsis	Added to inoculated soil	Induced the production of proline and enzyme activity (i.e SOD and POX) and the overexpression of <i>RD17</i> , <i>RD29A</i> , <i>ERD1</i> , <i>LEA14</i> genes.	Lu et al. (2018)
<i>B. amyloliquefaciens</i>	Grape	Drenching	Enhanced melatonin secretion and reduced H <sub>2</sub> O <sub>2</sub> , O <sub>2</sub> <sup>-</sup> , and MDA concentration.	Jiao et al. (2016)
<i>B. cereus</i> AR156, <i>B. subtilis</i> SM21, and <i>Serratia</i> sp. XY21	Cucumber	Applied directly to roots	Induced the production of monodehydro-ascorbate, proline, and antioxidant enzymes, and altered the expression of <i>cAPX</i> , <i>rbcL</i> , and <i>rbcS</i> genes.	Wang et al. (2012)
<i>Trichoderma</i> and <i>Pseudomonas</i>	Rice	Coated onto seeds	Increased the transcript levels of multiple genes involved in the antioxidant enzymes and phenylpropanoid biosynthesis pathway.	Singh D. P. et al. (2020)
<i>Pseudomonas</i> spp.	Soybean Arabidopsis	Drenching	Induced the expression of <i>DREB/EREB</i> , <i>PIP</i> , <i>TIP</i> , <i>P5CS</i> , and <i>GOLS</i> genes. Induced the expression of <i>RD29A</i> and <i>RD29B</i> genes.	Vaishnav and Choudhary (2019) and Liu et al. (2020)
<i>Bacillus</i> and <i>Pseudomonas</i>	Sorghum	Applied directly to roots	Higher production of signaling molecules (i.e., IAA, CK, SA, GA, JA, BRs, sphingosine, psychosine), osmolytes, and antioxidants, and reduced ET content.	Carlson et al. (2020)
<i>Sinorhizobium</i> sp.	Barrel clover	Drenching	Upregulated JA pathway translation and downregulated ET biosynthesis.	Staudinger et al. (2016)
<i>Bacillus</i> spp.	Guinea grass	Drenching	Higher proline production and lower MDA concentration and GR activity.	Moreno-Galván et al. (2020)
<i>Streptomyces</i> spp.	Tomato	Added to inoculated sand	Improved growth and leaf water content, antioxidant enzyme activity, proline and H <sub>2</sub> O <sub>2</sub> accumulation, and reduced <i>ERF1</i> and <i>WRKY70</i> gene expression.	Abbasi et al. (2020)
<i>Bacillus subtilis</i>	Arabidopsis Mustard	Applied directly to roots	Increased the expression of <i>RD29B</i> , <i>RAB18</i> , <i>RD20</i> , and <i>NCED3</i> genes. Increased the expression of <i>DREB1D</i> , <i>WRKY7</i> , and <i>CSD3</i> genes.	Woo et al. (2020)
<i>Enterobacter cloacae</i> , <i>Enterobacter</i> sp., <i>Ochrobactrum</i> sp., and <i>Microbacterium</i> sp.	Sorghum	Coated onto seeds	Improved growth fitness, osmotic adjustment, and proline accumulation, with the upregulation of proline biosynthesis genes <i>SbP5CS 1</i> and <i>SbP5CS 2</i> .	Govindasamy et al. (2020)
<i>Bacillus subtilis</i> and <i>Paenibacillus illinoensis</i>	Pepper	“watered in” via irrigation	De-regulation of vacuolar H <sup>+</sup> pyrophosphatases gene expression.	Vigani et al. (2019)
<i>Piriformospora indica</i>	Barley	Drenching	Induced the expression of genes involved in regulating stress signaling molecules, including proteins and enzymes orchestrating pivotal metabolic pathways, transporters, autophagy and up-regulation of plant oxidative stress-associated proteins.	Ghaffari et al. (2019)

(Continued)



TABLE 1 (Continued)

Microbe inoculation	Plant	Inoculation method	Tolerance strategy	Ref.
<i>Pseudomonas indica</i>	Rice	Coated onto seeds	Improved growth performances, biomass accumulation, mineral nutrition (zinc and phosphorus), and proline accumulation, with the upregulation of <i>P5CS</i> genes.	Saddique et al. (2018)
<i>Trichoderma</i> sp.	Rapeseed	Applied directly to roots	Downregulation of ET genes ( <i>ACO1</i> and <i>ERF1</i> ) and upregulation of <i>NCED3</i> and <i>PYL4</i> .	Poveda (2020)
<i>Rhizophagus irregularis</i>	Apple	Applied directly to roots	Enhanced <i>MdMAPK7-1</i> , <i>MdMAPK16-2</i> , <i>MdMAPK17</i> , and <i>MdMAPK20-1</i> transcripts.	Huang et al. (2020)
<i>Funneliformis mosseae</i>	Trifoliolate orange	Applied directly to roots	Increased the antioxidant enzyme (CAT and SOD) genes and activity and upregulation of polyamine metabolism-associated gene expression.	Zhang et al. (2020)
<i>Funneliformis mosseae</i>	Trifoliolate orange	Applied directly to roots	Increased expression of root tip aquaporins ( <i>PtTIP1;2</i> , <i>PtTIP1;3</i> , <i>PtTIP4;1</i> ).	Jia-Dong et al. (2019)
<i>Glomus clarum</i> , <i>Acaulospora scrobiculata</i> , and <i>Gigaspora rosea</i>	Bean	Applied directly to roots	Increased expression of eight aquaporin-associated genes.	Recchia et al. (2018)
<i>Funneliformis mosseae</i> , <i>F. geosporus</i> , <i>Claroideoglossum claroideum</i> , <i>Glomus microaggregatum</i> , and <i>Rhizophagus irregularis</i>	Rice	Applied directly to roots	Increased P and IAA concentrations	Chareesri et al. (2020)
<i>Glomus mosseae</i>	Wheat	Applied directly to roots	Upregulated proteins involved in cell wall integrity and carbohydrate production and downregulated stress-associated molecules (i.e., ET biosynthesis enzymes)	Bernardo et al. (2017)

ABA, abscisic acid; ACO1, aconitase1; APX, ascorbate peroxidase; BRs, brassinosteroids; CAT, catalase; CK, cytokinin; CSD3, copper/zinc superoxide dismutase 3; DREB, dehydration-responsive element-binding protein; EPS, exopolysaccharides; EREB, ethylene responsive element binding protein; ERF1, ethylene response factor; ET, ethylene; JA, jasmonic acid; HSP, heat shock protein; IAA, indole-3-acetic acid; GA, gibberellic acid; GOLS, galactinol synthase; LEA, late embryogenesis abundant; MAPK, Mitogen-activated protein kinase; MDA, malonyldialdehyde; NCED3, 9-cis-epoxycarotenoid dioxygenase3; P, phosphate; P5CS, delta1-pyrroline-5-carboxylate synthase; POX, peroxidase; PR10, pathogenesis-related protein 10; PYL, pyrabactin resistance-like; rbcL, ribulose biphosphate carboxylase large chain; rbcS, ribulose biphosphate carboxylase small chain; RD29A, desiccation-responsive protein 29A; SA, salicylic acid; SOD, superoxide dismutase; TIP, tonoplast intrinsic protein; VA, vacuolar H<sup>+</sup>-ATPase; VCs, volatile compounds.

distribution or allocation of diverse signaling molecules or defense metabolites as a result of drought may have an additional impact on microbiome assembly.

It is worth noting that in host-microbiome research, core-and-hub microbiota concepts are gaining traction (Singh B. K. et al., 2020). These refer to the microbiota that exist in a specific species regardless of environmental conditions, growing season, or management practices and perform critical host functions (Trivedi et al., 2020). Given their significance, it is crucial to understand how drought affects the 'core-and-hub' microbiota that may organize community-scale functions in plant-microbiome communications. An enlarged understanding of the ecological vectors that orchestrate microbiome response to water scarcity will promote our knowledge of microbiome traits that boost plant performances under changing environments.

## 2.2 Plant-mediated reshaping of microbiota composition in response to drought

Plant and microbiota have a two-way communication, both underground and aboveground, that enables them to sense and respond to stress conditions. In response to stress, plants release a

range of metabolites that attract specific microorganisms capable of enhancing their tolerance to stress (Bai et al., 2022). According to the 'cry for help' hypothesis, plants recruit particular microbiome communities that aid them in managing stress (Liu et al., 2020). This concept was first observed when plants grown in soils deficient in phosphorus and nutrient-supplying arbuscular mycorrhizal fungi (AMF), and nitrogen recruited nitrogen-fixing rhizobia (Carbonnel and Gutjahr, 2014; Nishida and Suzaki, 2018). The 'cry for help' assumption is also applicable to plants experiencing drought stress, as the microbiome composition in roots significantly changes by promoting actinobacteria and other gram-positive bacteria over gram-negative ones (Timm et al., 2018). Plants may selectively recruit drought-tolerant microbes that have evolved from repetitive drought periods, resulting in beneficial and efficient plant-microbiome interactions that enhance the performance of both host and microbes (Naylor and Coleman-Derr, 2018). Terhorst et al. (2014) demonstrated that drought-stressed *Brassica rapa* plants exhibit higher and more diverse bacterial richness around their roots in comparison to the controls.

Santos-Medellín et al. (2021) revealed that the above- and below-ground microbiome undergo a plant-driven change in response to water limitation, resulting in an increase in drought-tolerant endophytic monoderm bacteria that may help mitigate drought. The

same authors demonstrated how persistent drought can permanently impede plant endophytic microbiome growth. This effect persists even after the drought constraint is alleviated. Their research revealed how long-lasting drought stress may shift microbial community composition, which may affect plant fitness. They also identified promising candidates for microbiome engineering to create performant microbial assemblages against water deficit, including drought-resistant endophytic microorganisms that increased in abundance in the endosphere after drought stress. Active microorganism recruitment under stressful conditions appears to be a common evolutionary mechanism to promote plant performances. Nonetheless, the strategies that allow plant host to incorporate external signals during symbiotic microbes' recruitment and the host genetic characters controlling this recruitment are still under investigations. These processes are orchestrated by multilayer components involving plants, microorganisms, soil, and environmental traits that shape the final result. The accumulation of stress-related factors in plant roots during drought, including G3P and pipercolic acid, has been linked to actinobacteria enrichment in the rhizosphere (Knight et al., 2018; Caddell et al., 2020; Table 2). Understanding the underground signals communication is still in its early stages, particularly in drought-stressed hosts that shape their tolerant microbes.

A dynamic understanding of the role of metabolites and their genomic features is essential to comprehend the multilayered complexity of the 'cry for help' theory in host microbe assembly before and after drought conditions. This will provide new insight into creating drought-tolerant microbial consortia for sustainable agriculture. Recently, Bai et al. (2022) proposed a model based on the 'cry for help' hypothesis for plant microbiome recruitment under water scarcity (Figure 2). Under drought conditions, plants undergo molecular and metabolic readjustments and produce specific root metabolites. The root exudates may promote the reprogramming and restructuring of the microbiome by recruiting selective drought-tolerant microorganisms with a vast arsenal of functional enzymes. Subsequently, drought-resistant microbiota

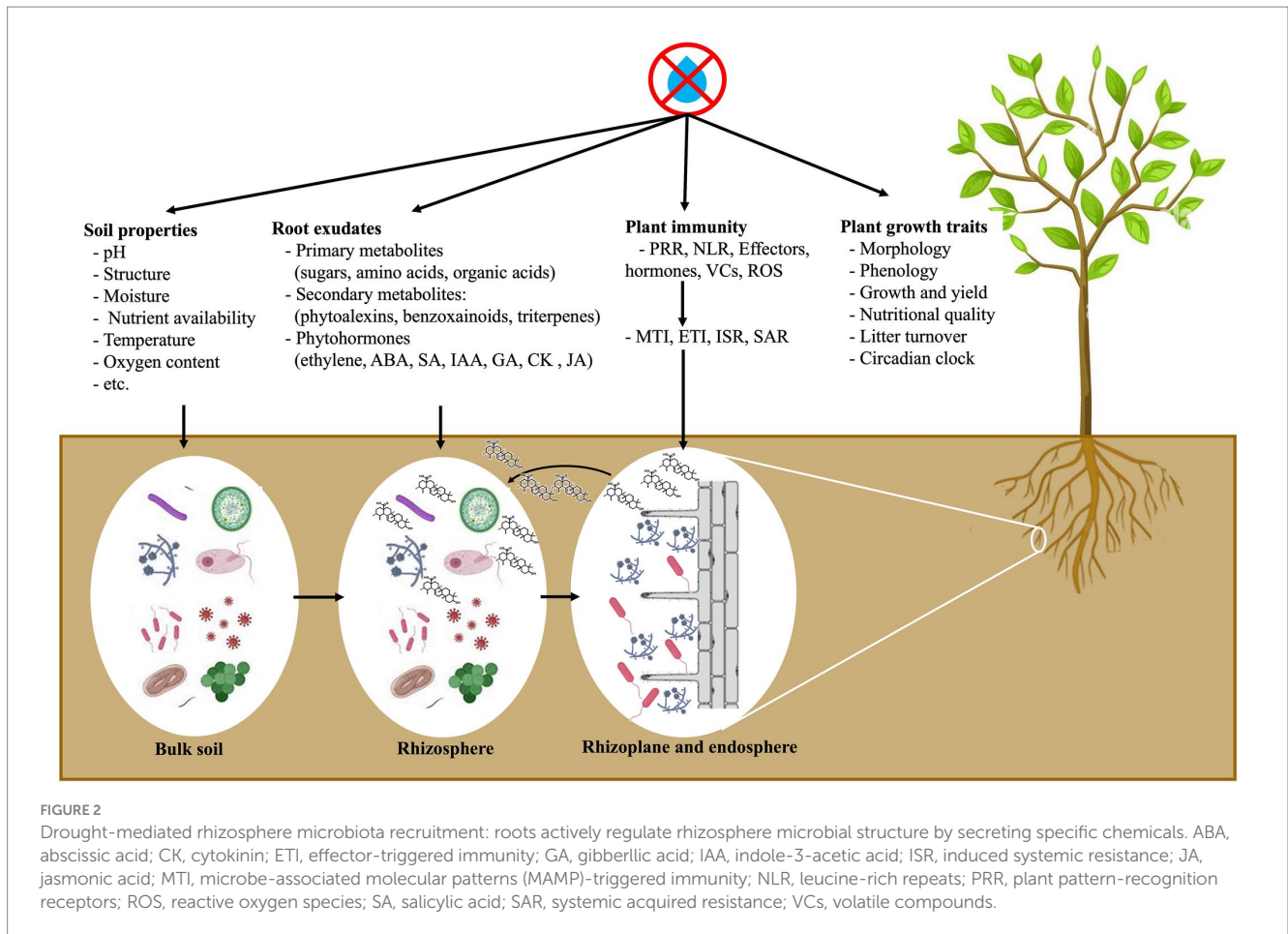
can mitigate stress impact and deliver nutrients to host plants via multiple direct and indirect mechanisms.

## 2.3 Microbes that get the scoop—plant genes, signaling integrators, and metabolic changes co-ordinating rhizosphere microbiome under drought

The plant and its associated microbiome form a harmonized and functional entity known as a holobiont (Bordenstein and Theis, 2015), in which evolutionary selection occurs not only between the host and the associated microbes but also among the microbes (Ait-El-Mokhtar and Baslam, 2023). To maintain the harmony of this association, systems of coordination among the microbial communities and with the host plant are necessary. Our understanding of the acquisition of microbes in the environment and the rules governing their association in the plant holobiont is very limited. It is widely believed that during root penetration into bulk soil, the soil microbiome progressively differentiates into the rhizosphere microbiome via contact with rhizodeposits, which have a significant effect on the microbiota composition (Tian et al., 2020; Figure 2). After this initial community shift, the microbiota composition is finely adjusted in specific compartments (rhizosphere, rhizoplane, or endosphere; Bulgarelli et al., 2013). Plant genetic factors, including root exudate quality and quantity and root morphology, have been known to shape the rhizospheric microbial communities (Sasse et al., 2018). Other factors, including the plant developmental stage, plant immune system, and season, have also been shown to play a significant role in shaping the rhizosphere microbiome (Hassani et al., 2018). The presence of a core microbiota in some crops, irrespective of fertilization management or soil origin, suggests that these communities are partly assembled and selected by plants. In general, it is believed that the plant selects its microbial associates via the action of its root exudates. Yet, this unidirectional recruitment is being questioned (Uroz et al., 2019) because the co-evolution of the plant-microbe holobiont suggests

TABLE 2 Plant-mediated reshaping of rhizosphere microbiota composition in response to drought.

Regulator/Genes/Key factors	Host plant	Pathways/Signals molecules shaping the microbiota	Effect on the microbiota	Effect of shifted microbiota on the host plant	Ref.
Unclear	<i>Sorghum bicolor</i>	Glycerol-3-phosphate	Monoderm bacteria (especially Actinobacteria)	Root growth promotion	Xu et al. (2018b)
Unknown	<i>Sorghum bicolor</i>	Pipercolic acid	Monoderm bacteria (Actinobacteria)	Root growth reduction	Caddell et al. (2020)
Unclear	<i>Oryza sativa</i>	Unclear	Actinobacteria (Streptomyces)	Root growth promotion	Santos-Medellin et al. (2021)
Unclear	<i>Oryza sativa</i>	Unclear	Actinobacteria and Chloroflexi	Root growth promotion	Santos-Medellin et al. (2017)
Unknown	<i>Populus deltoides</i>	Unknown	Proteobacteria, Actinobacteria, and Verrucomicrobia	-	Timm et al. (2018)
Unknown	18 plant species belonging to the Poaceae family	Unknown	Actinobacteria	-	Naylor et al. (2017)
Unknown	<i>Brassica rapa</i>	Unknown	Increased bacterial richness	-	Terhorst et al. (2014)

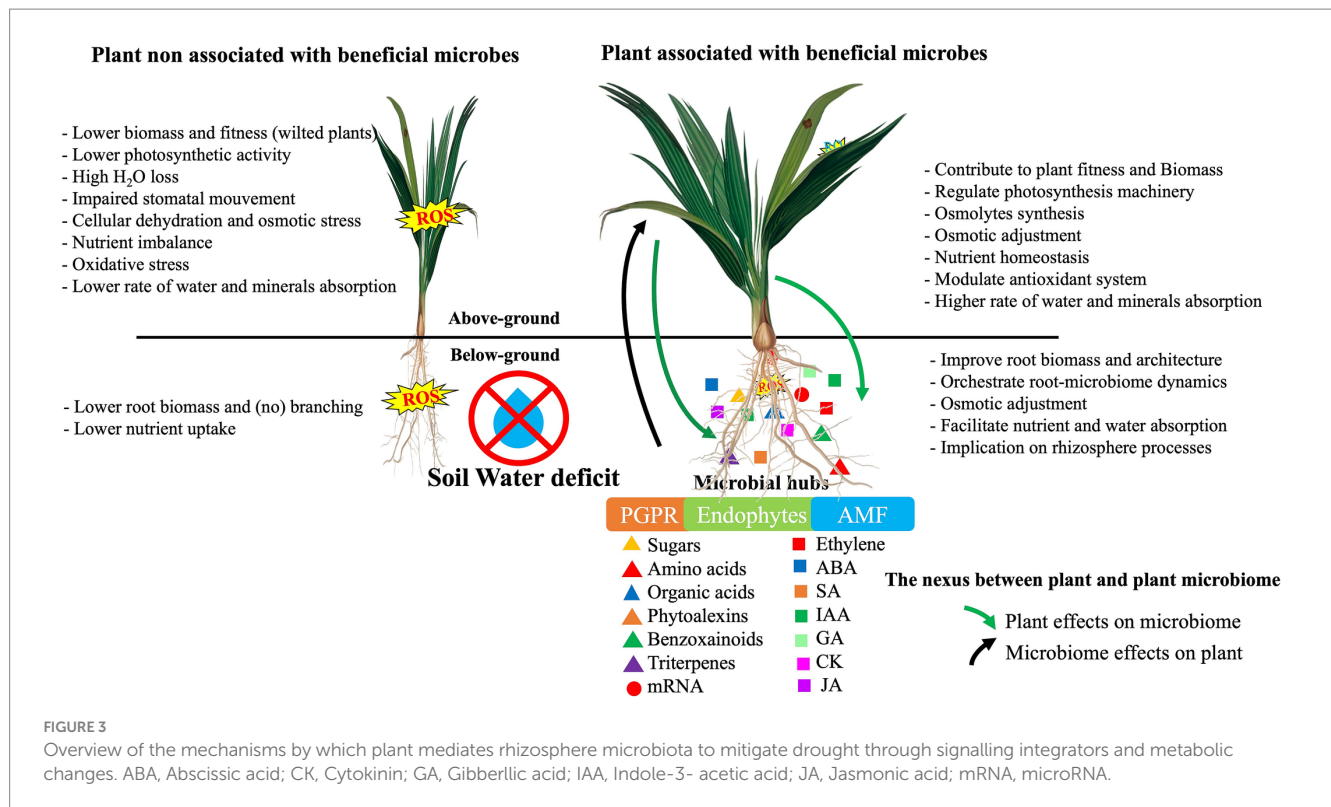


bidirectional interactions, particularly in terms of rhizosphere microbiome shaping (Figure 3).

Conventionally, root exudate secretion was thought to be a passive process facilitated by various pathways, such as diffusion across the root cell membrane, ionic channels, and vesicle transport (Baetz and Martinoia, 2014). The chemical characteristics of the exuded molecules determine the type of the secretion pathway. Diffusion is involved in the exudation of metabolites with low molecular weight, such as amino acids, sugars, carboxylic acids, and phenolics. This process is caused by the difference in the concentrations of compounds between root cell cytoplasm and rhizosphere, and it may be influenced by root membrane permeability, root cell integrity, and compound polarity (Badri and Vivanco, 2009). Ionic channel pathways are involved in the exudation of carbohydrates and particular carboxylates, including oxalate and malate (released in large amounts), which are transported through membranes via a transport mechanism performed by proteins rather than diffusion. Two types of anionic channels are involved in this process: SLOW Anion Channels (SLACs), which are activated in many seconds, and QUICK Anion Channels (QUACs), which take a few milliseconds to be activated (Dreyer et al., 2012). The third form of passive transport pathways is vesicle transport (exocytosis) responsible for the exudation of high molecular weight metabolites kept inside vesicles (Badri and Vivanco, 2009). Exuded compounds are produced by the endoplasmic reticulum or the Golgi apparatus and aid in pathogen defense (Weston et al., 2012). In contrast, the active transport pathway of root-secreted metabolites is

mediated by plasmatic membrane proteins (Baetz and Martinoia, 2014): ATP-Binding Cassette (ABC) and Multidrug and Toxic Compound Extrusion (MATE) (Kang et al., 2011). Protein-mediated root exudation may take three forms and depends on their specificity: transporters exuding multiple compounds, compounds secreted via various membrane transporters in the rhizosphere, and metabolites secreted by a single transporter. ABC transporters are classified as primary transporters owing to the use of ATP hydrolysis for the necessary energy to transport varied solutes (Jones and George, 2002; Orelle et al., 2018). The gene names encoding these transporters have evolved over time. Nevertheless, another classification has been established based on the organization of TMD and NBD domains, assembling the various members into nine families termed with letters ranging from A to I, despite the fact that family H does not exist in plants (Verrier et al., 2008). Some studies have looked into the involvement of ABC transporters in root exudation and highlighted their significance in this process (Badri et al., 2008, 2009; Olanrewaju et al., 2019).

Recent studies have shown that shifting from naturally occurring microbiome to adapted microbial communities to the stressful condition enables the plant holobiont to quickly adapt to changing environments (Pantigoso et al., 2022; Faist et al., 2023; Li et al., 2023). Rice provides an example of plant-mediated microbial abundance modulation, where under water deficiency, the microbiome composition shifts to a greater abundance of drought-resistant plant growth promoting rhizobacteria (PGPR) strains (Santos-Medellin



et al., 2017). Changes in root exudation caused by water shortage may be the source of the enhancement of several types of microorganisms. Stressful soil conditions, along with microbial composition changes, can influence rhizosphere microbial activity. The modulation of the rhizosphere microbiome is influenced not only by plants but also by microbes. By exuding phytohormones, antimicrobials, volatile compounds (VCs), and quorum-sensing, plants may regulate the plant environment and even benefit their hosts (Venturi and Keel, 2016). Under water limitation conditions, the rhizosphere microbiome is shaped by microbial interactions among members and their preferences for specific metabolites (Zhalnina et al., 2018). Microbial interactions may alter gene expression within communicating microbes (Sasse et al., 2018), indicating that microbial interactions affect both the function and shape of the microbiome. According to Uroz et al. (2019), both partners are ecological engineers of the holobiont because they regulate plant-associated microbes. Therefore, microbial communications (and plant-modulating microbiome) in the rhizosphere play a critical role in shaping plant-associated microbiome.

Using metatranscriptomic analysis to study the wheat holobiont under water deficiency, Pande et al. (2023) revealed that the microbial associates were the most responsive to water deficit. The majority of the differentially abundant (DA) genes were associated with bacteria in the rhizosphere and fungi in the roots when comparing drought-stressed wheat and control treatments. In the rhizosphere, Actinobacteria were overrepresented in positively regulated DA transcripts, while Acidobacteria and Proteobacteria were overrepresented in negatively regulated ones. These authors demonstrated that certain transcripts were more abundant in the roots and rhizosphere under severe water stress, including heat shock proteins (HSPs), as well as carbohydrate and amino acid transport and

metabolism-related transcripts. Another metatranscriptomic study reported that drought stress promoted the transcripts of Proteobacteria and Bacteroidetes, while reducing those of Actinobacteria and Acidobacteria (Tartaglia et al., 2023). This study also indicated an over-expression of universal stress proteins by Proteobacteria and Bacteroidetes in water-stressed treatment compared to the control. Furthermore, Xu et al. (2018a,b) revealed greater enrichment in various Actinobacteria and Chloroflexi taxa and a decline in the abundance of different Acidobacteria and Deltaproteobacteria taxa under drought conditions. This change was coupled with an increase in G3P-related transcripts in Actinobacteria.

In this cross-kingdom communication, there has been a recent surge of interest in small RNAs, specifically microRNAs, as active 'hormone-like' mediators in cell-to-cell communication (Leitão et al., 2020). *Arabidopsis* and *Botrytis cinerea*, a fungal pathogen, were the first to demonstrate the bi-directional cross-kingdom RNAi via sRNA trafficking (Wang et al., 2016). Still, multiple studies are emphasizing the function of microRNA exchanges in non-pathogenic associations with a focus on the host-microbiota communication in the gut (Liu et al., 2016; Bi et al., 2020; Casado-Bedmar and Viennois, 2022). Intestinal epithelial microRNAs have been reported to influence the composition of the gut microbiome by penetrating specific bacteria and controlling the transcription of a large number of genes involved in sugar degradation and housekeeping, thereby influencing the bacterial fitness (Gao et al., 2019). After their ingestion, plants secrete extracellular vesicles (EVs) in the gut, where specific bacteria can uptake them with their microRNA, causing an alteration in their gene expression (Mu et al., 2014; Teng et al., 2018). As a result, their metabolite production and secretion could be modified, resulting in differential growth of bacterial strains that interact with these specific bacteria. Following these advances, Middleton et al. (2021) propose



that plants and their associated rhizosphere microbes interact through microRNAs, that modulate the composition and activity of rhizospheric microbiota. Strikingly, hundreds of microRNAs have been found in host root tissues (Breakfield et al., 2012). It is therefore assumed that some microRNAs, selected through co-evolution with nearby microorganisms, could be secreted through EVs structure in the rhizosphere.

Taking a step further, Escudero-Martinez et al. (2022) applied metagenomics data to map the plant genetic factors regulating microbiota in the rhizosphere of domesticated and wild barley genotypes. The authors identified a small number of loci that have a significant impact on the rhizospheric microbiome composition. One of those loci, called *QRMC-3HS*, emerged as a major determining factor of microbiota composition. A comparative root RNA-seq profiling of soil-grown sibling lines with contrasting *QRMC-3HS* alleles and presenting distinct microbiotas enabled the identification of three primary candidate genes: *Nucleotide-Binding-Leucine-Rich-Repeat (NLR)* gene and two other genes from *QRMC-3HS*. The *NLR* gene encodes an NLR protein, one of two types of immune system receptors involved in the microbe proliferation recognition through effector recognition (Jones and Dangl, 2006). The first gene of *QRMC-3HS* is differently regulated in sibling lines with different microbiotas, and it is unclear how it mechanistically contributes to rhizospheric plant-microbiota interactions because it encodes an unknown protein. The second gene encodes a xyloglucan endotransglucosylase/hydrolase (*XTH*) enzyme involved in the cleavage and/or rearrangement of xyloglucans (Yang et al., 2019), which are the most abundant hemicellulosic compounds in plant primary cell walls (Ezquer et al., 2020). The *XTH* gene may still be involved in microbiota shaping through cell wall polysaccharide modification closely related to plant-microbe interactions (Vorwerk et al., 2004). In *Arabidopsis*, cell wall traits serve as recruitment cues for almost 50% of the endogenous root microbial communities (Bulgarelli et al., 2012). In addition, cell wall alterations underpin some of the gene ontology classes identified in genome-wide association mapping experiments carried out using this plant (Horton et al., 2014). Improved adaptation to soil physicochemical conditions may represent further involvement of *XTH* genes in plant-microbiome interactions. Han et al. (2017) previously reported that *XTH* genes are involved in drought stress tolerance.

## 2.4 Microbiome drivers of plant fitness benefits under drought

As previously discussed, soil microbes provide various benefits to plants, with root-associated microbiome playing a key role in determining host fitness and performance under various environments, including drought. Root microbiome composition is influenced by both plant and environmental factors. Plant-associated microbiome may boost host development under drought stress by stimulating different layers of plant tolerance mechanisms (Table 1). Among these microbes, PGPRs are abundant in the rhizospheric area and have been shown to be one of the most successful strategies for mitigating the adverse effect of water shortage on the host plant (Etesami and Jeong, 2018). PGPRs enhance crop plant resistance by increasing the production of osmolytes (including glycine betaine and

proline), accumulating secondary metabolites, and modulating the expression of a myriad of host drought-related genes.

Vurukonda et al. (2016) revealed that PGPRs associated with stressed plants are crucial for inducing systemic tolerance (IST). A metabolome study of drought-stressed *Sorghum bicolor* primed with *Bacillus* and *Pseudomonas* isolates showed an induction of signature metabolic profiles and biomarkers related to IST in the host (Carlson et al., 2020). The findings revealed substantial treatment-related differential metabolic reprogramming among rhizobacteria-treated and control plants. This was correlated to the ability of the selected isolates to preserve host plants against drought stress by up-regulating IAA, CK, SA, GA, JA, brassinosteroids (BRs), sphingosine, psychosine, osmolytes and antioxidants, and down-regulating ET production. Raheem et al. (2018) found that IAA and other auxins produced by PGPR bacteria enhance plant performance under drought stress, as demonstrated by *Bacillus amyloliquefaciens*, an auxin-producing bacteria isolated from *Acacia arabica* rhizospheric areas in arid climate. The production of exopolysaccharide by PGPRs is another cue inducing plant drought tolerance. Using a *Bacillus amyloliquefaciens* exopolysaccharide-deficient mutant (*epsC*), Lu et al. (2018) demonstrated that the *epsC* gene is a key gene involved in drought tolerance in *Arabidopsis* (Table 3). The authors highlighted the effect of ET and JA in inducing IST and up-regulating many drought-resilient genes (including *ERD1*, *LEA14*, *RD17*, and *RD29A*) in leaves. Staudinger et al. (2016) used proteomics to show that *Sinorhizobium* sp -inoculated *Medicago truncatula* grown under drought induced hormonal crosstalk and increased JA translational regulation, playing a role in increased leaf maintenance in nodulated plants during drought. PGPRs have been shown to accelerate the antioxidant enzymes and osmoprotectants biosynthesis in drought-stressed plants. By using various formulations of PGPRs isolated from *Megathyrus maximus* rhizosphere in dry areas, Moreno-Galván et al. (2020) showed that the isolates improved *Megathyrus* drought tolerance by up-regulating proline biosynthesis and down-regulating malondialdehyde (MDA) concentration and glutathione reductase activity. Recently, Singh D. P. et al. (2020) revealed that the overexpression of genes encoding enzymes responsible for phenylpropanoid has been linked to ROS scavenging in rice plants inoculated with *Pseudomonas* and *Trichoderma* and grown under water scarcity conditions. Similarly, upregulation of genes encoding *PiP*, *DHN*, and *DREB* contributes to the improvement of drought resistance in plants treated with PGPRs. Drought-stressed tomato plants treated with PGPRs yielded enhanced growth traits, water status, proline biosynthesis, antioxidant enzyme defense (i.e., ascorbate peroxidase, catalase, and glutathione peroxidase), and H<sub>2</sub>O<sub>2</sub> accumulation compared to the controls (Abbasi et al., 2020). The authors demonstrated that PGPR-treated tomato plants showed altered stress signaling and regulatory networks controlling the expression of target genes related to plant response to drought, such as *ERF1* and *WRKY70*. Woo et al. (2020) reported that *Bacillus subtilis* boosted drought resilience in *Arabidopsis* and *Brassica* by up-regulating the expression of drought-sensor genes, including *NCED3*, *RAB18*, *RD29B*, and *RD20* in *Arabidopsis* and *WRKY7*, *CSD3*, and *DREB1D* in *Brassica*.

Several studies have shown that specialized microbiome may alleviate plant drought stress (Mathur and Roy, 2021; Aslam et al., 2022; Singh et al., 2023). Endophytes, microorganisms living in the endosphere without inducing disease symptoms, confer stress

TABLE 3 Key genes influenced by the microbiome in drought resistance and their primary functions.

Microbe inoculation	Host plant	Genes	Major function	ref.
<i>Bacillus subtilis</i> GOT9	Arabidopsis	<i>RD29B, RAB18, RD20, NCED3, DREB1D, WRKY7, CSD3</i>	ABA pathways, resistant protein to biotic and abiotic stress	Woo et al. (2020)
<i>Bacillus amyloliquefaciens</i>	Arabidopsis	<i>epsC, RD17, RD29A, ERD1, LEA14</i>	EPS production and ET- and JA-mediated pathways	Lu et al. (2018)
<i>Bacillus subtilis, Paenibacillus illinoisensis</i>	Chili pepper	V-PPase genes	Osmoregulation	Vigani et al. (2019)
<i>Ochrobactrum</i> sp. EB-165, <i>Microbacterium</i> sp. EB-65, <i>Enterobacter</i> sp. EB-14, <i>E. cloacae</i> EB-48	Soybean	P5CS genes ( <i>SbP5CS 1</i> and <i>SbP5CS 2</i> )	Osmoregulation	Govindasamy et al. (2020)
<i>Pseudomonas simiae</i>	Soybean	<i>P5CS, GOLS, DREB/EREB, PIP, TIP</i>	Osmoregulation, water transport	Vaishnav and Choudhary (2019)
<i>Bacillus marisflavi</i> CRDT-EB-1	Mustard	<i>ABA2, ABA3, and NCED3</i>	ABA pathway	Gowtham et al. (2021)
<i>Trichoderma parareese</i>	Rapeseed	<i>ACCO1, ERF1, and NCED3</i>	ABA and ET pathways	Poveda (2020)
<i>Funneliformis mosseae</i>	Trifoliolate orange	AQP genes ( <i>PIPs, TIPs, NIPs</i> )	Water transport	Zou et al. (2019)
<i>Rhizophagus irregularis</i>	Apple	<i>MdIAA24, MdD27, MdCCD7, MdCCD8a, MdCCD8b</i> and <i>MdMAXa</i>	Mycorrhization regulation, SL production	Huang et al. (2021)
<i>Rhizophagus irregularis</i>	Apple	MAPKs ( <i>MdMAPK7-1, MdMAPK20-1, MdMAPK17, MdMAPK16-2</i> )	Signal transduction during biotic and abiotic stress	Huang et al. (2020)
<i>Piriformospora indica</i>	Rice	P5CS genes	Osmoregulation	Saddique et al. (2018)
<i>Funneliformis mosseae</i>	Trifoliolate orange	<i>PtSPMS, PtCuAO1, PtCuAO2, PtCuAO6, PtCuAO8, PtADC1, PtADC2, PtPAO1, PtPAO2, and PtPAO3</i>	Polyamine metabolism	Zhang et al. (2020)
<i>Funneliformis mosseae</i>	Trifoliolate orange	AQP genes ( <i>PtTIP1;2, PtTIP1;3, PtTIP4;1</i> )	Water transport	Jia-Dong et al. (2019)
<i>Glomus clarum, Acaulospora scrobiculata, Gigaspora rosea</i>	Bean	<i>PvPIP2;3</i>	Water transport	Recchia et al. (2018)
<i>Glomus intraradices</i>	Lettuce	<i>Lsnced</i> gene	ABA biosynthesis pathway	Testerink and Munnik (2005)
<i>Rhizophagus irregularis</i>	Black locust	AQP genes ( <i>RpTIP1;1; RpPIP1;3; RpTIP2;1; RpPIP2;1</i> ) and <i>RpAPX, RpGR</i>	Water transport, antioxidant defense system	He et al. (2016)
<i>Glomus intraradices</i>	Maize	AQP genes ( <i>ZmPIP1;1, ZmPIP1;3, ZmPIP1;4, ZmPIP1;6, ZmPIP2;2, ZmPIP2;4, ZmTIP1;2, ZmPIP2;5</i> )	Water transport	Li and Chen (2013)
<i>Glomus intraradices</i>	Chinese milkveth	<i>AsPT1, AsPT4</i>	P transport	Xie et al. (2013)
<i>Glomus intraradices</i>	Barrel medic	<i>AMT2;3</i>	P transport	Breullin-Sessoms et al. (2015)
<i>Funneliformis mosseae</i>	Common hoptree	<i>PtAHA2</i>	Osmoregulation	Cheng H. Q. et al. (2021)
<i>Rhizophagus irregularis</i>	Black locust	<i>RpFe-SOD, RpMn-SOD, RpPOD, RpCAT1;</i>	Antioxidant defense system	He et al. (2017)
<i>Rhizophagus intraradices</i>	Tomato	<i>TFT2, TFT3</i>	ABA signaling pathway	Xu et al. (2018a)
<i>Funneliformis mosseae</i>	Barrel medic	<i>Fm201, Ri14-3-3, RiBMH2</i>	Mycorrhizae establishment	Sun et al. (2018)
<i>Rhizophagus irregularis</i>	Tomato	<i>SICCD7</i>	SLs signaling pathway	Ruiz-Lozano et al. (2016)
<i>Funneliformis mosseae</i>	Common hoptree	<i>PtYUC3, PtYUC8, PtABC19, PtLAX2, PtPIN1, PtPIN3</i>	IAA signaling pathway	Liu et al. (2018)
<i>Funneliformis mosseae</i>	Sweet orange	<i>CsCDPK20, CsCDPK22</i>	Signal transduction during biotic and abiotic stress	Shu et al. (2020)

ABA, abscisic acid; ABCB19, ATP-binding cassette transporter B19; ACCO1, 1-aminocyclopropane-1-carboxylic acid oxidase; ADC1; Arginine Decarboxylase 1; AHA2, H<sup>+</sup>-ATPase; AMT, ammonium transporter; APX, ascorbate peroxidase; CAT, catalase; CCD, carotenoid cleavage dioxygenase; CDPK, Ca<sup>2+</sup>-dependent protein kinases; CSD, copper/zinc superoxide dismutase; CuAO1, Copper Amine Oxidase 1; D, Dwarf; DREB, dehydration-responsive element-binding protein; EPS, exopolysaccharides; ERD, early responsive to dehydration; EREB, ethylene responsive element binding protein; ERF, ethylene response factor; ET, ethylene; GR, glutathion reductase; JA, jasmonic acid; IAA, indole-3-acetic acid; Fm, *Funneliformis mosseae*; GOLS, galactinol synthase; LAX2, Like-Aux1 (AUX1) carrier 2; LEA, late embryogenesis abundant; MAX, more axillary growth; MAPK, mitogen-activated protein kinase; NCED, 9-cis-epoxycarotenoid dioxygenase; NIP, nodulin 26-like Intrinsic Protein; PAO1, Polyamine Oxidase 1; PIN, PIN-FORMED; PIP, prolactin induced protein; POD, peroxidase; PT, phosphate transporter; P5CS, delta1-pyrroline-5-carboxylate synthase; RAB, responsive to ABA; RD, desiccation-responsive protein; Ri, *Rhizophagus intraradices*; SLs, Strigolactone; SOD, Superoxide dismutase; SPMS, Spermine Synthase; TFT, Tomato Fourteen-Three-three; TIP, tonoplast intrinsic protein; V-PPase, vacuolar proton pumps H<sup>+</sup>-PPase. YUC3, YUCCA3.

resilience to host species and perform a significant function in the survival of some plants in high-stress environments. Various bacterial and fungal endophytes have been reported to increase plant drought resilience. Bacterial endophytes isolated from drought-stressed maize roots improved plant fitness due to biosynthesis of IAA, GA, and CK, 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity and siderophore biosynthesis (Sandhya et al., 2017). Drought-stressed sorghum plants treated with a consortium of root bacterial endophytes (*Enterobacter cloacae*, *Enterobacter* sp., *Ochrobactrum* sp., and *Microbacterium* sp.) resulted in higher growth and osmotic adjustment (Govindasamy et al., 2020). Drought tolerance mediated through microbial inoculation has been associated with enhanced proline accumulation and proline-related biosynthesis genes, *SbP5CS 1* and *SbP5CS 2*. Interestingly, Vigani et al. (2019) found that root endophytic bacteria conferred drought resistance in *Capsicum annuum* by modifying vacuolar H<sup>+</sup> pyrophosphatases (VPP) expression, which aided in preserving osmotic balance. Strains of *Bacillus* endophytes found in *Lepidium perfoliatum* roots were responsible for the formation of biofilm on roots, resulting in drought resistance and seedling germination (Li et al., 2017). *Piriformospora indica*, a well-known root fungal endophyte, colonizes the roots of many plant species and provides multifaceted amenities, including drought alleviation (Gill et al., 2016). Metabolome and proteome profiling analysis of barley plants inoculated with *P. indica*-grown under drought stress showed that inoculation redistributes resources, maintains the aquaporins (AQPs) presence, and promotes energy modulation, photorespiration protective proteins and transporters production, primary metabolism, and autophagy in water-stressed plants (Ghaffari et al., 2019). Inoculation of rice roots with *P. indica* increased growth, biomass accumulation, mineral nutrition (Zn and P), and upregulated *P5CS* genes in drought-stressed plants (Saddique et al., 2018). González-Teuber et al. (2018) reported that inoculating the roots of *Chenopodium quinoa* with the fungal endophyte *Penicillium minioluteum* primarily conferred drought tolerance through significant adjustments in below-ground biomass, photosynthesis, water-use efficiency (WUE), and photochemical efficiency.

AM symbiosis is one of the most complex and mutualistic interactions that plants have evolved to cope with droughts. Following a molecular dialog between the two partners involving “branching factors,” “mycorrhizal factors,” and common symbiotic signaling pathways, the AMF enters the plant roots and establish arbuscule formations ensuring nutrient exchange. Plant hormones act as central regulators of the development of the plant-AMF interaction (Santner et al., 2009; Charpentier et al., 2014; Etemadi et al., 2014), and auxins have potential key role in this interaction (Takeda et al., 2015; Jin et al., 2016). The modulation of AMF-mediated host drought tolerance is an extremely intricate process implicating multiple metabolites and pathways. Particularly, AMF can directly improve nutrients and water absorption and transport, boost host osmotic regulation, and increase plant gas exchange capacity, WUE, and antioxidant defense (Osakabe et al., 2014; Ruiz-Lozano et al., 2016). Zhang et al. (2019) found that a combination of *Funneliformis mosseae*, *Rhizoglyphus intraradices*, and *Diversispora versiformis* improved the survival of *Zenia insignis* subjected to water scarcity through regulating osmolytes accumulation, antioxidant enzyme activity, and plant N and P uptake. Drought-stressed trifoliolate oranges inoculated with *F. mosseae* have less oxidative stress via the increase of H<sub>2</sub>O<sub>2</sub> efflux from the root system (Santner et al., 2009; Jin et al., 2016). In addition, the regulation

of polyamine metabolism-associated gene transcripts by AMF has been identified to play a pivotal role in drought resilience (Zhang et al., 2020). Taking a step further downstream, several AM-specific host genes and proteins have been reported to play a key role in promoting plant water stress resilience. The different mechanisms involved in conferring drought resilience to mycorrhizal plants have been previously reviewed (Cheng S. et al., 2021; Wang et al., 2023). Drought-induced genes and compounds can be divided into: functional genes playing a direct role in stress [i.e., late embryogenesis abundant (LEA) proteins, AQPs, sugar, and proline] and regulatory genes implicated in the regulation of gene expression and the transduction signals (i.e., stress-related TFs) and signal molecules, such as calmodulin-binding protein. Many aspect of the molecular regulatory network linking AM symbiosis and drought stress have been elucidated, including the identification of several gene/protein functions (Bahadur et al., 2019; Ho-Plágaro and García-Garrido, 2022). Various TFs, such as *AP2/ERF* family, *GRAS* family, and *MYB* family have been found to be specifically induced by AMF under drought conditions, thereby contributing to the modulation of stress by phytohormones and other molecular signaling pathways (Wang et al., 2023). Jia-Dong et al. (2019) revealed that AM symbiosis significantly activated the expression of root tip AQPs *PtTIP1;2*, *PtTIP1;3*, and *PtTIP4;1* in drought-stressed trifoliolate orange. In the same vein, it has been reported that drought stress induced the up-regulation of eight AQP-associated genes in AMF-treated plants (Recchia et al., 2018). An interactive impact of AMF and drought was recorded on the over-expression of *MAPK* pathway gene that triggers an improvement in photosynthetic efficiency, osmolyte production, and antioxidant defense (Huang et al., 2020). Testerink and Munnik (2005) showed the role of ABA in up-regulating resistance genes expression to mitigate drought-induced damages. Under water limitation, lettuce inoculated with *G. intraradices* exhibited high expression of the *Lsnced* gene, which encodes a pivotal enzyme in the production of ABA. In contrast, the expression of this gene in roots was not affected by the exogenous application of ABA. This suggests that mycorrhizal plants adjust the endogenous ABA levels more efficiently and quickly than non-AM plants, leading to a more appropriate equilibrium between water acquisition and leaf transpiration under water deficit (Aroca et al., 2008). In a proteomic study on wheat, differential expression proteins involved in cell wall integrity and carbohydrate production were observed, while most stress-associated molecules, including enzymes involved in ET biosynthesis, were downregulated (Bernardo et al., 2017).

Recently, Poveda (2020) found an increase in the secretion of the fungal enzyme chorismate mutase by using mutant strains of *Trichoderma parareese*. This increase conferred tolerance to rapeseed plants grown under drought conditions by increasing gene expression (i.e., *NCED3* and *PYL4*) related to the hormonal pathways of ABA. Notably, colonization of *Trichoderma* sp. on rapeseed roots increased under stressed condition, initiating a myriad of host metabolic pathways. Comparative qRT-PCR analyzes with the chorismate mutase-silenced strain connected this enzyme to drought-tolerant mechanisms owing to its involvement in *ACCO1* (1-Aminocyclopropane-1-carboxylic acid oxidase) and *ERF1* downregulation, and ABA pathway genes *NCED3* upregulation. In addition, Bashyal et al. (2021) used transcriptome profiling of droughted- *Trichoderma harzianum*-inoculated rice and revealed the upregulation of 1,053 genes and the downregulation of 733 genes in stressed *T. harzianum*-inoculated plants. Most photosynthetic and



antioxidative genes, including plastocyanin, PSI subunit Q, PSII subunit PSBY, small chain of Rubisco, proline-rich protein, osmoproteins, stress-induced proteins, AQPs, and chaperonins, were exclusively expressed in stressed *T. harzianum*-inoculated rice. Using the enrichment analysis, the same authors showed that the metabolic (38%) and pathways involved in the synthesis of secondary metabolites (25%), phenyl propanoid (7%), carbon metabolism (6%), and glutathione metabolism (3%) were the most enriched pathways.

The co-inoculation with different members of plant microbiome was also reported to enhance host drought tolerance. Eshaghi Gorgi et al. (2022) studied the effect of the dual application of PGPR and AMF on biomass accumulation, water status, photosynthetic pigments, and proline content of drought-stressed *Melissa officinalis*. They demonstrated that the combined microbial treatment increased all these parameters under drought stress. The same authors also reported that leaves chemical composition of secondary metabolites was altered by PGPR+AMF inoculation. Another study showed that the co-inoculation of Common myrtle with *Funneliformis mosseae* and *Rhizophagus irregularis* AMF strains and *Pseudomonas fluorescens* and *P. putida* PGPR strains boosted seedlings survival, growth fitness, and (non-)enzymatic antioxidant accumulation while reducing electrolyte leakage, and MDA and proline concentrations under drought stress (Azizi et al., 2021). In the same vein, the combined application of *Glomus versiforme* and *Bacillus methylotrophicus* recorded significant drought resistance through improving growth and photosynthetic performances, nutrition status, phenols and flavonoids accumulation, antioxidant enzymatic system and ABA and IAA concentrations in tobacco plants under drought stress (Begum et al., 2022). Singh D. P. et al. (2020) revealed that *Trichoderma* and *Pseudomonas* primed rice seeds induced significant increase in the transcript levels of multiple genes involved in the antioxidant enzymes and phenylpropanoid biosynthesis pathway in seedlings grown under drought stress.

Several studies have revealed the significant beneficial effects of combining microbes and others biostimulants in mitigating drought stress. The application of AMF and organic amendment improved the tolerance of pistachio seedlings to drought stress through enhancing soil physicochemical and biological traits, as well as plant nutrient uptake (Paymaneh et al., 2023). Soussani et al. (2023) demonstrated that the application of AMF and/or compost promoted tomato growth, yield and fruit bioactive compounds, while reducing oxidative stress and enhancing the efficiency of the antioxidant enzyme system under water stress. The combined effect of AMF, PGPR, and compost boosted tomato growth fitness, fruit yield and quality, while increasing drought stress tolerance (Tahiri et al., 2022). A two-year field experiment showed that the application of different biostimulants such AMF, PGPR, and seaweed extract increased wheat root volume, membrane stability index, leaf relative water content (RWC), and photosynthetic pigment content, which promoted plant resilience under water shortage conditions (Najafi Vafa et al., 2022).

### 3 Concepts and mechanisms of plant-microbial adaptation to drought trends

The rhizosphere microbiome induces a profound influence on host physiology, and both monocrop and rotational crops exhibit

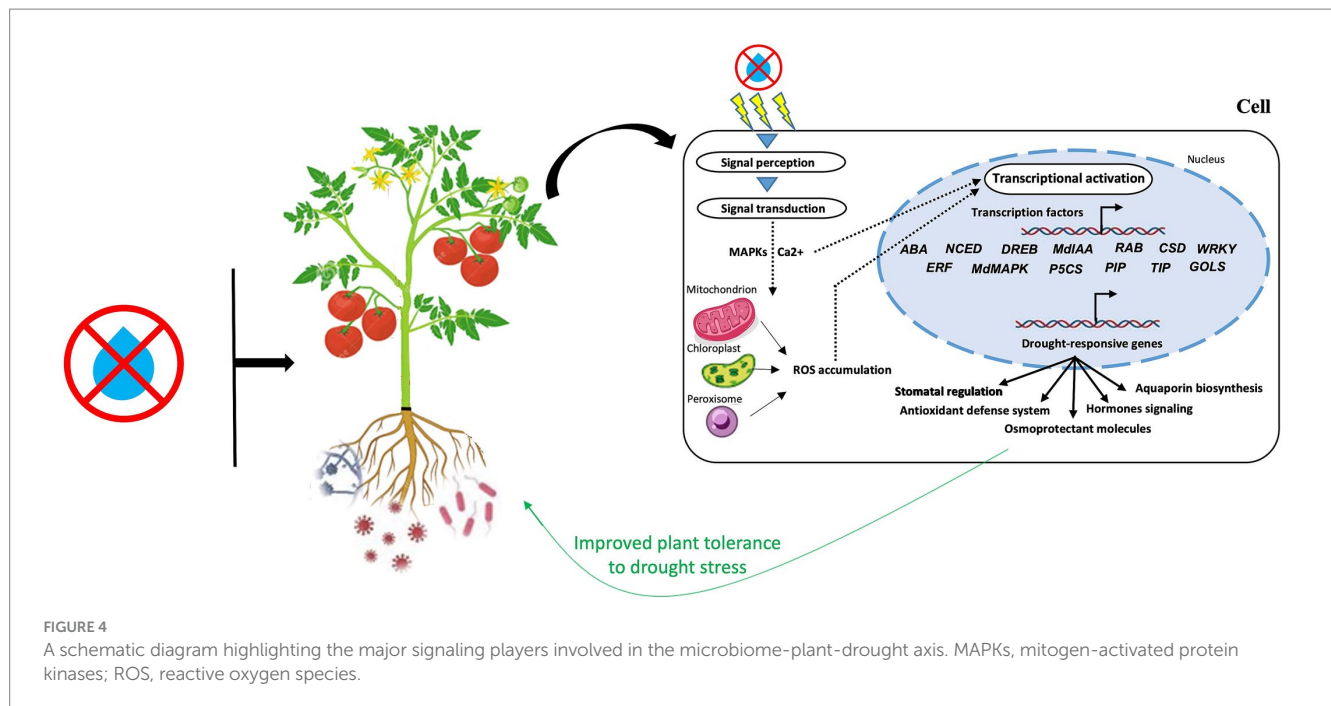
significant variations in the regulation of different genes related to phytohormones and plant defense system (Li et al., 2021). Managing aboveground biodiversity can increase the diversity of plant-associated microbiome and plant immunity, resulting in substantial economic and ecological benefits. Substantial progress has been made in understanding how drought affects the molecular machinery that drive the connection between aboveground and belowground diversity. In fact, drought can promote plants to support root biomass production or form novel and stronger associations with AMF to provide distant water from the rhizospheric area to the plants. These phenotypic and biotic alterations have the potential to significantly affect soil physical properties. Elucidating how combined changes in abiotic components affect plant adaptation allows for anticipating resilience and productivity. However, it will be necessary to understand the spatial and temporal dynamics of ecosystems and to consider multiple ecosystem dimensions, especially physical properties.

Plants possess cognitive capacities and may obtain, process, and memorize information that may adjust their behavior to (upcoming) natural signals (Michmizos and Hilioti, 2019). The cognitive abilities of plants can be extended to their surrounding environment either through root functions or beneficial symbiotic microorganisms (Parise et al., 2020). However, the operation of a plant cognitive system is still largely unknown given the lack of a nervous communication system, as is the case with animals. Well-identified learning and memory mechanisms at cellular and molecular levels may provide a plausible pathway toward adaptation built on prior stimuli such as prolonged water stress. However, determining the role of plant gnosophysiology—a newly emerging scientific field challenges conventional perspectives and delves into the concept that plants possess the ability to respond to stimuli, and learn from them, and make decisions ensuring their survival—and its relative contribution to drought resilience will require substantial theoretical and experimental evidence.

Due to the importance of plant and soil-rhizosphere microbiome diversity in boosting host defense and resilience to environmental constraints, a drought-related decrease in biodiversity has the potential to impact the abiotic resilience of plant communities with serious implications for adaptation. Enhanced plant diversity offers various PRR reservoirs capable of recognizing a variety of MAMPs, thereby boosting immunological defense mechanisms. Systemic signals can then be transmitted from one plant species to another via VCs (produced by microbes and plants) or root exudates, which impact primary productivity and host tolerance (Weisskopf et al., 2021).

By inducing the transcriptional reprogramming of numerous genes and TFs involved in a range of plant defense systems, microbial communities can assist host-plants endure water deficiency (Figure 4). A recent study revealed that under stressful conditions, microorganisms may produce ABA or ABA analogs and trigger essential genes that produce ABA, such *ABA2*, *ABA3*, and *NCED3* (Gowtham et al., 2021). ABA plays a variety of roles, from detecting environmental signals to activating transcription as an adaptive mechanism to regulating a range of developmental, physio-biochemical, and cellular, properties. According to Woo et al. (2020), *B. subtilis* strain GOT9 boosted water stress tolerance in *A. thaliana* by inducing the expression of several *NCED* genes, which control crucial ABA production-related enzymes. Additionally, a large





number of genes implicated in the control of ABA drought signaling pathways (Takahashi et al., 2018), including *DREB1D*, *RAB18*, *RD20*, *RD29B*, *CSD3*, *WRKY7*, and *ERF1* are induced by plant-associated microorganisms (Abbasi et al., 2020; Woo et al., 2020).

Furthermore, the transcriptional activity of MAPKs genes, including *MdMAPK7-1*, *MdMAPK16-2*, *MdMAPK17*, and *MdMAPK20-1*, which are crucial for signal transduction during stress, have been reported to increase in AMF-treated apple seedlings (Huang et al., 2020).  $Ca^{2+}$ -dependent protein kinases (CDPKs) and MAPKs perform a significant function in the signals transduction to the nucleus during drought stress through multiple TFs (i.e., *DREB*, *ABRE*, *MYB/MYC*, *WRKY*, and *NAC*) involved in drought-tolerant genes regulation (Ali et al., 2022). In the same vein, a recent study in maize reported that *pyrroline-5-carboxylate synthase* (*P5CS*) genes, responsible of proline production, including *SbpP5CS 1* and *SbpP5CS 2*, were upregulated under water stress (Govindasamy et al., 2020). Similar findings were made by Saddique et al. (2018), who found that *P. indica*-treated rice showed *P5CS* genes upregulation and improved phosphate and zinc uptake in order to alleviate the negative impact of water deficiency. In addition, *Pseudomonas simiae*-inoculated soybean enhanced fitness and water stress resistance through improving the transcription of several important genes, including water transporters (*TIP* and *PIP*) and osmoprotectants (*P5CS*, *DREB/EREB*, *GOLS*) (Vaishnav and Choudhary, 2019). The aforementioned alterations in the expression of proline-related genes were strongly linked with plant morphological and physiological adaptation to water deficit effects.

AQPs are considered as a main actor in the cell transport system. Jia-Dong et al. (2019) have suggested that these proteins are frequently linked to the process of nutrient exchange during mycorrhizal symbiosis. Zou et al. (2019) proposed an AMF-boosted mechanism that enhances the tolerance of trifoliolate orange to water

deficiency by up-and-down regulating the expression of specific AQPs genes. This study confirms the essential and direct involvement of these fungi in host water stress resistance. In fact, *MdIAA24* gene overexpression, which controls apples mycorrhizal symbiosis by regulating strigolactones production, was associated with general plant drought tolerance, including improvements in RWC, stomatal conductance, and osmotic adjustment (Huang et al., 2021). Metabolomic and proteomic investigations have revealed the upregulation of multiple essential genes controlling transporters, signaling proteins, major metabolic enzymes, and oxidative stress-related proteins following the application of *P. indica* in barley under drought condition (Ghaffari et al., 2019). However, further research in other species is necessary to determine whether these gene expression patterns are universal.

In addition to plants inoculated with beneficial microorganisms, pathogen-infected plants have also shown improved tolerance to drought stress. For instance, rice infected with brome mosaic virus (BMV) and beet plants infected with cucumber mosaic virus (CMV) have shown enhanced production of various antioxidants and osmoprotectants, which promote their tolerance to drought stress (Xu et al., 2008). Another study demonstrated that the viral protein 2b, which impacts host ABA signaling and RNA silencing pathways, provided drought tolerance to *Arabidopsis* plants in the case of CMV (Westwood et al., 2013). When *Nicotiana benthamiana* was treated with Yellowtail flower mild mottle virus, its ability to withstand water stress was also enhanced (Dastogeer et al., 2018). The effects of two ascomycete fungal endophytes isolated from wild Australian *Nicotiana* growing in an arid area that were examined in conjunction with this virus on plant gene expression and osmolytes and antioxidants production under drought stress were comparable to the virus effect. These outcomes indicated that the responses of plants infected with viruses and fungi to water deficiency are somewhat similar.

## 4 Surviving drought with new microbiome research approaches and applications in modern agriculture

### 4.1 Research approaches and applications—paving the way to harness the power of microbes to survive droughts

The ubiquitous presence of the soil microbiome and its impact on various aspects of plant functioning under drought stress have made it increasingly challenging to isolate specific aspects of the microbiome-plant-drought axis. This highlights the need for multidisciplinary interventions to uncover opportunities and strategies for enhancing crop drought resistance (Hartman and Tringe, 2019; Ali et al., 2022). Multidomain research approaches that combine plant resilience, microbiome recruitment, and the interactions among the different (a)biotic components of the ecosystem have proven to be valuable strategies. They establish connections that modulate microbiome composition and activity, leading to improved drought tolerance (Trivedi et al., 2022). Yet, the full potential of the host microbiome in sustainable agriculture is not yet fully realized due to multiple factors, including soil type, plant genotype, microbial interactions, agricultural practices, and the complex interplay among these components (Busby et al., 2017; Soman et al., 2017; Schmidt et al., 2019). Moreover, microbiome engineering faces challenges in achieving accurate and long-lasting positive effects on plants. Multiple interconnected factors, such as the richness and complexity of microbial communities and alterations in microbiota functioning during host development stages, contribute to the complexities that limit the effectiveness of microbiome engineering.

To maximize the benefits of plant microbiome assembly under drought stress, it is crucial to investigate the genetic complexity of both plants and their associated microbiome, the heterogeneity of their environment, and the metabolic patterns that influence the host microbiome. This requires the application of inclusive and systemic biological methods coupled with advanced multiomics techniques. While existing tools and methodologies have made significant advancement in understanding the effect of the microbiome on host resistance to water stress, there are still many gaps to be filled in order to make substantial progress toward microbiome-targeted approaches for enhancing crop production and resilience under drought stress.

Many approaches such as culture-dependent, culture-independent, and reductionist synthetic communities (SynCom) have been primarily used to study the root microbiome. However, reproducing a suitable natural conditions required for the development of different microbes in the laboratory is challenging, and a large number of them cannot be cultured, leading to a loss of microbiome information (Hill et al., 2000). However culture-dependent methods, including the reductionist SynCom method remain highly efficient for microbiome studies (Bai et al., 2015; Zhang et al., 2021). DNA fingerprinting and phospholipid fatty acid approaches, as culture-independent methods, focus on studying the composition and diversity of the entire microbiome community. However, these approaches provide less data in comparison to the current advances in metaomics, sequencing, and computational techniques (Jo et al., 2020). By utilizing advanced sequencing methods, studies have achieved unprecedented precision and comprehensiveness in understanding the composition of microbial communities under drought condition (Lundberg et al., 2012; Liu et al., 2019).

Furthermore, the development of metagenomics, metatranscriptomics, and metaproteomics approaches enable a thorough understanding of microbiome function under drought stress (Liu et al., 2021).

The census method, which includes metagenomic and amplicons statistics, offers a comprehensive understanding of plant associated-microbes, which is essential for studying natural microbiome facts. On the other hand, the reductionist SynCom method links plant molecular biology to microbial ecology (Guttman et al., 2014; Mendes et al., 2014; Bulgarelli et al., 2015; Edwards et al., 2015; Liu et al., 2019). The census approach provides data for the reductionist investigation of plant-microbiome interactions. By combining this information with data on isolated strains, an extensive range of representative SynCom can be created, providing accurate genetic information (Bulgarelli et al., 2012; Vorholt et al., 2017). These SynComs are then used to simulate plant-microbiome interactions, allowing the study of the components that orchestrate microbial communities and validate their monitoring functions and molecular strategies throughout plant growth and development, even under stressful conditions, such as drought (Bai et al., 2015; Castrillo et al., 2017; Chen et al., 2020; Finkel et al., 2020).

Multiomics approaches offer a valuable tool for addressing the challenging task of translating plant alterations at the genetic, proteomic, or metabolomic levels. The integration of multiomics data-driven science has significantly advanced our understanding of microbiome composition and functional responses in intricate environments, such as the rhizosphere, where the complex network of microbial connections orchestrates plant behavior under stressful conditions. The combination of these approaches has led to remarkable progress in plant-microbiome-related research.

Each technique employed in multiomics approaches brings unique advantages, but no single approach can provide a comprehensive understanding of the mechanisms governing the assembly of plant-associated microbiome under drought stress. Therefore, it is crucial to integrate various research approaches to pave the way toward a comprehensive understanding and utilization of the microbiome in future studies, with the aim of developing targeted strategies to boost plant resilience to water deficit stress.

Unlocking the intricate interactions between plant and their microbiome under water limitation and their implications for plant fitness and productivity are crucial steps toward harnessing the potential of the microbiome to promote host adaptation to environmental perturbation. Exploring the extent of these interactions at evolutionary, ecological, biochemical, and molecular levels can provide valuable insights for advancing our system-level understanding and inform microbial approaches to improve host resistance and fitness. Several key research directions should be prioritized in the future:

Gain a complete comprehension of how drought impacts the assembly and functions of the plant microbiome across different temporal and spatial scales.

Investigate the effect of drought on plant fitness and defense system, elucidating the specific alterations in photosynthates, root exudates, and defense mechanisms, and their influence on the assembly and functions of the plant microbiome.

Determine the changes in major signaling cascades and metabolite profiles and their interactions, elucidating their roles in shaping host plant and microbial functions and fitness.

Increase our understanding of the biosynthetic pathways, genetics, and mechanisms of action of drought-responsive

phytohormones, as well as their effects on plant-microbiome and microbe-microbe interactions.

Identify the frequency and duration of drought necessary for the eco-evolutionary adaptation of plant microbiome and the establishment of drought resilience in host plant.

Acquire cutting-edge knowledge about the molecular interactions that orchestrate plant-microbe interactions under drought conditions.

Develop methods for *in situ* manipulation of the plant and associated-microbiome to mitigate the detrimental effects of drought on crop productivity.

## 4.2 Eying the future—microbiome could hold keys to mitigating drought

Microorganisms exhibit remarkable resilience to harsh environments, triggering various signaling cascades and metabolic processes that enable them to swiftly adapt to changing conditions. The soil microbiome, with its manifold benefits for plants, has the ability to mitigate the adverse impact of drought on crops (Anli et al., 2020; Boutasknit et al., 2020; Ben-Laouane et al., 2021; Meddich et al., 2021). For instance, certain ectomycorrhizal fungal (EMF) species in the rhizosphere have been found to colonize the roots of specific pinyon pine genotypes, enhancing their drought resistance (Lau and Lennon, 2012). The varying drought tolerance among different genotypes can be attributed to the presence of these EMF communities, which represent an extended genetic repertoire of the host plant and may serve as a key strategy for drought resilience. The association between host plant and diverse bacterial/fungal communities, possessing potent metabolic and biogeochemical functions, can facilitate plant adaptation to water scarcity. Through long-term field and greenhouse studies coupled with microbial community sequencing, researchers have uncovered links between host-determined EMF communities and disparities in plant performance. Moreover, they have discovered that drought-resistant genotypes exhibit more intense colonization by *Geospora* EMF species. Adaptation has been a subject of extensive discussion in evolutionary biology and ecology. Gehring et al. (2017) revealed that the adaptation does not necessarily involve drastic changes in phenotype but rather subtle variations that affect how the host forms associations with microscopic rhizospheric fungi. Many questions remain unanswered; (1) What are the host traits that control specific interactions with microbial communities? Are they morphological, chemical, or even phenological? Speculation can be made regarding the involvement of genes and chemical signaling molecules that underlie host-mycorrhizal interactions, (2) How significant are plant-associated soil microbial communities in drought adaptation? The fact that genotypic difference in drought resistance were observed only in pinyon pine associated with microbes suggests that the plant's ability to form specific microbial associations is the primary driver of drought resistance.

Given that host genotypes shape distinct soil microbial communities that perform various biogeochemical and metabolic functions (Edwards et al., 2015; Wagner et al., 2016), the potential adaptation of plant traits controlling plant-microbe interactions becomes significant. A comprehensive understanding of host-microbiome interactions at biochemical and genomic levels will enhance our knowledge of drought adaptation and contribute to improved models of host responses to water deficiency. Recognizing that genotypes exhibit differential interactions with aboveground and

belowground microbes may revolutionize the strategies employed to enhance plant agronomic traits and sustain global food security in the face of increasing drought trends.

## 5 Conclusion

During periods of water deficiency, plants heavily rely on microbiome to perform essential functions, including nutrient uptake and stress adaptation. In this review, we have synthesized the current understanding of plant-microbiome interactions under drought stress, which ultimately shape the composition of root-associated microbes. However, there is a lack of research investigating the root-associated microbiota specifically under drought conditions. The limited knowledge about the intricate connections among microbes and their modulation under drought, as well as their complex communication with the host plant, highlight the need for further investigation. Therefore, it is imperative to conduct more research on the plant-microbiome-drought axis, with a particular emphasis on omics-based techniques that integrate genomics, metagenomics, proteomics and metabolomics. Such approaches will unravel the mechanisms orchestrating the adaptation of plant microbiome assembly to drought trends and provide insights to identify microbial communities that confer drought resilience and enhance plant performance under water deficient conditions.

## Author contributions

MA: Data curation, Formal analysis, Investigation, Methodology, Resources, Software, Validation, Writing – original draft. AM: Investigation, Supervision, Validation, Writing – review & editing. MB: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – review & editing.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.



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