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## Chapter

# Microbial Mitigation of Drought Stress in Plants: Adaptations to Climate Change

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## Abstract

The global temperature is constantly increasing due to the phenomenon of climate change. Plants have developed various mechanisms to defend themselves against environmental stresses including drought stress. Apart from indigenous biochemical, physiological, and molecular mechanisms of adaptation to stress, the plant-associated microbes may also play a crucial role in plant drought tolerance. The endophytic and rhizospheric microbes perform various functions and produce different enzymes and compounds that play an important role in plants' adaptation to various environmental stresses including drought stress. Some of the key mechanisms include production of growth hormones, siderophores, organic acids, induction of the ROS scavenging system, phosphate solubilization, and nitrogen fixation. However, the production of ACC deaminase in the plant-associated microbes has vital roles in reduction of ethylene levels under drought stress, resulting in improved plant growth and stress tolerance. Owing to the complex nature of drought tolerance, a multi-pronged approach would have to be adapted to further enhance the microbial-mediated drought tolerance in plants.

**Keywords:** microbial functions, rhizospheric microbes, ROS scavenging, ACC deaminase, osmolytes

## 1. Introduction

Climate change is the long-term shift in temperatures and weather patterns. These changes may be natural, such as through variations in the solar cycle or man-made activities. Different studies reveal that it mainly occurs due to anthropogenic activities taking place in a huge amount these days. Also, many other factors such as greenhouse effect, deforestation, urbanization, global warming, fossil fuels combustion, increased livestock farming, excessive use of fertilizers, and nitrous oxide emissions are included, which has resulted in increasing incidence of different abiotic and biotic stresses [1]. Currently, climate change is known to be the most serious contemporary challenge for humanity. The global climate conditions have been adversely affected due to different natural and unnatural activities, which have stimulated the rise in average temperature and carbon dioxide level. During the last century, the average global temperature soared up by 1.5 F, and it has been estimated that within a period

of 100 years that it might surge higher by additional 0.5–8.6 F [2]. These changes in climatic conditions have led to erratic events such as increase in rainfall and snowfall worldwide, excessive release of greenhouse gases, increase in air temperature, which renders soil dry and decreases its moisture content forming drought-like conditions, water scarcity, severe fires, rising sea levels, flooding, melting polar ice, catastrophic storms, declining biodiversity and an increase in pollution due to excessive CO<sub>2</sub> emissions, air pollutants, ground-level ozone, aerosols, methane, and others. By altering wind patterns, it also induces seasonal variations. In other words, it involves the altering of climatic or weather patterns that occur by emission of greenhouse gases, which are likely to be more erratic and extreme in the forthcoming years [3]. Moreover, these climate-changing parameters are known to affect different terrestrial macroorganisms such as plants. However, according to recent studies, other organisms and ecosystems may be impacted as well [4]; that is, it affects human health, their ability to grow food, housing, safety, and work; for example, some people living in small islands in developing states are already more vulnerable to climate impacts.

As a result of ever-growing population, there is an increased demand of food, which has resulted in intensive agricultural practices including excessive use of agro-chemicals, livestock generation (for meat and other source of income), and exploitation of water resources, which have further worsen the situation by release of GHG (due to agricultural activities) and resulting in pollution of natural resources. The uncontrolled deforestation mainly for development and agriculture has created imbalance in the natural process of carbon cycle, which has led to a rise in the concentration of carbon footprint and brought uneven pattern of climate causing a variety of adverse effects that have huge effect on agricultural production. Due to climate change, a very high rate of land degradation has been observed causing enhanced desertification and nutrient-deficient soil, which is characterized as a major global threat. According to Global Assessment of Land Degradation and Improvement (GLADA), a quarter of land area around the globe can now be marked as degraded. Lives of 1.5 billion people have been adversely affected by land degradation caused by anthropogenic activities and climate change, and also 15 billion tons of fertile soil is lost every year, which results in mass migrations. According to a report published by United Nations Environment Programme in 2017, about 500 million hectares of farmland has been abandoned due to drought and desertification resulting in major social and environmental constraints [5].

The climate alterations highly influence the growth behavior of different crop species. For example, it has a huge impact on mineral accumulation and nutrient acquisition in the plants. Changes in morphology, physiology, and plant productivity are the direct effects observed on the plants body. The organs and membranes of plants are impaired due to different stress conditions. Due to increased oxidative stress, the production of carbohydrates, proteins, and secondary metabolite in the plants is adversely influenced. Furthermore, it also highly affects soil fertility, irrigation measures, occurrence of pests and diseases, and also, stress incidence such as heat and drought are detected. Other ill effects of climate change on production strategies observed are effects on food demand, trade opportunities, and unequal distribution of products [6]. These variations thus cause a very damaging impact on plant growth, and their developmental patterns also significantly impact the diversity and activities of different plant-associated microbial communities as they possess a huge variety of microbiomes in phyllosphere and endophytes from surrounding soil and air [7]. This beneficial microbiome present in the plants

plays a vital role in regulating plant immunity, production of metabolites, nutrient uptake and acquisition, disease, and insect-pest management along with several other functions. The different microbes living in soil system comprise numerous PGPR, fungi, actinomycetes, algae, yeasts, cyanobacteria, and many more [8]. They help in transforming different organic substance into simpler form that can be assimilated by plants. Different microbiomes especially filamentous fungi and some bacterial species secrete a wide range of secondary metabolites, which are essential for plant development and many phenological responses [9]. Consequently, the microorganisms that are known for their positive effects on plant development and health might also be compromised due to climate change, in terms of exhibiting their desirable properties and their colonization capacity under certain conditions. Therefore, microorganisms present in the soil hold great importance in this regard, as they are vital constituent of nitrogen and carbon cycles and are also involved in the emission and removal of greenhouse gases such as CO<sub>2</sub> and CH<sub>4</sub>, which in turn are mostly responsible for the climate change.

## **2. Drought stress effects on agricultural production**

In nature, plants are exposed to various environmental stresses due to their sessile lifestyle. These different unfavorable factors negatively impact plant growth, productivity, and their geographic distribution. Plants may face many diverse stresses (e.g., drought, salinity, and pathogens) under field conditions individually or in combination, which might have a devastating effect on crop yield [10]. Water is the most essential resource for plants, and all the plant organs need to maintain 60–90% water content for sustainable activity. However, global climate change, caused by different anthropogenic activities and greenhouse gas emissions, has become more thoughtful worldwide, leading to drought conditions all over the world [11]. In agricultural technology, it is considered one of the main environmental stresses for plants. Due to the frequent changes in climate observed throughout the world, it has increased the severity of drought events for plants [12]. Important cereal crops are increasingly diminishing by over 10% yield due to drought stress, and it is still the main limiting factor of food production in numerous countries [13]. Decrease in plant metabolism and electrolyte disturbances in plant cells are major symptoms of drought stress, which automatically lead to their death. Because of inhibiting various morphological, physiological, and biochemical processes such as changes in leaf, root length, biomass photosynthesis, respiration, translocation, carbohydrate synthesis, nutrient metabolism, ion uptake, and growth promoters of plants are affected [14]. Also, it primarily prevents the photosynthesis system by causing an imbalance between light capture and utilization, due to which Rubisco activity is reduced and the amount of photosynthetic pigments, inhibiting leaf area and damaging the photosynthetic apparatus [15]. Similarly, it reduces the rate of carbon fixation by inhibiting metabolism or limiting carbon dioxide input into leaves. It also leads to various biochemical changes, such as an excessive accumulation of ROS including O<sup>2-</sup>, and H<sup>2</sup>O<sup>2</sup>, inside the host, which can further damage various tissues and cellular constituents such as nucleic acids and other biomolecules, resulting in cell death [16]. Furthermore, drought also lowers seedling vigor and affects germination by reducing water intake. Wilting, yellowing, discoloration, and leaf burning are the phenotypic signs observed in plants under drought condition [17]. Also, leaf senescence, drooping, leaf rolling, brittleness, scorching, limp leaves, premature fall, etiolation,

wilting, turgidity, flower sagging are the other symptoms observed [18]. Drought stress also alters carbon permeability and transport networks by lowering cation ( $\text{Ca}^{2+}$ ,  $\text{K}^+$ , and  $\text{Mg}^{2+}$ ) absorption by roots. They later can also limit development by preventing the activity of several critical enzymes that take part in nutrient digestion, uptake, translocation, and metabolism of plants [19]. It also has a negative impact on biogeochemical cycles, such as the nitrogen and carbon cycles, which further reduce the decomposition of organic matter that considerably lowers the uptake of water and minerals by the root system, thus increasing soil fertility. For instance, many drought-triggered plants decreasing in macronutrient absorption and translocation (K, N, and P) are found [20]. Many vital characteristics representing plant water relations in plants include relative water content (RWC), leaf water potential, stomatal conductance, transpiration rate, leaf, and canopy temperatures [21]. These traits have also been found to be affected considerably during drought stress in plants [22]. So the above information shows that water scarcity affects plants at all growth stages but causes maximum damage during critical growth phases, such as during the seed development stage or reproductive phase, thereby reducing seed size, number, and quality, which are primarily responsible for substantial yield losses [23].

### **3. Potential strategies to mitigate drought stress in plants**

Plants incorporate a wide range of morphological, physiological, and molecular defense responses contrary to drought, which prevents water loss, maintaining cellular water content, and water supply to vital parts [24]. Drought stress can be reduced through breeding, mass screening, and exogenous phytohormone production. Different strategies are used by plants to minimize stress, for example, by producing phytohormones (e.g., abscisic acid (ABA) and gibberellins) and low-molecular-weight osmolytes (e.g., amino acids and polyols) and by modifying succulent leaves to reduce transpiration loss [25]. Also, a significant plant defense strategy in response to drought is the transcriptional and translational reprogramming of key genes and proteins that are involved in signal perception and transduction, transcription factors, and upregulation of drought tolerant genes, all of which drive drought resilience [26]. Plants protect themselves from drought-induced reactive oxygen species (ROS) and other radicals owing to their efficient antioxidant system. During extended drought stress, they also synthesize an array of osmoprotectants such as prolines, soluble sugars, betaine, and spermines, to maintain cell turgor pressure. Over the past two decades, researchers have focused on transgenic approaches and other molecular breeding tools to increase drought resilience in different crops [27]. For instance, various biotechnological tools, such as CRISPR/Cas, RNAi, and transgenics, have made significant contributions to improving drought-resilient traits in both model and crop plants. But due to their high costs, complexity, ethical considerations, and toxicity concerns, their accessibility to farmers has been limited [27]. Furthermore, adaptive responses in plants are driven by complex genetic features involving several pathways, which have proven to be major impediments to long-term drought-tolerant crop improvement. Furthermore, the development of climate-resilient crops is required by integrating modern technological methods. The use of next-generation breeding approaches (genomic selection and genomic editing) and high-throughput phenotyping is desirable to develop crops that are exposed to different stresses [28]. Also, different bioinformatics tools have also been reported to overcome stress responses [29].

The recent advancement in genomics and genome editing technologies has been coming across various approaches of genetic study to produce climate-resilient crops [30]. Many other strategies are incorporated to grow climate-resilient/smart crop including SNP genotype, trait mapping, and plant breeding methods. The CRISPR/Cas technology has also been efficiently used in enhancing productivity in rice crop in fluctuating climatic conditions [31].

#### 4. Microbial mechanisms governing drought stress tolerance

Microbes have the potential to promote plant growth directly and indirectly through several mechanisms. The indirect activation of plant growth involves a series of events by which microbes prevent the inhibition of plant growth and development induced by pathogens [32]. During direct activation, microbes biosynthesize bacterial compounds that promote the uptake of nutrients from the soil and stimulate plant growth and development [33]. Microbes trigger local or systemic stress mitigation response mechanisms that enable plants to survive and overcome the negative effects of abiotic stress conditions. The mechanisms governing microbial-mediated stress tolerance may include such as drought stress and help plants sustain growth and development through the production, mobilization of nutrients, and induction of the levels of hormones and organic phytochemicals [34]. Below are the fundamental mechanisms governing drought stress tolerance in plants.

##### 4.1 Microbial production of aminocyclopropane-1-carboxylate deaminase

Aminocyclopropane-1-carboxylic acid (ACC) is a precursor of ethylene, and its production increases in plants during stress conditions. Plants enhance their ethylene production under drought stress, which inhibits plant growth by affecting root enlargement and seed germination. The production of higher ACC levels in plants is a strategy to combat severe drought stress [35]. A group of beneficial microbes have the potential to produce ACC deaminase that regulates plant growth and development by sequestering the plant-produced ACC, responsible for ethylene production in plants. A large number of microorganisms have been reported to produce ACC deaminase that in turn reduces ACC, thereby lowering the increased ethylene levels in plants under stress conditions [36]. These microbes play a vital role in plants' adaptation to stress conditions. In particular, drought stress tolerance has been achieved in several plants through the production of ACC deaminase. Some of the prominent examples of the microbial production of ACC deaminase and its mitigation effects on drought stress in several plants have been summarized (**Table 1**). The ACC deaminase production by *Bacillus subtilis* Rhizo SF 48 strain conferred maximum seed and plant growth promotion in tomato plants under drought stress [37]. The underlying biochemical mechanisms for this improved drought stress tolerance included induction in the proline, SOD, and APX activities, whereas reduction in the MDA and H<sub>2</sub>O<sub>2</sub> contents. The maize plant-associated rhizospheric microbial species; that is, *Pseudomonas aeruginosa*, *Enterobacter cloacae*, *Achromobacter xylosoxidans*, and *Leclercia adecarboxylata* were reported to produce ACC deaminase that resulted into enhanced drought stress tolerance. The plants showed improved grain yield plant<sup>-1</sup>, photosynthetic rate, and stomatal conductance, enhanced chlorophyll a, total chlorophyll, and carotenoid contents under drought stress [38, 42]. Chandra et al. [40] reported ACC deaminase production in the wheat-associated microbes, that is, *Variovorax paradoxus* RAA3,

Plant type	Microbe	Effects on growth	Biochemical changes	Reference
<i>Solanum lycopersicum</i>	<i>Bacillus subtilis</i> Rhizo SF 48.	Maximum seed (laboratory) and plant growth promotion (greenhouse)	Increased Proline, SOD and APX activity. Decrease in MDA, H <sub>2</sub> O <sub>2</sub> contents	Gowtham et al. [37]
<i>Zea mays</i>	<i>Leclercia adecarboxylata</i>	Enhanced shoot and root length, shoot fresh and dry weight and root fresh and dry weight in maize seedlings under axenic conditions	—	Danish et al. [38]
<i>Capsicum anuum</i>	<i>Bulkholderia cepacia</i> , <i>Citrobacter feurendii</i>	Plant growth promotion under stress conditions	—	Maxton et al. [39]
<i>Triticum aestivum</i>	<i>Variovorax paradoxus</i> RAA3; <i>Pseudomonas</i> spp. <i>Achromobacter</i> spp. <i>Ochrobactrum anthropi</i> DPC9	Improved wheat plant growth and foliar nutrient concentrations under glasshouse experiment	Positive changes in antioxidant properties	Chandra et al. [40]
grapevine ( <i>Vitis vinifera</i> L.)	Strains of <i>Pseudomonas</i> , <i>Enterobacter</i> , and <i>Achromobacter</i>	Increased plant height, biomass of shoot and root organs, relative water contents, and net photosynthetic rate of leaves	Significant changes in IAA, abscisic acid, and malondialdehyde	Duan et al. [41]
<i>Z. mays</i>	<i>Pseudomonas aeruginosa</i> , <i>Enterobacter cloacae</i> , <i>Achromobacter xylooxidans</i> and <i>L. adecarboxylata</i>	Grain yield plant <sup>-1</sup> , photosynthetic rate, stomatal conductance	Enhanced chlorophyll a, total chlorophyll and carotenoids contents under drought stress	Danish et al. [42]
<i>T. aestivum</i>	<i>Serratia marcescens</i> and <i>Pseudomonas</i> sp.	Improved harvest index	Improved water status, reactive oxygen species, osmolyte accumulation, chlorophyll and carotenoids content	Khan and Singh [43]
<i>Cyamopsis tetragonoloba</i>	Strains of <i>Pseudomonas</i> , <i>Enterobacter</i> , and <i>Stenotrophomonas</i>	—	—	Goyal et al. [44]
<i>Vigna mungo</i> L. and <i>Pisum sativum</i> L.	<i>Ochrobactrum pseudogrignonense</i> RJ12, <i>Pseudomonas</i> sp. RJ15 and <i>B. subtilis</i> RJ46	increase seed germination percentage, root length, shoot length, and dry weight of treated plants	An elevated production of ROS scavenging enzymes and cellular osmolytes; higher leaf chlorophyll content	Saikia et al. [45]

**Table 1.** Microbial ACC deaminase production confers drought stress tolerance in plants.

*Pseudomonas* spp. *Achromobacter* spp. and *Ochrobactrum anthropi* DPC9 that improved plant growth and foliar nutrient concentrations in the wheat plants subjected to drought stress under glasshouse conditions. The plants also showed positive changes in the antioxidant properties under drought stress. Similarly, the rhizospheric *Serratia*

*marcescens* and *Pseudomonas* sp. conferred drought stress tolerance to wheat plants, which showed improved harvest index, water status, reactive oxygen species scavenging, osmolyte accumulation, chlorophyll and carotenoid content [40]. Moreover, the rhizospheric *Ochrobactrum pseudogrignonense* RJ12, *Pseudomonas* sp. RJ15, and *B. subtilis* RJ46 exhibited increased seed germination percentage, root length, shoot length, and dry weight of treated plants, *Vigna mungo* L. and *Pisum sativum* L. under drought stress. The ACC deaminase production triggered the induction of ROS scavenging enzymes and cellular osmolytes, and higher leaf chlorophyll content. The microbial production of ACC deaminase showed growth improvement and drought stress tolerance in other plants such as *Capsicum annum*, *Vitis vinifera*, and *Cyamopsis tetragonoloba* [39, 41, 43].

## 4.2 Microbial production of phytohormone

Phytohormones such as indole acetic acid (IAA), gibberellins, ABA, ethylene, and cytokinin are organic chemical messengers that coordinate cellular events in plants and, therefore, play a crucial role in plant development and drought stress tolerance [44]. These phytohormones are generally produced by plants; however, they also produced by some plant-associated microorganisms. Phytohormones such as auxins indirectly regulate drought stress through modification of root growth and root hairs in a manner that enable plants to absorb maximum water and nutrients from the soil. In plants, auxins are produced through the tryptophan-dependent pathways [46]. Downward in the tryptophan pathway, indole-3-acetamide is produced that is converted into indole-3-acetaldoxime and tryptamine that further give indole-3-pyruvic acid, the final product [47]. The role of IAA in drought stress mitigation through inducing the drought signaling pathways has been reported in several studies [48]. Auxin production has the potential to induce the elongation of stems and coleoptiles of plants under stress conditions; thus, its production in the microbe-treated plants may trigger such modifications [49]. In a similar fashion, plant-associated microbes also induce the production of plant gibberellins. These are diterpenoids and are responsible for the hyperactive elongation of stems under stress conditions. Gibberellins are in association with carotenes and isoprene, bioactive compounds [50]. Carotenes protect the plant cells from harmful photodynamic reactions through triggering the photosynthesis, whereas isoprene regulates the turgor pressure that provides stability to the cell membranes [51]. In plants, the cytokinin biosynthesis increases in association with auxin and regulation of developmental responses under abiotic stress conditions. Cytokinin mediates in the phosphorylation of sugars leading to cellular accumulation in cells and also helps to prevent the reverse diffusion of sugars [52]. This cytokinin-mediated competitive phosphorylation enables plant cells to adapt to stress and provides protection against the damaging effects of oxidative stress [53]. Abscisic acid is generally known as a universal stress hormone because of its very important in plant adaptation to stress condition. In plants, the stomatal closure and inhibitor of stomatal opening are the underlying mechanisms of the ABA-mediated stress tolerance [54]. The ABA production also confers desiccation tolerance through regulation of gene expression [55].

The ethylene production in plants plays a significant role in regulation of plant growth and senescence. In interaction with other hormones, ethylene serves as a messenger hormone that regulates developmental processes, ranging from seed germination to the plant vegetative and reproductive stages [56].



The plant-associated microbes have the potential to produce phytohormones, which in turn help plants to adapt to the stress condition. Phytohormones mitigate stress through triggering a complex signaling network of genes and production of metabolites, which protect the inner cellular machinery and function as a response to environmental stress condition. The underlying mechanisms may include hormone regulation, and production of osmolytes and antioxidant enzymes.

#### **4.3 Osmotic adjustment**

Plants experience a sudden osmotic shock upon exposure to abiotic stresses. However, the plant-associated microbial communities and their interactions assist in osmotic adjustments. In response to drought stress, the plant-microbe interactions are governed by a series of biochemical and molecular changes leading to secretion of metabolites such as glycine, proline, organic acids, sugars, betaine, trehalose, calcium, chloride, and potassium ions. Proline is one of the most important osmolytes that is accumulated in plants and provides maintenance and protection to vital cellular organs as an adaptation to osmotic stress. Proline production has been reported in several rhizospheric bacteria [57]. Trehalose, a non-reducing sugar, is produced in plants under stress condition. Trehalose contains two glucose molecules that store energy for utilization under stress conditions. Trehalose biosynthesis in microbes is accelerated through the TPS/trehalose-6-phosphate phosphatases (TPS/TPP) pathway. Trehalose stabilizes turgor pressure and maintains osmotic adjustment in plant cells [58]. Production of organic acids has been one of the key mechanisms that microbes utilize to benefit the associated plants. Microbial inoculation of plants triggers the secretion of organic acids such as oxalic acid, malic acid, citric acid, and minerals, for example, chlorine, potassium, and sodium. These are very important for metabolic reactions, maintenance of osmoregulation, and nutrient availability in plant cells [59].

#### **4.4 Microbial production of exopolysaccharides for drought stress mitigation**

Exopolysaccharides are long-chain polymers of repeating sugar units (e.g., glucose, galactose, and rhamnose) [60]. Exopolysaccharides play a crucial role by forming hydrophilic biofilms, which provide protection against aridness during osmotic stress. Exopolysaccharides enhance the water-retaining potential and regulate the distribution of biological carbon sources in the soil. Microbes protect the roots from dehydration and maintain the moisture content by forming sheaths of exopolysaccharides [61]. Microbes release exopolysaccharides in the soil as slime ingredients comprising van der Waals linkages, anion adsorption interactions, and cation hydrogen bridges, which improve the biological properties of the soil [62]. The vital microbe-plant interaction regulates the production of biofilms, which facilitate microbial attachment to the plant roots, and imparts a strong root adhering capability. In conclusion, the microbial production of exopolysaccharide is one of the important strategies that protect plants against the damaging effects of abiotic stresses including drought stress [63].

#### **4.5 Effects of microbial volatile organic compounds against osmotic stress**

The plant growth-promoting microbes produce volatile compounds, which increase plant growth and development, iron uptake, photosynthesis, and overall

crop productivity. Organic acid production helps plants against disease-causing pathogens. The stress-induced organic compounds such as 2-pentylfuran, 3-hydroxy-2-butanone, and 2,3-butanediol play an important role in plant growth and development [64]. These compounds regulate stomatal closure and impart systemic stress resistance, and thus ensure plant growth and development under abiotic stress conditions [65]. These volatile compounds help boost plant growth by acting as insect repellents owing to their strong odor. The microbial production of these compounds triggers stress tolerance in the associated plants through inducing the biosynthesis of ROS scavengers and gene expression.

#### **4.6 Microbial induction of antioxidant machinery in plants**

The production of reactive oxygen species (ROS) is induced in plants under osmotic stress. These include hydrogen peroxide ( $H_2O_2$ ), superoxide, singlet oxygen, radicals, alkoxy radicals, and superoxide anion radicals. The ROS production triggers irreversible damages to lipids, proteins, and DNA, affecting the redox regulation [66]. Plants induce antioxidant defense systems involving enzymatic and non-enzymatic pathways to protect against the oxidative damage during osmotic stress. Several enzymes (e.g., glutathione reductase, superoxide dismutase (SOD), catalase, and ascorbate peroxidase) and non-enzymatic components (e.g., ABA, cysteine, and glutathione) catalyze the biosynthetic pathways of antioxidant pathways [67, 68]. The microbial inoculation of plants triggers the antioxidant biosynthetic pathways in the soil and, thus, confers drought stress tolerance. Kaushal and Wani [69] and Ilyas et al. [70] reported the secretion of phenolic components by various microbes (e.g., algae, zatinomycetes, and fungi) upon exposure of plants to stress condition. The microbe-plant interaction confers stress tolerance through regulating the ROS biosynthesis and maintaining a homeostatic balance between ROS and their removal. Overall, the ROS scavenging ability of PGPR regulates the antioxidant enzymes and may provide a solid barrier against abiotic stress.

#### **4.7 Stimulation of stress-response genes by plant-microbe interactions**

The microbial inoculation of plants confers stress tolerance by triggering the expression of genes involved in plant defense against abiotic stresses. Under drought stress in plants, the expression of stress-responsive genes is modulated, which is necessary for optimization of plant growth and development. There are numerous stress-responsive genes and proteins, which are involved in plant-microbe interactions and the resulting stress tolerance. These include sHSP, CaPR-10, dehydrin-like protein (Cadhn), 11-pyrroline-5-carboxylate reductase (P5CR), pyrroline-5-carboxylate dehydrogenase (P5CDH), and vacuolar ATPases [71]. Depending on the role of the encoded proteins, the expression of these stress-responsive genes can be categorized into functional or regulatory proteins as revealed by microarray studies. The stress-responsive functional proteins include water channel transporters, detoxification enzymes, osmolyte biosynthesis enzymes, macromolecule protection factors, and proteases [71, 72]. The stress-responsive genes encoding regulatory proteins include transcription factors, ABA biosynthetic factors, and phosphate kinases. The microbial-plant interaction-based expression and upregulation of stress-responsive genes can be harnessed as a powerful tool for enhancing plant drought stress tolerance.

## 5. Microbes and drought stress mitigation

### 5.1 Plant growth-promoting rhizospheric bacteria

The plant growth-promoting rhizobacteria (PGPR) have the potential to mitigate drought stress and alleviate the negative effects of climate change on plant growth and development in a sustainable way [73]. These microbes trigger the onset of biochemical changes, which enable the plant to set a response to alleviate drought stress [74]. The underlying mechanisms include optimization of exopolysaccharides and phytohormone production, antioxidant defense system, and cyclic metabolic pathways, involved in the deposition of sugars, polyamines, amino acids, and heat-shock protein synthesis [75]. Several studies have reported the positive effects of PGPR on plant growth and development under drought stress (**Table 2**). Particularly in wheat, the inoculation of PGPR mitigated drought stress. In one study, Li et al. [76] reported growth improvement in wheat plants upon inoculation with the Actinomycetes, *Streptomyces pactum* Act12. The bacterial inoculation significantly increased the overexpression of several genes including P5CS, EXPA6, SnRK2, and EXPA2. Overall, the root length, shoot length, and fresh biomass were significantly increased. Enhanced levels of sugars and antioxidant enzymes were detected in the exposed seedlings under stress condition. Inoculation of wheat plants with *Pseudomonas libanensis* EU-LWNA-33 increased the root length and biomass under drought stress [77]. The biochemical analysis revealed an increased production of osmolytes, that is, proline and glycine betaine. At the cellular level, proline and glycine betaine production regulates osmotic homeostasis, as well as the phosphorus solubilization and uptake. Phosphorus availability is a crucial factor in the overall growth and development of plants. In this study, the inoculated strains showed solubilization of phosphorus. In previous studies, Jochum et al. [79] reported drought stress tolerance in wheat and maize plants when inoculated with *Bacillus* sp. 12D6 and *Enterobacter* sp. 16i. The inoculation improved root length, surface area, and plant productivity. The study further revealed that *Bacillus* sp. 12D6 was comparatively more effective in countering drought stress. This enhanced drought stress mitigation was possible due to the production of phytohormones such as IAA and salicylic acid. In another study, Raheem et al. [80] isolated and investigated the impact of PGPR, namely *Bacillus*, *Moraxella*, *Enterobacter*, and *Pseudomonas*, on wheat plants under drought stress. Biochemical analysis of the inoculated stressed plants revealed production of increased levels of auxin that obviously helped plants to avoid the negative impact of drought stress. It was further concluded that the enhanced auxin production triggered by the *Bacillus* species improved the field capacity by 10% and crop yield by 34%. The drought stress mitigation effects of the plant growth-promoting bacteria (PGPB), *Azospirillum* were investigated in wheat plants [78]. The stressed plants showed drought tolerance, which was attributed to the microbial-mediated production of phytohormones, solutes, ACC deaminase, exopolysaccharides, chlorophyll synthesis, and increased mineral solubilization.

Drought stress imposes osmotic and oxidative stresses, which negatively affect the crops' growth and productivity. Microbial inoculation has been the most preferred strategy to reduce stress-associated losses in crop plants. In this connection, Kour et al. [81] investigated the effects of bacterial inoculation on foxtail millet crop subjected to drought stress. Inoculation of plants with *Acinetobacter calcoaceticus* EU-LRNA-72 and *Penicillium* sp. EU-FTF-6 showed drought stress tolerance. The drought stress mitigation was mainly due to the accumulation of osmolytes

Host plant	Microbe	Underlying mechanism	Reference
<i>Triticum aestivum</i>	<i>Streptomyces pactum</i> Act12	Increased overexpression of EXPA2, EXPA6, P5CS, and SnRK2, increased root length, shoot length, sugar content, MDA, and ABA	Li et al. [76]
<i>T. aestivum</i>	<i>Pseudomonas libanensis</i> EU-LWNA-33	Increased ACC deaminase, osmolytes, and P solubilization	Kour et al. [77]
<i>T. aestivum</i>	<i>Azospirillum</i>	Increased phytohormone, solute formation, and exopolysaccharide production	Priyanka et al. [78]
<i>T. aestivum</i> and <i>Zea mays</i>	<i>Bacillus</i> sp. (12D6) and <i>Enterobacter</i> sp. (16i)	Increased IAA and SA	Jochum et al. [79]
<i>T. aestivum</i>	PGPR ( <i>Bacillus</i> , <i>Enterobacter</i> , <i>Moraxella</i> , and <i>Pseudomonas</i> )	Increased auxin	Raheem et al. [80]
<i>Setaria italica</i>	<i>Acinetobacter calcoaceticus</i> EU-LRNA-72 and EU-FTF-6	Increased glycine betaine, chlorophyll a and b, proline, and sugars, decreased LPO	Kour et al. [81]
<i>Mentha piperita</i>	<i>Pseudomonas fluorescens</i> WCS417 <sup>r</sup> and <i>Bacillus amyloliquefaciens</i> (GB03)	Increased phenolic compounds and antioxidant defense	Chiappero et al. [82]
<i>Glycine max</i>	<i>Bacillus</i> strains UFGS1, UFGS2, UFGRB2, and UFGRB3	Expression of <i>Gmdreb1a</i> , increased stomatal conductance, transpiration and Fv/Fm	Martins et al. [83]
<i>Cicer arietinum</i>	<i>Pseudomonas putida</i> and <i>B. amyloliquefaciens</i>	Increased chlorophyll, antioxidant enzymes, and protein content	Kumar et al. [84]

**Table 2.**  
 Rhizospheric plant-growth-promoting bacteria and drought stress mitigation in plants.

(proline and glycine betaine) and increased levels of chlorophyll a and b contents. In this study, the increased proline and glycine betaine levels improved osmotic adjustment and membrane integrity, while the increased chlorophyll content resulted in plant growth and development.

In one study, Chiappero et al. [82] investigated the positive impact of PGPR inoculation on peppermint subjected to drought stress. Two rhizospheric bacteria, *Pseudomonas fluorescens* WCS417<sup>r</sup> and *Bacillus amyloliquefaciens* GB03, were used in the inoculation and drought experiment. The results revealed a significant improvement in drought stress tolerance, which was attributed mainly to the upregulation of the antioxidant defense system and phenolic components.

The effects of bacterial inoculation on drought stress were further tested in soybean plants [83]. The plants were inoculated with *Bacillus thuringiensis*, *Bacillus cereus*, and *B. subtilis* strains. The inoculation of plants with these strains resulted into an improved efficiency of the photosystem II (PS-II) and maintained the overall photosynthetic rates of the plants, transpiration rate, and stomatal conductance, which in turn improved the overall growth of inoculated plants compared with that of control plants. In addition, the genomic analysis revealed that the overexpression of *Gmdreb1a* might partly be responsible for drought stress mitigation.

The PGPBs have proven their potential as ecofriendly biofertilizers that can alleviate the negative effects of drought stress on plants. In a previous study, the PGPR strains, *Pseudomonas putida* and *B. amyloliquefaciens*, were isolated from alkaline

soils and then were used in the inoculation of chickpea plants under drought stress in the greenhouse and *in vitro* experiments [84]. The inoculation of plants with the strains in combination showed increased chlorophyll content, osmolyte production, and improved photosynthesis and biomass compared with plants inoculated with a single strain. In conclusion, the PGPR enhances the overall growth and development, as well as the biotic and abiotic stress tolerance of plants through a wide range of mechanisms.

## 5.2 Endophytic bacteria and fungi

Endophytes bacteria and fungi reside in different organs and tissues of plants and establish symbiotic relationship. The endophytes get their prepared food, while plants are benefited in different ways such as access to limited nutrients in the soil and biotic and abiotic stress tolerance. Endophytes have been specifically focused due to their crucial role in abiotic stress tolerance of plants [85]. It was previously reported that endophytes assist their host plants to increase their biomass under stress conditions [86]. However, different plant species showed variable levels of endophytic-mediated biomass accumulation under stress condition. For example, eudicots and C4 plants exhibited increased biomass accumulation compared with C3 and monocots [87].

Endophytic microbes play a very important role in reducing the damaging effects of abiotic stresses on plants. Several studies have demonstrated the drought stress mitigation in plants with endophytic bacterial inoculation (**Table 3**). Previously, Singh et al. [88] investigated the inoculation effects of endophytic bacterial strains, *Trichoderma* T42 and *Pseudomonas* on the growth and metabolic alterations in rice plants subjected to drought stress. The inoculated plants showed significantly improved metabolic activity such as induction of the antioxidant enzymes, and increases in the total polyphenolic content, which in turn, conferred oxidative stress tolerance. In another study, rice seedlings were treated with *Gluconacetobacter diazotrophicus* strain Pa15, and the drought stress tolerance was tested in the inoculated and uninoculated plants [89]. The plants were subjected to various drought stress levels for 15 days. The inoculated plants showed increased levels of proline and glycine betaine, which conferred the plants drought stress tolerance. Molecular analysis revealed relative expression of several genes such as *cat*, *gor*, *sod*, *BADH*, and *P5CR*. In conclusion, inoculation with *G. diazotrophicus* mitigated the effects of drought stress on rice plants.

The effects of bacterial inoculation on the growth of *Glycine max* were evaluated under drought stress [90]. Inoculation with bacterial strains, LHL10 and LHL06, produced positive improvement in plant growth under stress condition. The inoculated plants showed increased roots, shoot length, leaf area, and dry biomass. The underlying mechanisms included an increase in *HSP90* expression levels: lipid peroxidation, increased calcium levels, and phosphate solubilization. In a study, Kour et al. [91] investigated the effects of *Streptomyces laurentii* EU-LWT3-69 and *Penicillium* sp. EU-DSF-10 on sorghum plants subjected to drought stress. Bioavailability of phosphorus to plants is reduced under drought stress. However, the plant-associated microbes contain the active form of phosphate that is provided to plants to counter the stress effects. Both the strains used in the study might solubilize phosphate and ensure its availability to the plants. The biochemical alterations mediated by bacterial inoculation included an increase in the proline and glycine betaine levels and chlorophyll content, while a decrease in the lipid peroxidation. Overall, the study suggested that bacterial inoculation enabled the plants to grow better under the drought stress.

Microbial inoculation confers drought stress tolerance to the plants partly by an induction in the growth hormone levels and acquisition to soil mineral content. This was demonstrated in a study conducted by Kang et al. [100], in which the alfalfa plants were inoculated with two *Enterobacter ludwigii* strains, namely AFFR02 and Mj1212. The inoculated plants were assessed under drought stress for hormones and mineral concentrations. The results showed that the inoculated plants were more drought-tolerant than the uninoculated plants. Growth attributes such as fresh and dry biomass, root/shoot elongation, and stalk diameter were significantly higher in the inoculated plants than in the uninoculated plants. It was also observed that the treated plants accumulated higher levels of flavonoids, minerals, and ABA than those of untreated plants. In a previous study, Silambarasan et al. [92] used *Rhodotorula mucilaginosa* strain CAM4 in the inoculation of *Lactuca sativa* subjected to drought stress. The inoculated plants showed drought tolerance at various developmental stages. The treated plants showed a clear increase in the growth, dry biomass, root proliferation, and stem elongation as compared with the untreated plants. The inoculation caused a significant increase in the content of chlorophyll, carotenoids, and proline, while a decrease in the malondialdehyde (MDA) levels, indicating lipid peroxidation.

Fungal endophytic species have been extensively studied for their positive effects on plant growth, stress tolerance, and disease resistance. They exert their positive effects through production of growth hormones, siderophores, secondary metabolites, and phosphate solubilization. Several studies have demonstrated the drought stress-mitigating effects of fungal inoculation on plants (Table 3). Fungal endophytes, specifically isolated from desert plants, have shown promising results when used for stress mitigation in crop plants. Desert plants are usually exposed to high magnitudes of drought conditions and thus may harbor fungal endophytes that may confer drought and salt stress tolerance under arid environments. Jain et al. [101] used halotolerant fungal endophytic strains, namely *Neocamarosporium chichastianum*, *Neocamarosporium goegapense*, and *Periconia macrospinosa* in the inoculation of tomato and cucumber seedlings. The treated plants showed stress tolerance, which was evident from the increased plant growth, chlorophyll content, proline, and antioxidant enzyme levels.

Osmotic adjustment is one of the key physiological mechanisms, which have been observed in the drought-tolerant plants. Endophytic fungal strains confer drought tolerance in plants by maintaining osmotic balance and water uptake efficiency. In one study, Dastogeer et al. [94] investigated the role of the fungal endophyte *Neotyphodium coenophialum* in the drought tolerance of *Lolium arundinaceum*. The results revealed that the treated plants had high drought tolerance than the untreated plants. The underlying mechanism of this enhanced tolerance was dependent on the osmotic balance and improved water uptake efficiency, which in turn enhanced the gene expression and photosynthesis rate. In addition, drought tolerance was achieved in *Nicotiana benthamiana*, when inoculated with fungal endophytes isolated from a *Nicotiana* plant. Overall, the fungal endophytes contribute to the drought tolerance trait mainly by increasing the water-use efficiency, nutrient uptake and maintaining the ion homeostasis to induce stress tolerance in the associated plants.

### 5.3 Mycorrhizae

Mycorrhizae are fungal species that establish a symbiotic relationship with higher plants and play a significant role in plant growth, nutrient acquisition, soil fertility,

Microbe type	Host		Underlying mechanism	Reference
Endophytic bacteria	<i>Oryza sativa</i> L.	Trichoderma T42 and Pseudomonas	PAL expression, polyphenols	Singh et al. [88]
	<i>O. sativa</i> L.	Gluconacetobacter diazotrophicus Pa15	Expression of gor, cat, P5CR, sod, and BADH Increased proline and glycine betaine production	Filgueiras et al. [89]
	<i>Glycine max</i>	Endophytes (LHL10 and LHL06)	Expression of GmHsp90A2 and GmHsp90A1 increased SOD and decreased LPO	Bilal et al. [90]
	Foxtail millet	EU- LRNA-72 and EU-FTF-6	Increased glycine betaine, chlorophyll a and b, proline, and sugars	Kour et al. [81]
	<i>Sorghum bicolor</i> L.	Streptomyces laurentii EU-LWT3-69 and Penicillium sp. strain EU-DSF-10	Increased osmolytes, ACC and deaminase, solubilize P and reduced LPO	Kour et al. [91]
	<i>Lactuca sativa</i>	CAM4	Reduced MDA, and increased proline, chlorophyll a and b and carotenoids	Silambarasan et al. [92]
Endophytic fungi	Broccoli	YNA59	Increased sugar, protein, chlorophyll content, ABA, JA, and SA	Kim et al. [93]
	<i>Lolium Arundinaceum</i> , <i>Nicotiana benthamiana</i>	Neotyphodium coenophialum	Increased gaseous exchange and antioxidant enzyme production, altered gene expression and osmotic balance	Dastogeer et al. [94]
Mycorrhizae	<i>G. max</i>	Arbuscular mycorrhizal fungus	Increased proline, glycine, and soluble sugars, reduced MDA content	Grümberg et al. [95]
	<i>Fragaria ananassa</i> Duch.	Arbuscular mycorrhizal fungus	Increased Zn, AA enzyme and water uptake	Moradtab et al. [96]
	Trifoliolate orange	Funneliformis mosseae	Increased phenolic contents, terpenes, root exudates and coumarins, reduced alkanes, ester, and amides	Cheng et al. [97]
	<i>Triticum</i> spp.	Glomus mosseae	Decreased 6-SFT, SOD and sulfur metabolism; increased genetic diversity	Bernardo et al. [98]
	<i>Ephedra foliata</i> Boiss	AMF (Glomus etunicatum, Glomus intraradices, and Glomus mosseae)	Increased gene expression, mineral solubilization, hormone production, expression, osmolytes and antioxidant enzymes	Al-Arjani et al. [99]

**Table 3.**  
Microbial mitigation of drought stress in plants.

and biotic and abiotic stress tolerance. They have interspecific functionality and are generally host-specific [102]. The endophytic microbes induce stress tolerance in the associated plants mainly through producing phytohormones and induction of the synthesis of secondary metabolites. On the contrary, arbuscular mycorrhizae confer stress tolerance to host plants by maintaining a steady flow of water and nutrient absorption from the soil [103].

The role of arbuscular mycorrhizae in drought stress tolerance of plants has been documented in several previous studies (**Table 3**). In one study, the impact of inoculation of arbuscular mycorrhizal strains, namely *Septoglomus constrictum*, *Glomus* sp., and *Glomus aggregatum* was studied in soybean, which is highly sensitive to abiotic stress [95]. The plants were subjected to drought stress after inoculation, and the biochemical, physiological, and molecular attributes were investigated. The treated plants showed increased levels of soluble sugars, proline, and glycine betaine and reduced MDA levels. The increased osmolyte levels in the treated plants conferred increased protection against the drought stress, while the lowered MDA content reduced the osmotic stress. The induction of phenolic compounds is one of the key mechanisms through which plants generate a response not only to infectious diseases but also to drought stress. In one study, Cheng et al. [97] used *Funneliformis mosseae* in the inoculation of trifoliolate orange. The inoculated plants exhibited a marked increase in several growth attributes such as stem elongation, leaf number, leaf area, and root architecture. Biochemical analysis revealed induction in the contents of coumarin, terpene, and phenolic contents in the root exudates of the treated plants as compared with those of untreated plants. The drought stress tolerance in the inoculated plants was attributed to the induction of phenolic components, as they reduce oxidative stress in plants. In a similar study, a mycorrhizal fungal strain, *Glomus mosseae* was used to inoculate bread and durum wheat cultivars, and the plants were then exposed to drought stress [98]. The drought stress tolerance mechanism was evaluated through measurement of growth parameters and proteomics analysis. The inoculated plants showed increased dry weight, and the two genotypes responded differently to the fungal inoculation in terms of stress tolerance. A significant upregulation in the osmolytes concentrations was observed. Moreover, the inoculated plants accumulated lower ethylene levels an indication of stress tolerance.

Oxidative stress triggers the production of reactive oxygen species (ROS), which further causes irreversible damages to the macromolecules and key enzymes. Microbes have an ameliorating impact on oxidative stress in plants. Drought stress imposes oxidative stress on plants with associated growth and yield reduction. Plants respond to ROS generation by triggering the induction of ROS scavengers, which protect the cellular machinery. In one study, Zou et al. [104] used *Gigaspora margarita* and *Glomus intraradices* strains in the inoculation of host plants subjected to drought stress. Molecular analysis revealed upregulation of the expression of *GintSOD*, *GmarCuZnSOD*, *GintPDX1*, and *GintMT1* in the inoculated plants. Moreover, it was concluded that the drought stress tolerance mechanism also involved reduction in the cytoplasmic protein levels and regulation of redox status through synthesis of pyridoxamine. The drought-associated secondary stresses negatively impact both quality and quantity of crop plants. However, these negative effects can be efficiently mitigated through inoculation of various AMF strains. In one study, Al-Arjani et al. [99] isolated three AMF strains, namely *Glomus mosseae*, *Glomus etunicatum*, and *Glomus intraradices* from the rhizosphere of *Acacia gerrardii*. These strains were used to inoculate the *Ephedra foliata* Boiss plants,



subjected to drought stress. Compared with the untreated plants, the treated plants showed a significant increase in the chlorophyll and carotenoid contents. In addition, the treated plants showed increased levels of sucrose-phosphate synthase and osmolyte levels, which might be responsible for the enhanced drought stress tolerance. In another study, Moradtalab et al. [96] inoculated strawberry seedlings with AMF and silicon to evaluate their combined effects against drought stress. It was observed that the AMF and silicone inoculation caused a marked increase in the water uptake, mineral content, and overall biomass. The antioxidant defense system was also triggered, which reduced the drought-associated damages and conferred stress tolerance.

## **6. Conclusion and prospects**

Climate change tends to increase the global temperatures, which have devastated impacts on agricultural production. Furthermore, the rapid industrialization and increase in the world population have put a lot of burden on agriculture to produce more food and feed from the existing crop varieties, and land and water resources. Drought tolerance in plants is a multigenic trait and can be enhanced in a meaningful way by adoption of multi-pronged strategy. Endophytic and rhizospheric microbes have well-established mechanisms to support plants in nutrient acquisition, stress tolerance, and disease resistance. In this connection, microbes with high potential of osmolytes and siderophore production, phosphate solubilization, and nitrogen assimilation should be selected for plant inoculation. Also, the microbial induction of the genes involved in ROS scavenging may help plants to overcome the negative effects of drought stress. Inoculation experiments should involve mixtures or consortium of microbes rather than individual microbial strains. Some recent experiments have used mixtures of diverse microbial strains, and it was suggested that a microbial consortium would have broad impacts on the plant growth and productivity under drought stress. Furthermore, the modern and state-of-the-art gene sequencing and editing tools could be used in genomic studies, which would involve identification, cloning, and functional characterization of target genes in the selected microbes with high potential of conferring drought stress tolerance. These efforts could be combined with approaches of system biology studies, which would further explore the microbial-mediated alterations in metabolic profiles under drought stress. An important consideration would be to combine the complex genetic networks with those of metabolic events, which are lying at the core of plant-microbe interaction under environmental stresses including drought stress.

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## **Conflict of interest**

The authors declare no conflict of interest.

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