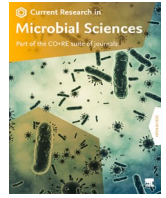




Contents lists available at ScienceDirect

Current Research in Microbial Sciences

journal homepage: www.sciencedirect.com/journal/current-research-in-microbial-sciences

Drought stress mitigation through bioengineering of microbes and crop varieties for sustainable agriculture and food security

Satish Kumar, Satyavir Singh Sindhu*

Department of Microbiology, CCS Haryana Agricultural University, Hisar, 125004, India

ARTICLE INFO

Keywords:

Drought
Plant growth promoting microbes
Phytohormone modulation
Osmolytes production
Antioxidants
Genetic engineering
Transgenic plants

ABSTRACT

Climate change and agriculture are intrinsically connected and sudden changes in climatic conditions adversely impact global food production and security. The climate change-linked abiotic stressors like drought and high temperatures are resulting in crop failure. The most severe abiotic stress drought significantly affect the stomatal closure, production of reactive oxygen species, transpiration, photosynthesis or other physiological processes and plant morphology, and adversely affect plant growth and crop yield. Therefore, there is an exigent need for cost effective and eco-friendly modern technologies to induce drought tolerance in crop plants leading to climate-adapted sustainable agricultural practices for sustained food production. Among many options being pursued in this regard, the use of plant growth promoting microbes (PGPMs) is the most sustainable approach to promote drought stress resilience in crop plants leading to better plant growth and crop productivity. These PGPMs confer drought resistance via various direct or indirect mechanisms including production of antioxidants, enzymes, exopolysaccharides, modulation of phytohormones level, osmotic adjustment by inducing the accumulation of sugars, along with increases in nutrients, water uptake and photosynthetic pigments. However, several technological and ecological challenges limit their use in agriculture and sometimes treatment with plant beneficial microbes fails to produce desired results under field conditions. Thus, development of synthetic microbial communities or host mediated microbiome engineering or development of transgenic plants with the capacity to express desired traits may promote plant survival and growth under drought stress conditions. The present review critically assesses research evidence on the plant growth and stress resilience promoting potentials of PGPMs and their genes as an approach to develop drought resilient plants leading to increased crop productivity. Effective collaboration among scientific communities, policymakers and regulatory agencies is needed to create strong frameworks that both promote and regulate the utilization of synthetic microbial communities and transgenic plants in agriculture.

1. Introduction

Sustainable agricultural practices are essential to meet demands of food for the ever-increasing population while minimizing the impact on the environment. However, global climate change, erratic rains, harsh

environmental conditions and progressive intensification of global agriculture have adversely affected soil health, microbial biodiversity and crop production (Malhi et al., 2021; Hartmann and Six, 2023). Dominant abiotic stresses comprise drought, salinity, temperature, freezing, intense light, changes in pH, flooding and heavy metals toxicity

Abbreviations: PGPMs, Plant growth-promoting microbes; ABA, Abscisic acid; SA, Salicylic acid; JA, Jasmonic acid; PGPB, Plant growth-promoting bacteria; ACC, 1-aminocyclopropane-1-carboxylate; ROS, Reactive oxygen species; ET, Ethylene; RWC, Relative water content; POD, Peroxidase; SOD, Superoxide dismutase; GR, Glutathione reductase; CAT, Catalase; APX, Ascorbate peroxidase; DHAR, Dehydroascorbate reductase; MDAR, Monodehydroascorbate reductase; MDA, Malondialdehyde; AMF, Arbuscular mycorrhizal fungi; FC, Field capacity; GSH, Glutathione; GSSG, Glutathione (oxidized form); CKs, Cytokinins; GA, Gibberellic acid; IAA, Indole acetic acid; VOCs, Volatile organic compounds; PGPR, Plant growth-promoting rhizobacteria; EPSs, Exopolysaccharides; EPB, EPS-producing bacteria; PSMs, Phosphate solubilizing microorganisms; PSMs, Phosphate solubilizing bacteria; KSMs, Potassium-solubilizing microorganisms; PGP, Plant growth-promoting; SMCs, Synthetic microbial communities; HMME, Host mediated microbiome engineering; P5CS, 1-pyrroline-5-carboxylic acid synthase enzyme; NCED, 9-cis-epoxycarotenoid dioxygenase; GWAS, Genome-wide association studies; RSA, Root system architecture; SNPs, Single-nucleotide polymorphisms; QTL, Quantitative trait locus WUE, Water utilization efficiency.

* Corresponding author.

E-mail addresses: kumarshaanu0822@gmail.com (S. Kumar), sindhuss@hau.ac.in (S.S. Sindhu).

<https://doi.org/10.1016/j.crmicr.2024.100285>

Available online 10 October 2024

2666-5174/© 2024 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY-NC license (<http://creativecommons.org/licenses/by-nc/4.0/>).

(Cramer et al., 2011; Teshome et al., 2020; Chaudhary and Sindhu, 2024). Among these different abiotic stresses, drought has affected approximately 64 % of global land area followed by cold (57 %), acidic soil (15 %) and flood (13 %), followed by low fertility (9 %) and salinity (6 %), respectively (Cramer et al., 2011; Phour and Sindhu, 2022). Thus, drought is one of the most important abiotic stresses that have deleterious impact on crop production and quality (Lesk et al., 2016; Ahluwalia et al., 2021; Zhang et al., 2022). Drought condition affects all aspects of plant growth including molecular, physiological, biochemical, hormonal, morphological and ecological traits (Ortiz et al., 2015; Gusain et al., 2024). Factors responsible for drought conditions includes evapotranspiration, uneven distribution of rainfall and varied water holding capacity of soil (Passioura and Angus, 2010; Devincentis, 2020). By year 2050, more than half of the cultivable land is expected to be affected by drought (Naylor and Coleman-Derr, 2018; Vociante et al., 2022). In different studies conducted, around 60 % of wheat yield is lost to drought followed by chickpeas and maize i.e., 40 and 21 % (Kasim et al., 2013; Daryanto et al., 2016; Khan et al., 2016).

Water comprises 80 to 95 % of plant body and is essential for reproduction, growth, and development of plants (Brodersen et al., 2019), thus any shortage in water will lead to abnormal plant growth leading to poor quality crop yield (Gupta et al., 2020; Deng et al., 2021). The solution seems to be developing high yielding crop plants with high water uptake potential or have some coping mechanisms against drought (Seleiman et al., 2021). Plants employ several morphological, physiological, and molecular responses in defense to combat drought stress (Phour and Sindhu, 2022; Bhanbhro et al., 2024). Further, osmolytes or osmo-protectants like soluble sugar, proline, betaine, spermines are synthesized by plant in order to maintain turgor pressure of cell. Secondary metabolites and antioxidant molecules have also been found to protect plants from drought (Siddique et al., 2016; Hasanuzzaman et al., 2020; Kaur et al., 2021). Other potent mechanisms that confer protection to drought in plants include abscisic acid (ABA) signalling, transcription factor activities and enhanced ion transport (Prakash et al., 2019; Kumar et al., 2019). Farmers also opt for water saving irrigation or drought tolerant cultivars to cope up with drought (Eisenstein, 2013). Thus, crop plants employ various adaptation strategies and pathways to tackle impact of climate change (Raza et al., 2019; Bhanbhro et al., 2024). However, under certain conditions, plant morphology or defense response fails to protect plant from drought and thus, there is a need to develop drought tolerance in plants by looking into gene regulation and cross talk between plants and microbes through signalling (Phour et al., 2020; Yadav et al., 2020; Shahid et al., 2020; Thomas-Barry et al., 2024).

Chemical priming of the plants with natural and synthetic chemicals is also applied in some cases for combating drought stress, which includes azelaic acid, salicylic acid (SA), piperolic acid, ABA, hydrogen peroxide, benzothiadiazole, jasmonic acid (JA) and β -aminobutyric acid (Savvides et al., 2016; Ali et al., 2019; Kaya et al., 2019). However, chemical priming is not a sustainable option as chemicals are expensive and toxic in nature, and may disturb the ecosystem after reaction with other chemicals in soil. In addition, chemicals may alter soil microbiota, biodiversity and fertility, and even affect crop production (Lin et al., 2019). Recently, utilization of beneficial plant-associated microbiomes as bioinoculants has emerged as cost effective and environment friendly solution for drought tolerance in sustainable agriculture practices (de Vries et al., 2020; Shah et al., 2021; Vociante et al., 2022; Muhammad et al., 2024). Various microorganisms help the plant in combating biotic and abiotic stress along with improving plant growth (Bender et al., 2016; Thirkell et al., 2017; Rubin et al., 2017; Ebrahimi-Zarandi et al., 2023). Such plant growth promoting bacteria (PGPB) including strains of *Azospirillum*, *Azotobacter*, *Bacillus*, *Klebsiella*, *Paenibacillus*, *Pseudomonas*, *Rhizobium* and *Serratia* obtained from phyllosphere, rhizosphere or endophytes have been demonstrated to contribute in drought mitigation (Abdelal et al., 2021; Kumar et al., 2022a, 2023; Manjunatha et al., 2022; Sati et al., 2023; Bittencourt et al., 2023). Such strains show

a diverse range of mechanisms for plant growth and stress mitigation by increasing nutrient availability (phosphorous, potassium and zinc) in soil, releasing plant growth promoting hormones, siderophores, 1-aminocyclopropane-1-carboxylate (ACC) deaminase and nitrogen fixation, and many more (Malik and Sindhu, 2011; Garcia et al., 2017; Li et al., 2020; Alkhatani et al., 2020; Kumar et al., 2022b; Chieb and Gachomo, 2023).

The molecular defense in plants against drought includes regulation at transcription and translation level, which could be reprogrammed or induced for drought tolerant genes (Fang and Xiong, 2015; Zandalinas et al., 2020; Wang et al., 2021; Kim et al., 2022). Various transgenic and molecular breeding tools are opted for developing drought resilient crops since last 20 years (Oladosu et al., 2019; Qaim, 2020; Khadka et al., 2020). RNAi, CRISPR/Cas and transgenics are some of the popular choices for developing drought resistant plants but this process is highly costly, and associated with toxicity and ethical issues (Shanker and Maheswari, 2017; Qaim, 2020; Jeon et al., 2023; Wang and Doudna, 2023). Hence, scientists are looking for and incorporating traits with the application of conventional plant breeding techniques that could aid in drought tolerance in plants, by which sustainable agriculture could be practiced (Khadka et al., 2020; Rasheed et al., 2022). However, such techniques are laborious and time consuming. On the other hand, molecular techniques for developing transgenic plants are associated with ethical issues, and could possibly cause environmental hazards.

While there have been numerous papers and reviews that discuss the genetic and physiological approaches that provide resistance to plants against drought stress and adapt to climate change (e.g., Ashraf, 2010; Marasco et al., 2012; Tardieu, 2022; Muhammad et al., 2024; Thomas-Barry et al., 2024). The potential contribution of some plant associated beneficial microbes to this challenge has also been discussed individually (although see, de Vries et al., 2020; Poudel et al., 2021; Shah et al., 2021; Bittencourt et al., 2023). The available information lacks the involvement of various microbial genes and their modulation during amelioration of drought stress. It necessitated the need for a comprehensive discussion on exploitation of microbial genetic resources during plant-microbe interactions to assist crop production under drought stress. In the present manuscript, a broad overview of the main strategies employed by plants and microorganisms has been provided that aids in increasing drought tolerance in crop plants. A more in-depth discussion was provided about various mechanisms and microbial genes to enhance drought tolerance. Novel approaches and strategies were explored for genetic engineering of microbial communities and host plants for increasing their efficacy towards drought stress mitigation in different crops.

2. Detrimental effects of drought stress on crops and plant responses to stress adaptation

Plants are affected more by varying environmental conditions due to their sessile nature. Harsh environmental conditions not only affect the growth and development of crop plants but also the geographic distribution of a single plant species (Bukhari et al., 2019; Teshome et al., 2020). Any kind of adverse condition results in some metabolic alterations and expression of stress responsive genes that ensure the plant survival under such conditions (Ahanger et al., 2017; Mostofa et al., 2018; Wang et al., 2021). Climate change due to human activities has adverse effects worldwide and drought is the most concerning stress as approximately 10 % of cereal crops yield is lost to drought (Lau et al., 2012; Shen et al., 2020). Therefore, it is essential to study the plant potential to tolerate water limitation specifically for the crops in arid and semi-arid regions (Sobhanian et al., 2020; Thomas-Barry et al., 2024). Various studies have been conducted to evaluate the impact of drought stress on plants from the initial growing stage to harvest. More studies are still needed towards the combined effects of both drought and heat on reproductive stage (Seleiman and Kheir, 2018). This section discusses the effect of drought on morphology, physiology, and

biochemistry of plants including changes in root and leaf shape, respiration, biomolecule synthesis, and physiological processes i.e., respiration, photosynthesis, translocation and ions uptake (Kapoor et al., 2020).

2.1. Stress symptoms caused by water deficiency and drought

Crops cultivated in areas that are chiefly dependent upon rainfall are at a higher risk of facing stress than the irrigated areas (Konapala et al., 2020; Thomas-Barry et al. 2024). Drought dependent symptoms intensify with the increasing time period of drought stress. The effect of drought on plant is dependent on soil type, growth stage of plant, time duration of drought, plant species and drought frequency (Zoghi et al., 2019). For instance, mild drought condition induces increase in root biomass, however, growth pattern remains same. On contrary, severe drought conditions typically affect the stomatal closure or transpiration, photosynthesis or other physiological processes, and plant morphology (Rao and Chaitanya, 2016; Gholami et al., 2022). Drought condition leads to low moisture content in soil, which indicates low water potential in leaves and stem causing high transpiration rates as compared to low water absorption from soil (Ristvey et al., 2019; Goche et al., 2020). Plants expand their roots to increase water uptake, which could reduce the transpiration rates so to cope up with drought stress (Martínez-Vilalta and García-Fórner, 2017). Also, the plant response towards water scarcity is based upon the drought intensity, presence of different stress conditions or the past drought experience (Thomason and Battaglia, 2020; Sadhukhan et al., 2023).

Drought threatens crop production due to reduction in photosynthesis, reduced amount of CO₂ captured due to stomatal closure, and increased photorespiration. Drought results into accumulation of salts in upper layers of soil, thus lowering the water potential and uptake of water and minerals from soil. Therefore, such situation is also responsible for micro- and macro-nutrients deficiency (Gholami et al., 2022). Stomata closure disrupts the carbon fixation and utilization rate by varying sugar concentrations, which latter generates reactive oxygen species (ROS) due to disturbance in photosynthesis (Chaves et al., 2009; Pinheiro and Chaves, 2011; Hou et al., 2024). Moreover, low water potential disturbs the redox homeostasis, which generates ROS and its production in chloroplast, mitochondria and peroxisomes could lower the CO₂ uptake in green leaves (Hasanuzzaman et al., 2020). Development of oxidative stress later affects the photosynthesis process in addition to electron transport chain, eventually results in malfunctioning of chloroplast and mitochondria (Rao and Chaitanya, 2016). It also causes lipid peroxidation, hence altering the structure and activity of enzymes like RuBisCo (Maswada et al., 2020). Water directly governs

the plant growth, for instance, cell enlargement is dependent more on water deficit compared to cell division (Humplík et al., 2017). Water scarcity is chiefly responsible for reducing the cell wall extensibility and turgor pressure. Thus, lowered plant metabolism and altered electrolyte balance can eventually cause plant death. Different studies have demonstrated decrease in the number of leaves and their sizes, retarded root growth, decreased production of seed and delayed seedling establishment under drought conditions (Osakabe et al., 2014).

Ethylene (ET) is the major phytohormone produced during drought and is responsible for leaf senescence in younger plants (Meena et al., 2017). Although, drought may affect plant functioning at any stage, but it is more lethal during seed development and reproductive stage, thus decreasing the number, size and quality of seeds, and crop yield (Queiroz et al., 2019). Phenotypic modifications induced by drought stress include leaf burning, wilting, yellowing and discoloration in leaf, closed flowers, etiolation, flower sagging, premature leaf senescence or fall, leaf drooping, scorching and limp leaves (Fig. 1) (Ullah et al., 2017; Khan et al., 2018; Ruehr et al., 2019). Some other rare symptoms include reduced canopy, stunted growth, twig and bark cracks, and necrosis (Toscano et al., 2019). Extreme drought may even lead to death of crop plants. Under water deficiency conditions, fruit cracking is also generally observed.

However, plant expresses a range of defense mechanisms varying from molecular to phenotypic level (Khadka et al., 2020; Bhanbhro et al., 2024). The most obvious defense strategy includes early flowering, fast growth and a short life cycle in addition to hairy leaves and cuticle to maintain high water potential in plant (Seleiman et al., 2021). Moreover, plants in drought prone areas adapt certain features like small leaf area, trichomes on both dorsal and ventral leaf surface, and limited expansion of new leaves, more root hair, increased root length and size, and better root growth for more absorption of water and nutrients from soil (Seleiman et al., 2021; Ranjan et al., 2022). Also, antioxidants production, osmotic regulation and salt accumulation are the underlying metabolic mechanisms to withstand drought condition (Hasanuzzaman et al., 2020; Zahedi et al., 2022). Other strategies that could help in avoiding the harmful effects of drought include sowing at a particular time, mulching, and application of osmotic protectors or plant beneficial microbes, maintaining soil nutrient pool, and selecting cultivars according to soil type (Gholami and Zahedi, 2019).

2.2. Drought related morphological changes

Now-a-days climate change and variations in environmental conditions is so high that plant experiences diversity of stresses including varying rainfall and drying conditions. Therefore, manipulating plant

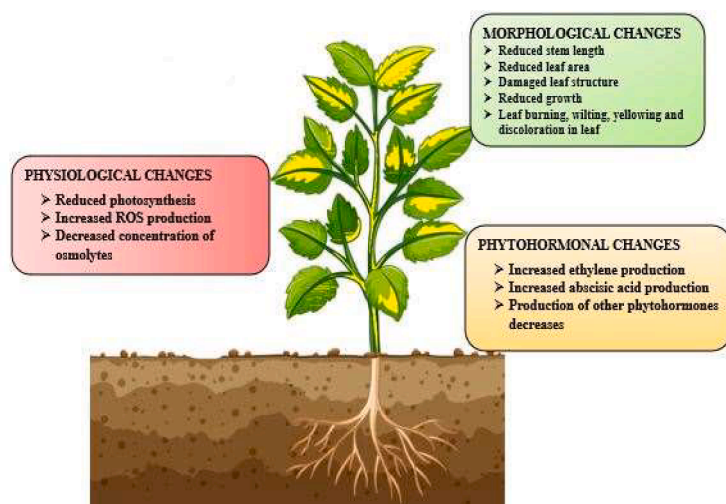


Fig. 1. Morphological, physiological and phytohormonal changes induced by drought stress.

physiology seems to be a fascinating option for overcoming stress conditions (Becklin et al., 2016). The most common response towards drought is generated through leaves (Pedersen et al., 2021) and changes in leaf thickness, altered leaf palisade, restricted cell division and elongation, and spongy leaf tissue occurs during water stress (Meng et al., 2021). Leaves capture the effects of drought in the form of stunted growth, reduced leaf area, number and size, atrophy, senescence, etiolation, and leaf shedding (Bhusal et al., 2020; Nadal et al., 2020; Pedersen et al., 2021). Every plant species shows different symptoms for instance; only marginal elongation of leaves is observed in sugarcane under drought conditions (Misra et al., 2020). Decrease in leaf area under water deficit conditions causes drop in leaf turgor pressure, decreased concentration of photo-assimilates and canopy temperature (Taiz et al., 2015). Thus, modification in leaf structure during drought conditions decreases the rate of transpiration and photosynthesis. Also, water is transpired mostly from the upper leaf epidermis, while the lower epidermis is less vulnerable to water loss causing a reduced pressure leading to wilted leaf with altered morphology. This mechanism is opted by conifers in xerophytic conditions, which retained more water by rolling in their leaves (Rueda et al., 2017). Reduced plant height is resulted due to delayed cell division and it is the most crucial symptom of drought (Li et al., 2020; Misra et al., 2020). Roots tend to uptake more nutrients from soil so as to sustain the plant during drought stress (Lobet and Draye, 2013). Another important adaptation in plants is increased number of vessels, reduced area of stele by decreasing the diameter of vessel and secondary root cortex cells (Thangthong et al., 2019). Moreover, water scarcity also reduces the root to shoot ratio (Zhang et al., 2019). Modifications in roots are necessary for plant survival under water stress in arid regions (Liu et al., 2023). This includes increase in root density and number of lateral roots, which will eventually aid in enhanced accumulation of nutrients (Strock et al., 2021), and water uptake compared to thinner roots (Ilyas et al., 2021).

2.3. Drought effects on physiology and biochemistry of plants

Numerous physiological and molecular mechanisms play central role in plant survival during unfavourable conditions so as to maintain homeostatic balance (Tardieu, 2022). Osmotic stress is induced due to water scarcity, which causes dehydration in cell due to restricted cell division and cell elongation. The major disfunction during drought includes decreased turgor, reduced chlorophyll content, chlorophyll peroxidation or other variations in chlorophyll, and reduced photosynthesis rate due to changes in stomata and leaf structure (Kaushal and Wani, 2016). With increasing time of drought, CO₂ uptake is also reduced due to altered functioning in plants and cannot be repaired even by increasing the external CO₂ concentration. The enzymatic activity of RuBisCo, electron transport chain and light harvesting capacity of photosynthetic apparatus are severely impaired during drought conditions, thus affecting photosynthesis process. The concentration of photosynthetic pigments is significantly reduced at the time of vegetative phase and pollination during drought stress. To minimize the effects of drought on biochemical and physiological processes, plants tries to maintain CO₂ in mesophilic intracellular space in order to restrict photosynthesis.

Plants suffer with low productivity and water use efficiency due to disturbed cycle of water and nutrients in plant during drought (Farooq et al., 2009; Li et al., 2009). Abid et al. (2018) observed that turgor pressure, water potential of leaf, and relative water content (RWC) decreases at tillering and jointing stage of wheat during drought, while an increase in osmotic adjustment was also reported. Osmotic regulation by plant is mediated via the accumulation of compatible solutes, which could reduce the water potential intracellularly (Yang et al., 2021). Osmotic regulators include mineral ions, organic osmolytes, nitrogen containing amides, amines and quaternary ammonium compounds, and sugars like trehalose, fructose, sucrose, maltose and mannitol (Bittencourt et al., 2023). Generally, drought is more severe during

flowering or reproductive growth stage contrary to vegetative growth stage, which eventually affects the crop yield and productivity in rice, chickpea, cowpea and wheat (Mafakheri et al., 2010; Ndiso et al., 2016; Zhang et al., 2018).

2.4. Drought induced oxidative stress and plant antioxidant response

Production of ROS is the most severe result of drought stress, which is produced within chloroplast, peroxisomes and mitochondria (Fig. 2) (Hasanuzzaman et al., 2020; Wu et al., 2022). ROS include hydrogen peroxide (H₂O₂), singlet oxygen (¹O₂) or superoxide radical (O₂⁻). ROS can be produced through the electron transport chain of respiration and photosynthesis processes (Dietz, 2016). They are normally produced in minor concentrations as signalling molecules for cell expression and protein production (Waszczak et al., 2018). However, higher ROS concentration causes damage to DNA, chloroplast and mitochondria, disturbs electron transport chain, and causes lipid peroxidation, alters the structure of proteins and denatures the enzymes, and modify the metabolic processes as well (da Silva et al., 2013; Li and Liu, 2016). The peptide bond is degraded by the ROS, which eventually damages the structure and functions of proteins, and other macromolecules either by carbonylation or glycosylation (Yang et al., 2021). Plants overcome the ROS stress by the action of antioxidant enzymes and the increased expression of related genes during the onset of drought conditions (Hou et al., 2021). The variations in the enzymatic activity of antioxidant enzymes such as peroxidase (POD) and superoxide dismutase (SOD) create a drought stress memory, which aids in producing adequate defense response during stress (Lukić et al., 2023). For instance, enhanced synthesis of SOD and peroxidase enzymes was observed in offsprings when the parent plants were grown under stress conditions in *Alopecurus pratensis* (Lukić et al. 2020; 2023). Liu et al. (2022) reported that transgenerational drought stress memory is induced by the over expression of anti-oxidative enzymes including glutathione reductase (GR), catalase (CAT), ascorbate peroxidase (APX), dehydroascorbate reductase (DHAR), SOD, POD and monodehydroascorbate reductase (MDAR). This latter is periodically oxidized and reduced, and metals bind to the enzyme, catalysing the conversion of O₂ to H₂O₂.

Usually, SOD has three different isoforms in plants, including Fe-SOD, Cu/Zn-SOD and Mn-SOD. Mn-SOD and Fe-SOD have one metal ion and can be found in chloroplast and mitochondria, while Cu/Zn-SOD exists in cytoplasm and chloroplast (Yang et al., 2021). Another important enzyme is catalase, which exist in tetrameric form containing four iron-containing heme group and functions in the conversion of H₂O₂ into H₂O and O₂. Catalase is primarily localized in peroxisomes where they detoxify H₂O₂ produced as a result of photorespiration by splitting the O–O bond. However, catalase only converts the excess amount of H₂O₂ into water and oxygen, and allows only a limited amount of H₂O₂ for cell signalling. Catalase produces iron peroxides by reacting with H₂O₂ followed by oxidation (Yang et al., 2021). Peroxidase enzyme functions similar to catalase and converts H₂O₂ into H₂O, thus preventing oxidative damage (Wu et al., 2022). Thus, CAT and POD enzyme secretion in drought stressed plants resulted in reduced concentration of H₂O₂ in offsprings (Lukić et al., 2023). Similarly, drought priming increases the concentration of malondialdehyde (MDA) by inducing chelation of ferrous ions, which are responsible for synthesis of MDA and lipids. Some of the non-enzymatic antioxidants include water soluble-glutathione, ascorbic acid and fat-soluble tocopherols (Ahmad et al., 2019; Laxa et al., 2019).

Glutathione (GSH; reduced form) and GSSG (GSH; oxidized form) could also scavenge free radicals to prevent oxidative damage. Glutathione peroxidase converts H₂O₂ into H₂O, while GSH is oxidized to GSSG. Similar to ascorbic acid, vitamin C could also act as antioxidant molecule in addition to enzymatic cofactor and it also functions additionally in the regulation of photosynthesis, cell division and signal transduction (Yang et al., 2021). During drought condition, oxygen free radical and H₂O₂ production was elevated in wheat flag leaves compared

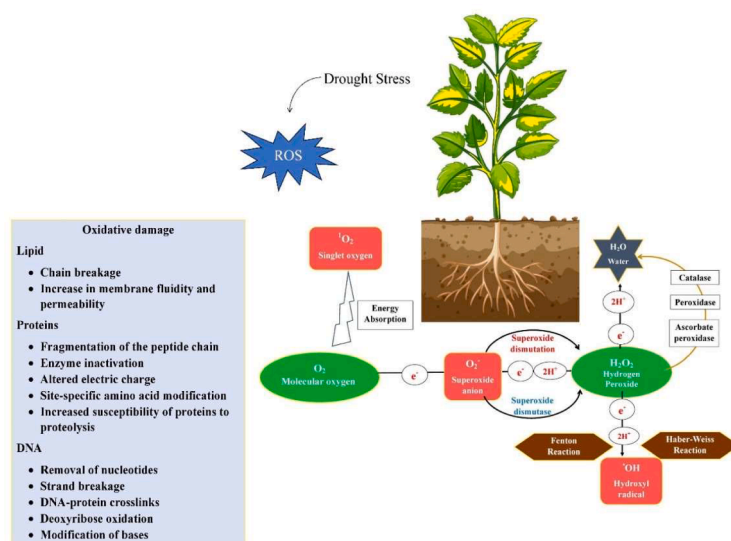


Fig. 2. Production of reactive oxygen species during drought stress and contribution of various antioxidant enzymes to prevent oxidative damage to macromolecules.

to the primed plants where their concentration was low (Wang et al., 2018). Enzymatic activity of different enzymes including CAT, APX and SOD was more in primed plant versus non primed plant. Priming elevates the activity of glutathione peroxidase enzymes during the second time exposure to drought, whereas, APX activity remains consistent. In another study, primed rice seedlings depicted increased SOD and POD due to oxidative stress generated under drought stress (Li et al. 2011). Primed plants resulted into five times more activity of SOD and a lower CAT activity compared to unprimed control (Yang et al., 2021). Similarly, primed *Nicotiana tabacum* (L.) produced peroxidase enzyme that reduced H_2O_2 concentration in plant cell during drought (Khan et al., 2020).

Arbuscular mycorrhizal fungi (AMF) establish symbiosis with plant roots and this symbiotic association promotes plant growth and development by establishing extra radical mycelial hyphae around the roots, and provide access to the inaccessible nutrients and water to the plants (Püschel et al., 2020; Tatewaki et al., 2023; Phour and Sindhu, 2024). In return, AMF procure shelter and carbon sources like lipids and sugars from the plant (Wang et al., 2023; Alotaibi et al., 2023). In addition, AMF induces enzymatic and microbial activity in soil, and also ameliorate biotic and abiotic stresses (Wanlin and Yan, 2024). The deleterious effect of ROS could be suppressed with the production of phenolics and flavonoids (Begum et al., 2021; Hassena et al., 2022; Haghaninia et al., 2024). Moreover, AMF stimulates the production of heat shock transcription factors in addition to non-enzymatic and enzymatic antioxidants which regulated signal transduction for balancing ROS production during stress conditions (Bahadur et al., 2019; Das and Sarkar, 2024). Combined treatment of AMF and biochar increased antioxidative enzymatic activity and reduced levels of proline and MDA in lavender under different irrigation levels (Haghaninia et al., 2024). Under mild drought stress conditions, increased production of flavonoid and phenolic in addition to borneol, linalool, camphor and linalyl acetate was observed.

AMF inoculation in *Bombax ceiba* under drought stress caused a hike in antioxidative enzymes such as CAT (318.5%), APX (34.1%) and GR by 22.8%, respectively (Li et al., 2022). Similarly in walnut, AMF exhibited increased activity of CAT by 340.4% and APX and GR by 106.3 and 77.2% compared to control plants (Ma et al., 2022). Further in tomato plants, CAT activity was increased by 42 and 57% during water and heat stress, respectively with the inoculation of two different AMF strains (Haddidi et al., 2020). In another study, Rasouli et al. (2023) evaluated the effect of AMF strain *Funneliformis mosseae* on the summer savory (*Satureja hortensis* L.) under different irrigation levels.

Inoculation of AMF at 30% field capacity (under drought stress) increased the levels of H_2O_2 , MDA, and antioxidant activity in addition to enhance enzymatic activity of guaiacol peroxidase, SOD and APX. Mycorrhization of Unnayan LT896 tomatoes with AMF strain *Paraglomus occultum* depicted higher CAT activity compared to control plants under drought stress (Alam et al., 2023). Whereas, H_2O_2 levels were maximum in control plant as compared to LT896 tomatoes treated with *Rhizophagus clarus*. On the other hand, APX activity was higher in Unnayan tomatoes when treated with *R. clarus* and *Acaulospora morrowiae*. AMF treated Minto super tomato (*Solanum lycopersicum* L.) plants depicted 42% and 66% increase in CAT and APX compared to control plants. Further, AMF treated plants showed increases in shoot dry weight and yield by 28 and 20%, respectively in comparison to control untreated plants.

2.5. Production of phytohormones associated with drought stress

Phytohormones production is a major strategy opted by plants to overcome stress conditions and to sustain their survival under harsh environmental conditions. Phytohormones also regulate key metabolic processes and contribute as signalling molecules under adverse environmental conditions (Salvi et al., 2021; Wu et al., 2022). Plant hormones include auxins, cytokinins (CKs), gibberellic acid (GA), jasmonic acid (JA), salicylic acid (SA), ethylene (ET), brassinosteroids, and strigolactone. Onset of drought stress induces ABA production leading its higher concentration in stressed plants, which functions as signalling sensor from root to shoot during drought stress (Chaves et al., 2003; Wang et al., 2009). It perceives the signal from environment and then accordingly produces adaptive response by regulating the cellular, biochemical, physiological characters. Other important functions of ABA include expression of stress related genes and modulation of transcription factors for increased resistance to stress (Kuromori et al., 2018; Takahashi et al., 2018; Manna et al., 2021). The drought signalling cascade mediated by ABA is perceived by three receptors i.e., GTGs, PYR/PLR/R-CARs and CHLH/ABAR, which then modulate lipid metabolism, stomatal closure, transpiration rate, seed germination, or seed dormancy and other plant developmental processes. The receptor protein phosphatases (PP2C) was identified as negative regulator of ABA in *Arabidopsis* knockouts of *abil-1* and *abi2-1* (Leung and Giraudat, 1998), while protein kinase (SnRK2/OST1) was identified as positive controller of ABA (Yoshida et al., 2002). Thus, ABA production could be modulated by regulatory genes/proteins, which subsequently affect the expression of stress related genes and transcription factors for increased resistance

to stress. ABA production is induced in roots with the onset of drought condition and later translocated to leaves through xylem where it shows protective response towards leaves (Wu et al., 2022). In addition, ABA together with CKs and JA controls stomatal opening and downregulates the transpiration (Daszkowska-Golec and Szarejko, 2013).

Several antioxidant enzymes and genes related to drought stress were upregulated including RD11, RD29A, RD29B, DREB2B, and DREB2A with increased concentration of auxins (Ilyas et al., 2020). Jung et al. (2015) identified a total of 31 Aux/IAA genes in rice (*Oryza sativa*) and some of which were induced by drought stress. It was found that the rice Aux/IAA gene OsIAA6 is highly upregulated by drought stress and its overexpression in transgenic rice improved drought tolerance, likely via the regulation of auxin biosynthesis genes. The OsIAA6 gene was specifically expressed in the axillary meristem of the basal stem, which is the tissue that gives rise to tillers in rice. Auxin production in *Arabidopsis* altered the concentration of glucosinolate (Salehin et al., 2019). Auxin promotes plant growth by stimulating root architecture and increasing the number of root hairs, which will allow more uptake of water and nutrients, thus indirectly aid in mitigation of drought stress (Contesto et al., 2010; Cassán et al., 2014; Egamberdieva et al., 2017).

Another active form of phytohormone includes gibberellic acid, GA1 and GA4, which are structurally tetracyclic diterpenoid carboxylic acid (Sponsel and Hedden, 2010). GA concentration should be low so to impart tolerance against drought, for instance; inhibition of GA production with paclobutrazol inhibitor in finger millet conferred tolerance to drought and resulted in no symptoms related to drought. This could be due to decreased rolling of leaves, which enhanced the plants withstand to lower moisture levels (Plaza-Wuthrich et al., 2016). Cytokinins are other phytohormones, which are synthesized in the roots and exported to other parts via xylem (Hai et al., 2020). Similar to GA functioning, CKs in low concentration increases the drought tolerance as observed from the overexpression of CKX1-4 in *Arabidopsis* (Nishiyama et al., 2011). CKs act as the antagonistic of ABA and prevent the stomatal closure under water limiting conditions (Hung et al., 2018). Similar results were reported by Prerostova et al. (2018) with decreased CKs production in sunflower during drought. Moreover, Ramireddy et al. (2018) observed that degradation of cytokinins due to overexpression of cytokinin oxidase/dehydrogenase gene promoted uptake of nutrients from soil by roots, thus improving tolerance of barley plants to drought.

Another class of phytohormones includes JA, which upregulated the stress related genes, and stimulated water uptake by roots via ABA independent and dependent pathways (Sanchez-Romera et al., 2014). JA plays a central role in crosstalk with ABA and other phytohormones, and induces the signalling cascade initiating the antioxidant activity, and regulates the stomata closing and opening (Singh et al., 2023). Polyhydroxylated sterol derivatives i.e., brassinosteroids also impart drought tolerance in plants (Kahlaoui et al., 2016). Increased concentration of H₂O₂ in cells initiated the signalling cascade of brassinosteroids by inducing transcription factors BES1 and BZR1 (Tian et al., 2018). Brassinosteroids induce the overexpression of antioxidant enzymes and decreases the ROS production (Divi et al., 2010). This mechanism helps in maintaining higher concentration of photosynthetic pigments and photosynthesis, and stomatal conductance in tomato and corn (Anwar et al., 2018).

Strigolactones phytohormones (carotenoid-derived lactone terpenoids) are synthesized in roots and then secreted in soil to induce symbiotic interactions between mycorrhizal fungi and plant roots leading to increases in uptake of water and minerals (Matusova et al., 2005; Stauder et al., 2018). Biosynthesis of strigolactones is mediated by a number of enzymes like eCCD7-8, DWARF 27 or D27 and MORE AXILLARY GROWTH 1 (MAX1) while the transporter protein mediates the secretion of strigolactones in soil (Sasse et al., 2015). Strigolactones together with ABA mitigates abiotic stress including drought in *Arabidopsis* (Liu et al., 2015a; Bhatt and Bhatt, 2020). However, in *Lotus japonicus* ABA is increased in woody sap, while strigolactones production was decreased in roots due to reduced water potential under

drought stress (Liu et al., 2015b).

Ethylene is another important phytohormone produced from methionine (Fusco and Carillo, 2023). ABA and ET positively regulate NADPH oxidase in six different genotypes of wheat (Hu et al., 2020a), and its production plays a crucial role in drought tolerance of rice by regulating ROS production and stomatal closure (Shi et al., 2020). Ethylene promotes ripening, seed germination, leaf growth and senescence under different stress conditions. SA is highly sensitive to the presence of ABA as observed with the overexpression of CBP60g (calmodulin-binding protein) in transgenic *Arabidopsis* plant (Wan et al., 2012), and SA producing plants depicted high resistance to disease and drought stress. Salicylic acid also controls stomatal movement, transpiration rate, photosynthesis, and antioxidant activity (Nazar et al., 2015). Application of SA could increase the concentration of dehydrin like proteins, heat shock proteins and chaperones, and regulates concentrations of Rubisco and chlorophyll along with protein kinase activity (Sun et al., 2009; Nazar et al., 2015). From above discussion, the crucial role of phytohormones in amelioration of drought stress is well established. However, the impact of different phytohormones on the drought-stressed root microbiome deserves further investigation.

3. Effects of drought on microbial population dynamics and functions

Recently, rapid and drastic changes in the global climate have exacerbated various environmental (abiotic) and biotic stresses for crops, which significantly threaten crop production and food security worldwide. Mild or severe drought conditions significantly affect the structure of soil microbial communities, their growth and survivability, as well as their biochemical functioning and soil fertility (Meisner et al., 2018; Siebielec et al., 2020; Bogati and Walczak, 2022), which subsequently affect yields of drought-sensitive crops (Nguyen et al., 2018; Bazany et al., 2022; Bogati and Walczak, 2022; Bittencourt et al., 2023). The major effects of drought on soil bacteria include increased osmotic stress and rising competition among microbial population for water and nutrients (Barnard et al., 2013; Chodak et al., 2015; Bogati et al., 2023). Further, water stress may induce alteration in genetic material like alkylation or oxidation of nucleic acid bases, removal of bases or formation of cross linking among nucleotides (Ngumbi and Kloepper, 2016). Moreover, drought stress induces the production of free radicals, which may result in lipid peroxidation, cause alteration in electron transport chains, or may induce conformational changes in proteins affecting the membrane structure and integrity (Bérard et al., 2015; Bogati et al., 2023). The climate change and plant community composition were reported modulate the structure and function of microbial communities. For instance, decreased soil moisture (drought) induced a highly active phosphate-solubilizing community, whereas opposite response was observed in the siderophore-producing community (Breitkreuz et al. 2021).

Microbial community structure in rhizosphere soil is also shaped by the root exudates released by host plant and surrounding soil environment (Dastogeer et al., 2020; Raza et al., 2021; Ali and Glick, 2024). Plants may stimulate the proliferation of specific beneficial microbes to help them in amelioration of these stresses by secreting a range of primary and secondary metabolites (Bakker et al., 2018; Liu et al., 2020; Bai et al., 2022; Dhungana et al., 2023). In addition, plant functional genes have been found to regulate root phenotypic traits and the secretion of root exudates, such as organic acids and hormones, which play important role in shaping the microbial community assembly in rhizosphere (Zhalnina et al., 2018; Zhang et al., 2019; Wang et al., 2020; Yu et al., 2021). Plant-microbe interactions under drought stress also influenced the synthesis or release of specific metabolites. For instance, *Pinus taeda* seedlings treated with root endophytic fungus *Serendipita indica* caused more than three times upregulation of eriocitrin, trans-aconitic acid, vitamin C, uric acid, α -ketoglutaric acid, vitamin A, stachydrine, coumalic acid, itaconic acid, calceolarioside B,

2-oxoglutaric acid, and citric acid synthesis in inoculated seedlings under drought stress in comparison to those of uninoculated seedlings (Wu et al. 2024).

Climate change affects the frequency and severity of droughts, which may cause significant perturbations of terrestrial ecosystems. The long-term impacts of droughts on ecosystem structure and functioning after the drought has subsided are often termed as 'drought legacies' (Müller and Bahn, 2022). Drought legacies involve changes at the species and the community scale as well as alterations of soil properties, which have consequences for ecosystem responses to subsequent drought. Canarini et al. (2021) conducted a long-term field experiment in mountain grassland in central Austria and suggested that the process of "ecological memory" is stimulated by recurring droughts and this provides resistance to future droughts due to the major role mediated by microorganisms. Thus, drought history of soils affects microbial population dynamics and functions such as enzyme activities involved in C, N, and P cycling, which can, in turn, affect plant's nutrition status and fitness (Canarini et al., 2021; Kelly et al., 2023). With increasing duration of drought conditions, the reduced microbial populations and their activity in litter soil was reported under birch trees after one month of drought conditions (Schimel et al., 1999). However, two months prevailing drought reduced the abundance of Bacteroidetes, Verrucomicrobia, and Proteobacteria while induced the dominance of Actinobacteria (Siebielec et al., 2020). The loamy soils are dominated by ten different actinomycetes genera including *Marmoricola*, *Gaiella*, *Pseudomonas*, *Sphingomonas*, *Aquihabitans*, *Flavobacterium*, *Solirubrobacter*, *Kribbella*, *Brevundimonas* and *Nocardioides*.

Several studies have further shown that this drought legacy affects the microorganisms associated with the rhizosphere and endosphere of crop hosts (Azarbad et al., 2020; Santos-medellín et al., 2021; Gebauer et al., 2022; Carter et al., 2023), and has a significant impact on plant growth, physiology, and phenology under drought (Lozano et al., 2022; Kuerban et al., 2023). For example, Azarbad et al. (2020) showed that under low soil moisture content, the rhizosphere of plants growing in soils with a history of water stress harbored significantly higher numbers of actinobacteria. Maize plants inoculated with a microbiota from a water-limited legacy soil were more tolerant to drought by producing longer roots and generating more organic carbon in the soil, potentially stimulating the microbiome, and slowing water loss in soil during drought (Carter et al., 2023). Ebrahimi-Zarandi et al. (2023) showed that actinobacteria are enriched in the rhizosphere and endosphere of crops enduring water deficit stress conditions. These actinobacteria, particularly the *Streptomyces* genus, employed various mechanisms including modulation of phytohormone levels, reinforcement of antioxidant enzymes, enhanced water and nutrient uptake to alleviate water deficit stress in crops.

Drought reduced the diversity of microorganisms from soil to the roots of different grasses and observed up to 20 % variance of microbial communities within different cereal species such as sorghum, maize, barley, and wheat under drought (Naylor et al., 2017). The enhanced the population of Actinobacterial species especially genus *Streptomyces* was demonstrated. In another study, genus *Streptomyces* was found as abundant actinobacteria taxa in the endosphere microbiome of 30 different angiosperm plants (Fitzpatrick et al., 2018; Santos-Medellín et al., 2021). Many researchers have reported the relative decrease in the population of Proteobacteria and Bacteroidetes under drought stress conditions (Dai et al., 2019; Simmons et al., 2020). Whereas, other studies showed higher microbial species richness in drought-sensitive genotypes in response to water deficit (Gaete et al., 2021; Kristy et al., 2022), indicating that drought-tolerant cultivars exert a stronger selection on microbial communities in the face of drought conditions. These results indicate that the host genetic factor at species and cultivar level is an important determinant in shaping root microbiomes under drought. Aparna and Devi (2022) reported that a rice landrace recruited a specific group of microorganisms during drought, potentially maintaining its rhizosphere functioning. Characterizing the root mycobiome of wild and

domesticated pearl millet grown in arid and semi-arid areas, Mofini et al. (2022) showed a higher relative abundance of saprotrophic fungal species in the wild millet. It suggests that wild plants probably provide a more appropriate ecological niche for saprotrophic fungi under drought, and could benefit from mineralization of nutrients driven by saprotrophs. By sharing the necessary phenotypes such as nitrogen fixation, increased plant nutrient availability, and acquisition of tolerance to drought, an intercropping system including legume-cereal can positively affect the composition of root microbial communities under drought stress (Singh and Mathimaran, 2019).

In rice plants, Si et al. (2021) found that drought exerts a negligible effect on the alpha diversity of rhizosphere bacterial communities, but substantially enriches *Actinobacteria* and decreases *Firmicutes* (Rosa et al., 2023). Specifically, the relative abundances of *Actinobacteria* and *Acidobacteria* were increased in peanut seedlings and podding stages under drought stress, whereas the relative abundances of *Cyanobacteria* and *Gemmatimonadetes* were increased in the flowering stage (Dai et al., 2019). Furthermore, in millet plants, Simmons et al. (2020) proved that drought intensity is correlated with the enrichment level of *Actinobacteria*. In conclusion, *Actinobacteria* enrichment within drought-stressed root microbiomes is strongly conserved among evolutionarily diverse plant species. Moreover, decreases in the phyla *Proteobacteria* and *Verrucomicrobia*, as well as increases in the ratio of Gram-positive to Gram-negative bacteria, are also frequently observed under drought conditions (Acosta-Martínez et al., 2014; Naylor and Coleman-Derr, 2018; Rosa et al., 2023).

Drought stress may reduce the colonization of ectomycorrhizal fungi, and alter their community structure in addition to changes in hyphal growth, and arbuscules production (Compant et al., 2010). Changes in the composition of root-associated fungal communities and increased fungal biodiversity in rice plants have also been reported, with the majority of identified OTUs belonging to the *Pezizomycotina* subphylum (Andreo-Jimenez et al., 2019).

A study was carried out to observe differences in relative abundance of Ascomycota and Basidiomycota during drought stress in seven different grasslands located in two continents (Ochoa-Hueso et al., 2018). The results depicted that the changes in relative abundance was negatively related to the rainfall. Further, rice plant responded to drought by inducing a shift in bacterial and fungal population in their root endosphere and rhizosphere (Santos-Medellín et al., 2017), and characterized an enrichment of *Actinobacteria* and *Chloroflexi* but a depletion of *Acidobacteria* and *Delta Proteobacteria*. In another study, specific fungal species have been identified in wheat roots under drought stress; for example, *Trichoderma longibrachiatum* and *T. velutinum* are only identified under drought stress, whereas *Zopfiella* sp., *M. hedericola*, *A. verrucaria*, *G. radicola*, and *A. salicis* are observed specifically in irrigated plant groups (Salamon et al., 2020). Whereas, a relatively more abundance of phytopathogenic fungi such as *Fusarium*, *Thielavia* and *Curvularia* was reported in number in tropical grassland soil under drought conditions (Oliveira et al., 2020). The meta-analysis studies demonstrated that bacterial communities are more vulnerable to drought stress compared to fungal communities (Fry et al., 2016). Significant enrichment in arbuscular mycorrhizal fungus (AMF) *Funneliformis* was also identified within the roots during drought, which is predominantly attributed to decreased P availability in drought soil (Augé, 2001; Carbone et al., 2021).

Bazany et al. (2022) observed that water deficit stress differentially shape bacterial, fungal, and protistan microbiome composition and influenced interkingdom microbial interactions in the rhizospheres of corn and sugar beet grown under irrigated and water deficit conditions. The water deficit treatment had a stronger influence than host species on bacterial composition, whereas the opposite was true for protists. Nishu et al. (2022) isolated *Pseudomonas fluorescens* DR397 from the drought-prone rhizospheric soil of soybean, which showed high metabolic activity at 21.25 Mpa. Transcriptomic analysis revealed that genome of DR397 possesses several genes related to the synthesis of

compatible solutes (choline and glycine-betaine), exopolysaccharides (alginate and cellulose), and secretion systems (type II, III, IV, and VI), as well as genes related to plant growth promotion (indole acetic acid, transketolase, and thiamine phosphate synthesis). The expression of these genes was significantly upregulated (8- to 263-fold change) only under drought conditions with plant root exudate treatment. Several other studies have shown a considerable effect on extracellular soil enzymes due to drought stress (Yan et al., 2020; Deng et al., 2021). Onset of drought or reduced precipitation suppressed the soil enzymes for instance, urease (-30.6 %), acid phosphatase (-5.1 %), phenol oxidase (-47.2 %) and β -1,4-glucosidase (-4.6 %). Moreover, nutrient acquisition i.e., C (-4.6), N (-17.6 %) and P (-5.1 %), respectively, was significantly affected (Steinweg et al., 2013).

The above examples indicate that drought legacies impact the selection of adapted microbial communities harboring beneficial functions after recurrent stress events to better tolerate subsequent drought (Canarini et al., 2021; Müller and Bahn, 2022). It is also observed that root exudates and soil organic amendments increase the diversity and/or activity of root microbiota, which may modulate drought tolerance (Preece and Peñuelas, 2016; Prescott et al., 2020; Mueller et al., 2024). Thus, plant-soil feedback and long-term adaptation to drought can determine the performance of plants as well as plant-associated communities under drought (Azarbad et al., 2020; Carter et al., 2023). In addition, soil amendment practices and the transition to new cropping systems can be considered for harnessing soil microbiome under water scarcity (Nawaz et al., 2023). However, the persistence of microbial communities under biotic and abiotic drivers needs to be considered for predictions of agricultural system responses (Bittencourt et al., 2023).

4. Role of microbial metabolites and associated genes in mitigation of drought stress

Recently, use of plant-associated beneficial microbes has emerged as a low cost, sustainable and environment friendly approach for increasing plant tolerance against abiotic stresses and for improving plant growth (Naylor and Coleman-Derr, 2018; Caddell et al., 2019; Liu et al., 2020; Gamalero and Glick, 2022; Islam et al., 2023). In addition,

plant microbiome offers high metabolic flexibility, fast growth, large population size, high physiological tolerance, great diversity and abundance in nature (Berg et al., 2016; Jiao et al., 2019). Beneficial microbes have been isolated from soil, phyllosphere and rhizosphere or as endophytes, which help plants for their survival under drought and other abiotic stresses (Ullah et al., 2019; de Vries et al., 2020; Poudel et al., 2021; Vocciante et al., 2022; Islam et al., 2023; Kumar et al., 2024). These beneficial microbes produced/secreted various phytohormones, growth regulators, volatile organic compounds (VOCs), organic acids, and enzymes like ACC deaminase and also enhanced availability of fixed nitrogen (N) and nutrient solubilization (Fig. 3) (Ahkami et al., 2017; Ahmad et al., 2021; Sindhu et al., 2022; Kumar et al., 2023; Gu et al., 2024). Recently, Gu et al. (2024) discussed the morpho-physiological, biochemical, and molecular mechanisms underlying the mitigation effect of microbes on crop drought stress. The complex interactions between crops and microbes were reviewed for improving drought resistance through the application of beneficial drought adaptive microbes. Thus, application of plant growth promoting rhizobacteria (PGPR) and mycorrhizal fungi as bioinoculants in plants results in better plant growth due to their growth promoting functions and increased drought tolerance (AlKahtani et al., 2020; Goswami and Deka, 2020; Kumar et al., 2022b) (Table 1).

Arbuscular mycorrhizal fungi (AMF) colonize upto 80 % of terrestrial plant roots including most crops and are most popularly applied as bioinoculants in agriculture (Brundrett and Tedersoo, 2018; Chen et al., 2018; Martín-Robles et al., 2018). Mycorrhizal fungi function efficiently in nutrient solubilization and nutrient uptake by plants due to enlarged surface area of roots and also enhance plant resistance to different stresses (Strullu-Derrien et al., 2018; Kumar et al., 2022a; Phour and Sindhu, 2024). AMF significantly regulate plant water relationships, which in return affect plant productivity (Rapparini and Peñuelas, 2014). Apart from mycorrhiza, certain plants may exist in mutualistic relationship with endophytic fungal strain, for instance; *Trichoderma*, which is easy to culture and could be easily applied and colonize within plant roots (Harman and Uphoff, 2019; Field et al., 2021; Khan et al., 2021). *Trichoderma* could effectively alter gene expression in plants and induce certain metabolic pathways, which could aid in mitigation of drought stress (Shoresh et al., 2010).

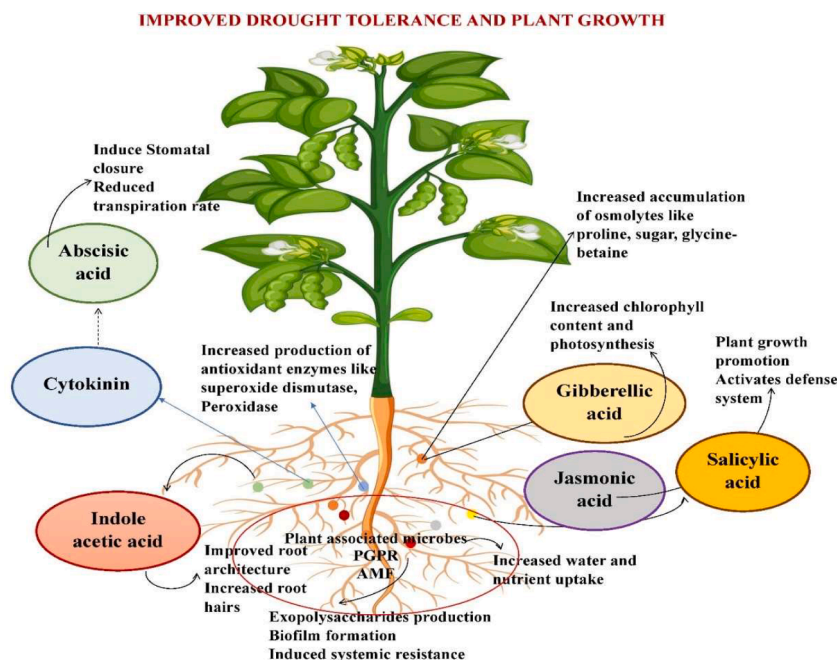


Fig. 3. Production of phytohormones, exopolysaccharides, antioxidant enzymes and osmolytes by beneficial microbes to activate plant defense system under drought stress.

Table 1

Amelioration of drought stress through the application of microbial strains and possible mechanisms.

Mechanism of action	Drought tolerant microbial strains	Host plant	Beneficial features related to drought mitigation	References
Phytohormonal activity	<i>Bacillus cereus</i> TCR17, <i>Myroides odoratimimus</i> TCR22 and <i>Providencia rettgeri</i> TCR21	Sorghum	Plant growth promotion, IAA production, confers drought tolerance	Bruno et al., 2020
	<i>Herbaspirillum seropedicae</i> Z-152 and <i>Azospirillum brasilense</i> SP-7	Maize	Increases plant biomass, osmoregulation, reduces ethylene and ABA production, and confers drought tolerance	Curá et al., 2017
	<i>Bacillus subtilis</i>	Chickpea	Increases metabolites production and influence phytohormone production	Khan et al., 2019b
	<i>Bacillus amyloliquefaciens</i> S-134	Wheat	Plant growth promotion, increases the production of IAA, ICA and ILA and enhances drought resistance	Raheem et al., 2018
	<i>Azospirillum brasilense</i>	Pennyroyal mint	Regulate auxin transport in root tip, root hair elongation, and increased ABA accumulation and improved drought tolerance	Asghari et al., 2020
ACC deaminase	<i>Bacillus</i> sp.	Potato	Increases the photosynthetic potential and upregulates genes related to ROS scavenging or antioxidant system	Gururani et al., 2013
	<i>Paenibacillus polymyxa</i> B and <i>Bacillus thuringiensis</i> AZP2	Wheat	Plant growth promotion, increases plant biomass and drought tolerance	Timmusk et al., 2014
	<i>Bacillus subtilis</i> TV12H and <i>B. megaterium</i> TV6D	Lettuce	Increases nutrient availability, stomatal conductance, and relative water content in leaves, and improves plant growth and crop yield	Maxton et al., 2018
	<i>Enterobacter cloacae</i> and <i>Achromobacter xylosoxidans</i>	Maize	Increases transpiration rate, chlorophyll content, photosynthesis, and stomatal conductance. Improves plant growth and crop yield	Danish et al., 2020
	<i>Bacillus cereus</i> AKAD A1-1, <i>P. otitidis</i> AKAD A1-2 and <i>Pseudomonas</i> sp. AKAD A1-3	Soybean	Increases relative water content, osmolytes concentration, maintains membrane integrity and confers drought tolerance and promotes plant growth	Dubey et al., 2021
Osmotic adjustment	<i>Pseudomonas fluorescens</i> YX2, <i>Klebsiella variicola</i> F2 and <i>Raoutella planticola</i> YL2	Maize	Increases relative water content, dry matter weight and accumulation of choline and glycine betaine	Gou et al., 2015
	<i>Bacillus polymyxa</i>	Tomato	Accumulation of proline, improvement in biochemical and physiological characters of plant	Shintu and Jayaram, 2015
	<i>Acinetobacter calcoaceticus</i> EU-FTF-6 and EU-LRNA-72	Foxtail millet	Significant increase in glycine betaine, proline, sugars, chlorophyll content and decreased LPO	Kour et al., 2020
	<i>Bacillus subtilis</i>	Chickpea	Increase proline, aids lipid peroxidation, enhanced antioxidant enzymes activities such as catalase, SOD, POD and APX	Khan et al., 2019
	<i>Glomus intraradices</i> , <i>Bacillus amyloliquefaciens</i> and AM fungi	Fennel Soybean	Improves leaf nutrients and regulates osmotic adjustment Improved osmoprotectant levels, i.e., phenol, flavonoid, glycine betaine contents, and antioxidant activities and glutathione-S-transferase activity	Zardak et al., 2018 Sheteiwiy et al., 2021
Exopolysaccharides	<i>Pseudomonas putida</i> GAP-P45	Sunflower	Increases plant growth, biomass and reduces drought stress	Sandhya et al., 2010
	<i>Rhizobium phaseoli</i> MR-2, <i>Mesorhizobium ciceri</i> CR-30 and <i>Azospirillum brasilense</i> NO-40	Wheat	IAA, EPS and CAT production, improves plant growth and biomass, and increases drought tolerance	Kasim et al., 2013
	<i>Azospirillum brasilense</i> and <i>Bacillus subtilis</i>	Wheat	Increases seed vigor index, germination rate, relative water content, chlorophyll content, concentration of osmolytes, and antioxidant enzymes activities and improves plant biomass	Ilyas et al., 2020
	<i>Bacillus amyloliquefaciens</i> 54	Tomato	Increases root vigor, relative water content, antioxidant enzymes activities, ABA production and decreases MDA content and upregulates <i>nced1</i> gene	Wang et al., 2019
Volatile organic compounds	<i>Bacillus altitudinis</i> FD-48	Rice	Promotes plant growth and drought tolerance	Narayanasamy et al., 2023
	<i>Bacillus subtilis</i> GB03	Arabidopsis	Promotes plant growth and drought tolerance	Tahir et al., 2017
	<i>Pseudomonas pseudoalcaligenes</i> and <i>Proteus vulgaris</i> JBL S2020	Maize Arabidopsis	Promotes plant growth and drought tolerance Increases root and shoot length, number of leaves, leaf area and plant fresh weight	Yasmin et al., 2021 Bhattacharyya et al., 2015
Antioxidant activity	<i>Pseudomonas chlororaphis</i> O6	Arabidopsis	Plant growth promotion and stimulate drought resistance	Cho et al., 2008
	<i>Pseudomonas</i> sp. M30-35 and <i>Bacillus</i> sp. WM13-24	Ryegrass	Increases antioxidant enzymes activities like SOD, CAT, POD, decreases relative membrane permeability, MDA content, hydrogen peroxide production and confers drought tolerance	He et al., 2021
	<i>Pseudomonas fluorescens</i> and <i>P. putida</i>	Common myrtle	Increases chlorophyll and carotenoid contents and employs enzymatic and non-enzymatic defense system, increases plant biomass	Azizi et al., 2021
	<i>Bacillus megaterium</i>	Wheat	Increases antioxidant enzyme activity such as CAT, GR, APX, POD and SOD, reduces oxidative stresses by decreasing MDA content and electrolyte leakage, and increases photosynthesis	Rashid et al., 2022
	<i>Bacillus</i> sp.	Guinea grass	Increases proline accumulation and decreases glutathione reductase activity	Moreno-Galván et al., 2020a
Stress responsive genes	Consortium containing <i>Azospirillum lipoferum</i> YB5, <i>A. nitroguajacolicus</i> YB3, <i>P. jessenii</i> R62 and <i>P. synxantha</i> R81	Rice	Increases enzymatic activity of APX, POD and CAT and decreases MDA content and H ₂ O ₂ production	Gusain et al., 2015
	<i>Pseudomonas putida</i> KT2440 and <i>P. fluorescens</i>	Maize	Down-regulated gene <i>WRKY18</i> , cold-related dehydrin 410 gene, lipoxygenase genes, <i>OPR7</i> gene (encoding 12-oxo-phytyldienoate reductase 7)	Ahmad et al., 2019
	<i>Gluconacetobacter diazotrophicus</i> PAL 5	Sugarcane	Activates ABA-dependent signalling genes	Vargas et al., 2014
	<i>Paenibacillus yonginensis</i> DCY84T	Arabidopsis	Induces the expression of stress responsive genes such as late embryogenesis abundant protein i.e., bab18 and early response to dehydration i.e., erd15	Sukweenadhi et al., 2015

(continued on next page)

Table 1 (continued)

Mechanism of action	Drought tolerant microbial strains	Host plant	Beneficial features related to drought mitigation	References
Nutrient and water uptake	<i>Pseudomonas chlororaphis</i> O6	Arabidopsis	Induces systemic drought tolerance	Cho et al., 2013
	<i>Paenibacillus polymyxa</i> CR1	Arabidopsis and soybean	Confers drought tolerance	Liu et al., 2020
	<i>Bacillus subtilis</i> GOT9	Mustard and Arabidopsis	Induces hyper-expression of stress related genes	Woo et al., 2020
	<i>Rhizophagus irregularis</i> , <i>R. intraradices</i> , <i>Funneliformis mosseae</i> and <i>F. geosporum</i>	Wheat	Improves nutrient allocation and nutrient composition in plant and increases grain number	Cabral et al., 2016
	<i>Rhizophagus irregularis</i>	Barrel clover	Improves hyphal water absorption rate	Püschel et al., 2020
	<i>Bacillus</i> spp strains KB122, KB129, KB133 and KB14	Sorghum	Improves plant growth and biomass, provides dark green colour to leaves, increases chlorophyll content, relative water content, soil moisture content	Grover et al., 2014
	<i>Enterobacter</i> sp. EB-14, <i>Ochrobactrum</i> sp. EB-165, <i>Microbacterium</i> sp. EB-65, and <i>E. cloacae</i> EB-48	Sorghum	Induces root development and topology, increases relative water content, proline levels and membrane stability index	Govindasamy et al., 2020
	<i>Bacillus cereus</i> P2 and <i>Planomicrobium chinese</i> P1	Sunflower	Increases root and shoot length, fresh and dry root weight, phenolic content, sugar and proline levels, chlorophyll and carotenoid content in leaves	Khan et al., 2018

In addition to symbiotic mycorrhizal fungi, phyllosphere inhabiting microorganisms act as a barrier against different biotic and abiotic stresses in plants, and enhance nutrient availability as well as various growth hormones i.e., zeatin, gibberellic acid, IAA and cytokinins for improving plant growth (Abadi et al., 2020; Khan et al., 2020; Wang et al., 2022; Kumar et al., 2023). Phyllosphere microbes of humid tropical ecosystems harbors nitrogenase enzyme that convert atmospheric nitrogen into ammonia, which could be utilized by plants (Abril et al., 2005). In addition, phyllosphere microbes also produce secondary metabolites including siderophores, antibiotics, hydrolytic enzymes, HCN, which prevent the growth of plant pathogens and suppress various plant diseases (Wu et al., 2009; Sahu and Sindhu, 2011; Sehrawat and Sindhu, 2019; Sehrawat et al., 2022). Production of other secondary metabolites by different phyllospheric microbes such as alkenyl glucosinolates, 2-phenyl, 4 penentyl, 3-butenyl and aromatic glucosinolates-2-phenylethyl, also acts as defense mechanism against plant pathogens and induces systemic resistances in plants (Vorholt, 2012; Wagi and Ahmad, 2017; Chaudhary et al., 2021).

Thus, plants treatment with beneficial microbes termed as microbial priming, is a fascinating approach for better crop performance under stress conditions. Due to the microbial priming effect, plants' response to a subsequent drought or stress conditions is quite prompt. For instance, priming with *Bacillus* in maize produced several metabolites that provided resistance against drought (Alamgir et al., 2018). Similarly, inoculation of rice with phyllospheric bacteria increased plant resistance against different biotic as well as abiotic stresses (Arun et al., 2020). In another study, drought tolerance, plant growth and biomass were improved with the application of *Mesorhizobium ciceri*, *Bacillus amyloliquefaciens*, *Rhizobium leguminosarum* and *Azospirillum brasilense* (Kumar et al., 2020). Similarly, drought tolerance in okra was enhanced with the inoculation of phosphobacterium (Pravivisa et al., 2019). Treatment of crop plants with fungi, termed as mycorrhization, also has been demonstrated to mitigate drought stress. For instance, mycorrhization with *Trichoderma harzianum* significantly alleviated the drought tolerance in rice (Khadka and Uphoff, 2019; Hewedy et al., 2020). Islam et al. (2023) discussed role of some key genes, such as ABA-responsive genes, transcription factor genes, aquaporin genes, and ROS-related genes in drought tolerance in tomato plants. Microbial interactions, notably with PGPR, mycorrhizal fungi, *Pseudomonas* and *Bacillus subtilis*, improved water and nutrient availability. These microorganisms produced antioxidants such as CAT and SOD to scavenge ROS, protected plant cells, and enhanced resistance to oxidative damage during drought.

During drought conditions, some microbial genes are differentially expressed for mitigating drought stress. For instance, enhanced expression of phenylpropanoid (PAL) gene and enzymatic activity was observed after microbial inoculation, which stimulated the accumulation of polyphenolics within plant cells (Singh et al., 2020). Such plants

depicted increased levels of ABTS, DPPH, Fe reducing power and chelation activity suggesting the role of polyphenolics as free radical scavengers. In addition, inoculation with microbes also increased enzyme activities of GR, POD, APX, and glutathione peroxidase. Similarly, soybean inoculation with *Pseudomonas simiae* strain AU protected plants from drought stress by altering the gene expression and phytohormones production pathway (Vaishnav and Choudhary, 2019). The drought tolerance was mediated with the overexpression of osmoprotectants (P5CS, GOLS), transcription factors (DREB/EREBB), and water transporters i.e., TIP and PIP. Such plants also caused the increased production of SA, ABA, proline and total soluble sugar in addition to reduced ET production, which strengthened the plant's drought tolerance. In another study, Sarkee et al. (2017) treated rice plants with *Pseudomonas fluorescens* strain Pf1 and elucidated the gene expression at reproductive stage of plants exposed to drought stress using differential display technique. From differentially expressed cDNAs, various genes including Hsp20, PKDP, aP2-EREBP, COX1, COC1 and bZIP1 were successfully identified, cloned and sequenced. These genes were upregulated with treatment of *P. fluorescens* Pf1 strain. Hence, effective colonization of Pf1 strain induced drought tolerance in the rice plants at reproductive stage. Omar et al. (2021) revealed the effect of drought tolerant strains i.e., *Rhizobium* sp. (4E11), *Bacillus megaterium* (4E3) and *Pseudomonas azotoformans* (3E9) on drought sensitive rice genotype Giza177 under drought conditions. Inoculating bacterial strains caused a hike in the activities of several enzymes, for instance; urease, dehydrogenase, alkaline phosphatase and nitrogenase in the tolerant genotype of rhizosphere. Moreover, inoculated plants showed enhanced expression of stress related genes including GST, GRAM, COX1, EREBP, DHN, NRAMP6, AP-2 and three different gene of expansin i.e., EXP3, EXP2 and EXP1 during drought stress. Moreover, enhanced tolerance in plants inoculated with 4E11 strain also depicted better plant growth under drought stress.

Kalleku et al. (2024) observed the effect of *Pseudomonas koreensis* strain S4T10 on plant physiology of wild type *Arabidopsis thaliana* Col-0 and atnced3 mutant plants under drought and salt stress. The strain induced the activity of SOD, polyphenol oxidase (PPO), POD and GSH for ROS scavenging. The gene expression of related antioxidant system including AtSOD, AtCAT1 and AtCAT3 was upregulated by treatment with *P. koreensis*. Whole-transcriptome sequencing of *Burkholderia phytofirmans* PsJN colonizing potato (*Solanum tuberosum* L.) plants was used to analyse *in planta* gene activity under plant stress. Inoculation of *B. phytofirmans* PsJN in potato plants upregulated the transcripts involved in cellular homeostasis and detoxification of ROS under *in vitro* conditions (Sheibani-Tezerji et al., 2015). Gene depicted the modulation of extracytoplasmatic function (ECF) group IV sigma factors, which are involved in cell surface signaling and allows bacteria to adjust their metabolism according to environmental changes. Around six ECF sigma

factor genes were differently expressed in potato plants inoculated with *B. phytofirmans* PsJN strain. Youssfi et al. (2024) reviewed the role of *Bacillus* species in enhancing plants' ability to alleviate drought stress mainly by producing water absorbing substances and enhancing the uptake of water and nutrient. Some *Bacillus* species also possess the ability to resist plant pathogens through several mechanisms, including antibiosis, competition, induced systemic resistance (ISR), and enriching the microbiome of the soil with important biological agents for management of plant diseases. Different fundamental mechanisms governing drought stress tolerance in plants involving expression of various metabolites and associated genes in microbes are discussed in this section.

4.1. Modulation of phytohormones produced by PGPMs in drought stress mitigation

Plant growth promoting microbes produce different phytohormones including auxins, CKs, GA, ET, ABA and JA, which contributes towards mitigation of biotic and abiotic stresses, and increases root or shoot length and plant growth (Cassán et al., 2014; Vurukonda et al., 2016; Orozco-Mosqueda et al., 2023). Phytohormones also control the processes of abscission, dormancy, and senescence (Ahmed and Hasnain, 2014). For instance, PGPR regulate the concentration of phytohormones such as ABA, indole acetic acid (IAA) and CKs (Egamberdieva et al., 2017; Namwongsa et al., 2019), and lowers ET levels (Belimov et al., 2015). Various strains of soil microbiota produce IAA, which are involved in plant-microbes interactions, mitigation of biotic stress and in regulation of plant growth (Jangu and Sindhu, 2011; Spaepen and Vanderleyden, 2011; Orozco-Mosqueda et al., 2023). Moreover, auxins suppress abiotic stress condition by strengthening the root structure, promoting root growth, or enhancing the number of root hairs; thus, increasing water and mineral uptake (Cassán et al., 2014; Egamberdieva et al., 2017).

Indole acetic acid has been demonstrated to induce drought signaling pathways under drought stress conditions. For instance, inoculation with three IAA producing thermotolerant PGPR strains including *Bacillus cereus* TCR17, *Providencia rettgeri* TCR21, and *Myroides odoratimimus* TCR22 in *Sorghum bicolor* increased plant growth under water stress conditions (Bruno et al., 2020). However, IAA at higher concentrations promotes lateral root formation and increases the number of root hairs, but reduces the length of primary roots (Vacheron et al., 2013). Moreover, higher IAA concentrations activate transcription of ACC synthase, which enhances the ET level. For example, *Ochrobactrum pseudogrigoenense* RJ12 produced 85 $\mu\text{g mL}^{-1}$ of IAA while *Bacillus subtilis* RJ46 and *Pseudomonas* sp. produced 72 and 68 $\mu\text{g mL}^{-1}$ of IAA. These three strains when applied in garden pea and black gram, suffering from osmotic stress of -0.73 MPa, increased the root length up to 10.2 and 12.1 cm, respectively (Saikia et al., 2018). Thus, IAA producing microbes may mitigate drought stress by promoting increased water uptake, permeability of water, upregulation of stress resistant genes and scavenging of reactive oxygen species (Etesami and Maheshwari, 2018; Ha-tran et al., 2021). Drought tolerance and root growth in wheat was enhanced by bacterization with *Bacillus amyloliquefaciens* S-134, which produced three different auxins i.e., IAA, indole-3-lactic acid (ILA) and indole-3-carboxylic acid (ICA) (Raheem et al., 2018).

Another hormone ABA modulated the root structure and increased the nutrient and water uptake in plants (Sah et al., 2016; Egamberdieva et al., 2017). Also, ABA increases antioxidant activity and enhances the accumulation of osmolytes to sustain plant growth under drought stress. Abscisic acid is involved in stomatal opening and closing, and its concentration is directly related to water availability to plants under drought conditions. It also regulates the transcription of certain genes, which are required under stress condition (Eldakak et al., 2013). Inoculation of *Arabidopsis* plant with *Phyllobacterium brassicacearum* STM196 (isolated from *Brassica napus* rhizosphere) elevated plants' tolerance to

drought (Bresson et al., 2013). The enhanced drought tolerance could be due to preventive action of ABA on oxidative stress induced damage (Guajardo et al., 2016). In addition, enhanced ABA levels also reduced the transpiration rate so to avoid water loss. Other phytohormones such as auxins, GA, JA, CKs, SA and brassinosteroids were increased in sorghum with the inoculation of rhizobacteria under drought conditions (Carlson et al., 2020). *Pseudomonas putida* H-2-3 produced GA, which suppressed the effect of drought on soybean (Kang et al., 2014). Taken together, the above examples illustrate that the phytohormone-producing microbiota can affect regulation of root development and benefit the host plant in drought stress mitigation.

4.2. Role of ACC deaminase in mitigation of drought stress

Ethylene production in plant is regulated by several factors such as light, plant hormones, temperature, nutrition and other biotic as well as abiotic stresses (Gamalero and Glick, 2015; Olanrewaju et al., 2017). ET in plants controls the physiological responses like senescence, aging, fruit ripening, nodule formation in roots, root formation, inhibition of formation of storage organs and flowering (Gururani et al., 2013; Chaudhary and Sindhu, 2015). Synthesis of ET, from ACC by ACC oxidase activity in plants, is increased during stress like drought, salinity, water logging, heavy metal, and disease development (Gamalero and Glick, 2015). Many microbial strains possess the ability for production of ACC deaminase enzyme, which degrades ACC molecule into α -ketobutyrate and ammonia; thus, prevent the formation of ET in plants (Zafar-ul-Hye et al., 2019; Danish et al., 2020; Thomas-Barry et al., 2024), and support the plant growth (Khandelwal and Sindhu, 2012; Chandra et al., 2019).

Moreover, ACC deaminase producing microbes also decreases the formation of ROS, thus reducing the impact of drought on plants. For instance, inoculation of ACC deaminase producing *Enterobacter* sp. and *Bacillus* sp. resulted in enhanced drought tolerance in *Mucuna pruriens* (Saleem et al., 2018). Likewise, Niu et al. (2018) described reduced effects of drought stress in *Setaria italica* upon inoculation with exopolysaccharides (EPSs) and ACC deaminase producing bacteria. *Enterobacter cloacae* in combination with biochar produced higher concentration of ACC deaminase and increased the crop yield by increasing nutrient availability and IAA content in maize (Danish et al., 2020). In similar studies, yield and productivity of wheat was increased in wheat under drought stress after inoculation with ACC deaminase producing strains of *Agrobacterium fabrum* and *Bacillus amyloliquefaciens* either individually or in combination (Zafar-ul-Hye et al., 2019). Chandra et al. (2019) also reported the role of ACC deaminase in amelioration of drought stress and plant growth improvement in wheat with individual application of *Variovorax paradoxus* RAA3 or combined application of *Pseudomonas* sp. DPB13, DPB15 and DPB16, and *Ochrobactrum anthropic* DPC9. PGPR inoculation improved the growth, nutrient concentration in leaves and regulated antioxidant activity of plants under drought stress. Due to these effects on the host plant, ACC deaminase-producing microbes support growth of crop plants under drought and reduced the deleterious effects of ET in plants under stress conditions (Khandelwal and Sindhu, 2013; Umaphathi et al., 2022; Ojuederie and Babalola, 2023). Thomas-Barry et al. (2024) obtained 15 rhizobacteria from dominant plant species grown in the hyperseasonal Aripo Savannas, which possessed ACC deaminase (ACCD) activities along with production of IAA and biofilm under stress induced conditions. The best performing co-culture, *Burkholderia* sp. UWIGT-83 and UWIGT-120 showed enhanced growth in germination assays and in greenhouse trials with *Capsicum chinense* (Moruga red hot peppers) under drought stress in comparison to uninoculated treatments.

4.3. Mitigation of drought stress in plants by osmoprotectants

Under drought stress, plants accumulate certain osmoprotectants including trehalose, proline, mannitol or glycine betaine and other

organic and inorganic ions like calcium, potassium, chloride ions or organic acid, which confers osmotic adjustments, reduces oxidative stress due to ROS, and stabilizes the subcellular plant structures (Huang et al., 2014). Moreover, AMF colonization in plants maintains the osmotic balance and increases the concentration of inorganic ions i.e., Ca^{2+} , Mg^{2+} and K^+ (Ruiz-Lozano, 2003), in addition to increased osmolytes concentration like polyamines, proline, and sugar (Rapparini and Peñuelas, 2014; Zhang et al., 2020). Proline is the most crucial osmolyte, which regulates the gene expression of stress-responsive genes and maintains the structural integrity of lipid bilayer and nucleic acid (Talaat and Shawky, 2015; Zhang et al., 2020), and conducts osmotic adjustment, inhibits free radical formation, and maintains the structural integrity of subcellular structure of plant cells (Ngumbi and Kloepper, 2016). PGPR strains retrieved from *Megathyrus maximus* produced proline and reduced the MDA levels and GR activity to overcome the deleterious effects of drought stress (Moreno-Galván et al., 2020a). Similarly, *Pseudomonas putida* inoculation in *Arabidopsis thaliana* increased the proline content followed by enhanced water uptake and induced biomass accumulation and chlorophyll concentration in plants (Ghosh et al., 2017). In addition to PGPR, AMF inoculation also induced proline accumulation in several plant species; for example, *Poncirus trifoliata* (Wu et al., 2017), *Cupressus arizonica* (Aalipour et al., 2020), *Olea europaea* (Ouledali et al., 2018) and *Juglans regia* (Behrooz et al., 2019).

The reduction in sugar levels due to environmental stress conditions degrades the cell membrane and cellular components of plant. Combined application of PGPR and plant growth regulators induced accumulation of soluble sugar and imparted tolerance to drought stress in chickpea along with improvement in photosynthetic efficiency (Khan et al., 2019b). Moreover, increased sugar level in plants contributes to the gene expression related to photosynthesis, and signalling of activation of various processes to cope up with water stress. Some bacteria produce trehalose under dry conditions where it functions as osmoprotectant and maintains membrane integrity, and protects dehydrated enzymes (Yang et al., 2009). Trehalose also acts as a signalling molecule for transcription of trehalose-6-phosphate synthase gene responsible for maintaining membrane structure (Vílchez et al., 2016).

Treatment of certain crop plants with bacteria, also termed as bacterization, accumulated several osmoprotectants and contributed in drought tolerance. For instance, bacterization with PGPR strains including *Pseudomonas fluorescens* YX2, *Klebsiella variicola* F2, and *Rouletella planticola* YL2 elevated the concentration of betaine, glycine and choline, and promoted plant growth in maize (Gou et al., 2015). Similarly, Govindasamy et al. (2020) reported increases in plant growth and osmotic adjustment in sorghum after the application of endophytes i.e., *Ochrobactrum* sp., *Enterobacter* sp. and *Microbacterium* sp. under drought stress. In another study, mycorrhization with AMF produced carbohydrates such as sucrose, fructose, or glucose as osmoprotectants and also promoted photosynthesis under drought conditions in crops like lettuce (Baslam and Goicoechea, 2012), maize (Hu et al., 2020b), and macadamia nut (Yooyongwech et al., 2013). The differential regulation of carbohydrates and proline occurs under drought stress, and the concentration of carbohydrates like sucrose, glucose and fructose were found higher in trifoliolate orange, while proline concentration was low in leaf exposed to drought stress (Wu et al., 2017).

4.4. Mitigation of drought stress by production of exopolysaccharides by PGPMs

Exopolysaccharides form an outer surface layer of microbial cell and stabilizes membrane under adverse environmental conditions (Mishra and Jha, 2013; Naseem et al., 2018). EPSs are secreted by plant associated microbes for strong adhesion to plant roots and supports plant survival against a range of abiotic stresses and under drought conditions as EPSs has high water retention competency (Sindhu and Dadarwal, 1994; Bhagat et al., 2021; Morcillo and Manzanera, 2021; Chauhan and

Upadhyay, 2023). The components of EPSs include macromolecules or polysaccharides, proteins, and uronic acid comprising 40 to 95 % of bacterial weight (Ojuederie et al., 2017). EPSs layer could be slime or capsular exopolysaccharides (Sindhu et al., 1999; Fukami et al., 2018), and prevent desiccation by retaining water and regulation of carbon diffusion under drought stress. The water retention capacity of EPSs could be as high as 70 g water per gram of polysaccharides (Flemming and Wingender, 2010; Chandra et al., 2021).

The production rate of EPS is highly dependent on environmental factors such as temperature, drought, pH, salinity, and nutrient availability. Various EPS-secreting bacteria including species of *Acinetobacter*, *Bacillus*, *Pseudomonas* and *Rhizobium* were demonstrated to promote plant growth under drought conditions (Naseem et al., 2024). These bacterial species form biofilm and increased drought tolerance of plants (Putrie et al., 2013; Ajjah et al., 2023). The biofilm formed by PGPR forms a covering over plant roots that retain water and protect them from desiccation (Rolli et al., 2015). The seed treatment with biofilm forming *Bacillus amyloliquefaciens* ALB629 produced five times more EPSs compared to its absence in common bean seedlings during drought stress conditions (Martins et al., 2018a). EPSs also promote microbial colonization and promote carbon diffusion under water deficit conditions (Ali et al., 2014). Silica induces more EPS production causing a hike in water retention of biofilm in addition to osmotic pressure and allows more plant-microbes interactions, thus producing healthy plants under drought stress conditions (Fetsiukh et al., 2021). Similarly, soil aggregation was increased during drought stress due to the application of EPSs producing *Bacillus* sp. strains HYTABP18, HYD-B17 and RMPB44 (Vardharajula, 2021).

Naseem et al. (2024) characterized EPS-producing bacteria (EPB) as *Pseudomonas aeruginosa* EPB9 and *Bacillus cereus* EPB17 from soil samples drawn from diverse ecologies (sub-humid and arid). Inoculation of both EPB strains significantly enhanced maize growth and soil-water retained until harvesting stage in drought-stressed soils. Higher water contents in soil and plant leaves, as well as fresh shoot and root weight were obtained with EPB9 (10d growth) treatment and plant leaf area and shoot length were greater with EPB17 (10d growth) inoculation. Bacterial EPS also caused higher protein and sugar, and lower proline contents in plants. Antioxidant enzymes (SOD, POD and CAT) remained lower with both EPB treatments due to reduced drought stress than in control.

4.5. Mitigation of drought stress by secretion of volatile organic compounds by PGPMs

Production of organic molecules in gaseous form by several PGPMs is known as volatile organic compounds, which are involved in improving plant growth during drought stress (Sharifi and Ryu, 2018). These VOCs are low-molecular-weight compounds (less than 300 Da) that can evaporate at room temperature and pressure (Bennett et al., 2012). Such compounds could act as elicitors inducing systemic resistance and strengthens the plant defense system (Timmusk et al., 2014; Panpatte et al., 2017). VOCs are produced by various microbes as extracellular degradation product of complex organic compounds or an end product of anaerobic fermentation (Choudhary et al., 2017). VOCs produced by PGPR significantly improve root branching, photosynthesis, seedling emergence, iron uptake, reduces disease incidence and increase plant growth and yield, and enhance drought tolerance (Terra et al., 2018; Martins et al., 2019).

VOCs produced by various microbes include different chemical compounds, for instance; alcohols, benzenoids, ketones, sulphides, alkenes, pyrazines and terpenes (Kanchiswamy et al., 2015; Lemfack et al., 2018). Apart from this, bacteria also produce certain antifungal compounds including HCN, phenazine-1-carboxylic acid, alcohols, and ammonia (Choudhary et al., 2008; Sehrawat et al., 2022). The role of volatile compound produced *Bacillus subtilis* and *B. amyloliquefaciens* in drought stress was elaborated by Asari et al. (2016) with reference to

Arabidopsis. These strains produced a range of volatiles like acetoin, 3-hydroxy-2-butanone and 2R- or 3R-buanediol, which showed increased plant growth due to upregulation of genes functioning in the maintenance of cell structure and phytohormones signalling like ET, SA and jasmonates. Similarly, Yasmin et al. (2021) reported increases in chlorophyll content, proline levels and antioxidant enzymes along with reduced MDA levels and electrolyte leakage throughout drought stress with the application of VOCs producing *Pseudomonas pseudoalcaligenes* in maize.

VOCs also act as signalling molecules and facilitate intercellular or organismal interaction due to their capacity to diffuse (Effmert et al., 2012; Bitas et al., 2013). The VOCs promoted drought tolerance in plants by increasing the concentration of choline and osmoprotectants such as glycine betaine (Liu and Zhang, 2015). VOCs were later identified as 2, 3 butanediol, which after 10 days of application increased the total leaf area by five times and enhanced plant growth. Other VOCs like indole and dimethylhexadecylamine (DMHDA) produced by different PGPR strains increased root hair density, improved root architecture and increased the root length along with volume and surface area in *Arabidopsis thaliana* (Bailly et al., 2014; Sharifi and Ryu, 2018). Moreover, VOCs regulates the gene expression of FIT1, IRT1 and FRO2 genes, which are responsible for iron uptake.

4.6. Antioxidant enzymes induced drought tolerance in plants by PGPMs

Drought induces ROS production, which damages the cellular structures, DNA, lipids and proteins due to their interference with cellular redox (Wu et al., 2014b), and thus impair normal plant functioning (Laxa et al., 2019). This necessitates an antioxidant system, which could remove ROS. Reactive oxygen species includes single oxygen (1O_2), hydroxyl radicals (OH), hydrogen peroxide (H_2O_2), superoxide anion radicals (O_2^-) and alkoxy radicals. Therefore, plants employ antioxidant system, which could be either enzymatic or non-enzymatic, and inhibit production of ROS; thus, protecting the host from oxidative damage under drought stress (Hasanuzzaman et al., 2020). Plant beneficial microbes alter the antioxidant activity of plant for promoting drought tolerance. Different antioxidant enzymes include GR, SOD, APX, and catalase. Non-enzymatic antioxidant activity is mediated via ascorbic acid, glutathione and cysteine (Kaushal and Wani, 2016; Ma et al., 2020). For instance, PGPR inoculation in Guinea grass reduced the GR activity, which promoted drought tolerance (Moreno-Galván et al., 2020a). Similarly, inoculation of *Bacillus* in maize lead to reduced activity of GR and APX under drought stress condition (Moreno-Galván et al., 2020b). AMF inoculation in plants significantly elevated the activity of enzymes such as SOD, CAT and POD under water deficit conditions (Essahibi et al., 2018; Liu et al., 2020). Paul et al. (2022) showed that inoculation of wheat (*Triticum aestivum*) seeds with biofilm-forming *Bacillus pseudomycooides* promoted antioxidant enzymes CAT, SOD, POD, and APX. Molecular gene expression studies showed that inoculation of *B. pseudomycooides* strongly expressed the *Dreb1* gene by silencing the expression of MYB gene, which synthesizes Myb protein (TaMpc1-D4), through secreted volatile compounds. Out of 45 volatile compounds identified, 2,6-ditert-butylcyclohexa-2,5-diene-1,4-dione and 3, 5-ditert-butylphenol compounds suppressed Myb protein's expression in response to drought.

4.7. Mitigation of drought stress through induction of stress responsive genes in plants

Drought response of any plant is regulated at genetic level and beneficial microbes trigger the gene expression to stimulate a better defense response under stress conditions. Microbes can also stimulate the expression of stress-resistance genes; for example, antioxidant (Murali et al., 2021), aquaporins (Quiroga et al., 2017; Kapilan et al., 2018; Symanczik et al., 2020), transcription factors (Barnawal et al., 2017; Manjunatha et al., 2022), and proline biosynthesis (Govindasamy

et al., 2020; Li et al., 2020) by modulation of hormonal levels. For instance, *Pseudomonas simiae* AU upregulated the expression of transcription factors i.e., EREB/DREB, water transporters including PIP and TIP, and osmoprotectant synthesis coding genes i.e., GOLS and P5CS upon inoculation of soybean in order to prevent the deleterious effect of drought (Vaishnav and Choudhary, 2019). Similar observation was recorded with the application of *Paenibacillus polymyxa* CR1 in *Arabidopsis*, which resulted in upregulation of dehydration-responsive genes, RD29A and RD29B for coping up with desiccation (Liu et al., 2020). Ghosh et al. (2017) reported upregulation of genes involved in biosynthesis of proline i.e., OAT (ornithine-1-aminotransferase), P5CR (11-pyrroline-5-carboxylate reductase), PDH1 (proline dehydrogenase 1) and P5CDH or 11-pyrroline-5-carboxylate dehydrogenase (P5CDH) with the inoculation of *Pseudomonas putida* GAP-P45 in *Arabidopsis thaliana*. Similarly, *Bacillus licheniformis* K11 inoculation in pepper plants induced the synthesis of vacuolar ATPase, small heat shock proteins, dehydrin like protein (Cadh) and other pathogenesis related protein (CaPR-10) (Lim and Kim, 2013). Moreover, *Bacillus marisflavi* strain CRDT-EB-1 produced ABA or abscisic acid analogs (xanthoxin and xanthoxic acid), which could induce the expression of ABA related genes like ABA2, ABA3 and NCED3 during drought conditions in mustard seedlings (Gowtham et al., 2021).

Upregulation of genes responsible for the phenylpropanoid synthesis and antioxidant enzymes production was observed by treatment of rice with *Trichoderma* and *Pseudomonas*, which enhanced stress tolerance (Singh et al., 2020). Genes like DHN responsible for dehydrin, PIP for plasma membrane intrinsic protein and DREB were also upregulated under drought stress. Improved drought tolerance in *Brassica campestris* was correlated with upregulation of drought tolerant genes such as CSD3, DREB1D, and WRKY7, while in *Arabidopsis thaliana*, it was attributed to the genes like NVED3, RD20, RaB18 and RD29B mediated by *Bacillus subtilis* GOT9 (Woo et al., 2020). Similar mechanism was observed in tomato by Abbasi et al. (2020) indicating the role of plant associated microbes in upregulation of drought tolerant genes ERF1 and WRKY70 and increased production of proline and antioxidant enzymes. Ou et al. (2022) showed that *Bacillus megaterium* HGS7 strain obtained from the rhizosphere soil of mulberry after drought stress, possessed multiple genes that contributed to plant growth promotion, stress tolerance enhancement, and antimicrobial compound production. *B. megaterium* HGS7 consistently exhibited antagonistic activity against phytopathogens and strong tolerance to abiotic stress *in vitro*. Moreover, this strain stimulated mulberry seed germination and seedling growth, and induced production of proline and antioxidant enzymes in mulberry trees.

Gene expression of SbP5CS1 and SbP5CS2 coding for pyrroline-5-carboxylate synthase was increased by endophytic root bacteria i.e., *Ochrobactrum* sp. EB-165, *Microbacterium* sp. EB-65, *Enterobacter* sp. EB-14 and *Enterobacter cloacae* strain EB-48 in sorghum and conferred drought tolerance and plant growth promotion (Govindasamy et al., 2020). *Pseudomonas putida* induced the gene expression of proline related gene P5CS in addition to enhancing phosphate and Zn uptake by rice seedling under drought conditions (Saddique et al., 2018). Mycorrhization of apple plants with AMF caused upregulation of gene expression i.e., MdMAPK20-1, MdMAPK7-1, MdMAPK16-2 and MdMAPK17 to ameliorate drought stress (Huang et al., 2020). MdIAA24 is the most commonly upregulated gene observed in apple due to AMF inoculation, which controls the synthesis of strigolactone, resulting in enhanced osmotic adjustments, relative water content and gas exchange capacity (Huang et al., 2021). Moreover, AMF produces a range of antioxidant enzymes for the amelioration of oxidative stress generated under drought conditions (Zou et al., 2021). Kim et al. (2022) reported that pepper (*Capsicum annuum*) plants inoculated with *Bacillus butanolivorans* KJ40 strain induced drought tolerance by activation of peroxidase and glutathione peroxidase and upregulation of gene expression of *Capsicum annuum* dehydrin (Cadh), small heat shock protein (sHSP), Δ 1-pyrroline-5-carboxylate synthetase (P5CS),

△1-pyrroline-5-carboxylate reductase (P5CR), ABA (bZIP transcription factor 1 and NCED1)-, JA (lipoxygenase 1; LOX1), and coronatine insensitive 1 (COI1)-related genes, as well as changing polyphenol content in KJ40-treated pepper plants under drought stress. Differential accumulation and alteration of polyphenol contents, including flavonoids, were observed in fruits of KJ40-treated plants, and capsaicin, dihydrocapsaicin, and naringenin were decreased. However, luteolin and catechin were increased compared to those of control plants.

Endophytic *Bacillus altitudinis* HNH7 and *B. velezensis* HNH9 strains possessed various PGP traits including proteolytic, amylolytic, lipolytic and cellulolytic activities, and solubilized iron by producing siderophores (Hasan et al., 2022). Inoculation of HNH7 and HNH9 strains promoted the growth of upland cotton plants by upregulating the expression of growth-linked genes, *EXP6*, *ARF1*, *ARF18*, *IAA9*, *CKX6* and *GID1b*. However, the expression of *ERF* and *ERF17* genes involved in ethylene biosynthesis was downregulated after treating the plants with HNH7 and HNH9 compared to the control. Furthermore, cotton plants treated with HNH7 and HNH9 strains exhibited a significantly higher rate of photosynthesis and stomatal conductance. Wu et al. (2024) performed proteome analysis of *Pinus taeda* seedlings treated with endophytic fungus *Serendipita indica* and revealed that two proteins, i.e., H9 × 056 and H9VDW5, only appeared in the needles of inoculated seedlings, and protein H9VNE7 was upregulated more than 11.0 times as that of uninoculated seedlings under drought stress. In addition, *S. indica* inoculation increased enrichment of water deficient-inducible proteins (such as LP3-1, LP3-2, LP3-3, and dehydrins) and those involved in ribosomal structures (such as A0A385JF23). *S. indica* inoculation also caused great changes in phenylpropanoid biosynthesis, cutin, suberine and wax biosynthesis, and 2-oxocarboxylic acid metabolism under drought stress. Hence, antioxidant system of AMF acts as active scavengers of ROS with amelioration of drought stress in crop plants.

4.8. Improvement in nutrient and water uptake under drought stress by PGPMs

Plants require nutrients for their optimum growth and development, and they are dependent on soil nutrient pool due to their sessile lifestyle. Various microbial strains increase the nutrient availability and their efficient utilization by plants under various stress conditions. Plant requires N, P, and potassium (K) along with trace amounts of iron (Fe) for their growth, but most of the soils are deficient of these nutrients (Khan et al., 2017; Kumar et al., 2022b; Sindhu et al., 2022). Among these nutrients, P exists both in organic as well as inorganic forms. Bista et al. (2018) studied the nutrient uptake potential of different drought tolerant and drought sensitive grasses including barley, bluestem, and corn. Under drought stress, proteins involved in phosphate uptake failed to keep up with normal functioning and thus, leads to reduced uptake of P. Moreover, this was more evident in plants harvested at mid and late drought periods. During drought stress, plant plasma membrane protein PHT-1 homologous to PHO84Pi of yeast aids in plant uptake of P (Nussaume et al., 2011). However, the PHT-1 levels were reduced under drought stress by 40 % in barley and 44 and 59 % in corn and bluestem, respectively. This resulted in reduced P content in corn by 48 %, barley and bluestem by 41 and 39 %, respectively. Thus, abiotic stress decreases the nutrient uptake due to reduced protein levels and impaired the plant growth and development of crops leading to poor crop yield. Therefore, farmers apply excessive amount of chemical fertilizers in order to fulfil plant's nutrient requirements; however, chemicals being toxic in nature affect the soil quality and causes environment pollution leading to public health hazards (Sindhu et al., 2017).

Phosphate solubilizing microorganisms (PSMs) are frequently applied as bioinoculants to mitigate the stress conditions and for plant growth promotion (Zhao et al., 2014; Alori et al., 2017; Bittencourt et al., 2023). Certain PSMs help in abiotic stress mitigation by producing siderophores and phytohormones, lowering ET levels by expression of

ACC deaminase enzyme, and upregulating the expression of antioxidant and dehydration response genes encoding CAT, APX, SOD, POD, and GR (Beneduzi et al., 2008; Ojuederie et al., 2019; Vocciante et al., 2022). For instance, Dubey et al. (2021) reported the improved biomass of soybean crops under drought conditions upon inoculation with three drought-tolerant phosphate solubilizing bacteria (PSB) strains i.e., *Pseudomonas* sp. AKAD A1-16, *P. ottidis* AKAD A-2 and *Bacillus cereus* AKAD A1-1. *Pseudomonas* sp. AKAD A1-16 produced ACC deaminase, which helped in stress mitigation.

Another important component of the soil microbial community is potassium solubilizing microorganisms (KSMs), which play important role in enhancing K availability to plants and strengthened plant defense mechanisms against various environmental stresses (Johnson et al., 2022; Bhattacharjee et al., 2023; Sharma et al., 2024). The release of K, aluminum and silicon by these KSMs through weathering of minerals along with secretion of phytohormones improved plant nutrition as well as plant growth (Höflich et al., 1994; Anwar et al., 2022). Currently, several efficient KSMs are being applied as biofertilizers for improving crop productivity in sustainable agriculture (Singh et al., 2022; Soumare et al., 2022; Sharma et al., 2024). For instance, inoculation of K solubilizing bacterial strains *Paenibacillus sabinae* and *Leptolyngbya* sp. RBD05 to saline-alkali soil alone or in combination, increased wheat growth, N:P ratio, K:Na ratio, proline content and SOD activity (Duan et al., 2023).

Drought stress also impairs the activity of nitrogenase enzyme leading to reduction in symbiotic N₂ fixation in legumes (King and Purcell, 2006; Arrese-Igor et al., 2011). Interestingly, about 60 % of legume production the developing world occurs under drought stressed conditions (Graham and Vance, 2003; Zhang et al., 2007). Majority of the isolates obtained from five cultivated leguminous plants, namely *Cicer arietinum*, *Lens esculentus*, *Phaseolus vulgaris*, *Pisum sativum* and *Vicia faba* grown in arid region of Egypt provided tolerance to various environmental factors including drought (Zahran et al., 1999). In another study, combined inoculation of ACC deaminase-containing *Bacillus subtilis* and *Pseudomonas stutzeri* along with *Mesorhizobium ciceri* significantly reduced ET production and improved chickpea growth under drought conditions (Swarnalakhmi et al., 2016). Similarly, enhanced drought tolerance, pod yield or biomass accumulation was observed in nodulated *Phaseolus vulgaris* and *Pisum sativum* as compared to non-nodulated nitrate-fed plants (Frechilla et al., 2000; Lodeiro et al., 2000).

Apart from N, P and K, Fe micronutrient is also essentially required by plants and Fe is the fourth most abundant mineral in soil (Pedraza, 2015; Dhankhar et al., 2023; Velez-Bermúdez and Schmidt, 2023), and it induces tolerance in plants against abiotic stress. Although Fe is present in abundant amount, yet the plant available ferric iron Fe³⁺ form is in scarce amount in soil. Therefore, deficiency of Fe in plants causes interveinal chlorosis and lowers crop yield (Tripathi et al., 2018). Thus, application of Fe or Zn (zinc) fertilizers in soil could promote plant growth and tolerance to several stress conditions (Rotaru et al., 2011; Pourgholam et al., 2013; Sehwat and Sindhu, 2024). Microbes residing within the plant rhizosphere produces Fe-chelating compounds called siderophores (Pedraza, 2015), which increases Fe availability to plants, and eventually improves plant growth. Some of the bacterial strains that produce carboxylate type siderophore include *Rhizobium meliloti* while hydroxamate and catecholate type of siderophores were produced by fluorescent pseudomonads (Ghavami et al., 2017). AMF strains belonging to the phylum Glomeromycota were also demonstrated to suppress the deleterious effects of drought by increasing nutrient availability (Li et al., 2019; Posta and Duc, 2019). Association of AMF with terrestrial plants helps in increasing nutrient and water uptake, modify root structure, promotes flowering and increases stress tolerance (Pozo et al., 2015; Wu et al., 2017), while AMF receives photosynthates for their growth from host plant (Li et al., 2019; Phour and Sindhu, 2024). Similarly, treatment of barley (*Hordeum vulgare* ssp. Nudum L.) with *Pacispora franciscana*, *Funneliformis mosseae*, *F.*

geosporum, *Rhizophagus irregularis* and *Glomus tenebrosum* increased uptake of N, P, K, Cu and Fe nutrients, improved activity of antioxidant enzymes and alleviated drought stress (Jerbi et al. 2022).

4.9. Increases in plant growth and crop yield using drought-tolerant microbes

Some PGPMs mitigate drought stress and promote root and shoot length, root hairs, biomass accumulation, number of leaves and phenological character like flowering. For instance, the symbiotic association between AMF and diverse plants boost root growth and productivity, plant biomass and leaf area index (Gholamhoseini et al., 2013). Significant improvement in drought and water deficit tolerance was reported in lettuce and tomato, sweet potato and strawberry, when exposed to AMF under immediate drought circumstances (Ruiz-Lozano et al., 2015; Yooyongwech et al., 2016; Moradtalab et al., 2019). In similar studies, bacterization of wheat with auxin-producing mixed culture comprising of *Bacillus simplex* D-1 and D-11 strains, *B. thuringiensis* D-2 and S-26, *B. amyloliquefaciens* S-134, *B. muralis* D-5, *M. pluranimalium* S-29 and *Pseudomonas stutzeri* S-80 increased the number of spikelets and tillers under drought stress (Raheem et al., 2018). Bakr et al. (2018) reported that mycorrhization of *Solanum lycopersicum* with AMF i.e., *Funneliformis mosseae*, *F. geosporum*, *Claroideoglomus etunicatum* and *Glomus microaggregatum* improved water use efficiency, stomatal conductance and water potential of leaves and conferred drought stress. In similar studies, inoculation of *Glomus intraradices* on *Solanum melongena* mitigated the adverse effects of drought stress and enhanced crop growth, dry biomass and yield (Badr et al., 2020). Co-application of TiO₂ nanoparticles and AMF increased water use efficiency and dry matter yield, improved essential oil quantity and quality of sage (*Salvia officinalis* L.) in drought stress conditions (Ostadi et al., 2022). Similarly, combined inoculation of PGPR and AMF consortium in tomato increased mineral accumulation, osmolyte accumulation, POD activity and plant growth, and also alleviated water stress effects (Tahiri et al., 2022).

Ahmad et al. (2019) inoculated *Zea mays* L. (cv. B73) with *Pseudomonas putida* KT2440 and *P. fluorescens* strains under drought stress and non-stress conditions. Both strains demonstrated significant improvement in root length, protein content, chlorophyll content, and root and shoot fresh masses as compared to uninoculated drought stressed plants. In another study, inoculation of sugarcane with *Bacillus megaterium* increased the expression of invertase gene (involved in conversion of sucrose to glucose and fructose), and it caused early growth of settings during drought stress (Chandra et al., 2018). In another study, inoculation of *Acinetobacter* sp. isolated from the cotton phyllosphere on drought susceptible cotton variety ADB-542 increased germination, plant biomass and number of bolls under drought conditions (Sharath et al., 2021). In similar studies, inoculation of rice seedling with phyllosphere bacterial strains enhanced plant growth under drought stress by increasing nutrient availability, EPSs secretion, soluble sugar levels, chlorophyll and protein content, and phytohormones production (Arun et al., 2020). Drought tolerance of *Oryza sativa* was increased with the application of phyllosphere bacteria *Bacillus megaterium* PB50 (Devarajan et al., 2021). Bacterization with P solubilizing *Enterobacter ludwigii* strains AFFR02 and Mj1212 in alfalfa promoted plant growth by secreting phytohormones and increasing nutrient availability leading to increased plant height, and plant weight under drought stress (Kang et al., 2021). PGPR treated alfalfa plants also showed higher levels of flavonoids and ABA.

Nishu et al. (2022) observed that inoculation of *P. fluorescens* DR397 on legume cultivars (*Pisum sativum* and *Phaseolus vulgaris*), increased shoot and root growths by 62.0 % to 149.1 % compared with the control group under drought conditions, whereas growth was hardly affected under well-watered conditions. In similar studies, drought stress tolerance of a susceptible soybean cultivar, MAUS 2 was improved through combined inoculation of selected rhizobia and AM fungus (Ashwin et al.,

2023). Shaffique et al. (2023) reported that treatment of soybean with *Bacillus pumilus* SH-9, possessing the ability to produce EPSs, siderophores, IAA and solubilized phosphate, promoted plant growth under drought stress. Further, the strain SH-9 could efficiently tolerate 30 % concentration of polyethylene glycol (PEG) 6000. Also, plant biomass and growth were increased by 20 % due to decreased levels of ABA and increased expression of different genes related to antioxidant enzymes like POD, GSH, SOD and APX and other transcription factors like GmDREB2, GmbZIP1, and GmNCED3. Subsequently, *Bacillus pumilus* SH-9 was used for inoculation of rice under drought stress (Shaffique et al., 2024). PGPR strain SH-9 significantly increased levels of CAT, APX and SOD, and could withstand 35 % of PEG6000 in rice. The strain positively influenced seeds vigor index, germination percent and germination rate index.

Mahreen et al. (2023) isolated eight different drought-tolerant PGPR strains from the rice rhizosphere that are tolerant to 20 % PEG-8000. All the strains exhibited the production of ACC deaminase, EPSs, IAA (14.3 to 46.2 µg ml⁻¹) and organic acid (72 to 178 µg ml⁻¹), and solubilized 51 to 356 µg ml⁻¹ of phosphate. A consortium consisting of *Bacillus cereus* NM-6, *B. subtilis* NM-2 and *Brucella haematophilum* NM-4 was prepared and its inoculation on rice improved the root length (17 %), increased root surface area (18 %), and seed vigor index i.e., 1009.2 to 1100 as compared to non-inoculated plants causing 630 to 957 seed vigor index. Moreover, consortium induced drought tolerance by production of antioxidant enzymes, increased proline levels by 85.8 to 122 %, membrane stability index and relative water content by 64 % and 51 %, respectively. In similar studies, consortium of PGPR strains including *Azotobacter vinelandii*, *Pseudomonas putida* and *Pseudomonas agglomerans* application was evaluated on *Festuca ovina* and it increased germination percentage, nutrient uptake, root and shoot length, plant dry weight, and plant biomass with their application under 30 % FC condition (Rigi et al., 2023). Therefore, single strain or consortium inoculation in plants could significantly increase plant tolerance to drought.

Wilmowicz et al. (2022) showed that inoculation of maize seeds by *Glomus* sp. and *Bacillus* sp. restored the proper photosynthetic activity of the plant under drought stress and stabilized the osmoprotectant content of the leaf. Mixed inoculation of maize seeds by *Glomus* sp. and *Bacillus* sp. was also related to the stabilization of cell redox status reflected by H₂O₂ content, antioxidant enzymes, and malondialdehyde level in leaves. In addition, drought response in maize was mediated by both microorganism-mediated modifications of cell wall composition and structure of leaves, such as downregulating pectin, affecting their methylation degree, and increasing hemicellulose content. In another study, combined inoculation of maize (*Zea mays* L.) plants with *Acaulospora laevis* (AMF) and *Bacillus subtilis* (PGPR) increased root colonization (104.6–113.2 %) and microbial biomass carbon (36.38–40.23 %), leaf photosynthetic rate (27.3–29.8 %) and grain yield under moderate to severe drought conditions as compared with uninoculated control (Khan et al., 2024). Higher root colonization was strongly linked with elevated ACC production, subsequently enhancing water use efficiency (21.62–12.77 %) and root nutrient uptake under moderate to severe drought conditions. Furthermore, co-inoculation with AMF-PGPR reduced cellular damage by lowering oxidative enzyme levels and increasing anti-oxidative enzyme activities, improving plant performance and grain yield under stressful environments. Mycorrhization of *Pinus massoniana* with ectomycorrhizal fungus *Cenococcum geophilum* showed increased water content, osmotic adjustment, photosynthesis rate, and antioxidant enzymes, which eventually improved drought tolerance (Zhang et al., 2024b). In another study, inoculation of wheat with AMF *Funneliformis mosseae* increased water use efficiency, growth, and yield (Duan et al., 2024), and soil was reported to have higher soil water content, nutrient availability and soil organic carbon to soil nitrogen ratio. Plants treated with AMF produced 28.5 % more grain compared to control under drought stress.

A comparative evaluation of microbial consortia versus single-strain inoculants was conducted in potato by Mamun et al. (2024). The effect

of six fungal and bacterial strains, and ten consortia on growth, nutritional status and drought stress protectants was compared. Presence of AMF *Rhizophagus irregularis* strain MUCL41833 improved the P nutritional status and root growth, while non-inoculated plants suffered with 70 % reduction in water supply and showed reduced shoot growth by 30 % and biomass of tuber by 50 % in addition to phosphate limitation. Consortium constituted of AMF and *Pseudomonas brassicacearum* strain 3Re2-7 and *Bacillus amyloliquefaciens* FZB42 suppressed the leaf damage under drought conditions. Also, NH_4^+ fertilization supplemented with AMF inoculation increased tuber biomass by 951 %, which was only 534 % with NH_4^+ fertilization alone. This was mediated by improved accumulation of osmolytes, increased concentration of hormones like JA, ABA and IAA in shoot and amplified antioxidant enzymes activity and reduced leaf damage under drought conditions. Bacterial inoculants also enhanced ROS detoxification and stimulated biomass allocation towards shoot growth at the expense of tuber development. Zhang et al. (2024a) established AM symbiosis between tomato plants and three AMF species i.e., *Rhizophagus intraradices*, *Funneliformis mosseae*, *R. irregularis*, under well watered or drought stressed conditions in pot experiment. AMF treatment significantly increased plant biomass under drought stress and the growth promoting effect of *R. irregularis* was lower than those of *R. intraradices* and *F. mosseae*, which was associated with higher mycorrhizal colonization and more consumption of lipids. On the other hand, drought tolerance capacity of *R. irregularis* was greater than those of *R. intraradices* and *F. mosseae*. These studies established that microbial consortia provide more tolerance to plants against drought stress.

Despite the growing recognition of the microbiota for increasing nutrient availability, plant growth and fitness in response to drought, harnessing of these interactions for increased drought resilience remains a significant challenge due to complex interactions between the host plant and its surrounding soil, which influence microbial community structure and function (Chen et al., 2019; Dong et al., 2023). In addition, poor colonization and establishment of inoculated microorganisms, and other cultural restrictions restricted the success of microbes in offering desired benefits to plant under field conditions (Goel et al., 1999; Sindhu et al., 2003). Moreover, only a small fraction of microbes is culturable under laboratory conditions, thus hidden potential of most of microbes is still unexplored (Tringe et al., 2005). Recently, use of advanced culture-independent techniques including high throughput DNA sequencing has resulted in finding new and novel unculturable microbial strains with great beneficial properties (Fitzpatrick et al., 2020). Thus, production of specific metabolites, phytohormones and antioxidant enzymes, understanding of interactions between different microbes and intercommunicating signalling mechanisms between plant and microbes is urgently needed to achieve full potential of plant associated microbes under drought stress (de Vries et al., 2018; de Nijs et al., 2019). For this, a better mechanistic understanding of the complex feedback between plants, soils, environment and microbes is needed to develop future strategies for prediction and mitigation of the drought stress impacts on growth of plants and crop yields.

5. Gene modulation during microbe-plant interactions to ameliorate drought stress

Recent rapid and drastic changes in the global climate have exacerbated various environmental (abiotic) and biotic stresses for crops, which significantly threaten the worldwide crop production and food security. Therefore, current research efforts are aimed at improving sustainable and healthy agricultural production through application of microbial communities or improving their traits/characteristics with microbiome-based rhizosphere engineering and synthetic biology approach, by increasing nutrient acquisition, and/or protecting plants from biotic and environmental stresses (Qiu et al., 2019; Ke et al., 2021; Phour and Sindhu, 2022; Neemisha et al., 2022; Gouesbet, 2023). Another novel approach involves the use of consortia of various microbes possessing different plant growth-promoting (PGP) traits as an

effective synthetic community to improve crop production under stressed environments (Lau et al., 2022; Shayanthan et al., 2022; Yin et al., 2022). Recent innovative omics technology including metagenomics, metabolomics, meta proteomics in addition to culture-based strategies may be applied to improve microbial colonization and plant-microbe interactions leading to improved plant growth and development (Jansson and Hofmockel, 2018; Mishra et al., 2022). For instance, culturomics- and metagenomics-based studies were performed recently on microbial community and its functions for assessing their performance in rhizosphere soils of desert farming systems (Lian et al., 2023). In addition, large-scale sequencing may be used to retrieve microbial genomes directly from a specific environment for comprehensive understanding of the diversity and functional potential of microbes. However, these novel genomic methods show species vulnerable to climate change disturbances, which may modify the structure and function of vast microbial communities. Hence, microbes are being engineered to derive desired result for improving soil health and plant growth (Tsolakidou et al. 2019; Ke et al. 2021).

Cosidering the role of different microbe-associated genes in drought tolerance, efforts are being made worldwide to improve drought tolerance in model as well as non-model plants (He et al., 2019; Zhang et al., 2020). It is established that several regulatory mechanisms are employed within the plants for increasing tolerance, averting drought or recovering from drought (Zhang et al., 2022; Kambona et al., 2023). Efforts have also been made to develop plants with increased drought tolerance with the aid of novel advanced techniques in genetic engineering and molecular breeding. However, the plant system is highly complex and thus, success rate is limited.

5.1. Bioengineering of microbes to improve efficacy of drought tolerance

Genetic engineering allows the manipulation of microbial communities for increasing plant tolerance to stress along with improvement in soil fertility and health leading to increases in plant growth and crop yield. In some cases, engineered microbiomes outcompetes the traditional microbial strains in producing more pronounced effects (Alnahhas et al., 2020; Karkaria et al., 2021). Therefore, microbiome engineering has become a popular choice because of associated benefits in comparison to single inoculation-based method. In addition, retrieving microbial community from wild crop plants and understanding their role in drought resistance could pave a way for developing SynComs (Fig. 4). SynComs are the synthetic microbial communities (SMCs), which are developed via microbiome engineering (Quides and Atamian, 2021; Monteoliva et al., 2022). Other microbiome engineering technique is 'host mediated microbiome engineering (HMME)'. A number of studies are based on the application of these HMME or SynComs techniques in various crops (Table 2). Recently, SynComs have been applied to crops like *Canavalia ensiformis* and *Crotalaria juncea* (Hernández-Álvarez et al., 2023), and *Medicago sativa* (Hansen et al., 2020). In most of the cases, efficacy of synthetic microbial communities has been found better than the conventional bioinoculants (Alnahhas et al., 2020; Karkaria et al., 2021), because SMCs allow synergistic action of different microbial strains, which offers multiple beneficial traits to plants. Hence, such SMCs are more robust and stable that work efficiently under different environmental conditions (Karkaria et al., 2021; Orozco-Mosqueda et al., 2021).

The microbial strains used to develop SMCs are indigenously isolated and characterized using culture dependent techniques and subsequently, screened for different desired traits/functions (Lemanceau et al., 2017; Vorholt et al., 2017; Armanhi et al. 2018). Different strains in SMCs employ either common or different mechanisms for mitigation of drought or other environmental stresses (Compant et al., 2019). Community profiling of the host plant is carried out to identify the strains with desired traits like effective colonization and survival under developmental stage (de Souza et al., 2020). Thus, SynComs is an application strategy that could develop inoculants, which are highly

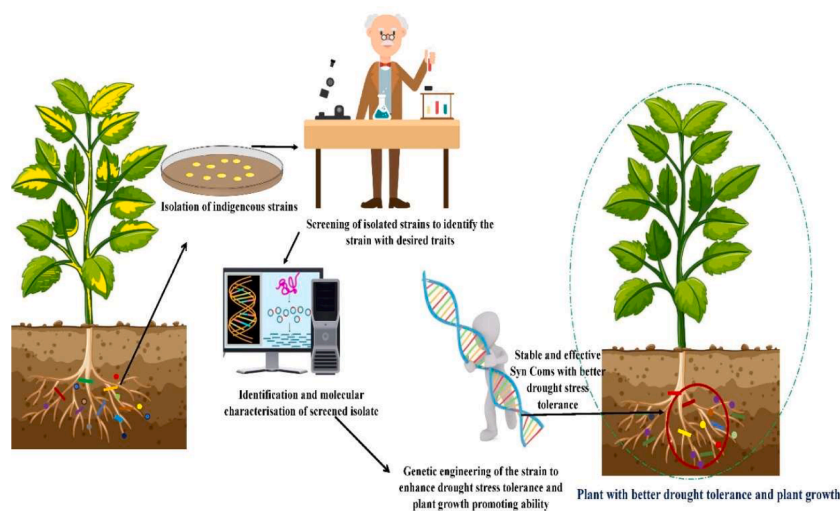


Fig. 4. Retrieving of microbial community from wild crop plants, their genetic engineering and development of SynComs for drought resistance.

efficient, shows increased plant-microbe or microbe-microbes interactions, and are integrated with plant beneficial characteristics (Arif et al., 2020; Petrushin et al., 2023).

Rolli et al. (2015) developed SynComs using strains of *Bacillus*, *Enterobacter*, *Delftia*, *Spingobacterium* and *Acinetobacter*, that increased drought tolerance and plant growth in grapevine. Similarly, plant height and weight were increased in maize with the application of SynComs consisting of strains of *Acinetobacter*, *Sphingomonas*, *Pseudomonas putida* and *Azospirillum brasilense* (Molina-Romero et al., 2017). Thus, SynComs have emerged as a helping tool in producing robust drought tolerant core microbiome, which confers drought resilience and further applied for producing drought resistance smart crops (Ali et al., 2022). With the advent of new technologies like machine learning, artificial intelligence and computational methods, more fine screening of beneficial microbes could be further accomplished (de Souza et al., 2020; Sindhu and Sindhu, 2023). However, plant-microbiome engineering has its own limitation due to complexity of microbial community and variation in function of microbiome during plant ontogeny. Therefore, HMME could be an alternative option by selecting microbiome based on the phenotype of host indirectly via propagation and cyclic differentiation to maintain microbial communities that benefit plants.

Microbial community directly or indirectly interacts with the host plant and could aid in shaping plant response to water stress. The focus of modern research is currently shifting towards the identification of beneficial microbial communities, engineering/manipulation of the rhizosphere microbes and their implications for maintaining long-term soil health and fertility (Hakim et al., 2021). Recent genetic engineering techniques could be applied to manipulate beneficial microbes for improving nutrient uptake, water acquisition and stress hormone regulation, which may enhance drought tolerance leading to plant growth promotion for their subsequent use as biofertilizer in different crop plants. For instance, Lian et al. (2023) applied culturomics- and metagenomics-based studies of microbial community and its functions for assessing their performance in rhizosphere soils of desert farming systems. In addition, use of large-scale sequencing to retrieve microbial genomes directly from a specific environment has given researchers a comprehensive understanding of the diversity and functional potential of microbes (Almeida et al. 2021). However, novel genomic methods show species vulnerable to climate change disturbances, which may modify the structure and function of vast microbial communities. Thus, focus of modern research is currently shifting towards the identification of beneficial microbial communities, engineering/manipulation of the rhizosphere and their implications for maintaining long-term soil health and fertility (Tsolakidou et al., 2019; Hakim et al., 2021).

Use of recent advanced and innovative techniques for identification, cloning and expression patterns of the genes related to drought stress mitigation may subsequently be applied to develop genetically manipulated microbial strains with enhanced PGP activities for their subsequent use as biofertilizer in different crop plants. Involvement of similar mechanisms for solubilization of P, K and Zn through production of acids (organic/inorganic) by various microbial strains (Amy et al., 2022; Sehrawat and Sindhu, 2024; Sharma et al., 2024), suggested that the genetic manipulation of PGPMS has the potential to produce significantly better strains with improved P, K and Zn solubilization efficacy (Chen et al., 2022). Recently, Yang et al. (2023) showed that K solubilizing *Priestia aryabhatai* strain SK1-7 upregulated the expression of the *maeA-1* gene to secrete more pyruvate into the medium for increasing feldspar dissolution. It needs to be determined whether P and Zn solubilization also results from the release of acids (malic and pyruvic acid) in the rhizosphere. Thus, current strategies for combating global warming by using metagenomics and other omics technologies may supply significant data inputs required to understand of the physiological reactions of the soil microbiome for supporting nutritional availability, soil functioning and plant growth promotion and by providing essential feedback to ecosystem health by alleviating the effects of climate change and drought stress (Fiodor et al., 2021; Gowda et al., 2022; Campos et al., 2023; Phour and Sindhu, 2023).

Under drought conditions, microbes may significantly alter the hormonal pathways and control the gene expression via antioxidant defense, hormone signalling, root modification, and stress responsive gene expression (Breitkreuz et al., 2021; Sayer et al., 2021; Yasmin et al., 2022). Two categories of genes are responsible for drought tolerance in plants, which include signal transduction factors such as transcription factors and protein kinases, while the second category includes proteins responsible for osmotic adjustments, protein modification, metabolism, ROS scavenging and transportation. Major genes related to drought tolerance in plants include proline encoding genes PAD4, P5CS and LEA and protein stabilization, and transcription factor DREB1A, which activates other drought responsive genes. Islam et al. (2023) reported different genes in tomatoes such as MdEPF2, *cwlnv*, AtGAMT1, SIADL1, ATHB-7, SIPIP2;1, SIPIP2;7, SIPIP2;5, osmotin, TAS14, SIMAPK3, and SLJUB1, which conferred drought tolerance. Priming of *Arabidopsis* with *Paenibacillus polymyxa* increased drought tolerance by activating certain genes like RAB18 and ERD15 (Timmusk and Wagner, 1999). In another study, *P. polymyxa* strain CR1 conferred drought resistance in soybean and *Arabidopsis* plants (Liu et al., 2020). Moreover, genes like RD29A and RD29B were upregulated with time in response to drought. Non ribosomal peptides and polyketide derived metabolites were produced

Table 2
Application of microbiome engineering (SynComs/HMME) for amelioration of drought stress in plants.

Synthetic microbial community			
Host plant	SynComs	Plant response	References
<i>Vitis vinifera</i> cv. <i>Barbera</i>	Strains of <i>Bacillus</i> sp., <i>Acinetobacter</i> sp., <i>Delftia</i> sp. <i>Enterobacter</i> sp. and <i>Sphingobacterium</i> sp.	Increased biomass of roots, reduced transpiration rates and enhanced water retention and drought tolerance	Rolli et al., 2015
<i>Populus deltoides</i> x p. <i>nigra</i> clone	Strains of <i>Rhizobium tropici</i> , <i>Sphingomonas vanoikuyae</i> , <i>Enterobacter asburiae</i> , <i>Acinetobacter calcoaceticus</i> , <i>Curtobacterium</i> sp., <i>Burkholderia vietnamiensis</i> , <i>Rahnella</i> sp., <i>Rhodotorula graminis</i> , <i>Burkholderia</i> sp.	Improved plant growth, and biomass, increased total nitrogen levels and drought tolerance	Khan et al., 2016
Maize	Strains of <i>Acinetobacter</i> sp., <i>Azospirillum brasilense</i> , <i>Pseudomonas putida</i> and <i>Sphingomonas</i> sp.	Enhanced plant growth and improved drought tolerance	Molina-Romero et al., 2017
Maize	<i>Burkholderia</i> sp., <i>Dyella</i> sp., <i>Enterobacter</i> sp., <i>Pantoea</i> sp., <i>Rhizobium</i> sp., <i>Stenotrophomonas</i> , <i>Microbacterium</i> sp., <i>Bosea</i> sp., <i>Chitinophaga</i> sp., <i>Asticcacaulis</i> , <i>Lysobacter</i> sp., <i>Pseudoxanthomonas</i> sp., <i>Sphingomonas</i> , <i>Chitinophaga</i> sp., <i>Stenotrophomonas</i> and 2 unidentified genera of Comamonadaceae and Streptomycetaceae	Increased plant growth and biomass (3.4 times) and increased root branching, and dark green leaves	Armanhi et al., 2018
Host-mediated microbiome engineering			
<i>Brassica rapus</i>	Microbes associated with wet environmental condition increased	Significant enhancement in plant growth and increased flower and fruit number with adapted microbiome	Lau and Lennon, 2012
<i>Brassica rapus</i>	Increased microbes associated with wet environmental conditions	Bacterial communities showed more abundance and richness while fungal communities showed less abundance. Nitrogen levels of soil were increased along with decrease in carbon to N ratio	Terhorst et al., 2014
Wheat	Abundance of Proteobacteria increased with 1.2-fold, while Acidobacteria and Actinobacteria decreased	Delayed symptoms of drought.	Jochum et al., 2019

by *P. polymyxa* to increase drought tolerance (Timmusk et al., 2015). The contribution of A26 Sfp-type 40-phosphopantetheinyl transferase gene (Sfp-type PPtase) was demonstrated in survival of wheat under drought conditions as its deactivation promoted biofilm formation. *Pseudomonas chlororaphis* O6 induced the gene expression of pdf-1.2 and VSP1 for the synthesis of JA, ethylene responsive gene HEL and PR1, and SA modulated gene for its colonization in *Arabidopsis* (Cho et al., 2013). Hence, a number of genes are regulated in augmenting the drought

tolerance of a plant.

Furthermore, inoculation of drought-tolerant microbes may alter or upregulate defensive pathways for alleviating abiotic stress. For instance, inoculation of AMF induced the expression of 1-pyrroline-5-carboxylic acid synthase enzyme (P5CS; involved in the proline synthesis) under drought stress condition. P5CS enzyme promotes cell water retention, thus improves the ability of plants to resist osmotic stress (Hu et al., 1992; Ruiz-Lozano et al., 2006). At the same time, the AMF has also been reported to upregulate 9-cis-epoxycarotenoid dioxygenase (NCED) gene expression for enhancing plant resistance to drought stress. NCED enzyme is involved in controlling ABA metabolism and it catalyses the oxidative cleavage of epoxy carotenoids into xanthoxins (Taylor et al., 2000; Chaffour et al., 2019).

Krishna et al. (2022) reported increased expression of stress-responsive genes like CAT, SOD, APX, DREB and P5CS due to the inoculation of PGPMs in tomato (*Solanum lycopersicum* L.) that enhanced drought tolerance and improved soil properties and fruit yield. Similarly certain genes were upregulated in soybean such as DREB/ERE transcription factor, P5CS and GOLS genes for osmoprotectants and water transporters genes i.e., PIP and TIP with the inoculation of *Pseudomonas simiae* AU for promoting plant survival under drought stress (Vaishnav and Choudhary, 2019). In a detailed study, Kaushal (2019) highlighted the role of different microbial communities including AMF or PGPR in regulation of different genes for providing drought tolerance to plants. Different genes which were upregulated includes miRNA's, Hsp20, SAMDC, CPA, ADC, AIH, ERD15, COC1, PtYUC3, PtYUC8, LbSKOR, jasmonate PR1, LbKT1, PKDP, COX1, 14-3-3, RAB18, AP2-EREBP, SPMS, bZIP1, VSP1, MYC2, and pdf1.2. Guarnizo et al. (2023) elaborated the role of *Pseudomonas mandelii* for interaction of *Helianthemum almeriense* with fungal species. *P. mandelii* also increased the nutrient uptake and expression of aquaporin coding AQP or TcaQP1 gene in *Terfezia clavaryi* and *Helianthemum* plant, which effectively increased water transport in ecto-endomycorrhizal fungal symbiont. The increased water uptake in both fungus and bacteria was essential to cope up with drought stress. *P. mandelii* not only promoted the colonization of fungus with plants but also increased ABA level and promoted plant survival under drought stress. Curá et al. (2017) reported hormonal regulation by *Herbaspirillum seropedicae* Z-152 and *Azospirillum brasilense* SP-7, along with reduced gene expression of ZmVP14 and genes coding for ABA and ET production in maize, respectively. Also, ABA dependent signalling genes were activated in the shoots of sugarcane by *Glucoacetobacter diazotrophicus* PAL5 in order to cope up with the effects of drought (Vargas et al., 2014). Similarly, concentrations of IAA and ABA were increased with the inoculation of *Shewanella putrefaciens* MCL-1 in pearl millet, while GA content was increased with *Cronobacter dublinensis* MKS-1. This suggested increased water uptake, proline level, improved root architecture, better plant growth and increased drought tolerance (Manjunatha et al., 2022).

Siraj et al. (2022) reported phytohormone production, P solubilization and siderophore production in *Microbacterium oxydans* strains AGH9, AGH5 and AGH3, isolated from the rhizosphere of *Calotropis procera* (Aiton) W.T. Aiton and *Achyranthes aspera* L. The production of ABA and JA was induced under drought stress in addition to increased gene expression of SlHsfA1a, SlHAKT1 and SlmiR159 in AGH3 strain. *Rhizophagus irregularis* (AMF) and *Bacillus subtilis* in combination promoted the expression of aquaporin genes and modulated ABA genes including ZmTIP1.1, ZmPIP1;3, ZmPIP2;2, and GintAQP1 for maintaining osmotic pressure in plant cell and thus, aided in plant survival under drought stress (Romero-Munar et al., 2023). Similarly, co-inoculation of two different endophytic fungi *Penicillium funiculosum* LHLO6 and *Paecilomyces formosus* LHL10 in soybean led to upregulation of drought responsive genes and heat shock proteins including GmRD20, GmDREB1B, and GmERD1. The endophytic fungal strains promoted plant growth under drought stress by increasing nutrient uptake, photosynthesis, biomass accumulation, and reducing oxidative stress (Bilal et al., 2020). This study also revealed high JA and ABA level in

non-inoculated plants under high temperature and drought stress. Ghosh et al. (2017) reported modulation in gene expression of proline biosynthesis in *Arabidopsis thaliana* after treatment with *Pseudomonas putida* GAP-P45. The quantitative real time expression analysis revealed prolonged but delayed upregulation of genes involved in proline catabolism i.e., $\Delta 1$ -pyrroline-5-carboxylate dehydrogenase (P5CDH), and proline dehydrogenase1 (PDH1) and genes involved in proline biosynthesis, i.e., $\Delta 1$ -pyrroline-5-carboxylate reductase/P5CR, $\Delta 1$ -pyrroline-5-carboxylate synthase1/P5CS1 and ornithine- Δ -aminotransferase/OAT. Therefore, rhizomicrobiome and co-inoculation of different strains has become a 'secret tool' for plants to utilize scarce soil nutrient resources and providing an effective mitigation strategy in crops exposed to drought stress.

5.2. Host based approach targeting microbiome evolution for drought stress mitigation

Manipulation of the host genotype is a promising approach for harnessing the plant-associated microbiota for increases drought resilience (Escudero-martinez and Bulgarelli, 2023). Genome-wide association studies (GWAS) represent a potentially powerful, unbiased method to connect host responsive microbes to the host genetic loci influencing their colonization (Deng et al., 2021). Host based approach is directed towards the improvement of plant functioning by targeting the evolution of microbiome (Mueller and Sachs, 2015). For selection of only desired phenotype, microbiome passing through all the multiple experiments is only selected at the end for the application as inoculum. Moreover, microbiome application in sequential plant growth cycle results in gradual evolution and domestication of the microbiome that is most suitable for plant phenotype. HMME is advantageous over SynComs due to selection of only desired microbes that has already acclimatized to plant system exposed to stress. In addition, HMME employs both culturable as well as non-culturable microbes, whereas SynComs explores only the culturable bacteria. HMME has been applied to increase drought resistance in wheat plant and Proteobacteria was confirmed as the most abundant bacterial phylum in soil with the use of 16S rRNA amplicon sequencing. In similar work, HMME application improved plant fitness on ecological context and increased drought tolerance (Lau and Lennon, 2012; Terhorst et al., 2014).

Root system architecture (RSA) and the spatial configuration of the plant root system plays a pivotal role in plant anchorage and efficient uptake of essential nutrients [e.g., N, P, and K and water] (Ryan et al. 2016; Gabay et al. 2023; Liu et al., 2023; Zheng et al. 2023). Under mild drought conditions, the biomass allocation into roots increases (Wach and Skowron, 2022), and root exudation is usually higher than that of well-watered controls (Tiziani et al., 2022). Specifically, drought increased the abundance of organic acids exuded by wheat (Anderson et al., 2023), and pearl millet (Ghatak et al., 2022), and also secondary metabolites in various plants (Ghatak et al., 2022; He et al., 2022). For instance, changes in plant metabolites of rice such as salicin, arbutin, glycolic acid phosphate influenced the growth of rhizosphere microorganisms and helped host plant to resist salt stress even after loss of *sst* gene (seedling salt tolerant) function (Lian et al., 2020). Furthermore, differences in the composition of root exudates was observed after disruption of ET signalling pathways and it included smaller amounts of esculetin, gallic acid, L-fucose, eicosapentaenoic acid, and higher amounts of β -aldehyde (Fu et al., 2021); these altered root exudate metabolites affect the growth, assembly and functioning of microbial taxa.

Moreover, plant characters could be altered with the help of genome editing that could allow the colonization of desired beneficial core microbiome. This strategy is more beneficial compared to traditional method of microbial inoculation. Song et al. (2021) observed that FERONIA, a kinase mutant in *Arabidopsis thaliana*, promoted colonization of *Pseudomonas fluorescens* in the rhizosphere by regulation of ROS. Also, other processes that could be engineered for altering the structural

microbial community includes hormonal biosynthesis or genes coding for plant exudates so to determine their function in shaping microbial community. Therefore, engineering plant microbiome is a promising tool for improving crop yield and productivity in addition to enhanced stress tolerance in plants.

Root system, its architecture and traits provide an avenue for breeding nutrient- and drought-resilient crops (Liu et al., 2023). Significant differences were identified in root traits using P efficient SC103 and inefficient BTx635 sorghum cultivars. Cultivar SC103 developed a larger root system with more and longer lateral roots, and enhanced shoot biomass, under both nutrient sufficient and deficient conditions. Under P deficiency, both cultivars exhibited an initial increase in lateral root development; however, SC103 still maintained the larger root biomass. Although N deficiency and drought stress inhibited both root and shoot growth, for both sorghum cultivars, SC103 again maintained the better growth performance under N deficiency and drought. Martínez-Barradas et al. (2024) evaluated drought tolerance of most widely cultivated cultivar 'Zorzal' of common bean (*Phaseolus vulgaris* L.) in Chile under drought stress. Plants were subjected to severe drought stress by suspending irrigation. 'Zorzal' cultivar expressed diverse traits associated with drought tolerance, and maintained stable leaf RWC and a better ROS scavenging and stable root biomass system than 'Arroz Tuscola' (a susceptible cultivar of the same gene pool) during the drought condition. Zeist et al. (2024) tested seven wild accessions, three *Solanum lycopersicum* var. *cerasiforme* accessions, and six commercial cultivars to select drought-tolerant tomato plants. Intra- and interspecific crosses were performed and from the crosses *S. lycopersicum* \times *S. pennellii*, two F₂BC₁ populations were obtained. The genotypes were subjected to water deficit. Among the tested *cerasiform* accessions, the RVC 66 accession was the least affected by the reduced water supply. The LA 716 accession (*S. pennellii*) was the most promising to introgress drought tolerance-related genes and had the highest tolerance to water deficit, followed by 'LA 1401' (*S. galapagense*) and 'LA 1967' (*S. chilense*). The crossing between 'LA 716' and the commercial tomatoes 'Clara' and 'Redenção' (most susceptible to water deficit) allowed the development and selection of drought-tolerant F₂BC₁ genotypes. Since host traits involved in microbiome assembly are complex and multifactorial (e.g., plant immune system, metabolites, and root traits), it has been suggested that this approach may not work in a predictable way (Raaijmakers and Kiers, 2022).

5.3. Redesigning of crop varieties and development of transgenic crops with improved drought stress tolerance

The application of beneficial microbes in soil is a sustainable and efficient approach to ameliorate drought stress. However, sometimes introduced microbial strains fail to reproduce the same effect in field as observed under laboratory conditions due to poor colonization of inoculated microbial strain, or failure in production of particular metabolite, and variable inoculant delivery (Sindhu and Dadarwal, 2000; Sindhu et al., 2003). Therefore, producing of transgenic plants or cultivars via genetic engineering is another alternative strategy to improve drought stress tolerance in plants (Manepalli et al., 2022; Pixley et al., 2023). Metabolic pathways are manipulated either to target root morphology and/or for secretion exudates to increase uptake of nutrients and enhance chlorophyll content. Thus, manipulation of the host genotype is a promising approach for harnessing the crop microbiota for increases drought resilience (Escudero-martinez and Bulgarelli, 2023). Moreover, analyses of high-throughput phenotyping and plant genomics, and integration of large-scale environmental metagenomics (e.g., in different geographic locations and different sites) with metabolomics, may provide wider insights into plant-microbiota interactions. For instance, genes located around single-nucleotide polymorphisms (SNPs) associating with fungi are involved in the plant immune system, abiotic stress responses and cell wall remodeling processes in drought-stressed rice (Andreo-Jimenez et al., 2023).

Conventional breeding techniques have been applied since last few decades; however, such techniques are labour and time consuming, and costly (Ashraf, 2010). Traditional methods of plant breeding also transform the undesirable genes and require several cycles of breeding, and selection for the desired outcome. Traditional breeding methods fail often due to the role of numerous genes in conferring drought resistance traits to plant. Therefore, genetically manipulating the plant for drought resistance is a more effective approach. The most significant step for genetic manipulation in plants is to collect the necessary data of elite material through doubled-haploid and speed-breeding methods related to genes involved in different abiotic stresses including drought as well as biotic stress, the availability of computing power and novel algorithms (Jeon et al., 2023). Plant breeders target for developing drought tolerant crops using genetic modification (Yang et al., 2010; Mwadzini et al., 2016). Recently, CRISPR-Cas is also being used as a tool for genome editing, which enables altering of genes directly in crop plants without permanently introducing foreign genetic material (Wang and Doudna, 2023). Most of the breeding and genome editing work is targeting commercial traits, crops and cropping systems for improving food security in developed countries (Pixley et al., 2022; Marks et al., 2023). Hence, transgenics are based upon the transfer of desired genes and conferring better traits in plants for the better resistance towards water deficit stress (Ashraf, 2010; Rabara et al., 2014). Transgenics works wonder as it is based on modifying either single or group of desired genes as compared to conventional breeding techniques (Gosal et al., 2009; Manepalli et al. 2022). Several techniques used for genetic manipulation for producing drought tolerant crops includes quantitative trait locus (QTL) mapping, marker-assisted breeding, and introgression from wild gene pool (Gupta et al., 2017; Bhatta et al., 2018; Przewieslik-Allen et al., 2019; Vala et al., 2023; Bhanbhro et al., 2024).

However, drought tolerance in plants is a complex quantitative polygenic trait and is regulated by a number of genes; therefore, the molecular or physiological basis of drought tolerance is difficult to understand (Hu and Xiong, 2014; Senapati et al., 2018). In addition, success rate of transgenic development is limited because the process requires skill to efficiently incorporate the genes. Moreover, the success of transgenics is also dependent upon the physiological effects of foreign gene after incorporation. The major pathways that could be targeted for improving drought tolerance include modulating the expression of stress responsive gene, activation of distinct stress-response pathways in plants, synthesis of various synergistic or antagonistic signaling molecules, stress hormones, ABA synthesis, and transcription factors (Suzuki et al., 2005; Liu et al., 2020; Osakabe et al., 2020; Manepalli et al., 2022). For instance, ABA signaling and osmotic stress signal transduction activated SnRK2 kinase, it regulated the activity of transcription factor and ion channels through phosphorylation resulting in expression of genes regulating stomatal closure (Takahashi et al., 2020). Certain genes were inserted within plant genome to produce transgenics with better production of organic acids, phosphatases, better P uptake and translocation, and carbohydrate utilization within the plant (Koyama et al., 2000). However, the major drawback associated with increasing the gene expression of stress responsive genes includes slower plant growth, which hinders the application of transgenics (Hussain et al., 2018).

Table 3 enlists various transgenic crops developed through genetic engineering to mitigate abiotic stresses. The overexpression of OsNAC45 gene in *Oryza sativa* improved tolerance to drought and salt stress (Yu et al., 2018). Additionally, it reduced the accumulation of ROS and increased lignin levels in the roots, and contributed to normal seedling root development under stress conditions. Significantly increased expression of transcription factor WRKY8 and stress responsive genes SIAREB, SIDREB2A and SIRD29 in tomato (*Solanum lycopersicum*) conferred resistance to the drought, salt stress and pathogen (Gao et al., 2019).

Cross talk between QTL, their interactions and cloning reveal the molecular basis of genes conferring stress tolerance (Nakashima et al.,

Table 3
Development of transgenic crops having improved tolerance to drought stress.

Transgenic Plants	Gene transferred	Abiotic stress tolerance	Mechanism involved	References
Wheat	Aquaporin gene <i>TdPIP2; 1</i>	Drought and salt stress tolerance	Induction of antioxidative enzymes catalase and superoxide dismutase	Ayadi et al., 2019
	TF <i>TaWRKY31</i>	Drought stress tolerance	Activation of stress responsive genes and antioxidant activities	Ge et al., 2024
	R2R3 MYB gene, <i>TaMpc1-D4 TaVQ4-D</i>	Drought stress tolerance Drought stress tolerance	Negatively regulates drought tolerance Upregulation of reactive oxygen species-scavenging-related genes and stress related genes	Le et al., 2020 Zhang et al., 2023
Rice	<i>CcCCR</i>	Drought, salt and cold stress	Higher leaf chlorophyll content, proline, reducing sugars, CAT, and SOD activities	Sunitha et al., 2017
	<i>OsMYB6</i> ; a MYB family gene	Drought and salinity stress	Higher proline content, higher CAT and SOD activities, lower REL and MDA content	Tang et al., 2019
	<i>CdCIPK21</i>	Drought and salt tolerance	Altered ABA sensitivity, antioxidant, proline accumulation and expression of ABA-dependent and ABA-independent stress responsive genes	Liu et al., 2023
Maize	<i>ZeEREB24</i>	Drought stress tolerance	Modulation the expression of drought stress genes	Ren et al., 2024
Tobacco	<i>TaMYB20</i>	Drought stress tolerance	Upregulation of auxin-related genes expression, improving root system architecture, maintenance of ROS balance, lower ion leakage and high relative water content	Azab et al., 2024
	<i>MaNCED1</i>	Drought and salt stress tolerance	Expression of auxin and ethylene signal pathway-related gene	Zhu et al., 2023
Chick pea	Aquaporins	Drought stress tolerance	Enhanced water-permeability of vacuolar and plasma membrane	Azeem et al., 2019
Faba bean	<i>PR10a</i>	Drought stress tolerance	Synthesis and accumulation of osmolytes	Hanafy et al., 2013

(continued on next page)

Table 3 (continued)

Transgenic Plants	Gene transferred	Abiotic stress tolerance	Mechanism involved	References	
Mung bean	<i>codA</i> gene	Drought and salt stress tolerance	encodes for osmoprotectant glycine betaine	Baloda et al., 2017	
	<i>VrbZIP</i>	Drought stress tolerance	Drought-responsive gene	Wang et al., 2018	
Alfalfa	<i>MicroRNA 156</i>	Drought stress tolerance	SPL13 silencing	Arshad et al., 2017	
	<i>AtEDT1</i>	Confers drought tolerance	Reduced membrane permeability and MDA content, higher soluble sugar and proline content, higher SOD, enhanced expression of drought-responsive genes	Zheng et al., 2017	
	<i>GsZFP1</i>	Confers drought and salt tolerance	Induction of stress-responsive marker gene	Tang et al., 2013	
Cowpea	<i>HaHB11</i>	Confers tolerance to water deficit and salinity	Morphological, physiological, and molecular changes	Cabello et al., 2017	
	<i>MsMYBH</i>	Drought resistance	Upregulation of genes	Si et al., 2024	
	<i>VuPLD1, VuNCED1, CPRD8, CPRD12, CPRD14, CPRD22</i>	Drought stress tolerance	ABA biosynthesis	Muchero et al., 2010	
Common bean	<i>DREB2</i>	Drought tolerance	ABA signaling pathway	Cortes et al., 2012	
Soybean	<i>WRKY20</i>	Drought tolerance	Higher antioxidant enzyme activities and more free proline content	Ning et al., 2017	
	<i>PgTIP1</i>	Drought and salt stress tolerance	Maintain homeostasis of water, salt ions and ROS	Van et al., 2018	
	<i>GmRACK1</i>	Drought and salt tolerance	Antioxidative enzymes activities	Li et al., 2018	
	<i>GmWRKY54</i>	Drought tolerance	Activating genes in abscisic acid and Ca ²⁺ signaling pathways	Wei et al., 2019	
	<i>miR166 ATHB14-LIKE</i>	Drought tolerance	Expression of ABA signaling pathway	Zhao et al., 2024	
	Sweet potato	<i>lbCBF3</i>	Drought and low temperature stress	Regulation of stress-responsive genes	Jin et al., 2017
		<i>NHX1 and eIF4A1</i>	Drought tolerance	Antioxidative enzymes activities and proline content	Zhang et al., 2019
Tomato	<i>SlbHLH22</i>	Drought and salt stress tolerance	helix-loop-helix transcription factor	Waseem et al., 2019	
Groundnut	<i>AtHDG11</i>	Drought and salt stress	Up-regulation of stress responsive genes, antioxidant enzymes, free proline	Banavath et al., 2018	

Table 3 (continued)

Transgenic Plants	Gene transferred	Abiotic stress tolerance	Mechanism involved	References
Apple	<i>MuWRKY3</i>	Drought tolerance	Transcription factor	Kiranmai et al., 2018
	<i>MsDREB6.2</i>	Drought tolerance	Results in cytokinin-deficient developmental phenotypes	Liao et al., 2017
	<i>MpSnRK2.10</i> protein kinase gene	Drought stress tolerance	Induction of stress responsive genes, enhancement of ABA signal transduction	Shao et al., 2019
Arabidopsis	<i>MdATG10</i>	Drought tolerance	Regulating stomatal movement and enhancing autophagic activity	Xiang et al., 2024
	<i>GmBIN2</i>	Drought and salt tolerance	Glycogen synthase kinase 3 gene	Wang et al., 2018
	<i>GmCaM4</i> and transcription factor, MYB2 <i>VfPIP1</i>	Drought tolerance	Upregulate several drought-responsive genes	Yoo et al., 2005
Arabidopsis	<i>OsNAM</i>	Improves drought resistance	Aquaporin/water transport	Cui et al., 2008
	<i>MePP2C24</i>	Conferred stress tolerance	Phytohormone regulation and fostering plant-rhizobacterium interaction	Tiwari et al., 2021
	<i>GmNAC19</i>	Drought stress tolerance	ABA signaling pathway	Zeng et al., 2024
Arabidopsis	<i>GmNAC19</i>	Drought stress and abscisic acid response	ABA signaling pathway	Zeng et al., 2024
	<i>GmNAC19</i>	Drought stress tolerance	Regulation of soluble protein, soluble sugar, proline and MDA and activities of antioxidant enzymes i.e., SOD, APX and CAT	Cui et al., 2024

2014; Medina et al., 2016). In order to develop crop cultivars with better stress resistance, the related transcription factors need to be identified, which can regulate the crop's phenotypes (Reynolds et al., 2015). Genetically modified plants demonstrated better resistance towards different environmental stress conditions compared to other plants (Shah et al., 2016; Nejat and Mantri, 2017). For instance, one of the plant specific transcription factor is *AP2/ERF* group, which is involved in stress response and related to plant growth improvement (Riechmann and Meyerowitz, 1998; Licausi et al., 2010). This group of transcription factors is divided into 4 different sub-groups based upon numbers and their similarity, and includes *ERF*, *AP2* (Apetala 2), *DREB* or dehydration-responsive element binding protein and *RAV* related to *AB13/VP1*. Among these 4 subgroups, *DREB* and *ERF* are the major groups responsible for biotic and abiotic stress response (Sharoni et al., 2010). *DREB* transcription factor functions in stress response to water limiting and cold stress conditions (Stockinger et al., 1997). Such transcription factors have been closely examined in various plant species such as rice, wheat, maize, barley, soybean, tomato, and *Arabidopsis* (Lata and Prasad, 2011; Mizoi et al., 2012). Moreover, *DREB1* genes have been inserted in other crops to develop transgenic crops with better stress resistance (Dubouzet et al., 2003; Qin et al., 2004). Transcription factor *DREB1* was also inserted in tobacco for increasing the tolerance to drought- and low-temperature stress (Kasuga et al., 2004) and *DREB1*

was upregulated in transgenic *Arabidopsis*, which showed better resistance towards salinity, cold and drought stress (Gilmour et al., 1998; Jaglo-Ottosen et al., 1998). Similarly, *DREB2* is reported to confer resistance to salinity, drought, and high temperature stress (Sakuma et al., 2002; Lucas et al., 2011). Transgenic rice was developed by over expressing the *OsDREB2A* gene, which provided resistance against drought and salinity (Mallikarjuna et al., 2011).

ERF is another larger subgroup of *AP2/EREBP* transcription factors (Dietz et al., 2010), which controls the stress tolerance genes in plants (Hao et al., 1998). In transgenic plants, *ERF* genes are over-expressed to increase the plant's tolerance to stress (Xu et al., 2008). *ERF* transcription factors also regulate the biosynthesis pathways of hormones in plants (Liang et al., 2008). Transgenic apple and tomato were developed with the addition of *MdMYB121* from apple to increase drought and salt tolerance (Cao et al., 2013). Similarly, transgenic tobacco and apple acquired *MdSIMYB1* gene from apple, which induced resistance in plants against drought, cold and salinity (Wang et al., 2014). In another study, transgenic wheat contained gene *TaPIMP1*, which conferred resistance against pathogen *Bipolaris sorokiniana*, in addition to drought (Zhang et al., 2012). Transgenic tobacco could withstand the infestation of *Ralstonia solanacearum* and abiotic stresses like salinity and drought due to the presence of *TaPIMP1* transcription factor (Liu et al., 2011).

The cultivation of rice (a high water demanding crop) is severely impacted by various abiotic and biotic stresses. Transgenic aromatic rice i.e., Pusa Sugandhi 2 was developed, which showed hyper expression of *AtDREB1A* and *OsRab16A* genes resulting in enhanced drought tolerance, leaf RWC, proline, and CAT levels and increased shoot and root lengths (Ganguly et al., 2020). In another study, drought resistance in rice was induced due to the expression of *OsNADK1* gene, which is localized in cytosol (Wang et al., 2020). This gene was involved in maintaining redox balance intracellularly in rice dwarf mutant. Another strategy for increased stress tolerance is due to increased production of cuticular wax. The transgenic rapeseed produced more cuticular wax induced by the overexpression of *BnCER1-2* and *BnKCS1-2* (orthologs of *ECERIFERUM*), *BnKCS1-1* (ortholog of 3-ketoacyl-CoA synthase). Moreover, transgenic rapeseed showed reduced water loss and increased tolerance to drought stress (Wang et al., 2020). Further, overexpression of such genes resulted in more dense wax crystals on leaf surface compared to wild type plants (Wang et al., 2020). Similarly, drought resistant transgenic cotton and *Arabidopsis* contained overexpressing gene *GbWRKY1* (Luo et al., 2020). The later gene acted as negative regulator of salinity and drought tolerance. Transcription factor R2R3-type MYB in wheat induced tolerance to multiple abiotic stresses (Li et al., 2020). Crops like soybean and maize were genetically modified for increasing drought tolerance (Li et al., 2018; Wei et al., 2019; Ren et al., 2024).

In some cases, drought resistance is mediated by the accumulation of proline in plant cells, therefore transgenic plant varieties showed more proline accumulation in wheat (Sawahel and Hassan, 2002), potato (*Solanum tuberosum*) (Hmida-Sayari et al., 2005), and tobacco (*Nicotiana tabacum*) (Kishor et al., 1995). The pathway responsible for proline synthesis includes the production of semialdehyde after the reduction of glutamate in the presence of enzyme P5CS, followed by reduction to produce proline. Enzyme P5CS is a rate limiting enzyme and is regulated by feedback inhibition (Zhang et al., 1995). Therefore, an attempt was made by Vendruscolo et al. (2007) to transform cDNA of gene responsible for P5CS synthesis of *Vigna aconitifolia* under inducible AIPC promoter via biolistics transformation method. Transgenic wheat depicted enhanced tolerance to water limitation conditions due to reduced MDA levels. Moreover, transgenic wheat had 50 % intact cellular membrane compared to 13 % in wild type wheat when exposed to water limitation for 14 days at booting stage. Transgenic lines of T2 generation containing *P5CS* gene when exposed to 8 days of water stress showed 18.5 times more proline accumulation compared to non-transgenic plants (Pavei et al., 2016). However, MDA levels were not reduced in such transgenics; hence there was no protection to cell membrane against

oxidative stress. Yang et al. (2021) reported over expression of *OE-SpP5CS* leading to increased proline levels in transgenic *Arabidopsis* during drought stress. Similarly, proline levels were increased due to overexpression of *PagP5CS1* gene in poplar plant under drought stress conditions (Ren et al., 2023). In potato, *P5CS* gene mediated tolerance against drought stress (Li et al., 2014).

Certain transgenics were developed by inserting the genes related to the biosynthesis of betaine and glycine; for instance, *COD*, *CDH*, *betaA* and *BADH* (Sakamoto and Murata, 2000; Wang et al., 2010; He et al., 2011). Gene *BADH* from *Atriplex hortensis* was transferred to wheat to induce betaine aldehyde dehydrogenase activity (Guo et al., 2000). Similarly, transgenic T6 wheat line was developed by inserting the *BADH* gene from *Atriplex hortensis*, which regulated under ubiquitin promoter from maize via microprojectile bombardment method (Wang et al., 2010). Transgenic plants depicted higher levels of glycine and betaine, along with increased photosynthesis rate due to better water status and antioxidant activity. This was evident from osmotic stress exposed (-1.88 MPa, 30 % PEG) transgenic and wild type Shi 4185. The same observation was recorded in transgenic wheat (T6 line) when exposed to water stress i.e., 78–82 % relative water content (Wang et al., 2010). He et al. (2011) developed transgenic wheat by inserting choline dehydrogenase encoding *betA* gene under maize ubiquitin promoter. When such plants were exposed to drought stress or 12–14 % RWC, they depicted less injury in addition to better root length and biomass due to enhanced levels of osmoprotectants glycine and betaine.

Enhanced photosynthesis rate and ROS scavenging activity were reported in some transgenic plants for increased tolerance to different abiotic stresses. This tolerance was mediated by transfer of *mtlD* gene from *Escherichia coli*, which was inserted in crops such as tobacco (Tarczynski et al., 1992; Karakas et al., 1997), rice (Pujni et al., 2007), *Arabidopsis* (Thomas et al., 1995) and peanut (Saxena et al., 2013; Bhauso et al., 2014). Transformation of wheat with the *mtlD* gene of *E. coli* induced the accumulation of mannitol though the wild wheat does not accumulate mannitol (Abebe et al., 2003). Another transgenic wheat line containing *SeCspA* and *SeCspB* from *E. coli* was developed by Yu et al. (2017). Transgenic wheat harbouring *SeCspA* depicted less wilting and reduced MDA levels, produced more proline and chlorophyll content, reduced water loss and more grain weight and yield compared to wild type. The expression of *A4-roIB* in the transformed cell cultures of *Arabidopsis* disturbed the homeostasis of numerous proteins involved in primary metabolism, phytohormone, chaperone and ROS signalling (Veremeichik et al. 2016; Bulgakov et al. 2018). Veremeichik et al. (2022) investigated the overexpression of *A4-roIB* gene from the pRiA4 of *Rhizobium rhizogenes*, which modulated two important processes, flavonoid biosynthesis and drought tolerance. In addition, the constitutive overexpression of *A4-roIB* activated the SA signaling system. An increase in flavonol accumulation and enhanced drought tolerance can be explained by the cooperative action of SA and ROS pathways.

In another study, over expression of *GhTPPA2* in tobacco resulted in enhanced TPPase activity (by 66 %), and sugar and starch content by 39 % and 27 %, respectively (Wei et al. 2024). Transgenic tobacco showed better growth under 100 mM mannitol stress, which could be attributed to metabolism of phosphate and carbohydrate, and photosynthesis. Further, *GhTPPA_2* induced soluble sugar accumulation, sugar metabolism and improved crop yield, which resulted in enhanced tolerance against drought stress. Transgenic wheat when exposed to drought, produced more anthocyanin and ABA, and showed greater drought tolerance compared to wild type. Enhanced leaf water content, antioxidant activity, soluble sugar and chlorophyll content, ABA levels and enzymes related abscisic acid signalling and anthocyanin content in wheat were reported by expression of *BnMYBL2-1* gene from *Brassica napus* (Gao et al., 2024). Gene *ChaWRKY40* enhanced drought tolerance of 'dawei' hazelnuts by positively regulating proline synthesis (Zhang et al., 2024). Increasing PEG-6000 concentration increased the expression of *ChaWRKY40* and *ChaP5CS*, which in turn increased the electrolyte leakage, and proline content. These studies suggested that

transgenics may improve physiological and molecular traits, which could improve drought stress tolerance in plants.

Another strategy involves the development of transgenic plants for higher drought tolerance by improving water utilization efficiency (WUE) leading to improved crop yields under drought stress. For instance, transgenic maize seedling exhibited enhanced survival rates due to better water utilization achieved by increasing the gene expression of ZmVPP1, ZmTIP1, and ZmSRO1d (Wang et al., 2016; Zhang et al., 2020; Gao et al., 2022). Moreover, the maize kernel yield was increased under drought conditions due to the overexpression of rice trehalose-6-phosphate phosphatase (TPP) (Nuccio et al., 2015), ZmSRO1d (Gao et al., 2022), ZmVPP1 (Wang et al., 2016), and ZmASR1 (Virilouvet et al., 2011). Under drought conditions, the expression of drought-inducible ZmEXPA4 gene decreased anthesis and silking interval (ASI) compared to wild type maize plant (Liu et al., 2021). An association study using a natural-variation population of maize revealed a significant relationship between the level of α -expansin4 (ZmEXPA4) expression and drought-induced increases in ASI. Furthermore, genetic manipulation of ZmEXPA4 expression using a drought-inducible promoter in developing maize ears reduced the ASI under drought conditions. Overexpression of expansin gene TaEXPA2 in transgenic wheat (Yang et al., 2020), ABA receptor gene TaPYL1-1B in wheat (Mao et al., 2022a), a NAC transcription factor TaNAC071-A in wheat (Mao et al., 2022b) or TaWRKY46 in transgenic wheat (Yu and Zhang, 2022) increased WUE and survival rates under drought stress compared to wild type plants. It has been reported that the wheat genes TaPYL1-1B and TaNAC071-A increased grain yield via increasing WUE (Mao et al., 2022a, b). Under drought stress, overexpression of MYB family gene, OsMYB6 (Tang et al., 2019), enhanced trehalose biosynthesis gene OsTPSP (Joshi et al., 2020), OsNAC14 (Shim et al., 2018), SiMYB56 involved in lignin biosynthesis and ABA signaling pathway (Xu et al., 2020), Osipa1 involved in activating ABA pathway (Zhu et al., 2022) improved WUE and increased survival rates compared to wild type rice plants. Transgenic rice plants having overexpression of OsTPSP (Joshi et al., 2020), OsNAC14 (Shim et al., 2018) or OsHYR (Ambavaram et al., 2014) genes showed higher grain yields than wild type plants under drought stress.

6. Regulatory challenges of implementing bioengineered crops and their economic and ethical implications

With the advent of advanced biotechnological tools, agriculture sector has seen a great boost in crop production via GM crops. The United States is a global leader and possesses 30 % of the whole market share of GM crops. Another largest GM cultivator is Canada, which accounts for 6 % of total global market share. However, use of genetic engineering technologies and GM crops in intensive agriculture practices for food production has potential health and environmental risks. These genetically transformed crops may have either positive or negative environmental impact depending on how and where they are used. Genetic engineering may either accelerate the damaging effects of agriculture or contribute to more sustainable agricultural practices and the conservation of natural resources. The main food safety concerns associated with transgenic products and foods derived from them relate to the possibility of increased allergens, toxins or other harmful compounds; horizontal gene transfer particularly of antibiotic-resistant genes and other unintended effects. Therefore, risk associated with such genetic engineering technologies must be evaluated and managed for the safe implementation (Aven, 2016; Glick, 2020).

Each country has their own set of regulations for the production, commercialization and trading of GM crops. For instance, three agencies are involved in the approval and evaluation of novel GM crops including the Environmental Protection Agency (EPA), United States Department of Agriculture (USDA) and Food and Drug Administration (FDA). However, the concerns for GM crops remain the same around the globe and should be strictly assessed for their potential risks (Podevin et al.,

2013). For instance, GM crops based on site directed nucleases (SDNs) mutagenesis (Tzfira et al., 2012; Podevin et al., 2013), especially SDN-1, are excluded from the GM regulations in various countries like South Africa, Germany, Argentina, Canada, Netherlands, Japan, and Australia. On the other hand, SDN-2 based GM crops are excluded from GM regulation in Germany in the EU, while SDN-3 based crops are enforced with GM regulations (McHughen, 2016).

Cultivation of GM crops and consumption of their products have been a debatable issue for their safety issues and long-term consequences on environment. Another concern regarding their safety is gene transfer to wild relatives or conventional crops, trait effects on non-target species and genetic modification over the time, which could potentially have direct effects including gene transfer and other unintended effects and may disturb environment and human health. In addition, transgenic crops may also entail positive or negative indirect environmental effects through changes in agricultural practices such as pesticide and herbicide use and cropping patterns. Therefore, environmental impacts need to be assessed on a case-by-case basis and post-release ecological monitoring is recommended to detect any unexpected events. Thus, it becomes essential to implement strict risk assessment and monitoring protocols for regular evaluation of potential risk of GM crops. Therefore, a regulatory body must assess ecological risk, gene flow and development of secondary pest resistance (Craig et al., 2008).

Several misconceptions are being circulated among public in recent past about consumption of GM crop products, which make people reluctant to adopt genetically engineered crop or products in different parts of world. Fortunately, currently available transgenic crops and foods derived from them have been found safe to eat and no verifiable untoward toxic or nutritionally deleterious effects have been reported from the consumption of foods obtained from GM crops (mainly maize, soybean and oilseed rape) anywhere in the world. Another issue regarding regulatory frameworks related to GM crops is time consuming, and expensive, which hinders the small traditional seed producing firms to enter the market (Tait, 2007). Since GM crops are entitled to different regulations depending upon their cultivation, import, export and consumption as food and feed (Eckerstorfer et al., 2019). Moreover, several international environmental non-governmental organizations have been active in campaigning against GM products, which caused poor public acceptance (Paarlberg, 2014). Therefore, regulatory framework must be standardized around the globe for the easy approvals of genetically engineered drought resistant crops, which will lead to increased acceptance by farmers. Moreover, their cultivation and consumption must be analyzed with strict consideration related to their governance and socio-economic impact to fully utilize their potential. In addition, policy makers must enforce clear regulations through transparent communications with public, public awareness programs and equitable access to technology to facilitate the smooth flow of genetically engineered crops in market. Furthermore, initiatives for technology transfer and capacity building is needed to promote cultivation of genetically engineered drought resistant crops irrespective of socio-economic disparities for promoting sustainable agriculture development.

7. Conclusions

With sudden changes in climate and increasing food demand by ever-growing global population, efficient and advanced cultivation techniques are needed to sustain food security under environmental stress conditions. Drought is one of the major threats to crop production, which adversely affect plant growth and crop yield. Application of drought-tolerant beneficial PGPMs as bioinoculants is a cost-effective sustainable option for inducing tolerance in farmer's field leading to increases in plant growth and crop yield under drought stress. These plant beneficial microbes employ various strategies including production of EPSs, phytohormones, osmolytes, VOCs and antioxidant

enzymes, and induce expression of drought responsive genes. Therefore, a better understanding of the physiological reactions of the beneficial soil microbiome is needed to predict effects of climate change on microbial community in soil and its functioning, which could be used to alleviate the effects of climate change by giving essential feedback to ecosystem health (Azeem et al., 2022; Bittencourt et al., 2023). Thus, soil microbial communities can be managed for monitoring, adaptation, and stress mitigation despite climate change's pragmatic uncertainties. A deeper awareness of changing climate effects on soil microbes' biogeochemical processes is further needed to make more accurate estimates of climate change for addressing future soil degradation and impact on food production. Genetic manipulation of soil microbiomes and host plants along with development of drought-tolerant transgenic crops also have great potential for supporting sustainable agriculture by reducing the competition from native microorganisms and increasing plant adaptation to drought stress. Engineered microbiomes may outcompete the traditional bioinoculants in enhancing plant stress tolerance and plant growth. However, the research in this aspect is still in infancy stage and associated with several hinderances. For instance, inconsistent results of engineered microbiomes in fields, limited knowledge of plant microbiome functioning under *in vivo* system, lack of appropriate method for preservation and application of microbiota, and complex plant-microbe-environmental interactions in soil are few limitations. However, plant associated microorganisms and their biengineering using synthetic biology approach may help in developing drought resilient plant system to harness more benefits in sustainable agriculture systems.

8. Future directions

Drought and other abiotic stresses to plants have been a global phenomenon since ancient times and have silently become a chronic problem. The evidences presented herein highlight the profound influence of drought stress on crop growth, in shaping the composition of root microbial communities and the intricate interplay between crops and microorganisms in drought-prone environments. We have systematically elucidated the underlying mechanisms governing how microorganisms can ameliorate the adverse effects of drought stress on crops. Nevertheless, a substantial research gap exists in the characterization of root exudates across diverse crop species. Given the pivotal role of root exudates in modulating root microbial communities, the application of exudates holds significant promise for mitigating the adverse effects of drought stress on crop growth. Hence, sustained efforts are required to characterize and quantify root exudates under drought stress conditions. Furthermore, a deeper exploration of distinct root or rhizobacterial microbes could enhance our understanding of their interconnectedness and their potential to fortify crops against drought stress. However, the research into the efficiency of drought-tolerant microbes as inoculants under drought conditions is limited.

In addition, due to the multigenic nature of stress tolerance and the long time required in these approaches, traditional breeding approaches to improve drought tolerance have largely failed. The molecular techniques have been developed over the last few decades to understand the mechanisms governing drought stress tolerance at the gene-level, which improved water utilization efficiency leading to improved crop yields under drought stress. The discovery of miRNAs regulating gene expression, post-translational modifications of proteins to accommodate more complex functions for the same set of gene(s) and the development of new CRISPR-based tools and modifications, has proved to be critical points in the understanding of drought and abiotic stress tolerance. Nevertheless, the application of beneficial drought adaptive microbes to crops could be a sustainable solution enabling plants to withstand stress conditions, paving the way for improved soil health, fertility and crop yields. Thus, considerable future research is required to identify efficient microbial strains as potential field bioinoculants with longer shelf-life and survival ability for promoting sustainable food production in arid

areas while bolstering environmental friendliness and agricultural sustainability.

Credit authorship contribution statement

Satish Kumar: Resources analysis, Data curation, Original draft preparation, Investigation, Figures designing.

Satyavir S. Sindhu: Conceptualization, Supervision, Formal analysis, Reviewing and Editing.

Authors' contributions

Both authors have equal contribution in compilation of this review chapter. Both authors have read and approved the final manuscript.

Funding

Being a review article, no funding was involved in compilation of the information in this review chapter.

Availability of data and materials

All the data, figures and tables have been submitted with the manuscript.

Ethics approval and consent to participate

The work submitted does not include any experiment related to animals.

Consent for publication

Not applicable. This is the review chapter and no data/figure has been copied or taken from any published article.

Availability of data and materials

Data reported in the review chapter include information compiled from different published articles. The minimal dataset used for interpretation has been compiled from the information of the findings reported in the different articles. All the articles have been included in the References section.

Declaration of competing interest

The authors declare that they have no competing interests.

Acknowledgements

Authors thank the faculty members of the Microbiology department for their excellent contributions in improving the quality of the manuscript.

References

- Aalipour, H., Nikbakht, A., Etemadi, N., Rejali, F., Soleimani, M., 2020. Biochemical response and interactions between arbuscular mycorrhizal fungi and plant growth promoting rhizobacteria during establishment and stimulating growth of *Arizona cypress* (*Cupressus arizonica* G.) under drought stress. *Sci. Hortic.* 261, 108923.
- Abadi, V.A.J.M., Sepehri, M., Rahmani, H.A., Zarei, M., Ronaghi, A., Taghavi, S.M., Shamshirpour, M., 2020. Role of dominant phyllosphere bacteria with plant growth-promoting characteristics on growth and nutrition of maize (*Zea mays* L). *J. Soil Sci. Plant Nutr.* 20, 2348–2363. <https://doi.org/10.1007/s42729-020-00302-1>.
- Abbasi, S., Sadeghi, A., Safaie, N., 2020. *Streptomyces* alleviate drought stress in tomato plants and modulate the expression of transcription factors ERF1 and WRKY70 genes. *Sci. Hortic.* 265, 109206.

- Abdelal, K., AlKahtani, M., Attia, K., Hafez, Y., Király, L., Künstler, A., 2021. The role of plant growth-promoting bacteria in alleviating the adverse effects of drought on plants. *Biology* 10 (6), 520.
- Abebe, T., Guenzi, A.A., Martin, B., Cushman, J.C., 2003. Tolerance of mannitol-accumulating transgenic wheat to water stress and salinity. *Plant Physiol.* 131, 1748–1755.
- Abid, M., Ali, S., Qi, L.K., Zahoor, R., Tian, Z., Jiang, D., Snider, J.L., Dai, T., 2018. Physiological and biochemical changes during drought and recovery periods at tillering and jointing stages in wheat (*Triticum aestivum* L.). *Sci. Rep.* 8 (1), 4615.
- Abril, A.B., Torres, P.A., Baucher, E.H., 2005. The importance of phyllosphere microbial populations in nitrogen cycling in the chaco semi-arid woodland. *J. Trop. Ecol.* 21, 103–107.
- Acosta-Martínez, V., Cotton, J., Gardner, T., Moore-Kucera, J., Zak, J., Wester, D., Cox, S., 2014. Predominant bacterial and fungal assemblages in agricultural soils during a record drought/heat wave and linkages to enzyme activities of biogeochemical cycling. *Appl. Soil Ecol.* 84, 69–82.
- Ahanger, M.A., Tomar, N.S., Tittal, M., Argal, S., Agarwal, R., 2017. Plant growth under water/salt stress: ROS production; antioxidants and significance of added potassium under such conditions. *Physiol. Mol. Biol. Plants* 23, 731–744.
- Ahkami, A.H., White III, R.A., Handakumbura, P.P., Jansson, C., 2017. Rhizosphere engineering: enhancing sustainable plant ecosystem productivity. *Rhizosphere* 3, 233–243.
- Ahluwalia, O., Singh, P.C., Bhatia, R., 2021. A review on drought stress in plants: Implications, mitigation and the role of plant growth promoting rhizobacteria. *Resour. Environ. Sustain.* 5, 100032.
- Ahmad, A., Aslam, Z., Naz, M., Hussain, S., Javed, T., Aslam, S., Raza, A., Ali, H.M., Siddiqui, M.H., Salem, M.Z., Hano, C., 2021. Exogenous salicylic acid-induced drought stress tolerance in wheat (*Triticum aestivum* L.) grown under hydroponic culture. *PLoS One* 16 (12), e0260556.
- Ahmad, I., Zaib, S., Alves, P.C.M.S., Luther, D.S., Bano, A., Shakeel, S.N., 2019. Molecular and physiological analysis of drought stress responses in *Zea mays* treated with plant growth promoting rhizobacteria. *Biol. Plant.* 63, 536–547. <https://doi.org/10.32615/bp.2019.092>.
- Ahmed, A., Hasnain, S., 2014. Auxins as one of the factors of plant growth improvement by plant growth promoting rhizobacteria. *Pol. J. Microbiol.* 63 (3), 261.
- Ajjah, N., Fiodor, A., Pandey, A.K., Rana, A., Pranaw, K., 2023. Plant growth-promoting bacteria (PGPB) with biofilm-forming ability: A multifaceted agent for sustainable agriculture. *Diversity* 15, 112. <https://doi.org/10.3390/d15010112>.
- Alam, M.Z., Choudhury, T.R., Mridha, M.A.U., 2023. Arbuscular mycorrhizal fungi enhance biomass growth, mineral content, and antioxidant activity in tomato plants under drought stress. *J. Food Quality* 2581608. <https://doi.org/10.1155/2023/2581608>.
- Alamgir, A.N.M., Alamgir, A.N.M., 2018. Phytoconstituents – Active and inert constituents, metabolic pathways, chemistry and application of phytoconstituents, primary metabolic products, and bioactive compounds of primary metabolic origin. *Therap. Use Med. Plants Extracts: Vol 2: Phytochem. Bioactive Comp.* 25–164.
- Ali, Q., Ali, S., Iqbal, N., Javed, M.T., Rizwan, M., Khaliq, R., Shahid, S., Perveen, R., Alamri, S.A., Alyemeni, M.N., Wijaya, L., 2019. Alpha-tocopherol fertigation confers growth physio-biochemical and qualitative yield enhancement in field grown wheat deficit wheat (*Triticum aestivum* L.). *Sci. Rep.* 9 (1), 12924.
- Ali, S., Glick, B.R., 2024. Root exudate metabolites alter food crops microbiomes, impacting plant biocontrol and growth. *Crops* 4, 43–54. <https://doi.org/10.3390/crops4010004>.
- Ali, S., Tyagi, A., Mushtaq, M., Al-Mahmoudi, H., Bae, H., 2022. Harnessing plant microbiome for mitigating arsenic toxicity in sustainable agriculture. *Environ. Pollut.* 300, 118940.
- Ali, S.Z., Sandhya, V., Venkateswar Rao, L., 2014. Isolation and characterization of drought-tolerant ACC deaminase and exopolysaccharide-producing fluorescent *Pseudomonas* sp. *Ann. Microbiol.* 64 (2), 493–502.
- AlKahtani, M.D., Fouda, A., Attia, K.A., Al-Otaibi, F., Eid, A.M., Eweis, E.E.D., Hijri, M., St-Arnaud, M., Hassan, S.E.D., Khan, N., Hafez, Y.M., 2020. Isolation and characterization of plant growth promoting endophytic bacteria from desert plants and their application as bioinoculants for sustainable agriculture. *Agron* 10 (9), 1325.
- Alnahhas, R.N., Sadeghpour, M., Chen, Y., Frey, A.A., Ott, W., Josić, K., Bennett, M.R., 2020. Majority sensing in synthetic microbial consortia. *Nat. Commun.* 11 (1), 3659.
- Alori, E.T., Glick, B.R., Babalola, O.O., 2017. Microbial phosphorus solubilization and its potential for use in sustainable agriculture. *Front. Microbiol.* 8, 971.
- Alotaibi, M.O., Ikram, M., Alotaibi, N.M., Hussain, G.S., Ghoneim, A.M., Younis, U., Naz, N., Danish, S., 2023. Examining the role of AMF-biochar in the regulation of spinach growth attributes, nutrients concentrations, and antioxidant enzymes in mitigating drought stress. *Plant Stress*, 100205.
- Ambavaram, M.M.R., Basu, S., Krishnan, A., Ramegowda, V., Batlang, U., Rahman, L., Baisakh, N., Pereira, A., 2014. Coordinated regulation of photosynthesis in rice increases yield and tolerance to environmental stress. *Nat. Commun.* 5 (2014), 5302.
- Amy, C., Avice, J.-C., Laval, K., Bressan, M., 2022. Are native phosphate solubilizing bacteria a relevant alternative to mineral fertilizations for crops? Part I. when rhizobacteria meet plant P requirements. *Rhizosphere* 21, 100476. <https://doi.org/10.1016/j.rhisp.2022.100476>.
- Anderson, A.J., Hortin, J.M., Jacobson, A.R., Britt, D.W., McLean, J.E., 2023. Changes in metal-chelating metabolites induced by drought and a root microbiome in wheat. *Plants* 12, 1209. <https://doi.org/10.3390/plants12061209>.
- Andreo-Jimenez, B., Beest, D.E., Kruijer, W., Vannier, N., Kadam, N.N., Melandri, G., Krishna, J.S.V., 2023. Genetic mapping of the root microbiota in rice and its role in drought tolerance. *Rice* 16, 26. <https://doi.org/10.1186/s12284-023-00641-4>.
- Andreo-Jimenez, B., Vandenkoornhuys, P., Le Van, A., Heutinck, A., Duhamel, M., Kadam, N., Jagadish, K., Ruyter-Spira, C., Bouwmeester, H., 2019. Plant host and drought shape the root associated fungal microbiota in rice. *Peer J* 7, e7463.
- Anwar, A., Liu, Y., Dong, R., Bai, L., Yu, X., Li, Y., 2018. The physiological and molecular mechanism of brassinosteroid in response to stress: a review. *Biol. Res.* 51.
- Anwar, A.R., Ala, A., Kuswinanti, T., Syam'un, E., 2022. The ability of potassium-solubilizing fungi isolated from leucite potassium rock deposits. *Biodiversitas* 23 (12), 6579–6586. <https://doi.org/10.13057/biodiv/d231257>.
- Aparna, S., Devi, N., 2022. Rhizosphere functioning and rhizo-microbiome of two contrasting genotypes of rice under drought-induced conditions. *Res. Square* 1–26. <https://doi.org/10.21203/rs.3.rs-2267712/v1>.
- Arif, I., Batool, M., Schenk, P.M., 2020. Plant microbiome engineering: expected benefits for improved crop growth and resilience. *Trends Biotechnol.* 38 (12), 1385–1396.
- Armanhi, J.S.L., De Souza, R.S.C., Damasceno, N.D.B., De Araujo, L.M., Imperial, J., Arruda, P., 2018. A community-based culture collection for targeting novel plant growth-promoting bacteria from the sugarcane microbiome. *Front. Plant Sci.* 8, 2191.
- Arrese-Igor, C., Gonzalez, E.M., Marino, D., Ladrera, R., Larrainzar, E., Gil-Quintana, E., 2011. Physiological response of legumes nodules to drought. *Plant Stress* 5, 24–31.
- Arshad, M., Feyissa, B.A., Amyot, L., Aung, B., Hannoufa, A., 2017. MicroRNA156 improves drought stress tolerance in alfalfa (*Medicago sativa*) by silencing SPL13. *Plant Sci.* 258, 122–136.
- Arun, K.D., Sabarinathan, K.G., Gomathy, M., Kannan, R., Balachandar, D., 2020. Mitigation of drought stress in rice crop with plant growth-promoting abiotic stress-tolerant rice phyllosphere bacteria. *J. Basic Microbiol.* 60 (9), 768–786.
- Asari, S., Matzén, S., Petersen, M.A., Bejai, S., Meijer, J., 2016. Multiple effects of *Bacillus amyloliquefaciens* volatile compounds: plant growth promotion and growth inhibition of phytopathogens. *FEMS Microbiol. Ecol.* 92 (6), fiw070.
- Asghari, B., Khademian, R., Sedaghati, B., 2020. Plant growth promoting rhizobacteria (PGR) confer drought resistance and stimulate biosynthesis of secondary metabolites in pennyroyal (*Mentha pulegium* L.) under water shortage condition. *Sci. Hortic.* 263, 109132.
- Ashraf, M., 2010. Inducing drought tolerance in plants: recent advances. *Biotechnol. Adv.* 28 (1), 169–183.
- Ashwin, R., Bagyaraj, D.J., Mohan Raju, B., 2023. Ameliorating the drought stress tolerance of a susceptible soybean cultivar, MAUS 2 through dual inoculation with selected rhizobia and AM fungus. *Fungal Biol. Biotechnol.* 10, 1–19.
- Augé, R.M., 2001. Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. *Mycorrhiza* 11 (1), 3–42.
- Aven, T., 2016. Risk assessment and risk management: Review of recent advances on their foundation. *Eur. J. Operat. Res.* 253 (1), 1–13. <https://www.sciencedirect.com/science/article/pii/S0377221715011479>.
- Ayadi, M., Brini, F., Masmoudi, K., 2019. Overexpression of a wheat aquaporin gene, *tdpip2; 1*, enhances salt and drought tolerance in transgenic durum wheat cv. Maali. *Intern. J. Mol. Sci.* 20 (10), 2389.
- Azab, O., Ben Romdhane, W., El-Hendawy, S., Ghazy, A., Zakri, A.M., Abd-ElGawad, A.M., Al-Doss, A., 2024. Ectopic expression of a wheat R2R3-type MYB gene in transgenic tobacco enhances osmotic stress tolerance via maintaining ROS balance and improving root system architecture. *Biology* 13 (2), 128.
- Azarbad, H., Tremblay, J., Giard-Laliberté, C., Bainard, L.D., Yergeau, E., 2020. Four decades of soil water stress history together with host genotype constrain the response of the wheat microbiome to soil moisture. *FEMS Microbiol. Ecol.* 96 (7). <https://doi.org/10.1093/FEMSEC/FIAA098>.
- Azeem, F., Bilal, A., Rana, M.A., Muhammad, A.A., Habibullah, N., Sabir, H., Sumaira, R., Hamid, M., Usama, A., Muhammad, A., 2019. Drought affects aquaporins gene expression in important pulse legume chickpea (*Cicer arietinum* L.). *Pak. J. Bot.* 51, 81–88.
- Azeem, M., Soundari, P.G., Ali, A., Tahir, M.I., Imran, M., Bashir, S., Zhang, Z., 2022. Soil metagenomics: a step forward in metagenomics. *Arch. Agron. Soil Sci.* 68 (12), 1645–1663.
- Azizi, S., Kouchaksaraei, M.T., Hadian, J., Abad, A.R.F.N., Sanavi, S.A.M.M., Ammer, C., Bader, M.K.F., 2021. Dual inoculations of arbuscular mycorrhizal fungi and plant growth-promoting rhizobacteria boost drought resistance and essential oil yield of common myrtle. *For. Ecol. Manag.* 497, 119478.
- Badr, M.A., El-Tohamy, W.A., Abou-Hussein, S.D., Gruda, N.S., 2020. Deficit irrigation and arbuscular mycorrhiza as a water-saving strategy for eggplant production. *Horticulturae* 6, 45.
- Bahadur, A., Batool, A., Nasir, F., Jiang, S., Mingsen, Q., Zhang, Q., Pan, J., Liu, Y., Feng, H., 2019. Mechanistic insights into arbuscular mycorrhizal fungi-mediated drought stress tolerance in plants. *Intern. J. Mol. Sci.* 20, 4199.
- Bai, B., Liu, W., Qiu, X., Zhang, J., Zhang, J., Bai, Y., 2022. The root microbiome: community assembly and its contributions to plant fitness. *J. Integr. Plant Biol.* 64, 230–243.
- Bailey, A., Groenhuizen, U., Schulz, S., Geisler, M., Eberl, L., Weiskopf, L., 2014. The inter-kingdom volatile signal indole promotes root development by interfering with auxin signalling. *Plant J.* 80 (5), 758–771.
- Bakker, P.A.H.M., Pieterse, C.M.J., de Jonge, R., Berendsen, R.L., 2018. The soil-borne legacy. *Cell* 172, 1178–1180.
- Bakr, J., Pék, Z., Helyes, L., Posta, K., 2018. Mycorrhizal inoculation alleviates water deficit impact on field-grown processing tomato. *Polish J. Environ. Stud.* 27, 1949–1958.
- Baloda, A., Madanpotra, S., 2017. Transformation of mungbean plants for salt and drought tolerance by introducing a gene for an osmoprotectant glycine betaine. *J. Plant Stress Physiol.* 5–11.
- Banavath, J.N., Chakradhar, T., Pandit, V., Konduru, S., Guduru, K.K., Akila, C.S., Podha, S., Puli, C.O., 2018. Stress inducible overexpression of AtHDG11 leads to

- improved drought and salt stress tolerance in peanut (*Arachis hypogaea* L.). *Front. Chem.* 6, 34.
- Barnard, R.L., Osborne, C.A., Firestone, M.K., 2013. Responses of soil bacterial and fungal communities to extreme desiccation and rewetting. *ISME J.* 7, 2229–2241.
- Barnawal, D., Bharti, N., Pandey, S.S., Pandey, A., Chanotiya, C.S., Kalra, A., 2017. Plant growth-promoting rhizobacteria enhance wheat salt and drought stress tolerance by altering endogenous phytohormone levels and TaCTR1/TaDREB2 expression. *Physiol. Plant.* 161 (4), 502–514.
- Baslam, M., Goicoechea, N., 2012. Water deficit improved the capacity of arbuscular mycorrhizal fungi (AMF) for inducing the accumulation of antioxidant compounds in lettuce leaves. *Mycorrhiza* 22, 347–359.
- Bazany, K.E., Wang, J.T., Delgado-Baquerizo, M., Singh, B.K., Trivedi, P., 2022. Water deficit affects inter-kingdom microbial connections in plant rhizosphere. *Environ. Microbiol.* 24 (8), 3722–3734. <https://doi.org/10.1111/1462-2920.16031>.
- Becklin, K.M., Anderson, J.T., Gerhart, L.M., Wadgymar, S.M., Wessinger, C.A., Ward, J. K., 2016. Examining plant physiological responses to climate change through an evolutionary lens. *Plant Physiol.* 172 (2), 635–649.
- Begum, N., Akhtar, K., Ahanger, M.A., Iqbal, M., Wang, P.P., Mustafa, N.S., Zhang, L.X., 2021. Arbuscular mycorrhizal fungi improve growth, essential oil, secondary metabolism, and yield of tobacco (*Nicotiana tabacum* L.) under drought stress conditions. *Environ. Sci. Pollut. Res.* 28, 45276–45295. <https://doi.org/10.1007/s11356021-13755-3>.
- Behrooz, A., Vahdati, K., Rejali, F., Lotfi, M., Sarikhani, S., Leslie, C., 2019. Arbuscular mycorrhiza and plant growth-promoting bacteria alleviate drought stress in walnut. *Hortic. Sci.* 54 (6), 1087–1092.
- Belimov, A.A., Dodd, I.C., Safronova, V.I., Shaposhnikov, A.I., Azarova, T.S., Makarova, N.M., Davies, W.J., Tikhonovich, I.A., 2015. Rhizobacteria that produce auxins and contain 1-amino-cyclopropane-1-carboxylic acid deaminase decrease amino acid concentrations in the rhizosphere and improve growth and yield of well-watered and water-limited potato (*Solanum tuberosum*). *Ann. Appl. Biol.* 167 (1), 11–25.
- Bender, S.F., Wagg, C., van der Heijden, M.G., 2016. An underground revolution: biodiversity and soil ecological engineering for agricultural sustainability. *Trends Ecol. Evol.* 31 (6), 440–452.
- Beneduzi, A., Peres, D., Vargas, L.K., Bodanese-Zanettini, M.H., Passaglia, L.M.P., 2008. Evaluation of genetic diversity and plant growth promoting activities of nitrogen-fixing bacilli isolated from rice fields in South Brazil. *Appl. Soil Ecol.* 39 (3), 311–320.
- Bennett, J.W., Hung, R., Lee, S., Padhi, S., 2012. 18 Fungal and bacterial volatile organic compounds: an overview and their role as ecological signaling agents. *Fungal Assoc.* 373–393.
- Bérard, A., Sassi, M.B., Kaisermann, A., Renault, P., 2015. Soil microbial community responses to heat wave components: drought and high temperature. *Clim. Res.* 66, 243–264.
- Berg, G., Rybakova, D., Grube, M., Köberl, M., 2016. The plant microbiome explored: implications for experimental botany. *J. Exp. Bot.* 67 (4), 995–1002.
- Bhagat, N., Sharma, S., Ambaradar, S., Raj, S., Trakroo, D., Horacek, M., Zouagui, R., Sbabou, L., Vakhlu, J., 2021. Microbiome fingerprint as biomarker for geographical origin and heredity in *Crocus sativus*: A feasibility study. *Food. Sustain. Geogr. Syst.* 5, 688393.
- Bhanbhro, N., Wang, H.J., Yang, H., Xu, X.J., Jakhar, A.M., Shalmani, A., Zhang, R.X., Baksh, Q., Akbar, G., Jakhro, M.I., Khan, Y., Chen, K.M., 2024. Revisiting the molecular mechanisms and adaptive strategies associated with drought stress tolerance in common wheat (*Triticum aestivum* L.). *Plant Stress* 11, 100298. <https://doi.org/10.1016/j.stress.2023.100298>.
- Bhatt, M.D., Bhatt, D., 2020. Strigolactones in overcoming environmental stresses. *Protect. Chem. Agents Ameliorat. Plant Abiotic Stress: Biochem. Mol. Perspect.* 327–341.
- Bhatta, M., Morgounov, A., Belamkar, V., Baenziger, P.S., 2018. Genome-wide association study reveals novel genomic regions for grain yield and yield-related traits in drought-stressed synthetic hexaploid wheat. *Intern. J. Mol. Sci.* 19, 3011.
- Bhattacharjee, K., Barua, S., Churungo, N.K., Joshi, S.R., 2023. Characterization of biomineralizing and plant growth-promoting attributes of lithobiontic bacteria. *Curr. Microbiol.* 80 (2), 80. <https://doi.org/10.1007/s00284-022-03176-x>, 20.
- Bhattacharyya, D., Garladinne, M., Lee, Y.H., 2015. Volatile indole produced by rhizobacterium *Proteus vulgaris* JBS202 stimulates growth of *Arabidopsis thaliana* through auxin, cytokinin, and brassinosteroid pathways. *J. Plant Growth Regul.* 34, 158–168.
- Bhauso, T.T., Radhakrishnan, T., Kumar, A., Mishra, G.G., Dobarja, J.J., Patel, K., Rajam, M.M., 2014. Overexpression of bacterial mtD gene in peanut improves drought tolerance through accumulation of mannitol. *Sci. World J.* 2014.
- Bhusal, N., Kim, H.S., Han, S.G., Yoon, T.M., 2020. Photosynthetic traits and plant-water relations of two apple cultivars grown as bi-leader trees under long-term waterlogging conditions. *Environ. Exp. Bot.* 176, 104111.
- Bilal, S., Shahzad, R., Imran, M., Jan, R., Kim, K.M., Lee, J.J., 2020. Synergistic association of endophytic fungi enhances *Glycine max* L. resilience to combined abiotic stresses: Heavy metals, high temperature and drought stress. *Ind. Crops Prod.* 143, 111931.
- Bista, D.R., Heckathorn, S.A., Jayawardena, D.M., Mishra, S., Boldt, J.K., 2018. Effects of drought on nutrient uptake and the levels of nutrient-uptake proteins in roots of drought-sensitive and-tolerant grasses. *Plants* 7 (2), 28.
- Bitas, V., Kim, H.S., Bennett, J.W., Kang, S., 2013. Sniffing on microbes: diverse roles of microbial volatile organic compounds in plant health. *Mol. Plant Microbe Interact.* 26 (8), 835–843.
- Bittencourt, P.P., Alves, A.F., Ferreira, M.B., da Silva Irineu, L.E.S., Pinto, V.B., Olivares, F.L., 2023. Mechanisms and applications of bacterial inoculants in plant drought stress tolerance. *Microorganisms* 11, 502. <https://doi.org/10.3390/microorganisms11020502>.
- Bogati, K., Walczak, M., 2022. The impact of drought stress on soil microbial community, enzyme activities and plants. *Agronomy* 12, 189.
- Bogati, K.A., Golińska, P., Sewerniak, P., Burkowska-But, A., Walczak, M., 2023. Deciphering the impact of induced drought in agriculture soils: changes in microbial community structure, enzymatic and metabolic diversity. *Agronomy* 13, 1417. <https://doi.org/10.3390/agronomy13051417>.
- Breitkreuz, C., Herzig, L., Buscot, F., Reitz, T., Tarkka, M., 2021. Interactions between soil properties, agricultural management and cultivar type drive structural and functional adaptations of the wheat rhizosphere microbiome to drought. *Environ. Microbiol.* 23 (10), 5866–5882.
- Bresson, J., Varoquaux, F., Bontpart, T., Touraine, B., Vile, D., 2013. The PGPR strain *Phyllobacterium brassicacearum* STM 196 induces a reproductive delay and physiological changes that result in improved drought tolerance in *Arabidopsis*. *New Phytol.* 200 (2), 558–569.
- Brodersen, C.R., Roddy, A.B., Wason, J.W., McElrone, A.J., 2019. Functional status of xylem through time. *Annu. Rev. Plant Biol.* 70, 407–433.
- Brundrett, M.C., Tedersoo, L., 2018. Evolutionary history of mycorrhizal symbioses and global host plant diversity. *New Phytol.* 220 (4), 1108–1115.
- Bruno, L.B., Karthik, C., Ma, Y., Kadirvelu, K., Freitas, H., Rajkumar, M., 2020. Amelioration of chromium and heat stresses in *Sorghum bicolor* by Cr⁶⁺ reducing-thermotolerant plant growth promoting bacteria. *Chemosphere* 244, 125521.
- Bukhari, S.A.H., Peerzada, A.M., Javed, M.H., Dawood, M., Hussain, N., Ahmad, S., 2019. Growth and development dynamics in agronomic crops under environmental stress. *Agronomic Crops: Volume 1. Production Technologies*, pp. 83–114.
- Bulgakov, V.P., Vereshchagina, Y.V., Bulgakov, D.V., Veremeichik, G.N., Shkryl, Y.N., 2018. The *A4-rolB* plant oncogene affects multiple signaling protein modules related to hormone signaling and plant defense. *Sci. Rep.* <https://doi.org/10.1038/s41598-018-20694-6>.
- Cabello, J.V., Giacomelli, J.I., Gomez, M.C., Chan, R.L., 2017. The sunflower transcription factor HaHB11 confers tolerance to water deficit and salinity to transgenic *Arabidopsis* and alfalfa plants. *J. Biotechnol.* 257, 35–46.
- Cabral, C., Ravnsov, S., Tringovska, I., Wollenweber, B., 2016. Arbuscular mycorrhizal fungi modify nutrient allocation and composition in wheat (*Triticum aestivum* L.) subjected to heat-stress. *Plant Soil* 408, 385–399.
- Caddell, D.F., Deng, S., Coleman-Derr, D., 2019. Role of the plant root microbiome in abiotic stress tolerance. *Seed Endophytes: Biol. Biotechnol.* 273–311.
- Campos, E.V.R., Pereira, A.E.S., Aleksieienko, I., do Carmo, G.C., Gohari, G., Santalla, C., Fraceto, L.F., Oliveira, H.C., 2023. Encapsulated plant growth regulators and associative microorganisms: nature-based solutions to mitigate the effects of climate change on plants. *Plant Sci.* 111688 <https://doi.org/10.1016/j.plantsci.2023.111688>.
- Canarini, A., Schmidt, H., Fuchslueger, L., Martin, V., Herbold, C.W., Zezula, D., Gündler, P., 2021. Ecological memory of recurrent drought modifies soil processes via changes in soil microbial community. *Nat. Commun.* 12, 5308. <https://doi.org/10.1038/s41467-021-25675-4>.
- Cao, Z.H., Zhang, S.Z., Wang, R.K., Zhang, R.F., Hao, Y.J., 2013. Genome wide analysis of the apple MYB transcription factor family allows the identification of MdoMYB121 gene conferring abiotic stress tolerance in plants. *PLoS ONE* 8, e69955.
- Carbone, M.J., Alaniz, S., Mondino, P., Gelabert, M., Eichmeier, A., Tekielska, D., Bujanda, R., Gramaje, D., 2021. Drought influences fungal community dynamics in the grapevine rhizosphere and root microbiome. *J. Fungi* 7, 686.
- Carlson, R., Tugizimana, F., Steenkamp, P.A., Dubery, I.A., Hassen, A.I., Labuschagne, N., 2020. Rhizobacteria-induced systemic tolerance against drought stress in *Sorghum bicolor* (L.) Moench. *Microbiol. Res.* 232, 126388.
- Carter, K.R., Nachtsheim, A.C., Dickman, L.T., Moore, E.R., Negi, S., Heneghan, J.P., Sabella, A.J., 2023. Drought conditioning of rhizosphere microbiome influences maize water use traits. *Plant Soil* 11 (2), e01476. <https://doi.org/10.1007/s11104-023-06204-2>, 22.
- Cassán, F., Vanderleyden, J., Spaepen, S., 2014. Physiological and agronomical aspects of phytohormone production by model plant-growth-promoting rhizobacteria (PGPR) belonging to the genus *Azospirillum*. *J. Plant Growth Regul.* 33, 440–459.
- Chandra, D., Srivastava, R., Gupta, V.V., Franco, C.M., Sharma, A.K., 2019. Evaluation of ACC-deaminase-producing rhizobacteria to alleviate water-stress impacts in wheat (*Triticum aestivum* L.) plants. *Can. J. Microbiol.* 65 (5), 387–403.
- Chandra, P., Tripathi, P., Chandra, A., 2018. Isolation and molecular characterization of plant growth-promoting *Bacillus* spp. and their impact on sugarcane (*Saccharum* spp. hybrids) growth and tolerance towards drought stress. *Acta Physiol. Plant* 40 (11), 199.
- Chandra, P., Wunna, A., Verma, P., Chandra, A., Sharma, R.K., 2021. Strategies to mitigate the adverse effect of drought stress on crop plants – influences of soil bacteria: a review. *Pedosphere* 31 (3), 496–509.
- Chaudhary, D., Sindhu, S.S., 2015. Inducing salinity tolerance in chickpea (*Cicer arietinum* L.) by inoculation of 1-aminocyclopropane-1-carboxylate acid deaminase containing *Mesorhizobium* strains. *Afr. J. Microbiol. Res.* 9, 117–124.
- Chaudhary, S., Sindhu, S.S., 2024. Microbiome-mediated remediation of heavy metals: Impact on soil health, crop production, and ecosystem sustainability. In: Parry, J.A., Li, W.J. (Eds.), *Microbiome-Assisted Bioremediation: Rehabilitating Agricultural Soils*. Academic Press, Elsevier, pp. 257–311. <https://doi.org/10.1016/B978-0-443-21911-5.00019-2>.
- Chaudhary, V., Runge, P., Sengupta, P., Doehlemann, G., Parker, J.E., Kemen, E., 2021. Shaping the leaf microbiota: plant-microbe-microbe interactions. *J. Exp. Bot.* 72, 36–56.

- Chauffour, F., Bailly, M., Perreau, F., Cuff, G., Suzuki, H., Collet, B., Frey, A., 2019. Multi-omics analysis reveals sequential roles for ABA during seed maturation. *Plant Physiol.* 180, 1198–1218.
- Chauhan, P.K., Upadhyay, S.K., 2023. Exo-polysaccharide producing bacteria can induce maize plant growth and soil health under saline conditions. *Biotechnol. Genet. Engin. Rev.* <https://doi.org/10.1080/02648725.2022.2163812>.
- Chaves, M.M., Flexas, J., Pinheiro, C., 2009. Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. *Ann. Bot.* 103 (4), 551–560.
- Chaves, M.M., Maroco, J.P., Pereira, J.S., 2003. Understanding plant responses to drought—from genes to the whole plant. *Funct. Plant Biol.* 30 (3), 239–264.
- Chen, L., Xin, X.L., Zhang, J.B., Redmile-Gordon, M., Nie, G.S., Wang, Q.Y., 2019. Soil characteristics overwhelm cultivar effects on the structure and assembly of root-associated microbiomes of modern maize. *Pedosphere* 29 (3), 360–373. [https://doi.org/10.1016/S1002-0160\(17\)60370-9](https://doi.org/10.1016/S1002-0160(17)60370-9).
- Chen, M., Arato, M., Borghi, L., Nouri, E., Reinhardt, D., 2018. Beneficial services of arbuscular mycorrhizal fungi—from ecology to application. *Front. Plant Sci.* 9, 1270.
- Chen, Y., Yang, H., Shen, Z., Ye, J., 2022. Whole-genome sequencing and potassium-solubilizing mechanism of *Bacillus aryabhattai* SK1-7. *Front. Microbiol.* 12, 722379. <https://doi.org/10.3389/fmicb.2021.722379>.
- Chieb, M., Gachomo, E.W., 2023. The role of plant growth promoting rhizobacteria in plant drought stress responses. *BMC Plant Biol.* 23, 407. <https://doi.org/10.1186/s12870-023-04403-8>.
- Cho, S.M., Kang, B.R., Han, S.H., Anderson, A.J., Park, J.Y., Lee, Y.H., Cho, B.H., Yang, K.Y., Ryu, C.M., Kim, Y.C., 2008. 2R, 3R-butenediol, a bacterial volatile produced by *Pseudomonas chlororaphis* O6, is involved in induction of systemic tolerance to drought in *Arabidopsis thaliana*. *Mol. Plant Microbe Interact.* 21 (8), 1067–1075.
- Cho, S.M., Kang, B.R., Kim, Y.C., 2013. Transcriptome analysis of induced systemic drought tolerance elicited by *Pseudomonas chlororaphis* O6 in *Arabidopsis thaliana*. *Plant Pathol. J.* 29 (2), 209.
- Chodak, M., Gołębiewski, M., Morawska-Ploskonka, J., Kuduk, K., Niklińska, M., 2015. Soil chemical properties affect the reaction of forest soil bacteria to drought and rewetting stress. *Ann. Microbiol.* 65, 1627–1637.
- Choudhary, D.K., Johri, B.N., Prakash, A., 2008. Volatiles as priming agents that initiate plant growth and defence responses. *Curr. Sci.* 595–604.
- Choudhary, D.K., Sharma, A.K., Agarwal, P., Varma, A., Tuteja, N., 2017. Volatiles and food security. Springer, Singapore.
- Compant, S., Samad, A., Faist, H., Sessitsch, A., 2019. A review on the plant microbiome: Ecology, functions, and emerging trends in microbial application. *J. Adv. Res.* 19, 29–37.
- Compant, S., Van Der Heijden, M.G., Sessitsch, A., 2010. Climate change effects on beneficial plant–microorganism interactions. *FEMS Microbiol. Ecol.* 73, 197–214.
- Contesto, C., Milesi, S., Mantelin, S., et al., 2010. The auxin-signaling pathway is required for the lateral root response of *Arabidopsis* to the rhizobacterium *Phyllobacterium brassicacearum*. *Planta* 232, 1455–1470.
- Cortes, A.J., This, D., Carolina, C., Madrinan, S., Blair, M.W., 2012. Nucleotide diversity patterns at the drought-related DREB2 encoding genes in wild and cultivated common bean (*Phaseolus vulgaris* L.). *Theor. Appl. Genet.* 125, 1069–1085.
- Craig, W., Tepfer, M., Degrassi, G., Ripandelli, D., 2008. An overview of general features of risk assessments of genetically modified crops. *Euphytica* 164 (3), 853–880.
- Cramer, G.R., Urano, K., Delrot, S., Pezzotti, M., Shinozaki, K., 2011. Effects of abiotic stress on plants: a systems biology perspective. *BMC Plant Biol.* 11 (1), 1–14.
- Cui, X., Tang, M., Li, L., Chang, J., Yang, X., Chang, H., Chen, Z., 2024. Expression patterns and molecular mechanisms regulating drought tolerance of soybean [*Glycine max* (L.) Merr.] conferred by transcription factor gene GmNAC19. *Intern. J. Mol. Sci.* 25 (4), 2396.
- Cui, X.H., Hao, F.S., Chen, H., Chen, J., Wang, X.C., 2008. Expression of the *Vicia faba* VPIP1 gene in *Arabidopsis thaliana* plants improves their drought resistance. *J. Plant Res.* 121, 207–214.
- Curá, J.A., Franz, D.R., Filosofio, J.E., Balestrasse, K.B., Burgueño, L.E., 2017. Inoculation with *Azospirillum* sp., *Herbaspirillum* sp. bacteria increases the tolerance of maize to drought stress. *Microorganisms* 5 (3), 41.
- da Silva, E.C., de Albuquerque, M.B., de Azevedo Neto, A.D., da Silva Junior, C.D., 2013. Drought and its consequences to plants – From individual to ecosystem. *Resp. Org. Water Stress* 18–47.
- Dai, L., Zhang, G., Yu, Z., Ding, H., Xu, Y., Zhang, Z., 2019. Effect of drought stress and developmental stages on microbial community structure and diversity in peanut rhizosphere soil. *Intern. J. Mol. Sci.* 20, 2265.
- Danish, S., Zafar-ul-Hye, M., Fahad, S., Saud, S., Brtnicky, M., Hammerschmidt, T., Datta, R., 2020. Drought stress alleviation by ACC deaminase producing *Achromobacter xylosoxidans* and *Enterobacter cloacae*, with and without timber waste biochar in maize. *Sustainability* 12 (15), 6286.
- Daryanto, S., Wang, L., Jacinthe, P.A., 2016. Global synthesis of drought effects on maize and wheat production. *PLoS One* 11 (5), e0156362.
- Das, S., Sarkar, S., 2024. Arbuscular mycorrhizal fungal contribution towards plant resistance to drought conditions. *Front. Fungal Biol.* 5, 1355999.
- Dastogeer, K.M.G., Tumpa, F.H., Sultana, A., Akter, M.A., Chakraborty, A., 2020. Plant microbiome – an account of the factors that shape community composition and diversity. *Curr. Plant Biol.* 23, 100161.
- Daszkowska-Golec, A., Szarejko, I., 2013. Open or close the gate–stomata action under the control of phytohormones in drought stress conditions. *Front. Plant Sci.* 4, 138.
- de Nijs, E.A., Hicks, L.C., Leizeaga, A., Tietema, A., Rousk, J., 2019. Soil microbial moisture dependences and responses to drying–rewetting: The legacy of 18 years drought. *Glob. Change Biol.* 25 (3), 1005–1015.
- De Souza, R.S.C., Armanhi, J.S.L., Arruda, P., 2020. From microbiome to traits: designing synthetic microbial communities for improved crop resiliency. *Front. Plant Sci.* 11, 1179.
- de Vries, F.T., Griffiths, R.I., Bailey, M., Craig, H., Giralanda, M., Gweon, H.S., Hallin, S., Kaisermann, A., Keith, A.M., Kretschmar, M., Lemanceau, P., 2018. Soil bacterial networks are less stable under drought than fungal networks. *Nat. Commun.* 9 (1), 3033.
- de Vries, F.T., Griffiths, R.I., Knight, C.G., Nicolitch, O., Williams, A., 2020. Harnessing rhizosphere microbiomes for drought-resilient crop production. *Science* 368, 270–274.
- Deng, L., Peng, C., Kim, D.G., Li, J., Liu, Y., Hai, X., Liu, Q., Huang, C., Shanguan, Z., Kuzyakov, Y., 2021. Drought effects on soil carbon and nitrogen dynamics in global natural ecosystems. *Earth-Sci. Rev.* 214, 103501.
- Devarajan, A.K., Muthukrishnan, G., Truu, J., Truu, M., Ostonen, I., Kizhaeral, S.S., 2021. The foliar application of rice phyllosphere bacteria induces drought stress tolerance in *Oryza sativa* (L.). *Plants* 10. <https://doi.org/10.3390/plants10020387>.
- Devincenzi, A.J., 2020. Scales of Sustainable Agricultural Water Management. University of California, Davis, CA, USA. Ph.D. Thesis.
- Dhankhar, R., Gupta, S., Gulati, P., 2023. Insights on plant–microbe interactions in soil in relation to iron dynamics. *Vegetos* 36, 750–767. <https://doi.org/10.1007/s42535-022-00467-3>.
- Dhungana, I., Kantar, M.B., Nguyen, N.H., 2023. Root exudate composition from different plant species influences the growth of rhizosphere bacteria. *Rhizosphere* 25, 100645. <https://doi.org/10.1016/j.rhisph.2022.100645>.
- Dietz, K.J., 2016. Thiol-based peroxidases and ascorbate peroxidases: why plants rely on multiple peroxidase systems in the photosynthesizing chloroplast? *Mol. Cells* 39 (1), 20.
- Dietz, K.J., Vogel, M.O., Viehhauser, A., 2010. AP2/EREBP transcription factors are part of gene regulatory networks and integrate metabolic, hormonal and environmental signals in stress acclimation and retrograde signalling. *Protoplasma* 245, 3–14.
- Divi, U.K., Rahman, T., Krishna, P., 2010. Brassinosteroid-mediated stress tolerance in *Arabidopsis* shows interactions with abscisic acid, ethylene and salicylic acid pathways. *BMC Plant Biol.* 10, 1–14.
- Dong, M., Kuramae, E.E., Zhao, M., Li, R., Shen, Q., Kowalchuk, G.A., 2023. Tomato growth stage modulates bacterial communities across different soil aggregate sizes and disease levels. *ISME Commun.* 3, 104. <https://doi.org/10.1038/s43705-023-00312-x>.
- Duan, H., Liu, W., Zhou, L., Han, B., Huo, S., El-Sheekh, M., Dong, H., Li, X., Xu, T., Elshobary, M., 2023. Improving saline alkali soil and promoting wheat growth by co-applying potassium solubilizing bacteria and cyanobacteria produced from brewery wastewater. *Front. Environ. Sci.* 11, 1170734. <https://doi.org/10.3389/fenvs.2023.1170734>.
- Duan, H.X., Luo, C.L., Zhou, R., Zhao, L., Zhu, S.G., Chen, Y., Zhu, Y., Xiong, Y.C., 2024. AM fungus promotes wheat grain filling via improving rhizosphere water and nutrient availability under drought and low density. *Appl. Soil Ecol.* 193, 105159.
- Dubey, A., Saiyam, D., Kumar, A., Hashem, A., Abd Allah, E.F., Khan, M.L., 2021. Bacterial root endophytes: Characterization of their competence and plant growth promotion in soybean (*Glycine max* (L.) Merr.) under drought stress. *Intern. J. Environ. Res. Public Health* 18 (3), 931.
- Dubouzet, J.G., Sakuma, Y., Ito, Y., Kasuga, M., Dubouzet, E.G., Miura, S., Seki, M., Shinozaki, K., Yamaguchi-Shinozaki, K., 2003. OsDREB genes in rice, *Oryza sativa* L., encode transcription activators that function in drought-, high-salt- and cold-responsive gene expression. *Plant J.* 33, 751–763.
- Ebrahimi-Zarandi, M., Etesami, H., Glick, B.R., 2023. Fostering plant resilience to drought with Actinobacteria: Unveiling perennial allies in drought stress tolerance. *Plant Stress* 10, 100242. <https://doi.org/10.1016/j.stress.2023.100242>.
- Eckerstorfer, M.F., Engelhard, M., Heissenberger, A., Simon, S., Teichmann, H., 2019. Plants developed by new genetic modification techniques-comparison of existing regulatory frameworks in the EU and non-EU countries. *Front. Bioengin. Biotechnol.* 7 (26), 1–16. <https://doi.org/10.3389/fbioe.2019.00026>.
- Effmert, U., Kalderás, J., Warnke, R., Piechulla, B., 2012. Volatile mediated interactions between bacteria and fungi in the soil. *J. Chem. Ecol.* 38, 665–703.
- Egamberdieva, D., Wirth, S.J., Alqarawi, A.A., Abd Allah, E.F., Hashem, A., 2017. Phytohormones and beneficial microbes: Essential components for plants to balance stress and fitness. *Front. Microbiol.* 8, 2104.
- Eisenstein, M., 2013. Plant breeding: Discovery in a dry spell. *Nature* 501 (7468), S7–S9.
- Eldakak, M., Milad, S.I., Nawar, A.I., Rohila, J.S., 2013. Proteomics: a biotechnology tool for crop improvement. *Front. Plant Sci.* 4, 35.
- Escudero-Martinez, C., Bulgarelli, D., 2023. Engineering the crop microbiota through host genetics. *Ann. Rev.* 61, 257–277. <https://doi.org/10.1146/annurev-phyto-021621-121447>.
- Essahibi, A., Benhiba, L., Babram, M.A., Ghoulam, C., Qaddoury, A., 2018. Influence of arbuscular mycorrhizal fungi on the functional mechanisms associated with drought tolerance in carob (*Ceratonia siliqua* L.). *Trees* 32, 87–97.
- Etesami, H., Maheshwari, D.K., 2018. Use of plant growth promoting rhizobacteria (PGPRs) with multiple plant growth promoting traits in stress agriculture: Action mechanisms and future prospects. *Ecotoxicol. Environ. Saf.* 156, 225–246.
- Fang, Y., Xiong, L., 2015. General mechanisms of drought response and their application in drought resistance improvement in plants. *CMLS* 72, 673–689.
- Farooq, M., Wahid, A., Kobayashi, N., Fujita, D., Basra, S., 2009. Plant drought stress: effects, mechanisms and management. In: Lichtfouse, E., Navarrete, M., Debacle, P., Veronique, S., Alberola, C. (Eds.), *Sustainable Agriculture*. Springer, Dordrecht/Netherlands, pp. 153–188. https://doi.org/10.1007/978-90-481-266-6-8_12.
- Fetsiukh, A., Conrad, J., Bergquist, J., Timmusk, S., 2021. Silica particles trigger the exopolysaccharide production of harsh environment isolates of growth-promoting rhizobacteria and increase their ability to enhance wheat biomass in drought-stressed soils. *Int. J. Mol. Sci.* 22 (12), 6201.

- Field, K.J., Daniell, T., Johnson, D., Helgason, T., 2021. Mycorrhizal mediation of sustainable development goals. *Plants People Planet* 3 (5), 430–432.
- Fitzpatrick, C.R., Copeland, J., Wang, P.W., Guttman, D.S., Kotanen, P.M., Johnson, M.T., 2018. Assembly and ecological function of the root microbiome across angiosperm plant species. *Proc. Natl. Acad. Sci. USA* 115, E1157–E1165.
- Fitzpatrick, C.R., Salas-González, I., Conway, J.M., Finkel, O.M., Gilbert, S., Russ, D., Teixeira, P.J.P.L., Dangel, J.L., 2020. The plant microbiome: from ecology to reductionism and beyond. *Annu. Rev. Microbiol.* 74, 81–100.
- Flemming, H.C., Wingender, J., 2010. The biofilm matrix. *Nat. Rev. Microbiol.* 8 (9), 623–633.
- Frechilla, S., Gonzalez, E.M., Royuela, M., Minchin, F.R., Aparicio-Tejo, P.M., Arrese-Igor, C., 2000. Source of nitrogen nutrition (nitrogen fixation or nitrate assimilation) is a major factor involved in pea response to moderate water stress. *J. Plant Physiol.* 157 (6), 609–617.
- Fry, E.L., Manning, P., Macdonald, C., Hasegawa, S., De Palma, A., Power, S.A., Singh, B.K., 2016. Shifts in microbial communities do not explain the response of grassland ecosystem function to plant functional composition and rainfall change. *Soil Biol. Biochem.* 92, 199–210.
- Fu, R., Feng, H., Dini-Andreote, F., Wang, Z., Bo, C., Cao, W., Yang, K., 2021. Modulation of the tomato rhizosphere microbiome via changes in root exudation mediated by the ethylene receptor NR. *Microorganisms* 9, 2456.
- Fukami, J., Cerezini, P., Hungria, M., 2018. *Azospirillum*: benefits that go far beyond biological nitrogen fixation. *Amb. Exp.* 8 (1), 73.
- Fusco, G.M., Carillo, P., 2023. Ethylene interplay with metabolites in crops. *The Plant Hormone Ethylene*. Academic Press, pp. 181–190.
- Gabay, G., Wang, H., Zhang, J., Moriconi, J.I., Burguener, G.F., Gualano, L.D., et al., 2023. Dosage differences in 12-oxophytodienoate reductase genes modulate wheat root growth. *Nat. Commun.* 14, 539. <https://doi.org/10.1038/s41467-023-36248-y>.
- Gaete, A., Pulgar, R., Hodar, C., Maldonado, J., Pavez, L., Zamorano, D., Pastenes, C., González, M., Franck, N., Mandakovic, D., 2021. Tomato cultivars with variable tolerances to water deficit differentially modulate the composition and interaction patterns of their rhizosphere microbial communities. *Front. Plant Sci.* 12, 688533. <https://doi.org/10.3389/fpls.2021.688533>.
- Gamalero, E., Glick, B.R., 2015. Bacterial modulation of plant ethylene levels. *Plant Physiol.* 169 (1), 13–22.
- Gamalero, E., Glick, B.R., 2022. Recent advances in bacterial amelioration of plant drought and salt stress. *Biology* 11, 437. <https://doi.org/10.3390/biology11030437>.
- Ganguly, M., Roychoudhury, A., Sengupta, D.N., Datta, S.K., Datta, K., 2020. Independent overexpression of OsRab16A and AtDREB1A exhibit enhanced drought tolerance in transgenic aromatic rice variety Pusa Sugandhi. *J. Plant Biochem. Biotechnol.* 29, 503–517. <https://doi.org/10.1007/s13562-020-00565-w>.
- Gao, H., Cui, J., Liu, S., Wang, S., Lian, Y., Bai, Y., Zhu, T., Wu, H., Wang, Y., Yang, S., Li, X., Zhuang, J., Chen, L., Gong, Z., Qin, F., 2022. Natural variations of ZmSRO1D modulate the trade-off between drought resistance and yield by affecting ZmRBOHC mediated stomatal ROS production in maize. *Mol. Plant.* 15, 1558–1574.
- Gao, S., Xu, J., Song, W., Dong, J., Xie, L., Xu, B., 2024. Overexpression of BnMYB2L-1 improves plant drought tolerance via the ABA-dependent pathway. *Plant Physiol. Biochem.* 207, 108293. <https://doi.org/10.1016/j.plaphy.2023.108293>.
- Gao, Y.F., Liu, J.K., Yang, F.M., Zhang, G.Y., Wang, D., Zhang, L., Ou, Y.B., Yao, Y.A., 2019. The WRKY transcription factor: WRKY8 promotes resistance to pathogen infection and mediates drought and salt stress tolerance in *Solanum lycopersicum*. *Physiol. Plant* 168 (1), 98–117.
- García, J.E., Maroniche, G., Creus, C., Suárez-Rodríguez, R., Ramirez-Trujillo, J.A., Groppa, M.D., 2017. In vitro PGPB properties and osmotic tolerance of different *Azospirillum* native strains and their effects on growth of maize under drought stress. *Microbiol. Res.* 202, 21–29.
- Ge, M., Tang, Y., Guan, Y., Lv, M., Zhou, C., Ma, H., Lv, J., 2024. TaWRKY31, a novel WRKY transcription factor in wheat, participates in regulation of plant drought stress tolerance. *BMC Plant Biol.* 24 (1), 27.
- Gebauer, L., Breitkreuz, C., Heintz-buschart, A., Reitz, T., Buscot, F., Tarkka, M., Bouffaud, M.L., 2022. Water deficit history selects plant beneficial soil bacteria differently under conventional and organic farming. *Front. Microbiol.* 13, 824437. <https://doi.org/10.3389/fmicb.2022.824437>.
- Ghatak, A., Schindler, F., Bachmann, G., Engelmeier, D., Bajaj, P., Brenner, M., Fragner, L., Guntur, R.K., Varshney, V.S., Chaturvedi, P., Weckwerth, W., 2022. Root exudation of contrasting drought-stressed pearl millet genotypes conveys varying biological nitrification inhibition (BNI) activity. *Biol. Fert. Soils.* 58, 291–306. <https://doi.org/10.1007/s00374-021-01578-w>.
- Ghavami, N., Alikhani, H.A., Pourbabaei, A.A., Besharati, H., 2017. Effects of two new siderophore-producing rhizobacteria on growth and iron content of maize and canola plants. *J. Plant Nutr.* 40 (5), 736–746.
- Gholamhosseini, M., Ghalavand, A., Dolatabadian, A., Jamshidi, E., Kholaei-Joghban, A., 2013. Effects of arbuscular mycorrhizal inoculation on growth, yield, nutrient uptake and irrigation water productivity of sunflowers grown under drought stress. *Agric. Water Manag.* 117, 106–114.
- Gholami, R., Hoveizeh, N.F., Zahedi, S.M., Gholami, H., Carillo, P., 2022. Melatonin alleviates the adverse effects of water stress in adult olive cultivars (*Olea europaea* cv. Sevillana & Roughani) in field condition. *Agric. Water Manag.* 269, 107681.
- Gholami, R., Zahedi, S.M., 2019. Reproductive behavior and water use efficiency of olive trees (*Olea europaea* L. cv *Konservolia*) under deficit irrigation and mulching. *Erwerbs-Obstbau* 61 (4).
- Ghosh, D., Sen, S., Mohapatra, S., 2017. Modulation of proline metabolic gene expression in *Arabidopsis thaliana* under water-stressed conditions by a drought-mitigating *Pseudomonas putida* strain. *Ann. Microbiol.* 67, 655–668.
- Gilmour, S.J., Zarka, D.G., Stockinger, E.J., Salazar, M.P., Houghton, J.M., Thomashow, M.F., 1998. Low temperature regulation of the *Arabidopsis* CBF family of AP2 transcriptional activators as an early step in cold-induced COR gene expression. *Plant J.* 16, 433–442.
- Glick, B.R., 2020. Introduction to plant growth-promoting bacteria. *Beneficial Plant-Bacterial Interactions*. Springer, Cham, Switzerland, pp. 1–37.
- Goche, T., Shargie, N.G., Cummins, I., Brown, A.P., Chivasa, S., Ngara, R., 2020. Comparative physiological and root proteome analyses of two sorghum varieties responding to water limitation. *Sci. Rep.* 10 (1), 11835.
- Goel, A.K., Sindhu, S.S., Dadarwal, K.R., 1999. Bacteriocin producing native rhizobia of green gram (*Vigna radiata*) having competitive advantage in nodule occupancy. *Microbiol. Res.* 154, 43–48.
- Gosal, S.S., Wani, S.S., Kang, M.S., 2009. Biotechnology and drought tolerance. *J. Crop. Imp.* 23, 19–54.
- Goswami, M., Suresh, D.E.K.A., 2020. Plant growth-promoting rhizobacteria—alleviators of abiotic stresses in soil: a review. *Pedosphere* 30 (1), 40–61.
- Gou, W.E.I., Tian, L.I., Ruan, Z.H.I., Zheng, P.E.N.G., Chen, F.U.C.A.I., Zhang, L., Cui, Z., Zheng, P., Li, Z., Gao, M.E.I., Shi, W.E.I., 2015. Accumulation of choline and glycinebetaine and drought stress tolerance induced in maize (*Zea mays*) by three plant growth promoting rhizobacteria (PGPR) strains. *Pak. J. Bot.* 47 (2), 581–586.
- Gouesbet, G., 2023. Deciphering macromolecular interactions involved in abiotic stress signaling: A review of bioinformatics analysis. *Methods Mol. Biol.* 2642, 257–294. <https://doi.org/10.1007/978-1-0716-3044-0-15>.
- Govindasamy, V., George, P., Kumar, M., Aher, L., Raina, S.K., Rane, J., Annapurna, K., Minhas, P.S., 2020. Multi-trait PGP rhizobacterial endophytes alleviate drought stress in a senescent genotype of sorghum [*Sorghum bicolor* (L.) Moench]. *3 Biotech.* 10, 1–14.
- Gowtham, H.G., Duraivadivel, P., Ayusman, S., Sayani, D., Gholap, S.L., Niranjana, S.R., Hariprasad, P., 2021. ABA analogue produced by *Bacillus marisflavi* modulates the physiological response of *Brassica juncea* L. under drought stress. *Appl. Soil Ecol.* 159, 103845.
- Graham, P.H., Vance, C.P., 2003. Legumes: Importance and constraints to greater use. *Plant Physiol.* 131, 872–877.
- Grover, M., Madhubala, R., Ali, S.Z., Yadav, S.K., Venkateswarlu, B., 2014. Influence of *Bacillus* strains on seedling growth and physiological parameters of sorghum under moisture stress conditions. *J. Basic Microbiol.* 54 (9), 951–961.
- Gu, Z., Hu, C., Gan, Y., Zhou, J., Tian, G., Gao, L., 2024. Role of microbes in alleviating crop drought stress: A review. *Plants* 13, 384. <https://doi.org/10.3390/plants13030384>.
- Guajardo, E., Correa, J.A., Contreras-Porcia, L., 2016. Role of abscisic acid (ABA) in activating antioxidant tolerance responses to desiccation stress in intertidal seaweed species. *Planta* 243, 767–781.
- Guarnizo, Á.L., Navarro-Ródenas, A., Calvo-Polanco, M., Marqués-Gálvez, J.E., Morte, A., 2023. A mycorrhizal helper bacterium alleviates drought stress in mycorrhizal *Helianthemum almeriense* plants by regulating water relations and plant hormones. *Environ. Exp. Bot.* 207, 105228.
- Gupta, A., Rico-Medina, A., Caño-Delgado, A.I., 2020. The physiology of plant responses to drought. *Science* 368 (6488), 266–269.
- Gupta, P.P., Balyan, S.S., Gahlaut, V., 2017. QTL analysis for drought tolerance in wheat: Present status and future possibilities. *Agronomy* 7, 5.
- Gururani, M.A., Upadhyaya, C.P., Baskar, V., Venkatesh, J., Nookaraju, A., Park, S.W., 2013. Plant growth-promoting rhizobacteria enhance abiotic stress tolerance in *Solanum tuberosum* through inducing changes in the expression of ROS-scavenging enzymes and improved photosynthetic performance. *J. Plant Growth Regul.* 32, 245–258.
- Gusain, S., Kumari, K., Joshi, R., 2024. Physiological, hormonal and molecular dynamics of root system architectural response to drought stress signaling in crops. *Rhizosphere* 31, 100922.
- Gusain, Y.S., Singh, U.S., Sharma, A.K., 2015. Bacterial mediated amelioration of drought stress in drought tolerant and susceptible cultivars of rice (*Oryza sativa* L.). *Afr. J. Biotechnol.* 14 (9), 764–773.
- Haddidi, I., Duc, N.H., Tonk, S., Rápo, E., Posta, K., 2020. Defense enzymes in mycorrhizal tomato plants exposed to combined drought and heat stresses. *Agronomy* 10, 1657.
- Haghaninia, M., Javanmard, A., Radicetti, E., Rasouli, F., Ruiz-Lozano, J.M., Sabbatini, P., 2024. Adoption of arbuscular mycorrhizal fungi and biochar for alleviating the agro-physiological response of lavender (*Lavandula angustifolia* L.) subjected to drought stress. *Plant Stress* 12, 100461. <https://doi.org/10.1016/j.plstress.2024.100461>.
- Hai, N.N., Chuong, N.N., Tu, N.H.C., Kisiala, A., Hoang, X.L.T., Thao, N.P., 2020. Role and regulation of cytokinins in plant response to drought stress. *Plants* 9 (4), 422.
- Hakim, S., Naqqash, T., Nawaz, M.S., Larabi, I., Siddique, M.J., Zia, R., Mirza, M.S., Imran, A., 2021. Rhizosphere engineering with plant growth-promoting microorganisms for agriculture and ecological sustainability. *Front. Sustain. Food Syst.* 5, 617157. <https://doi.org/10.3389/fsufs.2021.617157>.
- Hanafy, M.S., El-Banna, A., Schumacher, H.M., Jacobsen, H.J., Hassan, F.S., 2013. Enhanced tolerance to drought and salt stresses in transgenic faba bean (*Vicia faba* L.) plants by heterologous expression of the PR10a gene from potato. *Plant Cell Rep.* 32, 663–674.
- Hansen, B.L., Pessotti, R.D.C., Fischer, M.S., Collins, A., El-Hifnawi, L., Liu, M.D., Traxler, M.F., 2020. Cooperation, competition, and specialized metabolism in a simplified root nodule microbiome. *MBio* 11 (4), 10–1128.
- Hao, D., Ohme-Takagi, M., Sarai, A., 1998. Unique mode of GCC box recognition by the DNA-binding domain of ethylene-responsive element-binding factor (ERF domain) in plant. *J. Biol. Chem.* 273, 26857–26861.
- Harman, G.E., Uphoff, N., 2019. Symbiotic root-endophytic soil microbes improve crop productivity and provide environmental benefits. *Scientifica*, 2019.

- Hartmann, M., Six, J., 2023. Soil structure and microbiome functions in agroecosystems. *Nat. Rev. Earth Environ.* 4, 4–18. <https://doi.org/10.1038/s43017-022-00366-w>.
- Hasan, N., Khan, I.U., Farzand, A., Heng, Z., Moosa, A., Saleem, M., Canning, T., 2022. *Bacillus altitudinis* HNH7 and *Bacillus velezensis* HNH9 promote plant growth through upregulation of growth-promoting genes in upland cotton. *J. Appl. Microbiol.* <https://doi.org/10.1111/jam.15511>.
- Hasanuzzaman, M., Bhuyan, M.B., Parvin, K., Bhuiyan, T.F., Anee, T.I., Nahar, K., Hossen, M.S., Zulfiqar, F., Alam, M.M., Fujita, M., 2020. Regulation of ROS metabolism in plants under environmental stress: A review of recent experimental evidence. *Intern. J. Mol. Sci.* 21 (22), 8695.
- Hasanuzzaman, M., Bhuyan, M.H.M.B., Zulfiqar, F., Raza, A., Mohsin, S.M., Al Mahmud, J., Fujita, M., Fotopoulos, V., 2020. Reactive oxygen species and antioxidant defense in plants under abiotic stress: Revisiting the crucial role of a universal defense regulator. *Antioxidants* 9, 681. <https://doi.org/10.3390/antiox9080681>.
- Hasseina, A.B., Zouari, M., Labrousse, P., Decou, R., Soua, N., Khabou, W., Zouari, N., 2022. Effect of arbuscular mycorrhizal fungi on soil properties, mineral nutrition and antioxidant enzymes of olive plants under treated wastewater irrigation. *South Afr. J. Bot.* 148, 710–719.
- Ha-Tran, D.M., Nguyen, T.T.M., Hung, S.H., Huang, E., Huang, C.C., 2021. Roles of plant growth-promoting rhizobacteria (PGPR) in stimulating salinity stress defense in plants: A review. *Intern. J. Mol. Sci.* 22 (6), 3154.
- He, A., Niu, S., Yang, D., Ren, W., Zhao, L., Sun, Y., Meng, L., Zhao, Q., Paré, P.W., Zhang, J., 2021. Two PGPR strains from the rhizosphere of *Haloxylon ammodendron* promoted growth and enhanced drought tolerance of ryegrass. *Plant Physiol. Biochem.* 161, 74–85.
- He, C., Zhang, W., Gao, Q., Yang, A., Hu, X., Zhang, J., 2011. Enhancement of drought resistance and biomass by increasing the amount of glycine betaine in wheat seedlings. *Euphytica* 177, 151–167.
- He, D., Singh, S.K., Peng, L., Kaushal, R., Vilchez, J.I., Shao, C., Wu, X., Zheng, S., 2022. Flavonoid-attracted *Aeromonas* sp. from the *Arabidopsis* root microbiome enhances plant dehydration resistance. *ISME* 16, 2622–2632. <https://doi.org/10.1038/s41396-022-01288-7>.
- He, Z., Wu, J., Sun, X., Dai, M., 2019. The maize clade A PP2C phosphatases play critical roles in multiple abiotic stress responses. *Intern. J. Mol. Sci.* 20 (14), 3573.
- Hernández-Álvarez, C., Peimbert, M., Rodríguez-Martin, P., Trejo-Aguilar, D., Alcaraz, L. D., 2023. A study of microbial diversity in a biofertilizer consortium. *bioRxiv*. <https://doi.org/10.1101/2023.05.15.540786>, 2023.
- Hewedy, O.A., Abdel Lateif, K.S., Seleiman, M.F., Shami, A., Albarakaty, F.M., El-Meihy M., R., 2020. Phylogenetic diversity of *Trichoderma* strains and their antagonistic potential against soil-borne pathogens under stress conditions. *Biology* 9 (8), 189.
- Hmida-Sayari, A., Gargouri-Bouزيد, R., Bidani, A., Jaoua, L., Savouré, A., Jaoua, S., 2005. Overexpression of $\Delta 1$ -pyrroline-5-carboxylate synthetase increases proline production and confers salt tolerance in transgenic potato plants. *Plant Sci.* 169, 746–752.
- Hoflich, G., Wiehe, W., Kühn, G., 1994. Plant growth stimulation by inoculation with symbiotic and associative rhizosphere microorganisms. *Experientia* 50 (10), 897–905.
- Hou, P., Wang, F., Luo, B., Li, A., Wang, C., Shabala, L., Ahmed, H.A.I., Deng, S., Zhang, H., Song, P., Zhang, Y., 2021. Antioxidant enzymatic activity and osmotic adjustment as components of the drought tolerance mechanism in *Carex diruscula*. *Plants* 10 (3), 436.
- Hou, S., Rodrigues, O., Liu, Z., Shan, L., He, P., 2024. Small holes, big impact: Stomata in plant–pathogen–climate epic trifecta. *Mol. Plant* 17, 26–49. <https://doi.org/10.1016/j.molp.2023.11.011>.
- Hu, C.A., Delauney, A.J., Verma, D.P., 1992. A bifunctional enzyme ($\Delta 1$ -pyrroline-5-carboxylate synthetase) catalyzes the first two steps in proline biosynthesis in plants. *Proc. Natl. Acad. Sci. U.S.A.* 89, 9354–9358.
- Hu, C.H., Wang, P.Q., Zhang, P.P., Nie, X.M., Li, B.B., Tai, L., Liu, W.T., Li, W.Q., Chen, K. M., 2020a. NADPH oxidases: The vital performers and center hubs during plant growth and signaling. *Cells* 9 (2), 437.
- Hu, H., Xiong, L., 2014. Genetic engineering and breeding of drought-resistant crops. *Annu. Rev. Plant Biol.* 65, 715–741.
- Hu, Y., Xie, W., Chen, B., 2020b. Arbuscular mycorrhiza improved drought tolerance of maize seedlings by altering photosystem II efficiency and the levels of key metabolites. *Chem. Biol. Technol. Agric.* 7, 1–14.
- Huang, B., DaCosta, M., Jiang, Y., 2014. Research advances in mechanisms of turfgrass tolerance to abiotic stresses: from physiology to molecular biology. *Crit. Rev. Plant Sci.* 33 (2-3), 141–189.
- Huang, D., Ma, M., Wang, Q., Zhang, M., Jing, G., Li, C., Ma, F., 2020. Arbuscular mycorrhizal fungi enhanced drought resistance in apple by regulating genes in the MAPK pathway. *Plant Physiol. Biochem.* 149, 245–255.
- Huang, D., Wang, Q., Jing, G., Ma, M., Li, C., Ma, F., 2021. Overexpression of MdIAA24 improves apple drought resistance by positively regulating strigolactone biosynthesis and mycorrhization. *Tree Physiol.* 41 (1), 134–146.
- Huang, X., Hou, L., Meng, J., You, H., Li, Z., Gong, Z., Yang, S., Shi, Y., 2018. The antagonistic action of abscisic acid and cytokinin signaling mediates drought stress response in *Arabidopsis*. *Mol. Plant* 11 (7), 970–982.
- Humphrik, J.F., Bergounoux, V., Van Volkenburgh, E., 2017. To stimulate or inhibit? That is the question for the function of abscisic acid. *Trends Plant Sci.* 22 (10), 830–841.
- Hussain, H.A., Hussain, S., Khaliq, A., Ashraf, U., Anjum, S.A., Men, S., Wang, L., 2018. Chilling and drought stresses in crop plants: Implications, cross talk, and potential management opportunities. *Front. Plant Sci.* 9, 393.
- Ilyas, M., Nisar, M., Khan, N., Hazrat, A., Khan, A.H., Hayat, K., Fahad, S., Khan, A., Ullah, A., 2021. Drought tolerance strategies in plants: a mechanistic approach. *Plant Growth Regul.* 40 (3), 926–944.
- Ilyas, N., Mumtaz, K., Akhtar, N., Yasmin, H., Sayyed, R.Z., Khan, W., Enshasy, H.A.E., Dailin, D.J., Elsayed, E.A., Ali, Z., 2020. Exopolysaccharides producing bacteria for the amelioration of drought stress in wheat. *Sustainability* 12 (21), 8876.
- Islam, M.R., Islam, R., Dutta, T., Jhelom, F.R., 2023. Genetic and microbial insights into drought stress alleviation in tomato (*Solanum lycopersicum* L.). *Biol. Life Sci. Forum. MDPI* 27, 22. <https://doi.org/10.3390/IECAG2023-15223>.
- Jaglo-Ottosen, K.R., Gilmour, S.J., Zarka, D.G., Schabenberger, O., Thomashow, M.F., 1998. *Arabidopsis* CBF1 overexpression induces COR genes and enhances freezing tolerance. *Science* 280, 104–106.
- Jangu, O.P., Sindhu, S.S., 2011. Differential response of inoculation with indole acetic acid producing *Pseudomonas* sp. in green gram (*Vigna radiata* L.) and black gram (*Vigna mungo* L.). *Microbiol. J.* 1, 159–173.
- Jansson, J.K., Hofmøckel, K.S., 2018. The soil microbiome—from metagenomics to metaproteomics. *Curr. Opin. Microbiol.* 43, 162–168. <https://doi.org/10.1016/j.mib.2018.01.013>.
- Jeon, D., Kang, Y., Lee, S., Choi, S., Sung, Y., Lee, T.-H., Kim, C., 2023. Digitalizing breeding in plants: A new trend of next-generation breeding based on genomic prediction. *Front. Plant Sci.* 14, 1092584.
- Jerbi, M., Labidi, S., Laruelle, F., Tisserant, B., Dalpé, Y., Lounès-Hadj Sahraoui, A., Ben Jeddi, F., 2022. Contribution of native and exotic arbuscular mycorrhizal fungi in improving the physiological and biochemical response of hulless barley (*Hordeum vulgare* ssp. *nudum* L.) to drought. *J. Soil Sci. Plant Nutr.* 1–18.
- Jiao, W., Tian, C., Chang, Q., Novick, K.A., Wang, L., 2019. A new multi-sensor integrated index for drought monitoring. *Agric. For. Meteorol.* 268, 74–85.
- Jin, R., Kim, B.H., Ji, C.Y., Kim, H.S., Li, H.M., Kwak, S.S., 2017. Overexpressing IbCBF3 increases low temperature and drought stress tolerance in transgenic sweet potato. *Plant Physiol. Biochem.* 118, 45–54.
- Jochum, M.D., McWilliams, K.L., Pierson, E.A., Jo, Y.K., 2019. Host-mediated microbiome engineering (HMM) of drought tolerance in the wheat rhizosphere. *PLoS One* 14 (12), e0225933.
- Johnson, R., Vishwakarma, K., Hossen, M.S., Kumar, V., Hasanuzzaman, M., 2022. Potassium in plants: Growth regulation, signaling, and environmental stress tolerance. *Plant Physiol. Biochem.* 172, 56–69.
- Joshi, R., Sahoo, K.K., Singh, A.K., Anwar, K., Pundir, P., Gautam, R.K., Krishnamurthy, S.L., Sopory, S.K., Pareek, A., Singla-Pareek, S.L., Dhankher, O.M., 2020. Enhancing trehalose biosynthesis improves yield potential in marker-free transgenic rice under drought, saline, and sodic conditions. *J. Exp. Bot.* 71 (2020), 653–668.
- Jung, H., Lee, D.K., Do Choi, Y., Kim, J.K., 2015. OsIAA6, a member of the rice Aux/IAA gene family, is involved in drought tolerance and tiller outgrowth. *Plant Sci.* 236, 304–312.
- Kahlaoui, B., Misle, E., Khaskhoussy, K., Jaouadi, I., Hachicha, M., 2016. Brassinosteroids and drought tolerance in plants. *Water Stress Crop Plants: Sustain. Approach* 2, 600–607.
- Kalleku, J.N., Ihsan, S., Al-Azzawi, T.N.I., Khan, M., Hussain, A., Chebitok, F., 2024. Halotolerant *Pseudomonas koreensis* S4T10 mitigate salt and drought stress in *Arabidopsis thaliana*. *Physiol. Plant.* 176 (2), e14258. <https://doi.org/10.1111/pp1.14258>.
- Kambona, C.M., Koua, P.A., Léon, J., Ballvora, A., 2023. Stress memory and its regulation in plants experiencing recurrent drought conditions. *Theor. Appl. Genet.* 136, 26. <https://doi.org/10.1007/s00122-023-04313-1>.
- Kanchiswamy, C.N., Malnoy, M., Maffei, M.E., 2015. Chemical diversity of microbial volatiles and their potential for plant growth and productivity. *Front. Plant Sci.* 6, 151.
- Kang, S.M., Khan, M.A., Hamayun, M., Kim, L.R., Kwon, E.H., Kang, Y.S., Kim, K.Y., Park, J.J., Lee, J.J., 2021. Phosphate-solubilizing *Enterobacter ludwigii* AFFR02 and *Bacillus megaterium* Mj1212 rescues alfalfa's growth under post-drought stress. *Agriculture* 11 (6), 485.
- Kang, S.M., Radhakrishnan, R., Khan, A.L., Kim, M.J., Park, J.M., Kim, B.R., Shin, D.H., Lee, J.J., 2014. Gibberellin secreting rhizobacterium, *Pseudomonas putida* H-2-3 modulates the hormonal and stress physiology of soybean to improve the plant growth under saline and drought conditions. *Plant Physiol. Biochem.* 84, 115–124.
- Kaplan, R., Zaziri, M., Zwiazek, J.J., 2018. Regulation of aquaporins in plants under stress. *Biol. Res.* 51 (1), 1–11.
- Kapoor, D., Bhardwaj, S., Landi, M., Sharma, A., Ramakrishnan, M., Sharma, A., 2020. The impact of drought in plant metabolism: How to exploit tolerance mechanisms to increase crop production. *Appl. Sci.* 10 (16), 5692.
- Karakas, B., Ozias-Akins, P., Stushnoff, C., Sufferheld, M., Rieger, M., 1997. Salinity and drought tolerance of mannitol-accumulating transgenic tobacco. *Plant Cell Environ.* 20, 609–616.
- Karkaria, B.D., Fedorec, A.J., Barnes, C.P., 2021. Automated design of synthetic microbial communities. *Nat. Commun.* 12 (1), 672.
- Kasim, W.A., Osman, M.E., Omar, M.N., Abd El-Daim, I.A., Bejai, S., Meijer, J., 2013. Control of drought stress in wheat using plant-growth-promoting bacteria. *J. Plant Growth Regul.* 32, 122–130.
- Kasuga, M., Miura, S., Shinozaki, K., Yamaguchi-Shinozaki, K., 2004. A combination of the *Arabidopsis* DREB1A gene and stress-inducible rd29A promoter improved drought- and low-temperature stress tolerance in tobacco by gene transfer. *Plant Cell Physiol.* 45, 346–350.
- Kaur, H., Kohli, S.K., Khanna, K., Bhardwaj, R., 2021. Scrutinizing the impact of water deficit in plants: Transcriptional regulation, signaling, photosynthetic efficacy, and management. *Physiol. Plant.* 172 (2), 935–962.

- Kaushal, M., 2019. Microbes in cahoots with plants: MIST to hit the jackpot of agricultural productivity during drought. *Int. J. Mol. Sci.* 20 (7), 1769.
- Kaushal, M., Wani, S.P., 2016. Plant-growth-promoting rhizobacteria: drought stress alleviators to ameliorate crop production in drylands. *Ann. Microbiol.* 66, 35–42.
- Kaya, C., Ashraf, M., Wijaya, L., Ahmad, P., 2019. The putative role of endogenous nitric oxide in brassinosteroid-induced antioxidant defence system in pepper (*Capsicum annuum* L.) plants under water stress. *Plant Physiol. Biochem.* 143, 119–128.
- Ke, J., Wang, B., Yoshikuni, Y., 2021. Microbiome engineering: synthetic biology of plant-associated microbiomes in sustainable agriculture. *Trends Biotechnol.* 39 (3), 244–261.
- Kelly, C., Byrne, P.F., Schipanski, M.E., Schneekloth, J., Calderón, F., Fonte, S.J., 2023. Soil management legacy interacts with wheat genotype to determine access to organic N in a dryland system. *Agric. Ecosyst. Environ.* 345, 108336. <https://doi.org/10.1016/j.agee.2022.108336>.
- Khadka, K., Earl, H.J., Raizada, M.N., Navabi, A.A., 2020. Physio-morphological trait-based approach for breeding drought-tolerant wheat. *Front. Plant Sci.* 11, 715.
- Khadka, R.B., Uphoff, N., 2019. Effects of *Trichoderma* seedling treatment with System of Rice Intensification management and with conventional management of transplanted rice. *Peer J.* 7, e5877.
- Khan, A., Pan, X., Najeeb, U., Tan, D.K.Y., Fahad, S., Zahoor, R., Luo, H., 2018. Coping with drought: stress and adaptive mechanisms, and management through cultural and molecular alternatives in cotton as vital constituents for plant stress resilience and fitness. *Biol. Res.* 51.
- Khan, M.R., Parveen, G., Zaid, A., Wani, S.H., Jogaiah, S., 2021. Potential of *Trichoderma* species in alleviating the adverse effects of biotic and abiotic stresses in plants. In: Jogaiah, S. (Ed.), *Biocontrol Agents and Secondary Metabolites*. Woodhead Publishing, Sawston, pp. 85–112.
- Khan, M.S., Rizvi, A., Saif, S., Zaidi, A., 2017. Phosphate-solubilizing microorganisms in sustainable production of wheat: current perspective. *Probiot. Agroecosyst.* 51–81.
- Khan, N., Bano, A., Rahman, M.A., Guo, J., Kang, Z., Babar, M.A., 2019. Comparative physiological and metabolic analysis reveals a complex mechanism involved in drought tolerance in chickpea (*Cicer arietinum* L.) induced by PGRs and PGRs. *Sci. Rep.* 9 (1), 2097.
- Khan, R., Ma, X., Shah, S., Wu, X., Shaheen, A., Xiao, L., Wu, Y., Wang, S., 2020. Drought-hardening improves drought tolerance in *Nicotiana tabacum* at physiological, biochemical, and molecular levels. *BMC Plant Biol.* 20 (1), 1–19.
- Khan, W., Zhu, Y., Khan, A., Zhao, L., Yang, Y.-M., Wang, N., Hao, M., Ma, Y., Nepal, J., Ullah, F., Ur Rehman, M.M., Abrar, M., Xiong, Y.-C., 2024. Above and underground feedback loop of maize is jointly enhanced by plant growth-promoting rhizobacteria and arbuscular mycorrhizal fungi in drier soil. *Sci. Total Environ.* 917, 170417. <https://doi.org/10.1016/j.scitotenv.2024.170417>.
- Khan, Z., Rho, H., Firrincieli, A., Hung, S.H., Luna, V., Masciarelli, O., Kim, S.H., Doty, S. L., 2016. Growth enhancement and drought tolerance of hybrid poplar upon inoculation with endophyte consortia. *Curr. Plant Biol.* 6, 38–47.
- Khandelwal, A., Sindhu, S.S., 2012. Expression of 1-aminocyclopropane-1-carboxylate deaminase in rhizobia promotes nodulation and plant growth of clusterbean (*Cyamopsis tetragonoloba* L.). *Res. J. Microbiol.* 7, 158–170.
- Khandelwal, A., Sindhu, S.S., 2013. ACC deaminase containing rhizobacteria enhances nodulation and plant growth in clusterbean (*Cyamopsis tetragonoloba* L.). *J. Microbiol. Res.* 3, 117–123.
- Kim, S.T., Yoo, S.-J., Weon, H.-Y., Song, J., Sang, M.K., 2022. *Bacillus butanolivorans* KJ40 contributes alleviation of drought stress in pepper plants by modulating antioxidant and polyphenolic compounds. *Sci. Horticul.* 301, 111111. <https://doi.org/10.1016/j.scianta.2022.111111>.
- King, C.A., Purcell, L.C., 2006. Genotypic variation for shoot N concentration and nitrogen use efficiency in soybean. *Crop. Sci.* 46, 2396–2402.
- Kiranmai, K., Lokanadha Rao, G., Pandurangaiah, M., Nareshkumar, A., Amarathana Reddy, V., Lokesh, U., Venkatesh, B., Anthony Johnson, A.M., Sudhakar, C., 2018. A novel WRKY transcription factor, MuWRKY3 (*Macrotyloma uniflorum* lam. Verdc.) enhances drought stress tolerance in transgenic groundnut (*Arachis hypogaea* L.) plants. *Front. Plant Sci.* 9, 346.
- Kishor, P.B.K., Hong, Z., Miao, G.G., Hu, C.A.A., Verma, D.P.S., 1995. Overexpression of $\Delta 1$ -pyrroline-5-carboxylate synthetase increases proline production and confers osmotolerance in transgenic plants. *Plant Physiol.* 108, 1387–1394.
- Konapala, G., Mishra, A.K., Wada, Y., Mann, M.E., 2020. Climate change will affect global water availability through compounding changes in seasonal precipitation and evaporation. *Nat. Commun.* 11 (1), 3044.
- Kour, D., Rana, K.L., Yadav, A.N., Sheikh, I., Kumar, V., Dhaliwal, H.S., Saxena, A.K., 2020. Amelioration of drought stress in Foxtail millet (*Setaria italica* L.) by P-solubilizing drought-tolerant microbes with multifarious plant growth promoting attributes. *Environ. Sustain.* 3, 23–34.
- Krishna, R., Jaiswal, D.K., Ansari, W.A., Singh, S., Soumia, P.S., Singh, A.K., Kumari, B., Singh, M., Verma, J.P., 2022. Potential microbial consortium mitigates drought stress in tomato (*Solanum lycopersicum* L.) plant by up-regulating stress-responsive genes and improving fruit yield and soil properties. *J. Soil Sci. Plant Nutr.* 22 (4), 4598–4615.
- Kristy, B., Carrell, A.A., Johnston, E., Cumming, J.R., Klingeman, D.M., Gwinn, K., Syring, K.C., Skalla, C., Emrich, S., Cregger, M.A., 2022. Chronic drought differentially alters the belowground microbiome of drought-tolerant and drought-susceptible genotypes of *Populus trichocarpa*. *Phytobio. J.* 6, 317–330. <https://doi.org/10.1094/PBIOMES-12-21-0076-R>.
- Kuerban, M., Cong, W.F., Jing, J., Bezemer, T.M., 2023. Microbial soil legacies of crops under different water and nitrogen levels determine succeeding crop performance. *Plant Soil* 485, 167–180. <https://doi.org/10.1007/s11104-022-05412-6>.
- Kumar, A., Singh, S., Gaurav, A.K., Srivastava, S., Verma, J.P., 2020. Plant growth-promoting bacteria: biological tools for the mitigation of salinity stress in plants. *Front. Microbiol.* 11, 1216.
- Kumar, M., Kesawat, M.S., Ali, A., Lee, S.C., Gill, S.S., Kim, H.U., 2019. Integration of abscisic acid signaling with other signaling pathways in plant stress responses and development. *Plants* 8 (12), 592.
- Kumar, S., Chaudhary, T., Diksha, Sindhu, S.S., Chaudhary, D., Kumar, R., 2022a. Mycorrhizal fungi: An eco-friendly input for sustenance of soil fertility and plant health. In: Malik, D.K., Rathi, M., Kumar, R., Bhatia, D. (Eds.), *Microbes for humanity and its applications*. Daya Publishing House, New Delhi, pp. 21–74.
- Kumar, S., Diksha, Sindhu, S.S., Kumar, R., 2022b. Biofertilizers: An ecofriendly technology for nutrient recycling and environmental sustainability. *Curr. Res. Microbiol. Sci.* 3, 100094. <https://doi.org/10.1016/j.crmicr.2021.100094>.
- Kumar, S., Diksha, Sindhu, S.S., Kumar, R., 2024. Microbial endophytes: Prospects in biological control of plant pathogens and plant growth stimulation for sustainable agriculture. In: Egamberdieva, D., Parry, J.A., Davranov, K. (Eds.), *Plant Endophytes and Secondary Metabolites*. Elsevier, pp. 375–422. <https://doi.org/10.1016/B978-0-443-13365-7.00015-4>. Chapter 19.
- Kumar, S., Diksha, Sindhu, S.S., Kumar, R., Kumari, A., Panwar, A., 2023. Harnessing phyllosphere microbiome for improving soil fertility, crop production and environmental sustainability. *J. Soil Sci. Plant Nutr.* <https://doi.org/10.1007/s42729-023-01397-y>.
- Kuromori, T., Seo, M., Shinozaki, K., 2018. ABA transport and plant water stress responses. *Trends Plant Sci.* 23 (6), 513–522.
- Lata, C., Prasad, M., 2011. Role of DREBs in regulation of abiotic stress responses in plants. *J. Exp. Bot.* 62, 4731–4748.
- Lau, J.A., Lennon, J.T., 2012. Rapid responses of soil microorganisms improve plant fitness in novel environments. *Proc. Natl. Acad. Sci. U.S.A.* 109 (35), 14058–14062.
- Lau, S.E., Teo, W.F.A., Teoh, E.Y., Tan, B.C., 2022. Microbiome engineering and plant biostimulants for sustainable crop improvement and mitigation of biotic and abiotic stresses. *Discover. Food* 2, 9. <https://doi.org/10.1007/s44187-022-00009-5>.
- Laxa, M., Liebthal, M., Telman, W., Chibani, K., Dietz, K.J., 2019. The role of the plant antioxidant system in drought tolerance. *Antioxidants* 8 (4), 94.
- Lemanceau, P., Blouin, M., Muller, D., Moëne-Loccoz, Y., 2017. Let the core microbiota be functional. *Trends Plant Sci.* 22 (7), 583–595.
- Lemfack, M.C., Gohlke, B.O., Toguem, S.M.T., Preissner, S., Piechulla, B., Preissner, R., 2018. mVOC 2.0: a database of microbial volatiles. *Nucleic Acids Res.* 46 (D1), D1261–D1265.
- Lesk, C., Rowhani, P., Ramankutty, N., 2016. Influence of extreme weather disasters on global crop production. *Nature* 529 (7584), 84–87.
- Leung, J., Giraudat, J., 1998. Abscisic acid signal transduction. *Annu. Rev. Plant Biol.* 49 (1), 199–222.
- Li, X., Liu, F., 2016. Drought stress memory and drought stress tolerance in plants: biochemical and molecular basis. *Plants Physiol. Biochem.* <https://doi.org/10.1007/978-3-319-28899-4>.
- Li, D.H., Li, W., Li, H.Y., Guo, J.J., Chen, F.J., 2018. The soybean GmRACK1 gene plays a role in drought tolerance at vegetative stages. *Russ. J. Plant Physiol.* 65, 541–552.
- Li, H., Guo, Q., Jing, Y., Liu, Z., Zheng, Z., Sun, Y., Xue, Q., Lai, H., 2020. Application of *Streptomyces pactum* Act12 enhances drought resistance in wheat. *J. Plant Growth Regul.* 39, 122–132.
- Li, J., Meng, B., Chai, H., Yang, X., Song, W., Li, S., Lu, A., Zhang, T., Sun, W., 2019. Arbuscular mycorrhizal fungi alleviate drought stress in C3 (*Leymus chinensis*) and C4 (*Hemarthria altissima*) grasses via altering antioxidant enzyme activities and photosynthesis. *Front. Plant Sci.* 10, 499.
- Li, K., Gao, Y., Wu, J., 2014. Study on salt tolerance and drought resistance of potato transgenic P5CS gene 'Dongnong 303'. *Jiangsu Agric. Sci.* 42, 131–133.
- Li, X., Tang, Y., Li, H., Luo, W., Zhou, C., Zhang, L., Lv, J., 2020. A wheat R2R3 MYB gene TaMpc1-D4 negatively regulates drought tolerance in transgenic *Arabidopsis* and wheat. *Plant Sci.* 299, 110613. <https://doi.org/10.1016/j.plantsci.2020.110613>.
- Li, X., Zhang, L., Li, Y., 2011. Preconditioning alters antioxidative enzyme responses in rice seedlings to water stress. *Procedia Environ. Sci.* 11, 1346–1351. <https://doi.org/10.1016/j.proenv.2011.12.202>.
- Li, Y., Ye, W., Wang, M., Yan, X., 2009. Climate change and drought: a risk assessment of crop-yield impacts. *Clim. Res.* 39 (1), 31–46.
- Li, Z., Zhang, Y., Liu, C., Gao, Y., Han, L., Chu, H., 2022. Arbuscular mycorrhizal fungi contribute to reactive oxygen species homeostasis of *Bombax ceiba* L. under drought stress. *Front. Microbiol.* 13, 991781.
- Lian, T., Huang, Y., Xie, X., Huo, X., Shahid, M.Q., Tian, L., Lan, T., 2020. Rice SST variation shapes the rhizosphere bacterial community, conferring tolerance to salt stress through regulating soil metabolites. *mSystems* 5, e00721. -20.
- Lian, W.H., Mohamad, O.A.A., Dong, L., Zhang, L.Y., Wang, D., Liu, L., Han, M.X., Li, S., Wang, S., Antunes, A., Fang, B.Z., Jiao, J.Y., Li, W.J., 2023. Culturomics- and metagenomics-based insights into the microbial community and function of rhizosphere soils in Sinai desert farming systems. *Environ. Microb.* 18, 4. <https://doi.org/10.1186/s40793-023-00463-3>.
- Liang, H., Lu, Y., Liu, H., Wang, F., Xin, Z., Zhang, Z., 2008. A novel activator-type ERF of *Thinopyrum intermedium*, TiERF1, positively regulates defence responses. *J. Exp. Bot.* 59, 3111–3120.
- Liao, X., Guo, X., Wang, Q., Wang, Y., Zhao, D., Yao, L., Wang, S., Liu, G., Li, T., 2017. Overexpression of MsDREB 6.2 results in cytokinin-deficient developmental phenotypes and enhances drought tolerance in transgenic apple plants. *Plant J.* 89 (3), 510–526.
- Licausi, F., Giorgi, F.M., Zenoni, S., Osti, F., Pezzotti, M., Perata, P., 2010. Genomic and transcriptomic analysis of the AP2/ERF superfamily in *Vitis vinifera*. *BMC Genom.* 11, 719.

- Lim, J.H., Kim, S.D., 2013. Induction of drought stress resistance by multi-functional PGPR *Bacillus licheniformis* K11 in pepper. *Plant Pathol. J.* 29 (2), 201.
- Lin, W., Lin, M., Zhou, H., Wu, H., Li, Z., Lin, W., 2019. The effects of chemical and organic fertilizer usage on rhizosphere soil in tea orchards. *PLoS One* 14 (5), e0217018.
- Liu, B., Zhang, B., Yang, Z., Liu, Y., Yang, S., Shi, Y., Jiang, C., Qin, F., 2021. Manipulating ZmEXPA4 expression ameliorates the drought-induced prolonged anthesis and silking interval in maize. *Plant Cell* 33 (2021), 2058–2071.
- Liu, H., Zhou, X., Dong, N., Liu, X., Zhang, H., Zhang, Z., 2011. Expression of a wheat MYB gene in transgenic tobacco enhances resistance to *Ralstonia solanacearum* and to drought and salt stresses. *Funct. Integr. Genom.* 11, 431–443.
- Liu, L., Cao, X., Zhai, Z., Ma, S., Tian, Y., Cheng, J., 2022. Direct evidence of drought stress memory in mulberry from a physiological perspective: antioxidative, osmotic and phytohormonal regulations. *Plant Physiol. Biochem.* 186, 76–87.
- Liu, J., He, H., Vitali, M., Visentin, L., Charnikhova, T., Haider, I., Schubert, A., Ruyter-Spira, C., Bouwmeester, H.J., Lovisolio, C., Cardinale, F., 2015b. Osmotic stress represses strigolactone biosynthesis in *Lotus japonicus* roots: exploring the interaction between strigolactones and ABA under abiotic stress. *Planta* 241, 1435–1451.
- Liu, J., Osbourn, A., Ma, P., 2015a. MYB transcription factors as regulators of phenylpropanoid metabolism in plants. *Mol. Plant* 8 (5), 689–708.
- Liu, R., Huang, S., Huang, A., Chen, M., Luo, Y., Guo, Z., Lu, S., 2023. Overexpression of CdtCIPK21 from triploid Bermuda grass reduces salt and drought tolerance but increases chilling tolerance in transgenic rice. *J. Plant Physiol.* 286, 154006.
- Liu, W., Sikora, E., Park, S.W., 2020. Plant growth-promoting rhizobacterium, *Paenibacillus polymyxa* CR1, upregulates dehydration-responsive genes, RD29A and RD29B, during priming drought tolerance in *Arabidopsis*. *Plant Physiol. Biochem.* 156, 146–154.
- Liu, X.M., Zhang, H., 2015. The effects of bacterial volatile emissions on plant abiotic stress tolerance. *Front. Plant Sci.* 6, 774.
- Lobet, G., Draye, X., 2013. Novel scanning procedure enabling the vectorization of entire rhizotron-grown root systems. *Plant Methods* 9 (1), 1–11.
- Lodeiro, A., Gonzalez, P., Hernandez, Balague, L., Favelukes, G., 2000. Comparison of drought tolerance in nitrogen-fixing and inorganic nitrogen-grown common beans. *Plant Sci.* 154, 31–41.
- Lozano, Y.M., Aguilar-Trigueros, C.A., Ospina, J.M., Rillig, M.C., 2022. Drought legacy effects on root morphological traits and plant biomass via soil biota feedback. *New Phytol.* 236, 222–234. <https://doi.org/10.1111/nph.18327>.
- Lucas, S., Durmaz, E., Akpinar, B.A., Budak, H., 2011. The drought response displayed by a DRE-binding protein from *Triticum dicoccoides*. *Plant Physiol. Biochem.* 49, 346–351.
- Lukić, N., Kukavica, B., Davidović-Plavšić, B., Hasanagić, D., Walter, J., 2020. Plant stress memory is linked to high levels of anti-oxidative enzymes over several weeks. *Environ. Exp. Bot.* 178, 104166.
- Lukić, N., Schurr, F.M., Trifković, T., Kukavica, B., Walter, J., 2023. Transgenerational stress memory in plants is mediated by upregulation of the antioxidative system. *Environ. Exp. Bot.* 205, 105129.
- Luo, X., Li, C., He, X., Zhang, X., Zhu, L., 2020. ABA signaling is negatively regulated by GWRKY1 through JAZ1 and ABI1 to affect salt and drought tolerance. *Plant Cell Rep.* 39, 181–194. <https://doi.org/10.1007/s00299-019-02480-4>.
- Ma, W.Y., Qin, Q.Y., Zou, Y.N., Kúca, K., Giri, B., Wu, Q.S., Hashem, A., Al-Arjani, A.-B. F., Almutairi, K.F., Abd Allah, E.F., 2022. Arbuscular mycorrhizae induces low oxidative burst in drought-stressed walnut through activating antioxidant defense systems and heat shock transcription factor expression. *Front. Plant Sci.* 13, 1089420.
- Ma, Y., Dias, M.C., Freitas, H., 2020. Drought and salinity stress responses and microbe-induced tolerance in plants. *Front. Plant Sci.* 11, 591911.
- Mafakheri, A., Siosemardeh, A.F., Bahramnejad, B., Struik, P.C., Sohrabi, Y., 2010. Effect of drought stress on yield, proline and chlorophyll contents in three chickpea cultivars. *Aust. J. Crop. Sci.* 4 (8), 580–585.
- Mahreen, N., Yasmin, S., Asif, M., Yahya, M., Ejaz, K., Yousaf, S., Amin, I., Zulfiqar, S., Imran, A., Khaliq, S., Arif, M., 2023. Mitigation of water scarcity with sustained growth of rice by plant growth promoting bacteria. *Front. Plant Sci.* 14, 1081537.
- Malhi, G.S., Kaur, M., Kaushik, P., 2021. Impact of climate change on agriculture and its mitigation strategies: A review. *Sustainability* 13, 1318.
- Malik, D.K., Sindhu, S.S., 2011. Phyto-stimulatory effect of IAA-producing *Pseudomonas* strains on nodulation and plant growth of chickpea (*Cicer arietinum*). *Physiol. Mol. Biol. Plants* 17, 25–32.
- Mallikarjuna, G., Mallikarjuna, K., Reddy, M., Kaul, T., 2011. Expression of OsDREB2A transcription factor confers enhanced dehydration and salt stress tolerance in rice (*Oryza sativa* L.). *Biotechnol. Lett.* 33, 1689–1697.
- Mamun, A.A., Neumann, G., Moradtalab, N., Ahmed, A., Dupuis, B., Darbon, G., Nawaz, F., Declerck, S., Mai, K., Vogt, W., Ludewig, U., 2024. Microbial consortia versus single-strain inoculants as drought stress protectants in potato affected by the form of N supply. *Horticulture* 10 (1), 102.
- Manepalli, S.B., Tomar, S., Gaikwad, D.J., Maitra, S., 2022. Abiotic stress signaling in plants and transgenic technology as a triumph: A review. *J. Appl. Biol. Biotechnol.* 10 (5), 5–13. <https://doi.org/10.7324/JABB.2022.100501>.
- Manjunatha, B.S., Nivetha, N., Krishna, G.K., Elangovan, A., Pushkar, S., Chandrashekar, N., Aggarwal, C., Asha, A.D., Chinnusamy, V., Raipuria, R.K., Watts, A., 2022. Plant growth-promoting rhizobacteria *Shewanella putrefaciens* and *Cronobacter dublinensis* enhance drought tolerance of pearl millet by modulating hormones and stress-responsive genes. *Physiol. Plant.* 174 (2), e13676.
- Manna, M., Thakur, T., Chirom, O., Mandlik, R., Deshmukh, R., Salvi, P., 2021. Transcription factors as key molecular target to strengthen the drought stress tolerance in plants. *Physiol. Plant.* 172 (2), 847–868.
- Mao, H., Jian, C., Cheng, X., Chen, B., Mei, F., Li, F., Zhang, Y., Li, S., Du, L., Li, T., Hao, C., Wang, X., Zhang, X., Kang, Z., 2022a. The wheat ABA receptor gene TaPYL1-1B contributes to drought tolerance and grain yield by increasing water-use efficiency. *Plant Biotechnol. J.* 20 (2022), 846–861.
- Mao, H., Li, S., Chen, B., Jian, C., Mei, F., Zhang, Y., Li, F., Chen, N., Li, T., Du, L., Ding, L., Wang, Z., Cheng, X., Wang, X., Kang, Z., 2022b. Variation in cis-regulation of a NAC transcription factor contributes to drought tolerance in wheat. *Mol. Plant.* 15 (2022), 276–292.
- Marasco, R., Rolli, E., Ettoumi, B., Vignani, G., Mapelli, F., Borin, S., Abou-Hadid, A.F., El-Behairy, U.A., Sorlini, C., Cherif, A., Zocchi, G., Daffonchio, D., 2012. A drought resistance-promoting microbiome is selected by root system under desert farming. *PLoS One* 7, e48479.
- Marks, R.A., Ame'zquita, E.J., Percival, S., Rougon-Cardoso, A., Chibici-Revneanu, C., Tebele, S.M., Farrant, J.M., Chitwood, D.H., van Buren, R., 2023. A critical analysis of plant science literature reveals ongoing inequities. *Proc. Natl. Acad. Sci. U.S.A.* 120, e2217564120.
- Martínez-Barradas, V., Inostroza-Blancheteau, C., Tighe-Neira, R., Romero-Romero, J.L., Schwember, A.R., Arce-Johnson, P., 2024. Drought tolerance evaluation of 'Zorzal,' the most cultivated common bean in Chile, a country facing desertification. *Agric. Res.* 13, 41–52. <https://doi.org/10.1007/s40003-023-00679-2>.
- Martínez-Vilalta, J., García-Fórner, N., 2017. Water potential regulation, stomatal behaviour and hydraulic transport under drought: deconstructing the iso/anisohydric concept. *Plant Cell Environ.* 40 (6), 962–976.
- Martín-Robles, N., Lehmann, A., Seco, E., Aroca, R., Rillig, M.C., Milla, R., 2018. Impacts of domestication on the arbuscular mycorrhizal symbiosis of 27 crop species. *New Phytol.* 218 (1), 322–334.
- Martins, S.J., Faria, A.F., Pedroso, M.P., Cunha, M.G., Rocha, M.R., Medeiros, F.H.V., 2019. Microbial volatiles organic compounds control anthracnose (*Colletotrichum lindemuthianum*) in common bean (*Phaseolus vulgaris* L.). *Biol. Control* 131, 36–42.
- Martins, S.J., Medeiros, F.H., Lakshmanan, V., Bais, H.P., 2018. Impact of seed exudates on growth and biofilm formation of *Bacillus amyloxylicus* ALB629 in common bean. *Front. Microbiol.* 8, 2631.
- Maswada, H.F., Mazrou, Y.S., Elzaawely, A.A., Eldein, S.M.A., 2020. Nanomaterials. Effective tools for field and horticultural crops to cope with drought stress: A review. *Span. J. Agric. Res.* 18 (2), 15.
- Matusova, R., Rani, K., Verstappen, F.W., Franssen, M.C., Beale, M.H., Bouwmeester, H. J., 2005. The strigolactone germination stimulants of the plant-parasitic Striga and Orobanche are derived from the carotenoid pathway. *Plant Physiol.* 139 (2), 920–934.
- Maxton, A., Singh, P., Masih, S.A., 2018. ACC deaminase-producing bacteria mediated drought and salt tolerance in *Capsicum annum*. *J. Plant Nutr.* 41 (5), 574–583.
- McHughen, A., 2016. A critical assessment of regulatory triggers for products of biotechnology: Product vs. process. *GM Crops Food* 7 (3–4), 125–158.
- Meena, K.K., Sorty, A.M., Bitla, U.M., Choudhary, K., Gupta, P., Pareek, A., Singh, D.P., Prabha, R., Sahu, P.K., Gupta, V.K., Singh, H.B., 2017. Abiotic stress responses and microbe-mediated mitigation in plants: the omics strategies. *Front. Plant Sci.* 8, 172.
- Meisner, A., Jacquiod, S., Snoek, B.L., ten Hooften, F.C., van der Putten, W.H., 2018. Drought legacy effects on the composition of soil fungal and prokaryote communities. *Front. Microbiol.* 9, 294.
- Meng, D., Dong, B., Niu, L., Song, Z., Wang, L., Amin, R., Cao, H., Li, H., Yang, Q., Fu, Y., 2021. The pigeon pea CcCIPK14-CcCBL1 pair positively modulates drought tolerance by enhancing flavonoid biosynthesis. *Plant J.* 106 (5), 1278–1297.
- Mishra, A., Jha, B., Rosenberg, E., DeLong, E.F., Lory, S., Stackebrandt, E., 2013. Microbial exopolysaccharides. In: Thompson, F. (Ed.), *The Prokaryotes*. Springer, Berlin/Heidelberg, Germany, pp. 179–192.
- Mishra, A., Singh, L., Singh, D., 2022. Unboxing the black box – One step forward to understand the soil microbiome: A systematic review. *Microbial Ecol.* 2022 (1), 1–15. <https://doi.org/10.1007/S00248-022-01962-5>.
- Misra, V., Solomon, S., Mall, A.K., Prajapati, C.P., Hashem, A., Abd Allah, E.F., Ansari, M. I., 2020. Morphological assessment of water stressed sugarcane: A comparison of waterlogged and drought affected crop. *Saudi J. Biol. Sci.* 27 (5), 1228–1236.
- Mizoi, J., Shinozaki, K., Yamaguchi-Shinozaki, K., 2012. AP2/ERF family transcription factors in plant abiotic stress responses. *Biochim. Biophys. Acta Gene Regul. Mech.* 1819, 86–96.
- Mofini, M.T., Diedhiou, A.G., Simonin, M., Dondjou, D.T., Pignoly, S., Ndiaye, C., Min, D., Vigouroux, Y., Laplace, L., Kane, A., 2022. Cultivated and wild pearl millet display contrasting patterns of abundance and co-occurrence in their root microbiome. *Sci. Rep.* 12, 207. <https://doi.org/10.1038/s41598-021-04097-8>.
- Molina-Romero, D., Baez, A., Quintero-Hernández, V., Castañeda-Lucio, M., Fuentes-Ramírez, L.E., Bustillos-Cristales, M.D.R., Rodríguez-Andrade, O., Morales-García, Y. E., Munive, A., Muñoz-Rojas, J., 2017. Compatible bacterial mixture, tolerant to desiccation, improves maize plant growth. *PLoS One* 12 (11), e0187913.
- Monteoliva, M.I., Valetti, L., Taurian, T., Crociara, C.S., Guzzo, M.C., 2022. Synthetic communities of bacterial endophytes to improve the quality and yield of legume crops. *IntechOpen*.
- Moradtalab, N., Roghieh, H., Nasser, A., Tobias, E.H., Günter, N., 2019. Silicon and the association with an arbuscular-mycorrhizal fungus (*Rhizophagus clarus*) mitigate the adverse effects of drought stress on strawberry. *Agronomy* 9, 41. <https://doi.org/10.3390/agronomy9010041>.
- Morcillo, R.J., Manzanera, M., 2021. The effects of plant-associated bacterial exopolysaccharides on plant abiotic stress tolerance. *Metabolites* 11 (6), 337.
- Moreno-Galván, A.E., Cortés-Patiño, S., Romero-Perdomo, F., Uribe-Vélez, D., Bashan, Y., Bonilla, R.R., 2020a. Proline accumulation and glutathione reductase activity induced by drought-tolerant rhizobacteria as potential mechanisms to alleviate drought stress in Guinea grass. *Appl. Soil Ecol.* 147, 103367.

- Moreno-Galván, A.E., Romero-Perdomo, F.A., Estrada-Bonilla, G., Meneses, C.H.S.G., Bonilla, R.R., 2020b. Dry-caribbean *Bacillus* strains ameliorate drought stress in maize by a strain-specific antioxidant response modulation. *Microorganisms* 8 (6), 823.
- Mostofa, M.G., Ghosh, A., Li, Z.G., Siddiqui, M.N., Fujita, M., Tran, L.S.P., 2018. Methylglyoxal—a signaling molecule in plant abiotic stress responses. *Free Radic. Biol. Med.* 122, 96–109.
- Muchero, W., Je, V., Roberts, P.A., 2010. Restriction site polymorphism-based candidate gene mapping for seedling drought tolerance in cowpea [*Vigna unguiculata* (L.) Walp.]. *Theor. Appl. Genet.* 120, 509–518.
- Mueller, C.W., Baumert, V., Carminati, A., Germon, A., Holz, M., Kögel-Knabner, I., Peth, S., Schlüter, S., Uteau, D., Vetterlein, D., Teixeira, P., Vidal, A., 2024. From rhizosphere to detritosphere - Soil structure formation driven by plant roots and the interactions with soil biota. *Soil Biol. Biochem.* 193, 109396. <https://doi.org/10.1016/j.soilbio.2024.109396>.
- Mueller, U.G., Sachs, J.L., 2015. Engineering microbiomes to improve plant and animal health. *Trends Microbiol.* 23 (10), 606–617.
- Muhammad, M., Waheed, A., Wahab, A., Majeed, M., Nazim, M., Liu, Y-H., Li, L., Li, W. J., 2024. Soil salinity and drought tolerance: An evaluation of plant growth, productivity, microbial diversity, and amelioration strategies. *Plant Stress* 11, 100319. <https://doi.org/10.1016/j.stress.2023.100319>.
- Müller, L.M., Bahn, M., 2022. Drought legacies and ecosystem responses to subsequent drought. *Global Change Biol.* 28 (17), 5086–5103. <https://doi.org/10.1111/gcb.16270>.
- Murali, M., Singh, S.B., Gowtham, H.G., Shilpa, N., Prasad, M., Aiyaz, M., Amruthesh, K. N., 2021. Induction of drought tolerance in *Pennisetum glaucum* by ACC deaminase producing PGPR-*Bacillus amyloliquefaciens* through antioxidant defense system. *Microbiol. Res.* 253, 126891.
- Mwadingeni, L., Shimelis, H., Dube, E., Laing, M.D., Tsilo, T.J., 2016. Breeding wheat for drought tolerance: Progress and technologies. *J. Integr. Agric.* 15, 935–943.
- Nadal, M., Roig-Oliver, M., Bota, J., Flexas, J., 2020. Leaf age-dependent elastic adjustment and photosynthetic performance under drought stress in *Arbutus unedo* seedlings. *Flora* 271, 151662.
- Namwongsa, J., Jogloy, S., Vorasoot, N., Boonlue, S., Riddech, N., Mongkoltharunuk, W., 2019. Endophytic bacteria improve root traits, biomass and yield of *Helianthus tuberosus* L. under normal and deficit water conditions. *J. Microbiol. Biotechnol.* 29, 1777–1789. <https://doi.org/10.4014/jmb.1903.03062>.
- Narayananamy, S., Thankappan, S., Kumaravel, S., Ragupathi, S., Uthandi, S., 2023. Complete genome sequence analysis of a plant growth-promoting phyloplane *Bacillus altitudinis* FD48 offers mechanistic insights into priming drought stress tolerance in rice. *Genomics* 115 (1), 110550.
- Naseem, H., Ahsan, M., Shahid, M.A., Khan, N., 2018. Exopolysaccharides producing rhizobacteria and their role in plant growth and drought tolerance. *J. Basic Microbiol.* 58 (12), 1009–1022. <https://doi.org/10.1002/jobm.201800309>.
- Naseem, M., Chaudhry, A.N., Jilani, G., Alam, T., Naz, F., Ullah, R., Zahoor, M., Zaman, S., 2024. Exopolysaccharide-producing bacterial cultures of *Bacillus cereus* and *Pseudomonas aeruginosa* in soil augment water retention and maize growth. *Heliyon* 10, e26104. <https://doi.org/10.1016/j.heliyon.2024.e26104>.
- Nawaz, F., Rafeeq, R., Majeed, S., Ismail, M.S., Ahsan, M., Ahmad, K.S., Akram, A., Haider, G., 2023. Biochar amendment in combination with endophytic bacteria stimulates photosynthetic activity and antioxidant enzymes to improve soybean yield under drought stress. *J. Soil Sci. Plant Nutr.* 23, 746–760. <https://doi.org/10.1007/s42729-022-01079-1>.
- Naylor, D., Coleman-Derr, D., 2018. Drought stress and root-associated bacterial communities. *Front. Plant Sci.* 8, 2223.
- Naylor, D., Degraaf, S., Purdom, E., Coleman-Derr, D., 2017. Drought and host selection influence bacterial community dynamics in the grass root microbiome. *ISME J.* 11, 2691–2704. <https://doi.org/10.1038/ismej.2017.118>.
- Nazar, R., Umar, S., Khan, N.A., Sareer, O., 2015. Salicylic acid supplementation improves photosynthesis and growth in mustard through changes in proline accumulation and ethylene formation under drought stress. *S. Afr. J. Bot.* 98, 84–94.
- Ndiso, J., Chemining'Wa, G., Olubayo, F., Saha, H., 2016. Effect of drought stress on canopy temperature, growth and yield performance of cowpea varieties. *Int. J. Plant Sci.* 9 (3), 1–12.
- Neemisha Kumar, A., Sharma, P., Kaur, A., Sharma, S., Jain, R., 2022. Harnessing rhizobacteria to fulfil inter-linked nutrient dependency on soil and alleviate stresses in plants. *J. Appl. Microbiol.* 133 (5), 2694–2716. <https://doi.org/10.1111/jam.15649>.
- Nejat, N., Mantri, N., 2017. Plant immune system: Crosstalk between responses to biotic and abiotic stresses the missing link in understanding plant defence. *Curr. Issues Mol. Biol.* 23, 1–16.
- Ngumbi, E., Kloepper, J., 2016. Bacterial-mediated drought tolerance: current and future prospects. *Appl. Soil Ecol.* 105, 109–125.
- Nguyen, L.T., Osanai, Y., Anderson, I.C., Bange, M.P., Tissue, D.T., Singh, B.K., 2018. Flooding and prolonged drought have differential legacy impacts on soil nitrogen cycling, microbial communities and plant productivity. *Plant Soil* 431, 371–387.
- Ning, W., Zhai, H., Yu, J., Liang, S., Yang, X., Xing, X., Huo, J., Pang, T., Yang, Y., Bai, X., 2017. Overexpression of *Glycine soja* WRKY20 enhances drought tolerance and improves plant yields under drought stress in transgenic soybean. *Mol. Breed.* 37 (2), 19.
- Nishiyama, R., Watanabe, Y., Fujita, Y., Le, D.T., Kojima, M., Werner, T., Vankova, R., Yamaguchi-Shinozaki, K., Shinozaki, K., Kakimoto, T., Sakakibara, H., 2011. Analysis of cytokinin mutants and regulation of cytokinin metabolic genes reveals important regulatory roles of cytokinins in drought, salt and abscisic acid responses, and abscisic acid biosynthesis. *Plant Cell* 23 (6), 2169–2183.
- Nishu, S.D., No, J.H., Leea, T.K., 2022. Transcriptional response and plant growth promoting activity of *Pseudomonas fluorescens* DR397 under drought stress conditions. *Microbiol. Spectr.* 10 (4). <https://doi.org/10.1128/spectrum.00979-22>.
- Niu, X., Song, L., Xiao, Y., Ge, W., 2018. Drought-tolerant plant growth-promoting rhizobacteria associated with foxtail millet in a semi-arid agroecosystem and their potential in alleviating drought stress. *Front. Microbiol.* 8, 2580.
- Nuccio, M.L., Wu, J., Mowers, R., Zhou, H.P., Meghji, M., Primavesi, L.F., Paul, M.J., Chen, X., Gao, Y., Haque, E., Basu, S.S., Lagrimini, L.M., 2015. Expression of trehalose-6-phosphate phosphatase in maize ears improves yield in well-watered and drought conditions. *Nat. Biotechnol.* 33 (2015), 862–869.
- Nussaume, L., Kanno, S., Javot, H., Marin, E., Pochon, N., Ayadi, A., Nakanishi, T.M., Thibaud, M.C., 2011. Phosphate import in plants: focus on the PHT1 transporters. *Front. Plant Sci.* 2, 83.
- Ochoa-Hueso, R., Collins, S.L., Delgado-Baquerizo, M., Hamonts, K., Pockman, W.T., Sinsabaugh, R.L., Smith, M.D., Knapp, A.K., Power, S.A., 2018. Drought consistently alters the composition of soil fungal and bacterial communities in grasslands from two continents. *Glob. Chang. Biol.* 24, 2818–2827.
- Ojuederie, B.O., Babalola, O.O., 2023. Growth enhancement and extenuation of drought stress in maize inoculated with multifaceted ACC deaminase producing rhizobacteria. *Front. Sust. Food Syst.* 6, 1076844. <https://doi.org/10.3389/fsufs.2022.1076844>.
- Ojuederie, B.O., Babalola, O.O., 2017. Microbial and plant-assisted bioremediation of heavy metal polluted environments: a review. *Intern. J. Environ. Res. Public Health* 14 (12), 1504.
- Ojuederie, O.B., Olanrewaju, O.S., Babalola, O.O., 2019. Plant growth promoting rhizobacterial mitigation of drought stress in crop plants: Implications for sustainable agriculture. *Agronomy* 9 (11), 712.
- Oladosu, Y., Rafii, M.Y., Samuel, C., Fatai, A., Magaji, U., Kareem, I., Kamarudin, Z.S., Muhammad, I., Kolapo, K., 2019. Drought resistance in rice from conventional to molecular breeding: a review. *Intern. J. Mol. Sci.* 20, 3519.
- Olanrewaju, O.S., Glick, B.R., Babalola, O.O., 2017. Mechanisms of action of plant growth promoting bacteria. *World J. Microbiol. Biotechnol.* 33, 1–16.
- Oliveira, T.B., Lucas, R.C., de Scarcella, A.S.A., Contato, A.G., Pasin, T.M., Martinez, C. A., Polizeli, M.D.L.T.d.M., 2020. Fungal communities differentially respond to warming and drought in tropical grassland soil. *Mol. Ecol.* 29, 1550–1559.
- Omar, S.A., Fetyan, N.A.H., Eldenary, M.E., Abdelfattah, M.H., Abdelhalim, H.M., Wrobel, J., Kalaji, H.M., 2021. Alteration in expression level of some growth and stress-related genes after rhizobacteria inoculation to alleviate drought tolerance in sensitive rice genotype. *Chem. Biol. Technol. Agric.* 8, 41. <https://doi.org/10.1186/s40538-021-00237-4>.
- Orozco-Mosqueda, M.d.C., Flores, A., Rojas-Sánchez, B., Urtis-Flores, C.A., Morales-Cedeño, L.R., Valencia-Marin, M.F., Chávez-Avila, S., Rojas-Solis, D., Santoyo, G., 2021. Plant growth-promoting bacteria as bioinoculants: Attributes and challenges for sustainable crop improvement. *Agronomy* 11 (6), 1167.
- Orozco-Mosqueda, M.d.C., Santoyo, G., Glick, B.R., 2023. Recent advances in the bacterial phytohormone modulation of plant growth. *Plants* 12, 606. <https://doi.org/10.3390/plants12030606>.
- Ortiz, N., Armada, E., Duque, E., Roldán, A., Azcón, R., 2015. Contribution of arbuscular mycorrhizal fungi and/or bacteria to enhancing plant drought tolerance under natural soil conditions: effectiveness of autochthonous or allochthonous strains. *J. Plant Physiol.* 174, 87–96.
- Osakabe, Y., Osakabe, K., Shinozaki, K., Tran, L.S.P., 2014. Response of plants to water stress. *Front. Plant Sci.* 5, 86.
- Osakabe, Y., Yamaguchi-Shinozaki, K., Shinozaki, K., Tran, L.S.P., 2020. ABA control of plant macroelement membrane transport systems in response to water deficit and high salinity. *New Phytol.* 202, 35–49.
- Ostadi, A., Javanmard, A., Amani Machiani, M., Sadeghpour, A., Maggi, F., Nouraein, M., Morshedloo, M.R., Hano, C., Lorenzo, J.M., 2022. Co-application of TiO₂ nanoparticles and arbuscular mycorrhizal fungi improves essential oil quantity and quality of sage (*Salvia officinalis* L.) in drought stress conditions. *Plants* 11 (13), 1659.
- Ou, T., Zhang, M., Huang, Y., Wang, L., Wang, F., Wang, R., Liu, X., Zhou, Z., Xie, J., Xiang, Z., 2022. Role of rhizospheric *Bacillus megaterium* HGS7 in maintaining mulberry growth under extremely abiotic stress in hydro-fluctuation belt of three Gorges reservoir. *Front. Plant Sci.* 13, 880125. <https://doi.org/10.3389/fpls.2022.880125>.
- Ouledali, S., Ennajeh, M., Zrig, A., Gianinazzi, S., Khemira, H., 2018. Estimating the contribution of arbuscular mycorrhizal fungi to drought tolerance of potted olive trees (*Olea europaea*). *Acta Physiol. Plant* 40, 1–13.
- Paarlberg, R., 2014. A dubious success: The NGO campaign against GMOs. *GM Crops Food* 5, 223–228. <https://doi.org/10.4161/21645698.2014.952204>.
- Panpatte, D., Shukla, Y., Shelat, H., Vyas, R., Jhala, Y., 2017. Bacterial Volatile Organic Compounds: A New Insight for Sustainable Agriculture. *Microorganisms for Green Revolution*. Springer, Singapore.
- Passioura, J.B., Angus, J.F., 2010. Improving productivity of crops in water-limited environments. In: *Advances in Agronomy*, 106. Academic Press, Cambridge, MA, USA, pp. 37–75.
- Paul, G.K., Mahmud, S., Dutta, A.K., Sarkar, S., Laboni, A.A., Hossain, Md.S., Nagata, A., Karmaker, P., Razu, M.H., Kazi, T., Uddin, Md.S., Zaman, S., Islam, Md.S., Khan, M., Saleh, Md.A., 2022. Volatile compounds of *Bacillus pseudomycoides* induce growth and drought tolerance in wheat (*Triticum aestivum* L.). *Sci. Rep.* 12, 19137. <https://doi.org/10.1038/s41598-022-22354-2>.
- Pavei, D., Gonçalves-Vidigal, M.M., Schuelter, A.A., Schuster, I., Vieira, E.E., Vendruscolo, E.E., Poletine, J.J., 2016. Response to water stress in transgenic (P5CS gene) wheat plants (*Triticum aestivum* L.). *Aust. J. Crop Sci.* 10, 776.

- Pedersen, O., Sauter, M., Colmer, T.D., Nakazono, M., 2021. Regulation of root adaptive anatomical and morphological traits during low soil oxygen. *New Phytol.* 229 (1), 42–49.
- Pedraza, R., 2015. Siderophores Production by *Azospirillum*: Biological Importance, Assessing Methods and Biocontrol Activity. *Handbook for Azospirillum*. Springer, Cham, Switzerland, pp. 251–262.
- Petrushin, I.S., Vasilev, I.A., Markova, Y.A., 2023. Drought tolerance of legumes: physiology and the role of the microbiome. *Curr. Mol. Biol.* 45 (8), 6311–6324.
- Phour, M., Seharawat, A., Sindhu, S.S., Glick, B.R., 2020. Interkingdom signaling in plant-rhizomicrobiome interactions for sustainable agriculture. *Microbiol. Res.* 241, 126589.
- Phour, M., Sindhu, S.S., 2022. Mitigating abiotic stress: Microbiome engineering for improving agricultural production and environmental sustainability. *Planta* 256, 85. <https://doi.org/10.1007/s00425-022-03997-x>.
- Phour, M., Sindhu, S.S., 2023. Soil salinity and climate change: Microbiome-based strategies for mitigation of salt stress to sustainable agriculture. In: Parry, J.A. (Ed.), *Climate Change and Microbiome Dynamics*. Climate Change Management. Springer, Cham, pp. 191–243. https://doi.org/10.1007/978-3-031-21079-2_13.
- Phour, M., Sindhu, S.S., 2024. Arbuscular mycorrhizal fungi: An eco-friendly technology for alleviation of salinity stress and nutrient acquisition in sustainable agriculture. In: Parihar, M., Rakshit, A., Adholeya, A., Chen, Y. (Eds.), *Advances in arbuscular mycorrhizal fungal technology for sustainable agriculture II: Nutrient and crop management*. Springer, Cham.
- Pinheiro, C., Chaves, M.M., 2011. Photosynthesis and drought: can we make metabolic connections from available data? *J. Exp. Bot.* 62 (3), 869–882.
- Pixley, K.V., Cairns, J.E., Lopez-Ridaura, S., Ojiewo, C.O., Dawud, M.A., Drabo, I., Mindaye, T., Nebie, B., Asea, G., Das, B., Daudi, H., Desmae, H., Batieno, B.J., Boukar, O., Mukankusi, C.T.M., Nkalubo, S.T., Hearne, S.J., Dhugga, K.S., Gandhi, H., Snapp, S., Zepeda-Villarreal, E.A., 2023. Redesigning crop varieties to win the race between climate change and food security. *Mol. Plant* 16, 1590–1611.
- Pixley, K.V., Falck-Zepeda, J.B., Paarlberg, R.L., Phillips, P.W.B., Slamet-Loedin, I.H., Dhugga, K.S., Campos, H., Gutterson, N., 2022. Genome-edited crops for improved food security of smallholder farmers. *Nat. Genet.* 54, 364–367.
- Plaza-Wüthrich, S., Blösch, R., Rindisbacher, A., Cannarozzi, G., Tadele, Z., 2016. Gibberellin deficiency confers both lodging and drought tolerance in small cereals. *Front. Plant Sci.* 7, 643.
- Podevin, N., Davies, H.V., Hartung, F., Casacuberta, J.M., Nogue, F., 2013. Site directed nucleases: A paradigm shift in predictable, knowledge-based plant breeding. *Trends Biotechnol.* 31 (6), 375–383.
- Posta, K., Duc, N.H., 2019. Benefits of Arbuscular Mycorrhizal Fungi Application to Crop Production under Water Scarcity. *Drought (Aridity)*. Intech Open, London, UK.
- Poudel, M., Mendes, R., Costa, L.A.S., Bueno, C.G., Meng, Y., Folimonova, S.Y., Garrett, K.A., Martins, S.J., 2021. The role of plant associated bacteria, fungi, and viruses in drought stress mitigation. *Front. Microbiol.* 12, 3058.
- Pourgholam, M., Nemati, N., Oveysi, M., 2013. Effect of zinc and iron under the influence of drought on yield and yield components of rapeseed (*Brassica napus*). *Ann. Biol. Res.* 4 (4), 186–189.
- Pozo, M.J., López-Ráez, J.A., Azcón-Aguilar, C., García-Garrido, J.M., 2015. Phytohormones as integrators of environmental signals in the regulation of mycorrhizal symbioses. *New Phytol.* 205 (4), 1431–1436.
- Prakash, V., Singh, V.P., Tripathi, D.K., Sharma, S., Corpas, F.J., 2019. Crosstalk between nitric oxide (NO) and abscisic acid (ABA) signalling molecules in higher plants. *Environ. Exp. Bot.* 161, 41–49.
- Pravitsya, P., Jayaram, K.M., Yusuf, A., 2019. Biotic priming with *Pseudomonas fluorescens* induce drought stress tolerance in *Abelmoschus esculentus* (L.) Moench (Okra). *Physiol. Mol. Biol. Plants* 25, 101–112.
- Preece, C., Peñuelas, J., 2016. Rhizodeposition under drought and consequences for soil communities and ecosystem resilience. *Plant Soil* 409, 1–17.
- Prerostova, S., Dobrev, P.I., Gaudinova, A., Knirsch, V., Körber, N., Pieruschka, R., Fiorani, F., Brzobohatý, B., Černý, M., Spichal, L., Humplik, J., 2018. Cytokinin: Their impact on molecular and growth responses to drought stress and recovery in *Arabidopsis*. *Front. Plant Sci.* 9, 655.
- Prescott, C.E., Grayston, S.J., Helmissaari, H.S., Kastovska, E., Korner, C., Lambers, H., Meier, I.C., Millard, P., Ostonen, I., 2020. Surplus carbon drives allocation and plant-soil interactions. *Trends Ecol. Evol.* 35, 1110–1118.
- Przewieslik-Allen, A.M., Burridge, A.A., Wilkinson, P.P., Winfield, M.M., Shaw, D.D., McAusland, L., King, J., King, I.I., Edwards, K.K., Barker, G.L.A., 2019. Developing a high-throughput snp-based marker system to facilitate the introgression of traits from aegilops species into bread wheat (*Triticum aestivum*). *Front. Plant Sci.* 9, 1993.
- Pujni, D., Chaudhary, A., Rajam, M.V., 2007. Increased tolerance to salinity and drought in transgenic indica rice by mannitol accumulation. *J. Plant Biochem. Biotechnol.* 16, 1–7.
- Püschel, D., Bitterlich, M., Rydlová, J., Jansa, J., 2020. Facilitation of plant water uptake by an arbuscular mycorrhizal fungus: a Gordian knot of roots and hyphae. *Mycorrhiza* 30, 299–313.
- Putrie, R.F.W., Wahyudi, A.T., Nawangsih, A.A., Husen, E., 2013. Screening of rhizobacteria for plant growth promotion and their tolerance to drought stress. *Microbiol. Indonesia* 7 (3), 2–12.
- Qaim, M., 2020. Role of new plant breeding technologies for food security and sustainable agricultural development. *Appl. Econ. Perspect.* 42 (2), 129–150.
- Qin, F., Sakuma, Y., Li, J., Liu, Q., Li, Y.Q., Shinozaki, K., Yamaguchi-Shinozaki, K., 2004. Cloning and functional analysis of a novel DREB1/CBF transcription factor involved in cold-responsive gene expression in *Zea mays* L. *Plant Cell Physiol.* 45, 1042–1052.
- Queiroz, M.S., Oliveira, C.E., Steiner, F., Zuffo, A.M., Zoz, T., Vendruscolo, E.P., Silva, M.V., Mello, B.F., Cabral, R.C., Menis, F.T., 2019. Drought stresses on seed germination and early growth of maize and sorghum. *J. Agric. Sci.* 11 (2), 310.
- Quides, K.W., Atamian, H.S., 2021. A microbiome engineering framework to evaluate rhizobial symbionts of legumes. *Plant Soil* 463, 631–642.
- Quiroga, G., Erice, G., Aroca, R., Chaumont, F., Ruiz-Lozano, J.M., 2017. Enhanced drought stress tolerance by the arbuscular mycorrhizal symbiosis in a drought-sensitive maize cultivar is related to a broader and differential regulation of host plant aquaporins than in a drought-tolerant cultivar. *Front. Plant Sci.* 8, 1056.
- Raaijmakers, B.J.M., Kiers, E.T., 2022. Rewilding plant microbiomes. *Science* 378 (6620), 599–600. <https://doi.org/10.1126/science.abn6350>.
- Raheem, A., Shaposhnikov, A., Belimov, A.A., Dodd, I.C., Ali, B., 2018. Auxin production by rhizobacteria was associated with improved yield of wheat (*Triticum aestivum* L.) under drought stress. *Arch. Agron. Soil Sci.* 64 (4), 574–587.
- Ramireddy, E., Hosseini, S.A., Eggert, K., Gillandt, S., Gnad, H., von Wirén, N., Schmülling, T., 2018. Root engineering in barley: increasing cytokinin degradation produces a larger root system, mineral enrichment in the shoot and improved drought tolerance. *Plant Physiol.* 177 (3), 1078–1095.
- Ranjan, A., Sinha, R., Singla-Pareek, S.L., Pareek, A., Singh, A.K., 2022. Shaping the root system architecture in plants for adaptation to drought stress. *Physiol. Plant.* 174 (2), e13651.
- Rao, D.E., Chaitanya, K.V., 2016. Photosynthesis and antioxidative defense mechanisms in deciphering drought stress tolerance of crop plants. *Biol. Plant.* 60 (2), 201–218.
- Rapparini, F., Peñuelas, J., 2014. Mycorrhizal fungi to alleviate drought stress on plant growth. In: Miransari, M. (Ed.), *Use of Microbes for the Alleviation of Soil Stresses*. Springer, New York, pp. 21–42.
- Rasheed, A., Mahmood, A., Maqbool, R., Albaqami, M., Sher, A., Sattar, A., Khosa, G.B., Nawaz, M., Hassan, M.U., Al-Yahyai, R., 2022. Key insights to develop drought-resilient soybean: A review. *J. King Saud Univ. Sci.* 34, 102089.
- Rasouli, F., Amini, T., Skrovankova, S., Asadi, M., Hassanpourghadam, M.B., Ercisli, S., Buckova, M., Mrazkova, M., Mlcek, J., 2023. Influence of drought stress and mycorrhizal (*Funnelformis mosseae*) symbiosis on growth parameters, chlorophyll fluorescence, antioxidant activity, and essential oil composition of summer savory (*Satureja hortensis* L.) plants. *Front. Plant Sci.* 14, 1151467. <https://doi.org/10.3389/fpls.2023.1151467>.
- Raza, A., Razaq, A., Mehmood, S.S., Zou, X., Zhang, X., Lv, Y., Xu, J., 2019. Impact of climate change on crops adaptation and strategies to tackle its outcome: A review. *Plants* 8 (2), 34.
- Raza, W., Wei, Z., Jousset, A., Shen, Q., Friman, V.P., 2021. Extended plant metarhizobiome: understanding volatile organic compound signaling in plant-microbe metapopulation networks. *mSystems* 6, e0084921.
- Ren, R., Wang, H., Wu, C., Heng, Q., Chen, W., Sun, T., Zhang, L., He, H., Li, X., Zhang, Y., 2023. Full-length cloning and functional verification of PagP5CS1 from *Populus alba* × *P. glandulosa*. *J. Northeast. For. Univ.* 38, 90–96.
- Ren, Z., Fu, J., Abou-Elwafa, S.F., Ku, L., Xie, X., Liu, Z., Wei, L., 2024. Analysis of the molecular mechanisms regulating how ZmEREB24 improves drought tolerance in maize (*Zea mays*) seedlings. *Plant Physiol. Biochem.* 207, 108292.
- Reynolds, M., Tattaris, M., Cossani, C.M., Ellis, M., Yamaguchi-Shinozaki, K., Saint Pierre, C., 2015. Exploring genetic resources to increase adaptation of wheat to climate change. *Advances in Wheat Genetics: From Genome to Field*. Springer, Berlin/Heidelberg, Germany, pp. 355–368.
- Riechmann, J.L., Meyerowitz, E.M., 1998. The AP2/EREBP family of plant transcription factors. *Biol. Chem.* 379, 633–646.
- Rigi, F., Saberi, M., Ebrahimi, M., 2023. Improved drought tolerance in *Festuca ovina* L. using plant growth promoting bacteria. *J. Arid Land* 15 (6), 740–755.
- Ristvey, A.G., Belayneh, B.E., Lea-Cox, J.D., 2019. A Comparison of irrigation-water containment methods and management strategies between two ornamental production systems to minimize water security threats. *Water* 11 (12), 2558.
- Rolli, E., Marasco, R., Vigani, G., Ettoumi, B., Capelli, F., Deangelis, M.L., Gandolfi, C., Casati, E., Previtali, F., Gerbino, R., Pierotti Cei, F., 2015. Improved plant resistance to drought is promoted by the root-associated microbiome as a water stress-dependent trait. *Environ. Microbiol.* 17 (2), 316–331.
- Romero-Munar, A., Aroca, R., Zamarreño, A.M., García-Mina, J.M., Perez-Hernández, N., Ruiz-Lozano, J.M., 2023. Dual inoculation with *Rhizophagus irregularis* and *Bacillus megaterium* improves maize tolerance to combined drought and high temperature stress by enhancing root hydraulics, photosynthesis and hormonal responses. *Intern. J. Mol. Sci.* 24 (6), 5193.
- Rosa, A.P., Dias, T., Mouazen, A.M., Cruz, C., Santana, M.M., 2023. Finding optimal microorganisms to increase crop productivity and sustainability under drought—A structured reflection. *J. Plant Interact.* 18, 2178680.
- Rotaru, V., 2011. The effect of phosphorus and iron on plant growth and nutrient status of two soybean (*Glycine max* L.) cultivars under suboptimal water regime of soil. *Lucrări Stiint. Suplim. Agron.* 54 (1), 11–16.
- Rubin, R.L., van Groenigen, K.J., Hungate, B.A., 2017. Plant growth promoting rhizobacteria are more effective under drought: a meta-analysis. *Plant Soil* 416, 309–323.
- Rueda, M., Godoy, O., Hawkins, B.A., 2017. Spatial and evolutionary parallelism between shade and drought tolerance explains the distributions of conifers in the conterminous United States. *Glob. Ecol. Biogeogr.* 26 (1), 31–42.
- Ruehr, N.K., Grote, R., Mayr, S., Arneith, A., 2019. Beyond the extreme: recovery of carbon and water relations in woody plants following heat and drought stress. *Tree Physiol.* 39 (8), 1285–1299.
- Ruiz-Lozano, J.M., 2003. Arbuscular mycorrhizal symbiosis and alleviation of osmotic stress. *New perspectives for molecular studies*. *Mycorrhiza* 13, 309–317.
- Ruiz-Lozano, J.M., Aroca, R., Zamarreño, A.M., Molina, S., Andreo-Jiménez, B., Porcel, R., 2015. Arbuscular mycorrhizal symbiosis induces strigolactone biosynthesis under drought and improves drought tolerance in lettuce and tomato. *Plant Cell Environ.* 39 (2), 441–452. <https://doi.org/10.1111/pce.12631>.

- Ruiz-Lozano, J.M., Porcel, R., Aroca, R., 2006. Does the enhanced tolerance of arbuscular mycorrhizal plants to water deficit involve modulation of drought-induced plant genes? *New Phytol.* 171, 693–698.
- Ryan, P.R., Delhaize, E., Watt, M., Richardson, A.E., 2016. Plant roots: understanding structure and function in an ocean of complexity. *Ann. Bot.* 118, 555–559. <https://doi.org/10.1093/aob/mcw192>.
- Saakre, M., Baburao, T.M., Salim, A.P., Ffancies, R.M., Achuthan, V.P., Thomas, G., Sivarajan, S.R., 2017. Identification and characterization of genes responsible for drought tolerance in rice mediated by *Pseudomonas fluorescens*. *Rice Sci.* 24 (5), 291f298. <https://doi.org/10.1016/j.rsci.2017.04.005>.
- Saddique, M.A.B., Ali, Z., Khan, A.S., Rana, I.A., Shamsi, I.H., 2018. Inoculation with the endophyte *Piriformospora indica* significantly affects mechanisms involved in osmotic stress in rice. *Rice* 11 (1), 1–12.
- Sadhukhan, A., Prasad, S.S., Mitra, J., Siddiqui, N., Sahoo, L., Kobayashi, Y., Koyama, H., 2023. How do plants remember drought? *Planta* 256, 1–15.
- Sah, S.K., Reddy, K.R., Li, J., 2016. Abscisic acid and abiotic stress tolerance in crop plants. *Front. Plant Sci.* 7, 571.
- Sahu, G.K., Sindhu, S.S., 2011. Disease control and plant growth promotion of green gram by siderophore producing *Pseudomonas* sp. *Res. J. Microbiol.* 6, 735–749.
- Saikia, J., Sarma, R.K., Dhandia, R., Yadav, A., Bharali, R., Gupta, V.K., Saikia, R., 2018. Alleviation of drought stress in pulse crops with ACC deaminase producing rhizobacteria isolated from acidic soil of Northeast India. *Sci. Rep.* 8 (1), 3560.
- Sakamoto, A., Murata, N., 2000. Genetic engineering of glycine betaine synthesis in plants: Current status and implications for enhancement of stress tolerance. *J. Exp. Bot.* 51, 81–88.
- Sakuma, Y., Liu, Q., Dubouzet, J.G., Abe, H., Shinozaki, K., Yamaguchi-Shinozaki, K., 2002. DNA-binding specificity of the ERF/AP2 domain of *Arabidopsis* DREBs, transcription factors involved in dehydration-and cold-inducible gene expression. *Biochem. Biophys. Res. Commun.* 290, 998–1009.
- Salamon, S., Mikolajczak, K., Blaszczyk, L., Ratajczak, K., Sulewska, H., 2020. Changes in root-associated fungal communities in *Triticum aestivum* ssp. *spelta* L. and *Triticum aestivum* ssp. *vulgare* L. under drought stress and in various soil processing. *PLoS One* 15, e0240037.
- Saleem, A.R., Brunetti, C., Khalid, A., Della Rocca, G., Raio, A., Emiliani, G., De Carlo, A., Mahmood, T., Centritto, M., 2018. Drought response of *Mucuna pruriens* (L.) DC. inoculated with ACC deaminase and IAA producing rhizobacteria. *PLoS One* 13 (2), e0191218.
- Salehin, M., Li, B., Tang, M., Katz, E., Song, L., Ecker, J.R., Kliebenstein, D.J., Estelle, M., 2019. Auxin-sensitive Aux/IAA proteins mediate drought tolerance in *Arabidopsis* by regulating glucosinolate levels. *Nat. Commun.* 10 (1), 4021.
- Salvi, P., Manna, M., Kaur, H., Thakur, T., Gandass, N., Bhatt, D., Muthamilarasan, M., 2021. Phytohormone signaling and crosstalk in regulating drought stress response in plants. *Plant Cell Rep.* 40, 1305–1329.
- Sánchez-Romera, B., Ruiz-Lozano, J.M., Li, G., Luu, D.T., del Carmen Martínez-Ballesta, M., Carvajal, M., Zamarreño, A.M., García-Mina, J.M., Maurel, C., Aroca, R., 2014. Enhancement of root hydraulic conductivity by methyl jasmonate and the role of calcium and abscisic acid in this process. *Plant Cell Environ.* 37, 995–1008.
- Sandhya, V.S.K.Z., Ali, S.Z., Grover, M., Reddy, G., Venkateswarlu, B., 2010. Effect of plant growth promoting *Pseudomonas* on compatible solutes, antioxidant status and plant growth of maize under drought stress. *Plant Growth Regul.* 62, 21–30.
- Santos-Medellín, C., Edwards, J., Liechty, Z., Nguyen, B., Sundaresan, V., 2017. Drought stress results in a compartment-specific restructuring of the rice root-associated microbiomes. *mBio* 8, e00764. -17.
- Santos-medellín, C., Liechty, Z., Edwards, J., Nguyen, B., Huang, B., Weimer, B.C., Sundaresan, V., 2021. Prolonged drought imparts lasting compositional changes to the rice root microbiome. *Nat. Plants* 7, 1065–1077. <https://doi.org/10.1038/s41477-021-00967-1>.
- Sasse, J., Simon, S., Gübeli, C., Liu, G.W., Cheng, X., Friml, J., Bouwmeester, H., Martinioia, E., Borghi, L., 2015. Asymmetric localizations of the ABC transporter PaPDR1 trace paths of directional strigolactone transport. *Curr. Biol.* 25 (5), 647–655.
- Sati, D., Pande, V., Pandey, S.C., Samant, M., 2023. Recent advances in PGPR and molecular mechanisms involved in drought stress resistance. *J. Soil Sci. Plant Nutr.* 23 (1), 106–124.
- Savvides, A., Ali, S., Tester, M., Fotopoulos, V., 2016. Chemical priming of plants against multiple abiotic stresses: mission possible? *Trends Plant Sci.* 21 (4), 329–340.
- Sawahel, W.W., Hassan, A.H., 2002. Generation of transgenic wheat plants producing high levels of the osmoprotectant proline. *Biotechnol. Lett.* 24, 721–725.
- Saxena, S.S., Kaur, H., Verma, P., Petla, B.B., Andugula, V.V., Majee, M., 2013. Osmoprotectants: Potential for crop improvement under adverse conditions (Eds.). In: Tuteja, N., Singh, S.S. (Eds.), *Plant Acclimation to Environmental Stress*. Springer, New York, NY, USA, pp. 197–232.
- Sayer, E.J., Crawford, J.A., Edgerley, J., Askew, A.P., Hahn, C.Z., Whitlock, R., Dodd, I. C., 2021. Adaptation to chronic drought modifies soil microbial community responses to phytohormones. *Commun. Biol.* 4 (1), 516.
- Schimel, J.P., Gullledge, J.M., Clein-Curley, J.S., Lindstrom, J.E., Braddock, J.F., 1999. Moisture effects on microbial activity and community structure in decomposing birch litter in the Alaskan Taiga. *Soil Biol. Biochem.* 31, 831–838.
- Sehrawat, A., Sindhu, S.S., 2019. Potential of biocontrol agents in plant disease control for improving food safety. *Def. Life Sci. J.* 4, 220–225.
- Sehrawat, A., Sindhu, S.S., 2024. Zinc-solubilizing microorganisms: Contributions in nutrients availability and implications for crop productivity in sustainable agriculture (Eds.). In: Sayyed, R.Z., Noshin, Ilyas (Eds.), *Sustainable Plant Nutrition in a Changing World: Plant Holobiome Engineering for Climate-Smart Agriculture*. Springer, Singapore, pp. 183–213. <https://doi.org/10.1007/978-981-99-9388-8>.
- Sehrawat, A., Sindhu, S.S., Glick, B.R., 2022. Hydrogen cyanide production by soil bacteria: Biological control of pests and plant growth promotion. *Pedosphere* 32 (1), 15–38. [https://doi.org/10.1016/S1002-6106\(21\)60058-9](https://doi.org/10.1016/S1002-6106(21)60058-9).
- Seleiman, M.F., Al-Suhaibani, N., Ali, N., Akmal, M., Alotaibi, M., Refay, Y., Dindaroglu, T., Abdol-Wajid, H., Battaglia, M.L., 2021. Drought stress impacts on plants and different approaches to alleviate its adverse effects. *Plants* 10 (2), 259.
- Seleiman, M.F., Kheir, A.M., 2018. Saline soil properties, quality and productivity of wheat grown with bagasse ash and thiourea in different climatic zones. *Chemosphere* 193, 538–546.
- Senapati, N., Stratonovitch, P., Paul, M.J., Semenov, M.A., 2018. Drought tolerance during reproductive development is important for increasing wheat yield potential under climate change in Europe. *J. Exp. Bot.* 70, 2549–2560.
- Shaffique, S., Imran, M., Injamum-Ul-Hoque, M., Zainurin, N., Peter, O., Alomrani, S.O., Lee, L.J., 2024. Unraveling the new member *Bacillus pumilus* SH-9 of Bacillaceae family and its potential role in seed biopriming to mitigate drought stress in *Oryza sativa*. *Plant Stress* 11, 100318.
- Shaffique, S., Imran, M., Rahim, W., Alomrani, S.O., Yun, B.W., Lee, L.J., 2023. A newly isolated *Bacillus pumilus* strain SH-9 modulates response to drought stress in soybean via endogenous phytohormones and gene expression (Daegu, South Korea). *Plant Stress* 10, 100279.
- Shah, A., Nazari, M., Antar, M., Msimbira, L.A., Naamala, J., Lyu, D., Rabileh, M., Zajonc, J., Smith, D.L., 2021. PGPR in agriculture: A sustainable approach to increasing climate change resilience. *Front. Sustain. Food Syst.* 5, 667546. <https://doi.org/10.3389/fsufs.2021>.
- Shah, S.H., Ali, S., Hussain, Z., Jan, S.A., Ali, G.M., 2016. Genetic improvement of tomato (*Solanum lycopersicum*) with AtDREB1A gene for cold stress tolerance using optimized agrobacterium-mediated transformation system. *Intern. J. Agric. Biol.* 18, 471–782.
- Shahid, M.J., Ali, S., Shabir, G., Siddique, M., Rizwan, M., Seleiman, M.F., Afzal, M., 2020. Comparing the performance of four macrophytes in bacterial assisted floating treatment wetlands for the removal of trace metals (Fe, Mn, Ni, Pb, and Cr) from polluted river water. *Chemosphere* 243, 125353.
- Shanker, A.K., Maheswari, M., 2017. Small RNA and drought tolerance in crop plants. *Indian J. Plant Physiol.* 22, 422–433.
- Shao, Y., Zhang, X., van Nocker, S., Gong, X., Ma, F., 2019. Overexpression of a protein kinase gene MpSnRK2.10 from *Malus prunifolia* confers tolerance to drought stress in transgenic *Arabidopsis thaliana* and apple. *Gene* 692, 26–34.
- Sharath, S., Triveni, S., Nagaraju, Y., Latha, P.C., Vidyasagar, B., 2021. The role of phyllosphere bacteria in improving cotton growth and yield under drought conditions. *Front. Agron.* 3, 680466. <https://doi.org/10.3389/fagro2021680466>.
- Sharifi, R., Ryu, C.M., 2018. Revisiting bacterial volatile-mediated plant growth promotion: lessons from the past and objectives for the future. *Ann. Bot.* 122 (3), 349–358.
- Sharma, R., Sindhu, S.S., Glick, B.R., 2024. Potassium solubilizing microorganisms as potential biofertilizer: A sustainable climate-resilient approach to improve soil fertility and crop production in agriculture. *J. Plant Growth Regul.*
- Sharoni, A.M., Nuruzzaman, M., Satoh, K., Shimizu, T., Kondoh, H., Sasaya, T., Choi, I.R., Omura, T., Kikuchi, S., 2010. Gene structures, classification and expression models of the AP2/EREBP transcription factor family in rice. *Plant Cell Physiol.* 52, 344–360.
- Shayanthan, A., Ordoñez, P.A.C., Oresnik, I.J., 2022. The role of synthetic microbial communities (SynCom) in sustainable agriculture. *Front. Agron.* 4, 896307. <https://doi.org/10.3389/fagro.2022.896307>.
- Sheibani-Tezerji, R., Rattei, T., Sessitsch, A., Trognitz, F., Mitter, B., 2015. Transcriptome profiling of the endophyte *Burkholderia phytofirmans* PsJN indicates sensing of the plant environment and drought stress. *mBio* 6 (5), e00621. <https://doi.org/10.1128/mBio.00621-15>.
- Shen, M., Huang, W., Chen, M., Song, B., Zeng, G., Zhang, Y., 2020. (Micro) plastic crisis: unignorable contribution to global greenhouse gas emissions and climate change. *J. Clean. Prod.* 254, 120138.
- Shetiwy, M.S., Abd Elgawad, H., Xiong, Y.C., Macovei, A., Brestic, M., Skalicky, M., Shaghaleh, H., Alhaj Hamoud, Y., El-Sawah, A.M., 2021. Inoculation with *Bacillus amyloliquefaciens* and mycorrhiza confers tolerance to drought stress and improve seed yield and quality of soybean plant. *Physiol. Plant* 172 (4), 2153–2169.
- Shi, Y., Chang, Y.L., Wu, H.T., Shalmani, A., Liu, W.T., Li, W.Q., Xu, J.W., Chen, K.M., 2020. OsRbohB-mediated ROS production plays a crucial role in drought stress tolerance of rice. *Plant Cell Rep.* 39, 1767–1784.
- Shim, J.S., Oh, N., Chung, P.J., Kim, Y.S., Choi, Y.D., Kim, J.K., 2018. Overexpression of OsNAC14 improves drought tolerance in rice. *Front. Plant Sci.* 9 (2018), 310.
- Shintu, P.V., Jayaram, K.M., 2015. Phosphate solubilising bacteria (*Bacillus polymyxa*)—An effective approach to mitigate drought in tomato (*Lycopersicon esculentum* Mill. *Trop. Plant Res.* 2 (1), 2349–9265.
- Shoresh, M., Harman, G.E., Mastouri, F., 2010. Induced systemic resistance and plant responses to fungal biocontrol agents. *Annu. Rev. Phytopathol.* 48, 21–43.
- Si, J., Froussart, E., Viaene, T., Vazquez-Castellanos, J.F., Hamonts, K., Tang, L., Beirincx, S., De Keyser, A., Deckers, T., Amery, F., et al., 2021. Interactions between soil compositions and the wheat root microbiome under drought stress: From an *in silico* to *in planta* perspective. *Comput. Struct. Biotechnol. J.* 19, 4235–4247.
- Siddique, Z., Jan, S., Imadi, S.R., Gul, A., Ahmad, P., 2016. Drought stress and photosynthesis in plants. *Water Stress Crop Plants: Sustain. Approach* 1, 1–11.
- Siebielec, S., Siebielec, G., Klimkowicz-Pawlas, A., Gał azka, A., Grz adziel, J., Stuczyński, T., 2020. Impact of water stress on microbial community and activity in sandy and loamy soils. *Agronomy* 10, 1429.
- Simmons, T., Styer, A.B., Pierroz, G., Gonçalves, A.P., Pasricha, R., Hazra, A.B., Bubner, P., Coleman-Derr, D., 2020. Drought drives spatial variation in the millet root microbiome. *Front. Plant Sci.* 11, 599.

- Sindhu, D., Sindhu, S., 2023. Biological databases and resources: Their engineering and applications in synthetic biology. *Intern. J. Adv. Sci. Eng.* 9 (4), 3085–3098. <https://doi.org/10.29294/IJASE.9.4.2023.3085-3098>.
- Sindhu, S.S., Dadarwal, K.R., 1994. Biosynthesis of exopolysaccharides and its role during nodule development in *Rhizobium*-legume symbiosis (Eds.). In: Vashampayan, A., Prasad, A.B. (Eds.), *Biology and application of nitrogen-fixing organisms - Problems and prospectus*. Scientific Publishers, Jodhpur, pp. 189–240.
- Sindhu, S.S., Goyal, A., Sindhu, S., Goyal, S., 2017. Food and water-borne diseases (Ed.). In: Rana, M.K. (Ed.), *Human Health through Better Nutrition and Hygiene*. Brillion Publishing, New Delhi, pp. 399–442.
- Sindhu, S.S., Mor, S., Dadarwal, K.R., 1999. Cell surface polysaccharides of *Rhizobium* and nodule development on legume roots: Recent advances (Eds.). In: Gakhar, S.K., Mishra, S.N. (Eds.), *Recent Trends in Developmental Biology*. Himalaya Publishing House, New Delhi, pp. 204–240.
- Sindhu, S.S., Sehrawat, A., Glick, B.R., 2022. The involvement of organic acids in soil fertility, plant health and environment sustainability. *Arch. Microbiol.* 204, 720. <https://doi.org/10.1007/s00203-022-03321-x>.
- Sindhu, S.S., Sharma, H.R., Dadarwal, K.R., 2003. Competition among *Bradyrhizobium* strains for nodulation of green gram (*Vigna radiata*): use of dark nodule phenotype. *Folia Microbiol.* 48, 83–89.
- Singh, A.D., Kour, J., Kumar, P., Sharma, N., Sharma, P., Madaan, I., Sharma, I., Kapoor, N., Singh, A.P., Bhardwaj, R., 2023. Role of jasmonates in regulating physiological and molecular aspects of plants under abiotic stress. In: Sharma, A., Pandey, S., Bhardwaj, R., Zheng, B., Tripathi, D.K. (Eds.), *The Role of Growth Regulators and Phytohormones in Overcoming Environmental Stress*, Academic Press, 3, 137–173.
- Singh, D., Mathimaran, N., 2019. Bioirrigation: A common mycorrhizal network facilitates the water transfer from deep-rooted pigeon pea to shallow-rooted finger millet under drought. *Plant Soil* 440, 277–292. <https://doi.org/10.1007/s11104-019-04082-1>.
- Singh, D.P., Singh, V., Gupta, V.K., Shukla, R., Prabha, R., Sarma, B.K., Patel, J.S., 2020. Microbial inoculation in rice regulates antioxidative reactions and defense related genes to mitigate drought stress. *Sci. Rep.* 10 (1), 4818.
- Siraj, S., Khan, M.A., Hamayun, M., Ali, S., Khan, S.A., Hussain, A., Iqbal, A., Khan, H., Kang, S.M., Lee, I.J., 2022. *Microbacterium oxydans* regulates physio-hormonal and molecular attributes of *Solanum lycopersicum* under drought stress. *Agronomy* 12 (12), 3224.
- Sobhanian, H., Pahlavan, S., Meyfour, A., 2020. How does proteomics target plant environmental stresses in a semi-arid area? *Mol. Biol. Rep.* 47, 3181–3194.
- Song, Y., Wilson, A.J., Zhang, X.C., Thoms, D., Sohrabi, R., Song, S., Geissmann, Q., Liu, Y., Walgren, L., He, S.Y., Haney, C.H., 2021. FERONIA restricts *Pseudomonas* in the rhizosphere microbiome via regulation of reactive oxygen species. *Nat. Plants* 7 (5), 644–654.
- Soumare, A., Sarr, D., Diedhiou, A.G., 2022. Potassium sources, microorganisms, and plant nutrition – challenges and future research directions: A review. *Pedosphere* 33 (1), 105–115. <https://doi.org/10.1016/j.pedosph.2022.06.025>.
- Spaepen, S., Vanderleyden, J., 2011. Auxin and plant-microbe interactions. *Cold Spring Harb. Perspect. Biol.* 3 (4), a001438.
- Sponsel, V.M., Hedden, P., 2010. Gibberellin biosynthesis and inactivation. *Plant Hormon.: Biosynthes. Signal Transdu. Action!* 63–94.
- Stauder, R., Welsch, R., Camagna, M., Kohlen, W., Balcke, G.U., Tissier, A., Walter, M.H., 2018. Strigolactone levels in dicot roots are determined by an ancestral symbiosis-regulated clade of the phytoene synthase gene family. *Front. Plant Sci.* 9, 255.
- Steinweg, J.M., Dukes, J.S., Paul, E.A., Wallenstein, M.D., 2013. Microbial responses to multi-factor climate change: effects on soil enzymes. *Front. Microbiol.* 4, 146.
- Stockinger, E.J., Gilmour, S.J., Thomashow, M.F., 1997. *Arabidopsis thaliana* CBF1 encodes an AP2 domain-containing transcriptional activator that binds to the C-repeat/DRE, a cis-acting DNA regulatory element that stimulates transcription in response to low temperature and water deficit. *Proc. Natl. Acad. Sci. U.S.A.* 94, 1035–1040.
- Strock, C.F., Burridge, J.D., Niemiec, M.D., Brown, K.M., Lynch, J.P., 2021. Root metaxylem and architecture phenotypes integrate to regulate water use under drought stress. *Plant Cell Environ.* 44 (1), 49–67.
- Strullu-Derrien, C., Selosse, M.A., Kenrick, P., Martin, F.M., 2018. The origin and evolution of mycorrhizal symbioses: from palaeomycology to phylogenomics. *New Phytol.* 220 (4), 1012–1030.
- Sukwernadhi, J., Kim, Y.J., Choi, E.S., Koh, S.C., Lee, S.W., Kim, Y.J., Yang, D.C., 2015. *Paenibacillus yonginensis* DCY84T induces changes in *Arabidopsis thaliana* gene expression against aluminum, drought, and salt stress. *Microbiol. Res.* 172, 7–15.
- Sun, X., Xi, D.H., Feng, H., Du, J.B., Lei, T., Liang, H.G., Lin, H.H., 2009. The dual effects of salicylic acid on dehydrin accumulation in water-stressed barley seedlings. *Russ. J. Plant Physiol.* 56, 348–354.
- Sunitha, M., Srinath, T., Reddy, V.D., Rao, K.V., 2017. Expression of cold and drought regulatory protein (CcDDR) of pigeonpea imparts enhanced tolerance to major abiotic stresses in transgenic rice plants. *Planta* 245 (6), 1137–1148.
- Suzuki, N., Rizhsky, L., Liang, H., Shuman, J., Shulaev, V., Mittler, R., 2005. Enhanced tolerance to environmental stress in transgenic plants expressing the transcriptional co-activator Multiprotein Bridging Factor 1c. *Plant Physiol.* 139, 1313–1322.
- Swarnalakhmi, K., Yadav, V., Kumar, M.S., Dhar, D.W., 2016. Biofertilizers for higher pulse production in India: scope, accessibility and challenges. *Indian J. Agron.* 61, 173–181.
- Symanczik, S., Krueztzmann, J., Nehls, U., Boller, T., Courty, P.E., 2020. Expression of major intrinsic protein genes in *Sorghum bicolor* roots under water deficit depends on arbuscular mycorrhizal fungal species. *Soil Biol. Biochem.* 140, 107643.
- Tahir, H.A.S., Gu, Q., Wu, H., Raza, W., Safdar, A., Huang, Z., Rajer, F.U., Gao, X., 2017. Effect of volatile compounds produced by *Ralstonia solanacearum* on plant growth promoting and systemic resistance inducing potential of *Bacillus* volatiles. *BMC Plant Biol.* 17 (1), 1–16.
- Tahiri, A.I., Meddich, A., Raklami, A., Alahmad, A., Bechtaoui, N., Anli, M., Göttfert, M., Heulin, T., Achouak, W., Oufdou, K., 2022. Assessing the potential role of compost, PGPR, and AMF in improving tomato plant growth, yield, fruit quality, and water stress tolerance. *J. Soil Sci. Plant Nutr.* 22 (1), 743–764.
- Tait, P.J., 2007. Systemic Interactions in Life Science Innovation1. *Technol. Anal. Strateg. Manag.* 19, 257–277. <https://doi.org/10.1080/09537320701281524>.
- Taiz, L., Zeiger, E., Moller, I.M., Murphy, A., 2015. *Plant physiology and development* (No. Ed. 6). Sinauer Associates Incorporated.
- Takahashi, F., Suzuki, T., Osakabe, Y., Betsuyaku, S., Kondo, Y., Dohmae, N., Fukuda, H., Yamaguchi-Shinozaki, K., Shinozaki, K., 2018. A small peptide modulates stomatal control via abscisic acid in long-distance signalling. *Nature* 556 (7700), 235–238.
- Takahashi, Y., Zhang, J., Hsu, P.K., Ceciliato, P.H., Zhang, L., Dubeaux, G., Munemasa, S., Ge, C., Zhao, Y., Hauser, F., Schroeder, J.I., 2020. MAP3Kinase-dependent SnRK2-kinase activation is required for abscisic acid signal transduction and rapid osmotic stress response. *Nat. Commun.* 11 (1), 1–2.
- Talaat, N.B., Shawky, B.T., 2015. Plant-microbe interaction and salt stress tolerance in plants,” in *Managing Salt Tolerance* (Eds.). In: Hossain, M.A., Wani, S.H. (Eds.), *Plants: Molecular and Genomic Perspectives*. Press/Taylor & Francis Group, Boca Raton, MA, pp. 267–289.
- Tang, L., Cai, H., Ji, W., Luo, X., Wang, Z., Wu, J., Wang, X., Cui, L., Wang, Y., Zhu, Y., 2013. Overexpression of GsZFP1 enhances salt and drought tolerance in transgenic alfalfa (*Medicago sativa* L.). *Plant Physiol. Biochem.* 71, 22–30.
- Tang, Y., Bao, X., Zhi, Y., Wu, Q., Yin, X., Zeng, L., Li, J., Zhang, J., He, W., Liu, W., Wang, Q., 2019. Overexpression of a MYB family gene, OsMYB6, increases drought and salinity stress tolerance in transgenic rice. *Front. Plant Sci.* 10, 168.
- Tarczynski, M.M., Jensen, R.G., Bohnert, H.J., 1992. Expression of a bacterial mtD gene in transgenic tobacco leads to production and accumulation of mannitol. *Proc. Natl. Acad. Sci. U.S.A.* 89, 2600–2604.
- Tardieu, F., 2022. Different avenues for progress apply to drought tolerance, water use efficiency and yield in dry areas. *Curr. Opin. Biotechnol.* 73, 128–134.
- Tatewaki, Y., Higo, M., Isobe, K., 2023. Impacts of tillage practices on growth, phosphorus uptake, and yield of maize in controlled and field-based studies in relation to arbuscular mycorrhizal fungi. *Appl. Microbiol.* 3, 358–374.
- Taylor, I.B., Burbidge, A., Thompson, A.J., 2000. Control of abscisic acid synthesis. *J. Exp. Bot.* 51, 1563–1574.
- Terhorst, C.P., Lennon, J.T., Lau, J.A., 2014. The relative importance of rapid evolution for plant-microbe interactions depends on ecological context. *Proc. R. Soc. B – Biol. Sci.* 281 (1785), 20140028.
- Terra, W.C., Campos, V.P., Martins, S.J., Costa, L.S.A.S., da Silva, J.C.P., Barros, A.F., Lopez, L.E., Santos, T.C.N., Smant, G., Oliveira, D.F., 2018. Volatile organic molecules from *Fusarium oxysporum* strain 21 with nematocidal activity against *Meloidogyne incognita*. *Crop Protec.* 106, 125–131.
- Teshome, D.T., Zharare, G.E., Naidoo, S., 2020. The threat of the combined effect of biotic and abiotic stress factors in forestry under a changing climate. *Front. Plant Sci.* 11, 1874.
- Thangthong, N., Jogloy, S., Punjansing, T., Kvien, C.K., Kesmla, T., Vorasoot, N., 2019. Changes in root anatomy of peanut (*Arachis hypogaea* L.) under different durations of early season drought. *Agronomy* 9 (5), 215.
- Thirkell, T.J., Charters, M.D., Elliott, A.J., Sait, S.M., Field, K.J., 2017. Are mycorrhizal fungi our sustainable saviours? Considerations for achieving food security. *J. Ecol.* 105 (4), 921–929.
- Thomas, J.J., Sepahi, M., Arendall, B., Bohnert, H.J., 1995. Enhancement of seed germination in high salinity by engineering mannitol expression in *Arabidopsis thaliana*. *Plant Cell Environ.* 18, 801–806.
- Thomas-Barry, G., Martin St., C., Ramsubhag, A., Eudoxie, G., Miller, J.R., 2024. Multi-trait efficiency and interactivity of bacterial consortia used to enhance plant performance under water stress conditions. *Microbiol. Res.* 281, 127610. <https://doi.org/10.1016/j.micres.2024.127610>.
- Thomason, W., Battaglia, M., 2020. Early defoliation effects on corn plant stands and grain yield. *J. Agron.* 112 (6), 5024–5032.
- Tian, Y., Fan, M., Qin, Z., Lv, H., Wang, M., Zhang, Z., Zhou, W., Zhao, N., Li, X., Han, C., Ding, Z., 2018. Hydrogen peroxide positively regulates brassinosteroid signaling through oxidation of the brassinazole-resistant1 transcription factor. *Nat. Commun.* 9 (1), 1063.
- Timmusk, S., Abd El-Daim, I.A., Copolovici, L., Tanilas, T., Kännaste, A., Behers, L., Nevo, E., Seisenbaeva, G., Stenström, E., Niinemets, Ü., 2014. Drought-tolerance of wheat improved by rhizosphere bacteria from harsh environments: enhanced biomass production and reduced emissions of stress volatiles. *PLoS One* 9 (5), e96086.
- Timmusk, S., Kim, S.B., Nevo, E., Abd El Daim, I., Ek, B.O., Bergquist, J., Behers, L., 2015. Sfp-type PPTase inactivation promotes bacterial biofilm formation and ability to enhance wheat drought tolerance. *Front. Microbiol.* 6, 387.
- Timmusk, S., Wagner, E.G.H., 1999. The plant-growth-promoting rhizobacterium *Paenibacillus polymyxa* induces changes in *Arabidopsis thaliana* gene expression: a possible connection between biotic and abiotic stress responses. *MPMI* 12 (11), 951–959.
- Tiwari, S., Gupta, S.C., Chauhan, P.S., Lata, C., 2021. An OsNAM gene plays important role in root rhizobacteria interaction in transgenic *Arabidopsis* through abiotic stress and phytohormone crosstalk. *Plant Cell Rep.* 40 (1), 143–155.
- Tiziani, R., Miras-Moreno, B., Malacrin, A., Vescio, R., Lucini, L., Mimmo, T., Cesco, S., Sorgon, A., 2022. Drought, heat, and their combination impact the root exudation patterns and rhizosphere microbiome in maize roots. *Environ. Exp. Bot.* 203, 105071. <https://doi.org/10.1016/j.envexpbot.2022.105071>.

- Toscano, S., Ferrante, A., Romano, D., 2019. Response of Mediterranean ornamental plants to drought stress. *Horticulture* 5 (1), 6.
- Tringe, S.G., Von Mering, C., Kobayashi, A., Salamov, A.A., Chen, K., Chang, H.W., Podar, M., Short, J.M., Mathur, E.J., Detter, J.C., Bork, P., 2005. Comparative metagenomics of microbial communities. *Science* 308 (5721), 554–557.
- Tripathi, D.K., Singh, S., Gaur, S., Singh, S., Yadav, V., Liu, S., Singh, V.P., Sharma, S., Srivastava, P., Prasad, S.M., Dubey, N.K., 2018. Acquisition and homeostasis of iron in higher plants and their probable role in abiotic stress tolerance. *Front. Environ. Sci.* 5, 86.
- Tsolakidou, M.D., Stringlis, I.A., Fanega-Sleziak, N., Papageorgiou, S., Tsalakou, A., Pantelides, I.S., 2019. Rhizosphere-enriched microbes as a pool to design synthetic communities for reproducible beneficial outputs. *FEMS Microbiol. Ecol.* 95, fuz138.
- Tzfira, T., Weinthal, D., Marton, I., Zeevi, V., Zuker, A., Vainstein, A., 2012. Genome modifications in plant cells by custom-made restriction enzymes. *Plant Biotechnol. J.* 10 (4), 373–389.
- Ullah, A., Nisar, M., Ali, H., Hazrat, A., Hayat, K., Keerio, A.A., Ihsan, M., Laiq, M., Ullah, S., Fahad, S., Khan, A., Khan, A.H., Akbar, A., Yang, X., 2019. Drought tolerance improvement in plants: an endophytic bacterial approach. *Appl. Microbiol. Biotechnol.* 103, 7385–7397. <https://doi.org/10.1007/s00253-019-10045-4>.
- Ullah, A., Sun, H., Yang, X., Zhang, X., 2017. Drought coping strategies in cotton: increased crop per drop. *Plant Biotechnol. J.* 15 (3), 271–284.
- Umapathi, M., Chandrasekhar, C.N., Senthil, A., Kalaiselvi, T., Santhi, R., Ravikesavan, R., 2022. Isolation, characterization and plant growth-promoting effects of sorghum [*Sorghum bicolor* (L.) Moench] root-associated rhizobacteria and their potential role in drought mitigation. *Arch. Microbiol.* 204, 354. <https://doi.org/10.1007/s00203-022-02939-1>.
- Vacheron, J., Desbrosses, G., Bouffaud, M.L., Touraine, B., Moëgne-Loccoz, Y., Muller, D., Legendre, L., Wiatrowski-Dyé, F., Prigent-Combaret, C., 2013. Plant growth-promoting rhizobacteria and root system functioning. *Front. Plant Sci.* 4, 356.
- Vaishnav, A., Choudhary, D.K., 2019. Regulation of drought-responsive gene expression in *Glycine max* L. Merrill is mediated through *Pseudomonas simiae* strain AU. *J. Plant Growth Regul.* 38, 333–342.
- Vala, A.G., Tomar, R.S., Rathod, P.J., Kumar, R., 2023. Genomics approaches for enhancing abiotic stress tolerance in groundnut: A pathway to crop improvement. *Intern. J. Innov. Sci. Res. Technol.* 8 (5).
- Van, J., Cheng, C., Hu, Z., Chen, H., Cai, W., Yu, B., 2018. The Panax ginseng PgTIP1 gene confers enhanced salt and drought tolerance to transgenic soybean plants by maintaining homeostasis of water, salt ions and ROS. *Environ. Exp. Bot.* 155, 45–55.
- Vargas, L., Santa Brígida, A.B., Mota Filho, J.P., de Carvalho, T.G., Rojas, C.A., Vanechoutte, D., Van Bel, M., Farrinelli, L., Ferreira, P.C., Vandepoel, K., Hemery, A.S., 2014. Drought tolerance conferred to sugarcane by association with *Glucanacetobacter diazotrophicus*: a transcriptomic view of hormone pathways. *PLoS One* 9 (12), e114744.
- Veze-Bermúdez, I.C., Schmidt, W., 2023. Iron sensing in plants. *Front. Plant Sci.* 14, 1145510. <https://doi.org/10.3389/fpls.2023.1145510>.
- Vendruscolo, E.C.G., Schuster, I., Pileggi, M., Scapim, C.C., Molinari, H.B.C., Marur, C.C., Vieira, L.G.E., 2007. Stress-induced synthesis of proline confers tolerance to water deficit in transgenic wheat. *J. Plant Physiol.* 164, 1367–1376.
- Veremeichik, G.N., Bulgakov, V.P., Shkryl, Y.N., 2016. Modulation of NADPH-oxidase gene expression in A4-rolB-transformed calli of *Arabidopsis thaliana* and *Rubia cordifolia*. *Plant Physiol. Biochem.* 105, 282–289. <https://doi.org/10.1016/j.plaphy.2016.05.014>.
- Veremeichik, G.N., Shkryl, Y.N., Tatiana, V., Rusapetova, T.V., Silantjeva, S.A., Valeria, P., Grigorichuk, V.P., Velansky, P.V., Brodovskaya, E.V., Konnova, Y.A., Khopta, A.A., Bulgakov, D.V., Victor, P., Bulgakov, V.P., 2022. Overexpression of the A4rolB gene from the pRiA4 of *Rhizobium rhizogenes* modulates hormones homeostasis and leads to an increase of flavonoid accumulation and drought tolerance in *Arabidopsis thaliana* transgenic plants. *Planta* 256, 8. <https://doi.org/10.1007/s00425-022-03927-x>.
- Vílchez, J.I., García-Fontana, C., Román-Naranjo, D., González-López, J., Manzanera, M., 2016. Plant drought tolerance enhancement by trehalose production of desiccation-tolerant microorganisms. *Front. Microbiol.* 7, 1577.
- Virlouvet, L., Jacquemot, M.P., Gerentes, D., Corti, H., Bouton, S., Gilard, F., Valot, B., Trouverie, J., Tcherkez, G., Falque, M., Damerval, C., Rogowsky, P., Perez, P., Noctor, G., Zivy, M., Coursol, S., 2011. The ZmASR1 protein influences branched-chain amino acid biosynthesis and maintains kernel yield in maize under water limited conditions. *Plant Physiol.* 157 (2011), 917–936.
- Vocciante, M., Grifoni, M., Fusini, D., Petruzzelli, G., Franchi, E., 2022. The role of plant growth-promoting rhizobacteria (PGPR) in mitigating plant's environmental stresses. *Appl. Sci.* 12, 1231. <https://doi.org/10.3390/app12031231>.
- Vorholt, J.A., 2012. Microbial life in the phyllosphere. *Nat. Rev. Microbiol.* 10, 828–840. <https://doi.org/10.1038/nrmicro2910>.
- Vorholt, J.A., Vogel, C., Carlström, C.I., Müller, D.B., 2017. Establishing causality: opportunities of synthetic communities for plant microbiome research. *Cell Host Microbe.* 22 (2), 142–155.
- Vurukonda, S.S.K.P., Vardharajula, S., Srivastava, M., Skz, A., 2016. Enhancement of drought stress tolerance in crops by plant growth promoting rhizobacteria. *Microbiol. Res.* 184, 13–24.
- Wach, D., Skowron, P., 2022. An overview of plant responses to the drought stress at morphological, physiological and biochemical levels. *Polish J. Agron.* 50, 25–34. <https://doi.org/10.26114/pja.iung.435.2022.04>.
- Wagi, S., Ahmad, A., 2017. Phyllospheric plant growth promoting bacteria. *J. Bacteriol. Mycol.* 5, 00119.
- Wan, D., Li, R., Zou, B., Zhang, X., Cong, J., Wang, R., Xia, Y., Li, G., 2012. Calmodulin-binding protein CBP60g is a positive regulator of both disease resistance and drought tolerance in *Arabidopsis*. *Plant Cell Rep.* 31, 1269–1281.
- Wang, D.C., Jiang, C.H., Zhang, L.N., Chen, L., Zhang, X.Y., Guo, J.H., 2019. Biofilms positively contribute to *Bacillus amyloliquefaciens*-induced drought tolerance in tomato plants. *Intern. J. Mol. Sci.* 20 (24), 6271.
- Wang, G.G., Hui, Z., Li, F., Zhao, M.M., Zhang, J., Wang, W., 2010. Improvement of heat and drought photosynthetic tolerance in wheat by overaccumulation of glycine betaine. *Plant Biotechnol. Rep.* 4, 213–222.
- Wang, J., Li, C., Li, L., Reynolds, M., Mao, X., Jing, R., 2021. Exploitation of drought tolerance-related genes for crop improvement. *Intern. J. Mol. Sci.* 22, 10265.
- Wang, J.Y., Doudna, J.A., 2023. CRISPR technology: A decade of genome editing is only the beginning. *Science* 379, eadd8643.
- Wang, L., Xu, Q., Yu, H., Ma, H., Li, X., Yang, J., Chu, J., 2020. Strigolactone and karrikinsignaling pathways elicit ubiquitination and proteolysis of SMXL2 to regulate hypocotyl elongation in *Arabidopsis*. *Plant Cell* 32, 2251–2270.
- Wang, L., Zhu, J., Li, X., Wang, S., Wu, J., 2018. Salt and drought stress and ABA responses related to bZIP genes from *V. radiata* and *V. angularis*. *Gene* 651, 152–160.
- Wang, L.S., Chen, Q.S., Xin, D.W., Qi, Z.M., Zhang, C., Li, S.N., Jin, Y., Li, M., Mei, H.Y., Su, A.Y., 2018. Overexpression of GmBIN2, a soybean glycogen synthase kinase 3 gene, enhances tolerance to salt and drought in transgenic *Arabidopsis* and soybean hairy roots. *J. Integr. Agric.* 17, 1959–1971.
- Wang, M., Wang, Z., Guo, M., Qu, L., Biere, A., 2023. Effects of arbuscular mycorrhizal fungi on plant growth and herbivore infestation depend on availability of soil water and nutrients. *Front. Plant Sci.* 14, 1101932.
- Wang, R.K., Cao, Z.H., Hao, Y.J., 2014. Overexpression of a R2R3 MYB gene MdSIMYB1 increases tolerance to multiple stresses in transgenic tobacco and apples. *Physiol. Plant.* 150, 76–87.
- Wang, S., Wang, J., Zhou, Y., Huang, Y., Tang, X., 2022d. Prospecting the plant growth-promoting activities of endophytic bacteria *Cronobacter* sp YSD YN2 isolated from *Cyperus esculentus* L. var *sativus* leaves. *Ann. Microbiol.* 72, 1. <https://doi.org/10.1186/s13213-021-01656-2>.
- Wang, X., Li, B.B., Ma, T.T., Sun, L.Y., Tai, L., Hu, C.H., Liu, W.T., Li, W.Q., Chen, K.M., 2020. The NAD kinase OsNADK1 affects the intracellular redox balance and enhances the tolerance of rice to drought. *BMC Plant Biol.* 20, 11. <https://doi.org/10.1186/s12870-019-2234-8>.
- Wang, X., Zhang, X., Chen, J., Wang, X., Cai, J., Zhou, Q., Dai, T., Cao, W., Jiang, D., 2018. Parental drought-priming enhances tolerance to post-anthesis drought in offspring of wheat. *Front. Plant Sci.* 9, 261.
- Wang, Y., Beaitth, M., Chalifoux, M., Ying, J., Uchacz, T., Sarvas, C., Griffiths, R., Kuzma, M., Wan, J., Huang, Y., 2009. Shoot-specific down-regulation of protein farnesyltransferase (α -subunit) for yield protection against drought in canola. *Mol. Plant* 2 (1), 191–200.
- Wanlin, L.L., Yan, X., 2024. Effects of polystyrene microplastics, simulated acid rain and arbuscular mycorrhizal fungi on the growth of *Trifolium repens* and soil microbial community composition. *Pedosphere* 3, 424–437.
- Waseem, M., Rong, X., Li, Z., 2019. Dissecting the role of a basic helix-loop-helix transcription factor, SlbHLH22, under salt and drought stresses in transgenic *Solanum lycopersicum* L. *Front. Plant Sci.* 10, 734.
- Waszczak, C., Carmody, M., Kangasjärvi, J., 2018. Reactive oxygen species in plant signaling. *Annu. Rev. Plant Biol.* 69, 209–236.
- Wei, W., Liang, D.W., Bian, X.H., Shen, M., Xiao, J.H., Zhang, W.K., Ma, B., Lin, Q., Lv, J., Chen, X., Chen, S.Y., 2019. GmWRKY54 improves drought tolerance through activating genes in abscisic acid and Ca²⁺ signaling pathways in transgenic soybean. *Plant J.* 100 (2), 384–398.
- Wei, Y., Song, Y., Khan, M.A., Liang, C., Wang, Y., Guo, S., Zhang, R., 2024. GhTPPA2 enhancement of tobacco sugar accumulation and drought tolerance. *Gene* 894, 147969. <https://doi.org/10.1016/j.gene.2023.147969>.
- Wilmowicz, E., Kućko, A., Bogati, K., Wolska, M., Świdziński, M., Burkowski-But, A., Walczak, M., 2022. *Glomus* sp. and *Bacillus* sp. strains mitigate the adverse effects of drought on maize (*Zea mays* L.). *Front. Plant Sci.* 13, 958004. <https://doi.org/10.3389/fpls.2022.958004>.
- Woo, O.G., Kim, H., Kim, J.S., Keum, H.L., Lee, K.C., Sul, W.J., Lee, J.H., 2020. *Bacillus subtilis* strain GOT9 confers enhanced tolerance to drought and salt stresses in *Arabidopsis thaliana* and *Brassica campestris*. *Plant Physiol. Biochem.* 148, 359–367.
- Wu, C., Yang, Y., Wang, Y., Zhang, W., Sun, H., 2024. Colonization of root endophytic fungus *Serendipita indica* improves drought tolerance of *Pinus taeda* seedlings by regulating metabolome and proteome. *Front. Microbiol.* 15, 1294833. <https://doi.org/10.3389/fmicb.2024.1294833>.
- Wu, C.H., Bernard, S., Andersen, G., Chen, W., 2009. Developing microbe plant interactions for applications in plant-growth promotion and disease control, production of useful compounds, remediation and carbon sequestration. *Microbiol. Biotechnol.* 2, 428–440.
- Wu, H.H., Zou, Y.N., Rahman, M.M., Ni, Q.D., Wu, Q.S., 2017. Mycorrhizas alter sucrose and proline metabolism in trifoliolate orange exposed to drought stress. *Sci. Rep.* 7 (1), 42389.
- Wu, J., Wang, J., Hui, W., Zhao, F., Wang, P., Su, C., Gong, W., 2022. Physiology of plant responses to water stress and related genes: A review. *Forests* 13 (2), 324.
- Wu, Q.S., Zou, Y.N., Abd-Allah, E.F., 2014. Mycorrhizal association and ROS in plants. *Oxidative Damage to Plants*. Academic Press, pp. 453–475.
- Xiang, W., Guo, Z., Han, J., Gao, Y., Ma, F., Gong, X., 2024. The apple autophagy-related gene MdATG10 improves drought tolerance and water use efficiency in transgenic apple plants. *Plant Physiol. Biochem.* 206, 108214.
- Xu, Z.S., Chen, M., Li, L.C., Ma, Y.Z., 2008. Functions of the ERF transcription factor family in plants. *Botany* 86, 969–977.

- Yadav, S., Modi, P., Dave, A., Vijapura, A., Patel, D., Patel, M., 2020. Effect of Abiotic Stress on Crops (Eds.). In: Hasanuzzaman, M., Filho, M., Fujita, M., Nogueira, T. (Eds.), Sustainable Crop Production. Intech Open, Rijeka, Croatia.
- Yan, Z., Li, Y., Wu, H., Zhang, K., Hao, Y., Wang, J., Zhang, X., Yan, L., Kang, X., 2020. Different responses of soil hydrolases and oxidases to extreme drought in an alpine peat land on the Qinghai-Tibet Plateau, China. *Eur. J. Soil Biol.* 99, 103195.
- Yang, D., Ni, R., Yang, S., Pu, Y., Qian, M., Yang, Y., Yang, Y., 2021. Functional characterization of the *Stipa purpurea* P5CS gene under drought stress conditions. *Intern. J. Mol. Sci.* 22, 9599.
- Yang, H., Lu, L., Chen, Y., Yea, J., 2023. Transcriptomic analysis reveals the response of the bacterium *Priestia aryabhattai* SK1-7 to interactions and dissolution with potassium feldspar. *Appl. Environ. Microbiol.* 89 (5). <https://doi.org/10.1128/aem.02034-22>.
- Yang, J., Kloepper, J.W., Ryu, C.M., 2009. Rhizosphere bacteria help plants tolerate abiotic stress. *Trends Plant Sci.* 14 (1), 1–4.
- Yang, S., Vanderbeld, B., Wan, J., 2010. Narrowing down the targets: towards successful genetic engineering of drought-tolerant crops. *Mol. Plant.* 3 (3), 469–490.
- Yang, X., Lu, M., Wang, Y., Wang, Y., Liu, Z., Chen, S., 2021. Response mechanism of plants to drought stress. *Horticulture* 7 (3), 50.
- Yasmin, H., Bano, A., Wilson, N.L., Nosheen, A., Naz, R., Hassan, M.N., Ilyas, N., Saleem, M.H., Noureldien, A., Ahmad, P., Kennedy, I., 2022. Drought-tolerant *Pseudomonas* sp. showed differential expression of stress-responsive genes and induced drought tolerance in *Arabidopsis thaliana*. *Physiol. Plant* 174 (1), e13497.
- Yasmin, H., Rashid, U., Hassan, M.N., Nosheen, A., Naz, R., Ilyas, N., Sajjad, M., Azmat, A., Alyemeni, M.N., 2021. Volatile organic compounds produced by *Pseudomonas pseudoalcaligenes* alleviated drought stress by modulating defense system in maize (*Zea mays* L.). *Physiol. Plant* 172 (2), 896–911.
- Yin, C., Hagerty, C.H., Paulitz, T.C., 2022. Synthetic microbial consortia derived from rhizosphere soil protect wheat against a soilborne fungal pathogen. *Front. Microbiol.* 13, 908981. <https://doi.org/10.3389/fmicb.2022.908981>.
- Yoo, J.H., Park, C.Y., Cheol, J., Do Heo, W., Cheong, M.S., Park, H.C., Kim, M.C., Moon, B.C., Choi, M.S., Kang, Y.H., 2005. Direct interaction of a divergent CaM isoform and the transcription factor, MYB2, enhances salt tolerance in *Arabidopsis*. *J. Biol. Chem.* 280, 3697–3706.
- Yooyongwech, S., Phaukinsang, N., Cha-um, S., Supaibulwatana, K., 2013. Arbuscular mycorrhiza improved growth performance in Macadamia tetraphylla L. grown under water deficit stress involves soluble sugar and proline accumulation. *Plant Growth Regul.* 69, 285–293.
- Yooyongwech, S., Samphumphuang, T., Tisarum, R., Theerawitaya, C., Chaum, S., 2016. Arbuscular mycorrhizal fungi (AMF) improved water deficit tolerance in two different sweet potato genotypes involves osmotic adjustments via soluble sugar and free proline. *Sci. Hort.* 198, 107–117. <https://doi.org/10.1016/j.scienta.2015.11.002>.
- Yoshida, R., Hobo, T., Ichimura, K., Mizoguchi, T., Takahashi, F., Aronso, J., Ecker, J.R., Shinozaki, K., 2002. ABA-activated SnRK2 protein kinase is required for dehydration stress signaling in *Arabidopsis*. *Plant Cell Physiol.* 43 (12), 1473–1483.
- Yousfi, C.El., Soujja, H., Hammoudani, Y.El., Mohammed, H.Z., Mourabit, N., Aarab, S., 2024. Overview of insights into the role of *Bacillus* species in drought stress alleviation and plant disease management. *E3S Web. Conf.* 527, 03010. <https://doi.org/10.1051/e3sconf/202452703010>.
- Yu, P., He, X., Baer, M., Beirincx, S., Tian, T., Moya, Y.A.T., Zhang, X., 2021. Plant flavones enrich rhizosphere *Oxalobacteraceae* to improve maize performance under nitrogen deprivation. *Nat. Plants* 7, 481–499.
- Yu, S., Huang, A., Li, J., Gao, L., Feng, Y., Pemberton, E., Chen, C., 2018. OsNAC45 plays complex roles by mediating POD activity and the expression of development-related genes under various abiotic stresses in rice root. *Plant Growth Regul.* 84 (3), 519–531.
- Yu, T.T., Xu, Z.Z., Guo, J.J., Wang, Y.Y., Abernathy, B., Fu, J.J., Chen, X., Zhou, Y.Y., Chen, M., Ye, X.X., 2017. Improved drought tolerance in wheat plants overexpressing a synthetic bacterial cold shock protein gene *SeCspA*. *Sci. Rep.* 7, 44050.
- Zafar-ul-Hye, M., Danish, S., Abbas, M., Ahmad, M., Munir, T.M., 2019. ACC deaminase producing PGPR *Bacillus amyloliquefaciens* and *Agrobacterium fabrum* along with biochar improve wheat productivity under drought stress. *Agronomy* 9 (7), 343.
- Zahedi, S.M., Hosseini, M.S., Meybodi, N.D.H., Abadía, J., Germ, M., Gholami, R., Abdelrahman, M., 2022. Evaluation of drought tolerance in three commercial pomegranate cultivars using photosynthetic pigments, yield parameters and biochemical traits as biomarkers. *Agric. Water Manag.* 261, 107357.
- Zahrán, H.H., 1999. *Rhizobium*-legume symbiosis and nitrogen fixation under severe conditions and in an arid climate. *Microbiol. Mol. Biol. Rev.* 63, 968–989.
- Zandalinas, S.I., Fritschi, F.B., Mittler, R., 2020. Signal transduction networks during stress combination. *J. Exp. Bot.* 71 (5), 1734–1741.
- Zardak, S.G., Dehnavi, M.M., Salehi, A., Gholamhosseini, M., 2018. Effects of using arbuscular mycorrhizal fungi to alleviate drought stress on the physiological traits and essential oil yield of fennel. *Rhizosphere* 6, 31–38.
- Zeist, A.R., Henschel, J.M., Perrud, A.C., Silva Júnior, A.D., Zeist, J.N.O., Oliveira, G.J.A., Adriana, A.L., de Resende, J.T.V., 2024. Toward drought tolerance in tomato: Selection of F₂BC₁ plants obtained from crosses between wild and commercial genotypes. *Agric. Res.* 13, 26–40. <https://doi.org/10.1007/s40003-023-00678-3>.
- Zeng, J., Wu, C., Ye, X., Zhou, J., Chen, Y., Li, L., Hu, W., 2024. MePP2C24, a cassava (*Manihot esculenta*) gene encoding protein phosphatase 2C, negatively regulates drought stress and abscisic acid responses in transgenic *Arabidopsis thaliana*. *Plant Physiol. Biochem.* 206, 108291.
- Zhalnina, K., Louie, K.B., Hao, Z., Mansoori, N., da Rocha, U.N., Shi, S., Cho, H., 2018. Dynamic root exudate chemistry and microbial substrate preferences drive patterns in rhizosphere microbial community assembly. *Nat. Microbiol.* 3, 470–480.
- Zhang, C., Stratopoulos, L.M.F., Pretzsch, H., Rötzer, T., 2019. How do Tilia cordata Greenspire trees cope with drought stress regarding their biomass allocation and ecosystem services? *Forests* 10 (8), 676.
- Zhang, C.C., Lu, Q., Verma, D.P.S., 1995. Removal of feedback inhibition of $\Delta 1$ -pyrroline-5-carboxylate synthetase, a bifunctional enzyme catalyzing the first two steps of proline biosynthesis in plants. *J. Biol. Chem.* 270, 20491–20496.
- Zhang, F., Zou, Y.N., Wu, Q.S., Kuća, K., 2020. Arbuscular mycorrhizas modulate root polyamine metabolism to enhance drought tolerance of trifoliate orange. *Environ. Exp. Bot.* 171, 103926.
- Zhang, H., Sun, X., Dai, M., 2022. Improving crop drought resistance with plant growth regulators and rhizobacteria: Mechanisms, applications, and perspectives. *Plant Commun.* 3 (1).
- Zhang, J., Zhang, S., Cheng, M., Jiang, H., Zhang, X., Peng, C., Lu, X., Zhang, M., Jin, J., 2018. Effect of drought on agronomic traits of rice and wheat: A meta-analysis. *Intern. J. Environ. Res. Public Health* 15 (5), 839.
- Zhang, L.X., Li, S.X., Zhang, H., Liang, Z.S., 2007. Nitrogen rates and water stress effects on production, lipid peroxidation and antioxidative enzyme activities in two maize (*Zea mays* L.) genotypes. *J. Agron. Crop Sci.* 11, 387–397.
- Zhang, P., Chao, R., Qiu, L., Ge, W., Liang, J., Wen, P., 2024. *ChaWRKY40* enhances drought tolerance of 'dawei' hazelnut by positively regulating proline synthesis. *Forests* 15, 407. <https://doi.org/10.3390/f15030407>.
- Zhang, W., Xia, K., Feng, Z., Qin, Y., Zhou, Y., Feng, G., Zhu, H., Yao, Q., 2024a. Tomato plant growth promotion and drought tolerance conferred by three arbuscular mycorrhizal fungi is mediated by lipid metabolism. *Plant Physiol. Biochem.* 208, 108478. <https://doi.org/10.1016/j.plaphy.2024.108478>.
- Zhang, X., Zhang, J., He, J., Li, M., Matsushita, N., Geng, Q., Lian, C., Zhang, S., 2024b. Physiological and transcriptome responses of *Pinus massoniana* seedlings inoculated by various ecotypes of the ectomycorrhizal fungus *Cenococcum geophilum* during the early stage of drought stress. *J. Fungi* 10 (1), 71.
- Zhang, Z., Liu, X., Wang, X., Zhou, M., Zhou, X., Ye, X., Wei, X., 2012. An R2R3 MYB transcription factor in wheat, Ta PIMP1, mediates host resistance to *Bipolaris sorokiniana* and drought stresses through regulation of defense- and stress-related genes. *New Phytol.* 196, 1155–1170.
- Zhao, C., Ma, J., Yan, C., Jiang, Y., Zhang, Y., Lu, Y., Yan, J., 2024. Drought-triggered repression of miR166 promotes drought tolerance in soybean. *Crop J.* 12, 154–163.
- Zhao, K., Penttinen, P., Zhang, X., Ao, X., Liu, M., Yu, X., Chen, Q., 2014. Maize rhizosphere in Sichuan, China, hosts plant growth promoting *Burkholderia cepacia* with phosphate solubilizing and antifungal abilities. *Microbiol. Res.* 169 (1), 76–82.
- Zheng, G., Fan, C., Di, S., Wang, X., Xiang, C., Pang, Y., 2017. Over-expression of *Arabidopsis* EDT1 gene confers drought tolerance in alfalfa (*Medicago sativa* L.). *Front. Plant Sci.* 8, 1–14.
- Zheng, Z., Wang, B., Zhuo, C., Xie, Y., Zhang, X., Liu, Y., et al., 2023. Local auxin biosynthesis regulates brace root angle and lodging resistance in maize. *New Phytol.* <https://doi.org/10.1111/nph.18733>.
- Zhu, P., Li, J., Zhao, A., 2023. A mulberry 9-cis-epoxycarotenoid dioxygenase gene MaNCED1 is involved in plant growth regulation and confers salt and drought tolerance in transgenic tobacco. *Front. Plant Sci.* 14, 1228902.
- Zoghi, Z., Hosseini, S.M., Kouchaksaraei, M.T., Kooch, Y., Guidi, L., 2019. The effect of biochar amendment on the growth, morphology and physiology of *Quercus castaneifolia* seedlings under water-deficit stress. *Eur. J. For. Res.* 138, 967–979.
- Zou, Y.N., Wu, Q.S., Kuća, K., 2021. Unravelling the role of arbuscular mycorrhizal fungi in mitigating the oxidative burst of plants under drought stress. *Plant Biol.* 23, 50–57.