Jewel Journal of Scientific Research (JJSR) 9(1&2): 74–86, 2024
©Federal University of Kashere-Nigeria (Print ISSN: 2384 – 6267, Online ISSN 2756-651X)
https://journals.fukashere.edu.ng/index.php/jjsr

Arbuscular Mycorrhiza-Induced Drought Stress Mitigation on Savanna Species

***[1]Adamu, G., [2]Gaya, E. and [2]Buba, T.**
[1]Dept. of Forestry Technology, Federal Polytechnic Bauchi.
[2]Dept. of Biological Sciences, Abubakar Tafawa Balewa University Bauchi.
***Corresponding Author**: gadamu@fptb.edu.ng; +234 8067417735

Abstract

In many arid and semi-arid regions, drought stress continues to be the primary factor limiting crop and ecosystem productivity, highlighting the implications of climate change. Arbuscular mycorrhizal fungi (AMF) are a flexible group that forms plant–fungal symbiotic relationships that mitigate the effects of drought stress. Developing innovative management techniques to lessen the negative consequences of drought stress is imperative in order to improve ecosystem health and food security. By causing oxidative stress, altering membrane integrity, plant water relations, nutrient uptake, photosynthetic activity, photosynthetic apparatus, and anti-oxidant activities, drought stress dramatically affects plant growth and development. Plant resistance to drought stress can be considerably increased using AMF. AMF helps plants thrive under drought stress by preserving membrane integrity and enhancing plant water levels, nutrient and water uptake, and water-use efficiency (WUE). AMF also lessens the buildup of reactive oxygen species (ROS) by boosting antioxidant activities and gene expression that give plants resistance against drought-induced oxidative stress. It also enhances photosynthetic efficiency, osmolytes, phenols, and hormone accumulation. This review discussed the various roles that AMF plays in the various ways that plants react to drought stress. We have given a thorough overview of the various pathways that AMF mediates to help plants develop drought resistance.

Keywords: Drought stress, Arbuscular mycorrhiza, Biochemical, morphological, physiological mechanisms.

Received: 20th Mar., 2024 *Accepted:* 20th Sept, 2024 *Published Online:* 30th Sept, 2024

Introduction

In addition to providing food for humans and other animals and serving as the primary source of solar energy and organic carbon in ecosystems, plants are essential for maintaining the planet's biodiversity and regulating the climate (Prajapati *et al*., 2023). In the current context of anthropogenic global warming, forest and cultivated plants must adapt to the new conditions or perish (Kijowska-Oberc, *et al*., 2020). To meet these challenges, plants have evolved complex mechanisms that involve a wide range of signaling pathways and interactions with other organisms, including microbes (Cheng, *et al*., 2019).

Low soil water supply and high atmospheric water demand are the two main drivers of drought, a complex natural climate phenomenon that can pose serious risks to agricultural productivity and the ecosystem (Madadgar *et al*., 2017, Zhao *et al*., 2021). Drought can also cause widespread tree mortality and water shortages (Trugman, *et al.* 2021). Drought is one of the threats that harm the ecosystem that is most widely recognized (Vicente-Serrano, et al., 2020). It happens whenever there is a substantial rainfall deficit that results to hydrological imbalances and impacts the land's productive processes. Practically all climate areas experience droughts, whether the mean annual rainfall is high or low (Ault, 2020). It may have negative effects on human society, the environment, and agricultural production (Haile *et al,* .2020). Drought is considered a unique form of natural disaster that differs from others because of its gradual development (Staupe-Delgado and Rubin 2022). According to (Liu *et al*. (2018), a drought tends to start slowly, have long-lasting impacts that gradually worsen, and continue for a considerable amount of time even after it has ended. Between the early 1960s and 1986, the National Aeronautics and Space Administration (NASA) observed persistent drought events that caused about 900,000 km2 of former savanna grassland in the region of Africa to be badly decertified (Eze, 2018)). Furthermore, according to Shukla, *et al*., (2021), one-third of Africans reside in regions that are susceptible to drought. The drought has turned into a recurring occurrence. Drought stress, one of the major abiotic stresses, has a significant impact on crop production and threatens global food security (Begna, 2020). Changes in savanna structure, composition and function as a result of ongoing and future climate change can have major implications for human wellbeing and ecosystem process (Mishra, and Young, 2020). Drought stress profoundly influences arid and semiarid native seed germination, seedling development and establishment in natural habitats (Seleiman, *et al.,* 2021).

Plants cope with drought deficit conditions by acquiring drought avoidance and/or drought tolerance mechanisms, which include morphological, physiological, and biochemical responses (Yang *et al* and Chen, 2021). Water scarcity has a negative impact on many aspects of plant physiology (Seleiman, *et al*, 2021). For example, it decouples photosynthesis, disrupts enzyme structure, and reduces nutrient uptake and/or transport to the shoot, causing a hormonal and nutritional imbalance in the plant (Liao, *et al*., 2023). Furthermore, drought stress causes osmotic stress, which can lead to turgor loss, inhibiting plant growth and development (Ozturk, *et al*, 2021). Drought stress also causes the production of reactive oxygen species (ROS), which causes oxidative damage to carbohydrates, protein synthesis, and lipid metabolism.

Soil drought stress has become the primary limiting factor for plant growth in arid and semi-arid regions due to ongoing climate change (Naorem, *et al*, 2023). Plant-associated microbes, such as arbuscular mycorrhizal fungi (AMF), have the ability to regulate physiological and molecular responses to drought stress, and they have a strong ability to cope with drought-induced oxidative damage via enhanced antioxidant defense systems (Wang, et al., 2023). In arbuscule-containing root cortical cells, AMF causes a short-lived oxidative burst (Kobae, 2019). To scavenge ROS, AMF modulates a fungal network in enzymatic and non-enzymatic antioxidant defense systems (Zou, *et al*., 2021).

Plant and fungal metabolites facilitate and guarantee partner recognition, colonization, and the development of the symbiotic association in the myriad interactions that take place in the rhizosphere between plants and their AMF symbionts. This review focuses on the alterations in metabolites that arise from the colonization and establishment of AMF in plants.

Methodology.

Research publications were from the Web of Science, Google, Google Scholar, Science Direct, Springer, Wiley, Springer, and Science. The following keywords were used for searching literature: arbuscular mycorrhizal fungi and drought stress or AMF or AMF-induced or AMF inoculation and drought stress/alleviation/tolerance or stress mitigation. Other keywords include physiological mediation, biochemical mediation and morphological mediation.

Direct effect of droughts on savanna tree mortality

Global vegetation is predicted to be significantly impacted by more frequent and severe droughts brought on by climate change (Xu, *et al.,* 2019). Yet, studies conducted so far have concentrated on how susceptible trees are to aridness in forests, in savannas, where a thin covering of trees coexists with grass, little is known about trees and moisture deficit. Despite being widely distributed throughout the world and making up a substantial portion of tropical land area (Raven, *et al*., 2020), savannas have gotten significantly less attention than forests in physiological investigations and globally syntheses of drought susceptibility of trees. Predictions about how severely a drought would harm trees are complicated by these tree-grass interactions, which are frequently mediated by fire and herbivory (Case *et al.*, 2019). During drought plants respond physiologically and structurally to prevent excessive water loss according to species-specific water uses strategies which have consequences for carbon uptake by photosynthesis and release by total ecosystem respiration (Li *et al*., 2020). In savannas, potential effects of drought are uncertain (Sankaran, 2019). Drought is obviously a physiological challenge to savanna trees, with the potential to stunt or even kill them. Regardless of how dry their surroundings are, savanna trees may have limited hydraulic safety margins, much like trees in other biomes (López *et al.*, 2021). Some scholars have suggested that drought has been underestimated as a type of natural episodic disturbance limiting tree populations in these systems (Lloret, and Batllori, 2021). Severe droughts have been shown to cause significant mortality in some cases of savanna trees, both historical and recent (Smit and Bond, 2020). Tree species also differ inherently in their ability to withstand and recover from droughts. Tree mortality during droughts can arise from one or more non-exclusive mechanisms including hydraulic failure and loss of vascular transport capacity as a result of xylem cavitation, carbon starvation as a result of depletion of carbohydrate reserves, and increased susceptibility to herbivore and pathogen attacks (Salmon *et al*., 2019). Hydraulic failure occurs when droughts are particularly severe, causing the xylem and rhizosphere to cavitate (become filled with air-pockets), impeding water flow and eventually resulting in desiccation and death (Peters 2019). Trees may limit carbon fixation during less severe but longer-lasting droughts by closing their stomata to prevent hydraulic collapse. This can lead to carbon starvation over time when trees are unable to meet their ongoing metabolic requirement for carbohydrates (Tomasella *et al.*, 2019). The xylem water potentials at which cavitation happens varies depending on the species and is mostly dictated by the anatomical characteristics of the xylem, such as the pit membrane's porosity and the conduits' diameter, length, connectedness, and density (Zhao *et al*., 2020).

Drought in savannas can have a significant impact on tree survival and inhibit canopy closure. It is becoming more and more crucial to take into account how drought affects the vegetation structure of savannas as future drought severity and frequency are expected to rise (Jones *et al*., 2022)..

Mycorrhizal fungi-mediated tolerance to Drought

Eighty to ninety percent of vascular plant species have symbiotic relationships with soil microorganisms known as arbuscular mycorrhizal fungi (AMF) (Genre *et al*., 2020). They are widely distributed throughout the world's ecosystems, which are mostly determined by the range of recognized plant hosts (Ma *et al.*, 2023). AMF are categorized as belonging to the three classes (Glomeromycetes, Archaeosporomycetes, and Paraglomeromycetes) in the phylum Glomeromycota and subkingdom Mucoromyceta (Lakhdar *et al*., 2023). AMF comprise around 250 species, 25 genera, and 11 families (Alrajhei *et al.,* 2022). Glomeromycota are obligatory symbionts that depend on their host plants' carbon substrates up to 20% of plant-fixed carbon for survival (Prasad 2023). In exchange, the fungus enhances the availability of water and nutrients, including nitrogen and phosphate, to the host plant via the root-apoplast contact, arbuscules, and extraradical and intraradical hyphae (Diagne *et al*., 2020). This symbiosis has existed from the earliest land plant emergence, about 600 million years ago, according to molecular and fossil records

(Uwamungu *et al*., 2022). Most likely the most common beneficial relationship between plants and microbes is the Arbuscular mycorrhizal (AM) symbiosis (Noceto *et al*., 2021). According to many studies, they support several critical ecological processes and are critical for plant nutrition and growth under stress (Wahab *et al*., 2023).

According to Tedersoo *et al*. (2020) mycorrhizal symbiosis is the formation of a close, primarily mutualistic relationship between mycorrhizal fungus and plant roots. AMF are the most prevalent type of mycorrhizal fungi, found in soils worldwide (Madawala 2021). The plant and the fungus in this symbiosis identify one another through interacting chemical signals (Khalid and Keller 2021). To be more precise, strigolactones released by plant roots promote branching and pre-symbiotic hypha metabolism and are regarded as one of the most important elements in the established (Mitra *et al*., 2021).

Water scarcity is one of the most serious abiotic pressures threatening ecosystem development and output throughout the world (Gavrilescu 2021). Water stress produces morphological, biochemical, physiological, and molecular changes in plants that reduce output (Kumaret al., 2019). Plants, on the other hand, are frequently connected with microorganisms that can modify plant responses to water scarcity in nature (Zia *et al.*, 2021). AMF are among the most common beneficial microorganisms, colonizing the majority of plants. Aside from improving plant nutrition, AMF has been shown to boost plant performance under water shortages (Begum *et al*., 2019).

This review aims to provide an overview of the current understanding of AMF relationships with savanna tree species, specifically the mechanisms involved in mediating the impacts of drought on host plants. The biochemical process, the morphological mechanism, and the AMF physiological drought mitigation mechanism.

Physiological mediation

Water status

Water scarcity in the soil and atmosphere increases stress on vegetation and affects future agricultural productivity and forest survival, particularly in the face of climate change (Jones *et al.,* 2020). Recent research has revealed soil drying as a main source of global transpiration reduction, which is a more stressful factor than vapor pressure deficit (Liu *et al*., 2020). The hydraulic conductivities of the various elements (soil, root-soil interface, root, xylem, and leaf) forming the soil-plant continuum influence the leaf water potential (Pou *et al.,* 2022). The leaf water potentials at which stomata close depend on belowground hydraulic properties (root, soil, and their interface) (Abdalla *et al*., 2022).

Bourbia *et al*. (2021) demonstrated that in both herbaceous and woody species, a decrease in root hydraulic conductivity was associated with stomatal closure. To deal with the loss in conductivity at the root-soil interface, plants evolved a variety of mechanisms (Hallett, *et al.*, 2022).

AMF symbiosis, which occurs naturally between fungal and most plant species, has been shown to improve plant water interactions, particularly in drought-stressed conditions (Madouh, and Quoreshi, 2023). AMF colonization can trigger a variety of physiological responses to drought stress, including stomatal conductance sensitivity, CO_2 absorption, and declines in relative water content; additionally, AMF inoculation is expected to improve leaf water potential (Chandrasekaran *et al*., 2019).

Water uptake by the roots from the soil and its circulation throughout the plant parts are critical for all physiological developments. Water moves through membranes in a gradient-driven flow, which is regulated and mediated by water channels known as aquaporins (AQPs) (Likhtenshtein and Likhtenshtein, 2021). AQPs are pore-forming integral membrane proteins that belong to the family of major intrinsic proteins (MIPs) and are found in all living cells/organisms, forming huge families in plants. AQPs are classified into five subfamilies based on amino acid sequences: tonoplast intrinsic proteins (TIPs), plasma membrane-intrinsic proteins (PIPs), and NOD26-like intrinsic proteins (NIPs), which were discovered in legume symbiosomes but also exist in the endoplasmic reticulum and plasma membrane, small basic intrinsic proteins (SIPs) found only in the endoplasmic reticulum (ER) of dicot as well as uncharacterized intrinsic proteins (XIPs) found in the plasma membrane (Bahadur *et al.,* 2019). Some PIPs in plant roots show differential expression of genes coding for AQPs in response to AMF and drought stress. According to research, the AM symbiosis modulates the expression of critical AQP genes, as well as the tightly controlled root plant hydration status, hydraulic conductivity, and tolerance to water scarcity (Quiroga *et al*., 2019). In AM fungal-inoculated tomato plants, an enhancement in the water transport capacity of AMF roots, correlated with overexpression of NIP AQP-encoding gene (LeNIP3;1) (Wang *et al*.,2023). Conversely, in another study a NIP AQP gene (LjNIP1) was up-regulated specifically in the arbuscule-containing cells in mycorrhizal roots of *Lotus japonicus* (Quiroga, 2020). In contrast, under drought stress, *Funneliformis mosseae* exhibited higher expression levels of root PtTIP1;2, PtTIP1;3, and PtTIP4;1 of *Poncirus trifoliata* L. and lower expression levels of root PtTIP2;1 and PtTIP5;1 (Jia-Dong *et al*., 2019). It shows that root TIPs genes revealed diverse responses to mycorrhization, representing the multiple roles of AMF in water absorption under water stress.

Plant assimilate production is significantly reduced by drought stress, which also has a negative impact on photosynthesis. Drought stress decreases photosynthesis by rising ROS generation and lowering chlorophyll concentrations (Wahab *et al.,* 2022). Drought stress inhibits the synthesis of RuBisCO and increases the activity of the enzyme chlorophyllase, which degrades chlorophyll, thereby causing a decrease in photosynthesis (Sharma *et al*., 2020). On the other hand, under drought stress, AMF significantly raised the chlorophyll concentrations and maintained improved RuBisCO synthesis, which resulted in a notable rise in photosynthetic rate (Wahab *et al*., 2023). With increased stomata conductance brought about by AMF, more CO_2 can enter plant leaf tissues, increasing PS-II efficiency and, ultimately, photosynthetic efficiency under drought stress (Jajoo, and Mathur, 2021). Higher chlorophyll production under drought stress is maintained by AMF, which significantly reduces chlorophyllase activity while preserving the activity of genes and enzymes involved in chlorophyll synthesis (Begum *et al.*, 2019b).

Morphological mediation.

Calleja-Cabrera *et al.* (2020), during the initial stages of climatic change, there is a steady reduction in shoot growth and maintenance of root growth, which leads to an increased root/shoot ratio. Osmotic stress and ion toxicity are the results of salt and ion accumulation in the upper soil layers during severe or moderate drought conditions (Zhang *et al*., 2022). Loose and wrinkled plant cell walls are the result of a decrease in the turgor pressure of plant cells when drought stress increases (Natonik-Białoń *et al.*, 2020). Plants that experience these biophysical consequences eventually lose water content and fresh weight, and their leaves become smaller and fewer in numbers (Bhattacharya and Bhattacharya, 2021). Under mild to moderate drought, roots undergo structural changes and modify their resource allocation (water and nutrients) to minimize dehydration (Seleiman *et al*., 2021). Research revealed that AMF colonization can modify morphological adaptation to improve the host plant's resistance to drought (Liu *et al*., 2023). Previous research during drought acclimation of AM rose plants showed reduced cuticle weight and less epicuticular wax in their leaves compared to non-AM plants (Hornstein, 2022). The inclination to abscise leaves would be the reason for the absence of wax in AM roses during drought adaptation. According to Boutasknit *et al.* (2020) mycorrhizal plants recover from wilting more quickly than non-mycorrhizal plants during drought recovery. However, stomatal density and guard cell size were unaffected by AMF inoculation in comparison to non-AMF treatments (Dehkordi *et a*l., 2021). Apart from leaf morphological adaptation, mycorrhization also employs root morphological adaptation as a strategy during drought stress. Under well-watered and drought-stressed conditions, research revealed considerably greater root total length, projected area, surface area, average diameter, volume, and number of first-, second-, and third-order lateral roots in AMF trifoliate orange seedlings compared to non-AMF seedlings (Meena *et al*., 2022).. Additional morphological investigations demonstrated modifications to the palisade's plant vascular architecture, starch storage, and photosynthesis (Liu and Wei, 2021).

The root morphological alterations caused by AMF may be attributed to the control of endogenous polyamine metabolism and phytohormone equilibrium, particularly the activation of root putrescine synthetases through arginine and ornithine decarboxylase as well as root indole-3-acetic acid (IAA) (Karunanantham *et al*.,2022)..

Biochemical mediation

During the process of AMF symbiosis against drought stress, a variety of signaling molecules, such as ethylene, ABA, cytokinins, salicylic acid (SA), jasmonic acid (JA), and auxin, have the capacity to function as phytohormones under certain circumstances (Gontia-Mishra *et al*., 2020).

Biochemical signaling molecules are emitted by both symbionts prior to any physical contact, triggering the other to start first reactions (Boyno and Demir, 2022). Strigolactones are a class of carotenoid-based phytohormones that are secreted by plants to regulate several aspects of their development (Boyno *et al*., 2023). During the pre-contact stage, strigolactones are released into the rhizosphere, where these labile signaling molecules draw AMF to recognize a particular host in their region. When AMF recognize strigolactones, they initiate oxidative metabolism, which improves hyphal branching and growth and leads to physical engagement with host plant roots, ultimately leading to symbiosis (Mitra *et al*., 2021b).

There are two more pronounced biochemical mechanisms for AMF drought stress mediation. The first process is the direct absorption of water by hyphae and its subsequent transport to the host plant, which increases the water content and scavenges the production of ROS, including superoxide anion radical ($O_2\cdot-$), hydrogen peroxide (H_2O_2), hydroxyl radicals ($\cdot OH$), and singlet oxygen ($^1O_2$) (He *et al.*, 2020). In plants, oxidative stress is accompanied by drought stress and arises from the generation of ROS (Sachdev *et al*., 2021). However, a substantial amount of research indicates that the build-up of ROS under drought stress results in structural damage to proteins, carbohydrates, lipids, and DNA, which eventually results in membrane damage and cell death (Singh *et al*., 2022).

The second process involves an AMF association-induced increase in the production of both enzymatic and non-enzymatic antioxidants (Afshari *et al*., 2022). The function of both enzymatic and non-enzymatic antioxidant in plants is to control and scavenge ROS. Ascorbate peroxidases (APX), superoxide dismutase (SOD), catalase (CAT), glutathione reductase (GR), guaiacol peroxidase (G-POD), and glutathione peroxidase (GPX) are examples of enzymatic antioxidants. Among the non-enzymatic antioxidants include tocopherol, flavonoids, carotenoid, ascorbate (ASC), and glutathione (GSH) (Ho *et al*., 2020). Increased transcription levels of enzymatic antioxidants and/or components of ascorbate and glutathione biosynthesis have been found to be associated with the influence of AMF symbiosis on antioxidant capacity, indicating the intricate transcriptional regulation of the antioxidant machinery (Zou *et al*., 2021).

There is still much to learn about the fundamental processes generating the signaling molecules that interact with the plant-fungus interaction. AMF symbiotic plants produce more ABA, a phytohormone known as the "abiotic stress hormone," during droughts in order to deal with the corresponding stresses (Karunanantham *et al.*, 2022). Many investigations have emphasized the mechanistic insights into the increased ABA production in the AMF host plant to provide tolerance against drought stress (Mathur and Roy 2021).

AMF triggers ABA production in response to drought stress, raising ABA levels in plants and encouraging stomatal closure to reduce transpiration water loss (Ilyas *et al*., 2021).

Since sugar is one of the primary sources of carbon supplied by the plants to the AMF, it plays a significant regulatory role in the symbiotic relationship between the two organisms (Salmeron-Santiago *et al.*, 2021). From 26–29 days after germination, hexoses, including glucose, were observed in the roots during the AMF colonization. But, the non-mycorrhizal roots showed higher sugar levels than the mycorrhizal roots at 40 days after germination (Gupta *et al.*, 2021). Abiotic stress-stricken plants showed an increase in sugar content, especially when associated with AMF. Sugar and lipid upregulation during water stress were observed in AMF plants, which was in line with the plants' increased biomass (Yadav *et al*., 2023). Similar sugar accumulations have been observed in plants colonized by AMF under various abiotic stress conditions. Different AMF species may accumulate sugars differently. As an illustration, trifoliate orange seedlings cultivated in drought had greater levels of sucrose, glucose, and fructose in their leaves when inoculated with *Paraglomus occultum* as opposed to *Funneliformis mosseae* (Posta and Duc, 2020).

As the building blocks of proteins and enzymes, amino acids also serve as signaling molecules and help plants cope with environmental stress (Ali *et al.*, 2019). The AMF spores can use N from the soil to synthesize amino acids, or they can directly extract the amino acids from the soil (Jansa *et al*., 2019). When compared to non-mycorrhizal plants, arbuscular mycorrhizal plants absorbed more amino acids from the soil (Kaur and Suseela 2020)]. Previous research has shown that AMF colonization in plants can result in an increase, decrease, or no variation in the amount of amino acids present (Kaur and Suseela 2020).

Proline is one of the important osmolytes that plants accumulate to counteract the effects of drought stress. It does this by stimulating the activity of various antioxidant enzymes, such as catalase, peroxidase, and superoxide dismutase, among others. Proline also has a notable ability to bind and hydrate enzymes, which helps to stabilize and protect macromolecules (Bogati and Walczak, 2022)

Conclusion

Plant morphological, physiological, and biochemical responses are disrupted by drought stress, which results in a significant reduction in plant growth and development. Nonetheless, AMF significantly enhances the growth and development of plants and protects them from the damaging effects of aridness. AMF inoculation preserves the integrity of the membrane and the water status of the plant, guards the photosynthetic apparatus from oxidative stress caused by aridity, and enhances the synthesis of photosynthetic pigments, all of which promote better plant growth and development under drought stress. Plant performance in conditions of water deficiency is significantly improved by AMF, which also enhances the accumulation of osmolytes, hormones, gene expression, and antioxidant activities. AMF-mediated improvements in plant development under DS are mostly due to these and other factors, including increased aquaporin expression, improved water uptake, and increased water usage efficiency.

There are still numerous unsolved concerns regarding the role of AMF in reducing the negative impacts of drought stress, despite recent advancements in this area. Areas of further research may include Identification of AMF species that are more effective in drought stress alleviation, elucidation of the molecular mechanisms underlying AMF-mediated drought stress tolerance in plants and development of AMF-based biofertilizers that can be used to enhance crop productivity under drought stress conditions.

References

Abdalla, M., Ahmed, M. A., Cai, G., Wankmüller, F., Schwartz, N., Litig, O., and Carminati, A. (2022). Stomatal closure during water deficit is controlled by below-ground hydraulics. *Annals of botany*, 129(2): 161-170.

Afshari, M., Rahimmalek, M., Sabzalian, M. R., Szumny, A., Matkowski, A., and Jezierska-Domaradzka, A. (2022). Mycorrhizal Colonization Modulates the Essential Oil Profile and Enzymatic and Non-Enzymatic Antioxidants to Mitigate the Adverse Effects of Water

Deficit in Salvia subg. Perovskia. *Biology*, 11(12): 1757

Alrajhei, K., Saleh, I., and Abu-Dieyeh, M. H. (2022). Biodiversity of arbuscular mycorrhizal fungi in plant roots and rhizosphere soil from different arid land environment of Qatar. *Plant Direct*, 6(1): e369.

Ali, Q., Haider, M. Z., Shahid, S., Aslam, N., Shehzad, F., Naseem, J. and Hussain, S. M. (2019). Role of amino acids in improving abiotic stress tolerance to plants. In *Plant Tolerance to Environmental Stress*. CRC Press. pp. 175-204

Ault, T. R. (2020). On the essentials of drought in a changing climate. *Science*, 368(6488): 256-260.

Bahadur, A., Batool, A., Nasir, F., Jiang, S., Mingsen, Q., Zhang, Q., and Feng, H. (2019). Mechanistic insights into arbuscular mycorrhizal fungi-mediated drought stress tolerance in plants. *International Journal of Molecular Sciences*, 20(17): 4199

Begum, N., Qin, C., Ahanger, M. A., Raza, S., Khan, M. I., Ashraf, M. and Zhang, L. (2019). Role of arbuscular mycorrhizal fungi in plant growth regulation: implications in abiotic stress tolerance. *Frontiers in Plant Science*, 10: 1068

Begum, N., Ahanger, M. A., Su, Y., Lei, Y., Mustafa, N. S. A., Ahmad, P. and Zhang, L. (2019). Improved drought tolerance by AMF inoculation in maize (*Zea mays)* involves physiological and biochemical implications. *Plants*, 8(12): 579

Begna, T. (2020). Effects of drought stress on crop production and productivity. *International Journal of Research Study in Agricultural Science*, 6: 34-43

Bhattacharya, A., and Bhattacharya, A. (2021). Effect of soil water deficit on growth and development of plants: a review. *Soil Water Deficit and Physiological Issues in Plants*, 393-488.

Bogati, K., and Walczak, M. (2022). The impact of drought stress on soil microbial community, enzyme activities and plants. *Agronomy*, 12(1): 189

Bourbia, I., Pritzkow, C., and Brodribb, T. J. (2021). Herb and conifer roots show similar high sensitivity to water deficit. Plant Physiol. 186: 1908–1918. doi: 10.1093/plphys/kiab207.

Boutasknit, A., Baslam, M., Ait-El-Mokhtar, M., Anli, M., Ben-Laouane, R., Douira, A. and Meddich, A. (2020). Arbuscular mycorrhizal fungi mediate drought tolerance and recovery in two contrasting carob (*Ceratonia siliqua* L.) ecotypes by regulating stomatal, water relations, and (in) organic adjustments. *Plants*, 9(1): 80

Boyno, G., and Demir, S. (2022). Plant-mycorrhiza communication and mycorrhizae in inter-plant communication. *Symbiosis*, 86(2): 155-168.

Boyno, G., Rezaee Danesh, Y., Demir, S., Teniz, N., Mulet, J. M., and Porcel, R. (2023). The Complex Interplay between Arbuscular Mycorrhizal Fungi and Strigolactone: Mechanisms, Sinergies, Applications and Future Directions. *International Journal of Molecular Sciences*, 24(23): 16774.

Calleja-Cabrera, J., Boter, M., Oñate-Sánchez, L., and Pernas, M. (2020). Root growth adaptation to climate change in crops. *Frontiers in Plant Science*, 11: 544.

Case, M. F., Wigley-Coetsee, C., Nzima, N., Scogings, P. F., and Staver, A. C. (2019). Severe drought limits trees in a semi-arid savanna. *Ecology*, 100(11): e02842.

Chandrasekaran, M., Chanratana, M., Kim, K., Seshadri, S., and Sa, T. (2019). Impact of arbuscular mycorrhizal fungi on photosynthesis, water status, and gas exchange of plants under salt stress–a meta-analysis. *Frontiers in Plant Science*, 10: 457.

Cheng, Y. T., Zhang, L., and He, S. Y. (2019). Plant-microbe interactions facing environmental challenge. *Cell Host and Microbe*, 26(2): 183-192.

Dehkordi, R. A., Roghani, S. R., Mafakheri, S., and Asghari, B. (2021). Effect of biostimulants on morpho-physiological traits of various ecotypes of fenugreek (*Trigonella foenum-graecum* L.) under water deficit stress. *Scientia horticulturae*, 283: 110077.

Diagne, N., Ngom, M., Djighaly, P. I., Fall, D., Hocher, V., and Svistoonoff, S. (2020). Roles of arbuscular mycorrhizal fungi on plant growth and performance: Importance in biotic and abiotic stressed regulation. *Diversity*, 12(10): 370.

Eze, J. N. (2018). Drought occurrences and its implications on the households in Yobe State, Nigeria. *Geoenvironmental Disasters*, 5(1): 1-10.

Genre, A., Lanfranco, L., Perotto, S., and Bonfante, P. (2020). Unique and common traits in mycorrhizal symbioses. *Nature Reviews Microbiology*, 18(11): 649-660.

Gavrilescu, M. (2021). Water, soil, and plants interactions in a threatened environment. *Water*, 13(19): 2746.

Gontia-Mishra, I., Sapre, S., Deshmukh, R., Sikdar, S., and Tiwari, S. (2020). Microbe-mediated drought tolerance in plants: current developments and future challenges. *Plant Microbiomes for Sustainable Agriculture*, 351-379.

Gupta, S., Thokchom, S. D., and Kapoor, R. (2021). Arbuscular mycorrhiza improves photosynthesis and restores alteration in sugar metabolism in *Triticum aestivum* L. grown in arsenic contaminated soil. *Frontiers in Plant Science*, 12: 640379

Haile, G. G., Tang, Q., Li, W., Liu, X., and Zhang, X. (2020). Drought: Progress in broadening its understanding. *Wiley Interdisciplinary Reviews: Water*, 7(2): e1407.

Hallett, P. D., Marin, M., Bending, G. D., George, T. S., Collins, C. D., and Otten, W. (2022). Building soil sustainability from root–soil interface traits. Trends in Plant Science, 27(7): 688-698.

He, J. D., Zou, Y. N., Wu, Q. S., and Kuča, K. (2020). Mycorrhizas enhance drought tolerance of trifoliate orange by enhancing activities and gene expression of antioxidant enzymes. *Scientia Horticulturae*, 262: 108745.

Ho, T. T., Murthy, H. N., and Park, S. Y. (2020). Methyl jasmonate induced oxidative stress and accumulation of secondary metabolites in plant cell and organ cultures. *International Journal of Molecular Sciences*, 21(3): 716.

Hornstein, E. D. (2022). *Genetic Engineering to retrace the Evolutionary loss of arbuscular mycorrhizae, with implications for sustainable agriculture*. North Carolina State University.

Ilyas, M., Nisar, M., Khan, N., Hazrat, A., Khan, A. H., Hayat, K. and Ullah, A. (2021). Drought tolerance strategies in plants: a mechanistic approach. *Journal of Plant Growth Regulation*, 40: 926-944.

Jajoo, A., and Mathur, S. (2021). Role of arbuscular mycorrhizal fungi as an underground saviuor for protecting plants from abiotic stresses. *Physiology and Molecular Biology of Plants*, 1-15.

Jansa, J., Forczek, S. T., Rozmoš, M., Püschel, D., Bukovská, P., and Hršelová, H. (2019). Arbuscular mycorrhiza and soil organic nitrogen: network of players and interactions. *Chemical and Biological Technologies in Agriculture*, 6(1): 1-10.

Jia-Dong, H., Tao, D., Hui-Hui, W., Ying-Ning, Z., Qiang-Sheng, W., and Kamil, K. (2019). Mycorrhizas induce diverse responses of root TIP aquaporin gene expression to drought stress in trifoliate orange. *Scientia Horticulturae*, 243: 64-69.

Jones, M. M., Fletcher Jr, R., Kruger, L., Monadjem, A., Simelane, P., and McCleery, R. (2022). Drought limits large trees in African savannas with or without elephants. *Austral Ecology*, 47(8): 1668-1684.

Jones, J. A., Wei, X., Archer, E., Bishop, K., Blanco, J. A., Ellison, D. and Creed, I. F. (2020). Forest-water interactions under global change. *Forest-water Interactions*, 589-624.

Kaur, S., and Suseela, V. (2020). Unraveling arbuscular mycorrhiza-induced changes in plant primary and secondary metabolome. *Metabolites*, 10(8): 335.

Karunanantham, K., Lakshminarayanan, S. P., Ganesamurthi, A. K., Ramasamy, K., and Rajamony, V. R. (2022). Arbuscular mycorrhiza—A health engineer for abiotic stress alleviation. In *Rhizosphere Engineering* Academic Press. pp. 171-198

Khalid, S., and Keller, N. P. (2021). Chemical signals driving bacterial–fungal interactions. *Environmental Microbiology*, 23(3): 1334-1347.

Kijowska-Oberc, J., Staszak, A. M., Kamiński, J., and Ratajczak, E. (2020). Adaptation of forest trees to rapidly changing climate. *Forests*, 11(2): 123.

Kobae, Y. (2019). The Infection Unit: Overlooked conceptual units for arbuscular mycorrhizal function. *Root Biology-Growth, Physiology, and Functions*, 1-13.

Kumar, R., Berwal, M. K., and Saroj, P. L. (2019). Morphological, physiological, biochemical and molecular facet of drought stress in horticultural crops. *International Journal of Bio-resource and Stress Management*, 10(5): 545-560.

Lakhdar, A., Trigui, M., and Montemurro, F. (2023). An Overview of Biostimulants' Effects in Saline Soils. *Agronomy*, *13*(8): 2092.

Liao, Z., Fan, J., Lai, Z., Bai, Z., Wang, H., Cheng, M. ... and Li, Z. (2023). Response network and regulatory measures of plant-soil-rhizosphere environment to drought stress. *Advances in Agronomy*, 180: 93.

Likhtenshtein, G. I., and Likhtenshtein, G. I. (2021). Hydration of Cells and Tissues. *Biological Water: Physicochemical Aspects*, 439-479.

Li, Q., Zhao, M., Wang, N., Liu, S., Wang, J., Zhang, W. and Du, N. (2020). Water use strategies and drought intensity define the relative contributions of hydraulic failure and carbohydrate depletion during seedling mortality. *Plant Physiology and Biochemistry*, 153: 106-118.

Lloret, F., and Batllori, E. (2021). Climate-induced global forest shifts due to heatwave-drought. *Ecosystem collapse and climate change*, 155-186.

Liu, L., Gudmundsson, L., Hauser, M., Qin, D., Li, S., and Seneviratne, S. I. (2020). Soil moisture dominates dryness stress on ecosystem production globally. *Nature Communications*, 11(1): 4892.

Liu, C. Y., Hao, Y., Wu, X. L., Dai, F. J., Abd-Allah, E. F., Wu, Q. S., and Liu, S. R. (2023). Arbuscular mycorrhizal fungi improve drought tolerance of tea plants via modulating root architecture and hormones. *Plant Growth Regulation*, 1-10.

Liu, Y., and Wei, X. (2021). Dark septate endophyte improves the drought-stress resistance of Ormosia hosiei seedlings by altering leaf morphology and photosynthetic characteristics. *Plant Ecology*, 222: 761-771.

López, R., Cano, F. J., Martin-StPaul, N. K., Cochard, H., and Choat, B. (2021). Coordination of stem and leaf traits define different strategies to regulate water loss and tolerance ranges to aridity. *New Phytologist*, 230(2): 497-509.

Ma, X., Xu, X., Geng, Q., Luo, Y., Ju, C., Li, Q., and Zhou, Y. (2023). Global arbuscular mycorrhizal fungal diversity and abundance decreases with soil available phosphorus. *Global Ecology and Biogeography*, 32(8): 1423-1434.

Madawala, H. M. S. P. (2021). Arbuscular mycorrhizal fungi as biofertilizers: Current trends, challenges, and future prospects. *Biofertilizers*, 1: 83-93

Madadgar, S., AghaKouchak, A., Farahmand, A., and Davis, S. J. (2017). Probabilistic estimates of drought impacts on agricultural production. *Geophysical Research Letters*, 44(15): 7799-7807.

Madouh, T. A., and Quoreshi, A. M. (2023). The function of arbuscular mycorrhizal fungi associated with drought stress resistance in native plants of arid desert ecosystems: A review. *Diversity*, 15(3): 391.

Mathur, P., and Roy, S. (2021). Insights into the plant responses to drought and decoding the potential of root associated microbiome for inducing drought tolerance. *Physiologia Plantarum*, 172(2): 1016-1029.

Meena, K. K., Kumar, P., Sorty, A. M., Bitla, U., and Pathak, H. (2022). Ecology of Arbuscular Mycorrhizae and Influence on Drought Tolerance in Crop Plants. In *Microbial BioTechnology for Sustainable Agriculture*. Singapore: Springer Nature Singapore. 1*:* 261-285.

Mishra, N. B., and Young, K. R. (2020). Savannas and grasslands. In *Terrestrial Ecosystems and Biodiversity*. CRC Press. pp. 235-247.

Mitra, D., Rad, K. V., Chaudhary, P., Ruparelia, J., Sagarika, M. S., Boutaj, H., and Panneerselvam, P. (2021). Involvement of strigolactone hormone in root development, influence and interaction with mycorrhizal fungi in plant: Mini-review. *Current Research in Microbial Sciences*, 2: 100026

Mitra, D., BE, G. S., Khoshru, B., De Los Santos Villalobos, S., Belz, C., Chaudhary, P. and Mohapatra, P. K. D. (2021). Impacts of arbuscular mycorrhizal fungi on rice growth, development, and stress management with a particular emphasis on strigolactone effects on root development. *Communications in Soil Science and Plant Analysis*, 52(14): 1591-1621.

Naorem, A., Jayaraman, S., Dang, Y. P., Dalal, R. C., Sinha, N. K., Rao, C. S., and Patra, A. K. (2023). Soil constraints in an arid environment—challenges, prospects, and implications. *Agronomy*, 13(1): 220.

Natonik-Białoń, S., Borowska-Wykręt, D., Mosca, G., Grelowski, M., Wrzalik, R., Smith, R. S., and Kwiatkowska, D. (2020). Deformation of a cell monolayer due to osmotic treatment: a case study of onion scale epidermis. *Botany*, 98(1): 21-36.

Noceto, P. A., Bettenfeld, P., Boussageon, R., Hériché, M., Sportes, A., van Tuinen, D. and Wipf, D. (2021). Arbuscular mycorrhizal fungi, a key symbiosis in the development of quality traits in crop production, alone or combined with plant growth-promoting bacteria. *Mycorrhiza*, 31(6): 655-669.

Ozturk, M., Turkyilmaz Unal, B., García-Caparrós, P., Khursheed, A., Gul, A., and Hasanuzzaman, M. (2021). Osmoregulation and its actions during the drought stress in plants. *Physiologia plantarum*, *172*(2), 1321-1335.

Posta, K., and Duc, N. H. (2020). Benefits of arbuscular mycorrhizal fungi application to crop production under water scarcity. *Drought Detect Solut*.

Prajapati, S. K., Kumar, V., Dayal, P., Gairola, A., Borate, R. B., and Srivastava, R. (2023). The Role of Carbon in life's Blueprint and Carbon Cycle Understanding Earth's Essential Cycling System: Benefits and Harms to our Planet. *International Journal*, *1*(1), 21-32.

Peters, J. M. (2019). *Hydraulic Vulnerability of Australian Forests to Drought*. PhD Dissertation Western Sydney University.

Pou, A., Rivacoba, L., Portu, J., Mairata, A., Labarga, D., García-Escudero, E., and Martín, I. (2022). How Rootstocks Impact the Scion Vigour and Vine Performance of *Vitis vinifera* L. cv. Tempranillo. *Australian Journal of Grape and Wine Research*, *2022*.

Prasad, K. (2023). Symbiotic Endophytes of Glomalin AM Fungi, Rhizobium, and PGPR Potential Bio stimulants to Intensive Global Food Production for Sustainable Agriculture System. *Journal of Microbes and Research*, 2(2): 2836-2187.

Quiroga, G., Erice, G., Ding, L., Chaumont, F., Aroca, R., and Ruiz-Lozano, J. M. (2019). The arbuscular mycorrhizal symbiosis regulates aquaporins activity and improves root cell water permeability in maize plants subjected to water stress. *Plant, Cell and Environment*, 42(7): 2274-2290.

Quiroga, G. G. (2020). Deciphering the contribution of maize aquaporins regulated by arbuscular mycorrhizae to the transport in planta of water and/or solutes of physiological importance under drought. *Plants*, 9(2): 148

Raven, P. H., Gereau, R. E., Phillipson, P. B., Chatelain, C., Jenkins, C. N., and Ulloa Ulloa, C. (2020). The distribution of biodiversity richness in the tropics. *Science Advances*, 6(37): eabc6228.

Salmon, Y., Dietrich, L., Sevanto, S., Hölttä, T., Dannoura, M., and Epron, D. (2019). Drought impacts on tree phloem: from cell-level responses to ecological significance. *Tree Physiology*, 39(2): 173-191.

Sachdev, S., Ansari, S. A., Ansari, M. I., Fujita, M., and Hasanuzzaman, M. (2021). Abiotic stress and reactive oxygen species: Generation, signaling, and defense mechanisms. *Antioxidants*, 10(2): 277

Sankaran, M. (2019). Droughts and the ecological future of tropical savanna vegetation. *Journal of Ecology*, 107(4): 1531-1549.

Salmeron-Santiago, I. A., Martínez-Trujillo, M., Valdez-Alarcón, J. J., Pedraza-Santos, M. E., Santoyo, G., Pozo, M. J., and Chávez-Bárcenas, A. T. (2021). An updated review on the modulation of carbon partitioning and allocation in arbuscular mycorrhizal plants. *Microorganisms*, 10(1): 75

Seleiman, M. F., Al-Suhaibani, N., Ali, N., Akmal, M., Alotaibi, M., Refay, Y. and Battaglia, M. L. (2021). Drought stress impacts on plants and different approaches to alleviate its adverse effects. *Plants*, 10(2): 259

Singh, A., Mehta, S., Yadav, S., Nagar, G., Ghosh, R., Roy, A., and Singh, I. K. (2022). How to cope with the challenges of environmental stresses in the era of global climate change: An update on ROS stave off in plants. *International Journal of Molecular Sciences*, 23(4): 1995

Sharma, A., Kumar, V., Shahzad, B., Ramakrishnan, M., Singh Sidhu, G. P., Bali, A. S. and Zheng, B. (2020). Photosynthetic response of plants under different abiotic stresses: a review. *Journal of Plant Growth Regulation*, 39: 509-531.

Shukla, S., Husak, G., Turner, W., Davenport, F., Funk, C., Harrison, L., and Krell, N. (2021). A slow rainy season onset is a reliable harbinger of drought in most food insecure regions in Sub-Saharan Africa. *Plos one*, 16(1): e0242883.

Smit, I. P., and Bond, W. J. (2020). Observations on the natural history of a savanna drought. *African Journal of Range and Forage Science*, 37(1): 119-136.

Staupe-Delgado, R., and Rubin, O. (2022). Challenges associated with creeping disasters in disaster risk science and practice: considering disaster onset dynamics. *International Journal of Disaster Risk Science*, 13(1): 1-11.

Seleiman, M. F., Al-Suhaibani, N., Ali, N., Akmal, M., Alotaibi, M., Refay, Y. and Battaglia, M. L. (2021). Drought stress impacts on plants and different approaches to alleviate its adverse effects. *Plants*, 10(2): 259

Tedersoo, L., Bahram, M., and Zobel, M. (2020). How mycorrhizal associations drive plant population and community biology. *Science*, 367(6480): eaba1223

Tomasella, M., Petrussa, E., Petruzzellis, F., Nardini, A., and Casolo, V. (2019). The possible role of non-structural carbohydrates in the regulation of tree hydraulics. *International Journal of Molecular Sciences*, 21(1): 144

Trugman, A. T., Anderegg, L. D., Anderegg, W. R., Das, A. J., and Stephenson, N. L. (2021). Why is tree drought mortality so hard to predict?. *Trends in Ecology and Evolution*, 36(6): 520-532.

.Uwamungu, J. Y., Shi, G., Wang, Y., Paliwal, A., Jadhav, R. R., and Wani, A. W. (2022). Arbuscular mycorrhizal fungi (AMF) for sustainable soil and plant health. In *Microbial and Biotechnological Interventions in Bioremediation and Phytoremediation*. Cham: Springer International Publishing. pp. 135-152

Vicente-Serrano, S. M., Quiring, S. M., Pena-Gallardo, M., Yuan, S., and Dominguez-Castro, F. (2020). A review of environmental droughts: Increased risk under global warming? *Earth-Science Reviews*, 201: 102953

Wang, Y., Zou, Y. N., Shu, B., and Wu, Q. S. (2023). Deciphering molecular mechanisms regarding enhanced drought tolerance in plants by arbuscular mycorrhizal fungi. *Scientia Horticulturae*, 308: 111591

Wahab, A., Abdi, G., Saleem, M. H., Ali, B., Ullah, S., Shah, W. and Marc, R. A. (2022). Plants' physio-biochemical and phyto-hormonal responses to alleviate the adverse effects of drought stress: A comprehensive review. *Plants*, 11(13): 1620

Wahab, A., Muhammad, M., Munir, A., Abdi, G., Zaman, W., Ayaz, A. and Reddy, S. P. P. (2023). Role of arbuscular mycorrhizal fungi in regulating growth, enhancing productivity, and potentially influencing ecosystems under abiotic and biotic stresses. *Plants*, 12(17): 3102.

Wang, Y., Zou, Y. N., Shu, B., and Wu, Q. S. (2023). Deciphering molecular mechanisms regarding enhanced drought tolerance in plants by arbuscular mycorrhizal fungi. *Scientia Horticulturae*, *308*, 111591.

Xu, C., McDowell, N. G., Fisher, R. A., Wei, L., Sevanto, S., Christoffersen, B. O. and Middleton, R. S. (2019). Increasing impacts of extreme droughts on vegetation productivity under climate change. *Nature Climate Change*, 9(12): 948-953.

Yang, X., Lu, M., Wang, Y., Wang, Y., Liu, Z., and Chen, S. (2021). Response mechanism of plants to drought stress. *Horticulturae*, 7(3): 50

Yadav, P., Yadav, B., Deka, D., and Narayan, O. P. (2023). Role of arbuscular mycorrhizas in regulating physiological and molecular aspects of plants under abiotic stress. In *The role of growth regulators and phytohormones in overcoming environmental stress*. Academic Press. pp. 399-433.

Zhao, J., Feng, H., Xu, T., Xiao, J., Guerrieri, R., Liu, S. and He, X. (2021). Physiological and environmental control on ecosystem water use efficiency in response to drought across the northern hemisphere. *Science of the Total Environment*, 758: 143599

Zhao, H., Jiang, Z., Ma, J., and Cai, J. (2020). What causes the differences in cavitation resistance of two shrubs? Wood anatomical explanations and reliability testing of vulnerability curves. *Physiologia Plantarum*, 169(2): 156-168.

Zhang, X., Yang, H., and Du, T. (2022). Osmotic adjustment of tomato under mild soil salinity can enhance drought resistance. *Environmental and Experimental Botany*, 202: 105004.

Zia, R., Nawaz, M. S., Siddique, M. J., Hakim, S., and Imran, A. (2021). Plant survival under drought stress: Implications, adaptive responses, and integrated rhizosphere management strategy for stress mitigation. *Microbiological Research*, 242: 126626.

Zou, Y. N., Wu, Q. S., and Kuča, K. (2021). Unravelling the role of arbuscular mycorrhizal fungi in mitigating the oxidative burst of plants under drought stress. *Plant Biology*, 23: 50-57.