Mechanistic Insights into Arbuscular Mycorrhizal Fungi-Mediated Drought Stress Tolerance in Plants

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Abstract: Arbuscular mycorrhizal fungi (AMF) establish symbiotic interaction with 80% of known land plants. It has a pronounced impact on plant growth, water absorption, mineral nutrition, and protection from abiotic stresses. Plants are very dynamic systems having great adaptability under continuously changing drying conditions. In this regard, the function of AMF as a biological tool for improving plant drought stress tolerance and phenotypic plasticity, in terms of establishing mutualistic associations, seems an innovative approach towards sustainable agriculture. However, a better understanding of these complex interconnected signaling pathways and AMF-mediated mechanisms that regulate the drought tolerance in plants will enhance its potential application as an innovative approach in environmentally friendly agriculture. This paper reviews the underlying mechanisms that are confidently linked with plant–AMF interaction in alleviating drought stress, constructing emphasis on phytohormones and signaling molecules and their interaction with biochemical, and physiological processes to maintain the homeostasis of nutrient and water cycling and plant growth performance. Likewise, the paper will analyze how the AMF symbiosis helps the plant to overcome the deleterious effects of stress is also evaluated. Finally, we review how interactions between various signaling mechanisms governed by AMF symbiosis modulate different physiological responses to improve drought tolerance. Understanding the AMF-mediated mechanisms that are important for regulating the establishment of the mycorrhizal association and the plant protective responses towards unfavorable conditions will open new approaches to exploit AMF as a bioprotective tool against drought.

Keywords: arbuscular mycorrhizal fungi; drought tolerance mechanisms; phytohormones; biochemical responses; aquaporins

1. Introduction

Drought stress, one of the major abiotic stresses, drastically affects crop production and jeopardizes food security globally [1]. Plants cope with drought deficit condition by recruiting drought avoidance and/or drought tolerance mechanisms, which include morphological, physiological, and molecular
responses [2,3]. Water deficit condition negatively affects several aspects of plant physiology [4]. For instance, it uncouples photosynthesis, disorders the structure of enzymes, reduces nutrient uptake and/or transport to the shoot, therefore prompting a hormonal and nutritional imbalance in the plant [5–7]. In addition, drought stress results in osmotic stress that can lead to turgor loss, thereby, leading to inhibition in plant growth and development [5]. Drought stress also induces the production of reactive oxygen species (ROS), resulting in oxidative damage to carbohydrates, protein synthesis, lipid metabolisms, and alternatively leading to the membrane damage and cell death in plant tissues [8,9].

Plants greatly rely on root-associated microflora to mitigate various environmental stresses i.e., drought stress [10,11]. Amongst them, the arbuscular mycorrhizal fungi (AMF), which belong to the phylum Glomeromycota, establish a symbiotic relationship with the host plants. AMF take photosynthetic products, including carbohydrates, from the host plant roots [12,13]. AMF not only increase water and nutrient uptake to mitigate the negative impact of drought but also improve stomatal regulation [14]. For instance, improved stomatal conductance has been reported in AMF-inoculated Poncirus trifoliata and Rosmarinus officinalis plants under drought stress [15–17]. In addition, to an increase in water use efficiency (WUE), AMF regulate various mechanisms to reduce oxidative damage under drought stress and represent a promising avenue to improve next-generation agriculture [18]. In response to drought stress, the development of AMF-mediated mechanisms includes modifications in the content of plant hormones, such as strigolactones, jasmonic acid (JA), and abscisic acid (ABA), and improvement in plant water status by increasing hydraulic conductivity [19]. In Solanum lycopersicum, AMF enhanced the plant drought tolerance by regulating the 14-3-3 genes (TFT1-TFT12) in the ABA signaling pathway and improved the plant water relations [20].

The current review is a refreshing contrast on previous reports and unique in its approach as not only giving an up-to-date insight into present knowledge pertaining AMF-mediated drought stress tolerance at biochemical, molecular, and morphological levels but also examining the latest significant contributions by researchers on the role of AMF in improving different aspects of plant/crop performance under drought stress.

2. The Influence of Drought Stress on AMF Diversity and Growth

AMF attribute widely in the context of upgrading soil structure and its water holding capacity. AMF species diversity depends highly on the mode of new methodology and application [21]. In different ecosystems, approximately 250 AMF species have been recognized to date [22]. On one side, AMF favor enhanced tolerance-related responses to drought stress [23], which substantially improve plant growth and crop production [24,25]. On the contrary, there is a direct effect of water shortage on AMF development cycle, which hampers the AMF spore germination, colonization capacity, sporulation, and extra-radical hyphal elongation [1].

Over the modern decades, a major focus is to understand how AMF composition and diversity is affected by drought stress. The AMF species are found to be lower in the water-deprived soils, relative to normal soils, with a distribution of Glomeraceae as the “global family”. These AMF species show an opportunistic behavior because they utilize their energy mostly in the production of more descendants. In addition, AMF species have evolved characteristics that are advantageous in dry environments [26]. Some of the AMF isolates or individual species can tolerate drought stress and are extensively distributed [27]. Native AMF ecotypes have come up after a long span of adaptation to the soils of extreme characteristics [28]. A number of investigations pointed out that Glomus species are typical of semi-arid Mediterranean ecosystems and are able to grow under water deficit conditions [27,29–33].

3. AMF and Host Plant Association During Drought Stress

Plants respond to drought stress by adopting different strategies, which allow them to avoid stress and/or enhance drought tolerance. Although these modifications have vital significance to most of the plant species, they have not been confirmed as a common response in host plant species with
different evolutionary trajectories [34–36]. These plant adaptive strategies allow the plant to withstand water-limiting conditions by maintaining a higher water status. Plant roots have highly plastic traits that can be modulated by AMF to enhance water uptake and/or minimize water loss. This dehydration tolerance is associated with survival and sustained physiological adaptations, when the leaf water potential is low, promote the ability of leaves to endure dehydration [37]. Fascinatingly, upon a perception of drought stress, most of the plants immediately ask for AMF help, by secreting rhizosphere signaling molecule (a class of phytohormones), so-called “strigolactone” [38]. Recently, the role of AMF inoculation to alleviate drought stress has been receiving great attention [39]. Mycorrhizal association with host plants increases the hydration status at whole-plant level, as characterized by leaf relative water content (LRWC) [40,41], while a detailed review of the literature shows that leaf water potential was not static in some experiments [42,43] (Table 1). Although the AMF colonization-mediated adaptive mechanisms in plants have been firmly established, several questions still remain open.

Mycorrhizal association with the plants under drought stress enhances plant performance by improving plant growth [44], water status, and nutrient accumulation [45]. During this process, AMF-colonization improves the establishment of extensive hyphal networks and glomalin secretion, which in turn, assist in water and nutrient uptake, and thereby, enhance soil structure (Figures 1 and 2) [46,47]. Besides, studies suggested that AMF develop drought-adaptive strategies through the extra-radical hyphae, and influence plant mechanisms, such as photosynthetic rate, root hydraulic conductivity, and root architecture [48–50]. AMF-mediated responses constitute an array of multifaceted mechanisms which include induction of drought-responsive genes and activation of different metabolic pathways. Studies to date have explored the vital role of AM symbiosis in ameliorating drought by up and down-regulating the numerous biochemical and physiological pathways. AMF amend the water regulation in the host plants by triggering hormonal signaling or by stimulating osmolytes. ABA is one of the non-nutritional mechanisms by which AM symbiosis regulates stomatal conductance and other physiological traits in response to drought stress [51].

### Table 1. Summary of drought stress effects on morphological, physiological, and biochemical differences in different experimental set-ups and plant species.

| Plant Species | AMF Species | AMF Variables | Plant Variables | Reference |
|---------------|-------------|---------------|-----------------|-----------|
| Calotropis procera Ait | Glomus intraradices | Col%↑ | N↑, K↑ | [52] |
| Cynophala flexuosa L. | AMF | Col%↑ | LRWC↑, Pn↑ (Cycle 2), leaf construction cost↑ (Cycle 2), SLA↑ (Cycle 1) | [41] |
| Glycine max L. | AMF | Col%↑ | Soil moisture (%), LAI↑, growth performance↑ | [44] |
| Glycyrrhiza uralensis Fisch. ex DC. | Rhizophagus irregularis | Col%↑, A%↑ | Leaf proline concentrations↑, P↑, C:N↑, Pn↑, WUE↑, C:P↑, N:P↑ | Root ABA↑ | [7] |
| Ipomoea batatas (L.) Lam. | Commercial inoculum containing Glomus sp. and Acaulospora sp. | Plant growth↑, tubers per plant↑, tuber fresh weight↑ | P content↑, soluble sugars↑, leaf osmotic potential↑, chlorophyll degradation↑, photosynthetic pigments↑, maximum quantum yield of PSII (Fv/Fm)↑, photon yield of PSII (ΦPSII)↑, net photosynthetic rate↑ | Proline↑ | [53] |
In roots and shoots, the osmotic stress induced by drought is tolerated by host plant via altering biochemical responses which mostly comprise of enhanced metabolites biosynthesis, such as sugars and proline, that function as osmolytes \[12,19\]. These metabolic compounds contribute to reducing the osmotic potential, and thereby, the leaf water potential in drought exposed plants \[59,60\]. These lower levels of potentials allow mycorrhizal plants to sustain high organ hydration and turgor level which maintain overall physiological activities of the cells and especially linked to the photosynthetic apparatus \[61\]. AMF plants counteract water deficit-induced oxidative stress by enhancing the

### Table 1. Cont.

| Plant Species | AMF Species | AMF Variables | Plant Variables | Physiological | Biochemical | Reference |
|---------------|-------------|---------------|-----------------|---------------|-------------|-----------|
| Pelargonium graveolens (L.) Herit. | Funneliformis mossea, Rhizophagus irregularis | Col%, hyphal length | Plant growth performance | Nutrient absorption, WRC, water potential, stomatal resistance | MDA, H₂O₂, CAT, APX, SOD, GPX | \[54\] |
| Phoenix dactylifera L. | Funneliformis monosporum, Rhizophagus clarus, Glomus deserticola A | Plant growth performance | | | | \[25\] |
| Poncirus trifoliata (L.) | Diversispora versiformis | Col%, hyphal length, root morphology | LWP | IAA, MeJA, NO | \[37\] |
| Poncirus trifoliata (L.) | Funneliformis mossea | Col% | Shoot root, total biomass, surface area of lateral roots | O₂, H₂O₂, MDA | \[55\] |
| Poncirus trifoliata (L.) | Funneliformis mossea, Paraglomus occulatum | Col% | Plant height, stem diameter, leaf number, leaf, stem, and root dry weight | LRWC | Leaf sucrose, glucose, fructose, leaf proline concentration | \[40\] |
| Poncirus trifoliata (L.) | Funneliformis mossea | Col% | Plant height, shoot and root biomass, root hair density, length, diameter | | Root IAA | \[56\] |
| Poncirus trifoliata (L.) | Funneliformis mossea, Paraglomus occulatum | Col% | Root biomass, taproot length, number of lateral roots | | | \[1\] |
| Solanum lycopersicum L. mutant notabilis and its wild-type | Rhizophagus intraradices | Col%, Col% | Shoot biomass | Shoot and root P concentrations, WUE, Tr | ABA | \[20\] |
| Solanum lycopersicum L. | Funneliformis mossea, Rhizophagus intraradices | Plant height, root fresh weight | Stomatal density, WUE, Tr | ABA, H₂O₂, proline | \[18\] |
| Zea mays L. | Rhizophagus irregularis | Col% | P, WUE, Rehydration rate, leaf moisture percentage | Proline, C, N, P, ABA, MDA | \[57\] |
| Zea mays L. | Rhizophagus irregularis | Col% | Shoot dry weight, root dry weight | gs, Lpr, Lo | Root ABA | \[58\] |

\(^{1}\) and \(^{2}\) indicate increasing and decreasing responses. AMF, arbuscular mycorrhizal fungi; WUE, water use efficiency; Tr, transpiration rate; ABA, abscisic acid; Col, AMF colonization; P, phosphorus; C:N, carbon: nitrogen; Pn, photosynthetic rate; C.P, carbon: phosphorus ratio; N:P, nitrogen:phosphorus; LAI, leaf area index; LRWC, leaf relative water content; PEUE, photosynthetic energy use efficiency; SLA, specific leaf area; CAT, catalase; POD, peroxidase; APX, ascorbate peroxidase; SOD superoxide dismutase; N, nitrogen; K, potassium; gs, stomatal conductance; Lpr, hydrostastic root hydraulic conductivity; Lo, osmotic root hydraulic conductivity; IAA, indoleacetic acid; O₂, superoxide radical; H₂O₂, hydrogen peroxide; MDA, malondialdehyde; LWP, leaf water potential; MeJA, methyl jasmonate; NO, nitric oxide; GPX, glutathione peroxidase; ns, non-significant.
antioxidant compounds production which scavenges ROS and improves the antioxidant enzymatic activities. AMF root colonization increases root growth, hydraulic properties, and root architecture, and consequently, induces the development of a greatly functional root system to uptake water nutrients [23]. In the meanwhile, AMF hyphae in the soil establish the beneficial pathways for water and nutrient acquisition and transport, providing better beneficial exploitation of nutrient and water reservoirs in the soil, the area where only the AMF could grow, in turn surpassing nutrient and water depletion zones around the plant roots. AMF symbiosis activates the molecular mechanisms to cope with stress impacts, i.e., the activation of functional protein genes, such as aquaporins membrane transporters, and potentially, sugar and ion transporters in fungi and roots. Enhanced transport of root translates water and nutrient acquisition into improved hydration in the aboveground plant parts, thereby affects the biochemical and physiological processes. Moreover, AMF symbiosis improves the plant resistance to drought stress by secondary responses, such as enhancing the soil structural stability, in turn, enhancing the soil water retention (Figure 1).

![Figure 1](image-url)

**Figure 1.** Arbuscular mycorrhizal fungi (AMF) symbiosis helps plants to maintain and regulate different processes in plants to cope with deleterious effects of drought stress, through either direct or indirect interaction, on plant growth performance. “+” and “−” symbols indicate an increase and a decrease in the production and accumulation of specific compounds.

4. Mechanisms of AMF-Mediated Drought Stress Tolerance

Drought stress is responsible for the deterioration in the soil and presents severe threats to agriculture worldwide. Most of the research over the last few years has focused on symbiotic mechanisms of AMF for protecting plants against drought stress, which verdict, symbiosis often marks an increased accumulation of osmoregulators, nutrient uptake, WUE and photosynthetic rate [57]. From a research viewpoint, efforts from both AMF and drought stress fields have improved our understanding of these mechanisms. In this regard, more recently, it was confirmed that AM symbiosis-specific downstream responses control a combination of morphological, biochemical,
and physiological plant characteristics (Table 1). In this section of the current review, we will insight the most important mechanisms of AMF-mediated drought stress tolerance in plants.

4.1. AMF-Assisted Drought Stress Tolerance at Biochemical Level

The AMF function against water stress episodes and facilitate the drought-exposed plants by regulating their biochemical mechanisms, where two mechanisms are more pronounced to explain the low oxidative damage in AMF-inoculated plants. The first mechanism involves the direct water absorption by hyphae and its transfer to the host plant, increasing the water content and scavenging the generation of ROS, such as hydroxyl radicals (·OH), singlet oxygen (¹O₂), hydrogen peroxide (H₂O₂), and superoxide anion radical (O₂⁻) [55]. Oxidative stress is accompanied by drought stress in plants and develops due to the production of ROS (Figure 1) [62]. A great body of evidence exists, though, that shows the accumulation of ROS under drought stress causes damage in the structure of carbohydrates, lipids, proteins, and DNA, which ultimately leads to the membrane damage and cell death [9,63,64].

The second mechanism entails an enhancement in the production of enzymatic and non-enzymatic antioxidants induced by symbiotic association [52,65]. The capacity of the antioxidant machinery governed by enzymatic and non-enzymatic antioxidant [54,66] work in plants to control and scavenge ROS [54,65,67]. Enzymatic antioxidants include ascorbate peroxidases (APX), superoxide dismutase (SOD), catalase (CAT), glutathione reductase (GR), guaiacol peroxidase (G-POD) and glutathione peroxidase (GPX). The non-enzymatic antioxidants include glutathione (GSH), ascorbate (ASC), carotenoid, flavonoids, and tocopherol [7,68–70]. For example, AMF symbiosis lowered the oxidative stress in maize plants under drought conditions and was also observed to provide profit in terms of non-systematic oxidative stress [71] (Figure 1). However, further studies are required to explore the actual AMF mechanisms and functions involved in the production of antioxidants and alteration in ROS metabolism. The influence of AMF symbiosis on the antioxidant capacity has been established to correlate with an increased transcription levels of enzymatic antioxidants and/or ascorbate and glutathione biosynthesis components, signifying the complex transcriptional regulation of the antioxidant machinery [65,72]. Additionally, some studies have focused on proteomic approaches, whereby the proteomic replies specific to AMF in water-deficient plants will help elucidate how mycorrhization provokes nutrient uptake, plant growth, and stress-tolerance responses. Antioxidants act not only as a direct ROS scavenger but also as a key sensor of the cellular redox status, so they trigger a number of signaling events to tightly control cellular ROS levels.

Many types of signaling molecules have the potential to act under specific conditions as phytohormones including ethylene, ABA, cytokinins, salicylic acid (SA), jasmonic acid (JA), and auxin during the process of AMF symbiosis against drought stress (Table 1, Figure 2) [19,56,73,74]. Due to the considerations regarding the length of the current review, this section will only discuss recent progress to understand the signaling and communication events between AMF and the host plant that can be useful for a more precise characterization of the AMF plant symbiosis under drought stress. Readers are suggested to excellent reviews for understanding the role of AMF-dependent phytohormones against drought stress [19,24,39,75,76].

Development in symbiosis starts with the signaling that happens earlier to the physical contact between the symbionts, where both symbionts release biochemical signaling molecules which stimulate preparatory responses in the other [6,77]. Molecular dialogue begins by strigolactones, a group of carotenoid-based phytohormones, released by the plant, controlling various aspects of plant development [78]. Strigolactones are released into the rhizosphere, where these labile signaling molecules attract AMF to identify a specific host in their neighborhood during the pre-contact phase (Figure 2). AMF trigger oxidative metabolism, on recognition of strigolactones, which stimulates improvement of hyphal branching and growth, resulting in the occurrence of physical interaction with a host plant root and driving them to symbiosis [76,79,80] (Figure 2). Increased production of strigolactones has been reported in lettuce and tomato plants under drought in the presence
of *Rhizophagus irregularis*, indicating that AMF symbiosis induces strigolactones biosynthesis [6]. The expression of two tomato genes, *SICCD7* and *SICCD8*, involved in the biosynthesis of strigolactones was quantified. The expression of *SICCD8* was not altered, however, *SICCD7* expression was clearly up-regulated by increasing severity of the drought stress in host roots. Known aspects about the AM symbiosis and strigolactones mode of action suggest that it alleviates the negative effects of drought by regulating the plant physiology and development. These findings confirm the potential use of arbuscular mycorrhizas as biofertilizers to sustain crop production and agriculture development under unfavorable conditions. Strigolactones involvement in protecting AMF host plants against drought stress leads to the questions, whether it is a common symbiosis signaling pathway in a diversity of plant species. However further study is required to reveal the intrinsic mechanisms of strigolactones modulated by AM symbiosis against drought stress.

AMF-induced enhanced drought tolerance has been communicated so far, which alleviates the negative effects of drought stress by altering the hormonal profiles. The underlying mechanisms involved in the production of signaling molecules interacting with the plant-fungus association remain greatly unidentified. The phytohormone, ABA, considered as the ‘abiotic stress hormone’, increases under drought in AMF symbiotic plants to cope with the respective stress (Table 1, Figure 2). The simultaneous increase in the expression of plant genes encoding D-myo-inositol-3-phosphate synthase (IPS) and 14-3-3-like protein GF14 (14-3GF), which were responsible for ABA signaling transduction, was found to be involved in the activation of 14-3-3 protein and aquaporins (GintAQPF1 and GintAQPF2) in *Rhizophagus intraradices*. These findings suggest that coexpression of IPS and 14-3GF is responsible for the synergistic actions of the symbiotic partners in enhancing plant drought tolerance [81]. Various studies highlighted the mechanistic insights about the enhanced production of ABA in AMF host plant to confer tolerance against drought stress [82–84].

Apart from drought tolerance responses, production of ABA is essential for an appropriate establishment of AM colonization in plant roots [85], with evidence of its impact on the formation and functioning of arbuscules [85,86]. Hence an enhanced ABA biosynthesis in the AM symbiosis stressed plants serves to improve drought tolerance, whereas meanwhile, it increases and establishes AM symbiosis. The continuous adjustment of plants’ ABA levels in response to AM symbiosis elucidates its critical importance in communicating drought tolerance [81]. Various studies highlighted the mechanistic insights about the enhanced production of ABA in AMF host plant to confer tolerance against drought stress [82–84].

Another impact of drought stress on plant tissues is recognized in the context, a loss in intracellular water and osmotic damage. Osmotic stresses are involved in the inhibition of cell growth by restricting cellular expansion and cell wall extension, leading to a decrease in plant growth and development (Figure 1). Production of free amino acids is the vital osmolytes function in the osmotic adjustment of plants [89]. AMF symbiosis improved the growth performance and osmotic adjustment in *Macadamia tetraphylla* L. by the accumulation of different compounds, such as soluble sugar, proline, and free amino acids, under drought [90]. Osmotic adjustment assists plants to sustain water potential gradient for water flow from soil into roots [90,91]. It has been reported that the root colonization by AMF in *Medicago sativa* L. induces proline accumulation in leaves and roots against water deficit condition [92]. In water-deficient plants, proline frequently functions as an osmoprotectant, as a solute for the security of enzymes and proteins from denaturation. It also functions as a sink for energy, as an alleviator of cell acidity, and as a hydroxyl radical scavenger to control redox potential [60,93].
The AM symbiosis affects the metabolic regulation of organic acids emitted by leaves under drought episodes and improves the energetic position of the plant and works as an assistant to mitigate the drought deficit.

Classically, soluble sugar accumulation for adjusting the osmotic potential in plants in response to drought stress establishes an important plant-protective mechanism (Figure 1) [94]. AMF symbiosis is able to alter the pattern of gene expression encoding for \( \Delta 1 \)-pyrroline-5-carboxylate synthetase (p5cs) (showed lower p5cs transcript accumulation) in *Glycine max* and *Lactuca sativa* plants and protects host plants against drought [95]. Several studies have described the influence of AM symbiosis to maintain osmotic adjustments in terms of soluble sugar where AM-inoculation decreased the soluble sugars in drought-exposed plants, i.e., *Erythrina variegata* [35] and *Casuarina equisetifolia* [96] and improved the plant tolerance in host plants. On the contrary, many authors have documented the positive correlation between sugar accumulation and mycorrhization, which might be due to the sink effect on the fungus demanding sugars from plant shoot tissues [42,90]. The mechanisms involved in the mycorrhiza development, often lead to improved photosynthesis rate and accumulation in carbon compounds in the root systems of AMF colonized plants [1,97].

Proline is an amino acid, synthesized by plants in response to drought stress, and its activation results in an alteration in osmoprotectant, thereby helps in the maintenance of cell osmotic balance to mitigate the drought stress effects [98]. Additional evidence for proline suggests that it is actively involved in osmoregulation and scavenging of free radicals [90]. Proline acts as a molecular chaperone for stabilizing subcellular structures, thus protecting plant cells against damaging effects of drought episodes [99]. Multiple studies have demonstrated that in arbuscular mycorrhized plants proline accumulation leads to more enhanced stress tolerance than in non-AMF plants against drying conditions (Figures 1 and 2) [23,51]. In contrast, in *Antirrhinum majus* L. plants, although proline accumulation enhanced against drought stress, a lower level of proline was observed in AMF plants, as compared to non-AMF counterparts, and accounted to advance plant growth performance and biomass productivity [100]. In *Poncirus trifoliata* AMF decreased the activity of both P5CS and OAT in leaf, root, and total plant and increased tissue ProDH activity. This observation confirms that a decrease in proline accumulation in AMF plants might be derived from the integration of an inhibition of glutamate synthetic pathway of proline with an increase in proline degradation [101]. The AMF inoculation in water-deprived plants increased the accumulation of soluble nitrogenous compounds and free polyamines [102]. It can be concluded that fluctuations in proline levels by mycorrhization would be an adaptive strategy by plants in terms of drought avoidance or drought resistance to stress conditions. There is a profound gap to be abridged and coherent results concerning the expression patterns at molecular levels to be operated. To link and demarcate a lineage among genes specific for osmotic stress, proline accumulation, and delinking of AMF and non-AMF counterparts with proline synthesis need to be further analyzed.

During the onset and development of drought stress within a plant, all the major processes, including the plant metabolism, are affected. Beneficial effects of AMF symbiosis under drought stress may be due to alterations in basal energetic metabolism. Thus, changes in plant metabolism have also been reported in mycorrhizal plants grown at different drought stress levels. Maintenance of photosynthetic apparatus via the accumulation of protective molecules and osmolytes and/or the upregulation of antioxidant metabolism by AMF suggests the integration of biotechnological opportunities and their application for improving agricultural productivity.
Figure 2. Schematic diagram showing a complex network of mechanisms mediated by AMF to alleviate drought stress symptoms in plants. Through the establishment of mycorrhizal symbiosis and/or exudation of specific compounds like strigolactones, plants adapt different strategies to alleviate deleterious effects of stress. This plant–AMF association alters root physiology and plant growth by acting on different physiological, biochemical and molecular mechanisms that essentially enhance water and nutrient uptake. Altered root physiology impacts root-to-shoot cross-talk and contributes to the maintenance of homeostasis water, hormones, and ions in the plant. This alleviates the drought-induced growth impairment, and in turn, plants adapt their phenotype according to stress conditions by regulating the expression of stress-related genes and proteins. AMF symbiosis helps maintain the plant in water uptake, producing a large amount of external mycelium and increasing the effective root surface area by fungal hyphae or by increasing the lateral root formation. The exchange of water and nutrients between the two partners takes place through the arbuscules formed within the root cells of the host plant.

4.2. AMF-Mediated Drought Stress Tolerance at Morphological Level

The AMF extend the capacity of plants for adaptation to the drought environment. The establishment of particular AMF member in the rhizosphere can be regarded as niche colonization. As mentioned, the impact of the AMF colonization is believed to rely heavily upon the survival and growth of the host plant [103], which also mediate tolerance via colonization which is beneficial for both the host plants and AMF. For example, three Glomus species, G. macrocarpum, G. clarum, and G. etunicatum, exhibited considerable tolerance to soil drying [104]. This could be a strategy for survival, implemented by AMF, because spores are a form of resistance propagules that can survive under adverse conditions (Table 1). To date, significant evidence has been accumulated on AMF survival in drought stress. AMF have been revealed to tolerate drought stress by implementing morphological adaptation (i.e., avoidance strategy). This adaptive root conductance is communicated with changes in the morphogenetic types of roots. AMF has the potential to reduce the meristem activity of root apices resulting in the formation of enhanced adventitious roots. These AMF-mediated modifications in root morphology may assist in maintaining nutrient uptake and water balance in the host plant under drought stress.

In response to drought stress, a stimulation of AMF development phenomenon has been revealed where it acts as an AMF defense reaction to alleviate the negative effects of water deficit. In a previous study, when AMF spores were treated by storage in different soil water potentials, Glomus mosseae and G. deserticola showed better infectivity, indicating that surrounding of spores might have a strong impact on its efficiency in root colonization [59]. Previously, [105] reported that spore germination of Gigaspora margarita was independent of drought episodes. Whenever drought
stress has been investigated, AMF have demonstrated the ability to fix water uptake and improve plant nutrition through hyphal elongation. Moreover, better water status might trigger its action, resulting in increased activity and hydraulic conductivity of the roots [37,106,107]. Furthermore, AMF have the ability to perform the function of anastomosis (the capability to bring about vegetative cells’ inter-individual fusion) which is considered an imperative mechanism taking to AMF perseverance in dry conditions, particularly the anastomosis of disrupted mycelium to rebuild a linked network after facing water-deficit stress [108,109].

In contrast to above findings, even if AMF are ubiquitous in terrestrial ecosystems, including man-made habitats [110,111], many studies (Table 1) have revealed that the key stages in the AMF development cycle, such as spore germination, colonization, extraradical hyphal elongation, and sporulation, could be hindered by drought stress. A decrease in arbuscular and vesicle abundance in the roots of mycorrhiza was also observed in response to drought [112]. Several studies have described an inhibition in germinative hyphae elongation and spore germination upon drought stress [44,113]. The negative effect of drought on spore germination may influence the root colonization in the host plant. In fact, it is reported that drought stress can cause a serious decline in the formation of total root colonization (Table 1). This might be due to the inability of AMF spores to germinate and perceive an appropriate host plant root or might be due to the disruption at later steps in the process of colonization even after getting contact with the host [44,113,114]. Furthermore, this negative effect can be explicated either by an indirect impact because of inhibition in the root growth and or of a direct impact on the AMF development itself. Drought stress affects the post-symbiotic steps, including the post-colonization formation of extraradical mycelium and new spores.

4.3. Fungal Water Absorption and Transport Against Drought Stress in AMF Association

Uptake of water by the roots from the soil and its circulation across the whole plant parts are significant for all the physiological developments. Movement of water happens by a gradient-driven flow through membranes, a process which is regulated and mediated by water channels called aquaporins (AQP’s) [7,58,115]. AQP’s are a family of pore-forming integral membrane proteins that belong to the family of major intrinsic proteins (MIPs) and occur in all living cells/organisms and form large families in the plants. Based on the sequences of amino acid, AQP’s are divided into five subfamilies: Tonoplast intrinsic proteins (TIPs), plasma membrane-intrinsic proteins (PIPs), and NOD26-like intrinsic proteins (NIPIs) which were first recognized in legumes symbiosomes but they also exist in the endoplasmic reticulum and plasma membrane, small basic intrinsic proteins (SIPs) localized only in the endoplasmic reticulum (ER) of dicots, as well as uncharacterized intrinsic proteins (XIPs) found in the plasma membrane [18,116,117]. Plant AQP’s play a key role in AM symbiosis and might respond differently to subjected drought stress and AMF colonization (Figure 1) [118,119]. Differential expression of genes coding for AQP’s by AMF and drought stress is observed for some PIP’s in plant roots [119,120]. For instance, the expression of two AQP genes GintAQPF1 and GintAQPF2 was significantly enhanced, in extraradical mycelia of R. irregularis and mycorrhizal roots in response to drought stress, thus supporting the existence of a direct AMF involvement in plant tolerance to water deprivation [121,122]. Consistently, the increased expression of AQP’s genes in both root cortical cells containing arbuscules and extraradical mycelia under drought stress was reported, though possible mechanisms include direct water and nutrient uptake via extraradical hyphae, and better root system architecture [67,121,123,124]. This activity was inhibited by the presence of drought stress.

Previous studies clearly elucidated that AM symbiosis regulates the expression of key AQP genes and tightly programmed root plant water status as well as the hydraulic conductivity and tolerance under water deficiency [125,126]. 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;3) [18]. Conversely, in another study a NIP AQP gene (LjNIP1) was up-regulated specifically in the arbuscule-containing cells in mycorrhizal roots of Lotus japonicus [127]. 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 [128]. It shows that root TIPs genes revealed diverse responses to mycorrhization, representing the multiple roles of AMF in water absorption under water stress.

Osmotic root hydraulic conductivity is defined as an observation of plant water flow through cell-to-cell connected pathways, where it is greatly allied to the water channels activity or the density of the plasma membrane in the cells [129]. Upon drought perception, plants usually show a decline in root hydraulic conductivity [125,130] perhaps as an adaptive mechanism to prevent water loss. These observations are similar to some other studies [58]. The absence of strong correlation between AQP genes expression and hydraulic conductivity suggests that, with the enhancement in hydraulic conductivity in plants inoculated by AMF, it might be owed to other processes like enlarged expression and/or action in plants AQP genes due to post-translational modifications of these proteins [131] or changes in the density or size of plasmodesmata in AMF roots. The increase in osmotic root hydraulic conductivity (Lo) in AM plants can be associated with an enhanced expression in fungal or plant AQPs [132]. It is noteworthy that under drought stress episodes, AMF plants enhanced maize growth, especially in the case of drought-sensitive cultivar. This beneficial effect of AMF symbiosis was linked to a better efficiency of PSII, higher membrane stability and lower lipid peroxidation [53,58,133]. It was investigated lately that differential regulation of PIP AQP genes in six rice varieties was linked to drought stress tolerance. Recently, [7] found that the expression of root AQP gene PIP was significantly upregulated by moderate water deficit in AMF roots. Additional, study on the in-vivo transport capacities by these AQP genes is necessary to understand the specific role of these proteins in the AMF-induced drought tolerance.

Some plant genes encoding AQPs were induced by AMF colonization, as shown for RpPIP2;1 in Robinia pseudoacacia [134], which could be a way to upturn water flow in specific plant tissues, vital for host existence under drought stress. In this context, it was found that the AQP genes of AMF involve in water transport by mycorrhizal hyphae to the plant mate [122]. Likewise, in Phaseolus vulgaris and Nicotiana tabacum antisense type were colonized by AMF [135]. The AMF effects on AQP genes were reliant on the endogenous points of ABA in the host plant [10]. Though, in lettuce roots, the GintAQP1 gene expression was decreased by water deficit, even if the root AMF was improved [119]. Advanced studies are required to analyze the AQP genes regulation in plants exposed to water episodes, which allocates both the transport of water from AMF hyphae to the roots and the roles of AQP genes in AMF-facilitated plant water transport. Differential regulation of AQP-encoding genes by AMF symbiosis and water stress episodes has been detected for some PIPs in R. irregularis [120,135]. Thus, AMF symbioses lead to a decreased or an increased expression in AQP genes, but the functionality of AQP in mycorrhizal systems is still poorly understood. The facilitated water transport in AM symbiotic communication might also be connected to an enhanced membrane water permeability, demanding the up-regulation of AQPs under water deficit condition [136]. Some specific patterns of AQP regulation were identified in colonized roots, and these were linked to an overall enhancement in drought tolerance, as revealed by amended growth and water status of mycorrhizal plants [137].

5. Concluding Remarks and Future Perspectives

Drought episodes cause a significant reduction in agriculture productivity. Mycorrhizal symbiosis is a ubiquitous plant–microbe interaction, plays an important role in nutrient cycling that helps alleviate the deleterious effects of drought conditions by promoting plant performance and yield production. Consequently, this plant–fungus interaction has a great potential in an environmentally friendly sustainable agriculture. Surprisingly, although this symbiosis was established more than 450 million years, we are beginning to comprehend how its presence and functioning are maintained. In this review, we aimed at providing a brief remark towards the perspective of various protective mechanisms, including secondary metabolites, such as phytohormones and signaling molecules and metabolic pathways that play crucial roles to counteract drought under AMF. Among them, the classical approaches based on biochemical, physiological, and molecular responses have emerged.
as key mechanisms due to their multifunctional adaptive responses, open up a wide range of potentials in sustainable global food security. However, an in-depth understanding of the AMF-mediated drought tolerance mechanisms in plants is required to insight their full potential. Another important factor to consider is the signaling cross-talk that takes place during these adaptive practices. Deciphering how mycorrhizal plants act and interact in drought-protective processes will contribute to the design of responses to optimize AMF symbiosis not only in drought tolerance but also in other abiotic stresses.

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