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Benefits of Arbuscular Mycorrhizal Fungi Application to Crop Production under Water Scarcity

Katalin Posta and Nguyen Hong Duc

Abstract

Water deficit is one of the most severe abiotic stresses threatening crop growth and production on the globe. Water stress causes a series of morphological, biochemical, physiological, and molecular alterations that negatively influence plant productivity. However, in nature, plants are often associated with microbes that can modulate plant responses to water scarcity. Among beneficial microbes, arbuscular mycorrhizal fungi (AMF) are one of the most widespread symbiotic fungi colonizing the majority of agricultural plants. Besides an enhancement in plant nutrition, AMF have been reported to improve plant performance under water restrictions. In this chapter, we emphasize the benefits of AMF inoculation to crop production under water deficit based on related laboratory and field experiments. Variable outcomes and challenges of AMF application are also discussed for practical use in crop production under water scarcity.

Keywords: arbuscular mycorrhizal fungi, drought stress, water relations, crop productivity, plant tolerance, drought mitigation

1. Introduction

Water scarcity jeopardizes not only originally arid, semi-arid regions but also agricultural areas in which farmers obtain flourishing horticulture based on adequate water resources. Nonetheless, ongoing climate change supposed to amplify the frequency and severity of drought in different regions of the globe [1] can wipe out the so far achievements. Drought is the most devastating stress that remarkably diminishes crop productivity more than any other stress factor [2]. Water constraints provoke stomatal closure with a subsequent reduction of CO_2 influx resulting in a decrease in photosynthetic activity and carbon partitioning [3]. Also, water scarcity has a negative influence on nutrient supply, reducing phosphate availability. Severe drought profoundly affects plant physiology, growth, development, and reproduction, and exerts substantial losses in crop yield as well as reduces crop quality. In fact, over the past 35 years, worldwide drought inflicted yield decrease by 40% in maize and 21% in wheat production [4]. Thus, there is an urgent need to develop strategies to make agriculture more resilient and to alleviate the adverse impacts of water scarcity on crop yield. Among these strategies, there has been an increasing interest in beneficial soil microbes including arbuscular mycorrhizal (AM) fungi.

Notably, under natural conditions, plants frequently interact with microbes, which directly mediate plant responses to environmental adversities. Some microbe-plant interactions lead to a mitigation of stress-related damages and improvement of plant tolerance to stressful conditions [5]. As a crucial element of soils, microbes are an integral part of the agricultural ecosystem. Arbuscular mycorrhizal fungi (AMF) are ubiquitous soil microorganisms, which can form a symbiotic association with most terrestrial plants. These beneficial microbes have been proved to offer an array of benefits to host plants [6]. During mycorrhization, besides significant improvement of plant nutritional status, AMF can enhance plant performance and tolerance against several stresses, particularly drought stress [7]. The exploitation of AMF is considered as one of the most efficient practices to increase plant tolerance to environmental stresses [8]. Previous studies illustrate the substantial contribution of AM symbiosis to improved stress plant tolerance to water deficit by various mycorrhizal benefits such as strengthened water and nutrient uptake, alterations in host physiology, for example, photosynthesis, osmotic adjustment, phytohormones, and more efficient antioxidative systems [9–11]. This chapter presents the current knowledge on AMF application to crop production under water deficit. Variable benefits of AMF are also discussed to explain the reason why positive outcomes of AM colonization are not always the case. Finally, challenges of the fungal symbiont application are highlighted for practical use in crop production.

2. General features of AMF

AMF are obligate root symbionts inhabiting almost all terrestrial ecosystems. They can form a symbiotic association with around 80% of vascular plants and with approximately 90% of agricultural plants [12]. In this mutual association, the fungus receives 10–20% of total photosynthates [13] and lipids [14] from the host plant, whereas the plant is enhanced through uptake of water and mineral nutrient by the mycorrhizal partner [12]. AMF are the most common fungi in soils and represent 9–55% of the soil microbe biomass and 5–36% of the total soil biomass [15]. These fungi play a vital role in agricultural ecosystems, since they can improve plant nutrient, water status, and plant growth [12], enhance survival rate and development of seedlings, crop uniformity, and reproductive capacity [16], decrease the input of P and N fertilizer, and increase resistance or tolerance to environmental adversities [8, 17].

Currently, AMF are classified as a member of phylum Glomeromycota including four orders (Archaeosporales, Diversisporales, Glomerales, and Paraglomerales), with 11 families, 25 genera, and nearly 250 species [18]. However, data based on next-generation sequencing of root samples [19] and recent results [20] suggest that its number may be an order of magnitude higher. Spores of AMF which are the major survival units of AMF have multi-nucleate, heterokaryotic structures [21], and are formed singly, in clusters or sporocarps in the soil, and within root tissue in some mycorrhiza species as well (**Figure 1A–C**). The development of AM symbiosis starts with signaling taking place before physical contact between the plant and the fungus. Both partners produce molecular signals triggering preparative responses in the other [22]. The mycorrhization process can be divided into distinct steps, consisting of germinating spores, hyphae differentiation, appressorium formation, penetration of the host root, intraradical hyphae formation, intercellular growth along with developed external mycelium (extraradical hyphae), and arbuscule formation, subsequently exchanging nutrients and carbohydrates between the host and fungus [23].

The primary structures of AMF consist of coenocytic hyphae with unlimited growth in the rhizosphere called external hyphae, which penetrate the cortex
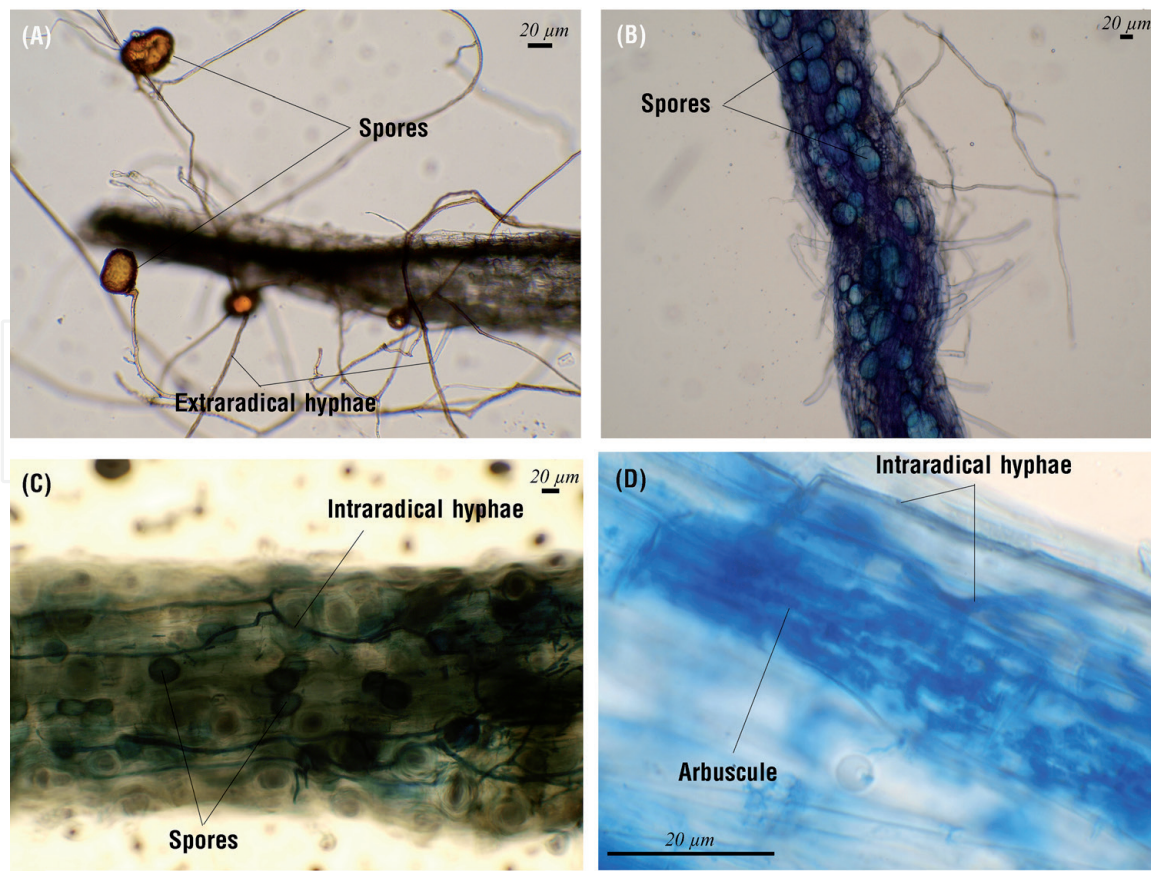
Figure 1.
Tomato roots without (A) and with (B–D) staining showing AM fungal structures. The presence of arbuscular mycorrhiza (AM) structures (arbuscules, vesicles, intraradical hyphae, and spore) was assessed by means of an Olympus BX51 light microscope with Nomarski interference contrast optics, using an objective of 40×. Scale Bar representing 20 μm.

layer of roots and form different organs. The extraradical hyphae merely in some species of Diversisporales [18] producing auxiliary cells could have functions in reproduction or nutrition and storage [24]. Mycelium outside the roots absorb mineral nutrients and water and subsequently transport them to the host plant via intraradical hyphae (**Figure 1C, D**) growing inside root cells [6]. Hyphae growing within roots form either the Paris-type or the Arum-type. The Paris-type is featured by intracellular mycelium development to shape coils, whereas the Arum-type is characterized by intercellular hyphae growth forming arbuscules [12] (**Figure 1D**), thereby establishing the nutrient exchange sites between AMF and the host plant [25]. Vesicles containing high quantity of lipids and glycogen are formed from intraradical hyphae at intercalary position (their terminal) in the root, functioning as nutrient storage, and propagules [23] but not all AMF produce vesicles.

AMF species isolates differ in the ability to spread mycelia, the viability, structure, and possibility of anastomosis [26, 27]. Taxonomic variation in mycelium structure among AMF families was also observed [28]. *Gigasporaceae* are prone to possess vigorous, thickly aggregated mycelium with densities from 6 to 9 m cm^{-3}, while *Acaulosporaceae* and *Glomeraceae* show a tendency to maintain thinly dispersed mycelium with densities from 1 to 2 m cm^{-3}.

3. Variable crop responses to AMF

Although a majority of plants are responsive to AMF, plant species in families *Amaranthaceae, Brassicaceae, Caryophyllaceae, Chenopodiaceae, Cyperaceae,*

Juncaceae, and *Urticaceae* are rarely or never colonized by the symbiotic fungus [29]. How AMF evaluate the AM host and nonhost status of plant species is not well known. The current hypothesis proposes that nonmycorrhizal plant species lost orthologs of important putative genes, required for symbioses [30], and/or cannot synthesize or degrade strigolactones, essential signals for symbiosis establishment [31], and/or their root exudates constitute antifungal products [29]. Under certain conditions, some nonhost species develop rudimentary AM phenotypes described by Cosme et al. [30] giving a more in-depth explanation of this question.

Utilization of AMF has become an appealing tool for sustainable agriculture due to the positive attributes of mycorrhizal symbiosis. Nevertheless, the opposite or neutral influence of AMF has also been found [32]. The obligate biotrophic life cycle of AMF which relies on photosynthates supplied by a nurturing autotrophic host is the key point; therefore, choosing the right partner (target plant) is crucial. Even though this widespread symbiont is thought to be a generalist due to low host specificity, each AMF species highly varies in the responsiveness to the host plant. Hence, the variable benefits of AM symbiosis exist among mycorrhiza species [10, 33]. The interaction between the host plant and AMF could range from mutualism to parasitism in which colonized plants exhibit a decrease in growth [34] owing to the carbon drainage in the host inflicted by the fungus [35]. Many factors that can affect the AM benefits to target plants include host plant genotypes, AMF species, and environmental conditions. Dissimilar plant responses to different AMF species under environmental adversities have been observed [11, 36]. Fascinatingly, AM benefits for plant fitness augment with adversity, supporting the concept of AM colonization as a 'health insurance' for host plants, in which the beneficial effects of AMF become more obvious under stressful environments [36]. Metabolites differentially accumulated in roots colonized by different fungal symbionts (*Rhizophagus irregularis*, *Funneliformis mosseae*, and *Claroideoglomus etunicatum*) under abiotic stresses, which may underlie their enhanced stress tolerance in host plants [36]. Cultivar differences in response to mycorrhizas have been reported in many crops such as tomato [37], pepper [38], wheat [39], maize [40], and some other crops [41]. For chickpea, only three of thirteen varieties with different genotypes and phenotypes were more positively responsive to AM mixed inoculation with *Diversispora eburnea*, *Claroideoglomus etunicatum*, and *Glomus* sp. [42]. More recently, twenty geographically different barrel clover (*Medicago truncatula*) accessions showed differences in their growth, stomatal conductance (g_s), and AM colonization in response to *Funneliformis mosseae* treatment [43]. Also, root hydraulic conductivity, expression of the mycorrhiza-induced phosphate transporter gene (*MtPT4*), and five aquaporin genes (*MtAQP1, MtPIP1, MtPIP2, MtNIP1,* and *MtNIP4*) vary with mycorrhizal treatment during further analysis of five accessions. In the case of wheat, old accessions have been shown to be more responsive to AMF than new ones [39].

Selection and breeding programs generally tend to maximize plant performance and crop yield under high-input production systems, which could cause the loss of genes, phytochemicals, and/or other plant traits which are necessary for the establishment of efficient symbioses. Modern cultivars could absorb phosphate without the AM assistance in soils with high phosphorus availability, decreasing the degree of AM dependence. As a consequence, AMF are less responsive to new lines. Recent research has proved that domestication decreased AM benefits for domesticated crops in exposure to high P supply [44]. However, in maize, which is highly mycorrhizal-dependent, modern breeding programs do not necessarily result in the less mycorrhizal colonization. Replicated field experiments with 225 genotypes consisting of hybrids, inbred lines, and landraces originating from different locations were conducted for two consecutive years to explore the variation in

mycorrhizal colonization [40]. The findings showed that AM colonization differed profoundly and continuously among genotypes, with substantially greater values in modern hybrids than old landraces and inbred lines.

4. Mechanisms of AMF mitigate drought stress in host plants

It is well known that AMF offer indispensable advantages to the host plant subjected to water shortage, with two major strategies that mycorrhizal plants use to deal with water deficit: drought mitigation and drought tolerance. Drought mitigation strategy is involved in indirect AM benefits and enhanced water uptake through the extensive hyphae network, enabling host plants to suffer less stress than non-AM plants, whereas drought tolerance includes a combination of direct AM benefits that improve plant's innate ability to cope with the stress (**Figure 2**).
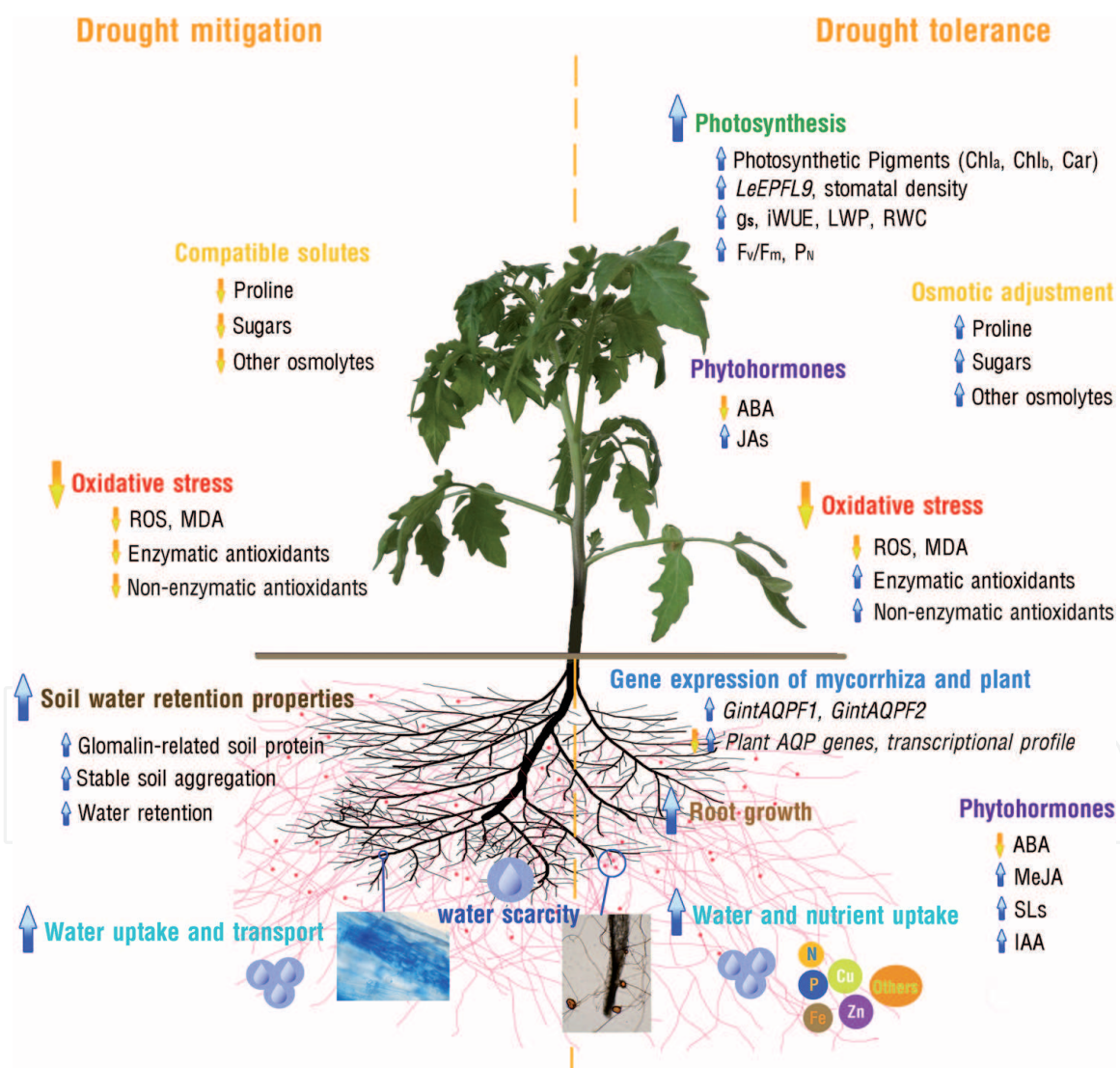
Figure 2.
Strategies of mycorrhizal plants to cope with water scarcity, that is, drought mitigation and drought tolerance. Multiple benefits/mechanisms could be simultaneously induced by arbuscular mycorrhizal fungi in the host plant exposed to water deficit. The blue arrows show increase/up-regulation, whereas the orange arrows indicate decrease/down-regulation, relative to control non-mycorrhizal plants. Italic words indicate genes. ABA, abscisic acid; AQP, aquaporin; Car, carotenoids; Chl_a, chlorophyll a; Chl_b, chlorophyll b; F_v/F_m, maximum quantum efficiency of PSII; g_s, stomatal conductance; IAA, indole-3-acetic acid; iWUE, intrinsic water use efficiency; JAs, jasmonates; LWP, leaf water potential; MDA, malondialdehyde; MeJA, methyl jasmonate; P_N, net photosynthesis rate; ROS, reactive oxygen species; RWC, relative water content; SLs, strigolactones.

4.1 Direct benefits of AM symbiosis for host plants under water deficit

4.1.1 Improved water and nutrient uptake through the hyphal network of AMF

An important benefit of AM colonization to the host plant under drought stress is a superior water allocation mediated by the fungal hyphal network, facilitating the colonized root access to water in a lower soil water potential [45]. Indeed, the host root system is extended by widespread extraradical mycelia, enabling colonized roots to reach more water and nutrient pools unavailable to uncolonized roots. Fungal hyphae diameters (3–7 μm) are much smaller than those of fine root hairs (5–20 μm); nevertheless, hyphal densities are ten-hundred times higher than root densities [46]. Hence, the absorption surface of mycorrhizal roots is improved substantially. It is calculated that the rate of water transport from external hyphae to the root ranged from 0.1 [47] to 0.76 μl H_2O h^{-1} per hyphal infection point [48], which is adequate to alter plant water relations [47]. Lettuce plants pretreated by *Rhizophagus irregularis*, *Funneliformis mosseae*, *Funneliformis coronatum* (formerly *Glomus coronatum*), and *Claroideoglomus claroideum* (*G. claroideum*) obtained 3–4.75 ml H_2O plant^{-1} day^{-1} higher than uncolonized plants, which might be related to the amount of extraradical mycelium and root colonization frequency [45]. Furthermore, AMF contribute approximately 20% to total plant water uptake [49], highlighting the role of the symbiosis in the water status of host plants.

The widespread extraradical mycelia also enhance the absorption of mineral nutrients in soils, which is more critical for host plants under water-stress conditions where nutrient mobility is limited. As soon as external hyphae transport water to the host, mineral nutrients also follow the water flow to the plant from the soil-root interface [50]. AM colonization is well known to improve phosphorus (P) nutrient into the host plants particularly under low-nutrient conditions, increasing stress tolerance in plants. Interestingly, plants possess a symbiotic inorganic phosphate (Pi) uptake pathway, and AM symbiosis has been proved to specifically induce the expression of genes encoding plant Pi transporters to enhance P acquisition, for instance, *LjPT4* in *Lotus japonicus* and *MtPT4* in *Medicago truncatula* [51], recently *LbPT3, LbPT4,* and *LbPT5* in *Lycium barbarum* [52]. Under water restrictions (moderate and severe), different expressions of five tomato *PT* genes (*LePT1-LePT5*) in the absence/presence of *Rhizophagus irregularis* or *F. mosseae* were observed [53]. *LePT4* was overexpressed in *R. irregularis*-colonized plants exposed to both water-stress levels, while this upregulation was in *F. mosseae*-infected plants subjected to severe water stress. A role of *PT4* genes in root tips, creating a connection among root branching, Pi-signaling mechanisms, and Pi-perception has been proposed [51]. In addition, on the fungal side, *R. irregularis PT* gene was up-regulated under moderate drought conditions [53]. Phosphate is taken up by mycorrhizal phosphate transporters and assimilated to polyphosphate translocated toward the plant. This process is facilitated by the activation of fungal aquaporins [54].

Apart from that, AM colonization enhances the rate of nitrogen (N)-assimilation of plants under drought [55] as a result of the direct uptake of NO_3^- or NH_4^+ by fungal hyphae [56]. Several NO_3^- and NH_4^+ transporters and metal transporters in AMF [57, 58] while mycorrhiza-inducible ammonium transporters in some plants have been identified [59, 60]; therefore, AMF considerably contribute to the total N uptake of the host. Increased N nutrient could promote protein synthesis and higher levels of compatible osmolytes in stressed AM plants. Other studies also confirmed that inadequacy of necessary macro- and micro-nutrients could be alleviated in mycorrhizal plants under water deficit [61, 62]. Hydraulic conductivity of colonized roots was enhanced to absorb more N, P, and K, leading

to a higher protein concentration in host plants under drought stress [63]. Thus, more vigorous uptake of water and nutrients may provide adequate necessary substances for better growth of mycorrhizal plants under such stress.

4.1.2 AMF-induced changes in expression of aquaporin genes, transcriptional profiles

The negative water potential in dried soils exerts the problem for plants to obtain adequate water amount, a process where aquaporins (AQPs) get involved in [64]. AQPs belonging to the large major intrinsic protein family of transmembrane proteins functioning as water channels are crucial in osmoregulation [64]. On top of that, their regulation of transcellular movement of many molecules such as small alcohols, boron, and osmolytes has been reported [65]. In AMF, the first AQP gene *GintAQP1* of *Rhizophagus irregularis* was cloned, with evidence of a compensatory mechanism between *GintAQP1* expressions and the host aquaporins under drought stress [66]. Furthermore, two AQP genes *GintAQPF1* and *GintAQPF2* present in *Rhizophagus irregularis* were upregulated under osmotic stress, assisting the fungus survival and contributing to the host plant tolerance to water stress [67, 68]. Upregulation of *RiAQPF2* in *Rhizophagus irregularis* was also found under water deficit [10], suggesting its putative involvement in host plant tolerance in response to drought.

On the plant side, AMF could induce changes in the expression of various AQP genes in the host in order to strengthen root hydraulic conductivity and host tolerance under water-stress conditions in several plants, such as maize [69–71], tomato [10, 11], black locust [72], trifoliate orange [73], olive [74], and *Populus x canadensis* plants [75]. AM-induced alterations in expression of plant AQPs could depend on stress duration as the observation in maize plants [69]. Under short-term water deficit, the AM symbiosis upregulated ten AQP genes with diverse aquaporin classes in roots inoculated with *Rhizophagus intraradices*, stimulating more water uptake in the host [69]. By contrast, under sustained water-stress conditions, AM-mediated downregulation of 6 different AQP genes was found, restricting plant water loss [69]. Intriguingly, drought-sensitive cultivars may gain higher physiological benefit from AM inoculation than drought-tolerant cultivars [71]. Downregulation of genes *TIP1;1, TIP2;3, PIP1;1, PIP1;3, PIP1;4, PIP1;6, PIP2;2,* and *PIP2;4* whereas only upregulation of *TIP4;1* were observed in drought-sensitive cultivar colonized by *Rhizophagus irregularis*, supporting the decrease in water loss in host plants subjected to drought stress [71]. Recent research also revealed a significant shift in the transcriptional regulation profiles with AQP genes as potential targets in mycorrhizal roots, in comparison to non-AM ones during a water stress event, which may influence some key metabolic pathways linked with drought response [76]. In parallel, it has been proposed that during drought stress a controlled mechanism mediated by the presence of arbuscules at cortical cells in roots fine-tuned the gene expression regulation in the host plant [76].

In general, fungal and plant AQPs work together in mycorrhizal plants under water restrictions. The simultaneous induction of both fungal and plant AQP genes together with differential regulation of drought-responsive genes in host plant indicates that AMF mediate colonized plant responses to drought stress.

4.1.3 Increased photosynthetic efficiency

Numerous reports illustrate that AMF could increase photosynthetic activity or protect the photosynthetic apparatus under water stress conditions [77, 78]. In fact, AM colonization considerably influences the stomatal behavior in the leaves of host

plants, determining the water vapor efflux, CO_2 gas exchange, and thus photosynthetic activity [79]. Stomatal conductance changed by AM inoculation is closely connected to leaf water potential and relative water content in host plants. Under water restrictions, the first response of plants is stomatal closure to limit water loss through transpiration. Additionally, reduction of CO_2 uptake and carbon assimilation whereas favoring photorespiration may occur in plants [80]. Upregulation of *LeEPFL9* involved in the regulation of stomatal development together with greater stomatal density was found in tomato plants colonized by *R. irregularis* [10]. Inoculation of *Septoglomus deserticola* or *S. constrictum* sustained stomatal opening in host plants under drought conditions, substantially contributing to the carbon assimilation [11]. Improvement of stomatal conductance (g_s) in mycorrhizal castor bean [78], black locust [72], and strawberry [81] plants exposed to water stress has been detected.

One of the widely known benefits of mycorrhizal inoculation is the improvement of host water status under drought stress. Leaf water potential (LWP) and relative water content (RWC) of plants were substantially higher in the presence of mycorrhiza [11, 81]. Several studies illustrated a higher water use efficiency or intrinsic water use efficiency in AM plants during water stress [10, 81, 82]. It is believed that photosynthetic activity correlates with chlorophyll content and stomatal conductance, which have been enhanced by AMF. Drought stress changes photosynthetic pigments and damages chloroplasts. Nonetheless, AM inoculation alleviates the damage of these parameters caused by the stress [77]. *Rhizophagus irregularis*-colonized castor bean plants subjected to water restriction increased contents of chlorophyll a (by 26%), b (30%), carotenoid (by 28.5%), and total chlorophyll (25.5%) in comparison to counterparts of non-AM plants [78]. These increases in AM plants may be attributed to the improved nutrient uptake, particularly N and Mg that are structural components of chlorophyll.

Mycorrhizal colonization has been found to alleviate the adverse impacts of drought stress on photochemical efficiency and photosystem II (PSII) reaction center [77, 83]. Under water deficit, application of AMF promoted a higher maximum quantum efficiency of PSII (F_v/F_m) [11], greater photosynthetic efficiency [84], transpiration rate, and net photosynthesis rate (P_N) [10, 81]. Although mycorrhizal plants usually have higher photosynthetic capacities, environmental factors such as high atmospheric drought or low radiation can decide the beneficial effects of mycorrhiza on photosynthesis [85].

4.1.4 Phytohormonal changes

Phytohormones not only modulate a plethora of events during plant development but also are essential signaling molecules for interaction between plants and AMF [86]. Changes in plant hormone homeostasis also affect plant tolerance against abiotic stresses [87, 88]. During mycorrhization, changes in levels of several plant hormones have been reported [86], hence may contribute to the improved host plant tolerance to subsequent stresses.

Abscisic acid (ABA) is the most fundamental stress hormonal signal, modulating transpiration rate, root hydraulic conductivity, and aquaporin expression [89]. The concentration of ABA is heightened in plant tissues under drought stress to induce stomatal closure for reduction of water loss and activate different stress-responsive genes, increasing plant tolerance to drought [90]. A lower ABA concentration was found in roots and leaves of mycorrhizal plants versus nonmycorrhizal plants under drought stress [9, 10, 91]. Downregulation of *SlNCED* gene, a critical ABA biosynthetic gene, in *Septoglomus constrictum*-infected roots under water stress concurred with the greater g_s and higher water status of tomato plants, indicating a higher stress tolerance in colonized plants compared to uninoculated plants [11].

Nonetheless, an increase in ABA concentration in trifoliate orange plants colonized by *F. mosseae* was also observed under drought stress [73]. The reason for this remains poorly understood, which requires further research.

The role of jasmonate (JA) in water uptake and transport, exerting influence on stomatal conductance, root hydraulic conductance, and regulating the expression and abundance of aquaporins in tomato plants has been revealed [91]. Tomato plants defective in JA synthesis altered the AM impacts on the host plant, interfering phytohormones and expression of AM-induced aquaporin genes. The content of JA and its precursors was higher in leaves of *Digitaria eriantha* plants infected by *Rhizophagus irregularis* under water deficit, relative to noninfected plants, which could enhance plant tolerance to the stress [92]. Likewise, mycorrhizal inoculation substantially increased methyl jasmonate (MeJA) in trifoliate orange plants exposed to drought stress [93]. Under water-stress conditions, significantly higher expression levels of JA-biosynthetic gene *SlLOXD* in roots and leaves of colonized tomato plants were detected, supporting plant response to drought stress by triggering a LOXD-mediated pathway [10, 11].

Strigolactones (SLs), as phytohormones, not only modulate the coordinated development of plants exposed to nutrient shortages but are also host detection signals for AM establishment in the host plant [94]. Upregulation of the SL-biosynthesis gene *SlCCD7* together with a greater content of SLs was found in *Rhizophagus irregularis*-inoculated tomato roots subjected to water-stress conditions, correlated with the increase in AM colonization rate [9]. The stimulated production of SLs promoting symbiosis establishment as a strategy of plants to cope with drought stress has been proposed.

Auxin is a key regulator in root-hair initiation, growth, and developmental processes [95, 96]. In a recent study, an increased content of indole-3-acetic acid (IAA) which is the dominant naturally occurring auxin was found in mycorrhizal tomato plants exposed to drought [91]. Similarly, stimulation of biosynthesis and transport of IAA in roots of trifoliate orange under water restrictions were demonstrated [97]. Under drought conditions, AM colonization overexpressed *PtYUC3* and *PtYUC8* involved in IAA biosynthesis, and downregulated auxin efflux carriers (*PtPIN1* and *PtPIN3*), while up-regulated auxin-species influx carriers (*PtABCB19* and *PtLAX2*) in roots, leading to significantly higher IAA accumulation in mycorrhizal roots versus non-AM roots [97]. Together with higher IAA, colonized trifoliate orange plants showed a significant increase in MeJA, nitric oxide, and calmodulin in roots, supporting greater root adaptation of morphology as a crucial strategy for drought adaptation [93].

Although important roles of phytohormones are irrefragable in plant responses to water stress, little attention has been paid to them in mycorrhizal plants. Previous studies have just revealed changes in concentrations and expression of genes encoding biosynthesis of few hormones in colonized plants during drought stress; thereby, further research is required to understand it.

4.1.5 Osmotic adjustment

In response to drought stress, plants accumulate compatible solute compounds or osmolytes functioning for osmotic adjustment to maintain a favorable gradient for water uptake [98]. Osmotic adjustment is essential for water influx, turgor maintenance, sustaining physiological activity in plants such as stomatal opening, photosynthesis, cellular expansion, and growth during the stress [98]. Compatible solutes include a variety of sugars, proline, glycine betaine, polyamines, and organic acids such as oxalate and malate [99]. Interestingly, discrepant observations in osmolyte accumulation have been reported in a wide range of mycorrhizal plants [10, 83, 100, 101].

Proline, an amino acid, plays a crucial role in osmoregulation and acts as an efficient scavenger of reactive oxygen species (ROS) [102] (discussed in Section 4.1.7). Enhanced drought tolerance with a higher proline concentration in mycorrhizal plants has been shown in many studies [10, 78, 100]; nevertheless, opposite results have also been reported [81, 83]. Inoculation of either *F. mosseae* or *Paraglomus occultum* in trifoliate orange plants substantially reduced leaf proline content but improved the host plant growth under water deficit [103]. These results suggest that AMF strongly altered leaf proline metabolism through regulating proline-metabolized enzymes, which is important for osmotic adjustment of the host plants.

Sugars are osmoprotectants, which contribute up to 50% of osmotic potential in plants [104, 105]. In general, under water stress, the higher accumulation of total soluble sugars offers a defense mechanism in mycorrhizal plants such as watermelon [100] and flax [106]. Concentrations of sucrose, glucose, and fructose were significantly heightened in leaves of mycorrhizal trifoliate orange seedlings exposed to drought, which could function as osmolytes to stabilize and protect structures and macromolecules in plants from the stress, therefore improving host plant tolerance [103]. AMF-mediated increases in leaf sugar metabolism by modulating sugar-metabolized enzymes notably contribute to the osmotic adjustment of colonized plants. However, contrast observations have been shown in olive trees [101] and maize [107] colonized by AMF, which may be due to the fact that host plants suffer less stress. Noticeably, under severe drought inoculation with *Rhizophagus clarus* significantly reduced soluble sugars in leaves of strawberry plants, but this parameter was remarkably enhanced in roots in response to mild and severe water stress [81]. These changes together with an improved water status and plant biomass suggest different strategies for the enhanced water status triggered by AMF in roots and leaves of strawberry.

In summary, increased accumulation of compatible solutes in AM-inoculated plants in exposure to water deficit is supposed to protect plants from the stress and curtail the plant osmotic potential, whereas the lower osmolyte accumulation in host plants is thought to be due to colonized plants successfully gaining drought mitigation.

4.1.6 Enhanced plant tolerance to oxidative stress

One of the consequences of water stress is the overproduction of reactive oxygen species (ROS) such as hydroxyl radicals ($\cdot OH$), superoxide radicals ($O_2\cdot^-$), singlet oxygen ($^1O_2$), and hydrogen peroxide (H_2O_2) mainly in chloroplasts and mitochondria. The excessive ROS results in unbalanced cellular homeostasis and then oxidative stress, damaging membrane lipids, proteins, and nucleic acids and even causing the death of cells [108]. To cope with oxidative stress, plants have evolved ROS scavengers in both nonenzymatic and enzymatic defense systems. Nonenzymatic antioxidants comprise phenolic compounds, glutathione, ascorbic acid, alkaloids, carotenoids, and tocopherol [109], which not only play a direct role in ROS removal but also serve as a substrate for the antioxidant enzymes in scavenging ROS [110]. Under water deficit, AMF ameliorate oxidative damage through augmented production of phenolic compounds and secondary metabolites detoxifying ROS in various plants [111–113]. AM inoculation also significantly increased the concentrations of anthocyanins and carotenoids [106] and ascorbic acid [82, 106] in plants in exposure to water constraints.

Another important ROS scavenger system is enzymatic antioxidants which could be enhanced in mycorrhizal plants including superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), guaiacol peroxidase, ascorbate peroxidase (APX), glutathione reductase (GR), dehydroascorbate reductase (DHAR), and

monodehydroascorbate reductase (MDHAR) [110]. The AM symbiosis has been reported to improve plant protection against oxidative stress by decreasing the level of lipid peroxidation (MDA) and H_2O_2 accumulation by strengthening significantly antioxidative enzymes SOD, POD, and CAT in roots and leaves under mild and severe drought [11, 81]. SOD and CAT are the most important ROS scavenging enzymes among the enzymatic antioxidants. These enzymes together with the cooperative enzymes (GR, MDHAR, DHAR, and APX) in the ascorbate-glutathione (ASA-GSH) cycle play pivotal roles in controlling overproduced ROS to maintain cellular homeostasis [114–116]. Remarkable increases in SOD, CAT, GR, APX, and MDHAR at transcription and enzymatic level correlated with lower $O_2^{·-}$, H_2O_2, and MDA have been revealed in drought-stressed mycorrhizal plants versus counterparts of non-AM plants, improving host protection against oxidative damage [101].

Higher nonenzymatic and enzymatic antioxidants in colonized plants help for the rapid and efficient elimination of excess ROS. Nevertheless, discrepant results, no change or decrease in ROS scavengers, have also been demonstrated [70, 117]. Results are not entirely consistent with all reports because of different ages of host plants [118] and/or the specific combination of mycorrhizal strains and plant species, even cultivars [11] (as discussed in Section 3) or successful drought mitigation in colonized plants.

4.2 Indirect benefits of AM symbiosis for host plants under water deficit

The hyphal network of AMF is believed to improve soil water retention properties in the mycorrhizosphere through its physical, biological, and chemical influences. It has been reported that AMF produce polysaccharides, glomalin, mucilages, and hydrophobins that act to bind soil particles, leading to soil aggregation with enhanced water-holding capacity in soil [119]. Glomalin, a stable glycoprotein, highly persists in the soil, defined as glomalin-related soil protein (GRSP) [120]. The higher amounts of GRSP in the soil, the more enhanced capacity of water retention was found since soil aggregation increased protection of C-rich debris from the decomposition of soil microbes [120, 121]. Indeed, fungal hyphae coated by GRSP sharp a hydrophobic layer into the aggregate surface, hence decreasing water loss within soil aggregates [122]. When the fungal hyphae form branching structures with glomalin, they physically stick micro-aggregates with macro-aggregates [119]. The physical interaction of external hyphae on soil particles forms stable aggregates [123] in general and under water deficit [124]. Moreover, mycorrhizosphere also influences soil aggregation through alterations in the soil microbial food web, habitats for soil microbes, and biological activities in the host rhizosphere, which could result in an enhancement in microaggregate soil structure [125]. Thus, soils possess well-structured property in the presence of AMF, maintaining relatively higher available water than poorly structured soils without mycorrhizal presence under water stress [126]. Notably, in artificial substrates, an enhancement in water retention and water transport within substrates inoculated with AMF was observed under severe drought, suggesting that host plants perceive less stress at the root surface as reducing substrate moisture [127]. Hence, AMF postponed the physiological stress response in host plants.

5. Altered plant growth, yield, and quality

It is often found that AM symbiosis can improve plant growth in numerous plants, such as lettuce [9], tomato [9, 11], strawberry [81], maize [128], black locust [72], digitgrass (*Digitaria eriantha*), a source of forage [92], and damask rose [129].

The substantial improvement in the growth of mycorrhizal plants could be a result of a combination of AMF-induced mechanisms of plant tolerance under drought conditions, notably enhanced water and nutrient uptake in host plants [60, 117], and increased photosynthetic activity (as discussed in Section 4.1.3) since plant size closely links with measured physiological parameters [11]. It is important because nutrient supply may improve plant drought tolerance for better plant establishment. The increased plant biomass and nutrient uptake in AM plants could be more pronounced during seedling growth stages and in a longer stress duration. For instance, significant increases in shoot dry weight (by 128–242%) and root dry weight (185–328%) in French lavender (*Lavandula dentata*) plants treated by either single autochthonous AMF (*Septoglomus contrictum, Diversispora aunantia, Archaespora trappei, Glomus versiforme,* and *Paraglomus occultum*) or their mixture were recorded, compared to uninoculated plants after 6 months of growth under drought conditions [60].

Besides positive mycorrhizal effects on plant growth, discrepant observations have also been reported. Four tomato recombinant inbred lines (RIL 20, 40, 66 and 100) and one commercial cultivar inoculated with *Rhizophagus irregularis* showed variable results under water stress [37]. AM application remarkably increased shoot dry weight of RIL 40 and RIL 60 lines under drought conditions while no changes were recognized in plants colonized by other AMF. Similar results were found in soybean using single isolates of *Septoglomus constrictum*, *Glomus* sp., *Glomus aggregatum*, or their mixture [130]. Taken together, the benefits of AMF application under water deficit are dependent on the specific combination of plant genotypes and AM isolates.

Another significant benefit of mycorrhizal inoculation is to increase crop yield in exposure to water constraints compared to nonmycorrhizal plants. An array of observations shows a significantly higher yield, importantly marketable yield in mycorrhizal plants subjected to water scarcity in maize [128], tomato [82], flax [131], cowpea [132], and damask rose [129]. Furthermore, AM symbiosis has shown to accelerate flowering and fruit development [133]. Interestingly, re-inoculation of AMF after transplanting seedlings in the field appears to be necessary to strengthen mycorrhizal benefits. This could be seen in the field investigation which with twice application of AMF considerably heightened the marketable fruit yield (by 51–71%) in plants subjected to 50% water supply regime in comparison with those with mycorrhizal inoculation once at sowing and uninoculated ones [82]. The beneficial effect of AMF application on relative water content and nutritional status in plants as well as enhanced shoot accumulation of photoassimilates through higher photosynthetic activity, and improved stress tolerance in the presence of drought could result in higher productivity in colonized plants. Also, fruits are often the main sink for P; therefore, enhanced P nutrient in host plants promotes higher fruit yield.

As a result of physiological changes during mycorrhization, both transcriptional and metabolic changes occur in host plants influencing crop quality as well. AM symbiosis not only modulates gene expression in tomato fruit, through a systemic impact, but also changes the phenology of flowering and fruit ripening as well as in the amino acid profile [133]. Under water shortage, AMF treatment has been explored to improve quality attributes including antioxidant compounds, carotenoids and anthocyanins [82, 134], essential oils [135], and alteration in seed quality of flax [131], hence highlighting the potential of using AMF in crop production, producing industrial and oil plants.

6. Challenges of AMF application

Microbial symbionts of plants such as AMF represent a huge, but an unrealized resource for improving yields, especially in the tropics [136]; however, lower

benefits to plants than the potential of these microorganisms are often found. To predict real benefits as well as all potentials of the fungal inoculation, implementation of field trials before AMF application on a large scale is indispensable in order to choose suitable inoculum or appropriately tune the best AM combination for target crop production systems. Moreover, various environmental factors influence the success of AMF application into the field.

Another critical issue is whether generic or tuned AM products should be utilized in sustainable crop production. One of the challenges of AMF inoculation under open field conditions is the native populations of AMF in soils, which are able to remarkably compete colonization niche with the introduced symbionts. Despite the fact that commercial AMF inoculants are usually advertised as compatible for a variety of host plants and field-cultivation conditions, the AM-induced benefits for crops are not always as expected [137]. The bridge between research and AM suppliers should be strengthened to recommend appropriate AM inocula for most benefits. Due to the specificity of AMF-host plant interaction as described in several places in the chapter, an attempt to exploit advantageous combinations is necessary. Fine-tuning commercial mycorrhizal products is vital to obtain optimum beneficial effects from mycorrhizal inoculation.

Even in some circumstances, the symbiotic effectiveness and adaptability of the indigenous fungi are more dominant than non-native ones [138, 139]; therefore, introduced AMF isolates could be less profitable than native ones [140]. Besides, there is an existence of functional diversity among different AMF species [36]. Remarkable differences in performance even among different geographical isolates belonging to the same mycorrhizal species have been described [141]. In such cases, isolation of indigenous mycorrhizal strains for inoculum production, then large-scale reintroduction of these native fungi in the field could be a feasible solution for a useful AMF application [142]. It is worth mentioning that selection of specific AM taxa for particular crops is the best approach to improve crop growth, and there is no 'one-size-fits-all' AMF [143]. In controlled environments, application of a single AMF is more effective than using a mixture of different AM taxa [143].

During the last decades, several molecular techniques have been used to characterize entire communities of mycorrhiza in soil [144, 145] and AMF inocula [146–148]. These techniques enable to monitor the introduced fungal symbiont both inside and outside the host during plant growth [149, 150]. Tracing the introduced AMF temporally and spatially could be implemented by high-throughput next-generation sequencing, which possibly verifies whether the introduced fungi favor substantial levels of colonization and explores how the inoculated AMF coexist and interact with the local community of AMF [136]. Advances in molecular techniques can further assist the adjustment or tuning of commercial inoculants to specific AMF combinations with host plants under crop production systems.

Another major limitation of mycorrhizal inoculation in horticulture and agriculture is farmer's awareness and acceptance and the relatively high cost of it. Furthermore, conventional breeding programs have overlooked plant characteristics facilitating mycorrhizal association, and plant breeders have selected varieties in favor of acquiring nutrients in high-input crop production systems without respect to the AMF role in soil nutrient management [151], resulting in the primary challenge to AMF application. Hence, modern breeding programs should consider AMF as an essential component of breeding traits in new cultivars, particularly those cultivated under environmental adversities such as drought stress in which AMF application has been proved to stimulate higher crop tolerance.

7. Conclusion and future perspectives

AM inoculation can offer multiple advantages to host plants in exposure to water scarcity, which could enable inoculated plants to avoid drought stress or tolerate water deficit better than nonmycorrhizal plants. Indeed, various direct and indirect AM-induced mechanisms in mycorrhizal plants could contribute to drought mitigation or tolerance. More importantly, improved crop yield and quality attribute in colonized plants under drought stress highlight the importance of AMF application in crop production as one of the promising practices under water constraints. However, variable plant responses to AMF and the discussed major challenges hinder possible fruitful outcomes of AM inoculation. Identification of the most appropriate combination of fungal inoculants and a given variety, cultivar, or accession grown under water scarcity, and understanding environmental factors deciding the positive results of the inoculation are crucial determinants for successful AMF application. Compatible combination of AMF with other beneficial microbes such as plant growth-promoting bacteria and/or *Trichoderma* offering synergistic effects on plant tolerance to stressful environments including drought stress is also a bright perspective [38, 106]. Besides that, further research is necessary to shed light on the specific functions of genes mediated by mycorrhiza, which could explore the exact AM-triggered mechanisms of plant adaptation under water deficit. Studies on quantitative trait loci (QTL) involved in mycorrhizal plant responses to drought stress are needed for breeding programs to create new cultivars with a combination of drought-tolerant traits and AM benefits.

Acknowledgements

Conflict of interest

We declare that we do not have any conflict of interest.

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