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Review

The Function of Arbuscular Mycorrhizal Fungi Associated with Drought Stress Resistance in Native Plants of Arid Desert Ecosystems: A Review

Tareq A. Madouh * and Ali M. Quoreshi

Desert Agriculture and Ecosystems Program, Environment & Life Sciences Research Center, Kuwait Institute for Scientific Research, P.O. Box 24885, Kuwait City 13109, Kuwait
* Correspondence: tmadouh@kisr.edu.kw

Abstract: Drought stress profoundly affects native desert plants' survival and performance. Among all the abiotic stresses, drought is considered a major constraint that influences the structure and functions of desert ecosystems. Arid desert ecosystems are characterized by prolonged drought, extreme temperatures, high solar radiation, water scarcity, high salinity, scarcity of soil nutrients, and poor soil structure. Such extreme desert environments are the toughest regions on earth, which present enormous challenges in conserving plant survival, growth and reproduction. Despite the predominance of these environmental conditions, native desert plant species that grow in desert environments develop complex adaptation strategies and resistance mechanisms to ameliorate the abiotic and biotic stresses in the extreme environments including changes in biochemical, physiological, and morphological levels. Arbuscular mycorrhizal fungi (AMF) form positive symbiotic associations with a considerable percentage of terrestrial plants as their host, induce distinct impacts on plant growth and protect plants from abiotic stresses. However, it is necessary to advance our understanding of the complex mechanisms associated with AMF-mediated and other dark septate endophytes (DSE)-mediated amelioration of native desert plants' drought stress resistance and associated biological adjustments such as changes in hormone balance, water and nutrient status, stomatal conductance and osmotic adjustment, antioxidant activity, and photosynthetic activity. This review provides an overview of the relationships of mycorrhiza and fungal endophytes involved in drought stress tolerance, summarizing the current knowledge and presenting possible mechanisms mediated by AMF to stimulate drought tolerance associated with native desert plants. We discuss the research required to fill the gaps and provide suggestions for future research.

Keywords: abiotic stresses; arbuscular mycorrhizal fungi; dark septate endophyte; desert ecosystems; drought resistance; drought stress tolerance; ecophysiology

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1. Introduction

In terrestrial ecosystems, plants are frequently exposed to environmental stresses. Among them, drought is considered one of the major abiotic factors hazards that occur in most global environments; it can also have significant economical, societal and environmental impacts [1]. In ecological settings of arid environments, particularly desert ecosystems, drought is directly connected to the total seasonal rainfall. Inadequacy of precipitation over an extended period results in a water scarcity [2]. Moreover, drought is predicted to increase in frequency and severity in several parts of the world due to reduced water availability [1] and the rise of the evaporation rate due to global climate change [3]. In warmer climates, such as arid and semi-arid regions, shifts in seasonal precipitation are particularly evident, which have escalated the risk of drought episodes [4]. Similarly, the desert ecosystem is under continuous drought stress and is vulnerable to even slight changes in water availability and soil moisture levels. It is reported that approximately 40% of the planet's total terrestrial area is considered to be water deficient arid dryland soils due to the scarcity of rainfall, high solar radiation and temperature fluctuations [5,6]. Extreme temperature fluctuations and high solar radiation are the major drivers of environmental challenges in arid desert ecosystems; these features can quickly heat up the desert with low vegetation coverage during the daytime and temperatures drop down considerably at night. The increased severity of drought in many regions and specifically the arid desert environment may pose considerable challenges for natural ecosystem restoration, habitat management, and even for crop production under farming systems [7]. Furthermore, drought stress profoundly influences desert native seed germination, seedling development and establishment in natural habitats [8,9]. Drought stress is the most crucial abiotic stress inhibiting native vegetation survival, growth and performance; however, desert plants have developed different strategies to adjust their levels of stress tolerance and drought resistance [10,11].

Among the adaptive strategies, symbiotic association with arbuscular mycorrhizal fungi (AMF), a ubiquitous type of soil microorganism, can establish symbiotic association with the roots of over 80% of plant species, and develop adaptive mechanisms with their host plants. The mycorrhizal association that prevails in desert ecosystems is capable of enhancing resistance to drought stress and tolerance, improving plants' ability to absorb water and nutrients. The existence of soil and root microorganisms in terrestrial ecosystems, particularly the arbuscular mycorrhizal fungi, is considered a crucial factor in the adaptation of plants to a wide range of ecological circumstances, and they participate in various ecological processes [12,13]. Desert ecosystems, however, are quite different from other biomes in relation to microbial community composition and functions; the biomes are leading drivers of desert systems, facilitating crucial ecosystem processes [14,15]. Desert vegetation has the morphological, physiological and biochemical adaptation ability that allows plants to tolerate extreme environmental conditions [16]. However, there is sparse information regarding the interaction of mycorrhizal fungi with native plants in desert ecosystems, particularly in the Kuwait desert regions and similar habitats. The aim of this review is to provide an overview of the relationships of mycorrhiza and fungal endophytes in drought stress resistance in native desert plants, and to summarize the current knowledge on mechanisms mediated by AMF and the need for future research.

2. Desert Plants Responses to Drought Stress

Drought stress stimulates a variety of physiological, morphological and biochemical responses to activate the adaptation mechanisms in plants to ameliorate the negative impacts of drought. Three main environmental conditions—acute water scarcity, extreme temperature fluctuations and salinity—are most associated with arid desert ecosystems. Of these, drought is the major abiotic stressor limiting plant survival, growth and reproduction in desert systems. Despite the severe environmental challenges, most native desert plants can tolerate and resist drought stress by increasing their water use efficiency through several functional and biological adjustments such as regulating stomatal activity [17,18], decoupling aboveground and belowground responses [18] and controlling nutrient reabsorptions [19–22]. Drought stress can alter the biochemical activities in plants for resisting drought stress and the alleviation of abiotic stress by increasing the activity of antioxidant enzymes superoxide dismutase (SOD), guaiacol peroxidase and ascorbate peroxidase (POD) [23]. Plants adapted to desert ecosystems are frequently exposed to diverse abiotic stresses; they are required to reduce transpiration demand associated with water stress to improve species survival and maintain stable populations and biodiversity [18].

To alleviate the negative impact of drought stress on desert plant performance, these plants must adapt by regulating their biological functions and processes. It is reported that drought stress has profound influence on plants' survival, growth, and development, mainly because of constraints in physiological, morphological, biochemical and molecular processes and pathways [24,25]. These constraints include reduced turgidity, osmoregulation, decreased carbon assimilation and gas exchange, decreased enzymatic activities and ion absorption, oxidative damage, osmotic adjustment and reduced relative water content in leaves, which decreases stomatal conductance and net photosynthesis [26,27]. It is believed that these processes occur within the plants' internal system as a response to drought stress.

Most of the major physiological processes such as photosynthesis, protein and energy synthesis, and metabolism of lipids are consistently affected in relation to water deficiency [28]. Therefore, drought stress has been shown to influence multiple biological processes and pathways in plants, which subsequently adjust their growth, biomass production and water relations to maintain their productivity [29–31]. Many plants show drought-stimulated accumulation of reactive oxygen species (ROS), which may cause oxidation of proteins, DNA materials, carbohydrates, and damage membrane integrity [32–34]. However, plants accumulate several osmolytes and different antioxidant enzymes to combat the influence of drought stresses [35,36]. Plants also synthesize important proteins in response to drought stress; these proteins secure the performance of ion channels, search for ROS, adjust antioxidant activities, aid gene expression, membrane integrity and water transportation and, consequently, enhance plant tolerance of environmental stress [37,38]. Extreme temperature and high radiation levels prevailing in desert environments can have distressing consequences for plants' viability and the production of ROS, which may harm DNA, proteins and membrane lipids [39]. Several other adaptive mechanisms reported in response to heat, high radiation, excessive light and temperature include changes in leaf orientation [40], with the formation of thick wax layers on leaf surfaces [41]; changing the angle of leaflets to avoid high levels of radiation [42]; the production of phenolic compounds [43], and altering photosynthetic processes to ease the absorbed energy in reducing oxygen to carbon dioxide [44].

Since severe water limitation is the key concern for natural vegetation development in desert environments, different desert plant species adopt various strategies to resist and survive water stress. Among these strategies drought escape, avoidance and/or building resistance to tolerate and adapt to drought stress. One universal strategy followed by desert annual plants is to keep their seeds dormant in the soil and to germinate when water is available [45]. In contrast, perennial plants adopt morphological adaptations by developing roots deeper into the soil to search for moisture. Other desert perennial plants may adopt a drought-deciduous strategy, becoming dormant or having partially dieback in response to drought stress.

Nonetheless, there is substantial evidence to indicate that AMF support host plants against various abiotic stressors such as drought [46,47] and other environmental stresses, i.e., heat, salinity, metals and extreme temperatures [48,49]. Li et al. [50] suggested that soil microbes such as AMF often regulate plant growth response to drought stress and alleviate drought damage via increasing photosynthesis, and antioxidant enzyme activities and reducing levels of malondialdehyde (MDA) in drought conditions. Colonization of these AMF can also stimulate various physiological responses to drought stress including stomatal conductance sensitivity, CO_2 assimilation, and decreases in relative water content; further, leaf water potential is likely to be improved by AMF inoculation [51,52]. A schematic representation of potential mechanisms mediated by AMF and dark septate endophytes (DSEs) to regulate drought stress tolerance and improve desert plants' performance and adaptation is shown in Figure 1.

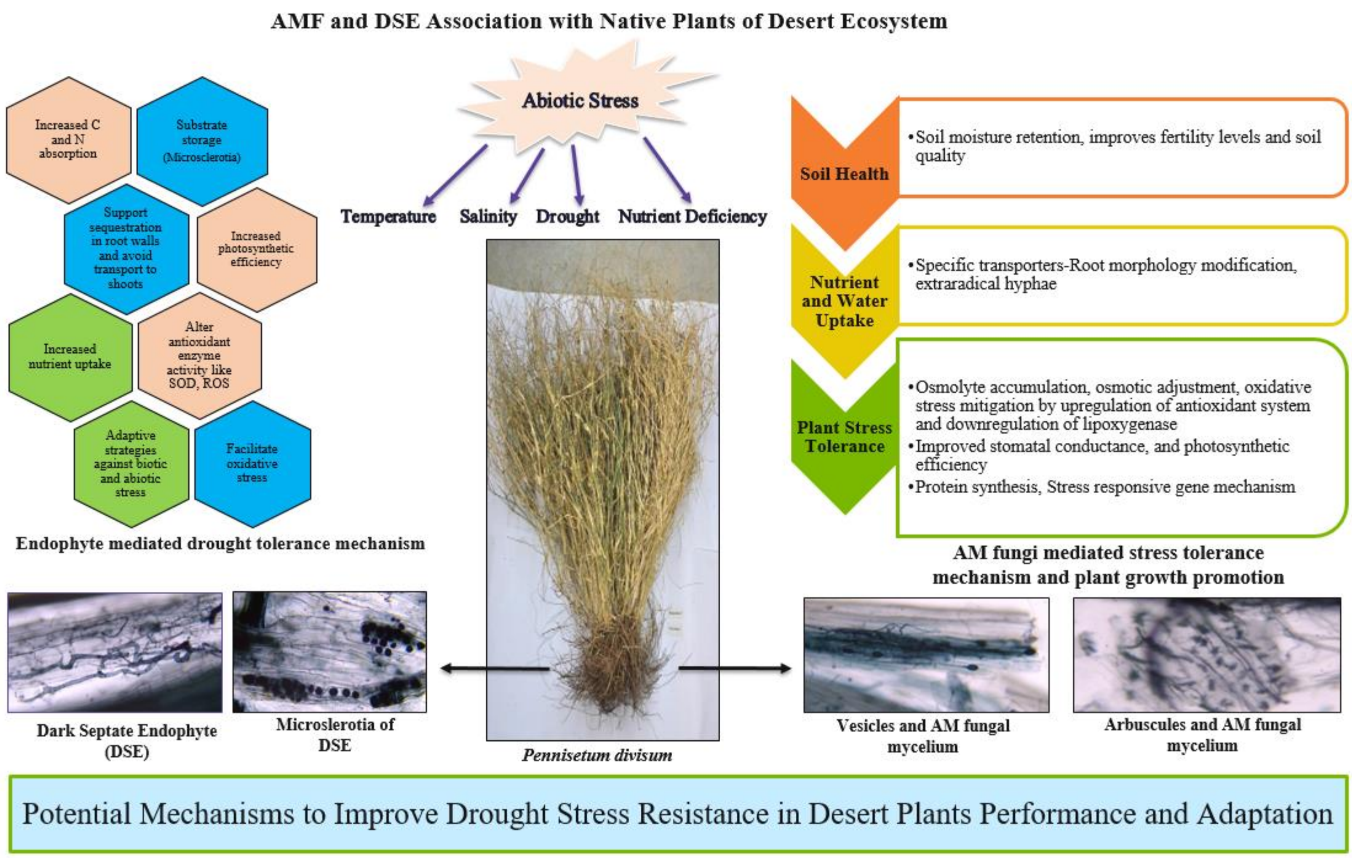

Figure 1. A schematic representation showing potential mechanisms mediated by AMF and DSEs to adopt and regulate drought stress tolerance and improve plant growth and performance of plants. Source images: Quoreshi et al. [53]. Other sources: Byregowda et al. [25], Cheng et al. [11] and Begum et al. [37].

3. Drought Stress Arbitrated Influences in Plants Stimulated by AMF

In desert ecosystems, drought intensely reduces plant survival and productivity; consequently, desert plants develop different strategies to combat drought stress tolerance. Plant-AMF's symbiotic relationships are known to enhance the adaptability of plants in stressed environments and improve tolerance of their host plants to drought stress [54]. Arbuscular mycorrhiza fungi are the most common obligate symbiotic fungi involved in host plants' interactions to complete their life cycles. The fungi colonize the plant root system and receive carbon from the host plant, while nutrients are provided from fungi to host plants in symbiosis, modulating plant growth and development [55,56]. Research evidence suggests that AMF symbiosis safeguards the host plants against drought stress by mediating several mechanisms such as morphological, biochemical and physiological attributes [36]. Furthermore, AMF symbiotic association permits plants to grow more effectively under abiotic and biotic stress environments [57]. AMF species are naturally occurring in most ecological ecosystems and are widespread across various environments [56]. AMF species usually developing a symbiotic association with host plants utilizing three methods from the soil: AMF spores, external mycelium and infected root segments [58]. AMF species are believed to be intuitive growth regulators of a vast majority of terrestrial ecosystems. They provide a range of important biological processes by improving plant nutrition, stress resistance and tolerance, soil structure and fertility [56]. Mineral nutritional features in AMF symbiosis have been studied comprehensively and revealed that AMF are efficient in considerably enhancing host plants' nutrient acquisition, particularly in nutrient deficient environments, and possess a symbiotic Pi uptake pathway [59–61]. Besides Pi uptake, nitrogen (N) and sulfur (S) can also be transported to host plant through AMF symbiosis via sulfur and NH_4 transporters [62–64]. In recent studies, the contribution of AMF symbiosis to increased micronutrient concentrations in plants has been reported [65,66].

The mechanisms that have been reported and essentially contribute to increased drought and salinity stress tolerance in plants are complex and further complicated with multiple responses with AMF (Table 1) and DSEs (Table 2). Tables 1 and 2 summarize the observed responses and their potential mechanisms involved in response to various abiotic stresses. Numerous researchers have reported improvements in soil health and quality influenced by AMF [67,68]. AMF colonization and extensive proliferation of fungal hyphae into soils enhances soil aggregation and stability as well as water holding ability, hence improving drought tolerance [69]. Many studies have shown that AMF association with host plants can regulate morphological adaptations to ameliorate drought stress tolerance of the host plants [70]. In addition, Rouphael et al. [71] reported that AMF assist plant nutrition by enhancing and relocating mineral nutrients beyond the depletion zones of plant rhizospheres. AMF colonization with host plants induces root morphological changes, improves root growth, root surface area, average diameter, and lateral roots, root-shoot ratio, and hydraulic characteristics. Mycorrhizal extension hyphae help penetrate soil pores to absorb water, resulting in roots' improved capacity to acquire water and nutrients from a distance [72,73]; this enhances drought resistance by influencing physiological and biochemical mechanisms [74]. Morphological studies further revealed changes in plant vascular architecture, starch storage and photosynthesis in the palisade mesophyll of AMF associated plants [70]. Furthermore, AMF interfere with the phytohormone profile of host plants, causing changes in phytohormones and thus bio-regulating plant performance and promoting tolerance to environmental stresses. AMF symbiosis is found to be highly correlated with enhanced plant tolerance and resistance to abiotic stresses such as drought and salinity in arid environments [75]. AMF appear to influence host plants in improving the tolerance processes and inhibit the reduction of primary metabolic pathways [49]. It is likely that AMF can enhance soil and plant development under stressful environments caused by abiotic factors [76,77]. AMF are the most effective soil microorganisms, helping in soil aggregation and stabilizing soil structure through growing fungal hyphae into the soil, thus producing glomalin [78–80]. Drought stress considerably affects photosynthesis by reducing chlorophyll content and raising the production of ROS. AMF symbiosis can improve chlorophyll synthesis and stimulate photosynthesis, as well as successive assimilate production, by decreasing the ROS formation [81]. In addition, increased osmotic adjustment is believed to be an essential component of drought tolerance mechanisms in arid desert plants. Maintaining osmolyte accumulation is an essential strategy adopted by plants to combat the negative influences of drought stress [36]. AMF colonization triggers the increased accumulation of several osmolytes and improves drought tolerance [82,83]. Alterations in ROS and antioxidant-protected systems mediated by mycorrhizal association are evaluated in detail by Wu et al. [84]. Apparently, AMF-associated plants possessed greater antioxidant enzyme activities and nonenzymatic antioxidant concentrations which probably help to protect against oxidative damage, consequently enhancing drought tolerance [70,85]. Furthermore, AMF increase the synthesis of phenolic compounds, which reinforces the antioxidant defense mechanisms and ultimately develops resistance and tolerance against drought stress [37,86]. Furthermore, AMF colonization may regulate gene expression to combat drought stress tolerance. Two groups of stress-related genes are known to respond different stresses. The first group act in stress tolerance, including late embryogenesis abundant (LEA) proteins, osmotin, mRNA-binding proteins, enzymes for osmolyte biosynthesis, and ROS–scavenging enzymes [87]. The second group includes protein factors involved in the regulation of signal transduction and gene expression that perhaps play a role in different stress responses [88]. Other published reports suggest that AMF symbiosis triggers different molecular mechanisms such as gene expression, aquaporins (AQP), membrane transporters, sugar and ion transporters to control the effects of drought stress [89]. AMF-attributed enrichment in expression of AQP which also improves nutrient and water uptake and helps mitigate drought stress effects.

Hence, fungal species are crucial constituents in supporting and maintaining plant functions and performance in a wide range of ecological systems. Zhao et al. [90] report that AMF species play a significant role in desert ecosystems by maintaining plant biodiversity, richness and development. AMF impact community structure by altering plant adaptation to restricted resources. However, it is likely that various adaptive mechanisms of an abundant diversity of shrubs and perennial grasses relate to AMF in the regulation of plant responses to stresses. Therefore, the association between AMF and plant adaptation may influence the potential mechanisms underlying plants' community dynamics in the resource-limited desert ecosystem [91], leading to enhancing plant survival and improving the level of resistance and tolerance under extreme desert ecosystem conditions.

Table 1. Various abiotic stresses, observed responses and potential mechanisms involved in relation to AMF association with the host plant species.

Stress	Observed Responses/Mechanisms with AMF Association	References
Drought	Increased sodium, potassium, catalase (CAT), peroxidases (POD), ascorbate peroxidase (APX), superoxide dismutase (SOD) by *Glomus intraradices* on *Calotropis procera* Ait. This improves the nutritive element concentration and antioxidant enzyme activity to decrease oxidative damage.	[92]
Drought	Improved leaf relative water content, photosynthetic energy use efficiency, specific leaf area in *Cynophalla flexuosa* L. This increases tolerance to recurring drought stress leading to high photosynthetic area.	[93]
Drought	Increased essential oil content, and oil yield and decreased malondialdehyde (MDA), hydrogen peroxide, catalase (CAT), ascorbate peroxidase (APX), superoxide dismutase (SOD), glutathione peroxidases (GPX) and improved nutrient concentration, plant biomass and essential oil content and glomalin related soil proteins (GRSP) in *Pelargonium graveolense* (L.) Herit.	[86]
Drought	Improved nitrogen metabolism by positively regulating nitrate and nitrite reductase activity, increased antioxidant enzyme activity, ascorbic acid contents, and reduction in glutathione level. This resulted in significant amelioration of oxidative damage to plant membranes by restricting the excess generation of reactive oxygen species (ROS). Greater content of proline, glucose, and total soluble protein such as hydrogen peroxide. Boosted phosphorous metabolism by increasing alkaline and acid phosphatase enzyme activity in *Ephedra foliata*.	[94]
Drought	Improvement in antioxidant system reducing hydrogen peroxide accumulation and lipid peroxidation. Increased Indole Acetic Acid (IAA) promoting growth. Increases root morphology (length, surface area and volume) in *Panicum turgidum*.	[95]

Table 1. *Cont.*

Stress	Observed Responses/Mechanisms with AMF Association	References
Drought	Increased levels of phenols, the activities of both peroxidase (POD) and polyphenolxydases after AMF treatment and increased leaf number and leaf area index in *Phoenix dactylifera*.	[96]
Drought	Increased contents of glomalin-related soil protein (GRSP) and increased soil structure and phosphorus content in *Medicago sativa*.	[97]
Drought	Increased catalase (CAT), superoxide dismutase (SOD), photosynthetic rate, stomatal conductance and intrinsic water use efficiency in *Leymus chinesis* and increased catalase activity and photosynthetic rate in *Hemarthria altissima*.	[50]
Drought	Increased c DNAs, named HaPIP1 water channel proteins, in *Helianthemum almeriense*.	[98]
Drought	Increased drought impact and increased turgor potential and mineral uptake of potassium, nitrogen, zinc, and iron in *Olea europaea*.	[73]
Drought	Increased catalase (CAT), ascorbate peroxidase (APX), increased endogenous level of cis-12-oxophytodienoc acid, jasmonic acid and 12-OH-JA; regulates stomatal conductance, lipid peroxidation, hydrogen peroxide in shoot and root of *Digitaria eriantha*.	[99]
Salinity	Increased shoot and root dry mass, stomatal conductance, soluble sugars, free alpha amino acid, sodium and potassium uptake in *Aeluropus littoralis*.	[100]
Salinity	Improved root and shoot biomass and phosphorus, zinc, and copper content in *Acacia nilotica*.	[101]
Salinity	Increased seedling weight, water content and phosphorus and nitrogen in *Leymus chinensis*.	[102]
Drought	Increased superoxide dismutase (SOD) and total peroxidase (POX) activity in *Phillyrea angustifolia*.	[103]
Drought	Increased plant growth, phosphorus uptake in *Salsola laricina*.	[104]

Table 2. Various abiotic stresses, observed responses and potential mechanisms involved in relation to Dark Septate Endophytes (DSE) association with the host plant species.

Stress	Observed Responses/Mechanism in Relation to Dark Septate Endophytes	References
Drought	Improved root dry weight, NPQ (non-photochemical quenching values, qP (photochemical quenching values), increased secondary metabolites such as polyphenols, flavonoids, anthocyanins and enhanced enzymatic activities related to secondary metabolism in sorghum seedlings.	[105]

Table 2. *Cont.*

Stress	Observed Responses/Mechanism in Relation to Dark Septate Endophytes	References
Drought	Improved plant growth, antioxidant enzyme activity and root development in *Artemisia ordosica*.	[106]
Drought	Increased root biomass. Increase in potassium, calcium content in root of *Ammopiptanthus mongolicus* by some DSE species.	[107]
Drought	Improved root biomass, total biomass, nutrient concentration and antioxidant enzyme activities in *Hedysarum scoparium* by some DSE strains	[50]
Drought	Increase in proline, chlorophyll content, antioxidant enzymatic activities and growth parameters in *Seidlitzia rosmarinus*, *Zygophyllum eichwaldii* and *Haloxylon ammodendron*.	[25]
Drought	Increased plant growth, photosynthetic parameters and P uptake in *Lolium perenne*.	[108]
Drought	Increase in plant height, stem girth, leaf characteristics, biomass and proline accumulation in *Chrysanthemum indicum*.	[109]
Drought	Increased accumulation of soluble sugars, decrease in MDA (malondialdehyde) and degradation of chlorophyll in leaves in *Alhagi sparsifolia*.	[110]

4. Role of Arbuscular Mycorrhizal Fungi in the Desert Ecosystem

Desert soil is mostly sandy soil (90–95%) found in arid and dry regions. It has a low content of nitrogen and organic matter with extremely high calcium carbonate and phosphates, making it infertile. Fine, dry sandy soils with little or no structure are features of desert ecosystems; they are commonly vulnerable to frequent wind erosion. Al-Whaibi [111] indicated that AMF form symbiotic association within desert plant species and their activities are significant to these plants. It has been demonstrated in many studies that mycorrhizal association enhances plant survival, growth, biomass, and mineral and water uptake under normal and drought conditions.

Among the biological and biophysical mechanisms, AMF appear to enhance soil aggregate stability [112] and maintain higher drought tolerance in an arid environment [113]. AMF symbiosis mechanisms are related to different adaptation mechanisms in plants including morphological modifications to drought stress that allow their tolerance to extreme desert environments [111,114,115]. The presence of AMF in root zones of multiple native desert plant species of Saudi Arabia facilitates nutrient uptake and increases the stabilization of and sand dunes. AMF enhance the stability of soil aggregates and lead to general improvement of soil's physical and chemical properties, moreover the lowest AMF spore quantities and species diversity were found in the root zones of plant species growing in the middle of the sand dune area [116]. Desert AMF community structure and diversity varies pursuant to the habitat complexity and ecological settings. Low diversity of specific AMF community composition tends to be related to extreme abiotic environments and the dispersal restriction in the desert ecosystems [117]. Plant diversity, ecosystem variability and productivity are highly influenced by AMF composition [118]. Plant growth response and reliance of host plants differs in relation to colonizing AMF specific species, leading to changes in their competitive abilities that affect plant community structure [119]. The abundance of AMF spores in rhizosphere of one plant species varies considerably from other species, irrespective of whether they are from a similar habitat [120]. This suggests that the host plant species determines the allocation of AMF within the ecological ecosystem and habitat structure. However, Klironomos et al. [121] reported that inconsistencies between AMF spore estimates tend to relate to each AMF species and its host, regardless of the ecosystem homogeneity. Furthermore, AMF diversity arrangements and distribution are primarily associated with the dominant plant species within the specific habitat, and season. Annual plants maintain a large amount of a fine mycorrhizal root network, whereas perennial plants have a much deeper root system supporting a relatively stable mycelial network deep in the soil profile [105]; this indicates that soil and root nutrients are the main influencing factors on determining AMF diversity and distribution.

5. Dark Septate Endophytes (DSEs) and Drought Stress Tolerance in Desert Plants

Plant tissue harbors a wide diversity of root endophytic fungi which are mainly beneficial symbionts, comprising DSEs [122]. These DSEs inhabit plant root tissues in different ecosystems, particularly in extreme desert ecosystems; they often form symbiotic associations with the epidermis and the cortex of plant roots in arid and semi-arid environments [106,123–126]. These sterile ascomycetous DSEs are categorized by melanized dark septate hyphae with microsclerotia that colonize the roots of numerous plant species, both intracellularly and extracellularly [127–129]. Arbuscular mycorrhizal fungi, the most important root endophytes, are extensively studied and well documented for their role in promoting resistance to drought stress, nutrient uptake and improvement in plant development. However, DSEs, which have recently gained more attention, may have very similar roles to AMF in improving stress tolerance responses, particularly in extreme arid desert environments. They have an extensive ecological dissemination and are often found colonized in a range of arid and semi-arid region plants [107,130]. Alleviating drought stress tolerance in plants by exploiting endophytes could be an effective approach to recuperate the successful restoration of water deficit desert soils [131,132]. However, our current knowledge on the characterization and function of DSEs, and their ecological significance in arid stressful environments, is inadequate. Several research results indicate that DSEs can stimulate drought resistance in plants in water-scarce conditions and increase plant growth by improving water, nutrient and carbon (C) uptake, enhanced activities of antioxidant enzymes, and facilitating oxidation stress [133–136]. DSEs association with plants can significantly demote the oxidative cellular damage in stressed plants by strengthening their antioxidative mechanisms [137]. They are also capable of developing adaptation strategies against heavy metals, supporting sequestration in root walls and avoiding transport to shoots [137]. Recent studies revealed that DSEs can defend a host plant by reducing heavy metal absorption in plant tissues and/or by sequestering heavy metals in root walls in insoluble form, consequently avoiding further translocation to shoots [51,138].

In a recent study, we observed the roots of native desert plants from the Kuwait desert that were colonized by distinctive dark septate hyphae with a dark brown color microsclerotia structure along with arbuscular mycorrhizal hyphae, vesicle and arbuscules (Figure 2, [53]). The presence of such DSEs' structures found in our study (Quoreshi et al., 2018) [53] of native desert plant species suggests that the DSEs might be crucial constituents of the roots in desert habitats, linked to adaptive drought and other environmental stress resistance mechanisms similar to AMF endophytes. They are found in the root cells that develop a typical structure such as septate hyphae, melanized cell walls, and microsclerotia in clusters. The microsclerotia may act as resting spores, like other fungi, and serve as storage for nutrient accumulation [139]. It is reported that DSEs have helpful ecological roles in plant survival, growth, nutrient and water uptake [140,141], offering enhanced plant resistance to a variety of environmental stresses [133,142,143].

Rodriguez et al. [48] suggest that many plants accept colonization with DSEs to enhance their survival and growth in severe environmental conditions that are triggered by drought, salinity and metal contamination in soils. This has also been reported to increased nutrient uptake for host plants. Such increased nutrient absorption by plants, when colonized by DSEs, may be related to the enhanced C and N absorption and elevated activities of antioxidant enzymes [50]. Many researchers reported that increased nutrient absorption by various plants is observed when inoculated with DSE isolates [50,107,136].

Several reports indicate that DSEs are extensively found in plants in arid and semiarid environments and can improve the tolerance of host plants to drought stress [106,126,144–146]. It is suggested that DSE fungi in water-limited environments normally show positive responses to host plants in terms of drought tolerance and resistance [106,126]. The mechanism is perhaps related to significantly increased superoxide dismutase (SOD) activity under drought stress to remove ROS and cope with oxidative damage. Therefore, DSEs may perform a vital function in plant survival and growth under water deficit conditions. However, the complete mechanisms mediated by DSEs which influence the tolerance of environmental stresses are not fully elucidated and require further research.

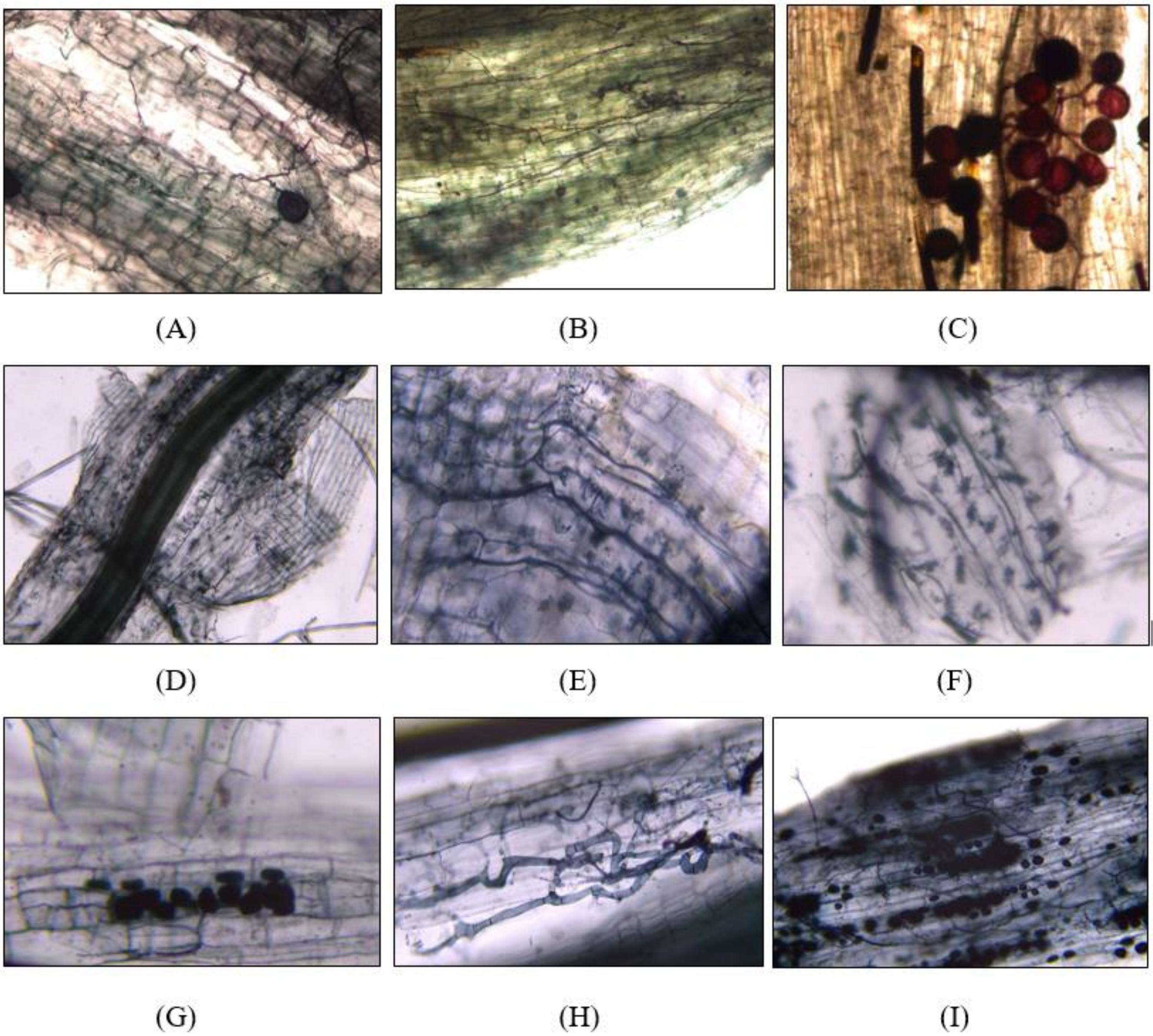

Figure 2. Pictures showing different structures of AMF and DSE colonization observed in root system of native desert plants of Kuwait. Vesicles observed in summer root samples of *Acacia pachyceras* (**A**), *Panicum turgidum* (**B**) and *Pennisetum divisum* (**C**). AMF arbuscules in winter root samples of *Cyperus conglomeratus* (**D**), *Pennisetum divisum* (**E**), *Stipa capensis* (**F**). Microslerotia clusters of DSE in *Rhanterium epaposum* (**G**), DSE hyphae in *Plantago boisseri* (**H**), Microsclerotia/resting spores of DSE in *Stipa capensis* (**I**). All these structures were observed under compound microscope. Source images: Quoreshi et al. [53].

6. Conclusions and Future Prospective

Arid desert ecosystems harbor varied plants and soil microorganisms including AMF which can enhance soil health conditions, improve plant stresses, and support plant growth and performance. This review highlighted the important functions of AMF in improving plant growth responses and adaptation under various abiotic stresses. It has been reported that AMF association with host plants boosts the tolerance of plants in a water limited environment; however, the drought tolerance and resistance mechanism is rather complex, and it may be involved in multiple-level controlled systems. In a desert ecosystem, natural habitats are exposed to wide range of environmental stresses with drought being the main limiting factor. Several research reports have identified the various biological roles of AMF in desert ecosystems, along with their association with native desert plants and their enhanced resistance to tolerate drought stress by complex physiological adjustments. In most natural environments, as well as the desert ecosystem, AMF species are thought to have a selective advantage for individual plants of the same species habitats. Therefore, understanding AMF symbiotic relationships with various native desert plants and their responses to environmental stresses, particularly drought stress, can be a vital contribution not only in determining plant community structure, but also in assisting restoration and re-vegetation schemes, as well as the reestablishment of degraded habitats.

Despite recent advances in knowledge on the function of mycorrhizal symbiosis in plants, the functions of AMF associated with native desert plants—assisting in their resistance to and tolerance of drought stress—are not entirely established: drought is considered a natural incident which occurs frequently and more intensely. There are numerous unanswered questions and the roles of nutrient uptake channels and signaling as well as ion transport systems, associated with desert plants in drought stressed environments, need to be investigated. Likewise, the role of AMF in seed germination mechanisms associated with drought stress conditions is unexplored. Furthermore, the main focus of future research should be dedicated to advanced molecular research on the identification of gene expression and how the gene products regulate AMF-mediating growth and nutrient, water uptake, and control them under stressful environments. More attention is needed to understand DSEs and their function in desert ecosystems as well as how plants combat drought stress and influence plant nutrition and productivity when colonized with DSEs. Future research should exploit the link between the native desert plants' adaptation to various environmental stresses combining AMF and DSEs symbiotic relationship in the desert ecosystems. Such research would increase our current knowledge of the role of endophytes in combating drought stresses. Nevertheless, AMF biotechnology should be explored as a potential bio-fertilizer enhancement for the restoration of disturbed desert habitats for successful and sustainable rehabilitation efforts.

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