ROLE OF ARBUSCULAR MYCORRHIZAL FUNGI IN AMELIORATING DROUGHT STRESS TO PLANTS

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Introduction

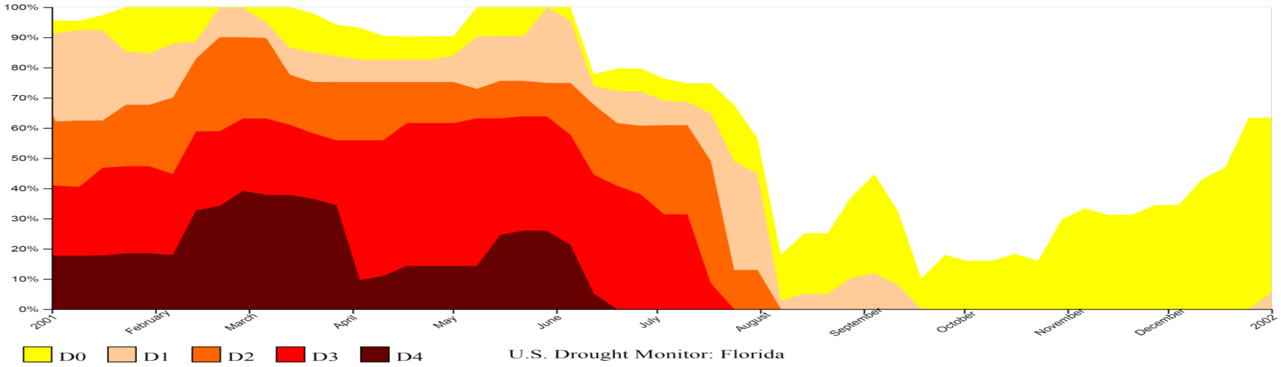
In agriculture, water is one of the most limiting natural factors for plant growth. The absence of irrigation or rainfall for a long time leads to soil moisture depletion and causes agricultural drought. Agricultural drought is the moisture deficit condition which results when the available water in the soil is not sufficient for normal plant growth. When soil moisture depletes below a critical value, water stress in plants develops as the absorption of water by the plant roots is less than the water loss from the plant. Under drought, the water is scarce for proper plant growth. When high temperature accompanies the drought period, evapotranspiration losses aggravate the water stress in plants (Farooq et al., 2012; Knox, 1988).

Water stress decreases the transpiration rate, photosynthetic rate, and other normal plant processes. Thus water stress negatively impacts crop growth and productivity (Farooq, et al., 2012; Ghobadi et al., 2013; Stagnari et al., 2016). In general, a long period without rainfall is considered a drought; however, because of the low water retention properties of sandy soils of Florida, crops experience water stress only after a few days without rain (Mylavarapu et al., 2016; Trenholms, 2000). Florida ranks high in terms of value and area of crop production among other states of the USA; however, this crop production is affected by periodic droughts (Florida Reports; National reports). In Florida since 2000, the most severe drought had occurred in February 2001 when average rainfall was 0.74 inches (FCC) and 39.14% of the land was affected by D4 category drought (Table 1, Figure 1). The longest drought lasted for 124 weeks from April 2006 to August 2008 (Florida|drought.gov).

Table 1 Categorization of drought impacts in FL by National Drought Mitigation Center

Category	Intensity	Characteristics
D0	Abnormally Dry	Small brush fires increases
		Increased landscape irrigation is needed; voluntary water conservation is requested
D1	Moderate drought	Burns bans are possible
		Trees and bushes begin browning
		Water supply decreases
D2	Severe Drought	Pasture is drying; hay yields are low
		Large increase of wildfire abundance; fire danger is elevated; burn bans are implemented
		Air and water quality are poor; water salinity is high; river and lake levels are low
D3	Extreme Drought	Fire danger is extreme; fire restrictions increase
		Saltwater species replace freshwater species; sea intrusion
		Nesting bird populations grow with increased nesting area; mosquitoes increase
D4	Exceptional Dry	Ground water declines rapidly
		Large municipalities use alternative water sources, borrow water

Figure 1: FL drought period of 2001 (Ref: Florida|drought.gov)



Since 2010, the average annual precipitation in Florida ranges from 48 to 61 inches, and most of this precipitation occurs in the rainy season from June to September (FCC). Moreover, increasing FL population will further increase water demand (Dijl et al., 2015; USCB).

EFFECT OF WATER DEFICIT STRESS ON PLANT(S)

Drought stress negatively affects crop yield and yield quality by hindering plant processes as it causes physiological injuries and metabolic changes. During drought, less or no available water in the root zone causes less water uptake by the plant roots, leading to tissue dehydration and osmotic stress. Tissue water deficit stress triggers many changes in gene expression. As a result, many metabolites accumulate in the cell, increasing its water potential and inhibiting water uptake by roots. Absicic acid (ABA) hormone is one of the principal regulators of signaling pathways for gene expression and metabolite production for physiological processes, and it accumulates in response to osmotic stress (Bray, 2004). ABA inhibit root growth and triggers ethylene production that causes plant abscission and senescence (Iqbal et al., 2017).

Water stress impairs the electron transport system of cell organelles, and there is an overflow of electrons from the mitochondria, chloroplast, plasma membrane, and peroxisomes into the cell (Bhattacharjee, 2019). This imbalance in electron flow leads to the excessive production of reactive oxygen species (ROS) such as free radical superoxide anion ($O2^{\cdot -}$), singlet oxygen ($^1O_2$), hydrogen peroxide (H_2O_2), hydroxyl radical ($OH\cdot$), and malondialdehyde (MDA). Accumulation of ROS causes oxidative stress and disrupts normal metabolism by causing oxidative damage such as oxidation of proteins, peroxidation of lipids, and damage to nucleic acids that could lead to cell death (Kusuvaran et al., 2016; Sharma et al., 2012).

Plants close their stomata in response to water stress to prevent water loss via transpiration. Stomata closure reduces the $CO2$ influx and adversely impact plants' photosynthetic capacity thus plant growth and productivity (Osakabe et al., 2014). Furthermore, decreased soil moisture under drought conditions reduces the nutrient movement in the soil matrix and thus uptake by the roots. In addition, water stress hinders the transport of mineral nutrients from the root surface to shoots due to decreased transpiration rate, altered membrane permeability, and the dysfunction of membrane-active transporters (da Silva et al., 2011).

Nonetheless, the extent of adverse effects of drought on plant growth and yield depends upon plant genetic potential, stage of the plant growth, and the severity and duration of drought (Aroca and Ruiz-Lozano, 2012; Stagnari et al., 2016). Moreover, experiments have shown the ability of plant-associated microbes such as arbuscular mycorrhizal fungi (AMF) on the water allocation efficiency of the plant from the soil under water deficit conditions. In addition to this, AMF enhances plant resistance to drought stress by influencing various physiological processes (Zou et al., 2018; Zhang et al., 2018a). In this article, we will discuss the potential of AMF in increasing agricultural productivity under drought conditions by discussing various protective mechanisms adopted by AMF-plant symbiosis.

ARBUSCULAR MYCORRHIZAL FUNGI (AMF)

The symbiosis between AMF (phylum Glomeromycota) and the roots of the terrestrial plants dates back 450 million years ago and is universally recognized as one of the most important mutualistic symbiosis on the Earth. Interestingly, more than 80% of plant species can form a symbiotic relationship with AMF.n However, the AMF colonization density is dependent on AMF taxa, plant preference for AMF species, and the ecosystems where the symbionts have evolved (Klironomos, 2003; Smith et al., 2009; Smith and David 2010).

The symbiotic association between fungi and the plant roots is called mycorrhizae. The AMF is endomycorrhiza as its hyphae which are fine, tubular filaments penetrate the cell walls and enclose themselves in the cell membrane of cortical cells of the plant roots. A well-established AMF and plant symbiosis include two colonization phases: the internal phase and the external phase. In the internal phase, fungi form a mass of hyphae called mycelium and colonize the root cortex cells. Mycelium establishes oval and branched structures called vesicles and arbuscule, respectively. Vesicles are storage organs of lipids food for AMF. Highly branched tree-like-shaped arbuscule is the site of nutrient exchange between fungi and the host. In the external phase, the fungi develop highly branched extraradical hyphae (ERH) in the soil. The hyphae of the fungal structure are very fine (diameter ~ 2-5 µm) and lengthier than plant roots, thus penetrating deeper into the soil micropores where plant roots, because of their relatively larger diameter, cannot (Smith and David, 2010).

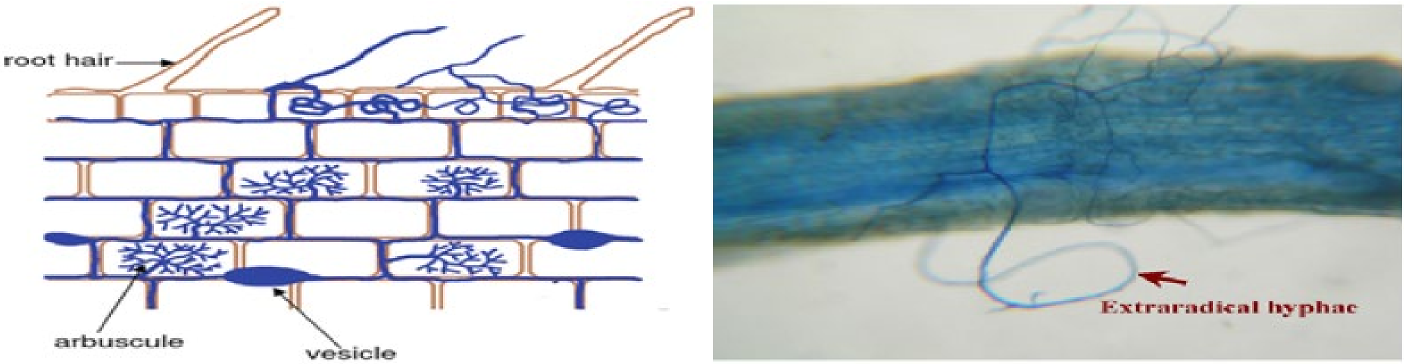


Figure 2: Vesicle, Arbuscule, and Extraradical hyphae of AMF. Ref: Wu et al., 2013; Priyadharsini et al., 2015

AMF depend on host plants for food, such as carbohydrates and lipids (Parihar et al., 2020), throughout their life. In return, AMF enhances the ability of the host to absorb water and nutrients from the soil by extending the root absorbing area and increasing plants' tolerance to adverse conditions (2020, Diagne). Many studies have testified that AMF improves plant tolerance to drought stress and increases plant growth, yield, and yield quality despite the negative impact of water stress on AMF colonization (Meddich et al., 2015; Ouledali et al., 2018). Nonetheless, AMF demonstrates functional diversity because of the plant mycorrhizal dependence, plant preference for individual AMF, the environment, and functional specialization among AMF (Klironomos, 2003; Koomen et al., 1987; Thirkell et al., 2020).

AMF MEDIATED WATER STRESS TOLERANCE IN PLANTS

AMF contributes to crop productivity and ecosystem sustainability through its beneficial effects on soil health and plant performance. This symbiosis helps plants to cope with drought stress by improving soil health and altering plants' physiological, morphological, and biochemical characteristics and or physiochemical properties of the rhizosphere.

Table 2: Studies that showed increased plant biomass and yield of citrus crop under water deficit conditions in AMF-Plant symbiosis.

Increase Plant Biomass or Yield		
PLANT SPECIES	AMF SPECIES	REFEENCE
Tangerine (*Citrus tangerine*)	*Glomus versiforme*	Wu and Xia, 2006a
Trifoliate orange (*Poncirus trifoliate* (L) Raf.)	*Glomus mossae*	Wu et al., 2006b
Trifoliate orange (*Poncirus trifoliate*(L.) Raf.)	*Glomus mossae/ Glomus versiforme/Glomus diaphanum*	Wu et al., 2008
Trifoliate orange (*Poncirus trifoliate*(L.) Raf.)	*Glomus diaphanum/Glomus mosseae/Glomus versiforme*	Wu et al., 20011b
Tangerine (*Citrus tangerine* Tanaka)	*Glomus versiforme*	Wu et al., 2006c

AMF-mediated changes in Soil Quality

Good soil structure, aggregate stability, water holding capacity, and soil microbial diversity are indicators of good soil quality (Maikhuri and Rao, 2012). Arbuscular mycorrhization plays a vital role in improving soil quality. The extraradical hyphae (ERH) of the AMF bind and hold the soil particles and compresses the soil by exercising physical force, reorienting clay particles, and maintaining air-filed soi porosity. The ERH itself and the exudates from the ERH add to soil biomass. The glomalin and glomalin-related soil proteins are major exudates produced by AMF. Glomalin is a hydrophobic, heat and water-stable glycoprotein. The hydrophilic fungal wall can adhere to the hydrophobic soil surface after coating by hydrophobic GRPS (Rilling and Mummey, 2006). It acts as a glue to bind soil particles together, thus playing a role in enhancing soil aggregate stability (Rilling and Mummey, 2006; Wright and Upadhyaya, 1996; Cornejo et al*.,* 2008a). Improved soil structure and aggregate stability protect soil organic matter by decreasing soil loss due to wind or water erosion (Mardhiah et al., 2016). Better soil structure and increased organic matter accumulation lead to increased soil water holding capacity (Auge, 2001), nutrient storage (Rilling and Daniel, 2006), and facilitate root penetration. AMF symbiosis also shifts rhizospheric microbial structure and diversity through AMF mediated root exudates (Vázquez et al., 2000).

There is a direct correlation between soil quality/health and plant growth and productivity as soil plays vital functions in plant growth. AMF improves soil quality by increasing water-stable soil aggregates, adding biomass, and reorienting the soil aggregates. Therefore, AMF indicates the potential to improve plant health and productivity via improving soil quality (Maikhuri and Rao, 2012).

AMF Mediated Improved Nutrient and Water Status of Plants

The AMF symbiosis enhances plant water and nutrient status under water deficit conditions by increasing water and nutrient uptake (Barros et al., 2018). The AMF plants have greater uptake of water and nutrients by overcoming the water and nutrient depletion zone in the rhizosphere because of increased surface area by ERH (Wu et al., 2013). Furthermore, mycorrhizae may change the hyphal diameter based on the size of the soil pores, allowing them to access pores that are inaccessible to plants' roots due to their considerably larger diameter (Drew et al., 2003). In addition to ERH, AM colonization increases root hair length and density by forming and elongating lateral roots, thus increasing host root surface area and volume. As a result, the host's increased soil exploration enhances contact with water and nutrients available in the soil (Wu et al., 2013; Zou et al., 2017).

Interestingly, organic and inorganic nutrient forms are absorbed and transported from soil to the plant through specific transporters in this symbiosis (Kikuci et al., 2016; Cappellazzo et al., 2008). The uptake of nutrients, especially less mobile in the soil as phosphorus, potassium, and magnesium benefit from AMF symbiosis. In addition to these, AMF also enhances plant nitrogen status, the highly mobile nutrient in soil (Garg and Bhandari, 2016). Furthermore, the ERH turnover acts as a source of minerals and increases the availability of plant minerals (Riling et al., 2001). However, AMF species–Plant (inter/intra-species)–environment combinations give a wide range of responses to nutrient uptake, including positive, negative, and no effect (El Amerany et al., 2020; Munier-Lamy et al., 2007).

AM symbiosis improves plants' water use efficiency which is the measure of the ratio of the net photosynthetic rate to transpiration rate of leaves (Satander et al., 2017). Additionally, upregulation of host and fungal hyphae plasma membrane intrinsic proteins, aquaporin (AQP), gene expressions boosts hyphal and root water absorption rates (Quiroga et al., 2017; Li et al., 2013). These aquaporin proteins regulate the water flow by acting as a water channel and are also important in the osmoregulation of root cells (Bárzana et al., 2014; Maurel et al., 2008; Quiroga et al., 2017). Above all, compared to adequate water situations, hyphal and root water absorption is faster under water deficit conditions in AM plants by activating less resistant pathways for water radial flow across the cortex (Zhang et al., 2018aa; Quiroga et al., 2017; Li et al., 2013). The increased hydraulic conductivity might also be due to enhanced water status because of the symbiosis that triggers AMF action to increase its hydraulic conductivity because plants decrease their hydraulic conductivity under water deficit conditions to reduce water loss through transpiration. In addition to water, AQP can also transport nutrients and low molecular weight molecules such as ammonium, CO2, glycerol (Kruse et al., 2006). However, AM symbiosis has diverse response patterns of AQP genes depending upon all the variables of the symbiosis. Therefore the symbiosis has been found to up-regulate, down-regulate, or have no change in host AQP gene expression (Quiroga et al., 2017; Zou et al., 2019). Another factor for improved water status of AM plants is reduced hyphal water redistribution, where water flows out of the hyphae back to the rhizosphere. The hydrophobic sheath of glomalin on the AM hyphae protects nutrients and water loss while transporting from the hyphal tip to the plant and vice versa (Zou et al., 2018; Allen, 2007; Driver et al., 2005). Increased water status of AMF plants also aids plant productivity by modulating molecular responses under water-scarce conditions, such as oxidative damage mitigation.

Table 3: Increased Water Use Efficiency (WUE) and Nutrient Uptake by Citrus plants in symbiosis with AMF under water deficit conditions.

INCREASED WATER USE EFFICIENCY		
PLANT SPECIES	AMF SPECIES	REFERENCE
Tangerine (*Citrus tangerine*)	*Glomus versiforme*	Wu and Xia, 2006a
Trifoliate orange (*Poncirus trifoliate* (L) Raf.)	*Glomus mossae*	Wu et al., 2006b
***Citrus tangerine* Hort. Ex Tanaka**	*Glomus mosseae/ Glomus geosporum/ Glomus versiforme/ Glomus etunicatum/ Glomus diaphanum*	Wu et al., 2007b
Trifoliate orange (*Poncirus trifoliata* L. Raf.)	*Funneliformis mosseae*	He et al., 2020
Trifoliate orange (*Poncirus trifoliata* L. Raf.)	*Funneliformis mosseae*	Huang et al., 2014

Trifoliate orange (*Poncirus trifoliata* L. Raf.)	*Funneliformis mosseae*		Huang et al., 2017
Trifoliate orange (*Poncirus trifoliata* L. Raf.)	*Funneliformis mosseae*		Wu et al.,2019
Trifoliate orange (*Poncirus trifoliata* L. Raf.)	*Funneliformis mossease, Paraglomus occultum*		Zhang et al., 2018a
Trifoliate Orange (*Poncirus Trifoliate*)	*Funneliformis mosseae*		Wang et al., 2017
INCREASED NUTRIENT UPTAKE			
CROP SPECIES	**AMF SPECIES**	**NUTRIENT**	**REFERENCE**
Tangerine (*Citrus tangerine*)	*Glomus versiforme*	K, Ca^{2+}, Mg^{2+}	Wu and Xia, 2006a
Trifoliate orange (*Poncirus trifoliate* (L) Raf.)	*Glomus mossae*	P	Wu et al., 2006b
Trifoliate orange (*Poncirus trifoliate*(L.) Raf.)	*Glomus versiforme*	K, Ca^{2+}	Wu et al., 2007a
Trifoliate orange (*Poncirus trifoliate*(L.) Raf.)	*Glomus diaphanum/Glomus mosseae/Glomus versiforme*	P	Wu et al, 20011b
Trifoliate orange (*Poncirus trifoliata*)	*Glomus versiforme*	P, K, Ca^{2+}, Mn^{2+}, Fe^{2+}, Zn^{2+}	Wu et al., 2009b

The Role of AMF in Mitigating Oxidative damage

Drought stress induces the production of reactive oxygen species (ROS) called oxidative burst, which causes oxidative damage to plants (Zou et al., 2021). ROS production is an initial response of plants to water stress and acts as a signaling molecule at low concentrations to trigger plant responses to drought. However, when the ROS concentration exceeds a level, it causes oxidative damage to the host (Miller et al., 2010). The multiple roles of ROS make it necessary to keep the ROS level in control to prevent it from complete elimination and keep it below a level that could cause oxidative damage (Zou et al., 2021).

Table 4: List of some Enzymatic and Non-Enzymatic Antioxidants in plants

ENZYAMATIC ANTIOXIDANTS	NON ENZYATIC ANTIOXIDANTS
Superoxide Dismutase (SOD)	Ascorbic acid (AsA)
Catalase (CAT)	Carotenoids
Guaiacol Peroxidasae (G-POD)	Glutathione (GSH)
Glutathione Reductase (GR)	Tocopherol
Monodehydroascorbate Reductase (MDHAR)	Ascorbate (ASC)
Dehydroascorbate Reductase (DHAR)	Phenolic Compounds • Polyphenols ○ Flavonoids
Ascorbate Peroxidase (APX)	
Phenylalanine ammonia lyase (PAL)	

Glutathione Peroxidase (GPX)	○ Phenolic Acid and Derivatives
Ref: Sharma et al., 2012	

Increased enzymatic and nonenzymatic antioxidants (Table 3) in AM plants mitigate the oxidative burst. Antioxidants regulate defensive mechanisms and protect plants from oxidative damage by acting as reducing agents, directly scavenging ROS, and or triggering signaling events to control cellular ROS levels (Table 4). Researchers have found a decrease in the production of MDA value, O2._ levels, and lower H2O2 in mycorrhizal plants compared to non-mycorrhizal plants (Bahadur et al., 2019; Sharma et al., 2012; Zou et al., 2015; Zou *et al.,* 2021).

Table 5: List of Some Antioxidants and their functions

ANTIOXIDANT	FUNCTION	REFERENCE
Phenolic compounds	Protect ells from oxidative damage by detoxifing ROS and neutralizing the radicals.	Sharma et al., 2012
AsA	Important reducing substrate for H_2O_2	Noctor and Foyer, 1998
GSH	Maintain the normal reduced state of cells by decreasing cellular ROS levels, such as of H_2O_2, DHA, Improve photosynthetic performance.	Ruiz-Sánchez *et al.,* 2010; Ruiz-Lozano *et al.,*2001
SOD	Detoxifies superoxide radical and H_2O_2	Sharma et al., 2012
APX	Scavenges ROS , Changes H_2O_2 to water by generating NADP+ and also remove water in the presence of substrate provided by GR and DHAR	Benhiba et al., 2015; Sharma et al., 2012
GR, mono, and dehydroascorbate reductases	detoxify H_2O_2 and O_2^-, prevent the formation of OH radicals	Sharma et al., 2012
Carotenoids	protect the photosynthetic machinery from photo-oxidative damage by quenching excess $^1O_2$ from light energy	Sharma et al., 2012
Flavonoids	Directly scavenge ROS, stimulate spore germination, arbuscule formation, and mycorrhizal hyphal growth	Salloum et al 2018; Mirjani et al 2019

Mycorrhization up-regulates polyamines (PAS) and fatty acids (FAs) production. PAs and FAs modulate antioxidant systems under stress conditions. For example, increased PAs reduces H2O2 accumulation and electron supply system impairment. PAs and FAs are important regulators of plant cell membrane stability, integrity, and function. Moreover, increased PAs in mycorrhization improve host roots growth and N assimilation, thereby improving host tolerance to drought stress (Wu et al., 2013; Zou et al., 2021).

The AMF could mitigate the oxidative damage to non-arbuscule containing root cortical cells by restricting oxidative burst partly only to arbuscule containing cells of the root cortex (Zou et al., 2021). Nonetheless, many studies prove that the AM root also triggers ROS generation, especially in mycorrhizal-containing root cortical cells (Fester and Hause, 2005; Zou et al., 2021). This phenomenon is central to the fungal colonization process as ROS levels are dynamic while fungal colonization. The initial fungal colonization is ensured by H2O2 generation in mycorrhizal-containing root cortical cells, which are eliminated quickly by carotenoids, SOD, and CAT (Segal and Wilson, 2018).

Table 6: Examples of increased antioxidant enzymes in Citrus ccrop in symbiosis with AMF under water deficit condition.

INCREASE IN ANTIOXIDANT ENZYMES		
CROP SPECIES	AMF SPECIES	REFERENCE
Trifoliate orange (*Poncirus trifoliate*(L.) Raf.)	*Glomus mossae/ Glomus versiforme/Glomus diaphanum*	Wu et al., 2008
Trifoliate orange (*Poncirus trifoliata* L. Raf.)	*Glomus verssiforme/ G. mosseae/ G. geosporum/ G.diaphanum/ G. etunicatum*	Qiangsheng and Yousang, 2006a
Trifoliate orange (*Poncirus trifoliata* L. Raf.)	*Funneliformis mosseae*	He et al., 2020
Trifoliate orange (*Poncirus trifoliata* L. Raf.)	*Funneliformis mosseae*	Huang et al., 2014
Citrus (*Citrus tangerina* Hort. Ex Tanaka)	*Glomus etunicatum, G. mosseae*	Qiu-Dan et al., 2013

AMF and PHYTOHORMONES

Phytohormones are plant hormones that are crucial for plant development. They are also involved in the development of AMF symbiosis with plant roots (Ludwig-Müller, 2010). Strigolactones produce signals required for the germination of AMF spores and the commencement of the infection process between the host and the AMF. SLs also play a vital role in various development processes of both symbionts, for example, hyphal branching, shoot branching, and root development (Mostofa et al., 2018). Cytokinins (CK) and jasmonic acids (JA) also regulate AMF colonization. JA at low concentration stimulates whereas at high concentration hinder AMF colonization and development. An increase in JA raises the level of abscisic acid (ABA), while a decrease in JA lowers the level of ABA (Ludwig-Muller, 2010; de Ollas et al., 2016). Under normal conditions, a low level of ABA is essential for plant vegetative growth and contributes to the plant's susceptibility to AMF infection (Herrera-Medina et al., 2007). ABA generates signals to increase auxin synthesis and promote lateral root length (Ludwig-Muller, 2010; Zhang et al., 2006) because auxin regulates root and shoot architecture in plants. Moreover, different auxins are responsible for developing different stages of colonization (Ludwig-Muller, 2010).

Water deficit stress alters plant phytohormone production. ABA levels increase (Oleudeli et al., 2019; Zhang et al., 2006) whereas, SLs levels decrease under stressed conditions (Ruiz-Lozano et al., 2016). ABA is known as the stress hormone because of its rapid accumulation to stimulate plant responses to stress. In most plants, ABA mediates stomatal closure and leaf growth to reduce water loss via transpiration. Increased ABA reduces AQP activity via the ABA-dependent signaling pathway, thus reducing leaf hydraulic conductivity (de Ollas et al., 2016; Oludeli et al., 2019; Zhang et al., 2006). SLs also boost plant tolerance to drought stress by regulating various molecular and physiological processes in the aboveground organs of plants. SLs play a role in modulating ABA-mediated stomatal closure in different plant species, promoting leaf senescence and inhibiting shoot branching (Mostofa et al., 2018). Moreover, ABA and JA signaling pathway interacts at several points in response to drought stress (de Ollas et al., 2016). JA levels have a positive correlation with crop yield (Yosefi et al., 2018). AMF colonization increase JA (Fernandez-Lizarazo et al., 2016), SLs (Ruiz-Lozano et al., 2016) and decrease ABA level in host compared to non-mycorrhizal plants (Chitarra et al., 2016; Oludeli et al., 2019). SLS inhibits CK, a negative stress tolerance regulator (Mostofa et al., 2018).

Table 7: Effect of AMF symbiosis with citrus plant on ABA level under water deficit condition.

EFFECT ON ABA LEVEL			
CROP SPECIES	AMF SPECIES		REFERENCES
Trifoliate orange (*Poncirus trifoliata* L. Raf.)	*Funneliformis mosseae*	D	Wu et al., 2019
Trifoliate Orange (*Poncirus Trifoliate*)	*Funneliformis mosseae*	I	Wang et al., 2017

Osmotic adjustment by AMF in Plants

Osmotic adjustment (OA) by increasing cellular solute concentration is probably the crucial cellular response to lowered plants' osmotic potential under DS in plants. Organic solutes (aspartic acid, protein, sugars, proline, glycinbetain) and inorganic solutes (Ca2+, K+, Mg2+) are the two types of solutes (Wu et al., 2013). Increased solute concentration maintains plant water potential, thus promoting dehydration avoidance (Kiani et al., 2007) and increasing crop soil water uptake (Chimenti et al., 2006). The OA stabilizes subcellular membranes and macromolecular structures under DS.

Many studies have shown that AM colonization enhances OA under DS (Wu et al., 2013). K+ ion is essential for cell turgor, and osmotic pressure of vacuole and AM colonization increases its uptake under drought stress (Evelin et al., 2012). Higher net accumulation of proline, non-structural carbohydrates, Ca2+, K+, sucrose, and fructose in roots and leaves, and glucose in plant roots has been noticed in AM pants compared to non-AM plants under DS (Khalafallah et al., 2008; Wu et al., 2013). However, the concentration of proline, one of the chief osmoprotectants, decreased in some AM compared to non-mycorrhizal plants under DS. It might be because of better water conditions because of the symbiosis (Wu et al., 2013). Therefore, mycorrhization contributes to yield maintenance by maintaining OA and alleviating the negative effect of DS on plant growth (Chimenti et al., 2006).

Table 8: Effect on solute concentration in AM citrus plants under water deficit conditions (D: Decrease; NA: not noticed by the researcher).

EFFECT ON SOLUTE CONCENTRATION				
		PROLINE	OTHER SOLUTES	REFERENCE
Tangerine (*Citrus tangerine*)	*Glomus versiforme*	D	Increase soluble sugars of leaves and roots , the soluble starch of leaves, the total non-structural carbohydrates of leaves and roots	Wu and Xia, 2006a
Trifoliate orange (*Poncirus trifoliate* (L) Raf.)	*Glomus mossae*	D	Increase soluble sugar content	Wu et al., 2006b
Trifoliate orange (*Poncirus trifoliate*(L.) Raf.)	*Glomus versiforme*	D	Increase soluble sugar, soluble starch, total non-structural carbohydrates in leaves and roots	Wu et al., 2007a
Tangerine (*Citrus tangerine* Tanaka)	*Glomus versiforme*	NA	Increase soluble protein in roots	Wu et al., 2006c
Citrus tangerine	*Glomus mosseae/ Glomus*	NA	Increase soluble sugar, starch, non	Wu et al.,

Hort. Ex Tanaka	*geosporum/ Glomus versiforme/ Glomus etunicatum/ Glomus diaphanum*		structural carbohydrates, soluble protein concentration	2007b
Trifoliate orange (*Poncirus trifoliata* L. Raf.)	*Glomus verssiforme/ G. mosseae/ G. geosporum/ G.diaphanum/ G. etunicatum*	NA	Increase Soluble sugars in leaves and roots, soluble starch in leaves, soluble protein in leaves	Qiangsheng and Yousang, 2006a
Trifoliate orange (*Poncirus trifoliata*)	*Funneliformis mosseae, Paraglomus occultum*	D	Increase fructose and glucose cncentration, Lower sucrose accumulation	Zhang et al., 2018b

AMF mediated crop Photosynthesis

Drought limits crop development by bringing down photosynthesis due to stomatal closure and membrane damage (Farooq et., 2012). AM colonization has shown an increase in plant photosynthesis under water stress. Both stomatal and non-stomatal factors are involved in the photosynthesis enhancement of mycorrhizal plants. Better water use efficiency of AM plant maintains higher tissue water status, thus higher stomatal conductance as improved water content protects guard cell turgidity for opening and closing of the stomata. Moreover, AMF symbiosis also promotes stomata number in many cases (Chitarra et al., 2016). Increased stomatal conductance enhances transpiration, CO2 intake, and assimilation (Auge et al., 2015; Yang et al., 2014).

Increased N, Mg, P status in AM plants also bolster photosynthesis. N and Mg are central components of chlorophyll and, P is a vital component of ATP, the "energy unit" of the plant cell. Chlorophyll absorbs the sunlight required for photosynthesis, and ATP transfers energy in the photosynthetic cycle (Atkin et al., 2000; Fleischer, 1935). The accumulation of osmolytes, antioxidants in mycorrhizal plants protects the photosynthetic apparatus from oxidative damage. For example, the production of carotenoids (antioxidant) protects photosynthetic apparatus from destruction by scavenging singlet oxygen (Table 3) (Satander et al., 2017; Young, 1991). Stimulated photosynthesis in symbiosis adds to the plant's nutrient use efficiency and carbon balance (Barros et al., 2018).

Table 9: AMF mediated photosynthesis in citrus plants under water deficit stress.

INCREASED PHOTOSYNTHETIC EFFICIENCY (J)/STOMATAL CONDUCTANCE (I)			
CROP SPECIES	AMF SPECIES	Crop Trait	REFERENCES
Rough Lemon (*Citrus jambhiri* Lush)	*Glomus fasciculatus*(Thaxter) Gerd and Trappe	J & I	Levy et al., 1980
Carrizo citrange (*Poncirus trifoliate* (L.) Raf. × *Citrus sinensis* (L.) asbeck	*Glomus intraradices* Schench & Smith	J	Graham et al., 1984
Tangerine (*Citrus tangerine*)	*Glomus versiforme*	J & I	Wu and Xia, 2006a
***Citrus tangerine* Hort. Ex Tanaka**	*Glomus mosseae/ Glomus geosporum/ Glomus versiforme/ Glomus etunicatum/ Glomus*	I	Wu et al., 2007b

	diaphanum		
***Citrus jambhiri* Lush.**	*Glomus fasciculatus*	I & J	Levy et al., 1980
Trifoliate orange (*Poncirus trifoliata* L. Raf.)	*Funneliformis mosseae*	J	He et al., 2020
Trifoliate Orange (*Poncirus Trifoliate*)	*Funneliformis mosseae*	I & J	Wang et al., 2017

SUMMARY

Water scarcity in plants reduces yield and deteriorates yield quality by hampering plant processes. In infield and indoor experiments, AMF symbiosis has lessened the negative effect of water stress on crop production; however, results vary depending upon all the factors included in the symbiosis. AMF increases the water holding capacity of soil by improving soil structure and aggregate stability. In addition to this, AMF colonization strengthens the tolerance of the host to water deficit stress by mediating several physiological processes *viz.:* maintenance of root hydraulic properties, water, and nutrient uptake, avoiding water loss, reducing tissue osmotic potential, and plant gas exchange. AM plants have improved photosynthesis because of decreased biochemical alteration under drought stress. Therefore by alleviating the detrimental effects of drought stress on the plant, mycorrhizal symbiosis promotes plant growth. These results suggest AMF sustains agricultural production by stimulating nutrient concentration, plant growth, and yield under adverse conditions such as water stress. Consequently, AMF-plant symbiosis has high potential in sustainable agriculture by improving crop resilience to adverse growing conditions.

Figure 3: Mechanisms involved in increasing drought tolerance in AMF associated plants.

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