ABSTRACT

The expansion of areas affected by drought worldwide has a negative effect on yield and crops production, making water deficits the most significant abiotic stress that limits the growth and development of plants. The use of arbuscular mycorrhizal fungi (AMF) is a strategy that mitigates the effects of this stress in a sustainable way, given the increase in the tolerance to water deficit stress in plants inoculated with these fungi; however, the exact mechanism is unknown because the response depends on the water-deficit stress type and is specific to the AMF and the plant. This review describes the mechanisms that explain how the AMF colonization of roots can modify the response of plants during a water deficit, as well as its relationship with physiological processes that determine yield, photosynthesis and photoassimilate partitioning. These mechanisms may include modifications in the content of plant hormones, such as strigolactones, jasmonic acid (JA) and abscisic acid (ABA). The JA appears to be involved in the stress signal in mycorrhizal plants through an increase of ABA concentrations and, at the same time, ABA has a regulating effect on strigolactone concentrations. Also, there is improvement of plant water status, stomatal conductance, nutritional status and plant responses to cope with a water deficit, such as osmotic adjustment, and antioxidant activity. These modifications cause an increase in CO₂ assimilation and photoassimilate production, improving plant growth during a drought.

Key words: micorrhizae, hormonal control, stomatal conductance, nutritional status, antioxidants, photosynthesis.

RESUMEN

La extensión de áreas afectadas por la sequía en todo el mundo tiene un efecto negativo en la producción y rendimiento de los cultivos, haciendo que el déficit hídrico sea el estrés abiótico más limitante del crecimiento y desarrollo de las plantas. El uso de hongos micorrízicos arbusculares (HFMA) es una estrategia que mitiga los efectos de este estrés de una manera sostenible, numerosos estudios han demostrado un aumento en la tolerancia a déficit hídrico en plantas inoculadas con estos hongos. Sin embargo, aún se desconoce el mecanismo exacto por el cual los HFMA inducen esta tolerancia ya que se ha encontrado que la respuesta depende del tipo de estrés hídrico y además es específica, tanto a nivel del HFMA como de la planta. Esta revisión describe los mecanismos potenciales que explican cómo la colonización de las raíces por HFMA puede modificar el comportamiento de la planta durante el estrés por déficit hídrico, así como su relación con procesos fisiológicos determinantes de la producción como la fotosíntesis y la partición de fotoasimilados. Estos mecanismos incluyen modificaciones en las plantas en el contenido de hormonas como las estrigolactonas, el ácido jasónico (JA) y el ácido abscísico. The JA parece estar involucrado en las señales de estrés en las plantas micorrizadas incrementando la concentración del ácido abscísico (ABA) y, a su vez el ABA regula el efecto de las estrigolactonas. Igualmente hay una mejora del estado hídrico de la planta, la conductancia estomática, el estado nutricional y un aumento de la respuesta de la planta para contender con el déficit hídrico como el ajuste osmotico y la actividad antioxidante. Estas modificaciones causan un aumento en la asimilación de CO₂ y la producción de fotoasimilados mejorando el crecimiento de las plantas en condiciones de sequía.

Palabras clave: micorriza, control hormonal, conductancia estomática, estado nutricional, antioxidantes, fotosíntesis.

Introduction

Currently, the scarcity of water is a problem seen around the world and it is expected that climate change will accelerate the severity of droughts (Kahil et al., 2015). Under this scenario, the agricultural use of water is limited, resulting in an increase in areas affected by water deficits, causing significant losses in crops and reducing average yields by more than 50% (Wang et al., 2003). For these reasons, water-deficit stress is the most important...
abiotic stress that limits plants growth and development (Yang et al., 2008).

One of the main effects of water-deficit stress on plant development is related to a reduction in water uptake and, therefore, in the nutrient uptake (Sardans et al., 2007). This restriction results from the decrease in transpiration rate and alteration in the active transport and permeability of membranes (Sardans et al., 2007), which affect the biochemical and physiological processes as well as the metabolism of nutrients and plant growth regulators, photosynthesis, respiration, and translocation of photoassimilates, reducing plant growth (Jaleel et al., 2008).

Since crops production and, therefore, food security depend on the management of limiting factors, it is necessary to develop efficient strategies that allow for the improvement of crop yield under water-deficit stress (FAO, 2012). Recently, it has been observed that the symbiotic interaction of plants with AMF, in addition to being important from the agricultural and ecological point of view (Yang et al., 2008), could be a sustainable mitigation practice for water-deficit stress (Aroca, 2012).

AMF are obligate symbiotic fungi that need host plants in order to complete their life cycles (Schüßler et al., 2001) and colonize approximately 90% of plant species in the world and the majority of cultivatable species (Bonfante and Genre, 2010). This interaction is mainly based on the exchange of carbon from the host plant and nutrients from the fungi to the host plant in a symbiotic system (Atul-Nayyar et al., 2009). Additionally, AMF allow host plants to grow more efficiently under biotic and abiotic stress conditions (Gholamhoseini et al., 2013). It has been reported that the AMF effect increases with the intensity of water deficit (Miransari et al., 2008); however, the effect is not predictable and the magnitude and type of response depend on the AMF and plant species and on the degree of the prevailing water-deficit stress (Zhongjun et al., 2007) (Tab. 1).

It has been reported that the response of the plant-AMF symbiosis to a water deficit results from the combination of nutritional, physical, and cellular effects that mitigate this water deficit (Augé, 2001). The mechanisms that explain how AMF can affect the response of host plants coping with water deficit stress include, 1) modification of hormonal balance (Estrada-Luna and Davies, 2003), 2) improvement of plant water status by increasing hydraulic conductivity through an increase of water absorption by the external hyphae (Augé et al., 2007), 3) osmotic adjustment (Porcel and Ruiz-Lozano, 2004), 4) increase in antioxidant activity (Goicoechea et al., 2005) and 5) higher nutrients absorption (Al-Karaki, 2006). This paper describes these potential tolerance mechanisms for water-deficit stress in mycorrhizal plants and the relationship with the physiological process that determines the yield, photosynthesis and photoassimilate partitioning.

**Modification of hormonal balances**

AMF produce changes in isoprenoids content in leaves of tomato plants (Solanum lycopersicum L.), favoring the production of essential instead of nonessential isoprenoids, especially in water stress conditions or after JA applications (Asensio et al., 2012) (Tab. 1). The increasing production of essential isoprenoids has been associated with the increasing demand and biosynthesis of compounds derived from carotenoids such as ABA and strigolactones in mycorrhizal plants under water-deficit stress conditions (Asensio et al., 2012). The literature mostly includes ABA, strigolactones, and JA as the plant hormones related to the mycorrhizal interaction in water deficit conditions (Ludwig-Müller, 2010).

**Abscisic acid and strigolactones.** Contrasting effects have been observed for ABA concentrations in mycorrhizal plants in water deficit conditions, which reflects the complexity of interactions. In some plants, the beneficial effect of symbiosis with AMF in stress conditions has been attributed to increases of transpiration and water absorption by roots (Augé, 2001) and it is associated with lower concentrations of ABA (Aroca et al., 2013); however, in plants such as tomato, a water stress significantly increases the ABA content, with or without of mycorrhizal colonization (Asensio et al., 2012). These changes in hormonal levels can be highly dependent on AMF genotype (Ludwig-Müller, 2010); it has been determined that, in water-deficit stress conditions, the symbiosis with AMF regulates the ABA content (Estrada-Luna and Davies, 2003). ABA can be indispensable for sustaining AMF colonization, particularly in unfavorable conditions for plants, such as water-deficit stress (Ludwig-Müller, 2010). In fact, in tomato, ABA increases the susceptibility of plants to AMF colonization and appears to play an important role in the development and functionality of arbuscules (Herrera-Medina et al., 2007).

A significant correlation has been reported between ABA production and strigolactones (Aroca et al., 2013). Strigolactones correspond to a new class of plant hormones that regulate the architecture and reproductive development of plants (Foo and Reid, 2013), but the function for which they were initially recognized for is the intermediation capacity
in the mycorrhizal symbiosis process, where they act as a molecular signal in unfavorable conditions for plants (López-Ráez et al., 2010).

ABA and strigolactones are apocarotenoids (Auldridge et al., 2006) and their biosynthesis is analog (Walter et al., 2010). One of the possible roles of ABA comes from its regulating effect on the strigolactone concentrations. For example, tomato plants that were deficient in the synthesis of ABA or treated with ABA specific inhibitors demonstrated a reduced capacity for strigolactone biosynthesis (López-Ráez et al., 2010).

**Jasmonic acid and abscisic acid.** The biochemical and molecular responses to AMF colonization in host plants also include the activation of the JA signal pathway (Tejeda-Sartorius et al., 2008). Particularly, JA appears to be involved in the stress signal in mycorrhizal plants through an increase of ABA concentrations (Asensio et al., 2012).

Other JA functions include the development and functionality of arbuscules together with ABA (Isayenkov et al., 2005). The increase of JA could be related to the variation of the root osmotic potential, caused by an increase of carbohydrates from shoots (Ludwig-Müller, 2010). It has been suggested that sugar could induce the expression of genes related to JA biosynthesis, which could elevate the JA level and produce an increase in the sink strength through the extracellular invertase, whose expression is induced in mycorrhizal roots (Schaarschmidt et al., 2006).

The narrow relationship found between ABA and AMF colonization in water deficit conditions, as well as the functionality of the arbuscules suggests that the association between AMF and some plants could be one strategy to deal with a water deficit, probably regulated by the interaction of ABA with other hormones.

**Improvement of plant water status**

It has been demonstrated that AMF participate in the uptake and transport of water in host plants (Augé, 2004). In sunflowers (Helianthus annuus L.) with a water deficit, independently colonizing AMF species (Funnelliformis mosseae or Glomus hoi) had a positive effect that has been observed on the water use efficiency (WUE), as compared to non-inoculated plants (Gholamhoseini et al., 2013) (Tab. 1). This suggests that the stomatal conductance, transpiration rate, hydraulic conductivity and water potential of leaves can be higher in mycorrhizal plants with a water-deficit stress (Augé, 2004) and that the decrease in leaves and xylem water potentials, because of the decrease in the soil water potential, is lower in mycorrhizal plants (Sánchez-Blanco et al., 2004).

As a consequence of a decrease in the soil water content, there is stomatal closure that decreases net photosynthesis in plants (Goicoechea et al., 2005). In this way, AMF could increase net photosynthesis by improving the plant water status because the increase of stomatal conductance could result in a greater diffusion of CO₂ within the mesophyll (Boldt et al., 2011).

**Hydraulic conductivity in extraradical hyphae and roots.** One of the possible mechanisms for tolerance improvement of mycorrhizal plants to water deficit could be related to the increase in hydraulic conductivity of roots (Augé et al., 2008). This increase results from a larger root system due to AMF hyphae that increase the exploration area in soil, which has a direct effect on the relative water content (RWC) (Meddich et al., 2015) (Tab. 1), water potential, transpiration rate, and crop yield (Augé, 2001).

Living hyphae that are involved in water transport (Allen, 2009) possess a diameter between 2 µm and 5 µm and can penetrate smaller soil pores that are inaccessible to root hairs (10 µm to 20 µm diameter) and thereby absorb water that is not available to non-mycorrhizal plants (Marulanda et al., 2003). In addition, AMF have demonstrated a beneficial effect on soil structures, specifically generating stable aggregates due to the production of a glycoprotein known as glomalin (Wu et al., 2008).

As a consequence, soil colonization may be as important as root colonization in the AMF effect on water relationship in host plants (Augé et al., 2007). It has been postulated that differences between AMF species regarding efficiency of irrigation water in production are due to differences in their ability to produce external mycelium (Augé, 2004) and that the length of hyphae is an important parameter for the characterization of AMF functionality (Cseresnyés et al., 2013).

**Stomatal conductance.** The existence of variations in the stomatal conductance during water deficit periods has been demonstrated although the effect of AMF is not always apparent and is unpredictable (Augé et al., 2015). In mycorrhizal plants, such as rosemary (Rosmarinus officinalis L.) (Sánchez-Blanco et al., 2004), tangerine (Citrus tangerine) (Wu and Xia, 2006) and rice (Oryza sativa L.) (Ruiz-Sánchez et al., 2011) under water deficit and inoculated with AMF, an increase in the stomatal conductance has been observed.
Membrane conductivity. Some studies have demonstrated that the symbiosis with AMF induces the expression of genes coding for aquaporins (Ruiz-Lozano, 2003). In tobacco plants (Nicotiana tabacum L.), it has been demonstrated that inoculation with AMF not only increases the expression of genes coding for aquaporins, but also reflects a greater absorption of water by the plants (Porcel et al., 2005). In contrast, it was found that, in lettuce (Lactuca sativa L.) and soy plants (Glycine max L.) inoculated with F. mosseae and R. irregularis, the water-deficit stress rapidly and intensely decreased the expression of some aquaporin genes (PIP), as compared with non-inoculated plants, presenting a less negative hydric potential and higher RWC (Porcel et al., 2006). These differences in the expression could indicate differential mechanisms for modifying the hydraulic conductivity and avoiding water loss at the cellular level.

Osmotic adjustment

It has been observed that most mycorrhizal plants have a better osmotic adjustment than non-mycorrhizal plants (Porcel and Ruiz-Lozano, 2004). For example, AMF colonization of pistachio (Pistacia vera L.) increased tolerance to water deficits by increasing accumulation of compounds for osmotic adjustment (Abbaspour et al., 2012) (Tab. 1). Sweet potato (Ipomoea batatas (L.) Lam.) plants inoculated with a mix of Glomus sp. and Acaulospora sp. demonstrated a greater decrease in the osmotic potential than non-mycorrhizated plants, indicating higher osmotic adjustment ability (Yooyongwech et al., 2016) (Tab. 1). However, inoculation of plants subjected to water deficit does not always induce osmotic adjustment (Augé, 2001). Proline is one of the most important osmolytes for osmotic adjustment and its accumulation has been reported in inoculated plants such as white clover (Medina et al., 2010), Sweet potato (Yooyongwech et al., 2016), Loquat (Eriobotrya japonica Lindl.) (Zhang et al., 2015), rice (Ruiz-Sánchez et al., 2011) and pistachio (Abbaspour et al., 2012) in water stress (Tab. 1). Nevertheless, some plants do not increase proline concentration as a tolerance mechanism to water deficits. For example, mycorrhizal plants of the Indian coral tree (Erythrina variegata L.) displayed high tolerance to a water-deficit stress, associated with an accumulation of chlorophylls and carotenoids, but not proline (Manoharan et al., 2010).

Antioxidant activity

Two mechanisms have been proposed to explain the low oxidative damage in plants subjected to water deficits and inoculated with AMF. The first consists of the direct water absorption by hyphae and its transfer to the host plant, increasing the water content and decreasing the generation of reactive oxygen species (ROS). Caravaca et al. (2005) reported that non-inoculated plants of Myrtus communis and Phillyrea angustifolia subjected to a drought increased their superoxide dismutase (SOD) and total peroxidase (POX) activity as compared to inoculated plants because these plants had a lesser oxidative stress.

The second mechanism entails an increase in the production of enzymatic and non-enzymatic antioxidants induced by the symbiosis with AMF (Abbaspour et al., 2012), especially in water-deficit conditions (Zou et al., 2014; Amiri et al., 2015). Recently, maize plants under water deficit conditions have been found to be benefited by the AMF symbiosis not only by a lower oxidative stress, but also by local restriction and non-systemic oxidative stress (Bárzana et al. 2015) (Tab. 1). However, the exact mechanism involved is not yet clear and requires further experiments to better understand the actual function of AMF in the changes of reactive oxygen metabolism and antioxidants production.

Higher nutrients absorption

It has been established that the increase of pigment levels, stomatal conductance, transpiration rate and CO₂ assimilation rate in mycorrhizal plants subjected to water deficit is caused by a better nutritional supply. This would explain why host plants of corn (Zea mays L.) (Zhao et al., 2015) and loquat (Zhang et al., 2014) inoculated with different species.
of mycorrhizal fungi and subjected to moderate and severe water stress significantly improve contents of nitrogen (N), phosphorus (P) and magnesium (Mg) among others in shoots, as compared to non-inoculated plants (Tab. 1).

However, this behavior has not been observed in all plants. For example, it has been determined that differences of various photosynthetic parameters observed in tomato plants, cv. 'Moneymaker', inoculated with *F. mosseae* are not the consequence of increases in P induced by the fungi in the plants (Boldt et al., 2011).

**Phosphorus.** Since P is less mobile in soils with little water, an increase in its acquisition as a consequence of association with AMF is important for improvement of water relations in host plants (Augé, 2004). It has been observed that, although the P absorption during water deficit is reduced, the reduction rate is lower in inoculated plants. This has been observed in marigold (*Tagetes erecta* L.) (Asrar and Elhindi, 2011), wheat (*Triticum aestivum* L.), (Al-Karaki et al., 2004), tangerine (Wu and Xia, 2006), sorghum (*Sorghum bicolor* L.) and squash (*Cucurbita pepo* L.) (Augé et al., 2007). These variations in the P absorption rate can increase roots growth in comparison with non-inoculated plants (Miransari et al., 2007), which can be favorable for the uptake of water and nutrients.

**Nitrogen.** AMF can make the assimilation of N more efficient in plants, increasing the activity of the enzyme Nitrate Reductase (NR), which is induced by the increase of the substrate (Garg, 2013). Increase in N status in mycorrhizal is due to increasing N transport through hyphae, which also increases P concentration, that is required for the phosphorylation of NR when there are low concentrations of N (Caravaca et al., 2005). Likewise, in mycorrhizal plants, aquaporins could be related to the increase in N due to its participation in the low affinity transport of ammonium (Uehlein et al., 2007).

**Photosynthesis, partitioning and production of photoassimilates**

It is known that plants subjected to water-deficit stress decrease photosynthesis because of an accumulation of ROS that damages the photosynthetic apparatus (Abbaspour et al., 2012), which can limit the supply of NADPH and ATP to the Calvin cycle. As a consequence of AMF symbiosis, plants improve the water status, which increases photosynthesis by increasing stomatal conductance and, therefore, CO₂ fixing (Boldt et al., 2011). This relationship between the stomatal opening and the relative increase in the photosynthetic activity have been described in corn (Estrada et al., 2013), guava (*Psidium guajava* L.) (Estrada-Luna et al., 2000) and rosemary (Sánchez-Blanco et al., 2004) although other plants, such as the ‘Iceberg’ rose hybrid, do not present this relationship (Klingeman et al., 2005).

On the other hand, high photosynthetic rates in mycorrhizated plants subjected to water deficit can also be explained by non-stomatal factors (Sánchez-Blanco et al., 2004), mainly by photosynthetic pigments contents and efficiency of photosynthetic apparatus. The increase of photosynthetic pigments in plants inoculated with AMF in a water deficit has been observed in the marigold (Asrar and Elhindi, 2011), Indian coral tree (*Manoharan* et al., 2010), sweet potato (*Yooyongwech* et al., 2016) and tangerine (Wu and Xia, 2006). In this way, symbiosis avoids the photoinhibition and photodestruction of photosynthetic apparatus by ROS in stress conditions (Asrar and Elhindi, 2011), which has been interpreted as a higher tolerance of mycorrhizal plants, as compared to non-mycorrhizal plants.

A water stress decreases the efficiency of photosystem II (PSII) (Fv/Fm) and it has been reported that AMF have a positive effect (Sánchez-Blanco et al., 2004) or no effect (Garcia-Sánchez et al., 2014) on this parameter. Rice (Ruiz-Sánchez et al., 2010), sweet potato (*Yooyongwech* et al., 2016), corn (*Estrada* et al., 2013), tomato (Boldt et al., 2011), olive (*Olea europaea* L.) and black hawthorn plants (*Rhamnus lycioides* L.) (Caravaca et al., 2003) present significant increases in Fv/Fm, which probably decrease the photoserepiration and ROS production (*Estrada* et al., 2013). As a consequence of this modification, there is an increase in the ability of the plant to use the excitation energy more efficiently for CO₂ assimilation. This increase in the CO₂ assimilation causes a higher accumulation of ATP and reducing equivalents, which could result in a higher quantity of carbohydrates destined to ensure demands of AMF (Boldt et al., 2011).

It has been observed that, in Indian coral tree plants in a water deficit, the symbiosis with *F. mosseae* increases the contents of chlorophylls, carotenoids, and proteins, but also reduces the contents of sugars, starches and proline (*Manoharan* et al., 2010). Likewise, in trifoliate orange (*Poncirus trifoliata* L.) in water stress, high chlorophylls and carotenoids contents and low sugars and starches quantities have been observed in plants inoculated with *Glomus versiforme* (Wu et al., 2006). These behaviors can be explained by the increase in the sink strength of AMF, which conducts a greater removal of sugars from plants,
increasing the demand for photoassimilates (Kaschuk et al., 2009). The transfer of organic carbon to AMF is not necessarily an energy load for the plant if its photosynthesis is limited by the sink (Smith and Smith, 2012).

The mutualistic relationship is only efficient if the gains in water and nutrients by the plant are greater than the carbon supply to the fungi (Torres et al., 2011). This is possible through two mechanisms, the first involves competition from the AMF for the carbon partitioned towards the fungi at expense of the production of other organs, such as roots, which can be beneficial due to a positive effect of extraradical colonization on the water status of the mycorrhizated plants (Miransari et al., 2008). The second mechanism has AMF that increase the growth of the roots and the level of carbohydrates in the organ, altering its morphology and producing a greater absorption area, which can be considered a mechanism of tolerance for water deficit (Sánchez-Blanco et al., 2004; Caravaca et al., 2005; Roldán et al., 2008; Wu et al., 2008).

Finally, as has been demonstrated in numerous studies, AMF positively affect plant growth (Tab. 1), modifying the water balance and nutrient absorption in a water deficit (Subramanian et al., 2006). As a consequence, AMF are experiencing an increased use as an inoculum in sustainable production systems (Jeffries et al., 2003) because of the fact that their application can produce economic benefits, especially in crops of high commercial value (Borde et al., 2011).

**Conclusion**

AMF increase the tolerance of plants to a water deficit; however, the complexity and diversity of responses caused by the symbiosis against environmental stresses have prevented the establishment of a clear mechanism and appear to have differential modulations according to the species of AMF, plant species and the conditions in which the symbiosis is set. Another important component in the complexity of this relationship could be the susceptibility of the plant to a water deficit and the effect that this one has in its physiology and metabolism since the presence of an additional sink during a stress condition cannot always be supported by the plant. Thus, it is probable that, only in a mild or moderate water stress, where the symbiosis quickly generates a benefit for the plant, the symbiotic association be advantageous. Although the advances in the last decade have confirmed, for many mycorrhizal plants, an increase of tolerance to a water deficit as a result of multiple-level controlled mechanisms, a more holistic approach is required to understand this phenomenon.

**Acknowledgments**

This work was supported by a study grant from a project co-financed by Colciencias, code 1101-569-33833.

**TABLE 1.** Recent studies (since 2011) showing the effect of AMF on plants subjected to a drought stress.

| Plant species           | AMF                                          | Effect                                      | Reference           |
|-------------------------|----------------------------------------------|---------------------------------------------|---------------------|
| *Ipomoea batatas* (L.) Lam. | Commercial inoculum containing *Glomus* sp. and *Acaulospora* sp. | Increased Growth, P content, Proline, Soluble sugars, Leaf osmotic potential, Photosynthetic pigments, Maximum quantum yield of PSII (Fv/Fm), Photon yield of PSII (фPSII), Net photosynthetic rate, Tuber fresh weight | Chlorophyll degradation Yooyongwech et al. (2016) |
| *Eriobotrya japonica* Lindl. | *Funneliformis mosseae* | Increased Growth, Leaf water (leaf), Proline, Osmotic adjustment (root) | Decreased Lipid peroxides (leaf and root) Zhang et al. (2015) |
| Plant species       | AMF                                                                 | Effect                                      | Reference               |
|--------------------|----------------------------------------------------------------------|---------------------------------------------|-------------------------|
| Zea mays L.        | *Rhizophagus irregularis*                                            | Increased Growth                           | Zhao et al. (2015)      |
|                    |                                                                     | P content                                  |                         |
|                    |                                                                     | WUE                                         |                         |
|                    |                                                                     | Rehydration rate                           |                         |
|                    |                                                                     | Leaf moisture percentage                   |                         |
|                    | *Funneliformis monosporum, Rhizophagus clarus and Glomus deserticola* |                                             |                         |
|                    | Funneliformis mosseae, *Rhizophagus irregularis*                     | Increased Growth                           | Meddich et al. (2015)   |
|                    |                                                                     | Nutrient absorption                        |                         |
|                    |                                                                     | RWC                                         |                         |
|                    |                                                                     | Stomatal resistance                        |                         |
|                    | Pearlgonium graveolens (L.) Herit.                                   | Essential oil content and                 | Amiri et al. (2015)     |
|                    |                                                                     | Oil yield                                  |                         |
|                    |                                                                     | Catalase activity                          |                         |
|                    |                                                                     | Ascorbate activity                         |                         |
|                    |                                                                     | Peroxidase activity                        |                         |
|                    |                                                                     | Glutathione activity                       |                         |
| Zea mays L.        | *Rhizophagus irregularis*                                            | Increased Proline                          | Bárzana et al. (2015)   |
|                    |                                                                     | Systemically MDA accumulation              |                         |
|                    | *Eriobotrya japonica* Lindl.                                          |                                             |                         |
|                    | *Acaulospora laevis, Glomus mosseae, and Glomus caledonium*           | Increased Growth                           | Zhang et al. (2014)     |
|                    |                                                                     | Plant height                               |                         |
|                    |                                                                     | Leaf area                                  |                         |
|                    |                                                                     | Leaf number                                |                         |
|                    |                                                                     | N, P, K, Ca, Mg, Zn, Cu content            |                         |
| Citrullus lanatus  | (Thunb.) Matsum. & Nakai                                             | Mixed inoculum of                         | Omirou et al. (2013)    |
| (L.) Matsum. & Nakai| *Rhizophagus irregularis and Funneliformis mosseae*                  | Increased WUE                             |                         |
|                    |                                                                     | Yield (fruit)                              |                         |
|                    |                                                                     | P and N content (root)                     |                         |
| Helianthus annuus L.| *Funneliformis mosseae and Glomus hoi*                              | Increased Growth                           | Gholamhoseini et al. (2013) |
|                    |                                                                     | Seeds quality                              |                         |
|                    |                                                                     | N and P content (leaves and seeds)         |                         |
| Knaúia arvensis (L.)| Coult.                                                              | *Glomus sp. and complex of AMF inoculum obtained from rhizosphere soil of K. arvensis plants* | Doubková et al. (2013) |
|                    |                                                                     | Increased Growth                           |                         |
|                    |                                                                     | P content                                  |                         |
| Helianthus annuus L.| *Funneliformis mosseae and Claroideoglomus etunicatum*              | P and N content                            | Heidari and Karami (2012) |
|                    |                                                                     | Oil percentage (seeds)                     |                         |
| Solanum lycopersicum L.| Commercial inoculum containing Funneliformis mosseae and *Rhizophagus irregularis* | Foliar production of essentials isoprenoids | Asensio et al. (2012)   |
| Pistacia vera seedlings L.| *Claroideoglomus etunicatum*                                        |                                             | Abbaspour et al. (2012) |
|                    |                                                                     |                                             |                         |
|                    |                                                                     |                                             |                         |
| Plant species          | AMF                                                                 | Effect                                | Reference                                      |
|-----------------------|----------------------------------------------------------------------|---------------------------------------|------------------------------------------------|
| *Poncirus trifoliata* (L.) Raf. | *Rhizophagus diaphanus, Funneliformis mosseae* and *Glomus versiforme* | Increased: higher soil acid and total phosphatase activities<br>Decreased: soil available P contents | Wu et al. (2011)                                |
| *Oryza sativa* L.       | *Rhizophagus irregularis*                                              | Growth: efficiency of photosystem II<br>Efficiency of photosystem II<br>Glutathione<br>Stomatal conductance<br>Ascorbate and proline | Ruiz-Sánchez et al. (2011)                      |
| *Trifolium repens* L.   | Mixture of *Glomus* species                                            | RWC<br>Stomatal conductance           | Benabdellah et al. (2011)                       |
| *Cicer arietinum* L.     | *Rhizophagus irregularis*                                              | Yield<br>P content (seed and root)     | Erman et al. (2011)                            |
| *Tagetes erecta* L.      | *Septoglomus constrictum*                                              | Growth: photosynthetic pigments<br>Phosphorous content<br>Flower quality | Asrar and Elhindi (2011)                        |

¥ Indicates different responses among the AMF; WUE, water use efficiency; RWC, relative water content.

**Literature cited**

Abbaspour, H., S. Saeidi-Sar, H. Afshari, and M. Abdel-Wahhab. 2012. Tolerance of mycorrhiza infected pistachio (*Pistacia vera* L.) seedling to drought stress under glasshouse conditions. J. Plant Physiol. 169, 704-709. Doi: 10.1016/j.jplph.2012.01.014

Al-Karaki, G.N. 2006. Nursery inoculation of tomato with arbuscular mycorrhizal fungi and subsequent performance under irrigation with saline water. Sci. Hortic. 109, 1-7. Doi: 10.1016/j.scienta.2006.02.019

Al-Karaki, G., B. McMichael, and J. Zak. 2004. Field response of wheat to arbuscular mycorrhizal fungi and drought stress. Mycorrhiza 14, 263-269. Doi: 10.1007/s00572-003-0265-2

Allen, M.F. 2009. Bidirectional water flows through the soil-fungal-plant mycorrhizal continuum. New Phytol. 182, 290-293. Doi: 10.1111/j.1469-8137.2009.02815.x

Amiri, R., A. Nibakht, and N. Etemadi. 2015. Alleviation of drought stress on rose geranium [*Pelargonium graveolens* (L.) Herit.] in terms of antioxidant activity and secondary metabolites by mycorrhizal inoculation. Sci. Hortic. 197, 373-380. Doi: 10.1016/j.scienta.2015.09.062

Aroca, R. (ed.). 2012. Plant responses to drought stress: from morphological to molecular features. Springer-Verlag Berlin; GmbH & Co. K, Heidelberg, Germany.

Aroca, R., J.M. Ruiz-Lozano, A.M. Zamarreño, J.A. Paz, J.M. Garcia-Mina, M.J. Pozo, and J. A. López-Ráez. 2013. Arbuscular mycorrhizal symbiosis influences stigloactone production under salinity and alleviates salt stress in lettuce plants. J. Plant Physiol. 170, 47-55. Doi: 10.1016/j.jplph.2012.08.020

Asensio, D., F. Rapparini, and J. Peñuelas. 2012. AM fungi root colonization increases the production of essential isoprenoids vs. nonessential isoprenoids especially under drought stress conditions or after jasmonic acid application. Phytochemistry 77, 149-61. Doi: 10.1016/j.phytochem.2011.12.012

Asrar, A.-W. and K.M. Elhindi. 2011. Alleviation of drought stress of marigold (*Tagetes erecta*) plants by using arbuscular mycorrhizal fungi. Saudi J. Biol. Sci. 18, 93-98. Doi: 10.1016/j.sjbs.2010.06.007

Atul-Nayyar, A., C. Hamel, K. Hanson, and J. Germida. 2009. The arbuscular mycorrhizal symbiosis links N mineralization to plant demand. Mycorrhiza 19, 239-246. Doi: 10.1007/s00572-008-0215-0

Augé, R.M. 2001. Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. Mycorrhiza 11, 3-42. Doi: 10.1007/s005720100097

Augé, R.M. 2004. Arbuscular mycorrhizae and soil/plant water relations. Can. J. Soil Sci. 84, 373-381. Doi: 10.4141/S04-002

Augé, R.M., H.D. Toler, J.L. Moore, K. Cho, and A.M. Saxton. 2007. Comparing contributions of soil versus root colonization to variations in stomatal behavior and soil drying in mycorrhizal *Sorghum bicolor* and *Cucurbita pepo*. J. Plant Physiol. 164, 1289-1299. Doi: 10.1016/j.jplph.2006.08.005

Augé, R.M., H.D. Toler, C.E. Sams, and G. Nasim. 2008. Hydraulic conductance and water potential gradients in squash leaves showing mycorrhiza-induced increases in stomatal conductance. Mycorrhiza 18, 115-21. Doi: 10.1007/s00572-008-0162-9

Augé, R.M., H.D. Toler, and A.M. Saxton. 2015. Arbuscular mycorrhizal symbiosis alters stomatal conductance of host plants more under drought than under amply watered conditions: a meta-analysis. Mycorrhiza 25, 13-24. Doi: 10.1007/s00572-014-0585-4

Auldridge, M.E., D.R. McCarty, and H.J. Klee. 2006. Plant carotenoid cleavage oxygenases and their apocarotenoid products. Curr. Opin. Plant Biol. 9, 315-21. Doi: 10.1016/j.pbi.2006.03.005

Bárszana, G., R. Aroca, and J.M. Ruiz-Lozano. 2015. Localized and non-localized effects of arbuscular mycorrhizal symbiosis on accumulation of osmolytes and aquaporins and on antioxidant systems in maize plants subjected to total or partial...
Estrada, B., R. Aroca, J.M. Barea, and J.M. Ruiz-Lozano. 2013. Arbuscular mycorrhizal fungi influence water relations, gas exchange, abscisic acid and growth of micropropagated chile ancho pepper (Capsicum annuum) plantlets during acclimatization and post-acclimatization. J. Plant Physiol. 160, 1073-1083. Doi: 10.1078/0176-1617-00989

FAO. 2012. Coping with water scarcity an action framework for agriculture and food security. Rome.

Fernández-Lizarazo and Moreno-Fontseca: Mechanisms for tolerance to water-deficit stress in plants inoculated with arbuscular mycorrhizal fungi. A review

187
Omirou, M., I.M. Ioannides, and C. Ehaliotis. 2013. Mycorrhizal symbioses. Soil Biol. Biochem. 41, 1233-1244. Doi: 10.1016/j.soilbio.2009.03.005

Klingeman, W.E., M.W. Van Iersel, J.G. Kang, R.M. Augé, J.L. Moore, and P.C. Flanagan. 2005. Whole-plant gas exchange measurements of mycorrhizal "Iceberg" roses exposed to cyclic drought. Crop Prot. 24, 309-317. Doi: 10.1016/j.cropro.2004.08.012

López-Ráez, J., W. Kohlen, T. Charnikhova, P. Mulder, A.K. Undas, M.J. Sergeant, F. Verstappen, T.D.H. Bugg, A.J. Thompson, C. Ruyster-Spira, and H. Bouwmeester. 2010. Does abscisic acid affect strigolactone biosynthesis? New Phytol. 187, 343-354. Doi: 10.1111/j.1469-8137.2010.03291.x

Ludwig-Müller, J. 2010. Hormonal responses in host plants triggered by arbuscular mycorrhizal fungi. pp. 169-190. In: Koltaï, H. and Y. Kapulnik (eds.). Arbuscular mycorrhizas: physiology and function. Springer Netherlands, Dordrecht, Germany. Doi: 10.1007/978-90-481-9489-6_8

Manoharan, P.T., V. Shanmugaiah, N. Balasubramanian, S. Mathinayagam, M.P. Sharma, and K. Muthuchelian. 2010. Contribution of six arbuscular mycorrhizal fungal isolates to water uptake by Lactuca sativa plants under drought stress. Physiol. Plant. 119, 526-533. Doi: 10.1111/j.1399-3054.2003.00196.x

Meddich, A., F. Jaiti, W. Bourzik, A. El Asli, and M. Hafidi. 2015. Influence of AM fungi on the growth and physiological status of Erythrina variegata Linn. grown under different water stress conditions. Eur. J. Soil Biol. 46, 151-156. Doi: 10.1016/j.ejsoil.2010.01.001

Marulanda, A., R. Azción, and J.M. Ruiz-Lozano. 2003. Contribution of six arbuscular mycorrhizal fungal isolates to water uptake by Lactuca sativa plants under drought stress. Physiol. Plant. 119, 526-533. Doi: 10.1111/j.1399-3054.2003.00196.x

Medich, A., F. Jaiti, W. Bourzik, A. El Asli, and M. Hafidi. 2015. Use of mycorrhizal fungi as a strategy for improving the drought tolerance in date palm (Phoenix dactylifera). Sci. Hortic. 192, 468-474. Doi: 10.1016/j.scienta.2015.06.024

Medina, A., A. Roldán, and R. Azcón. 2010. The effectiveness of arbuscular-mycorrhizal fungi and Aspergillus niger or Phanerochaete chrysosporium treated organic amendments from olive residues upon plant growth in a semi-arid degraded soil. J. Environ. Manage. 91, 2547-2553. Doi: 10.1016/j.jenvman.2010.07.008

Miransari, M., H.A. Bahrami, F. Rejali, and M.J. Malakouti. 2008. Using arbuscular mycorrhiza to alleviate the stress of soil compaction on wheat (Triticum aestivum L.) growth. Soil Biol. Biochem. 40, 1197-1206. Doi: 10.1016/j.soilbio.2007.12.014

Miransari, M., H.A. Bahrami, F. Rejali, M.J. Malakouti, and H. Torabi. 2007. Using arbuscular mycorrhiza to reduce the stressful effects of soil compaction on (Zea mays L.) growth. Soil Biol. Biochem. 39, 2014-2026. Doi: 10.1016/j.soilbio.2007.02.017

Omirou, M., I.M. Ioannides, and C. Ehaliotis. 2013. Mycorrhizal inoculation affects arbuscular mycorrhizal diversity in watermelon roots, but leads to improved colonization and plant response under water stress only. Appl. Soil Ecol. 63, 112-119. Doi: 10.1016/j.apsoil.2012.09.013

Porcel, R., R. Aroca, R. Azción, and J.M. Ruiz-Lozano. 2006. PIP aquaporin gene expression in arbuscular mycorrhizal Glycine max and Lactuca sativa plants in relation to drought stress tolerance. Plant Mol. Biol. 60, 389-404. Doi: 10.1007/s11103-005-4210-y

Porcel, R., M. Gómez, R. Kaldenhoff, and J.M. Ruiz-Lozano. 2005. Impairment of NaAQP1 gene expression in tobacco plants does not affect root colonisation pattern by arbuscular mycorrhizal fungi but decreases their symbiotic efficiency under drought. Mycorrhiza 15, 417-23. Doi: 10.1007/s00572-005-0346-5

Porcel, R. and J.M. Ruiz-Lozano. 2004. Arbuscular mycorrhizal influence on leaf water potential, solute accumulation, and oxidative stress in soybean plants subjected to drought stress. J. Exp. Bot. 55, 1743-1750. Doi: 10.1093/jxb/erh188

Roldán, A., P. Díaz-Vivancos, J.A. Hernández, L. Carrasco, and F. Caravaca. 2008. Superoxide dismutase and total peroxidase activities in relation to drought recovery performance of mycorrhizal shrub seedlings grown in an amended semi-arid soil. J. Plant Physiol. 165(7):715-722. Doi: 10.1016/j.jplph.2007.02.007

Ruiz-Lozano, J.M. 2003. Arbuscular mycorrhizal symbiosis and alleviation of osmotic stress. New perspectives for molecular studies. Mycorrhiza 13, 309-317. Doi: 10.1007/s00572-003-0237-6

Ruiz-Sánchez, M., E. Armada, Y. Muñoz, I.E. García de Salamone, R. Aroca, J.M. Ruiz-Lozano, and R. Azcón. 2011. Azospirillum and arbuscular mycorrhizal colonization enhance rice growth and physiological traits under well-watered and drought conditions. J. Plant Physiol. 168, 1031-1037. Doi: 10.1016/j.jplph.2010.12.019

Ruiz-Sánchez, M., R. Aroca, Y. Muñoz, R. Polón, and J.M. Ruiz-Lozano. 2010. The arbuscular mycorrhizal symbiosis enhances the photosynthetic efficiency and the antioxidative response of rice plants subjected to drought stress. J. Plant Physiol. 167, 862-869. Doi: 10.1016/j.jplph.2010.01.018

Sánchez-Blanco, M.J., T. Ferrández, M.A. Morales, A. Morte, and J.J. Alarcón. 2004. Variations in water status, gas exchange, and growth in Rosmarinus officinalis plants infected with Glomus deserticola under drought conditions. J. Plant Physiol. 161, 675-682. Doi: 10.1078/0176-1617-01191

Sardans, J., J. Peñuelas, and R. Ogaya. 2007. Drought’s impact on Ca, Fe, Mg, Mo and S concentration and accumulation patterns in the plants and soil of a Mediterranean evergreen Quercus ilex forest. Biogeochemistry 87, 49-69. Doi: 10.1007/s10533-007-9167-2

Schaarschmidt, S., T. Roitsch, and B. Hause. 2006. Arbuscular mycorrhiza induces gene expression of the apoplastic invertase LI6N in tomato (Lycopersicon esculentum) roots. J. Exp. Bot. 57, 4015-4023. Doi: 10.1093/jxb/erl172

Schüßler, A., D. Schwarzott, and C. Walker. 2001. A new fungal phylum , the Glomeromycota: phylogeny and evolution*. Mycol. Res. 105, 1413-1421. 10.1017/S0953756201005196

Smith, S.E., and F.A. Smith. 2012. Fresh perspectives on the roles of arbuscular mycorrhizal fungi in plant nutrition and growth. Mycologia 104, 1-13. Doi: 10.3852/11-229

Subramanian, K.S., P. Santhanakrishnan, and P. Balasubramanian. 2006. Responses of field grown tomato plants to arbuscular mycorrhizal fungal colonization under varying intensities of drought stress. Sci. Hortic. 107, 245-253. Doi: 10.1016/j.scienta.2005.07.006

Tejeda-Sartorius, M., O. Martinez de la Vega, and J.P. Délano-Frier. 2008. Jasmonic acid influences mycorrhizal colonization in tomato plants by modifying the expression of genes involved in carbon sink strength of rhizobial and arbuscular mycorrhizal symbioses. Soil Biol. Biochem. 41, 1233-1244. Doi: 10.1016/j.soilbio.2009.03.005
in carbohydrate partitioning. Physiol. Plant. 133, 339-353. Doi: 10.1111/j.1399-3054.2008.01081.x

Torres, Y.A., C. Busso, O. Montenegro, L. Ithurrart, H. Giorgetti, G. Rodriguez, D. Bentivegna, R. Brevedan, O. Fernández, M. de la Merced Mujica, S. Baioni, J. Entio, M. N. Fioretti, and G. Tucat. 2011. Defoliation effects on the arbuscular mycorrhizas of ten perennial grass genotypes in arid Patagonia, Argentina. Appl. Soil Ecol. 49, 208-214. Doi: 10.1016/j.apsoil.2011.05.004

Uehlein, N., K. Fileschi, M. Eckert, G.P. Bienert, A. Bertl, and R. Kaldenhoff. 2007. Arbuscular mycorrhizal symbiosis and plant aquaporin expression. Phytochemistry 68, 122-129. Doi: 10.1016/j.phytochem.2006.09.033

Walter, M.H., D.S. Floss, and D. Strack. 2010. Apocarotenoids: hormones, mycorrhizal metabolites and aroma volatiles. Planta 232, 1-17. Doi: 10.1007/s00425-010-1156-3

Wang, W., B. Vinocur, and A. Altman. 2003. Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. Planta 218, 1-14. Doi: 10.1007/s00425-003-1105-5

Wu, Q.-S., and R.-X. Xia. 2006. Arbuscular mycorrhizal fungi influence growth, osmotic adjustment and photosynthesis of citrus under well-watered and water stress conditions. J. Plant Physiol. 163, 417-425. Doi: 10.1016/j.jplph.2005.04.024

Wu, Q.-S., R.-X. Xia, and Y.-N. Zou. 2006. Reactive oxygen metabolism in mycorrhizal and non-mycorrhizal citrus (Poncirus trifoliata) seedlings subjected to water stress. J. Plant Physiol. 163, 1101-1110. Doi: 10.1016/j.jplph.2005.09.001

Wu, Q.-S., R.-X. Xia, and Y.-N. Zou. 2008. Improved soil structure and citrus growth after inoculation with three arbuscular mycorrhizal fungi under drought stress. Eur. J. Soil Biol. 44, 122-128. Doi: 10.1016/j.ejsobi.2007.10.001

Wu, Q.-S., Y.-N. Zou, and X.-H. He. 2011. Differences of hyphal and soil phosphatase activities in drought-stressed mycorrhizal trifoliolate orange (Poncirus trifoliata) seedlings. Sci. Hortic. 129, 294-298. Doi: 10.1016/j.scienta.2011.03.051

Yang, Y., Y. Chen, and W. Li. 2008. Arbuscular mycorrhizal fungi infection in desert riparian forest and its environmental implications: a case study in the lower reach of Tarim River. Prog. Nat. Sci. 18, 983-991. Doi: 10.1016/j.pnsc.2008.02.009

Yooyongwech, S., T. Samphumhuang, R. Tisarum, C. Theerawitaya, and S. Cha-Um. 2016. Arbuscular mycorrhizal fungi (AMF) improved water deficit tolerance in two different sweet potato genotypes involves osmotic adjustments via soluble sugar and free proline. Sci. Hortic. 198, 107-117. Doi: 10.1016/j.scienta.2015.11.002

Zhang, Y., Q. Yao, J. Li, Y. Hu, and J. Chen. 2014. Growth Response and nutrient uptake of Eriobotrya japonica plants inoculated with three isolates of arbuscular mycorrhizal fungi under water stress condition. J. Plant Nutr. 37, 690-703. Doi: 10.1080/01904167.2013.868478

Zhang, Y., Q. Yao, J. Li, Y. Wang, X. Liu, Y. Hu, and J. Chen. 2015. Contributions of an arbuscular mycorrhizal fungus to growth and physiology of loquat (Eriobotrya japonica) plants subjected to drought stress. Mycol. Prog. 14(10). Doi: 10.1007/s11557-015-1108-1

Zhao, R., W. Guo, N. Bi, J. Guo, L. Wang, J. Zhao, and J. Zhang. 2015. Arbuscular mycorrhizal fungi affect the growth, nutrient uptake and water status of maize (Zea mays L.) grown in two types of coal mine spoils under drought stress. Appl. Soil Ecol. 88, 41-49. Doi: 10.1016/j.apsoil.2014.11.016

Zhongqun, H., H. Chaoxing, Z. Zhang, Z. Zhirong, and H. Wang. 2007. Changes of antioxidative enzymes and cell membrane osmosis in tomato colonized by arbuscular Mycorrhizae under NaCl stress. Colloids Surf., B. Biointerfaces. 59, 128-133. Doi: 10.1016/j.colsurfb.2007.04.023

Zou, Y.N., Y.M. Huang, Q.S. Wu, and X.H. He. 2014. Mycorrhiza-induced lower oxidative burst is related with higher antioxidant enzyme activities, net H2O2 effluxes, and Ca2+ influxes in trifoliolate orange roots under drought stress. Mycorrhiza 25, 143-152. Doi: 10.1007/s00572-014-0598-z