Mechanisms for tolerance to water-deficit stress in plants inoculated with arbuscular mycorrhizal fungi. A review

Mecanismos de tolerancia al estrés por déficit hídrico en plantas inoculadas con hongos micorrízicos arbusculares. Una revisión

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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 absicic 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 CO_2 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 jasmónico (JA) y el ácido absícico. 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 osmótico y la actividad antioxidante. Estas modificaciones causan un aumenta en la asimilación de CO_2 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

Received for publication: 2 February, 2016. Accepted for publication: 30 June, 2016.

Doi: 10.15446/agron.colomb.v34n2.55569

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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 restriction 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 (Zhongqun *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 extracelular 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 (*Funneliformis 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 CO_2 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 (*Oriza sativa* L.) (Ruíz-Sánchez *et al.,* 2011) under water deficit and inoculated with AMF, an increase in the stomatal conductance has been observed

(Table 1); however, white clover (*Trifolium repens* L.) have displayed a decrease in stomatal conductance and an increase in the RWC in the same conditions (Benabdellah *et al.,* 2011), both associated with a more water use efficiency (Tab. 1).

However, this symbiosis does not always generate the expected results in terms of the water status of plants. For example, in roses inoculated with *Rhizophagus irregularis* in water deficit conditions, the hydration of buds and the aesthetic appearance during water deficit did not significantly improve (Klingeman *et al.,* 2005). Likewise, it has been reported that tomato plants inoculated with AMF in water deficit conditions did not present differences in the RWC, as compared to non-mycorrhizal plants (García-Sánchez *et al.,* 2014).

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 (Ruíz-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 CO_2 assimilation rate in mycorrhizal plants subjected to a water deficit is caused by a better nutritional supply. This would explain why host plants of corn (*Zea mayz* 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, CO_2 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 (García-Sánchez *et al.,* 2014) on this parameter. Rice (Ruíz-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 photorespiration 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 CO_2 assimilation. This increase in the CO_2 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
		Increased	Decreased	
Ipomoea batatas (L.) Lam.	Commercial inoculum containing *Glomus* sp. and *Acaulospora* sp.	Growth P content Proline Soluble sugars Leaf osmotic potential Photosynthetic pigments Maximum quantum yield of PSII (Fv/Fm) Photon yield of PSII (ϕPSII) Net photosynthetic rate Tubers per plant Tuber fresh weight	Chlorophyll degradation	Yooyongwech *et al.* (2016)
Eriobotrya japonica Lindl.	*Funneliformis mosseae*	Growth Leaf water (leaf) Proline Osmotic adjustment (root)	Lipid peroxides (leaf and root)	Zhang *et al.* (2015)

Plant species	AMF	Effect		Reference
		Increased	Decreased	
Zea mays L.	*Rhizophagus irregularis*	Growth P content WUE Rehydration rate Leaf moisture percentage	C:P ratio N:P ratio	Zhao *et al.* (2015)
Phoenix dactylifera L.	*Funneliformis monosporum*, *Rhizophagus clarus* and *Glomus deserticola* ¥	Growth Nutrient absorption RWC Water potential	Stomatal resistance	Meddich *et al.* (2015)
Pelargonium graveolens (L.) Herit.	*Funneliformis mosseae*, *Rhizophagus irregularis*	Essential oil content and Oil yield Catalase activity Ascorbate activity Peroxidase activity Glutathione activity	MDA accumulation H_2O_2 accumulation	Amiri *et al.* (2015)
Zea maiz L.	*Rhizophagus irregularis*	Proline	Systemically MDA accumulation	Bárzana *et al.* (2015)
		Aquaporins were differently regulated		
Eriobotrya japonica Lindl.	*Acaulospora laevis*, *Glomus mosseae*, and *Glomus caledonium*	Growth Plant height, Leaf area Leaf number N, P, K, Ca, Mg, Zn, Cu content		Zhang *et al.* (2014)
Citrullus lanatus (Thunb.) Matsum. & Nakai	Mixed inoculum of *Rhizophagus irregularis* and *Funneliformis mosseae*	WUE Yield (fruit) P and N content (root)		Omirou *et al.* (2013)
Helianthus annuus L.	*Funneliformis mosseae* and *Glomus hoi* ¥	Growth Seeds quality N and P content (leafs and seeds)		Gholamhoseini *et al.* (2013)
Knautia arvensis (L.) Coult.	*Glomus sp.* and complex of AMF inoculum obtained from rhizosphere soil of *K. arvensis* plants	Growth P content	Proline	Doubková *et al.* (2013)
Helianthus annuus L.	*Funneliformis mosseae* and *Claroideoglomus etunicatum*	P and N content Oil percentage (seeds)		Heidari and Karami (2012)
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*	Growth P, K, Zn and Cu content Soluble sugars Proteins Flavonoids Proline Peroxidase activity		Abbaspour *et al.* (2012)

Plant species	AMF	Effect		Reference
		Increased	Decreased	
Poncirus trifoliata (L.) Raf.	*Rhizophagus diaphanus*, *Funneliformis mosseae* and *Glomus versiforme*	Growth Hgher soil acid and total phosphatase activities P contents (leaf and root)	Soil available P contents	Wu *et al.* (2011)
Oryza sativa L.	*Rhizophagus irregularis*	Growth Efficiency of photosystem II Stomatal conductance Ascorbate and proline	Glutathione Lipid peroxidation	Ruíz-Sánchez *et al.* (2011)
Trifolium repens L.	Mixture of *Glomus* species	RWC	Stomatal conductance	Benabdellah *et al.* (2011)
Cicer arietinum L.	*Rhizophagus irregularis*	Yield P content (seed and root)		Erman *et al.* (2011)
Tagetes erecta L.	*Septoglomus constrictum*	Growth Photosynthetic pigments Phosphorous content Flower quality		Asrar and Elhindi (2011)

¥ Inidicates diferent responses among the AMF; WUE, water use efficiency; RWC, relative water content.

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