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Mechanisms for Tolerance to Drought Stress in Plants Inoculated with (AM) Arbuscular Mycorrhizal Fungi: A Review

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Abstract: ***The expansion of areas affected by drought stress through out the world has anegative impact on yield as well as production of crops, making drought stress the most significant abiotic stress that limits the growth of plants. The use of (AMF) arbuscular mycorrhizal fungi is aeffective strategy that combat the impact of this drought stress in a very sustainable manner, given the increase in the tolerance to drought stress in plants inoculated with these fungi; however, the exact mechanism is unknown due to the response depends particularlyon the drought stress type and is specific to the (AMF) arbuscular mycorrhizal fungi and the plant. This review describes the mechanisms that explain how exactlythe AMF colonization in roots can modify the plantresponse during a drought stress, 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, like jasmonic acid (JA) and absicic acid (ABA). The JA appears to be involved in the stress signal in mycorrhizal plants through an increase ABA concentration. Also, there is enhancement of plant water status, stomatal conductance, nutritional status and responses of plant to cope up with a water deficit, antioxidant activity and osmotic adjustment. These modifications cause an increase in CO2 assimilation and photoassimilate production, improving plant growth during a drought stress.***

Keywords: micorrhizae, hormonal control, stomatal conductance, nutritional status, antioxidants, photosynthesis

1. Introduction

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

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

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

AMF are obligate symbiotic fungi in order to complete their life cycles fungi need host plants (Schüßleret al., 2001) and approximately colonize 90% of plant species around the world and the majority of cultivatable species (Bonfante and Genre, 2010). This interaction is based mainly 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, under biotic and abiotic stress conditions AMF allow host plants to grow more efficiently (Gholamhoseiniet al., 2013). It has been reported that the effect of AMF increases with the intensity of water deficit (Miransariet al., 2008); however, the effect is not predictable exactly and the type of response and magnitude depend on the plant species and AMF and on the degree of the prevailing drought stress (Zhongqunet al., 2007).

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 exactly AMF can affect the response of host plants coping with drought stress include, 1) hormonal balance modification (Estrada-Luna and Davies, 2003), 2) plant water status improvement by enhancing 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 antioxidantactivity (Goicoechea et al., 2005) and 5) higher absorption of nutrients (Al-Karaki, 2006). This paper describes these potential tolerance mechanisms for drought stress in mycorrhizal plants and the relationship with the physiological process that determines the yield, photosynthesis and photoassimilate partitioning.

Jasmonic acid and abscisic acid.

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

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

The narrow relationship found between AMF colonization and ABA in droughconditions, as well as thearbuscules functionality suggests that the association between plants and AMFcould be one strategy to copewith drought, which probably regulated by ABA interaction with other hormones.

Improvement of plant water status

It has been clearly demonstrated that AMF play important role in the uptake and transport of water in host plants (Augé, 2004). In sunflowers (Helianthus annuusL.) plants with a water deficit, independently colonizing AMF species (Funneliformismosseae or Glomus hoi) had a positive impact that has been observed on the (WUE) water use efficiency, as compared to non-inoculated plants (Gholamhoseini et al., 2013). This suggests that in mycorrhizal plants the stomatal conductance, transpiration rate, hydraulic conductivity and water potential of leaves can be higher 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 result of a decrease in the soil water content, there is stomatal closure that decreases net photosynthesis in plants (Goicoechea et al., 2005). In this manner, AMF could increase net photosynthesis by enhancing 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 behind tolerance improvement of mycorrhizal plants to water deficit could be related to the enhancement in hydraulic conductivity of roots (Augé etal., 2008). This increase results from a larger root systemdue to AMF hyphae that increase the exploration area in soil, which has a direct impact onon the (RWC) relative water content (Meddichet al., 2015), water potential, transpiration rate and crop yield (Augé, 2001).

Living hyphae that are involved in transport of water (Allen, 2009) possess a diameter between 2 µm and 5 µm and can penetrate even those smaller soil pores that are inaccessible to root hairs (10 µm to 20 µm diameter) and thereby absorb water that is not easily available to non-mycorrhizal plants (Marulanda et al., 2003). In addition, AMF have also demonstrated a beneficial impact on soil structures, specifically generating stable aggregates due to the production of a glycoprotein calledas 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 drought stress has been demonstrated although the impact of AMF is not always apparent and is always unpredictable (Augé et al., 2015). In various 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 drought stress and inoculated with AMF, an increase in the stomatal conductance has been observed; however, white clover (Trifolium repens L.) have displayed a marked decrease in stomatal conductance and an increase in the RWC in the same conditions (Benabdellah etal., 2011), both associated with a more water use efficiency.

However, this particular symbiosis does not always generate the expected results in terms of the plants water status . For example, in roses inoculated with Rhizophagusirregularisduring drought stress conditions, the hydration of buds and the aesthetic look during drought stress did not significantly improve (Klingeman et al., 2005). Likewise, it has been observed that tomato plants inoculated with AMF during drought stress did not represent the differences in RWC, as compared to non-inoculated plants (García- Sánchez et al., 2014).

Membrane conductivity

Some studies have explained that the symbiosis with AMF induces the expression ofgenes coding for aquaporins (Ruiz-Lozano, 2003). In tobacco plants (Nicotiana tabacum L.), it has been explained that inoculation with AMF not only enhance the expression of genes coding for aquaporins, but also enhance the absorption of water by the plants (Porcel et al., 2005). In contrast, it was reported that, in lettuce (Lactucasativa L.) and soy plants (Glycine max L.) inoculated with F. mosseae and R. irregularis, the drought stress rapidly and intensely decline the expression of some aquaporin genes (PIP), as compared to the non-inoculated plants, presenting a less negative hydric potential and increase in RWC (Porcelet al., 2006). These marked differences in the expression could reflect differential mechanisms to modifyingthe hydraulic conductivity and avoiding loss of water at the cellular level.

Osmotic adjustment

It has been examined that most of the mycorrhizal plants have a better osmotic adjustment as compared to the non-mycorrhizal plants (Porcel and Ruiz-Lozano, 2004). For example, AMF colonization of pistachio (PistaciaveraL.) enhance the tolerance to drought by increasing accumulation of compounds for osmotic adjustment (Abbaspour et al., 2012).Sweet potato (Ipomoea batatas (L.) Lam.) plantsinoculated with a mixture of Glomus sp. and Acaulosporasp.reported a greater decline in the osmotic potential than non-inoculated plants, indicating higher osmotic adjustment ability (Yooyongwech et al., 2016). However, inoculation of plants subjected to drought stressnot 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 like 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. Nevertheless, some plants do not enhance proline concentration as a tolerance mechanism to drought stress. For example, mycorrhizal plants of the indian coral tree (Erythrina variegata L.) displayed very high tolerance to drought stress, associated with an accumulation of chlorophylls and carotenoids, but notthe proline content (Manoharanet al., 2010).

Antioxidant activity

Two important mechanisms have been proposed in order to explain the low oxidative damage in plants subjected to drought stress and inoculated with AMF. The first oneconsists of the direct absorption of water by hyphae and its transfer to the host plant, enhancing the water content and declining the generation of reactive oxygen species (ROS). Caravaca et al. (2005)reported that plants of Myrtuscommunis which are non-inoculatedand Phillyreaangustifoliasubjected to a drought stress increased their superoxide dismutase (SOD) and total peroxidase (POX) activity as compared to those of 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 drought stress conditions (Zou et al., 2014; Amiri et al., 2015). Recently, maize plants under drought stress 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). However, the exact mechanism involved behind is not yet clear and requires further moreexperiments to better understand the actual role of AMF in the changes of reactive oxygen metabolism and antioxidants production.

Higher nutrients absorption

It has been observed that the increase of pigment levels, stomatal conductance, rate of transpiration and CO2 assimilation rate in inoculated plants subjected to a drought stressis caused by a better nutritional supply. This would explain why the host plants of corn (Zea mayz L.) (Zhao et al., 2015) and loquat (Zhang et al., 2014) inoculated with different speciesof mycorrhiza and subjected to moderate and severe drought stress significantly enhance the contents of nitrogen (N), phosphorus (P) and magnesium (Mg) among others in shoots, as compared to the plants which are non-inoculated.However, thisparticular behaviour has not been observed in all plants. For example, it has beenreported that differences of various photosynthetic parameters reported 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.

As phosphorus is less mobile in soils with little amount of water, an increase in its acquisition as a consequence of association with AMF is very important for enhancement of water relations in host plants (Augé, 2004). It has also been observed that, althoughthe P absorption during drought stress 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 (Sorghumbicolor L.) and squash (Cucurbita pepo L.) (Augé etal., 2007). These variations in the absorption rate of P can enhance roots growth in comparison with non-inoculated plants (Miransari et al., 2007), which can be favorable for the uptake and nutrients uptake.

Nitrogen

AMF can makeN assimilation 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 the level of N status in inoculated plants is due to increasing N transport through hyphae, which also increases concentration of P, that is required for the phosphorylation of NR when there are low concentrations of N (Caravaca et al., 2005). Same way, 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 drought stress decrease photosynthesis because of an accumulation of ROS that damages the photosynthetic apparatus (Abbaspour et al., 2012), which can also limit the supply of NADPH and ATP to the Calvin cycle. As a consequence of AMF symbiosis, plants improve the water status, which enhances thephotosynthesis by increasing stomatal conductance and, therefore, CO2 fixing (Boldt et al., 2011). This relationship between the stomatal opening and the relative increase inthe 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 represent this relationship (Klingemanet al., 2005).On the other hand, high photosynthetic rates in inoculated plants subjected to drought stress can also be described 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 drought stress has been reported 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 manner, symbiosis avoids the photoinhibition and photodestruction of photosynthetic apparatus by ROS in stress conditions (Asrar and Elhindi, 2011), which has been concluded as a higher tolerance of inoculatedplants, as compared to non-inoculated plants.

A water stress decreases the efficiency of photosystem II (PSII) (Fv/Fm) and it has been reported that AMF have a positive impact (Sánchez-Blanco et al., 2004) or no impact (García-Sánchez et al., 2014) on this parameter. Rice (Ruíz Sánchez et al., 2010), sweet potato (Yooyongwech etal. 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 marked increases inFv/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 CO2 assimilation. This marked 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 also been observed that, in indian coral tree plants in a drought stress, the symbiosis with F. mosseaeenhances the contents of chlorophylls, carotenoids, and proteins, butalso reduces the contents of sugars, starches and proline (Manoharan et al., 2010). Likewise, in trifoliate orange (Poncirus trifoliata L.) in drought 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 marked increase in the sink strength of AM fungi, which conducts a greater removal of sugars from plants, increasing the demand for photoassimilates (Kaschuk etal., 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 important mechanisms, the firstwhich involves the competition from the AM fungi 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 impact of extraradical colonization on the water status of the mycorrhizated plants (Miransari et al., 2008). The second mechanism has AM fungi that enhancethe growth of the roots and the level of carbohydrates in the organ, altering its morphology and producing a greater area for absorption, which canbe considered a mechanism of tolerance for drought stress (Sánchez-Blanco et al., 2004; Caravaca et al., 2005; Roldán et al., 2008; Wu et al., 2008).

Finally, as has been demonstrated in various studies, AM fungi positively affect the plantgrowth, modifying the water balance and absorption of nutrient in a drough stress (Subramanian et al., 2006). As a consequence, AM fungi 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 economicbenefits, especially in crops which are of high commercial value (Borde et al., 2011).

2. Conclusion

AM fungi enhances the tolerance of plants to a drought stress; however, the complexity and diversity of responses caused due to the symbiosis against environmental stresses have prevented the establishment of a clear mechanism behind and appear to have differential modulations according to the species of AM fungi, plant species and the typical 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 drought stress and the impact that this one hasin its physiology and metabolism since the presence of an additional sink during a stress situation cannot always be supported by the plant. Thus, probably, only in a mild or moderate drought 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 drought stress as a result of multiple-level typecontrolled mechanisms, a more holistic approach is to be required to understand this phenomenon.

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