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Abscisic acid, and abscisic acid-induced water stress tolerance in mycorrhizal herbaceous and olive (*Olea europaea*) plants

Ácido abscísico, y tolerancia al estrés hídrico inducido por ácido abscísico en plantas herbáceas y de olivo (*Olea europaea*) micorrizadas

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ABSTRACT

The worldwide expansion of drought-affected areas has a negative effect on crop yield and production, making water stress the most significant abiotic stress, limiting plant growth and development. The use of arbuscular mycorrhizal fungi (AMF) is a strategy that mitigates the effects of this kind of stress in a sustainable way, which occurs due to the increased tolerance to water stress in plants inoculated with these fungi. Modern agriculture is facing the challenge of ensuring global food demand. However, climate change is causing an increase in temperature that leads to severe droughts in some areas. Numerous biotechnological techniques are being used to overcome this drought stress. Among them, the use of AMF is considered an efficient approach to mitigate such stress. AMF provide water stress tolerance through biochemical and physiological mechanisms. Some of the well-known mechanisms include modification of hormonal balances comprising strigolactones, abscisic acid, gibberellic acid, salicylic acid, and jasmonic acid. The symbiosis of AMF changes the expression of the aquaporins (water transporting channels) present in the plasma membrane and tonoplast, improving plant water status.

Keywords — Arbuscular mycorrhizas; olive; phytohormones; stress tolerance; water stress.

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RESUMEN

La expansión de áreas afectadas por la sequía en el mundo tiene un efecto negativo en el rendimiento y la producción de cosechas, haciendo que el estrés hídrico sea el estrés abiótico más significativo que limita el crecimiento y desarrollo de las plantas. El uso de hongos micorrízicos arbusculares (HMA) es una estrategia que alivia los efectos de este estrés de una manera sostenible. Esto es debido al incremento en la tolerancia al estrés hídrico en plantas inoculadas con estos hongos. La agricultura moderna está enfrentando el desafío para asegurar una demanda global de alimentos. Sin embargo, el cambio climático está causando un incremento de temperatura que conduce a la producción de severas sequías en algunas áreas. Numerosas técnicas biotecnológicas se están utilizando para superar los efectos producidos por este estrés. Entre ellas, se piensa que el uso de los HMA es un excelente enfoque para reducir tales efectos. Los hongos micorrízicos arbusculares proveen tolerancia al estrés hídrico por medio de mecanismos bioquímicos y fisiológicos. Algunos de los mecanismos incluyen la modificación de los balances hormonales comprendiendo los ácidos abscisico, giberélico, salicílico y jasmónico, y las strigolactonas. La simbiosis de los HMA cambia la expresión de las acuaporinas (canales que transportan agua) de la membrana plasmática y el tonoplasto, lo cual mejora el estado hídrico de la planta.

Palabras clave — Estrés hídrico; fitohormonas; micorrizas arbusculares; olivo; tolerancia al estrés.

INTRODUCTION

Anthropogenic activities, such as desertification, imprudent utilization of water and industrialization lead to pollution and consequently cause climate changes (Perera & Nadeu, 2022). Climate change is multi-faceted, and includes changing concentrations of greenhouse gases in the atmosphere, rising temperatures, changes in precipitation patterns, and increasing frequency of extreme weather events (e.g., Sisco *et al.*, 2017).

Plant growth is controlled directly by plant water stress and only indirectly by soil water stress. Plant water stress depends on the relative rates of water absorption and water loss rather than on soil water supply alone. Therefore, it is not safe to assume that a given degree of soil water stress always will be accompanied by an equivalent degree of plant water stress. Plant water stress should be measured directly in research on the effects of water supply on plant growth and plant processes if the results are to be interpreted correctly. In this review, we focused on the effects of water stress on plant developmental processes (e.g., phytohormones production), and on the phytohormones-induced water stress tolerance in mycorrhizal olive plants. Drought is one of the most important factors that limits crop production worldwide (Qi *et al.*, 2022). For example, approximately 67% of crop losses were reported in the U.S.A. due to drought stress during the last 50 years. Severe drought conditions determine increasing and forcing up food prices. On the other hand, world population is increasing day by day and may reach over 9.8 billion in 2050 (United Nations, 2017). Fulfilling food requirements of a burgeoning population, the agriculture food must be increased up to 70% (Sah *et al.*, 2016). We need to develop technologies and

policies regarding climate change and drought stress, efficient water use, control of the growing human population, and production of drought-tolerant crops.

In response to water stress conditions, plants have evolved biochemical mechanisms to maintain constant cellular water potential and/or relative water content (Soltys-Kalina *et al.*, 2016). These processes are controlled by numerous phytohormones which are the basic mediators to tolerate or avoid the negative effects of water stress. This review mainly focuses on the abscisic acid-induced drought tolerance in mycorrhizal herbaceous and olive plants.

PHYTOHORMONES

Phytohormones are the key regulators of plant growth and developmental processes as well as crucial for biotic and abiotic stress response throughout their life cycle (Sah *et al.*, 2016; Ullah *et al.*, 2017). In addition to various other phytohormones, abscisic acid (ABA) is considered the main hormone which intensifies water stress tolerance in plants through various morpho-physiological and molecular processes including stomata regulation, root development, and initiation of ABA-dependent pathways (Aslam *et al.*, 2022). Phytohormones perform as chemical messengers in response to various abiotic stresses, like water stress. After stress signal perception, phytohormones release which activate various plant physiological and developmental processes including stomatal closure, root growth stimulation, and accumulation of osmolytes to avoid water stress conditions (Fahad *et al.*, 2016).

ABA is a weak acid that was first isolated as an abscission-accelerating substance (Lee *et al.*, 2021). ABA, which is not directly involved in the process of abscission, is a major stress hormone that participates in various crucial physiological processes during the plant life cycle, including stress responses, development and reproduction (Dong *et al.*, 2015). ABA is synthesized in the plastids and cytoplasm and derived from zeaxanthin, a plant pigment. A cluster of NCED (9-cis-epoxycarotenoid dioxygenase) genes are thought to be involved in ABA synthesis (Huang *et al.*, 2015). There are other phytohormones (e.g., jasmonic acid, salicylic acid, ethylene, auxins, gibberellins, cytokinins, and brassinosteroids) that congregate the challenges of water stress (Chen *et al.*, 2017; Liu & Zhang, 2017; Lo *et al.*, 2017). However, these hormones are usually cross talk with each other to increase the survival of plants under water stress conditions (Verma *et al.*, 2016). On the other hand, the transgenic approach is currently the most accepted technique to engineer the genes responsible for the synthesis of phytohormones in response to water stress.

Osmotic stress promotes the synthesis of ABA, which activate gene expression and adaptive physiological changes (Rowe *et al.*, 2016). ABA levels increase during stress conditions and decrease when stress is relieved. In addition, ABA concentration is higher in the younger than in the mature leaves. As leaves develop and mature, the ABA concentration declines and older leaves export ABA to younger ones. At the same time, the sensitivity of stomata to ABA increases throughout leaf development (Haworth *et al.*, 2018). Upon stress arrival, signal perception occurs through the plasma membrane, ABA synthesis is initiated, which occurs mostly

in the plastids, with the exception of xanthoxin conversion to ABA, which takes place in the cytoplasm (Ma *et al.*, 2018). Generally, ABA synthesis occurs in the roots. It is then transported via vascular tissues, and it shows responses in a variety of cells, such as guard cells and others (Postiglione & Muday, 2020). ABA must be translocated from the cells where it is synthesized via intercellular transport into the neighboring tissues (Silva, 2020). As a weak acid, ABA is a charged anion (i.e., ABA⁻) in the cytoplasm (pH 7). In the more acidic cell wall (pH 5.5), some is left uncharged (ABAH). This presumably enhances the movement of ABA into but not out the cells, while cell-to-cell ABA transport is enhanced by transporters [i.e., plasma membrane-bound ATP-binding cassette (ABC) transporters, which hydrolyze ATP to transport it, and a family of low-affinity nitrate transporters]. ABA perception and signal transduction are mediated by two pathways, which are ABA-dependent and ABA-independent. Water stress predominantly induces gene expression through the initiation of an ABA-independent pathway (Soma *et al.*, 2021). These pathways have been reviewed in detail (Kuromori *et al.*, 2018).

ABA-dependent signaling pathways play a critical role in stress-responsive gene expression during various stresses, especially osmotic stress. ABA receptors are important elements for ABA signal transduction. Various receptors have been identified in different sub-cellular compartments, including the plasma membrane, nucleus, cytosol, and chloroplast envelope. ABA content is low under normal conditions, and SnRK2 protein kinase activity is inhibited by PP2C phosphatases, which leads to dephosphorylation. The cellular ABA level increases when plants are exposed to water stress, and ABA then binds to PYRABACTIN RESISTANCE1/PYR1- LIKE/REGULATORY COMPONENTS OF ABA RECEPTORS (i.e., PYR/PYL/RCARs, respectively) which in turn bind and inactivate protein phosphatases 2C (PP2Cs, Ullah *et al.*, 2017). Thus, PYR/PYL/RCARs are necessary for ABA responses, and various genes encode these receptors. The sucrose nonfermenting 1-related protein kinase 2 (SnRK2s) is auto activated when it dissociates from PP2Cs. The SnRK2s are protein kinases that promote ABA responses (Yang *et al.*, 2019); SnRK2.2, SnRK2.3, and SnRK2.6 have been proven to be involved in ABA response (Hasan *et al.*, 2022). In addition, there are 76 PP2Cs in *Arabidopsis* but only clade A participates in ABA signaling (Wang *et al.*, 2023). Even more, ABA-dependent signaling pathway has several branches controlled by various transcription factors including MYB, MYC and NAC. In addition, ABA-responsive elements (ABREs) are also involved in ABA signaling (de Ollas & Dodd, 2016). Calcium-dependent protein kinases (CDPKs) also participate in ABA signaling (Shi *et al.*, 2018). Two CDPKs (i.e., CPK4 AND CPK11) have been reported to be involved in the regulation of ABA signaling in *Arabidopsis* (Shi *et al.*, 2018). Activated SnRK2s phosphorylate downstream targets and trigger ABA-induced physiological and molecular responses including germination, stomata regulation, root development and photosynthesis (Wang *et al.*, 2018). ABA regulates many stress-related genes to enhance water stress tolerance in plants (Shen *et al.*, 2017).

ARBUSCULAR MYCORRHIZAL FUNGI

AMF belong to the phylum Glomeromycota, encompassing ten out of eleven families: Acaulosporaceae, Ambisporaceae, Archaesporaceae, Claroidoglomeraceae, Diversisporaceae, Gigasporaceae, Glomeraceae, Pacisporaceae, Paraglomeraceae, and Sacculosporaceae (<http://www.amf-phylogeny.com/>, accessed on 1 June 2023). Given their status of obligate biotrophs, the AMF life cycle cannot be completed in the absence of host plants. It starts with an asymbiotic phase, during which spores germinate in response to physical factors such as moisture, temperature and pH, producing hyphae with a limited lifespan (Giovannini *et al.*, 2020). In the presence of root exudates from host plants, a differential hyphal morphogenesis occurs, with germling hyphae reorienting the direction of elongation and initiating a differential branching pattern (Giovannini *et al.*, 2020): this pre-symbiotic phase is followed by physical contact between AMF hyphae and host roots, with the differentiation of appressoria, which give rise to hyphae growing intercellularly within the root cortex, eventually penetrating in root cells and producing highly branched hyphal tree-like structures similar to haustoria, the arbuscules. The extraradical hyphae of AMF of one plant root system forage for the soil nutrients and induce the root colonization of the nearby plants, which leads to the formation of common mycorrhizal networks that interconnect roots (Busso & Busso, 2022). Inoculation with AMF can increase the root length, surface area and volume of seedlings in nutrient-limited karstic soils. Mycorrhizal symbioses can secrete glomalin to help promoting soil aggregates for water and nutrients storage, through an extended hyphae to absorb water and nutrients from long distances. AMF can boost rhizosphere soil enzyme activities, and may help to drive carbon sequestration. AMF also improve plant growth by advancing soil quality through influencing its structure and texture. As a result, AMF and CMNs benefit plants through improving soil quality and enhancing morphological (e.g., hyphal length, tillering, number of stolons per individual), physiological (e.g., water use efficiency) and productive (e.g., fresh and dry shoot and root weights) traits (Busso & Busso, 2022).

As obligate biotrophs, AMF receive photosynthetic products and lipids from root cells (Giovannini *et al.*, 2020). When addressing the regulation of such an intimate plant-microbe interaction as AMF, plant hormones are primer targets. The colonization of a plant root by AMF often improves growth and stress tolerance of the whole plant, besides the most important feature of the mutualistic symbiosis (Begum, 2019). In particular, AMF can alleviate water stress conditions. Indeed, a number of cases have been reported where the beneficial effects of AMF on plant performance became apparent under water stress conditions (Chen *et al.*, 2020). Although reports are not unanimous on this point, the beneficial consequences of AMF colonization regarding water stress seem to contribute not only towards a better mineral nutrition of plants, but encompass a more direct improvement of the plant water status. In addition, reduced levels of ABA and, accordingly, improved photosynthetic parameters have been described for above-ground parts of AMF plants (Ren *et al.*, 2019). Given this context, it makes sense that root ABA is necessary for a sustained colonization by AMF. This might ensure that roots become colonized

particularly strongly when it is most needed (i.e., under water stress conditions, when ABA levels are high).

AMF produce changes in isoprenoids content in leaves of some plant species, favoring the production of essential instead of nonessential isoprenoids, especially in water stress conditions or after jasmonic acid applications (Karunanantham *et al.*, 2022). 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 conditions (Goyal *et al.*, 2020). Contrasting effects have been observed for ABA concentrations in mycorrhizal plants exposed to water stress conditions, which reflects the complexity of interactions. In some plant species, the beneficial effect of symbiosis with AMF under stress conditions has been attributed to increases of transpiration and water absorption by roots (Busso & Busso, 2022) and it is associated with lower concentrations of ABA (Torres *et al.*, 2018). However, in some plant species, water stress has significantly increased the ABA content, with or without mycorrhizal colonization (Ouledali *et al.*, 2019). It has been determined that, in water-deficit stress conditions, the symbiosis with AMF regulates the ABA content (Liang *et al.*, 2021). In fact, in some plant species, ABA increases the susceptibility of plants to AMF colonization and appears to play an important role in the development and functionality of arbuscules (Chareesri *et al.*, 2020).

Strigolactones correspond to a new class of plant hormones that regulate the architecture and reproductive development plants (Zwanenburg *et al.*, 2016), 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 (Goyal *et al.*, 2020). One of the possible roles of ABA comes from its regulating effect on the strigolactone concentrations (Visentin *et al.*, 2020).

The biochemical and molecular responses to AMF colonization in host plants also include the activation of the jasmonic acid signal pathway (Bahadur *et al.*, 2019). Particularly, jasmonic acid appears to be involved in the stress signal in mycorrhizal plants through an increase of ABA concentration (Wang *et al.*, 2020). Gibberellic acids modulate arbuscule formation in a dose-dependent manner (Liao *et al.*, 2018). The narrow relationship found between ABA and AMF colonization in water stress conditions, and the functionality of the arbuscules suggests that the association between AMF and some plants could be one strategy to deal with a water stress, probably regulated by the interaction of ABA with other hormones.

There are involved a complex sequence of events and intracellular modifications in the fungal penetration and establishment in the host roots (Carotenuto *et al.*, 2019). Compatibility between plant roots and AMF implies a clear and selective recognition by the plant host that distinguishes the beneficial effects of the AMF. The elucidation of the recognition mechanisms and molecules involved in the AMF interaction is the key to understanding the phenomenon of compatibility. Biochemical and morphogenetic events mediated by phytohormones during AMF formation have been suggested in this context, and certain roles for phytohormones have been suggested in AMF (Liao *et al.*, 2018). In the colonization of a plant root by

AMF, that not only improves growth and stress tolerance of the whole plant, there have been implicated alterations in the homeostasis of plant hormones. There are a large number of publications showing that the levels of plant hormones like ABA, strigolactones, gibberellic acids, and auxin actually change upon the establishment of AMF (Liao *et al.*, 2018; Bahadur *et al.*, 2019).

PHYTOHORMONES-INDUCED WATER STRESS TOLERANCE IN MYCORRHIZAL HERBACEOUS AND OLIVE (*OLEA EUROPAEA*) PLANTS

Some plant species evolved to avoid water stress whereas others adopted water stress tolerance strategies, like the olive (Kokkotos *et al.*, 2020). In this respect, root colonization by AMF plays a crucial role in the response of plants to water stress (Bahadur *et al.*, 2019). It allows an integrative water stress response combining avoidance and tolerance strategies (Rapparini & Peñuelas, 2014).

A key factor in the response of olive trees to water stress is the presence of AMF in the soil (Calvo-Polanco *et al.*, 2016). Under constraining conditions, mycorrhizas improve the resilience of plants against environmental stresses like water stress, AMF also improve the growth of olive trees and their resistance to transplantation stress (Bizos *et al.*, 2020). Crucial factors to reach high productivity of olive trees is the enhancement of soil fertility and the fulfillment of its water requirements (Merwad *et al.*, 2015). This plant species is known for its strong tendency for alternate bearing, with higher yields produced every second year. This tendency is enhanced by low fertility, high temperatures and water stress (Kour *et al.*, 2018). Ennajeh *et al.* (2006) reported various morphological and physiological traits involved in the plant resistance to water stress in the leaves of the olive cultivars 'Meski' (water stress sensitive) and 'Chemalali' (water stress tolerant). The relative water content (RWC), net photosynthesis rate and stomatal conductance decrease in the leaves of both cultivars by withholding irrigation. Since this decrease was greater in 'Meski' than in 'Chemalali', the former cultivar was more sensitive to water stress. Leaf trichome and stomatal densities were higher in 'Chemalali' than in 'Meski'. However, the desiccation curves were comparable when leaves of both cultivars were kept in the dark. This implied that the two varieties had similar leaf cuticle transpiration. Leaves of both cultivars accumulated soluble sugars and proline under severe water stress, possible for osmotic adjustment. Both cultivars showed the same levels of RWC at which soluble sugar concentrations started to increase and decline. However, more soluble sugars were accumulated by the leaves of the 'Meski' variety. Lower soluble sugar and higher proline concentrations were determined on detached than attached leaves of 'Chemalali'. The authors suggested that it was possible that soluble sugars were diverted to proline synthesis in response to injury. The RWC levels at which proline accumulation started and ended were higher in 'Meski' than in 'Chemalali'. In the study of Ennajeh *et al.* (2006), high leaf trichome and stomatal densities and effective osmotic adjustment with proline may explain the greater water stress tolerance in 'Chemalali' than in 'Meski'.

The role of mycorrhizas in plants' response to water stress has been well documented in olive trees (Calvo Polanco *et al.*, 2016). The contribution of AMF to plants' tolerance of water stress is partly due to the larger volume of soil explored by roots and the extra-radical hyphae (Zhang *et al.*, 2016), and more efficient stomatal regulation by controlling the ABA metabolism (Torres *et al.*, 2018). Bizos *et al.* (2020) reported that the AMF species *Rhizophagus irregularis* and *Glomus mosseae* stimulated the root growth improving the resistance of olive plants to environmental and transplantation stresses. However, Bompadre *et al.* (2014) inoculated olive plants with two strains of the AMF *Rhizophagus irregularis* (GC2 and GA5), which have different strategies of colonization *in vitro* and in soil conditions. The GC2 strain had a high density of external mycelium, slow growing at the beginning of *in vitro* culture which increase with the proportion of mycelium ramification, and few number of big spores ($160.52 \pm 19.8 \text{ cm}^2$; $87.4 \pm 0.4 \text{ }\mu\text{m}$) (Silvani, 2011). Its spores and mycelium are limited to the vicinity of the roots where the colonization takes place. In contrast, GA5 presents little external mycelium at the beginning of culture but then increases its density forming a mycelium little branched, has a higher growth rate, and its spores are smaller and more abundant than GC2 ($293.4 \pm 81.8 \text{ cm}^2$; $70.8 \pm 0.5 \text{ }\mu\text{m}$) (Silvani, 2011). In olive seedlings, AMF increase growth, nutrients uptake, and root hydraulic conductivity (Calvo-Polanco *et al.*, 2016). They also help to reduce damage due to soil dryness by the activation of antioxidant defenses (Sepahvand *et al.*, 2021). Under field conditions prevalent in semi-arid olive-growing areas in southwestern Argentina there might be fairly long periods of water stress interrupted by sporadic torrential rains of spring and summer.

A wide variety of biotic and abiotic stresses needs to be overcome by plant species which affect their growth, development and production. Within the major factors that will determine those parameters is water stress. Within the Phyto-geographical Province of the southern "Caldenal", in southwestern Argentina, are common, large oscillations in total annual rainfall and water stress episodes (Peláez *et al.*, 2021). Olive orchards in this region includes water stress-tolerant cultivars. This is because they have morpho-anatomical adaptations and physiological and biochemical defense mechanisms (Ennajeh *et al.*, 2006; Khabou *et al.*, 2014). These olive cultivars differ in their water stress tolerance which can be exploited to improve their performance under water stress (Ennajeh *et al.*, 2009). Mycorrhization has been evaluated as a promising biological approach to mitigate the impact of water stress on the productivity of olive trees. Several studies have shown that mycorrhiza have a large beneficial effect on several aspects of plant physiology like root growth and morphology (Jaborova *et al.*, 2021). Chandrasekaran (2022) reported that mycorrhizal inoculated plants were less affected by water deficiency than those non-inoculated through developing more root biomass. Their results highlight the importance of the production of mycorrhizal plants to alleviate the field water stress mainly in arid and semiarid areas.

By modulating metabolic and physiological processes, plants adapt to their environment. They may interact with some organisms through symbiotic associations to allow this adaptation. The AMF symbiosis is beneficial for the plant under water stress conditions. AMF may influence the hormonal balance of the plant to

determine an integrated response to water stress. For example, the olive trees form beneficial associations with AMF (Ouledali *et al.*, 2018). ABA is a major phytohormone that can be induced by AMF colonization in water stress-stressed olive plants (Ouledali *et al.*, 2019). The plant's resistant to water stress is reinforced by AMF (Xu *et al.*, 2018).

The key phytohormone modeling the stomata behavior under water stress conditions is ABA (Ouledali *et al.*, 2019). However, Ouledali *et al.* (2019) reported that in AMF-inoculated plants of the olive cultivar 'Zarrazi', the ABA amount increased under moderate water stress and even further under water relief, but decreased under severe water stress. However, stomatal closure was not correlated with leaf ABA content in the study of Ouledali *et al.* (2019). The results of these authors showed that ABA is not the key factor controlling the stomatal closure in these AMF-inoculated olive plants under water stress conditions. They indicated that other AMF-related factors are involved in the control of stomata regulation in mycorrhizal olive plants exposed to severe water stress conditions, allowing a suitable stomata behavior.

In AMF-inoculated olive plants of the cultivar 'Zarrazi', water stress caused a decrease in conductance and leaf transpiration rate. Guard cells respond to various stimuli including plant hormones and elicitors (Agurla *et al.*, 2017). The major plant hormone inducing stomatal closure is ABA (Ouledali *et al.*, 2019). On the other hand, Hu *et al.* (2013) indicated that exogenous application of a synthetic cytokinin on *Poa pratensis* L. promoted stomatal reopening following drought-induced closure, leading to an enhanced stomatal conductance. Ren *et al.* (2019) reported that higher stomatal conductance rates are associated with lower ABA content in the leaves in mycorrhizal plants. In turn, Schmidt *et al.* (2017) reported that the arbuscular mycorrhiza fungus *Rhizophagus intraradices* increased the concentrations of numerous cytokinins in the leaves of the C₄ perennial grass *Miscanthus × giganteus* J.M. Greff & Deuter. AMF-symbiosis can thus influence the production of ABA and cytokinins in roots exposed to drying soil to regulate stomatal opening and limit water loss (Hu *et al.*, 2013; Schmidt *et al.*, 2017; Ren *et al.*, 2019). AMF-inoculated plants can regulate better their ABA level than AMF-non-inoculated plants (Ruiz-Lozano *et al.*, 2009). This results in a suitable balance between leaf transpiration and root water uptake during water stress. AMF-symbiosis could modulate the stomatal behavior through the regulation of the 14-3-3 genes in the ABA signaling pathway to improve water stress tolerance (Xu *et al.*, 2018). Therefore, the results of Ouledali *et al.* (2019) suggest that AMF-inoculation of the olive cultivar 'Zarrazi' helped somehow to maintain transpiration and stomatal conductance in plants of that cultivar under water stress conditions.

When water stress was moderate, and in the leaves of the AMF-inoculated olive plants of the cultivar 'Zarrazi', stomata closure was well correlated with ABA accumulation. Nevertheless, AMF-inoculated olive plants closed their stomata despite the lower leaf ABA concentrations under severe water stress (Ouledali *et al.*, 2019). These authors suggested the eventual presence of an AMF-dependent signal replacing ABA in olive when dehydration is severe. The lower ABA concentration may be caused by a (1) negative feed-back exerted by the AMF-induced signal on the ABA-biosynthesis pathway, or (2) competition for a shared common precursor

between ABA and the signal. Parwez *et al.* (2022) reported the role of ABA in regulation of different physiological mechanisms through integration of environmental cues via its positive and negative crosstalks with other phytohormones (like auxin, gibberellin, cytokinin, ethylene, salicylic acid, brassinosteroids, jasmonic acid, strigolactones, and melatonin). Munemasa *et al.* (2019) showed that the ethylene signaling inhibits jasmonate signaling as well as ABA signaling in guard cells of *Arabidopsis thaliana*, and revealed the signaling crosstalk mechanism. Both an ethylene precursor 1-aminocyclopropane-1-carboxylic acid, and an ethylene-releasing compound ethephon, induced transient stomatal closure, and also inhibited methyl jasmonate-induced stomatal closure as well as ABA-induced stomatal closure. While the ethylene inhibition of methyl jasmonate-induced stomatal closure was abolished in the ethylene-insensitive mutant *etr1-1*, the methyl jasmonate-induced stomatal closure was impaired in the ethylene-overproducing mutant *eto1-1* of *Arabidopsis* (Munemasa *et al.*, 2019).

Canales *et al.* (2021) explored the strategy set up by two oat cultivars to cope with drought based on root morphological, anatomical, physiological and molecular studies. These authors found a dramatic and rapid ABA increase in the susceptible genotype resulting in a tight and rapid reduction of stomatal conductance; despite this, leaf water potential decreased concomitantly due to a decrease in the root hydraulic conductivity. Contrarily, the resistant genotype, showed a mild and slow increase in ABA that allowed maintaining transpiration longer. They linked this response to an increase in root hydraulic conductance through an increase in total root length, in the length of the thinnest roots and a rise in root conductivity. Ren *et al.* (2019) reported that under water-stressed conditions, inoculation of *Zea mays* with *Funneliformis mosseae* greatly reduced leaf ABA content, and postponed the decline in photosynthetic rate, stomatal conductance and osmotic adjustment. Ouledali *et al.* (2019) informed that leaf transpiration rate and stomatal conductance became very low in the mycorrhizal olive cultivar Zarrazi, and reached zero in non-mycorrhizal plants, when dehydration became severe. Therefore, in this water stress tolerant cultivar, stomatal regulation was efficient (Ouledali *et al.*, 2018).

AMF symbiosis induces strigolactone biosynthesis under water stress and improves water stress tolerance in lettuce and tomato (Ruiz-Lozano *et al.*, 2016). Both being derives from carotenoids, strigolactones share their biosynthetic precursors with ABA (Stauder *et al.*, 2018). ABA functions at multiple levels to regulate the symbiosis with AMF (Martín-Rodríguez *et al.*, 2016). Liu *et al.* (2015) proposed that a transcriptionally regulated, early strigolactones decrease under osmotic stress is needed (but not sufficient) to allow the physiological increase of ABA in roots. Visentin *et al.* (2016) in tomato showed that genetic strigolactone depletion may affect ABA concentration and stomatal sensitivity to ABA. Thus, stomatal regulation under water stress in olive could partially be modulated by an AMF-dependent interplay between ABA and strigolactones.

Formenti & Rasmann (2019) informed that the mechanisms of AM fungal-mediated increased resistance include a manipulation of the hormonal cascades, such as the systemic activation of jasmonic acid dependent defenses. AMF colonization of trifoliolate orange (*Poncirus trifoliata*) by *Funneliformis mosseae* notably regulated the

changes in root phytohormone levels under drought conditions (Liu *et al.*, 2017). This was by increasing the indole-3-acetic acid, ABA, methyl jasmonate, zeatin riboside, and brassinosteroids concentrations (Liu *et al.*, 2017). These results concluded that AMF enhanced drought tolerance in trifoliolate orange through modulation of root phytohormones. Herrera-Medina *et al.* (2007) demonstrated that ABA contributed to the susceptibility of tomato to infection by AM fungi, and that it seems to play an important role in the development of the complete arbuscule and its functionality. The narrow relationship found between ABA and AMF colonization under water stress conditions, and the functionality of the arbuscules, suggests that the association between AMF and some plants could be one strategy to deal with water stress, probably regulated by the interaction of ABA with other hormones. Liao *et al.* (2018) informed a new component of the ABA pathway, the Protein Phosphatase 2A (PP2A) holoenzyme subunit, *PP2AB'1*. They reported that the positive effect of ABA on the AMF colonization, requires a Protein Phosphatase 2A (PP2A) holoenzyme subunit, *PP2AB'1*. Thus, ABA signaling appears to play an important positive role in AMF colonization, and this function is predominantly via the promotion of the PP2A holoenzyme complex.

Ouledali *et al.* (2018) either inoculated or not one-year-old olive plants with AMF and exposed these plants to a 40-day-water stress period. They showed that mycorrhizal plants were less affected by water stress than non-mycorrhizal plants proving the involvement of the AMF in the alleviation of the water stress impact on olive tree. The turgor potential in mycorrhizal plants exhibited positive values during the whole treatment period, while it was negative in non-mycorrhizal plants mainly under severe stress intensity. Moreover, the stomatal function was less affected by water stress in mycorrhizal than in non-mycorrhizal plants. The maximum of mycorrhizas relative water stress alleviation rate (RDAR) was estimated to be 40% for relative water content, 36% for the osmotic potential, 86% for turgor pressure, 16% for stomatal conductance and 27% for leaf transpiration rate. The osmotic adjustment by proline was earlier in mycorrhizal than in non-mycorrhizal plants. The inoculation with AMF also improved the mineral uptake of K, N, Zn and Fe. After 40 days of water stress, mycorrhizal olive plants survived but non-mycorrhizal plants did not. Thus, inoculation of young olive trees with the AMF improved their resilience to drought.

CONCLUSION AND FUTURE CONSIDERATIONS

The tolerance of plants to water stress is increased by AMF. However, the symbiosis under environmental stresses have caused a complexity and diversity of responses. In turn, this have prevented the establishment of a clear mechanism and it appears to have different modulations according to the species of AMF, the plant species, and the conditions under which the symbiosis is set. The plant susceptibility to a water stress, and the effect that this one has on its physiology and metabolism because of the presence of an additional sink during a stress condition, cannot always be supported by the plant. This is another important component in the complexity of

this relationship. Therefore, it is likely that where the symbiosis quickly generates a benefit for the plant, the symbiotic association is advantageous, only under exposure to a mild or moderate water stress. For many mycorrhizal plants, it has been confirmed an increase in water stress tolerance as a consequence of multiple-level controlled mechanisms. This indicates that a more holistic approach is required to understand this phenomenon.

To cope with water stress, novel and dynamic approaches are currently desirable; thereby, engineering genes responsible for phytohormones synthesis could be a great approach to maintain and improve the productivity.

So far little progress has been made at the molecular level to understand the mechanisms of this miraculous organism which include the involvement of aquaporins, some binding protein genes (BiPs), mitogen-activated protein kinase (MAPK) pathway genes, and stress responsive genes like proline dehydrogenase, invertase, proline synthetase, etc. However, with the advancement of new age molecular techniques it seems possible that the unravelling of this mystery is not far away.

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