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Biochemical and physiological mechanisms allowing olive trees to survive and produce under water stress conditions

Mecanismos bioquímicos y fisiológicos que le permiten sobrevivir y producir a los árboles de olivo expuestos a condiciones de estrés hídrico

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ABSTRACT

The beneficial properties of olive (*Olea europaea* L.) edible fruits and their oil play an important part in our diet. Severe summer conditions, including low rainfall, excessive heat load and high daily irradiance, characterize arid and semiarid regions where olive is produced. Although it is highly aggravated by other stresses, water stress is usually the most critical during summer-time. Under severe water stress conditions, a cultivar of any olive tree needs specific biochemical and physiological mechanisms in order to survive and be productive. It is well-known that these water stress resistance mechanisms generally act simultaneously. Nevertheless, water stress adaptability not only integrates the water stress resistance concept (i.e., escape, avoidance and/or tolerance to water stress) but also the recovery capacity. All of them play a major role in plants' growth and survival, especially when plants are continuously exposed to repeated events of water stress and adequate water levels during their lifetime. Water stress, heat and high irradiance, especially in association with each other, also damage plant functions. As a result, different resistance mechanisms are adopted by plants. This review summarizes each of these mechanisms.

Keywords — *Olea europaea*; drought; water stress; resistance mechanisms.

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RESUMEN

Las propiedades benéficas de los frutos comestibles del olivo (*Olea europaea* L.) y su aceite han tenido un rol importante en nuestra dieta. Las regiones árida y semiárida donde se produce el olivo están usualmente caracterizadas por condiciones severas de verano, incluyendo poca lluvia, calor excesivo y alta irradiación a menudo diariamente. Entre los constituyentes del estrés durante el verano, el estrés hídrico es usualmente el más crítico, aunque el mismo es altamente exacerbado por los otros. Bajo condiciones severas de estrés hídrico, un cultivar de cualquier árbol de olivo puede necesitar mecanismos bioquímicos y fisiológicos específicos que le permitan sobrevivir y ser productivo. Se conoce bien que estos mecanismos de resistencia al estrés hídrico generalmente actúan simultáneamente. De todas formas, la adaptación al estrés hídrico integra mucho más que el concepto de resistencia al mismo (dado por mecanismos que permiten el escape, o la evitación y/o tolerancia al estrés hídrico). La capacidad de recuperación también juega un rol fundamental en el crecimiento y supervivencia de las plantas. Esto toma especial importancia cuando las plantas están continuamente expuestas durante su vida a ciclos repetidos de estrés hídrico y niveles adecuados de agua después del mismo. Aunque se considera que la estrés hídrico es el principal factor estresante, otros como el calor y la alta irradiancia, especialmente en asociación mutua, también reducen las funciones de la planta. Como resultado, diferentes mecanismos de resistencia son adoptados por la vegetación terrestre. Esta revisión resume cada uno de estos mecanismos.

Palabras clave — *Olea europaea*; sequía; estrés hídrico; mecanismos de resistencia.

INTRODUCTION

The cultivation of olive trees has played a vital role on human nutrition. The beneficial properties of the edible fruits and their oil have played an important part in our diet. This may be one of the reasons why Argentina is currently the main producer and exporter of olive oil in South America. Olive yield raises to 40.000 tn and 37.200 tn. are exported on average, occupying the eleventh and sixth place in the world, respectively. The main countries where the olive oil is directed to are The United States, Spain and Brazil (Lupín *et al*., 2018). To a national level the consumption of olive oil is of 7.500 tn (Roldán, 2020).

In the southwestern region of the Buenos Aires Province can be found the semiarid, arid and subhumid-arid pampas where olive trees are cultivated. The olive growing in this region is an activity which did not arrest its growth since the end of the decade of 1990 (Goñi, 2020). The culture of olive is ecologically suitable in this region (Lupín & Picardi, 2016). The olives generate income for the involved enterprises, growth of the gross product, and a positive environmental effect, which contribute to the welfare of the population of the region in the long-term (Picardi de Sastre *et al*., 2015). The Ingeniero White seaport in Bahía Blanca provides a competitive advantage to the region. This port has the greatest depth in the country, an adequate transporting system, and the provision of associated services necessary for the marketing and general development of the activity (Cincunegui *et al*., 2019). In 2016, 48 agropecuarian settlements were established in the region with 2.598 ha of implanted olives.

Large oscillations in total annual rainfall are common in southwestern Buenos Aires, Argentina (Busso & Fernández, 2018). As a result, olive orchards include water stress-tolerant species in this region. This is because they have physiological, biochemical, and morpho-anatomical adaptations (Ennajeh *et al*., 2006; Karimi *et al*., 2018). Since these species differ in their water stress tolerance, this can be exploited to improve the performance of olive cultivars under water stress (Ennajeh *et al*., 2009).

Knowledge of the main biological factors influencing final harvest is becoming increasingly necessary to obtain reliable crop estimates, and thus ensure optimized, effective private crop management. This knowledge is also of great value to public agricultural institutions for the planning of government subsidies (Sinclair and Seligman, 2000). Effective olive crop forecasting is proving to be essential in optimizing human and economic resources for olive-fruit harvesting, marketing strategies and global commercial distribution.

Drought defense mechanisms generally act simultaneously (Elhami *et al*., 2015). Under severe drought conditions, a cultivar of any olive tree may need morphological, physiological, biochemical and/or anatomical modifications in order to survive and be productive. Drought adaptability integrates much more than the drought resistance concept (i.e., drought escape, drought avoidance and drought tolerance). Recovery capacity also plays a fundamental role in plants' growth and survival. This takes special importance where plants are continuously exposed to repeated cycles of drought re-watering during their life. Nevertheless, compared to development during drought, the study of recovery has been often neglected. Although drought is considered the primary stressor, others such as heat and high irradiance, especially in association with each other, also impairs plant functions and, therefore, different resistance mechanisms are adopted by plants. This review summarizes each of these mechanisms.

MECHANISMS WHICH AFFECT OLIVE CULTIVAR PERFORMANCE UNDER WATER STRESS

Biochemical-Physiological.— High water-use efficiency and net photosynthetic rates under water stress are often sought as mechanisms to select olive drought-resistant cultivars (Brito *et al.*, 2019b). The variability in water stress tolerance of plants can be reflected by differences in photosynthetic intensity under different leaf water potentials (Bhusal *et al*., 2019). Resistance to water stress requires a series of coordinated events, such as osmotic adjustment; it prevents the occurrence of oxidative stress damage and maintain the native structures of macromolecules and membranes (Parvanova *et al*., 2004). Osmoregulation occurs in most plant species under limiting water conditions (Ozturk *et al*., 2020). However, the extent of this adjustment is species-, and even cultivar-dependent (Abdallah *et al*., 2017). Indeed, low soil-water potentials induce plants to accumulate various compatible osmolytes such as soluble sugars and amino acids (Ahmad *et al*., 2014). Sugars are the first compounds responsible for osmoregulation in leaves (Santos *et al*., 2021). Amino acids accumulate later. Proline synthesis is closely related to sugar metabolism and the accumulation of proline in dehydrated plants is a result both of *de novo* synthesis and inactivation of degradation (Wu *et al*., 2017). Ceccarelli *et al*. (2004) proposed to use proline accumulation to breed for drought-resistance.

Several studies have investigated the relationship between gas exchange and water potential (WP) in olive leaves (e.g., Ahumada-Orellana *et al*., 2019). Flowers & Ludlow (1986) reported that leaves of pigeon pea (*Cajanus cajan* (L.) millsp.) with different levels of osmotic adjustment died at water potentials between –3.4 and –6.3 MPa, but all leaves died at a similar relative water content (32%). These authors emphasized that leaves died when relative water content reached a lethal value, rather than when a lethal leaf water potential was reached. A recent study, however, reported that time to incipient mortality differed between populations of *Pinus ponderosa*, but occurred at the same RWC and WP (Sapes & Sala, 2021). RWC and WP were accurate predictors of drought mortality risk. These results highlight that variables related to water status capture critical thresholds during drought-induced mortality and the associated dehydration processes. Sapes & Sala (2021) emphasized that both WP and RWC are promising candidates for large-scale assessments of drought-induced mortality risk. Juenger & Verslues (2023), nevertheless, propose that increased use of water potential, a physical measure of the free energy status of water, as a fundamental descriptor of plant water status can enhance the insight gained from many drought-related experiments and facilitate data integration and sharing across laboratories and research disciplines.

Vieira *et al.* (2017) showed that the RWC decreased according to the soil water restriction, causing reduction in stomatal conductance and decrease of 76.4% in net photosynthesis in plants of *Vatairea macrocarpa* exposed to 25% field capacity. These authors determined that water restriction decreased the chlorophyll content, but increased carotenoid content and also improved the antioxidant activities of superoxide dismutase (SOD), ascorbate peroxidase (APX) and catalase (CAT). In addition, high levels of sugars (sucrose, raffinose) and amino acids (proline, tryptophan, valine, glutamine and GABA) were observed in drought stressed plants, contributing to osmoregulation and as sources of carbon and nitrogen after rehydration. Decreases in carbon assimilation promoted a reduction of the leaf area, however an increase in the root surface area was observed. However, the analized parameters became similar to the control plants after rewatering, indicating that the severe water stress did not impair the survival of young plants. Instead, adjustments were made to protect them against drought such as the maintenance of the assimilatory metabolism at minimal levels (Vieira *et al.*, 2017). A large number of stomata permit a better CO_2 supply under water stress conditions, while more trichomes reduce water loss (Bertolino *et al*., 2019).

An efficient control of the stomatal aperture helps to maintain xylem water potential values above the safety threshold for loss of hydraulic conductance (Fernández, 2014). Strong evidence shows that stomatal conductance decreases as plant leaf water potential becomes more negative (Castro *et al*., 2019). Nadal-Salas *et al*. (2021)

reported that under sustained drought, stomatal regulation in response to evaporation demand may not be enough to mitigate hydraulic tension and prevent embolism (i.e., air bubbles) formation in the xylem, reducing xylem hydraulic conductance. Reduced xylem conductance limits water transport from soil to the leaves, which may lead to dehydration of cambium and apical meristems, canopy dieback, and ultimately tree death (e.g., Hesse *et al*., 2019). Brito *et al*. (2019b) informed that the wilting point for olive ranges approximately between -2.5 MPa and -3.5 MPa or even has a huge capacity to sustain values below -8 MPa. These authors also informed that rainfed olive trees with a leaf water potential of around -8 MPa extracted 40 mm of water below the conventional wilting point (-1.5 MPa). This amount has significant importance to rainfed orchards in arid regions since it represents around 10-15% of annual transpiration (Orgaz *et al*., 2008). During recovery, olive trees typically show a conservative behavior, rapidly restoring water status, but exhibiting a slow recovery of stomatal conductance (Brito *et al*., 2018).

Torres-Ruiz *et al*. (2015) determined that neither hydraulic nor non-hydraulic factors were able to explain the delay in the full recovery of stomatal conductance. These authors proposed two explanations. One explanation involved the restoration of certain aquaporins activities, not affecting leaf hydraulic conductance directly, but the balance of osmolytes in the cells. The other explanation involved the occurrence of a metabolic limitation, as the increase in ABA in guard cells under drought induces the expression of hexokinases, which accelerates the stomatal closure. On the other hand, the hexokinases are also involved in sugar sensing and stimulation of the osmolytes balance that should be restarted after the recovery of water status. Additionally, Brito *et al*. (2018) showed that in line with a delay in stomatal conductance restoration, the intense ABA signal in droughted olive leaves after stress relief was stronger closer to the upper epidermis, suggesting its re-localization after rehydration and a ''memory'' effect, which might enable a rapid response under drought restoration. Olive trees pre-exposed to drought also recover the net assimilation rate faster than stomatal conductance after stress relief (Brito *et al*., 2018).

Olive trees decrease the water potential of their tissues, establishing a particularly high gradient between leaves and roots to ensure the hydraulic conductance and the maintenance of water flow from roots to leaves (Dichio *et al*., 2009). The olive tree displays a strong capacity to osmotic adjustment –the active accumulation of solutes – both in leaves and roots under drought conditions (Abdallah *et al*., 2017). This mechanism decreases the osmotic potential, creating a soil-plant water gradient, which enables the extraction of water from the soil at a water potential below the conventional wilting point (Dichio *et al*., 2006). Osmotic adjustment is linked with active osmotic regulation mechanisms, an increase in solute concentration resulting from symplastic water loss (Dichio *et al*., 2006) and an accumulation or *de novo* synthesis of solutes within cells (Sanders & Arndt, 2012). Two major classes of solutes can lower the osmotic potential of tissues: inorganic cations and anions and organic compatible solutes, such as sugars, sugar alcohols, amino acids (i.e., proline), and quaternary ammonium compounds (notably glycine betaine) (Patakas *et al*., 2002; Sanders & Arndt, 2012). Some of the organic solutes can also protect cellular proteins, enzymes and cellular membranes and allow the metabolic machinery to continue functioning (Bacelar *et al*., 2009; Sanders & Arndt, 2012). On the other hand, changes in cell wall elasticity can also contribute to drought adaptability, as demonstrated in different olive genotypes (Bacelar *et al*., 2009). Changes in cell wall elasticity also participate to drought adaptability in Damask rose (*Rosa damascena* Mill.) (Al-Yasi *et al*., 2020). Increases and decreases in cell wall elasticity may aid survival under low water availability in these studies. More elastic cell walls can shrink more easily when subjected to stress, helping the maintenance of higher turgor pressure and protecting cell walls from rupturing (Srivastava *et al*., 2017). More rigid cells may help to maintain lower water potentials at any given volume than elastic ones, resulting in a higher gradient of water potential between the soil and the plant, thereby promoting more effective water uptake from drying soils (Patakas *et al*., 2002).

Cellular aquaporin water channels (AQPs) constitute a large family of transmembrane proteins present throughout all kingdoms of life, playing important roles in the uptake of water and many solutes across the membranes (Faize *et al*., 2020). These authors reported the first comprehensive study and systematic genome-wide analysis of AQP gene families in *O. europaea* L. They highlighted several novel findings explaining (1) the structural conservation and possible functional diversity of AQPs in wild (*O. europaea* var. sylvestris) and domesticated (*O. europaea* cv. Picual) olive tree varieties and (2) their involvement in cell responses to various biotic and abiotic environments. Their results allowed to increase our knowledge of the molecular mechanisms behind the actions of AQPs in olive domestication. These authors emphasized that further studies are required to (1) determine the functions of the individual selected genes identified on *O. europaea* cv. Picual and (2) reveal more functional mechanisms for these genes. Finally, Faize *et al*. (2020) suggested that the integration of bioinformatics analysis with biological experiment validations will provide further understanding of the key roles that some AQPs play in development processes and stress tolerance in domesticated olive trees. Secchi *et al.* (2007b) also studied the molecular bases of water transport in olive characterizing cDNAs from *Olea europaea* cv "Leccino" related to the aquaporin (AQP) gene family. These authors showed that a phylogenetic analysis of the corresponding polypeptides confirmed that they were part of water channel proteins localized in the plasma membrane and in the tonoplast. Additionally, Secchi *et al.* (2007b) found that the downregulation of AQP genes may result in reduced membrane water permeability and may limit cellular water loss during periods of water stress. The change in aquaporins activity may serve to ensure that during stress, water moves to where it is required or is retained where it is more critical (Šurbanovski & Grant, 2014). Aquaporins may also be important in whole-plant rehydration during the recovery period; they are essential in vessels refilling after drought-induced embolism (Secchi *et al.*, 2007a; Secchi *et al*., 2007b). Aquaporins' responses can be correlated with the isohydric and anisohydric behavior of plants, which can eventually switch from one to another in response to changing environmental conditions or to fruit load, as it was stated by Naor *et al*. (2013) for the olive tree. Finally, as aquaporins accumulate in cells around stomatal cavities and in guard cells themselves, they may also be involved in the regulation of stomatal conductance (Perez-Martin *et al*., 2014).

The regulation of the antioxidant system is one of the most relevant mechanisms against oxidative stress caused by reactive oxygen species (ROS). Reactive oxygen species play a double role in plant physiology. However, if ROS would act as signaling molecules or might cause oxidative stress to the tissues depend on the refined balance between its production and scavenging (Mattos & Moretti, 2015). The increase in carotenoids and the carotenoids/chlorophylls ratio is considered one of the mechanisms developed by the olive tree to protect the photosynthetic apparatus against photooxidation (Abdallah *et al*., 2017). Even more, the increment of some antioxidant enzymes activities (e.g., ascorbate peroxidase, catalase, superoxide dismutase, glutathione reductase) and/or in non-enzymatic antioxidant mechanisms (e.g., the accumulation of phenolic compounds, tocopherols, carotenoids, ascorbate and glutathione) were commonly described in olive trees under drought conditions (Petridis *et al*., 2012; Abdallah *et al*., 2017). Also, it was demonstrated that upon re-watering, olive trees still exhibited higher levels of hydrogen peroxide (H_2O_2), a known signaling ROS, possibly to keep the antioxidant system on alert (Abdallah *et al*., 2017). Even more, olive trees that were drought-primed showed an alleviation in oxidative stress in relation to plants exposed to drought for the first time (Abdallah *et al*., 2017). Resistant cultivars preserve their relative water content at a higher drought stress level than susceptible ones under similar conditions (Karimi *et al*., 2015). Therefore, since relative water content remains higher in the leaves of plants that better tolerate drought stress, it is widely utilized as an authentic index for screening drought-tolerant cultivars.

Water stress and disturbance of ions homeostasis cause overproduction of reactive oxygen species (ROS) and oxidative stress, which damage lipids, nucleic acids, and proteins and destroys the membrane integrity (Gao *et al*., 2015). The olive tree can accumulate compatible solutes thus increasing osmotic potential to promote a soil-plant water gradient, which can extract water from the soil potentially even below the wilting point. To survive the toxic effects of reactive oxygen species (ROS), the olive tree has evolved an efficient antioxidant defense system. Meanwhile, under severe drought conditions, ROS production often increases lipid peroxidation, malondialdehyde production, and DNA and protein degradation (Nikoleta-Kleio *et al*., 2020). Plant resistance to water stress has been correlated to a higher capacity for osmotic adjustment with proline in the ´Chemlali' olive cultivar (Ennajeh *et al*., 2015). Thus, olive cultivars manifest different levels of water stress tolerance depending on the genotype (Gholami *et al*., 2019).

Severe drought stress (50% deficit irrigation) strongly decreased photosynthetic pigments, in particular, chlorophyll (Chl) a, and b (Dias *et al*., 2018). A relative decrease in Chl a content and efficiency of photosystem II are effective adaptive strategies for drought tolerance (Hejnák *et al*., 2015). Water stress elicits a strong stomatal closure as the earliest response, with a consequent decrease of carboxylation capacity of photosynthesis because of a decrease in CO_2 availability (Flexas & Medrano, 2002). This leads to a progressive accumulation of NADPH and ATP, which ultimately results in downregulation of feedback inhibition of the photosynthetic electron transport (Wang *et al*., 2018).

In these conditions, there is a reduction in the synthesis of chlorophylls as a photoprotective mechanism; in fact, the Chl loss reduces the amounts of photons absorbed via leaves allowing the leaf tissues to reduce photooxidation and overcome the severe stress period (Vasques *et al.*, 2016). Chlorophyll loss and pigment photooxidation are considered obvious symptoms of oxidative stress as a consequence of water stress. Based on this fact, preserving a high level of antioxidative enzyme activities, and enhancing the capacity of host plants against oxidative damage can contribute greatly to drought stress alleviation (Ma *et al.*, 2020).

In the study of Calvo-Polanco *et al.* (2019), the drought treatment induced a significant reduction in the leaf Chl content of olive trees. These pigments are crucial components for Photosystems II and I and light-harvesting complexes, and oxidative stress can cause their photo-oxidation and degradation, affecting photosynthesis more than the restriction of CO_2 caused by stomatal closure during water stress (Allakhverdiev, 2020). However, the drought stress-related restriction to CO_2 uptake caused by leaf stomata closure varies among plant species, so drought tolerance depends on the cultivar (Wang *et al.*, 2011).

During Chl degradation under drought stress, α-tocopherol, an antioxidant involved in the O^-_2 scavenging, can be synthesized through the phytol recycling pathway. The accumulation of this photoprotective molecule with a decline of Chl content is an effective strategy for highly drought-tolerant plants to survive (Hortensteiner & Krautler, 2011). Chl a under drought stress could be degraded more compared to Chl b, indicating to be a more sensitive photosynthetic pigment prone to degradation to decrease the amount excitation energy reaching Chl a at the reaction center, and the electron transfer to an impaired electron transport chain under stress. The decrease in Chl a content and efficiency of photosystem II could be adaptive strategies for drought tolerance (Hejnák *et al.*, 2015). Nevertheless, chlorophyll degradation occurs from Chl a, while to degrade Chl b, it must be first converted to Chl a by two sequential enzymes, Chl b reductase and hydroxyl methyl Chl a reductase. Therefore, if the transcription or activity of these two enzymes is decreased by drought stress, Chl b accumulates compared to Chl a (Reshmi & Rajalakshmi, 2012).

Soluble carbohydrates (e.g., glucose, fructose, and sucrose), and amino acids such as proline, are the major solutes supporting osmotic adjustment in olive trees (Rahemi *et al.*, 2017). Plant growth mostly depends upon storage carbohydrates especially soluble sugars as a mobilized form (Sami *et al.*, 2016). Under drought stress, the accumulation of soluble carbohydrates as an osmotic adjustment is able to decrease the water potential of the cells to increase and/or maintain water influx and assist in maintaining tissue turgor. The accumulation of osmoprotectants such as sugar (e.g., mannitol and sucrose) and phenolic compounds is an initial mechanism to induce enhancement of resistance in olive to drought stress (Mechri *et al.*, 2020). Proline is one of the most widely distributed compatible compounds, which accumulates in plants under abiotic stress conditions (Carillo *et al.*, 2008). The increase of proline levels as an osmoprotectant may facilitate water retention, and are considered as an adaptive mechanism (Zahedi *et al.*, 2021). Accumulation of proline in the leaves under acute water stress was observed in several olive genotypes (Elhami *et al.*, 2015).

It is not clear if its accumulation in tissues under dehydration is a stress symptom, a stress response, or an adaptation strategy.

Plants activate several mechanisms such as increasing the accumulation of certain osmolytes to provide a level of resistance to drought stress. For example, proline can also play a key role in reactive oxygen species (ROS) scavenging (Parihar *et al.*, 2015). It has been found able to act as ROS scavenger, protect and stabilize membranes and macromolecules, and promote the expression of stress-responsive genes presenting elements responsive to proline (Gholami *et al.*, 2022).

The increase of phenolics was commonly reported in olive plants exposed to water stress (Ben-Abdallah *et al.*, 2017). They play an important antioxidative role by participating in several mechanism as free radical scavengers, peroxidase enzyme substrates, oxidative and oxygen reactions' blockers, and metal ion chelators (Posmyk *et al.*, 2009). The mechanisms involved in the plant reaction to induced water limitation enhance the antioxidative enzymatic activities (Chai *et al.*, 2015). Gholami & Zahedi (2019) found that the highest amount of malondialdehyde (MDA) was observed in olive cultivars under 50% deficit irrigation. MDA is one of the final products of polyunsaturated fatty acids peroxidation by ROS in the cells, and is then indicated as an index of the level of membrane lipid peroxidation in plants under stress. Previous studies indicated that the accumulation of MDA increased significantly in response to drought stress (Khoyerdi *et al.*, 2016). Elhami *et al.* (2015) demonstrated that a 40% water deficit in olive plants enhance the peroxidase (POD) activity compared with full irrigation (100% field capacity). Even more, changes in the activity of catalase (CAT) and POD due to abiotic stresses have been previously shown in olive crops (Ben-Abdallah *et al.*, 2017). The enhancement in antioxidative activity and metabolites was also reported on olive trees under water stress (Prioietti *et al.*, 2013). An imbalance between ROS synthesis and the antioxidant defense system may occur under severe water stress conditions (Brito *et al.*, 2018). This will cause an accumulation of ROS, lipid peroxidation, and cell damage, with consequences on plant growth and development, and finally yield performance (Ahmadipour *et al.*, 2018). The enhancement in activities of antioxidant enzymes (POD and CAT) is required for adjusting the balance by detoxification of excess ROS (Abdul-Kareem *et al.*, 2022). In general, plant develop a complicated antioxidant defensive strategy to induce ROS scavenging under drought stress (Ahumada-Orellana *et al.*, 2017). CAT is essential to assimilate and detoxify H_2O_2 in peroxisomes (Haider *et al.*, 2018) and POD is also in charge of the H_2O_2 decomposition (Gao *et al.*, 2016). Tolerant rootstocks exhibited less MDA and H_2O_2 but higher activities of antioxidant enzymes (CAT and POD) to cope with ROS in a study among 6 different citrus rootstocks (Hussain *et al.*, 2018). Nevertheless, the fine tuning of ROS scavenging enzymes and antioxidant system can also allow to maintain a beneficial low ROS concentration able to play a key role in ROS-hormones integrated signal events triggering stress-specific defense or tolerance responses. A controlled ROS increase, in particular, may be linked to the drought perception/sensing and activation of (1) ABA and other hormones, (2) homologs of respiratory burst oxidase homolog, and (3) calcium fluxes via ABA-dependent or independent signaling pathways (Verma *et al.*, 2019). In fact, ROS can activate a positive feedback loop involving ABA and resulting in higher ROS/ABA levels able to modulate gene expression and cellular responses to cope with drought stress (Yoshida *et al*., 2019). ABA-induced transcription factors (TFs) may also play an important role in promoting drought tolerance through ROS signaling (e.g., Devireddy *et al*., 2021). Similarly to ABA, brassinosteroids (BR) have been found able to boost the transcription of Respiratory Burst Oxidase Homolog1 (RBOH1) and the activity of NADPH oxidase thus increasing the concentration of apoplastic H_2O_2 under drought (Xia *et al*., 2015). In olive trees, the adaptability to recurrent drought episodes mediated by salicylic acid (SA) occurs by improving the balance between ROS production and scavenging, the plant ionome regulation, and promoting root development (Brito *et al*., 2019a). The same effect on root enlargement can be determined by other phytohormones, that can have a crosstalk with ROS playing a decisive role to allow plants to adapt to drought. In fact, ROS accumulation can reduce auxin accumulation and/or signaling, altering plant shoot growth in order to enlarge roots while reducing the surface of evapo-transpiring organs, lowering stomatal density and/or conductance (Cortleven *et al*., 2019).

Brito *et al*. (2019b) suggested that the lower amounts of Ca and K and the higher amount of Na under drought stress could be related to drought stress susceptibility.

CONCLUSIONS

The plant adaptive responses to water stress are given by resistance strategies. These strategies may be given by avoidance and/or tolerance mechanisms. We can summarize the avoidance olive tree strategies to improve water stress adaptability depending on the ability to **(1)** extract water from the soil (e.g., high root density close to trunk surface; large root system; small and dense xylem vessels; hydraulic redistribution; nighttime stomatal conductance; high root/canopy ratio, and capacity to decrease water potential) and **(2)** restrict water losses (e.g., paraheliotropism; small and sclerophyllous leaves; leaf mesophyll compactness; hypostomatous leaves; small and dense stomata; dense trichome layer; high root/canopy ratio; reduced stomatal conductance, and aquaporins regulation). In brief, tolerance mechanisms include the ability to sustain large internal water stress and metabolic activity (e.g., aquaporins regulation, osmotic adjustment; high carotenoids and carotenoids/chlorophyll ratios, and efficient enzymatic and non-enzymatic antioxidant responses). Finally, the rehydration recovery capacity can be achieved by a conservative behavior (e.g., slow stomatal conductance renewal; rapid water status restauration; aquaporins regulation; ABA persistence in leaves, and H_2O_2 persistence to keep the antioxidant system in alert). The identification of the most tolerant cultivars can be exploited both for future more in-depth studies on the molecular mechanisms underlaying water stress tolerance, and to design new agronomic strategies for olive cultivation to be translated directly into the field to improve oil production even under stress conditions.

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