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Anatomical and morphological changes in scion of some olive grafting combinations under water deficit

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All relevant data are within the paper and its Supporting Information files.

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Abstract: Effects of water stress deficit were studied on xylem anatomical features and some growth parameters among six olive grafting combinations; Amygdalifolia/Arbequina (Am/Ar), Amygdalifolia/Koroneiki (Am/Ko), Amygdalifolia/Zard (Am/Z), Conservallia/Koroneiki (Co/Ko), Conservallia/Zard (Co/Z) and Conservallia/Arbequina (Co/Ar) of about three-year-old olive trees (*Olea europaea* L.) under greenhouse conditions. To realize this, a factorial experiment was conducted in a completely randomized design (CRD). The results showed that rootstocks exhibited significant effects on scions xylem anatomical physiognomies, such as vessel lumen area (VLA) and vessel diameter (VD) and additionally on some growth indices including main stem length (SL), lateral shoot number (LSN) and graft union-cross sectional area (GU-CSA). Xylem anatomical characteristics including VLA, porosity, vessel frequency (VF) and VD of scions decreased when they were grafted onto Arbequina and Koroneiki rootstocks, but increased onto Zard rootstock. All growth parameters showed a decrease under drought stress, while this reduction was more pronounced for Zard rootstock than the other rootstocks. However, Co/Z showed the highest VF and the lowest vulnerability index (VI) and exhibited a better performance at the end of recovery.

1. Introduction

Olive (*Olea europaea* L.), as an evergreen tree, is often under severe drought stress conditions in summer. While withstanding a high level of drought situations (Lo Gullo and Salleo, 1988), the resistance level depends on cultivar and genetic characteristics of the plant (Bacelar *et al*., 2006; Therios, 2009). The ability of acclimation to water deficit includes morphological, physiological, biochemical and anatomical mechanisms (Bacelar *et al*., 2006; Therios, 2009) as inhibition of cell expansion, leaf area limitation, dense cuticles and trichomes, shoot growth cessation and foliar chemistry changes (Bacelar *et al*., 2007; Guerfel *et al*., 2009).

Rootstocks can enable the scion for normal growth under water deficit (Turner, 1986). In fact, grafting of commercial cultivars on tolerant rootstocks is a specific technique of acclimation to environmental stresses as a rapid tool compared to breeding methods (Flores *et al*., 2010). Knowledge about anatomical characteristics of rootstock and scion is essential to understand their interactions under drought conditions. Some researchers suggested that vigor reduction induced by dwarfing rootstock may contribute to change water transfer at the graft union (Soumelidou *et al*., 1994; Atkinson *et al*., 2003). Other investigations have been focused on the role of tree water status, determining the vegetative structure of grafted tree (Basile *et al*., 2003; Solari *et al*., 2006). It has also been emphasized that sensitivity to drought is related to vessel dimension (Lo Gullo *et al*., 1995; Trifilo *et al*., 2007). Xylem vessels of plants subjected to drought are in danger of emboli and dysfunction. Therefore, drought-adapted trees or shrubs usually have narrower vessels with concomitant in the higher number of vessels per mm^2 compared to the drought-sensitive trees (Carlquist, 2001). In a study by Trifilo *et al.* (2007) it has been reported that dwarfing rootstocks effectively reduce grafted plant size, although they are not essentially responsible for higher tolerance to drought by scions improving tree resistance to water deficit. It is an ordinary trend to increase root, stem vessel diameter, and decrease vessel density with tree height in some fruit and forest trees (Zach *et al*., 2010). Many xylem traits such as xylem-to-phloem ratio, vessel density, and vessel size influence dramatically the rootstock growth ability (Meland *et al*., 2007; Trifilo *et al*., 2007), playing an important role in hydraulic conductance of root and stem (Tombesi *et al*., 2010; Zach *et al*., 2010). Thus, number and diameter of vessels are two main characteristics determining hydraulic conductance (Tyree and Ewers, 1991). Smaller and fewer vessels in the scion and graft union of cherry trees could be related to hydraulic resistance and a decreased growth of scion (Olmstead *et al*., 2006). Anatomical parameters such as vessel frequency, vessel lumen area and percentage of vessels on wood cross section are reliable to preselect tree vigor. It has been widely accepted that reduced plant growth via increased hydraulic resistance derives from graft union and xylem conduit structure (Goncalves *et al*., 2007; Tombesi *et al*., 2010).

A comprehensive understanding of grafted trees vulnerability to drought derived from different scion/rootstock combinations will be useful in orchards situated in semi-arid regions experiencing drought stress. In fact, olive trees grow in Mediterranean basin with low summer rainfall while irrigation is not a popular practice. Using cloned rootstocks that potentially control scion vigor is a very necessary factor for establishing new olive orchard as an innovative cultivation method (Baldoni and Fontanazza, 1989; Rugini *et al*., 1996). Information on xylem anatomical responses of grafted olives under drought stress conditions are few. It has been assumed that different olive rootstocks may induce various anatomical and morphological modifications in the scions (Therios, 2009). Hence, the aim of the present study was to investigate xylem anatomical changes of scions' stems and morphological alterations of some olive grafting combinations under water deficit conditions.

2. Materials and Methods

Plant materials and experiment location

Olive (*Olea europaea* L.) current-season-growth shoots as scion (cvs. Amygdalifolia and Conservallia) were cleft grafted onto three rootstocks of two years old rooted cuttings (cvs. Koroneiki, Arbequina and Zard) in winter 2015. These grafted plants were transplanted in 12 L plastic pots containing a substrate mixture of field soil, sieved sand, and humus in a 1:1:1 (V: V: V) proportions and was placed in a greenhouse 1100 m above sea level; with a latitude 35°56' N, and longitude of 50°58' E and temperature of 28±3°C during the day and 23±3°C at night. The physical and chemical properties of pots soil mixture are presented in Table 1.

Treatments

All grafted olive trees were irrigated at field

Table 1 - Physical and chemical properties of the soil used in this study

Soil characteristics	Value
Physical properties	
Sand (%)	39
Silt (%)	38
Clay (%)	23
Texture	Loam
Chemical properties	
Organic carbon (%)	1.19
Electrical conductivity (dS/m)	2.68
pH	7.78
N (%)	0.12
P (mg/kg)	28.6
K (mg/kg)	360

capacity (FC) until the start of experiment. Moisture content of the substrate was calculated with Time Domain Reflectometry (TDR) in two opposite sides of the containers in each pot at a depth of 20 cm and then an average was calculated. The experiment was carried out in July 2016. The graft combinations were Amygdalifolia/Koroneiki (Am/Ko), Amygdalifolia/Zard (Am/Z), Amygdalifolia/Arbequina (Am/Ar), Conservallia/Koroneiki (Co/Ko), Conservallia/Zard (Co/Z) and Conservallia/Arbequina (Co/Ar). Then, they were divided into two groups; group one was irrigated at FC as control and the group two was subjected to water shortage by withholding irrigation for a period of 4 weeks (WS), (n=6). Three grafted plants were used for anatomical measurements (n=3) and three were subjected to re-watering for determination of viability and recovery. After three weeks of re-watering (recovery period), the stem length was measured in different graft combinations.

Xylem anatomical measurements

After 4 weeks of water deficit, stem pieces (2cm above the graft union) were collected early in the morning from experimental plants in both groups and immediately fixed in FAA (formalin, acetic acid, ethanol, 1:1:1, V:V:V) in the late summer 2016. Stem pieces were cross-sectioned using a sliding microtome (GLS1, WSL, and Switzerland). Cross sections with the thickness of ~10 µm were stained with 0.1 % (w/v) safranin (staining in red lignified cell walls) and 1% (w/v) Astra-blue (staining in blue-green cellulosic walls) and observed at different magnification under a light microscope (FLUO3, BEL Engineering, Italy) equipped with a digital camera (EUREKAM, BEL Engineering, Italy) connected to a computer. The last annual rings in microscopic sections were investigated both under bright filed and fluorescence lights. The vessel lumen area (VLA), vessel diameter (VD), vessel frequency (VF=number of vessels/mm^2), vulnerability index (VI= VD/VF), and porosity (total vessel lumen area/ total analyzed area ×100) were measured using Image J software (https://imagej.nih.gov/ij/). VI was calculated to assess vessel susceptibility to damage as a reliable indicator during the water deficit. VD was calculated using the mean value of the vessel lumen area [VLA = (VD/2)^2 π], to estimate idealized diameter.

Morphological parameters

In order to evaluate the growth indices of grafted plants under the period of water stress deficit, main stem length growth (SL) was calculated based on a difference between the stem length above graft union at the beginning and at the end of the drought period. Stem diameter (middle of the graft union) was measured with a hand caliper at the end of the drought period (4 weeks) in two opposite sides and an average was applied to calculate the graft union cross sectional area (GU-CSA) in mm^2. Lateral shoot number (LSN) was recorded by counting the shoots in the main stem (above the graft union) at the beginning and at the end of the drought period. Leaf number, above the graft union, was recorded at the beginning and at the end of the drought period and then a difference was calculated as LN (the leaves having more than 1 cm length were counted). Leaf area (LA, cm^2) was measured using leaf area meter at the end of the drought period and an average of five full-expanded leaves was used for the analysis.

Data analysis

A factorial experiment was conducted in a completely randomized design (CRD) with 9 replications. Treatments included 6 graft combinations and 2 levels of irrigation. Normal distribution of data was investigated using Shapiro-Wilk test. Data were analyzed by SPSS version 20.0 statistics software using multivariate analysis of variance (MANOVA) and means were compared by Duncan's multiple range test at probability of 5%. Pearson's correlation coefficients were tested among the analyzed characteristics, using values from 36 graft combinations.

3. Results

Xylem anatomical properties

Statistical analysis of the data showed significant effects of the rootstocks on the scion VLA, SL, LSN, GU-CSA and VD. The main effects of rootstocks showed that Koroneiki induced the highest values of VLA (514.5 µm^2) and VD (25.4 µm) in the scion, which was significantly greater than those of induced by zard rootstock. However, there was no significant difference among three rootstocks in porosity, VF, and VI (Table 2).

The interactions between graft combinations and water stress on scion xylem anatomical characteris-

Table 2 - The effects of different rootstocks on xylem anatomical properties of scion

Rootstock	Vessel lumen area (µm^2)	Porosity (%)	Vessel frequency (n/mm^2)	Vessel diameter (µm)	Vulnerability index
Arbequina	464.1 a	5.3 a	107.8 a	24.2 a	0.28 a
Koroneiki	514.5 a	6.9 a	133.4 a	25.4 a	0.27 a
Zard	371.7 b	4.5 a	119.4 a	21.2 b	0.23 a

tics showed that water shortage caused a decrease in the vessel lumen area (VLA) of both scions (Amygdalifolia and Conservallia) grafted onto the Arbequina and Koroneiki rootstocks (Fig. 1). On the contrary, it increased VLA in both scions grafted onto Zard rootstock (Fig. 1A). Arbequina and Koroneiki rootstocks decreased porosity and VF of Amygdalifolia and Conservallia scions under water shortage conditions; however, Zard rootstock increased porosity and VF of both scions (Amygdalifolia and Conservallia) (Figs. 1B and 1C). Water shortage increased vessel diameter in Am/Z and Co/Z combinations compared with the corresponding controls (Fig. 1D). The highest VI was observed in Co/Ar and Co/Ko whilst the lowest gained in Co/Z under water stress conditions (Fig. 1E).

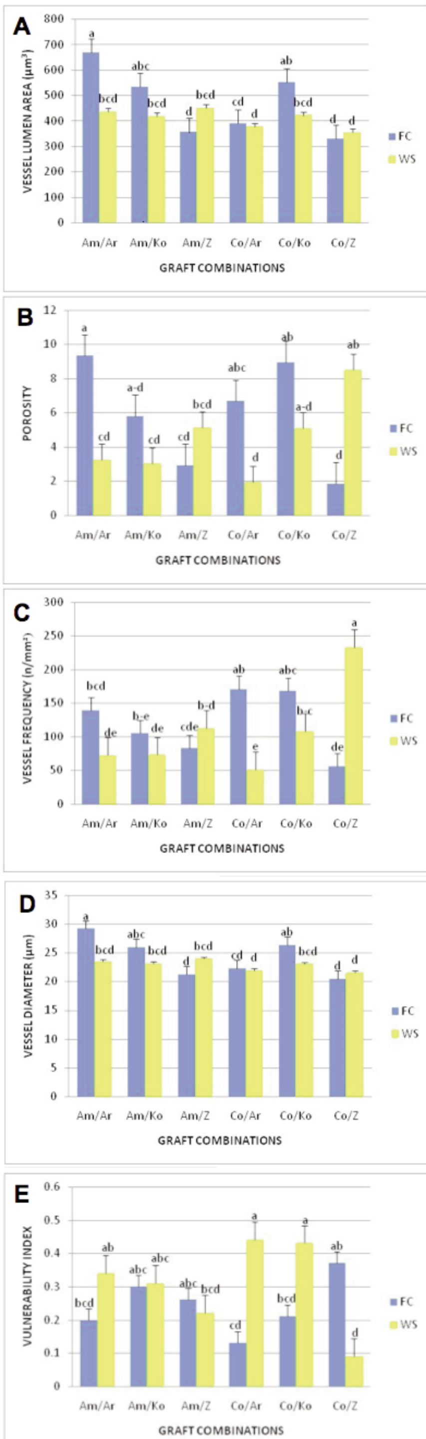

Fig. 1 - Interaction effects of graft combinations (Am/Ar, Am/Ko, Am/Z, Co/Ar, Co/Ko, Co/Z) and water stress deficit on vessel lumen area (A), porosity (B), vessel frequency (C), vessel diameter (D) and vulnerability index (E). Am (Amagdalifolia), Ar (Arbequina), Ko (Koroneiki), Co (Conservalia) and Z (Zard). Vertical bars indicate SE. Each value represents the mean ± SE of 3 replicates. Means with the same letters are not significantly different (P>0.05) using Duncan Multiple Range Test.

Scion morphological characteristics

Regardless of the scion types and irrigation levels, rootstocks affected some growth characteristics of scion; Koroneiki rootstock exhibited the highest value of scion stem length (SL), which was significantly greater than that of Zard rootstock (Table 3). This rootstock had the lowest graft union cross sectional area (GU-CSA). Arbequina presented the greatest GU-CSA and lateral shoot number (LSN). Koroneiki showed the highest leaf area (4.86 cm^2) and leaf number (24.38), however, they were not significantly different from the other rootstocks (Arbequina and Zard) (Table 3).

Table 3 - The effects of different rootstocks on xylem anatomical properties of scion

Rootstock	Leaf number	Leaf area (cm^2)	Lateral shoot number	Stem lenght (cm)	Graft union cross sectional area (mm^2)
Arbequina	18.33 a	4.10 a	1.00 a	3.95 ab	55.74 a
Koroneiki	24.38 a	4.86 a	0.71 ab	5.80 a	44.45 b
Zard	18.42 a	3.92 a	0.25 b	1.85 b	47.13 ab

In all graft combinations, water stress deficit significantly decreased the number of leaves and lateral shoot number; however, these reductions were not significant in Co/Ko combination (Figs. 2A and 2C). Drought stress also decreased leaf area in all graft combinations, although this reduction was only significant in Co/Ar combination (Fig. 2D). Water stress deficit declined scion stem length (SL) in all graft combinations such that there was no growth in Am/Z and Co/Z and stem length reduction was not significant in Co/Ko combination compared to the control (Fig. 2B). Drought stress significantly reduced GU-CSA in Am/Ar and Am/Ko while had not significant effect on other graft combinations (Fig. 2E*)*. All grafted plants continued to grow as a result of re-watering on scions stem length growth. However, the resulting SL were significantly lower than the controls except in the case of Co/Z. Am and Co scions, exhibiting no SL growth under water stress deficit conditions onto Zard rootstock, showed a SL elongation which were not significantly different from the corresponding controls (Fig. 3). Fluorescence microscopy helped us to distinguish tree ring boundaries since the intensity of emitted light by these specimens diminished from early wood to late wood (Figs. 4C and 5A) or were different between these two sub-annual areas (Fig. 5C). The fluorescence

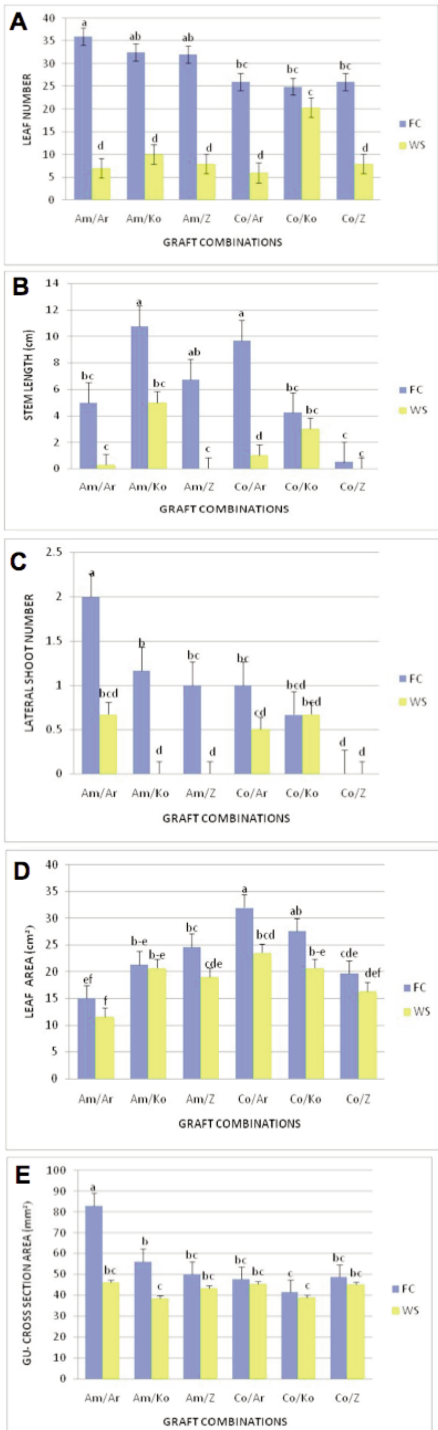

Fig. 2 - Interaction of graft combinations (Am/Ar, Am/Ko, Am/Z, Co/Ar, Co/Ko, Co/Z) and water stress deficit on leaf number (A), stem length (B), lateral shoot number (C), leaf area (D) and gu-cross section area (E). Am (Amygdalifolia), Ar (Arbequina), Ko (Koroneiki), Co (Conservallia) and Z (Zard). Vertical bars indicate SE. Each value represents the mean ± SE of 3 replicates. Means with the same letters are not significantly different (P>0.05) using Duncan Multiple Range Test.

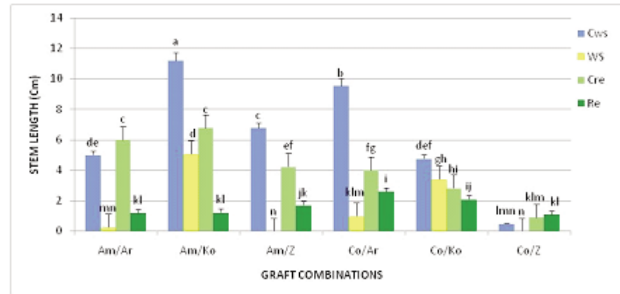

Fig. 3 - Stem length of graft combinations (Am/Ar, Am/Ko, Am/Z, Co/Ar, Co/Ko, Co/Z) under water stress deficit (WS) and Recovery (Re) and their controls (Cws), (Cre), respectively. Am (Amygdalifolia), Ar (Arbequina), Ko (Koroneiki), Co (Conservallia) and Z (Zard). Vertical bars indicate SE. Each value represents the mean ± SE of three replicates. Means with the same letters are not significantly different (P>0.05) using Duncan Multiple Range Test.

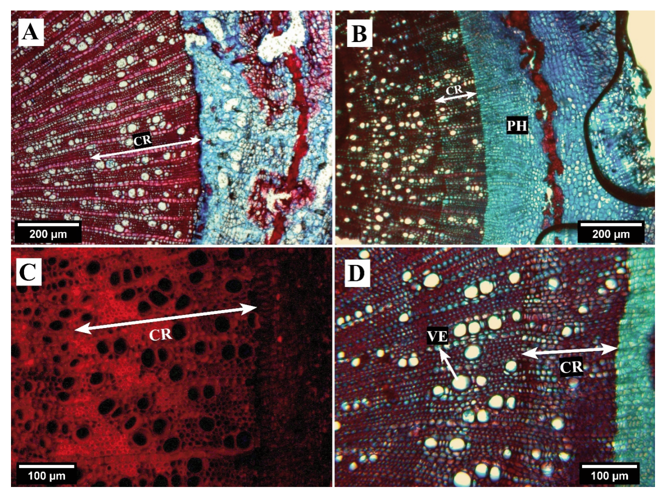

Fig. 4 - Micrographs of Am/Ko (Amygdalifolia/Koroneiki) combination of olive stem (2 cm above graft union) under bright field (A, B, D) and blue fluorescence light (D). Water-stressed samples (B and D) formed narrower rings with smaller vessels comparing with the control (A and C) (CR= current annual ring, VE= vessel, PH= phloem).

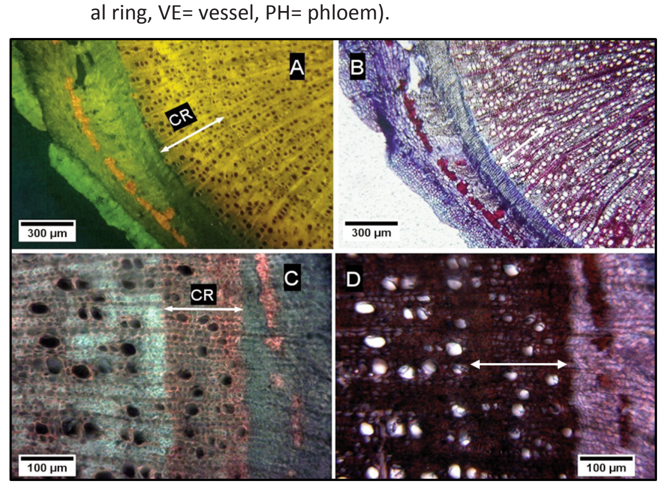

Fig. 5 - Micrographs of Co/Ar (Conservallia/Arbequina) combination of olive stem (2 cm above graft union) under irrigation (A and B) and water deficit conditions (C and D). The right-hand photos (B and D) were taken from samples under bright field light while A and C are the corresponding samples, respectively, under UV and blue fluorescence light, CR= current annual ring.

emission light in the late wood of control samples was different in intensity and/or color compared with those of under stress (Fig. 5). It seemed that the late ed fibers in water stressed samples are chemically different from control samples.

4. Discussion and Conclusions

Xylem anatomical properties

Vessel number and VD are considered as the main factors determining the hydraulic conductance (Tyree and Ewers, 1991). In addition, it has been hypothesized that VD and VF may affect drought tolerance. Thus, the highest VF value in Zard might explain its better performance under drought stress in comparison with the two other rootstocks analyzed in this study (Fig. 1C). These results are consistent with the anatomical analysis in cherry rootstocks (Goncalves *et al*., 2007; Meland *et al*., 2007; Zoric *et al*., 2012), while dispute the results on apple tree (Bauerle *et al*., 2011) due to genetic-dependent responses of different tree species. Since all plants in this study were grown at the same conditions, xylem anatomical differences among the control rootstocks may have a genetic basis; as it has been supposed that low vigor rootstocks may hereditary produce smaller vessels (Beakbane and Thompson, 1947). Correlation of an increase of VD and a decrease in VF with tree height demonstrated in many other investigations (Trifilo *et al*., 2007; Zach *et al*., 2010). Cloned rootstocks are less vigorous, having changes in the anatomy of xylem vessel, which may clarify their effects on shoot behavior (Atkinson *et al*., 2003). In the current research, Zard induced a narrower vessel formation compared with Arbequina and Koroneiki, confirming the results of a previous study on olive tree (Trifilo *et al*., 2007). Interestingly, Zard caused Conservallia to produce the highest number of xylem vessels (VF) under water stress in comparison with the scions grafted onto other rootstocks (Fig. 1C). Zard rootstock also increased VF in Am scion in lesser degree than Co. Vessel frequency (VF) is often increased by drought (Sterck *et al*., 2008; Fichot *et al*., 2011) through improving the hydraulic conductance (Scoffoni *et al*., 2012). A decreased VF has also been reported under drought stress (Corcuera *et al*., 2004), which is in line with the current results on the scions grafted onto Arbequina and Koroneiki rootstocks, suggesting drought may contradictorily influence olive different rootstocks. The drought stress increased the VI in Am/Ar, Co/Ar, Co/Ko and Am/Ko combinations, while decreased in two other combinations (Am/Z and Co/Z). It is generally accepted that cultivars with smaller and frequent vessels exhibit low VI (Carlquist, 1977), a rationale for a better water transport by Co/Z. This finding is consistent with that of Salvia (Hargrave *et al*., 1994), and suggests wider vessels (greater VD) might be more sensitive to abnormal function performance compared with vessels having smaller diameter. Additionally, it is supposed that scions may be more susceptible to show embolism onto invigorating rootstocks during water stress (Hargrave *et al*., 1994).

Scion morphological properties

Leaf expansion is the most sensitive characteristic to water deficits, because turgor reduction is the earliest significant biophysical effect of water stress, and leaf expansion is a turgor-dependent activity (Taiz and Zaiger, 2003). Limited leaf area resulted in a low photosynthesis and consequently decreased the shoot length (Marron *et al*., 2002), the number of leaves and the number of lateral shoots. Although SL reduction is expected under drought stress, differences among graft combinations can be originated from genetic elements of rootstocks (Goncalves *et al*., 2007). Vessel diameter reduction may cause a reduced growth in the scions grafted onto dwarf rootstocks and ultimately result in diminishing stomatal conductance and photosynthesis. The differences in scions growth can be caused by root hydraulic, which plays an important role in the control of olive plant growth (Nardini *et al*., 2006). Thus, it can be suggested that plant height and leaf area reduction may be correlated to a low cell development under water deficit in some species, implying the lowest values of SL and LA by Zard rootstock in this study. Although Zard rootstock stopped SL under water deficit conditions, however, it increased porosity and VF. It might be concluded that this rootstock employed assimilation for changing the pattern of xylem vessel as an alternative to elongating SL. Drought reduces the leaf number per plant. In fact, leaf area extension depends to water status, temperature, and assimilation supplied for growth, which may be affected by drought in a plant. LA reduction in the current study is in consistent with results in *Populus* and *Ziziphus* (Suther and Patel, 1992; Thakur and Sood, 2005).

In relation to correlation between measured traits, VLA and VF didn't show any correlation (r= 0.19). On the other hand, Porosity (%), is positively affected by both of these variables. Usually, when

VLA is decreased in an angiosperm plant, a decrease in water flow capacity is compensated by increasing the number of produced vessels. Hence, VLA and VF are usually negatively correlated (Oladi *et al*., 2014). However, in this research, the water deficiency resulted in a simultaneous decrease of both features (except for Zard rootstock), suggesting a different strategy employed by olive tree. Positive correlation between VD and GU-CSA demonstrated that vigorous rootstocks with higher GU-CSA had larger vessels, facilitating transfer of more water to aerial parts. A correlation value of 0.31 between LN and VD suggests that larger vessels might result in higher number of leaves in grafted trees. There is a relatively high correlation between LN and SL (r= 0.71), exhibiting a longer SL probably due to more leaf numbers on different rootstocks under irrigation and deficit conditions. Recent studies have shown that differences among rootstocks in either root size or scion extension influence soil-water-plant relationship (Clearwater *et al*., 2007; Cohen *et al*., 2007; Rodriguez-Gamir *et al*., 2010). Xylem vessel traits may determine hydraulic conductance extent and subsequently affect the current season vegetative growth. It seems VF is the main anatomical difference among the studied rootstocks. Several investigations suggested smaller and fewer vessels in graft union can contribute to water flow resistance, resulting in growth reduction (Olmstead *et al*., 2006; Goncalves *et al*., 2007) as observed in the case of Zard rootstock.

In this research, water stress deficit decreased the growth indices of all grafting combinations and among them, Zard rootstock inhibited any growth. Considering anatomical analysis, Zard rootstock induced higher porosity and VF in both scions (Am and Co) and exhibited the lowest VI under water stress conditions. In contrast, although Koroneiki and Arbequina showed some growth under water stress, however, induced high VI in both scions (Am and Co) and they did not attain the same performance compared to the control at the end of recovery. However, Co/Z combination showed the best performance compared to the control at the end of recovery.

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