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The olive tree: a paradigm for drought tolerance in Mediterranean climates

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Abstract

Olive tree (*Olea europaea* L.) is commonly grown in the Mediterranean basin where prolonged droughts may occur during the vegetative period. This species has developed a series of physiological mechanisms to tolerate drought stress and grow under adverse climatic conditions that can be observed in numerous plants of the Mediterranean macchia. These mechanisms have been investigated through an experimental campaign carried out over both irrigated and drought-stressed plants in order to comprehend the plant response under stressed conditions and its ability to recover. Experimental results show that olive plants subjected to water deficit lower the water content and water potentials of their tissues, establishing a particularly high potential gradient between leaves and roots, and stop canopy growth but not photosynthetic activity and transpiration. This allows the continuous production of assimilates as well as their accumulation in the various plant parts, so creating a higher root/leaf ratio if compared to well-watered plants. Active and passive osmotic adjustment due to the accumulation of sugars (in particular mannitol and glucose), proline and other osmolytes has a key role in maintaining cell turgor and leaf activities. At severe drought-stress levels, the non-stomatal component of photosynthesis is inhibited and a light-dependent inactivation of the photosystem II occurs. Finally, the activities of some antioxidant enzymes involved in the scavenging of activated oxygen species and in other biochemical pathways, increase during a period of drought. The present paper provides an overview of the driving mechanisms adopted by olive trees to face drought stress with the aim of better understand plant-soil interactions.

1 Introduction

The Mediterranean-climate regions are characterised by a cycle of temperatures out of phase with the rainfall forcing producing mild to cool rainy winters and dry summers. The hydrological variability of Mediterranean climate regions is due to a combination of

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rainfall (irregularly distributed in time and space) and heterogeneous land topography. The existing variety of climatic condition in these areas is due to the specific configuration of land surface and distance from sea (Fiorentino et al., 2006). The climatic forcing of Mediterranean areas induces a temporal variability in the soil moisture dynamics that is strongly affected by seasonal fluctuations between humid and dry conditions. This behaviour is clearly due to the characteristic climatic conditions of the region that moves from rainy winters to dry summers characterised by low air humidity, high solar radiation and consequently high rates of evapotranspiration. In these periods, water becomes a limiting factor producing prolonged and intense drought stress in plants.

Mediterranean vegetation dealing with this peculiar soil moisture dynamics has developed a number of physiological mechanisms to tolerate drought stress and grow under adverse climatic conditions (Lo Gullo and Salleo, 1988). Olive tree (*Olea europaea* L.) is one of the most typical and economically important tree culture species belonging to the Mediterranean area and it presents most of the characteristics of a typical drought-tolerant plant. In fact, as for many Mediterranean species adapted to semi-arid climates (Lo Gullo and Salleo, 1988), olive tree is able to tolerate the low availability of water in soil by means of morphological, physiological and biochemical adaptations acquired in reply to periods of water shortage often lasting throughout the spring-summer period (Connor and Fereres, 2005). In this species, a series of strategies act synergically against drought stress, such as the regulation of stomata aperture and transpiration (Moreno et al., 1996; Nogués and Baker, 2000), the regulation of gas exchange (Moriani et al., 2002), a very developed osmotic adjustment (Chartzoulakis et al., 1999), the regulation of the antioxidant system (Bacelar et al., 2007), the appearance of leaf anatomical alterations (Chartzoulakis et al., 1999), and the ability of extracting water from the soil due to a deep root system (Fernandez et al., 1997) and to a high water potential gradient between canopy and root system (Tombesi et al., 1986). Olive trees is confirmed to be economical and sparing users of soil water, with an efficient xylem sap transport and the maintenance of significant rates of gas exchange even during drought stress (Tognetti et al., 2004). For these reasons, olive tree can be

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defined as a model-plant for drought tolerance in Mediterranean climates.

The olive is the emblematic tree of the Mediterranean regions and constitutes an integral and significant part of the Mediterranean environment and culture, however, its ecological importance has only recently been acknowledged (Loumou and Giourga, 2003). Olive growing is often confined to slopes or fairly ragged land and occupies important parts of mountains and hills (Favia and Celano, 2005). Its culture reduces soil erosion and favors the preservation of a high bio-diversity (Loumou and Giourga, 2003).

Understanding the mechanisms by which olive plants face drought stress under extreme environmental condition is essential for selecting more drought-tolerant cultivars and hence for saving water resources in semi-arid environments. In this paper, we show some recent studies carried out to provide complete picture of the response of olive plants subjected to drought and to better explain their high degree of resistance to this specific abiotic stress. The information here obtained may improve our knowledge regarding the temporal variability of plant soil atmosphere continuum in this typical species of Mediterranean semi-arid regions.

2 Materials and methods

2.1 Description of the first experiment

The first experiment was carried out at Metaponto (Southern Italy, Basilicata Region – 40°24' N, 16°48' E). Trials were carried out in controlled conditions on two-year old own-rooted olive plants (*Olea europaea* L., cv. “Coratina”). Both irrigated and drought-stressed plants were studied. Drought stress levels were defined on the basis of the values of leaf water potential (Ψ_w) measured pre-dawn using a pressure chamber (PMS Instrument Co. Corvallis, OR, USA), according to Turner (1981). The effects of different levels of soil water deficit on water relations, gas exchange, osmotic adjustment, activity of antioxidant enzymes and markers of oxidative stress were studied on

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olive plants grew uniformly outdoors in 0.016m^3 vases containing loamy sand (73.2% sand, 13.3% silt and 13.5% clay). Pots were covered with plastic film and aluminium foil in order to avoid evaporation from the soil surface and to minimize temperature increase inside the containers. All plants were weighed each evening in order to calculate the amount of water transpired. In the case of irrigated plants, the soil water content was integrated every evening providing the amount of water lost through transpiration during the day in order to keep a relative saturation of 85%. On the other hand, drought-stressed olive plants were watered applying a gradual and controlled reduction for the first ten days and successively irrigation ceased. Once the maximum levels of Ψ_w had been reached, all plants were rewatered to create optimal soil water conditions. During this period the amount of water added daily was equal to the transpired amount.

2.2 Description of the second experiment

The second study site was located at Lavello (Southern Italy, Basilicata region – $41^\circ 03' \text{N}$, $15^\circ 42' \text{E}$), a semi-arid area with average annual rainfall of 670 mm concentrated in the October–February period and monthly average temperatures ranging from 5.7 to 24.1°C . This experimental site is characterised by intense and frequent dry conditions as one may observe from the probability density function of the relative saturation of soil, s (given by the ratio between the soil water content, θ , and the soil porosity, n), obtained via numerical simulation (Fig. 1). Numerical analysis were performed adopting the simulation scheme for soil water balance proposed by Rodríguez-Iturbe et al. (1999) adopting recorded rainfall and evapotranspiration data over a period of 40 years in order to account for the seasonal fluctuations of the climatic forcing. The distribution refers to the study area adopted in the field experiment and looks like a gamma distribution (e.g. Isham et al., 2005). The probability distribution displays dry conditions ($s \leq 0.3\text{--}0.4$) with a high frequency and also an elevated dispersion mainly due to the seasonal fluctuations.

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In this experiment, the relationships between canopy and roots were examined on own-rooted olive plants, cv. Coratina, planted in 1992 at distances of 6×3 m and monitored throughout a period of seven years after planting. Irrigation was suspended in part of the plot, whereas the rest was irrigated using a localized system (microjets discharging 80 L h⁻¹ over a 1 m-radius). The soil was a sandy loam (53.3% sand, 29.0% silt and 17.7% clay).

3 Tolerance strategies against drought stress

3.1 Gas exchange and water relations

In olive plants, morphological and anatomical features such as microphyllia, the thick leaf cuticle with large amounts of waxy substances, the hairiness of the leaf abaxial surface and the high specific weight of the leaves (sclerophylly) are means developed by this species to reduce water loss. Transpiration rates in olive are higher than in most other fruit tree species under both well-watered and drought conditions, and the various tissues can withstand very negative values of water potential (Xiloyannis et al., 2003).

The first experiment, carried out on two-year old plants, was aimed to investigate on the effects of drought stress on plant transpiration and photosynthesis. The measured relative saturation of soil in drought stressed plants during the first experiment is described in Figs. 1, 2a, where the drying phase lasted 22 days and there after soil water content was kept fairly constant for one month. During this experiment, the transpiration was monitored and showed an interesting behaviour when compared with the trend of relative soil saturation (Fig. 2b). In particular, transpiration occurs at the maximum rate as long as soil moisture is sufficient to permit the normal course of plant physiological processes but, when relative soil saturation becomes lower than 0.35, the transpiration is inhibited and it decreases almost linearly with the soil water content.

In normal conditions, plant transpiration can be computed as a function of relative

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soil saturation following the expression given by Laio et al. (2001)

$$E(s) = \begin{cases} E_{\max} \frac{s-s_w}{s^*-s_w} & s_w \leq s \leq s^* \\ E_{\max} & s^* \leq s \leq 1 \end{cases} \quad (1)$$

where E_{\max} is the maximum rate of transpiration that during the experiment was fairly constant (see VPD – Vapor Pressure Deficit in Fig. 2a, s^* is the relative soil saturation at the initial stomata closure and s_w correspond to the relative saturation of soil at the wilting point. Nevertheless, another relevant aspect for a correct description of the soil-plant continuum is that transpiration is inhibited during the rewatering phase even if the soil saturation is above s^* (Fig. 2b). This is likely due to the potential damages induced by the prolonged water-stress in plants (Fig. 2b). In this case, olive tree is able to recover their functionality within one month, but during this period transpiration was significantly reduced and Eq. (1) should be applied accounting for this reduction in the potential transpiration rate.

Reduction of soil water content from a relative saturation of soil of 0.7 to approximately 0.4 induces in olive plants a slight drop in pre-dawn leaf water potential (Ψ_w) (from -0.5 to -0.9 MPa). At this value, daily transpiration per unit of leaf area is reduced of about 55% while photosynthesis decreases approximately of 30% if compared to well-irrigated plants (Fig. 3). However, unlike in other species, leaves continue to function even at Ψ_w of -6.0 MPa. In dry condition, olive leaves can use for transpiration about 60% of their water reserves without irreversible damage, contributing to the demands of transpiration as stress increases, up to extreme values of -7.0 MPa, when relative water content reaches 40%. This value is considerable if compared with that of other fruit species such as kiwifruit, which uses for transpiration a limited amount of water (about 9%) from its reserves under conditions of severe water deficit (Nuzzo et al., 1997).

During periods of water shortage, high gradients of water potential between leaves (-7.0 MPa), roots (-3.5 MPa) and soil are formed, facilitating water uptake even at soil water potentials of about -2.5 MPa. If we assume that the soil volume explored by the

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roots of a mature olive orchard is approximately $15\,000\text{ m}^3\text{ ha}^{-1}$ and that the soil has a volumetric field capacity of 40%, the additional water available between -1.5 MPa (the soil water potential at which most tree species die) and -2.5 MPa is about 570 m^3 per hectare. One hectare of a mature olive orchard will consume around 10 m^3 of water per day under these conditions, so that this amount of water is sufficient to maintain a minimum level of activity in stressed plants for 50–60 days (Dichio et al., 2003).

During the first days of recovering following a drought phase, olive plants recover only partially leaf water potential but recover completely the maximum efficiency of photosystem II calculated as F_v/F_m , where F_v is the variable fluorescence and F_m maximal fluorescence measured on dark-adapted leaves by means of a leaf chamber fluorometer. (Table 1). This suggests that olive plants are have a strong mechanism for photosystem II repair after long-term photoinhibition and drought stress. Moreover, transpiration rates in the first two weeks of the rewatering period are much lower than the values of well-watered plants and their complete recovery occurs after four weeks of rewatering (Fig. 2b). A similar inhibition during the first days of rewatering was also observed for photosynthetic rates (Table 1). It is important to note that the extent of gas exchange inhibition is related to the level of drought stress previously experienced by plants (Angelopoulous et al., 1996). These persisting deficits in leaf gas exchange are not due to non-recovery of cell turgor but to other factors probably involving the hormonal and biochemical balance, the efficiency of the conducting system and the water absorption capacity of roots.

3.2 Osmotic adjustment and cell wall properties

Another important mechanism adopted by olive tree to face water deficit is osmotic adjustment. This physiological process is due to the accumulation of organic osmolytes in the cytosol compartment of cells and it can play a key role in turgor maintenance of plant tissues. The recognised metabolic benefits of osmolyte accumulation may depend on either active accumulation of compatible solutes within cells (active osmotic

adjustment; active $\Delta\Psi_{\pi}$) or loss of water from the plant tissues (passive osmotic adjustment; passive $\Delta\Psi_{\pi}$) or both. In plants subjected to a severe drought stress, leaf osmotic potential (Ψ_{π}) at full turgor decrease from -2.06 ± 0.01 MPa to -2.81 ± 0.03 MPa, whereas Ψ_{π} at turgor-loss decrease from -3.07 ± 0.16 MPa to -3.85 ± 0.12 MPa (Dichio et al., 2003).

Under drought stress conditions, olive tree sets on active and passive $\Delta\Psi_{\pi}$ not only in leaves, but also in roots increasing its ability to extract water from dry soil. In fact, an active $\Delta\Psi_{\pi}$ of 1.42 MPa was also observed in roots having a 1–4 mm-diameter (Dichio et al., 2006). This physiological response reduces the osmotic component (Ψ_{π}) of the total water potential (Ψ_w), and allows a favourable soil-plant water gradient which enables plants to extract water from soil at water potential below the wilting point (Dichio et al., 2006) and to maintain gas exchange, growth and productivity during drought periods (Xiloyannis et al., 1988; Dichio et al., 2002). The passive concentration of solutes within cells is the most important mechanism to maintain cellular turgor. In fact, the contribution of passive $\Delta\Psi_{\pi}$ represents approximately 60% of the total osmotic adjustment, while the remaining 40% is due to active $\Delta\Psi_{\pi}$ (Table 2).

The ex-novo synthesis of osmotically active compounds takes place in both leaves and roots and regards mainly sugars and proline. Extracts of leaves and roots of well-watered olive revealed that the most predominant sugars are mannitol and glucose, which account for more than 80% of the total soluble carbohydrates (Cataldi et al., 2000). At a Ψ_w of -6.0 MPa, in olive tissues mannitol increased of about 97% and it was about 15% more concentrated than glucose. Moreover, it was found that the contribution to total Ψ_{π} in severe-stressed plants made by glucose and mannitol combined was -0.32 MPa and an increase in malic and citric acid concentrations occurred. The levels of glucose, sucrose and stachyose decreased in thin roots at all the levels of water deficit, whereas medium roots exhibited no differences in the levels of these carbohydrates. Inorganic cations largely contribute to Ψ_{π} at full turgor and remained almost unchanged during the period of drought stress, except for the amount of Ca^{2+} which increased of 25% in water-stressed plants. The amount of malates in-

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creased both in leaves and roots during the dry period, whereas citrates and oxalates decreased. The results support the hypothesis that the observed decreases in Ψ_w and active $\Delta\Psi_\pi$ in leaves and roots of drought-stressed plants are due to an active accumulation of mannitol, Ca^{2+} and malates within cells.

5 In olive plants, a rapid increase of proline at Ψ_w lower than -3.0 MPa was observed both in leaves and roots. In particular, proline level in olive leaves reaches $1.59\pm 0.03\ \mu\text{mol mg}^{-1}\text{ DW}$ at severe water deficit and gives a considerable contribute to the decrease of Ψ_w (Sofa et al., 2004b). Finally, the maintenance of negative values of active $\Delta\Psi_\pi$ during the rewatering phase suggests this can be a strategy for this
10 species to withstand other possible periods characterized by water deficit (Dichio et al., 2006).

The elasticity and plasticity of cells depend on the composition and structure of the cell wall. An increase in elastic modulus (ε) is expected when cell walls become more rigid or thicker, and higher values of elastic modulus bring tissues to the turgor-
15 loss point faster than lower values for a given percentage of dehydration. Such a response favors drought avoidance by stomatal control of transpiration for relatively small water losses and is beneficial when there is limited water. As drought-stress increases, the maximum elastic modulus in olive leaf tissues raises from $11.6\pm 0.95\text{ MPa}$ to $18.6\pm 0.61\text{ MPa}$ (Fig. 4) (Dichio et al., 2003). This suggests that a drought-stressed
20 olive tree activates metabolic processes to produce substances that increase cell tissue rigidity, likely by regulating some enzymes involved in lignin biosynthesis such as peroxidases (Sofa et al., 2004a). High values of elastic modulus, together with low values of Ψ_π can be responsible for the observed high gradients of water potential between leaves and soil and thus can facilitate water extraction from the soil.

25 3.3 Regulation of antioxidant enzymes and markers of oxidative stress

Drought stress is often associated with increased cellular levels of activated oxygen species (AOS), such as superoxide anion (O_2^-), hydrogen peroxide (H_2O_2), hydroxyl

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radical (HO) and singlet oxygen ($^1\text{O}_2$) (Smirnoff, 1993). AOS are very reactive compounds able to oxidize and damage cell macromolecules and for this reason plants have enzymatic antioxidant mechanisms to remove them.

Olive tree is able to up-regulate the enzymatic antioxidant system as plants enter water deficit conditions (Table 3). This response protects cellular apparatus during water deficit conditions and limits cellular damage caused by AOS. In fact, the activities of drought on the activities of ascorbate peroxidase (APX) and catalase (CAT) in leaves show a marked three-fold increase, reaching values of 13.77 ± 0.55 units mg^{-1} DW and 11.78 ± 0.18 units mg^{-1} DW, respectively; the activities of superoxide dismutase (SOD) and peroxidase (POD) increased both in leaves and roots (Sofa et al., 2004a). Peroxidase isoenzymes are involved in lignin biosynthesis and thus participate in the modulation of cell wall properties during plant growth. For this reason, the observed increases in peroxidase activity could reflect the changed mechanical properties of the cell wall, which in turn, can be correlated with drought adaptation. In contrast, polyphenol oxidase (PPO) activity decreases during the progression of stress in all the tissues studied (Sofa et al., 2004a). Drought stress can improve the antioxidant action of phenols by inhibiting polyphenol oxidase and consequently by maintaining the phenol compounds pool in the reduced state. Moreover, the proteolytic activity of polyphenol oxidase suggests that the enzyme could be involved in removing the proteins damaged by activated oxygen species.

Significant increases of lipoxygenase (LOX) activity and malondialdehyde (MDA) content were also observed during the progressive increment of drought stress in both leaf and root tissues of olive plants (Sofa et al., 2004b). The increases in malondialdehyde levels and lipoxygenase activity suggest that the water deficit is associated with the peroxidation of membrane lipids caused by activated oxygen species and with the photodamage of photosynthetic apparatus.

During a rewatering treatment following a drought period, the activities of antioxidant enzymes and the levels of malondialdehyde decrease during the rewatering period in both leaves and roots. By contrast, polyphenol oxidase activity increases during

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rewatering in both leaf and root tissues (Sofa et al., 2004b).

3.4 Growth parameters

The second experiment, carried out in field, highlighted the different growth rates of olive tree's organs between drought-stressed and well-watered plants. Non-irrigated olive plants have higher values of root dry weight/leaf area ratio, volume of explored soil/leaf area ratio, and therefore have greater water availability per unit of leaf area (Celano et al., 1999; Palese et al., 2000). Moreover, root system of drought-stressed olive plants is deeper (up to 1.5 m) if compared to well-watered ones while root density remains similar in the two treatments (Dichio et al., 2002). This data demonstrate the positive effect of water availability on the growth of both canopy and roots, and the ability of olive tree to explore the deeper soil layers when grown under water deficit.

The results from the second experiment showed that lower soil water availability determines a greater growth reduction in the above-ground organs than in the underground organs (roots and stump) (Fig. 5). The greater decrease in canopy growth with respect to root growth in drought conditions is a mechanism which improves water availability per unit of leaf area, enabling plants to resist long water deficit periods while keeping the leaves photosynthetically active.

4 Conclusions and final remarks

Experimental results provide a deep overview of the different mechanisms developed by olive tree in order to deal with water limited conditions. A summary of drought stress effects on this species is given in Fig. 6, where the inhibition of physiological processes due to the decrease in pre-dawn leaf water potential (Ψ_w) is depicted.

The first effect of the decrease in Ψ_w is a reduction in cell turgor and gas exchange. If compared to a mean response of a plant to drought stress (Hsiao, 1973), olive tree is able to maintain cell turgor at much lower Ψ_w values. This is likely due to the stiffness

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of cell walls related to the high values of elastic modulus, that increase with drought intensity, and to the reduced water losses from cells. The inhibition of photosynthesis begins very soon and is accompanied by a decrease in transpiration. This suggests that, in olive plants subjected to water deficit, photochemical processes are affected not only by photoinhibition and photo-oxidation but stomatal factors are also involved. Moreover, shoot growth rate seems to be more sensitive to the decrease in Ψ_w if compared to root growth rate and this can be the cause of the higher root/shoot ratio of drought-stressed plants (Fig. 5). At the values of Ψ_w below -1.5 MPa, when gas exchange and growth rates are inhibited, the degradation of cell membranes due to lipid peroxidation takes place.

The regulation of stomata closure is one of the first effects of drought stress on olive tree's physiology and it is gradual with the decrease of Ψ_w . The stomata closure starts to be more relevant for values of Ψ_w below -2.5 MPa and at this point it is followed by a strong decrease in cell turgor (Fig. 6). For values of Ψ_w below -3.2 MPa, the osmotic adjustment due the accumulation of proline, sugars and other osmolytes is completely active and allows the conservation of water in olive tissues. Soon after, respiration is negatively affected by disturbances in cell metabolism.

The patterns described in Fig. 6 and the comparisons with other Mediterranean plant species (Lo Gullo and Salleo, 1988) give evidence for a high degree of tolerance of olive tree against water deficit and a concerted and gradual series of adaptation mechanisms against this abiotic stress. The analyses here discussed may be useful to better understand the physiological mechanisms adopted by a model-plant for water stress tolerance in a Mediterranean ecosystem.

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Table 1. Trends of pre-dawn leaf water potential (Ψ_w), net photosynthetic rates (A) and maximum efficiency of photosystem II (F_v/F_m) during the rewatering of severely stressed plants.

Days of rewatering	Ψ_w (MPa)	A ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	F_v/F_m
1	-6.50	6.6±0.78	0.643±0.081
2	-1.30	7.8±1.12	0.742±0.043
3	-0.85	9.4±1.01	0.772±0.063
4	-0.80	11.1±1.2	0.789±0.045
5	-0.80	9.7±1.1	0.798±0.054
Control	-0.45	22.1±0.95	0.816±0.036

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Table 2. Passive, active and total osmotic adjustment measured predawn in leaves of drought-stressed olive plants. Each value represents the mean of three measurements (\pm SE) from three plants having a similar value of pre-dawn leaf water potential.

Pre-dawn leaf water potential (MPa)	Osmotic adjustment (MPa)		
	Passive	Active	Total
-1.7	0.21 \pm 0.03	0.13 \pm 0.02	0.34 \pm 0.05
-3.3	0.56 \pm 0.08	0.30 \pm 0.05	0.86 \pm 0.10
-5.4	1.38 \pm 0.12	1.04 \pm 0.13	2.42 \pm 0.28

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Table 3. Activities of superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), guaiacol peroxidase (POD), polyphenol oxidase (PPO) and lipoxygenase (LOX) in leaves and roots of drought-stressed and well-watered control olive plants. Each value represents the mean of three measurements (\pm SE) from three plants having a similar value of pre-dawn leaf water potential. Stars refer to differences between well-watered and drought-stressed plants at $P=0.05$.

Pre-dawn leaf water potential (MPa)		Enzyme activity (units mg^{-1} dry weight)					
		SOD	APX	CAT	POD	PPO	LOX
Leaves	–0.4 (control)	15.21 \pm 0.82	3.88 \pm 0.20	4.52 \pm 0.18	29.21 \pm 1.24	33.49 \pm 0.87	149.93 \pm 7.35
	–1.6	30.73 \pm 0.89*	7.36 \pm 0.07*	6.81 \pm 0.05*	39.06 \pm 1.97*	26.55 \pm 0.85*	240.10 \pm 9.12*
	–4.3	31.69 \pm 1.90*	12.11 \pm 0.26*	11.44 \pm 0.74*	48.17 \pm 2.01*	24.13 \pm 1.34*	461.35 \pm 28.20*
	–5.7	25.17 \pm 1.06*	13.77 \pm 0.55*	11.78 \pm 0.18*	40.66 \pm 0.73*	20.36 \pm 0.91*	492.43 \pm 34.29*
	–0.4 (control)	7.99 \pm 0.20	0.36 \pm 0.01	2.08 \pm 0.02	23.88 \pm 0.34	38.19 \pm 0.99	54.45 \pm 2.57
Roots	–1.6	11.20 \pm 0.28*	0.42 \pm 0.01*	3.10 \pm 0.07*	39.05 \pm 1.56*	35.63 \pm 0.74*	59.27 \pm 1.20*
	–4.3	15.94 \pm 0.59*	0.56 \pm 0.02*	2.74 \pm 0.10*	47.77 \pm 2.11*	21.43 \pm 0.43*	55.21 \pm 2.54*
	–5.7	17.19 \pm 0.49*	0.51 \pm 0.02*	2.58 \pm 0.07*	44.56 \pm 1.27*	19.05 \pm 0.33*	50.79 \pm 1.42*

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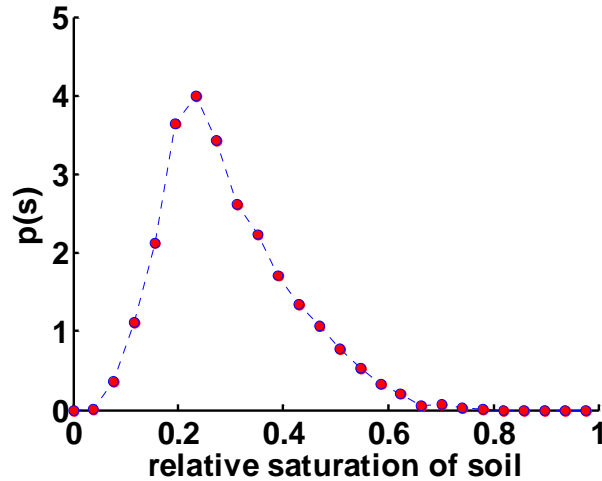


Fig. 1. Probability density function of the relative saturation of soil obtained simulating the soil water balance over 40 years in Lavello, a Mediterranean area of Southern Italy.

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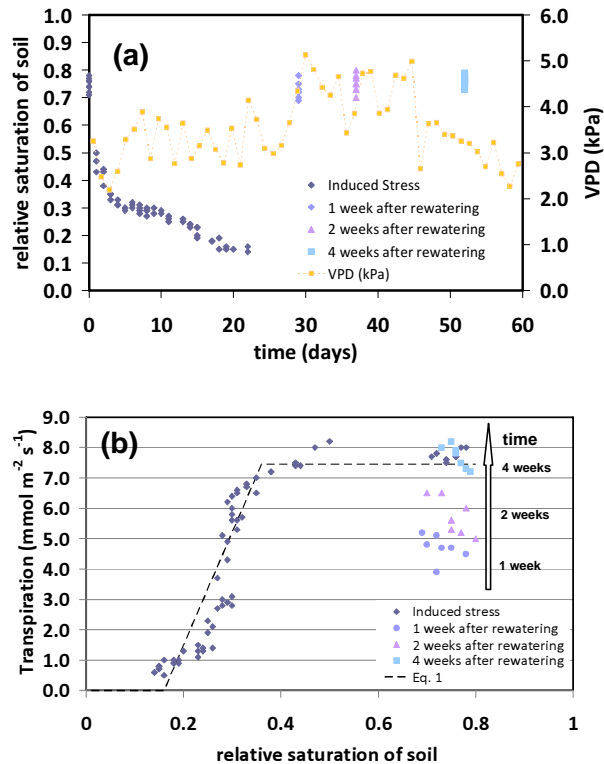


Fig. 2. (a) Measurements of soil saturation during an experiment where olive plants were driven toward drought-stressed conditions and watered afterwards. (b) Measured transpiration as a function of the relative saturation of soil. The dashed line describes the loss function with parameters: $E_{\max}=7.45 \text{ mmol m}^{-2} \text{ s}^{-1}$, $s^*=0.36$, and $s_w=0.16$.

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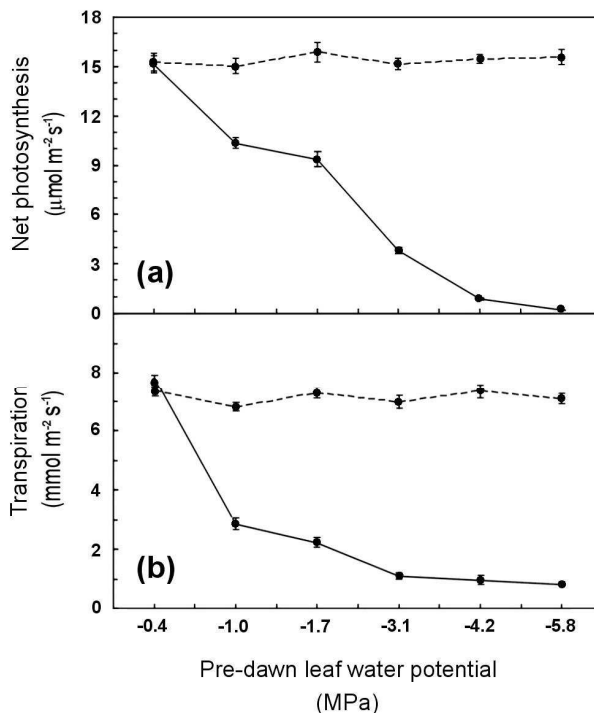


Fig. 3. Trends of net photosynthesis **(a)** and transpiration **(b)** in drought stressed (continuous lines) and irrigated (dashed lines) during a drought stress period. Each value represents the mean of three measurements (\pm SE) from three plants having a similar value of pre-dawn leaf water potential.

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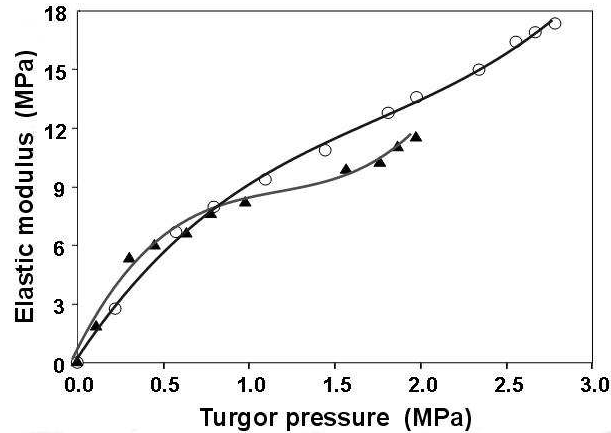


Fig. 4. Relationship between the bulk elastic modulus and turgor potential shown by representative leaves for well-watered (▲) and drought-stressed (pre-dawn leaf water potential = -5.2 MPa) (○) olive plants.

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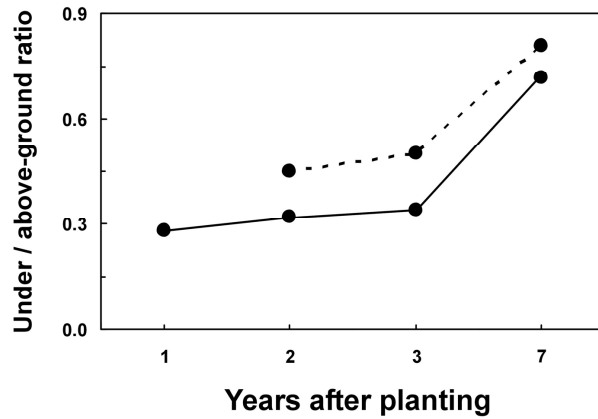


Fig. 5. Dry matter ratio between under- and above-ground tree parts in irrigated (solid line) and drought-stressed (dotted line) olive plants.

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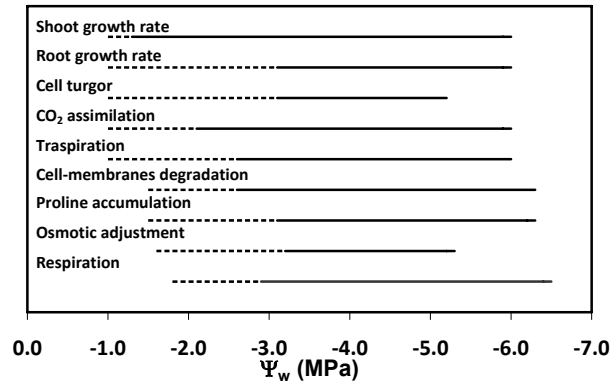


Fig. 6. Effects of the decrease in pre-dawn leaf water potential (Ψ_w) on physiological processes of olive plants. Dashed lines describe the Ψ_w intervals where physiological processes are partially inhibited or induced, while continuous lines describe the intervals where those processes are strongly affected by drought stress.

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