

Shade effect on photosynthesis and photoinhibition in olive during drought and rewatering

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ABSTRACT

Olive tree (*Olea europaea* L.) is commonly grown under environmental conditions characterised by water deficit, high temperatures and irradiance levels typical of Mediterranean semi-arid regions. Measurement of gas exchange, chlorophyll content, chlorophyll fluorescence and photoinhibition was carried out on two-year-old olive trees (cv. 'Coratina') subjected to a 21-day period of water deficit followed by 23 days of rewatering. At the beginning of the experiment, plants were divided in to two groups and subjected to different light regimes: exposed plants (EP) under a mean photosynthetically active radiation (PAR) at mid-day of $1800 \mu\text{mol m}^{-2} \text{s}^{-1}$ and shaded plants (SP) under a mean PAR of $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$. The effect of drought and high irradiance levels caused a reduction of gas exchange and photosystem 2 (PSII) efficiency, in terms of quantum yield of PSII (Φ_{PSII}) both in EP and SP. Shading conditions allowed plants to maintain a high photosynthetic activity at low values of stomatal conductance, whereas in EP the reductions in photosynthetic efficiency and intrinsic water efficiency were due to non-stomatal components of photosynthesis. The decrease in photosynthetic activity and the increase of photoinhibition under drought were more marked in EP than in SP. Full sunlight caused in EP a higher non-photochemical quenching, whereas SP showed a better photochemical efficiency. The information here obtained can be important to understand the mechanisms by which olive plants can minimize photoinhibition when subjected to simultaneous abiotic stresses.

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1. Introduction

The Mediterranean-type summer is characterised by high air temperatures and recurrently dry periods, which are predicted to occur more frequently in the future as a consequence of the global warming (Osborn et al., 2000). Hereby, plants regularly experience drought as combined with high radiation stress, determining plant growth and survival.

Olive tree (*Olea europaea* L.) is a woody species typically cultivated in the Mediterranean basin, where plants are often exposed to long periods of water deficit and high irradiance levels during the dry season (Connor and Fereres, 2005). If compared to other fruit tree species, olive tree is able to tolerate the low availability of water in the soil by means of morphological and physiological adaptations acquired in reply to perennial drought stress conditions (Connor and Fereres, 2005; Bacelar et al., 2007). In this species, a series of strategies act synergically against drought, such as the reduction of gas exchange (Moriani et al., 2002), a very developed osmotic adjustment (Dichio et al., 2006), the up-regulation of some antioxidant enzymes (Sofo et al., 2005),

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 and to a high water potential gradient (Fernández et al., 1997).

The photosynthetic processes are mainly driven by irradiance, however at levels above the photosynthetic saturation point excessive radiation may reduce photosystem 2 (PSII) efficiency (i.e. photoinhibition) (Demmig-Adams et al., 1995). The adverse impact of some abiotic stresses (i.e. drought, high radiation and air temperature) on photosynthetic apparatus of various endemic and non-endemic Mediterranean species has been widely investigated (Gratani and Varone, 2004; Flexas et al., 2004; Montanaro et al., 2007), revealing that the effects of low water status on the susceptibility of PSII to photodamage are species-specific (Valladares and Pearcy, 2002). It has been demonstrated that during water deficit olive tree achieve water conservation and photo-protection by the regulation of stomata aperture and the reduction in transpiration occur (Bongi and Long, 1987; Angelopoulos et al., 1996; Fernández et al., 1997).

Physiological and structural leaf responses to various irradiance-drought scenarios have shown that shading conditions could ameliorate (or at least not aggravate) the drought impact (Quero et al., 2006). However, under limiting irradiance availability (i.e. shade), the effect (positive, negative, or independent) of a shortage

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of a further resource (e.g. water) on leaf performance is still debated. Recently, Gregoriou et al. (2007) have reported that long-term shading could dramatically lower the photosynthetic capacity and yield in olive mainly as a consequence of anatomical modifications induced by shade.

Till now, the effects of shading on the photosynthetic machinery of olive have not been adequately explored. Therefore, this study investigates the impact of temporarily shade on the response of photosynthesis to excessive light combined with water shortage both in terms of CO₂ assimilation, as measured by leaf gas exchange, and of functionality of the photosynthetic apparatus, as assessed by chlorophyll fluorescence measurements. Potted olive trees under natural irradiance and artificially shaded were compared during drought and rewatering to provide additional information on the response of olive trees to different water-irradiance scenarios.

2. Materials and methods

2.1. Plant material and experimental design

Trials were conducted on two-year-old own-rooted *O. europaea* L. plants, cv. 'Coratina', measuring 130–150 cm in height and having a similar vegetative behaviour. The study site was located at the 'Pantanello' Agricultural Experimental Station in Metaponto (Southern Italy – N40°24', E16°48'). The experimental period started on July 1 and ended on August 26, 2005. Olive plants grew uniformly outdoors in 0.016 m³ pots containing 73.2% sand, 13.3% silt and 13.5% clay. The soil mixture was fertilized with 3.5 g per pot of slow release nitrogen complex fertilizer (Nitrophoska Gold 15N–9P–16K + 2Ca + 7Mg; Compo Agricoltura, Cesano Maderno, MI, Italy).

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 measure daily plant water consumption. Soil water content was maintained at a constant value of around 85% of water holding capacity by integrating the amount of water lost through transpiration during the day. At the beginning of the experiment, plants were divided in to two groups: 30 exposed plants (EP) and 30 shaded plants (SP). Exposed plants were maintained under prevailing environmental light (photosynthetically active radiation [PAR] range under clear sky = 1700–1900 μmol m⁻² s⁻¹ at 1200 h), whereas, starting from July 1, SP were kept in semi-shading conditions of about 67% of environmental radiation (PAR range = 1100–1300 μmol m⁻² s⁻¹ at 1200 h) by means of a neutral shading net (Arrigoni, CO, Italy, model 2591WO). Radiation spectral distribution above and under the net was measured at the beginning of the experiment at 1200 h using a portable spectroradiometer (LI-1800; Li-Cor Inc., NE, USA) (Fig. 1).

Starting from July 13, 26 plants per group were subjected to gradual water depletion for 21 days. During the first 10 days of the drought period, plants received in the evening (2000 h) 80% of their water consumption, in order to allow the induction and expression of adaptation mechanisms against drought. Successively, starting from day 11 of drought application, plants were not irrigated. The degree of drought stress in plants was defined by means of the values of leaf water potentials measured pre-dawn (LWP). After reaching the maximum level of water stress (August 3), plants were rewatered. The rewatering period lasted 23 days and during this period the amount of water added daily was equal to the transpired amount. Measurements during the rewatering period were carried out after 7 and 23 days from the beginning of water recovery.

Environmental parameters for each day of the experimental period were monitored by a weather station placed within 200 m of the experimental plot. Leaf-to-air vapour pressure deficit (VPD)

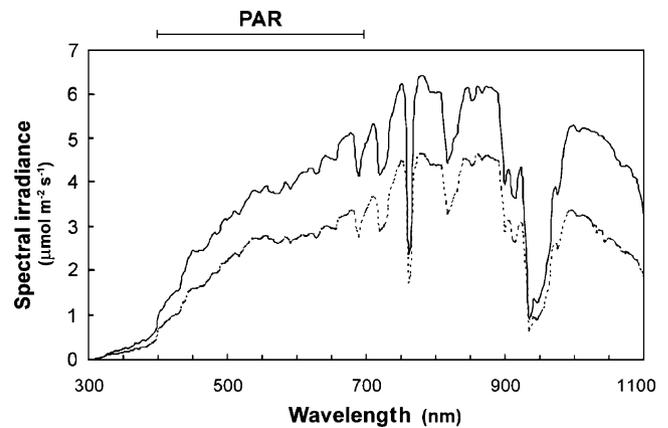


Fig. 1. Radiation spectral distribution above (continuous line) and under (dashed line) the shading net.

was calculated according to Goudrian and Van Laar (1994). The values of PAR were recorded at 1-min interval and daily integrated values were logged.

2.2. Water potential and gas exchange

Pre-dawn leaf water potential was measured both in EP and SP at each level of drought and rewatering on fully expanded leaves selected from each plant along the median segment of new-growth shoots. The values of LWP were measured at pre-dawn (at 0400–0500 h) using a Sholander pressure chamber (PMS Instrument Co., OR, USA).

Leaf gas exchange, temperature and chlorophyll fluorescence were measured using a programmable, open-flow portable system (LI-6400; Li-Cor Inc., NE, USA) operated at 500 μmol s⁻¹ flow rate with a leaf chamber fluorometer (LI-6400-40; Li-Cor Inc., NE, USA). The measurements of gas exchange were carried out at 0900–1000 h on horizontally positioned leaves taken from three EP and three SP having the same LWP. Temperature inside the leaf chamber was maintained equal to environmental air temperature by instrument automatic temperature regulation. The values of adaxial leaf temperature (T_{leaf}) were measured at 0900–1000 h by the instrument thermocouple inside the leaf chamber. The study of the relationships between net photosynthetic rate, stomatal conductance (g_s) and intrinsic water use efficiency (A/g_s) was carried out according to Flexas et al. (2004).

On leaves of each plant, quantum yield of PSII (Φ_{PSII}), photochemical quenching (qP) and non-photochemical quenching (NPQ) were determined. The value of PAR inside the leaf chamber (light with a 90% red fraction at a wavelength of 630 nm and a 10% blue fraction at 470 nm) was 850 μmol m⁻² s⁻¹. This value was chosen keeping into account the average light saturation point for olive (800–900 μmol m⁻² s⁻¹) and the mean environmental irradiance at 0900–1000 h monitored by the LI-6400 external quantum light sensor.

The values of Φ_{PSII} , a reliable indicator of PSII efficiency (Genty et al., 1989), were calculated as

$$\Phi_{PSII} = \frac{F'_m - F_t}{F'_m}$$

where F_t is the steady state fluorescence yield and F'_m is the maximum fluorescence yield under actinic light.

The values of qP were determined according to Maxwell and Johnson (2000) as

$$qP = \frac{F'_m - F_t}{F'_m - F'_o}$$

The values of NPQ were calculated according to Drake and Read (1981) as

$$\text{NPQ} = \frac{F_m - F'_m}{F_m - F'_o}$$

where F'_o is the minimal fluorescence in the dark of a light-adapted leaf.

2.3. Light response and fluorescence relaxation analysis

The same leaves chosen for gas exchange and fluorescence measurements were used for recording light response and fluorescence relaxation curves. Light response curves were recorded for each level of drought and rewatering at 0900–1100 h, to have the maximum PAR, with a 90% red/10% blue actinic light. Light curves were carried out starting from the highest light intensity (1800, 1600, 1200, 800, 400, 200, 100, 50 and 0 $\mu\text{mol PAR m}^{-2} \text{s}^{-1}$) at 15-min interval, in order to give the stomata time to equilibrate at each level.

Photosynthetic parameters were calculated from the equation of the light response curve of photosynthesis (Johnson et al., 1993):

$$A = \frac{A_{\max}(I - I_c)\alpha_c}{A_{\max} + (I - I_c)\alpha_c}$$

where A and A_{\max} are the net photosynthetic rate and the maximum net photosynthetic rate respectively (expressed in

$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), α_c the maximum quantum yield of photosynthesis ($\mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ PAR}$), I the light intensity and I_c is the light compensation point ($\mu\text{mol PAR m}^{-2} \text{ s}^{-1}$). Dark respiration rate (R_d) ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was calculated at the light compensation point as $R_d = \alpha_c I_c$.

Fluorescence relaxation curves were recorded at 0900–1100 h at the beginning of drought treatment, at the end of the drought period and at the end of the rewatering period according to the method of Walters and Horton (1991). Quenching was allowed to relax in the darkness after illumination and F_m was recorded at regular intervals of 5 min, with relaxation being followed over 45 min. Extrapolation from the graph ($\log F_m$ against time) of F_m values recorded when actinic light was removed, allowed the calculation of F'_m , that indicates the value of fluorescence attained if only slowly relaxing quenching was present in the light. Slowly relaxing non-photochemical quenching (NPQ_s) was calculated according to Maxwell and Johnson (2000) as $\text{NPQ}_s = (F_m - F'_m)/F'_m$.

3. Results

3.1. Environmental conditions

During the drought period, the levels of daily PAR exhibited a constant trend with high values between 50 and 70 $\text{mol m}^{-2} \text{ day}^{-1}$, except for some cloudy days (Fig. 2A). The analysis of radiation

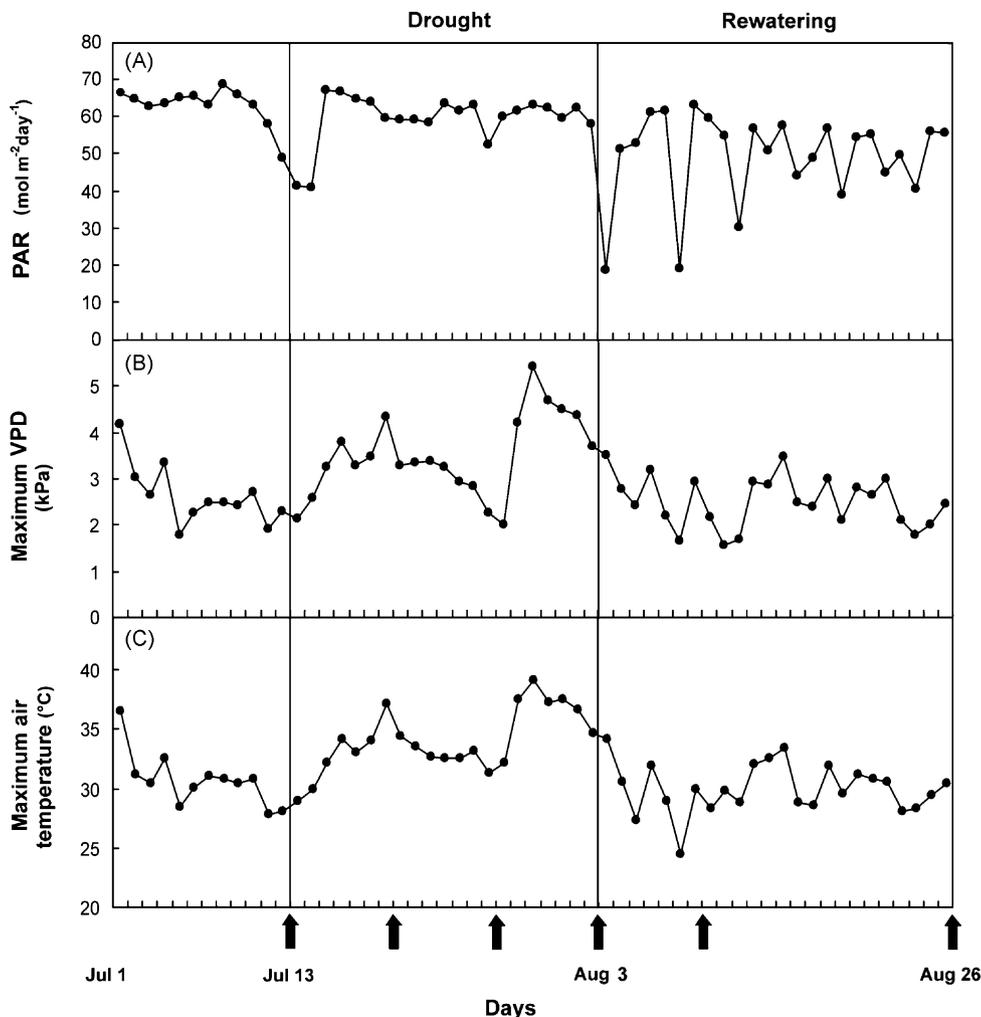


Fig. 2. (A) Daily photosynthetic active radiation (PAR), (B) maximum vapour pressure deficit (VPD) and (C) maximum air temperature at the field site during the experimental period. Arrows indicates the measuring days.

spectral distribution showed that the shading net transmitted evenly in all wavelengths and that radiation under the net decreased proportionally by about 33%. Maximum vapour pressure deficit ranged from 2.0 to 5.4 kPa and during the rewating it was on average basis equal to 2.9 kPa (Fig. 2B). In the measuring days, maximum air temperatures ranged between 34.2 °C (August 3) and 29.0 °C (July 13), with a mean value of 31.6 °C during the whole experimental period (Fig. 2C).

3.2. Water potential, gas exchange and leaf temperature

In all plants under drought, LWP of selected plants gradually decreased reaching a mean value of -6.5 MPa after 21 days and successively recovered completely during rewating. Net photosynthesis (A) and stomatal conductance (g_s) decreased with increasing drought (Fig. 3A and B). Throughout the drought stage, g_s in SP was lower than in EP (Fig. 3B), whereas A was higher in SP than in EP (Fig. 3A). At the end of the rewating period, g_s in EP (0.19 ± 0.02 mol H₂O m⁻² s⁻¹) did not reach the values of the same plants at the beginning of the experiment (0.24 ± 0.02 mol H₂O m⁻² s⁻¹), whereas SP showed a complete recovery of g_s

(Fig. 3B). Rewatering caused a complete recovery of A in SP (Fig. 3A). Moreover, EP did not show a complete recovery of A values at the end of the rewating period (Fig. 3A).

The values T_{leaf} increased at moderate and severe drought stress, declined in correspondence of the beginning of rewating and successively maintained a constant trend until the end of the experiment (Fig. 3C). During both drought and rewating, T_{leaf} values in EP were significantly higher than in SP (Fig. 3C).

3.3. Fluorescence parameters

The values of Φ_{PSII} decreased during the drought period and then recovered during the rewating period (Fig. 4A). Shading conditions in SP induced a protection of PSII, maintaining Φ_{PSII} higher if compared to EP (Fig. 4A). At the end of the rewating period, Φ_{PSII} in EP (0.22 ± 0.03) did not reach the values of the same plants at the beginning of the experiment (0.29 ± 0.03) (Fig. 4A). The values of qP in SP were higher than in EP, whereas the pattern of NPQ was opposite (Fig. 4B). Generally, the trends of qP and NPQ both in EP and SP showed a depression during the period of drought and then a partial or total recovery at the end of rewating (Fig. 4B).

The values of R_d decreased throughout the drought period (Fig. 5A). At a LWP of -6.5 MPa, R_d was significantly lower in EP (-3.97 ± 0.09 μ mol CO₂ m⁻² s⁻¹) than in SP (-3.50 ± 0.05 μ mol CO₂ m⁻² s⁻¹) (Fig. 5A). The values of I_c were higher in EP than in SP and increased during water deficit (Fig. 5B). A complete recovery of R_d and I_c occurred during rewating both in EP and SP (Fig. 5A and B). The analysis of relaxation curves shows that NPQ₅ increased with increasing drought, starting from 0.42 ± 0.02 and 0.38 ± 0.04 at the beginning of the experiment up to a maximum of 0.58 ± 0.04 and

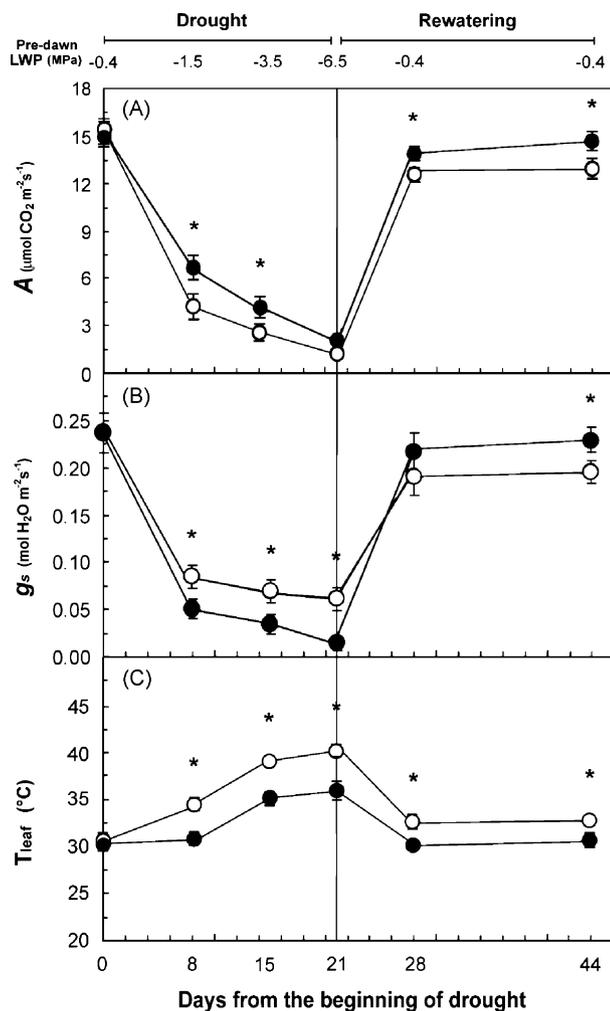


Fig. 3. (A) Net photosynthetic rate (A), (B) stomatal conductance (g_s) and (C) adaxial leaf temperature (T_{leaf}) in exposed (open symbols) and shaded (closed symbols) plants at different levels of drought and rewating. The values of pre-dawn LWP represent the mean of three measurements (\pm S.E.) on each of three selected plants, whereas the measurements of gas exchange and T_{leaf} were conducted at 0900–1000 h in replicates of three readings on each of three leaves per plant from three plants having the same pre-dawn LWP. Values with the asterisk are significantly different between exposed and shaded plants ($P < 0.05$, according to Student's t -test).

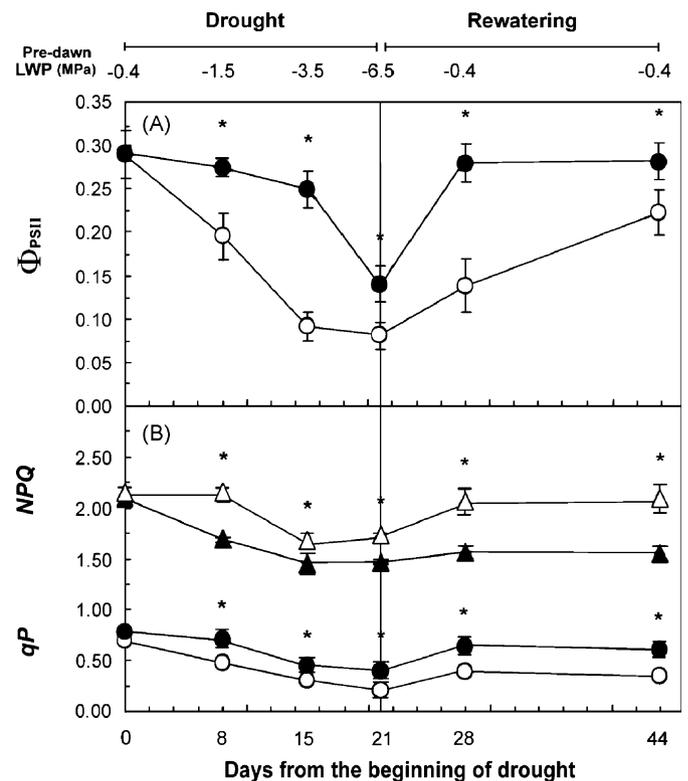


Fig. 4. (A) Quantum yield of PSII (Φ_{PSII}) and (B) photochemical quenching (qP , circles) and non-photochemical quenching (NPQ, triangles) in exposed (EP, open symbols) and shaded (SP, closed symbols) plants at different levels of drought and rewating. The measurements of chlorophyll fluorescence were conducted at 0900–1000 h in replicates of three readings on each of three leaves per plant from three plants having the same pre-dawn LWP, whereas the values of chlorophyll content represent the mean of three measurements (\pm S.E.) on each of three selected plants having the same pre-dawn LWP. Statistics like in Fig. 3.

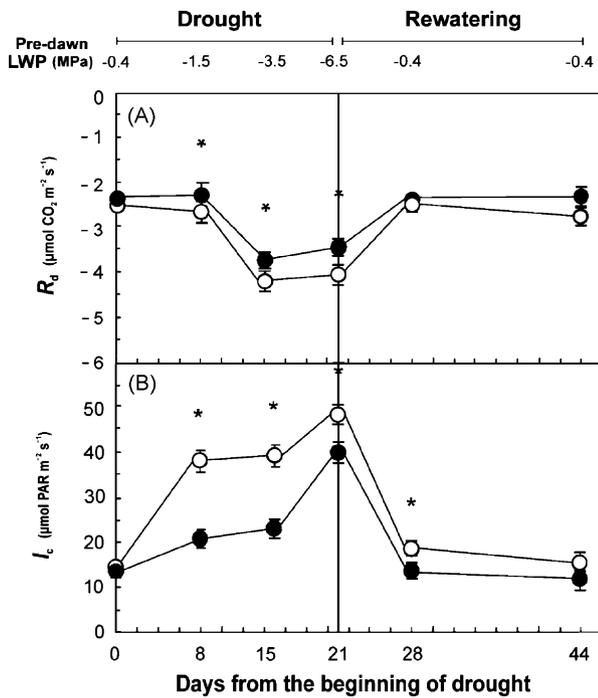


Fig. 5. (A) Dark respiration rate (R_d) and (B) light compensation point (I_c) in exposed (open symbols) and shaded plants (closed symbols) at different levels of drought and rewatering. The values (at 0900–1100 h) represent the mean of three measurements (\pm S.E.) from three plants having the same pre-dawn LWP. Statistics like in Fig. 3.

Table 1

Slowly relaxing non-photochemical quenching (NPQ_s) in exposed and shaded plants at the beginning of the experiment (well-watering conditions), at the maximum level of drought and at the end of the rewatering period. The values (at 0900–1100 h) represent the mean of three measurements (\pm S.E.) from three plants having the same pre-dawn LWP. Values followed by different letters (uppercase letters between columns and lowercase between rows) are significantly different ($P \leq 0.05$, according to Student's t -test).

	NPQ_s		
	Beginning of the experiment	Maximum level of drought	End of rewatering
Exposed	0.42 ± 0.02 Ba	0.58 ± 0.04 Aa	0.45 ± 0.08 Ba
Shaded	0.38 ± 0.04 Ba	0.49 ± 0.02 Ab	0.32 ± 0.03 Bb

0.49 ± 0.02 in EP and SP, respectively. Successively, both in EP and SP the values of NPQ_s recovered completely at the end of rewatering (Table 1). In EP, NPQ_s was generally higher than those found in SP throughout the whole experimental period (Table 1).

4. Discussion

Olive has been defined a tolerant tree able to face a series of abiotic stresses but in this species photoinhibitory processes during drought and rewatering were not studied in detail (Connor and Fereres, 2005).

In SP, the synergical effect of drought and reduced light caused a lower stomatal conductance, whereas the following rewatering determined a more efficacious recovery of stomatal conductance (g_s), showing a reversed trend with respect to the drought period (Fig. 3B). This phenomenon has also been observed by Gregoriou et al. (2007), that measured lower values of g_s in shaded olive plants. During the rewatering phase, the values of photosynthetic rates (A) in SP remained higher than the respective values of EP (Fig. 3A), implying a better

photosynthetic performance in plants under shade conditions. The positive shade effect on photosynthetic machinery is also highlighted by fluorescence analysis. Quantum yield of PSII (Φ_{PSII}) in SP were significantly higher than the values found in EP (Fig. 4A). The results obtained from light response curves (Fig. 5) corroborate the data on photosynthesis obtained from gas exchange and fluorescence measurements. In fact, the values of light compensation point (I_c) in SP were lower if compared to EP because, in these plants, dark respiration rates (R_d) were higher and thus a little net photosynthesis was required to bring the net CO_2 exchange to zero (Fig. 5).

On the basis of gas exchange data pooled from the experiment (Fig. 3A and B), it appears that shading determined higher values of A in the g_s range of 0.05 – $0.20 \text{ mol m}^{-2} \text{ s}^{-1}$, so confirming the beneficial effect of reducing excessive radiation on plant carbon gain. According to Flexas et al. (2004), information on the PSII status can be also inferred by the analysis of intrinsic water use efficiency (A/g_s) (Fig. 6B). As drought stress intensified, stomatal conductance decreased from maximum values till about $0.20 \text{ mol m}^{-2} \text{ s}^{-1}$ and, correspondingly, A/g_s increased progressively in both treatments (Fig. 6B), suggesting that stomata closure is the main limiting factor. As g_s dropped to about $0.10 \text{ mol m}^{-2} \text{ s}^{-1}$, A declined in both treatments, more sharply in EP than in SP (Fig. 6A). In SP, the higher A/g_s values observed in the g_s range of 0.10 – $0.20 \text{ mol m}^{-2} \text{ s}^{-1}$ suggest that shade reduced metabolic restriction of photosynthesis, as confirmed by the limited decline of Φ_{PSII} recorded in SP leaves if compared to EP (Fig. 4A). At g_s lower than $0.10 \text{ mol m}^{-2} \text{ s}^{-1}$, A/g_s in EP decreased, reflecting impaired photosynthetic metabolism in these plants, whereas the respective values in SP were higher (Fig. 6B).

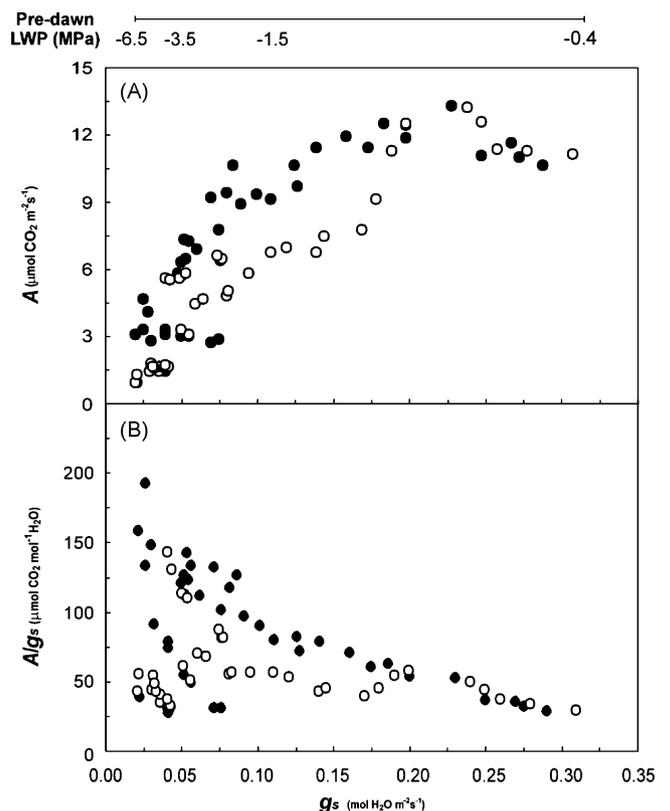


Fig. 6. (A) Relationship between net photosynthetic rate (A) and stomatal conductance (g_s) in exposed (open symbols) and shaded (closed symbols) plants. (B) Relationship between intrinsic water use efficiency (A/g_s) and stomatal conductance (g_s) in exposed (open symbols) and shaded (closed symbols) plants. Values represent measurements conducted at 0900–1000 h throughout the drought period in replicates of three readings on each of three leaves per plant.

Most of the studies of light effects on photoinhibition on tree species demonstrate that high irradiance levels cause a higher degree of photoinhibition (Gamon and Pearcy, 1989; Kamaluddin and Grace, 1992; Kitao et al., 2000; Einhorn et al., 2004). In particular, Kamaluddin and Grace (1992) found a high degree of photoinhibition that last several days in plants adapted to hard shading conditions ($\text{PAR} = 40 \mu\text{mol m}^{-2} \text{s}^{-1}$) and then immediately placed at higher light levels ($\text{PAR} = 1200 \mu\text{mol m}^{-2} \text{s}^{-1}$). Slowly relaxing non-photochemical quenching is due to energy-dissipative processes induced upon exposure of plants to light and relaxes within hours of ceasing illumination (Ruban and Horton, 1995). This parameter indicates both a damage of the reaction centres and a protective energy dissipation in the light-harvesting antenna of PSII and thus measures the degree of photoinhibition (Walters and Horton, 1991). The analysis of fluorescence relaxation curves shows that the values of NPQ_s at the maximum level of drought ($\text{LWP} = -6.5 \text{ MPa}$) were higher in EP than in SP (Table 1), confirming a significantly higher degree of photoinhibition in plants under full sunlight than in shaded ones. In fact, the differences in T_{leaf} between EP and SP during the whole experimental period (Fig. 3C) were partially due to the different radiation regimes but likely also to the higher degree of heat dissipation of EP (Fig. 4B).

Air temperature interacted with light in determining the stomatal and non-stomatal responses to drought of olive plants. In fact, the higher leaf temperatures observed in EP (Fig. 3C) were accompanied by lower values of net photosynthesis (Fig. 3A) and photosynthetic efficiency (Fig. 4A). Our results are in accordance with the results of Bonggi and Long (1987), which observed that in olive tree an increase in leaf temperature above 32°C causes a marked decline in photosynthetic rate, and that the synergical effects of high temperature (38°C) and high light ($\text{PAR} = 1200 \mu\text{mol m}^{-2} \text{s}^{-1}$) determine a sharp decrease in quantum yield of PSII.

It is known that light harvesting in plants is finely regulated (Ruban and Horton, 1995; Demmig-Adams et al., 1995). This regulation is important to adjust the dissipation rate of absorbed radiation and to use only the excitation energy requested for photosynthetic electron transport at the rate allowed by the assimilation reactions in the photosynthetic apparatus (Horton et al., 1996). The higher values of non-photochemical quenching in EP (Fig. 4B) could indicate that these plants were able to better regulate thermal dissipation by xanthophyll cycle during drought (Johnson et al., 1993; Demmig-Adams et al., 1995). By contrast, shading conditions determined a better light use efficiency by means of photochemical processes (qP), with a concomitant reduction of light proportion destined to heat dissipation (NPQ) (Fig. 4). This is also confirmed by the analysis of light response curves of EP, where lower values of R_d (Fig. 5A) indicate that SP used a higher proportion of light energy for photosynthetic processes.

Results showed that reducing excessive irradiance may alleviate non-stomatal limitations to photosynthesis in water stressed plants confirming the hypothesis of shade as lessening the effects of drought and excessive irradiance. Olive is surely a Mediterranean species with a high degree of tolerance against drought and other adverse environmental factors (Bonggi and Long, 1987; Connor and Fereres, 2005; Bacelar et al., 2007) however, in some extreme conditions (Fig. 2), artificial reduction of abiotic stresses (e.g. light) may be beneficial for plant carbon balance in semi-arid areas.

References

- Angelopoulos, K., Dichio, B., Xiloyannis, C., 1996. Inhibition of photosynthesis in olive trees (*Olea europaea* L.) during water stress and rewatering. *J. Exp. Bot.* 47, 1093–1100.
- Bacelar, E.A., Santos, D.L., Moutinho-Pereira, J.M., Lopes, J.L., Gonçalves, B.C., Ferreira, T.C., Correia, C.M., 2007. Physiological behaviour, oxidative damage and anti-oxidative protection of olive trees grown under different irrigation regimes. *Plant Soil* 292, 1–12.
- Bonggi, G., Long, S.P., 1987. Light-dependent damage to photosynthesis in olive leaves during chilling and high temperature stress. *Plant Cell Environ.* 10, 241–249.
- Chartzoulakis, K., Patakas, A., Bosabalidis, A.M., 1999. Changes in water relations, photosynthesis and leaf anatomy induced by intermittent drought in two olive cultivars. *Environ. Exp. Bot.* 42, 113–120.
- Connor, D.J., Fereres, E., 2005. The physiology of adaptation and yield expression in olive. *Hortic. Rev.* 31, 155–229.
- Demmig-Adams, B., Adams III, W.W., Logan, B.A., Verhoeven, A.S., 1995. Xanthophyll-cycle-dependent energy dissipation and flexible photosystem II efficiency in plants acclimated to light stress. *Aust. J. Plant Physiol.* 22, 249–260.
- Dichio, B., Xiloyannis, C., Sofo, A., Montanaro, G., 2006. Osmotic adjustment in leaves and roots of olive tree (*Olea europaea* L.) during drought stress and rewatering. *Tree Physiol.* 26, 179–185.
- Drake, B.G., Read, M., 1981. Carbon dioxide assimilation, photosynthetic efficiency, and respiration of a Chesapeake Bay Salt Marsh. *J. Ecol.* 69, 405–422.
- Einhorn, K.S., Rosenqvist, E., Leverenz, J.W., 2004. Photoinhibition in seedlings of *Fraxinus* and *Fagus* under natural light conditions: implications for forest regeneration? *Oecologia* 140, 241–251.
- Fernández, J.E., Moreno, F., Girón, I.F., Blázquez, O.M., 1997. Stomatal control of water use in olive tree leaves. *Plant Soil* 190, 179–192.
- Flexas, J., Bota, J., Cifre, J., Escalona, J.M., Galmés, J., Gulias, J., Lefi, E.K., Martínez-Cañellas, S.F., Moreno, M.T., Ribas-Carbó, M., Riera, D., Sampol, B., Medrano, H., 2004. Understanding down-regulation of photosynthesis under water stress: future prospects and searching for physiological tools for irrigation management. *Ann. Appl. Biol.* 144, 273–283.
- Gamon, J.A., Pearcy, R.W., 1989. Photoinhibition in *Vitis californica*: interactive effects of sunlight, temperature and water status. *Plant Cell Environ.* 13, 267–275.
- Genty, B., Briantais, J.M., Baker, N.R., 1989. The relationship between quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. *Biochim. Biophys. Acta* 990, 87–92.
- Goudrian, J., Van Laar, H.H. (Eds.), 1994. Modeling Potential Crop Growth Processes. Kluwer Academic, Dordrecht, pp. 238–240.
- Gratani, L., Varone, L., 2004. Adaptive photosynthetic strategies of the Mediterranean maquis species according to their origin. *Photosynthetica* 42, 551–558.
- Gregoriou, K., Pontikis, K., Vemmos, S., 2007. Effects of reduced irradiance on leaf morphology, photosynthetic capacity, and fruit yield in olive (*Olea europaea* L.). *Photosynthetica* 45, 172–181.
- Horton, P., Ruban, A.V., Walters, R.G., 1996. Regulation of light harvesting in green plants. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 47, 655–684.
- Johnson, G.N., Young, A.J., Scholes, J.D., Horton, P., 1993. The dissipation of excess excitation energy in British plant species. *Plant Cell Environ.* 16, 673–679.
- Kamaluddin, M., Grace, J., 1992. Photoinhibition and light acclimation in seedlings of *Bischofia javanica*, a tropical forest tree from Asia. *Ann. Bot.* 69, 47–52.
- Kitao, M., Lei, T.T., Koike, T., Tobita, H., Maruyama, Y., 2000. Susceptibility to photoinhibition of three deciduous broadleaf tree species with different successional traits raised under various light regimes. *Plant Cell Environ.* 23, 81–89.
- Maxwell, K., Johnson, G.N., 2000. Chlorophyll fluorescence—a practical guide. *J. Exp. Bot.* 51, 659–668.
- Montanaro, G., Dichio, B., Xiloyannis, C., 2007. Response of photosynthetic machinery of field-grown kiwifruit under Mediterranean conditions during drought and re-watering. *Photosynthetica* 45, 533–540.
- Moriana, A., Villalobos, F.J., Fereres, E., 2002. Stomatal and photosynthetic responses of olive (*Olea europaea* L.) leaves to water deficits. *Plant Cell Environ.* 25, 395–405.
- Osborn, C.P., Chuine, I., Viner, D., Woodward, F.I., 2000. Olive phenology as a sensitive indicator of future climatic warming in the Mediterranean. *Plant Cell Environ.* 23, 701–710.
- Quero, J.L., Villar, R., Marañón, T., Zamora, R., 2006. Interactions of drought and shade effects on seedlings of four *Quercus* species: physiological and structural leaf responses. *New Phytol.* 170, 819–834.
- Ruban, A.V., Horton, P., 1995. Regulation of non-photochemical quenching of chlorophyll fluorescence in plants. *Aust. J. Plant Physiol.* 22, 221–230.
- Sofo, A., Dichio, B., Xiloyannis, C., Masia, A., 2005. Antioxidant defences in olive tree during drought stress: changes in activity of some antioxidant enzymes. *Func. Plant Biol.* 32, 45–53.
- Valladares, F., Pearcy, R.W., 2002. Drought can be more critical in the shade than in the sun: a field study of carbon gain and photo-inhibition in a Californian shrub during a dry El Niño year. *Plant Cell Environ.* 25, 749–759.
- Walters, R., Horton, P., 1991. Resolution of components of non-photochemical chlorophyll fluorescence quenching in barley leaves. *Photosynth. Res.* 27, 121–133.