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ORIGINAL ARTICLE

Drought stress tolerance and photoprotection in two varieties of olive tree

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Abstract

The olive tree (*Olea europaea* L.) is adapted to tolerate severe drought and high irradiance levels. Relative electron transport rate (\mathcal{J}), photosynthetic efficiency (in terms of F_v/F_m and Φ_{PSII}), photochemical (qP) and non-photochemical quenching (NPQ) were determined in 2-year old olive plants (cultivars 'Coratina' and 'Biancolilla') grown under two different light levels (exposed plants, EP, and shaded plants, SP) during a 21-day controlled water deficit. After reaching pre-dawn leaf water potentials of about -6.5 MPa, plants were rewatered for 23 days. During the experimental period, measurements of gas exchange and chlorophyll fluorescence were carried out to study the photosynthetic performance of olive plants. The effect of drought stress and high irradiance levels caused a reduction of gas exchange, \mathcal{J} , Φ_{PSII} and F_v/F_m and this decrease was more marked in EP. Under drought stress, EP showed a higher degree of photoinhibition, a higher NPQ and a lower qP if compared to SP. Coratina was more sensitive to high light and drought stress and had a slower recovery during rewatering. The results confirm that photoprotection is an important factor that affects photosynthetic productivity in olive, and that the degree of this process varies between the cultivars. This information could give a more complete picture of the response of olive trees grown under stressful conditions of semi-arid environments, and could be important for the selection of drought-tolerant cultivars with a high productivity.

Keywords: Drought stress, light stress, *Olea europaea* L., photoinhibition, photoprotection.

Introduction

Among fruit tree species, the olive tree (*Olea europaea* L.) is able to tolerate a broad range of environmental stresses and such an uncommon capability is likely due to a variety of morphological and physiological adaptations (Lo Gullo & Salleo, 1988; Connor & Fereres, 2005; Bacelar et al., 2007). The olive tree has a high degree of drought tolerance due to a very developed osmotic adjustment and the appearance of leaf anatomical modifications (Chartzoulakis et al., 1999), an efficient regulation of stomata closure and transpiration (Fernández et al., 1997), and a higher water potential gradient between canopy and root system if compared with other fruit tree species (Xiloyannis et al., 2004).

In spite of the high level of tolerance of the olive tree against drought, in this species high levels of drought and radiation cause decreases in the rate of photosynthesis and the efficiency of photosynthetic

energy conversion, seriously damaging the photosynthetic systems of plants and causing photoinhibition (Angelopoulos et al., 1996; Sofu et al., 2004). It is known that an increase in the absorption of light by chlorophyll results in an increase in photosynthetic CO_2 fixation but, under strong light, photosynthesis is incapable of utilizing all the energy absorbed by chlorophyll. When exposed to light, plants can use energy for photosynthetic processes or dissipate it harmlessly as heat. The first process is photochemical quenching (qP), a parameter that estimates the degree of saturation of the PSII reaction centre (Johnson et al., 1993). The second process, called non-photochemical quenching (NPQ), is a photoprotective mechanism in conditions of excess light due to energy-dissipative processes induced upon exposure of plants to light, such as the xanthophyll cycle (Ruban & Horton, 1995). Non-photochemical fluorescence quenching arises from a number of processes in the thylakoid

membrane but the major fraction depends on the trans-membrane $\Delta p\text{H}$ and it can be an irreversible or slowly reversible process if associated with strong degrees of light stress or other abiotic stresses (Horton et al., 1996). However, whenever the utilization and dissipation of energy through photosynthesis, in combination with the photoprotective processes, are insufficient for dealing with the absorbed light, the photosynthetic apparatus may be damaged (Demmig-Adams et al., 1995; Nogués & Baker, 2000).

In the absence of other stress factors, leaves exposed to environmental light may be able to dissipate full sunlight entirely, through the combination of high rates of photosynthetic electron transport and high rates of thermal energy dissipation (Ruban & Horton, 1995). On the contrary, at irradiance levels close to light saturation point, even in the presence of stress factors, there is usually no excess of light energy and plants are more efficient in photochemical processes and production (Demmig-Adams & Adams III, 1992).

Olive is an economically important species of the Mediterranean area, so understanding the mechanisms by which olive plants face drought stress and light excess under extreme environmental conditions is essential for the improvement of olive yield and oil quality. The photosynthetic limitations of the olive tree under salt, chilling and high temperature stresses were thoroughly investigated (Bongi & Long, 1987; Loreto et al., 2003) but very little is known about photoinhibition and photoprotection under drought stress and high irradiance in this species. For this reason, two Italian olive cultivars with a different physiological and productive behaviour were compared: 'Coratina', that shows a high productivity and is sensitive to water deficit in the dry season (Xiloyannis et al., 2004), and 'Biancolilla', that has a high oil quality and is adapted to arid climates (Lo Bianco, personal communication). The photosynthetic performance and the role of thermal energy dissipation (NPQ) in photoprotection and photoinhibition were examined in plants subjected to drought stress under environmental light and semi-shade conditions. Photosynthesis and photoprotection were also monitored during a following rewatering.

Materials and methods

Experimental design

Trials were conducted on own-rooted 2-year-old *Olea europaea* L. plants, cv. 'Coratina' and 'Biancolilla', measuring 130–150 cm in height. The study

site was located at the 'Pantanello' Agricultural Experiment Station in Metaponto (Southern Italy – Basilicata Region – N 40° 24', E 16° 48'). The experimental period started on 1 July 2005 and ended on 26 August 2005. Olive plants grew uniformly outdoors in 0.016 m³ vases containing sandy clay soil (73.2% sand, 13.3% silt and 13.5% clay), with a bulk density of 1.52 g cm⁻³ and a field capacity of 17.6% (v/v). 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. Soil water content was maintained at a constant value of around 90% of water-holding capacity of the pot by integrating the amount of water lost through transpiration during the day. This value was chosen to have an equilibrated ratio between air and water in the soil, so allowing a better root growth. Soil water content was determined from the weight differences of soil samples before and after drying at 105 °C for 18 h.

At the beginning of the experiment (1 July), the plants of each cultivar were divided in two groups: 26 exposed plants (EP) and 26 shaded plants (SP). EP were grown under environmental light (photosynthetically active radiation [PAR] range under clear sky = 1700–1900 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at 12:00), whereas SP were kept in semi-shade conditions of about 67% of solar radiation (PAR range = 1100–1300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at 12:00) by means of a neutral shading net (Arrigoni, CO, Italy, model 2591WO). Starting from 13 July, plants were subjected to a gradual controlled water depletion for 21 d. During the first 10 d of the drought period, plants received in the evening (20:00) 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. After reaching values of pre-dawn leaf water potentials (Ψ_w) of about -6.5 MPa, starting from 3 August plants were subjected to a rewatering treatment by recovering soil water content (around 85% of water-holding capacity). The rewatering lasted 23 d and during this period the amount of water added daily was equal to the transpired amount. We defined two levels of rewatering: the first after 7 d from the beginning of water recovery and the second after 23 d.

Environmental parameters for each day of the experimental period were monitored by a weather station placed within 20 m of the experimental plot (Figure 1).

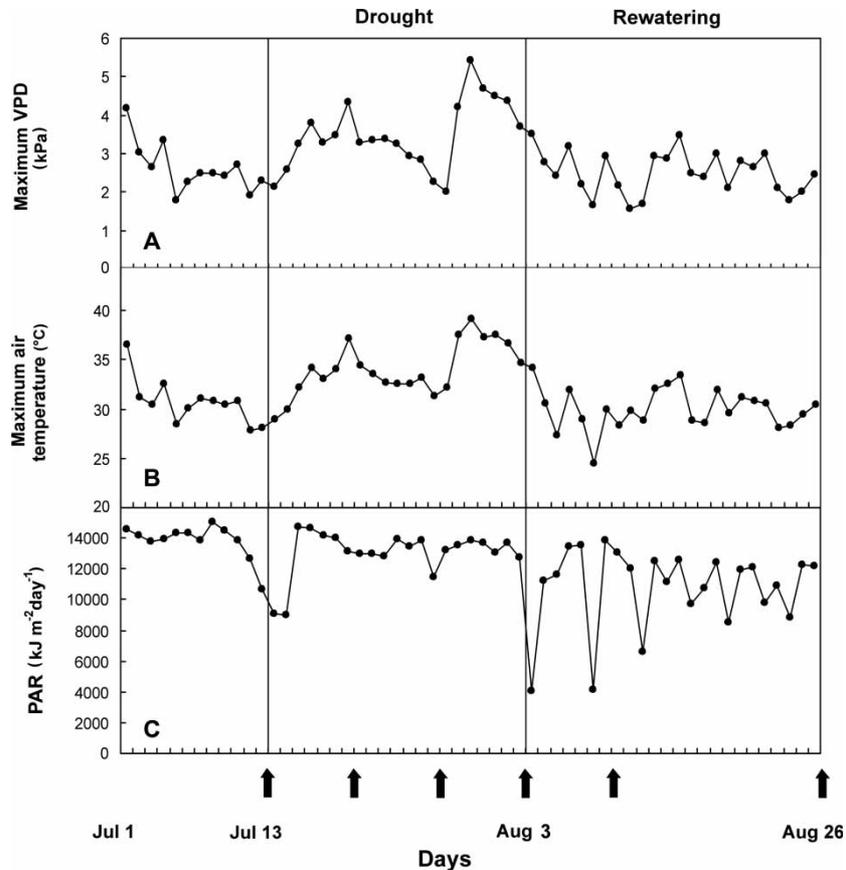


Figure 1. Maximum vapour pressure deficit (VPD), maximum air temperature and photosynthetically active radiation (PAR) at the field site during the experimental period. Arrows indicate the measuring days.

Plant water status and gas exchange

The values of Ψ_w were measured at pre-dawn (at 04:00–05:00) using a Sholander pressure chamber (PMS Instrument Co. Corvallis, OR, USA). Three plants having a similar value of Ψ_w for each cultivar were randomly chosen to measure gas exchange at each level of drought stress and rewatering. Measurements were carried out on leaves selected from each plant along the median segment of new-growth shoots. The measurements of gas exchange were carried out on clear days at 09:00–10:00 using a programmable, open-flow gas exchange portable system (LI-6400; Li-Cor, Inc.) operated at 500 $\mu\text{mol s}^{-1}$ air flow rate. During gas exchange measurements, light level inside the leaf chamber was maintained equal to the outdoor PAR by the LI-6400 external quantum light sensor ('Track PAR' function; 90% red light fraction at a wavelength of 630 nm and a 10% blue light fraction at 470 nm). Temperature inside the leaf chamber was equal to environmental air temperature and it was maintained constant during measurements by instrument automatic cooling. The values of adaxial leaf temperature (T_{leaf}) were measured at 09:00–

10:00 by the instrument thermocouple placed inside the leaf chamber.

Chlorophyll fluorescence and light response curves

The same plants used for gas exchange measurements were chosen to measure chlorophyll fluorescence at 09:00–10:00 using a leaf chamber fluorometer (LI-6400-40; Li-Cor, Inc.). The maximum quantum yield of PSII photochemistry (F_v/F_m) was calculated as $(F_m - F_o)/F_m$ (Oxborough 2004), where F_m is the maximum fluorescence in the dark and F_o is the minimum level of fluorescence. Measurements of (F_v/F_m) were carried out on leaves covered by homemade clip holders for 30 min before the measurements. The quantum yield of PSII (Φ_{PSII}) was calculated as $(F'_m - F_t)/F'_m$ (Oxborough, 2004), where F'_m is the maximum fluorescence in the light and F_t is the steady state fluorescence yield measured under actinic light. Relative electron transport rate (\mathcal{J}), i.e. the actual flux of photons that drives PSII, was given by:

$$J = [(F'_m - F_t)/(F'_m)]f \cdot I \cdot \alpha_{\text{leaf}} \quad (1)$$

where f is the fraction of absorbed quanta that is used by PSII (typically assumed to be 0.5 for C3

plants), I is incident photon flux density, and α_{leaf} is leaf absorptance.

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

$$qP = (F'_m - F_t)/(F'_m - F'_o) \quad (2)$$

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

The values of Stern-Volmer non-photochemical quenching (NPQ) were calculated using the initial F_m measured after the long darkness period and using the F'_m measured after the light exposure (Bilger & Björkman, 1990) as:

$$NPQ = (F_m - F'_m)/F'_m \quad (3)$$

The value of irradiance inside the leaf chamber during fluorescence measurements was fixed at $850 \mu\text{mol m}^{-2} \text{s}^{-1}$ (90% red light and 10% blue light). This value was chosen keeping into account the average light saturation point for olive ($800\text{--}900 \mu\text{mol m}^{-2} \text{s}^{-1}$).

For each cultivar, at the beginning of drought treatment, at the end of the drought stress period and at the end of the rewatering period, three plants were chosen for light response curves. Light response curves were recorded at 09:00–11:00 using a 90% red–10% blue actinic light. Light curves were carried out starting from the highest intensity ($1800 \mu\text{mol PAR m}^{-2} \text{s}^{-1}$) to the complete darkness at regular intervals of 15 min, in order to give the stomata time to equilibrate at each level. Net photosynthetic rate (A), \mathcal{J} , Φ_{PSII} , qP and NPQ were measured during light curve recording.

Statistical analysis

The values Ψ_w represent the mean of three measurements (\pm SE) on each of three selected plants, whereas the measurements of gas exchange and chlorophyll fluorescence were conducted in replicates of three readings on each of three leaves per plant from three plants having a similar Ψ_w . Statistical analysis was performed using ANOVA and significant differences were determined at $p \leq 0.05$, according to Student's t -test.

Results

Environmental conditions, plant water status and gas exchange

Vapour pressure deficit range was between 1.55 (on 11 August) and 5.43 kPa (on 29 July), with a mean value of 1.89 kPa (Figure 1A). In the measuring days, maximum air temperatures ranged between 39.2°C (on 29 July) and 24.5°C (on 8 August),

with a mean value of 31.6°C during the whole experimental period (Figure 1B). The levels of daily photosynthetic active radiation was high during all the experimental period, except for some cloudy days in July (12, 13 and 14) and in August (3, 8 and 12) (Figure 1C). Gas exchange and fluorescence measurements were carried out in clear days.

In all the plants, the values of Ψ_w decreased after the application of applied water deficit: mean values of about -1.5 MPa were reached after 8 days of drought stress, about -3.5 MPa after 15 days, and about -6.5 after 21 days (Figure 2A). Successively, the values of Ψ_w recovered during the rewatering period (Figure 1A).

With increasing drought stress, net photosynthetic rate (A) and stomatal conductance (g_s) decreased in both the cultivars (Figure 2B, C). In particular, starting from 8 days after drought stress, values of A in Coratina were significantly higher in SP than in EP, whereas during all the period of drought stress g_s in SP of both cultivars was significantly lower than in EP (Figure 2B). At the end of the rewatering period, in both Coratina and Biancolilla, A and g_s of EP did not reach the values of well-watered plants, whereas in SP they showed a complete recovery (Figure 2B, C). The values T_{leaf} increased during the drought stress period, declined in correspondence of the beginning of rewatering and successively maintained a constant trend until the end of the experiment (Figure 2D). Throughout the experiment, T_{leaf} in EP was significantly higher if compared to SP in both the cultivars, and Coratina showed higher values than Biancolilla (Figure 2D).

Chlorophyll fluorescence and light response curves

Relative electron transport rate (\mathcal{J}) in both the cultivars showed a similar trend, with strong declines due to drought stress and a recovery during rewatering (Figure 3A). The values of \mathcal{J} found in SP were significantly higher than those of EP during the drought period, in Coratina, or during the rewatering, in Biancolilla (Figure 3A). The values of F_v/F_m of EP and SP decreased with increasing drought stress and this decline was more pronounced in Coratina (Figure 3B). The patterns of Φ_{PSII} were similar to those of F_v/F_m but showed lower values (Figure 3C). In both cultivars, EP showed more marked decreases in F_v/F_m and Φ_{PSII} throughout the drought period and did not recovery fully Φ_{PSII} and F_v/F_m at the end of the rewatering period (Figure 3B, C).

Net photosynthetic rate (A) curves of both cultivars showed marked depressions at the maximum level of drought and a certain degree of recovery during rewatering (Figure 4A and 5A). Generally, A rates of Coratina were higher than in Biancolilla but,

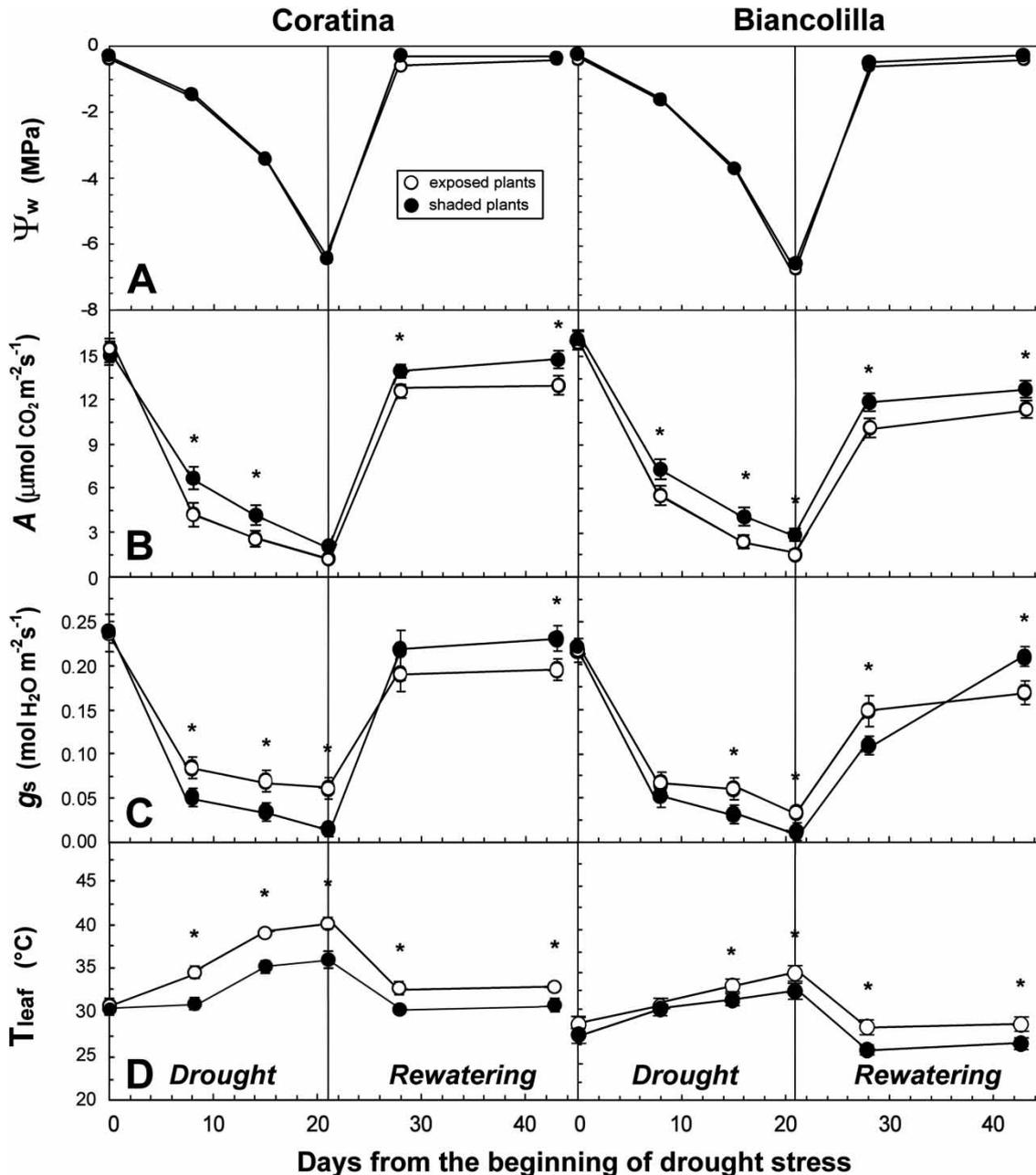


Figure 2. Pre-dawn leaf water potential (Ψ_w), net photosynthetic rate (A), stomatal conductance (g_s), maximum quantum yield of PSII (F_v/F_m) and quantum yield of PSII (Φ_{PSII}) in exposed and shaded olive plants of olive cultivars Coratina (left) and Biancolilla (right) during drought stress and rewatering periods. The values of Ψ_w represent the mean of three measurements (\pm SE) on each of three selected plants, whereas the other measurements were conducted in replicates of three readings on each of three leaves per plant from three plants having a similar Ψ_w . Values with the asterisk are significantly different ($P \leq 0.05$, according to Student's t -test).

in particular in EP, they showed a lower recovery (Figure 4A and 5A). In both the cultivars, the trends of \bar{f} reflected those of A , with higher values in SP, particularly at the highest PAR levels (Figure 4B and 5B). Well-watered, drought-stressed and rewatered plants of both cultivars showed a rapid initial decline in quantum yield (Φ_{PSII}) at low levels of PAR (500–1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) (Figure 4C and 5C). At higher light levels (PAR = 1000–2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$), the

values of Φ_{PSII} in SP light curves of both the cultivars reached a plateau and were significantly higher if compared to EP (Figure 4C and 5C).

Photochemical quenching (qP) had a decreasing trend with increasing PAR and were different between well-watered and drought-stressed plants (Figure 4D and 5D). In drought stress conditions and at the end of rewatering, the values of qP at high light levels in EP of both cultivars were significantly higher than in SP

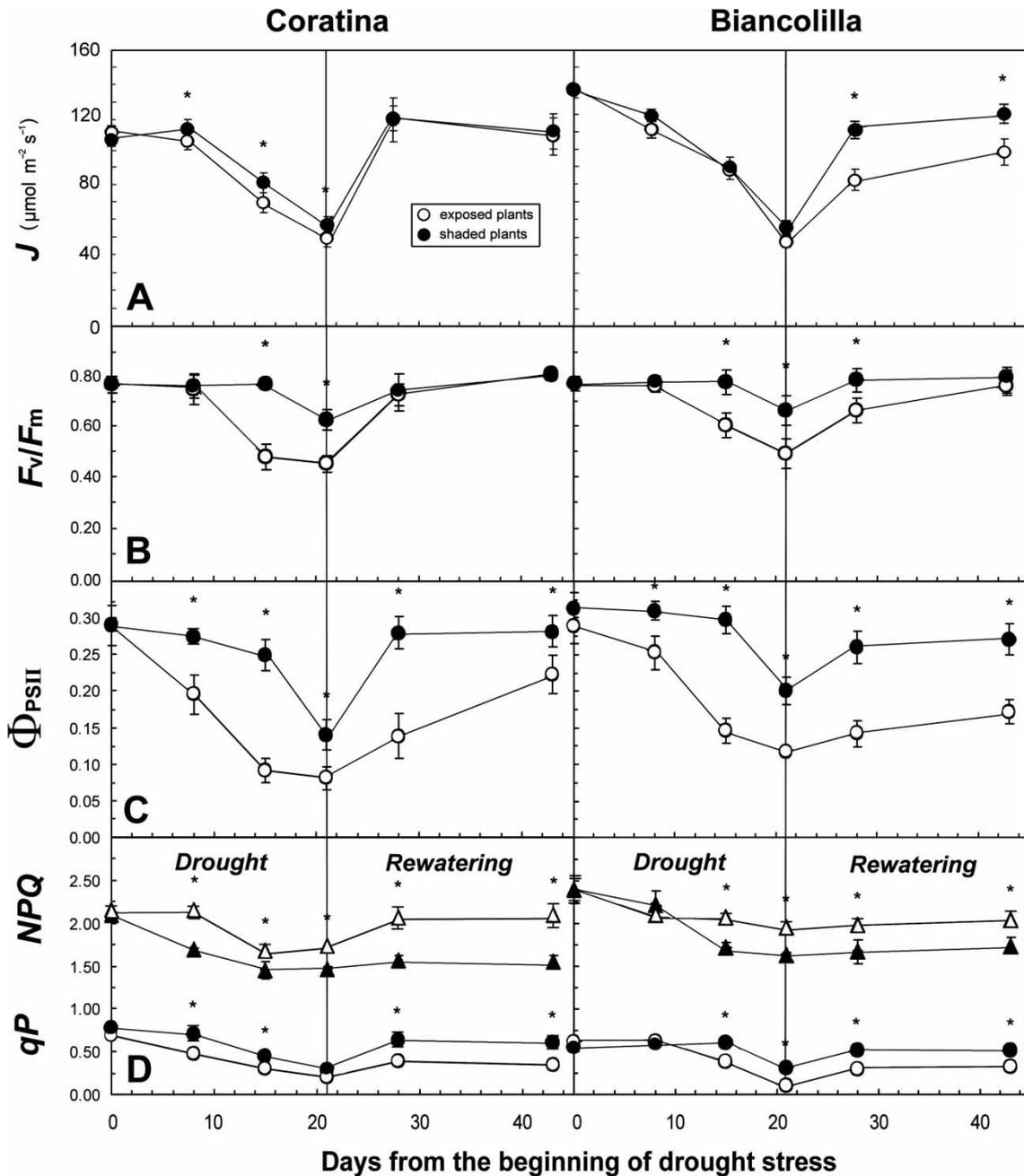


Figure 3. Relative electron transport rate (J), maximum quantum yield of PSII (F_v/F_m), quantum yield of PSII (Φ_{PSII}), photochemical quenching (qP ; circles) and non-photochemical quenching (NPQ ; triangles) in exposed and shaded olive plants of olive cultivars Coratina (left) and Biancolilla (right) during drought stress and rewatering periods. The measurements were conducted in replicates of three readings on each of three leaves per plant from three plants having a similar Ψ_w . Values with the asterisk are significantly different ($P \leq 0.05$, according to Student's t -test).

(Figure 4D and 5D). The results also show marked differences among Coratina and Biancolilla plants in the capacity for non-photochemical quenching (NPQ) (Figure 4E and 5E). In Biancolilla, NPQ of drought-stressed plants was much higher than in Coratina (Figure 4E and 5E). In both cultivars, a more rapid rise in NPQ at lower PAR in EP than in SP was observed (Figure 4E and 5E).

Discussion

Both Coratina and Biancolilla olive plants were strongly influenced by the different light levels. The higher light intensity, intensified by the contemporary application of drought stress, affected PSII efficiency and caused significant reductions in the values of A , Φ_{PSII} and F_v/F_m (Figure 2A and 3B, C). The higher values of photosynthetic parameters in shaded plants

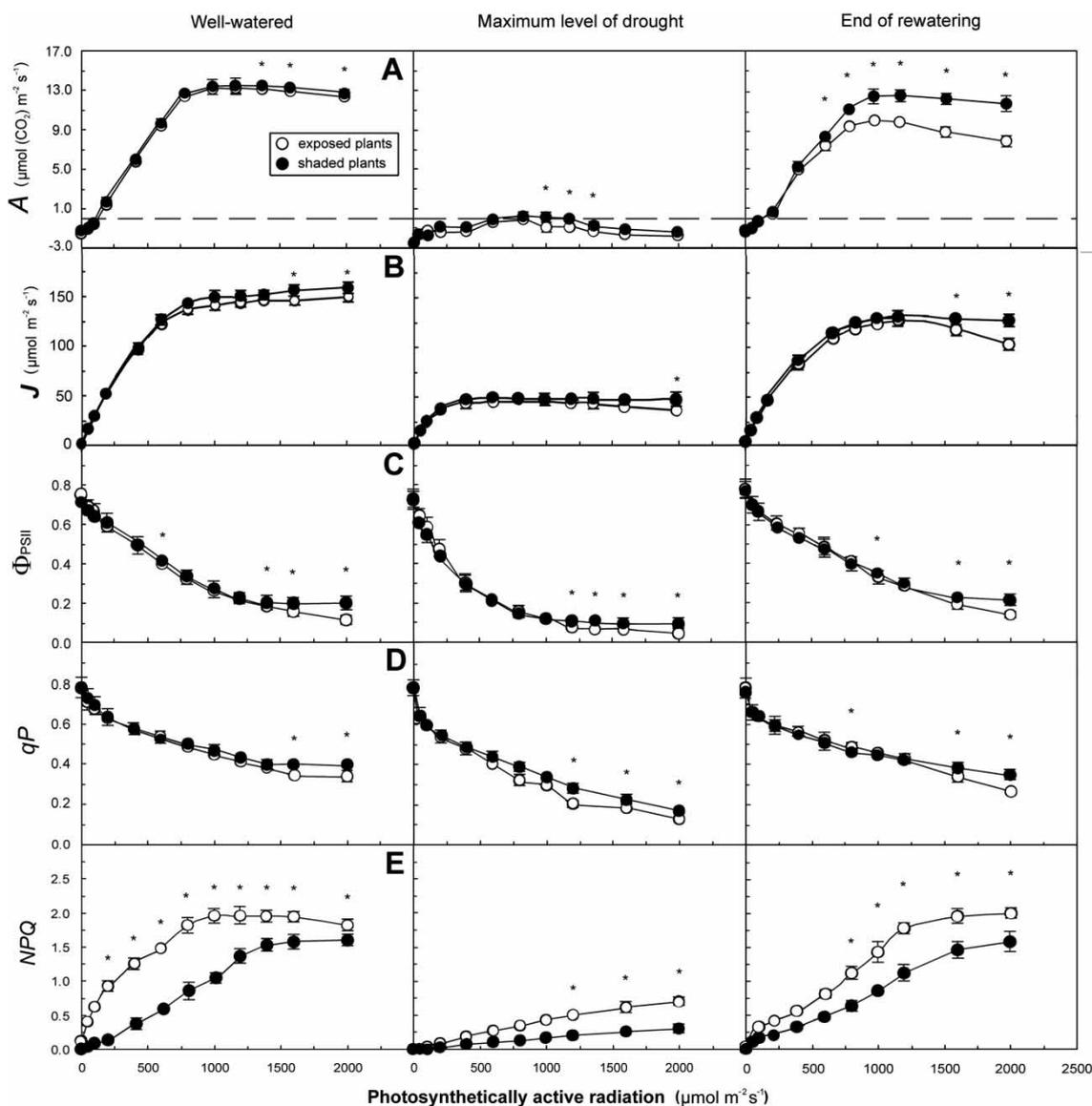


Figure 4. Light response curves of net photosynthetic rate (A), relative electron transport rate (J), quantum yield of PSII (Φ_{PSII}), photochemical quenching (qP) and non-photochemical quenching (NPQ) measured in exposed (black symbols) and shaded (white symbols) olive plants of the olive cultivar Coratina in well-watered conditions, at the maximum level of drought stress and at the end of the rewatering period. Statistics as in Figure 3.

(SP) (Figure 2B) likely occurred because in SP a large proportion of the absorbed light is used in photochemistry and not dissipated through non-photochemical processes as thermal dissipation (Demmig-Adams et al., 1995; Maxwell & Johnson, 2000). This was also confirmed by the data of relative electron transport rate in the two cultivars (Figure 3A). The reduction in photosynthetic efficiency due to high levels of irradiance was also observed in deciduous broadleaf trees (Kitao et al., 2000) and in tropical trees (Kamaluddin & Grace, 1992; Krause et al., 2001) but is not so common in cultivated tree crops, with few exceptions (Gamon & Pearcy, 1989).

The response of A , J and Φ_{PSII} to light from light response curves (Figure 4A–C and 5A–C) and their

punctual values measured during the experiment (Figure 2B and 3A, C) indicate that Coratina plants have higher photosynthesis rates in well-watered conditions but are more sensitive to high light and drought stress if compared to Biancolilla. Moreover, Coratina showed a slower recovery after the drought period and a higher photosynthesis depression in rewatered EP (Figure 2B and 4A). In contrary, Biancolilla presented lower values of A in well-watered conditions, a less marked photosynthesis decline during drought, and a considerable resilience during rewatering (Figure 2B and 5A).

The significant decreases in g_s found both in EP and SP with increasing drought (Figure 2C) indicate that the reduced PSII efficiency is not the only

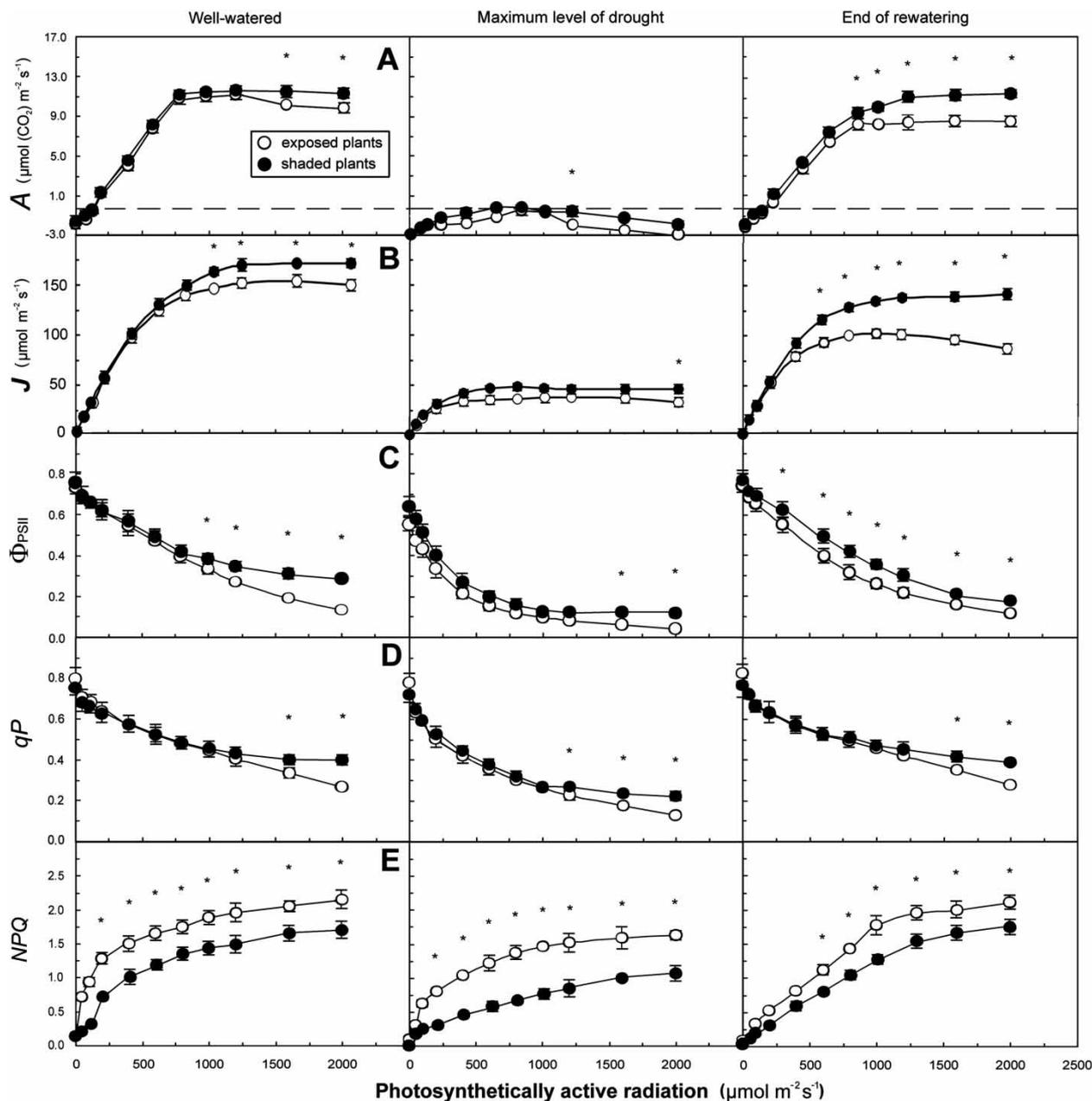


Figure 5. Light response curves of net photosynthetic rate (A), relative electron transport rate (J), quantum yield of PSII (Φ_{PSII}), photochemical quenching (qP) and non-photochemical quenching (NPQ) measured in exposed (white symbols) and shaded (black symbols) olive plants of the olive cultivar Biancolilla in well-watered conditions, at the maximum level of drought stress and at the end of the rewatering period. Statistics as in Figure 3.

limiting factor for photosynthesis in the olive tree (Angelopoulos et al., 1996) but stomatal regulation mechanisms are likely involved. During the rewatering period, SP of both cultivars recovered both A and PSII efficiency, while in EP they remained depressed (Figure 2B and 3B, C). This physiological response suggests that SP received a lower damage to photosynthetic apparatus and were able to restore quickly their normal physiological status during rewatering.

The differences in T_{leaf} between EP and SP during the whole experimental period (Figure 2D) were

partially due to the different radiation regimes but likely also to the higher degree of heat dissipation (NPQ) of EP (Figure 3D). Temperature interacted with light in determining the stomatal and non-stomatal responses to drought of olive plants. In fact, the higher temperatures of EP (Figure 2D) were accompanied by lower values of A and J (Figure 2B and 3A) and photosynthetic efficiency (Figure 3B, C). The results are in accordance with those of Bongi and Long (1987), who observed that in the olive tree an increase in leaf temperature above 32°C

causes a marked decline in photosynthetic rate and that the effects of high temperature (38 °C) and high light (PAR=1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$) determine a sharp decrease in quantum yield of PSII.

The regulation of light absorption in plants 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 cells (Johnson et al., 1993; Horton et al., 1996). In fact, if the onset of *NPQ* lags behind an increase in light intensity, transient over-excitation of photosynthetic apparatus may have photoinhibitory consequences (Ruban & Horton, 1995). In this study, light response curves highlight that the fluctuations of *NPQ* between EP and SP were wider than those of *qP* (Figure 4D, E and 5D, E). The values of *NPQ* in EP at the end of rewatering are comparable to those of well-watered plants (Figure 4E and 5E), indicating that in EP the mechanisms of energy dissipation by the xanthophyll cycle remained active even during the rewatering period. The light-dependent regulation of *NPQ* observed here for the olive tree was also found in some herbaceous plants (Johnson et al., 1993; Park et al., 1996) but in tree species was hitherto not observed. In fact, Einhorn et al. (2004) found that *Fraxinus* and *Fagus* acclimatize to different light regimes mainly by photochemical quenching (*qP*) whereas the regulation of thermal dissipation by *NPQ* is negligible. The results show that at a severe drought stress level (Ψ_w of about -6.5 MPa), the capacity of *NPQ* in cultivar Biancolilla was higher than in Coratina both in EP and SP (Figure 4E and 5E). These values indicate that Biancolilla is able to better regulate non-photochemical energy dissipation during drought stress and that *NPQ* is the main differentiating parameter between the two cultivars.

In conclusion, even though olive has a high degree of tolerance to drought if compared with other tree species (Lo Gullo & Salleo, 1988; Bacelar et al., 2007), the results confirm that photoprotection is an important factor that affects photosynthetic productivity in this species, and that the degree of this process varies between the cultivars. This information could give a more complete picture of the response of olive trees grown under stressful conditions of semi-arid environments, characterized by high light intensity and severe water deficit, and could be used for the selection of drought-tolerant cultivars with a high productivity. Finally, the results obtained could be of importance for the study of light competition within the olive tree's canopy, with positive repercussions on appropriate pruning techniques and canopy architecture.

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