Photosynthetic performance and light response of two olive cultivars under different water and light regimes

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Abstract

The olive tree (*Olea europaea* L.) is commonly grown in the Mediterranean area, where it is adapted to resist periods characterized by severe drought and high irradiance levels. Photosynthetic efficiency (in terms of F_v/F_m and Φ_{PSII}), photochemical (q_P) and nonphotochemical quenching (NPQ) were determined in two-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 the maximum level of drought stress, plants were rewatered for 23 days. During the experimental period, measurements of gas exchange and chlorophyll (Chl) fluorescence were carried out to study the photosynthetic performance of olive plants. The synergical effect of drought stress and high irradiance levels caused a reduction of gas exchange and photosynthetic efficiency and these decreases were more marked in EP. EP showed a higher degree of photoinhibition, a higher NPQ and a lower q_P if compared to SP. Coratina was more sensitive to high light and drought stress but also showed a slower recovery during rewatering, whereas Biancolilla showed a less marked photosynthesis depression during drought and a considerable resilience during rewatering. The results confirm that photoinhibition due to high light intensity and water deficit can be an important factor that affects photosynthetic productivity in this species.

Additional keywords: drought stress; light excess; *Olea europaea* L.; photoinhibition; water use efficiency.

Introduction

The synergical action of environmental stresses, such as drought and radiation, can seriously damage the photosynthetic systems of plants through photoinhibition, with a consequent decrease in the quantum yield of PSII (Demmig-Adams and Adams III 1992, Demmig-Adams *et al.* 1995). When exposed to light, plants can use energy for photosynthetic processes or dissipate it harmlessly as heat. The first process can be measured by photochemical quenching (q_P), a parameter that estimates the degree of saturation of the PSII reaction centre (Johnson *et al.* 1993). The second process can be followed by nonphotochemical quenching (NPQ) which is due to energy-dissipative processes induced upon exposure of plants to light, such as xantophyll cycle (Ruban and Horton 1995).

Among fruit tree species, 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 and Salleo 1988, Connor and Fereres 2005, Bacelar *et al.* 2007). 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). The photosynthetic limitations of olive tree under salt, chilling and high temperature stresses were deeply investigated (Bongi and Long 1987, Loreto *et al.* 2003) but very little is known about photoinhibition due to drought stress and high irradiance in this species.

For this study, two Italian olive cultivars with

a different physiological and productive behavior were compared: Coratina that show high productivity and resistance against drought stress (Xiloyannis *et al.* 2004) and Biancolilla with a high oil quality and particularly sensitive to water deficit (Lo Bianco, personal communication). The main aims of this research were to study: (*1*) the photosynthetic performance and (*2*) the photochemical and nonphotochemical quenching of Chl fluorescence in plants subjected to drought stress and to two different irradiance levels. Photosynthesis and photoinhibition were also monitored during a following rewatering. At low irradiance levels, there is no excess of light energy and plants are more efficient in photochemical processes and production (Demmig-Adams and Adams III 1992, Ruban and Horton 1995). 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.

Materials and methods

Plants and experimental design: Trials were conducted on own-rooted two-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 m^3 vases 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.

At the beginning of the experiment (July 1), 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 µmol m^{-2} s^{-1} at 12:00], whereas SP were kept in semi-shade conditions of about 67% of solar radiation (PAR range = 1100-1300 µmol m^{-2} s^{-1} at 12:00) by means of a neutral shading net (model *2591WO, Arrigoni Co.*, Italy). Starting from July 13, 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 the maximum level of water stress, starting from August 3 plants were subjected to a rewatering treatment by recovering soil water content to optimal values. 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 one after 7 d from the beginning of water recovery and the second one 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.

Water status, gas exchange and Chl fluorescence: The values of Ψ_w were measured at pre-dawn (at 04:00-05:00) using a Scholander pressure chamber (*PMS Instrument Co.*, Corvallis, OR, USA). Three plants having a similar value of pre-dawn leaf water potential (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-grown shoots. The measurements of gas exchange were carried out on clear days at 12:00–13:00 using a programmable, open-flow gas exchange portable system (*LI-6400, Li-Cor Inc.*, Lincoln, NE, USA) operated at 500 µmol s^{-1} 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).

The same plants used for gas exchange measurements were chosen to measure Chl fluorescence at 12:00–13:00 using a leaf chamber fluorometer (*LI-6400-40, Li-Cor Inc.*, Lincoln, NE, USA). On each plant of EP and SP, both sun-adapted and dark-adapted leaves were chosen to measure fluorescence parameters. On dark-adapted leaves (covered for 30 min before the measurements by homemade clip holders), the maximum quantum yield of PSII photochemistry was calculated as $F_v/F_m = (F_m - F_o)/F_m$ (Oxborough 2004), where F_m is the maximum fluorescence in the dark and F_o is the minimum level of fluorescence. On sun-adapted leaves, 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. The value of irradiance inside the leaf chamber a 90% red light and 10% blue light) during fluorescence measurements was 850 µmol m^{-2} s^{-1}. This value was chosen keeping into account the average light saturation point for olive (800 to 900 µmol m^{-2} s^{-1}) and the mean

environmental irradiance at 09:00–10:00 monitored by the *LI–6400* external quantum light sensor every 3 s.

Light-response curves: 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 µmol PAR $m^{-2}\ s^{-1}$) 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 (P_N), Φ_{PSII}, q_P and NPQ were measured during light curve recording.

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

$$q_P = (F'_m - F_t)/(F'_m - F'_o) \tag{1}$$

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

The values of Stern-Volmer 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 and Björkman 1990) as:

$$NPQ = (F_m - F'_m)/F'_m \tag{2}$$

Results

Environmental conditions and plant water status: Vapour pressure deficit range was between 1.55 (on August 11) and 5.43 kPa (on July 29), with a mean value of 1.89 kPa. The levels of daily photosynthetic active radiation were high during all the experimental period, except for some cloudy days in July (12, 13, and 14) and in August (3, 8, and 12). Gas exchange and fluorescence measurements were carried out on 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 MPa after 21 days (Tables 1 and 2). Successively, the values of Ψ_w recovered during the rewatering period (Tables 1 and 2).

Gas exchange and Chl fluorescence: With the increasing drought stress, P_N and g_s decreased in both the cultivars (Tables 1 and 2). In particular, starting from 8 d after drought stress, values of P_N 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 (Tables 1 and 2). At the end of the rewatering period, in both Coratina and Biancolilla, P_N and g_s of EP did not reach the values of well-watered plants, whereas in SP they showed a complete recovery (Tables 1 and 2).

The values of F_v/F_m of EP and SP decreased with increasing drought stress and this decline was more pronounced in Coratina (Tables 1 and 2). The patterns of Φ_{PSII} were similar to those of F_v/F_m but showed lower values (Tables 1 and 2). In both cultivars, EP showed more marked decreases in F_v/F_m and Φ_{PSII} throughout the drought period and did not recover fully Φ_{PSII} and F_v/F_m at the end of the rewatering period (Tables 1 and 2).

Light-response curves and Φ_{PSII}/NPQ correlation: P_N curves of both cultivars showed marked depressions at the maximum level of drought and a certain degree of recovery during rewatering (Figs. 1*A*, 2*A*). Generally, P_N rates of Coratina were higher than those in Biancolilla

Table 1. Pre-dawn leaf water potential (Ψ_w), net photosynthetic rate (P_N), 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 cultivar Coratina 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 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. 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).

		Drought stress July 11	July 20	July 27	Aug 2	Rewatering Aug 10	Aug 26
Exposed	Ψ_w [MPa]	-0.40 ± 0.04^{Aa}	-1.51 ± 0.11^{Ba}	-3.41 ± 0.07^{Ca}	-6.40 ± 0.10^{Da}	-0.50 ± 0.10^{Aa}	-0.40 ± 0.03^{Aa}
	P_N [µmol (CO_2) $m^{-2}\ s^{-1}$]	14.10 ± 1.10^{Aa}	3.63 ± 0.37^{Cb}	1.10 ± 0.12^{Db}	0.71 ± 0.09^{Da}	9.10 ± 0.92^{Bb}	11.76 ± 1.09^{Ba}
	g_s [mmol (H_2O) $m^{-2}\ s^{-1}$]	223.3 ± 26.2^{Aa}	56.4 ± 9.5^{Ca}	35.6 ± 7.0^{Da}	25.0 ± 4.4^{Da}	148.0 ± 15.9^{Bb}	155.7 ± 26.7^{Bb}
	F_v/F_m	0.79 ± 0.03^{Aa}	0.56 ± 0.09^{Bb}	0.22 ± 0.05^{Cb}	0.26 ± 0.02^{Cb}	0.60 ± 0.03^{Bb}	0.64 ± 0.03^{Bb}
	Φ_{PSII}	0.17 ± 0.01^{Aa}	0.10 ± 0.03^{Bb}	0.04 ± 0.01^{Cb}	0.05 ± 0.01^{Cb}	0.10 ± 0.02^{Bb}	0.12 ± 0.02^{Bb}
Shaded	Ψ_w [MPa]	-0.35 ± 0.04^{Aa}	-1.46 ± 0.02^{Ba}	-3.42 ± 0.06^{Ca}	-6.43 ± 0.08^{Da}	-0.30 ± 0.13^{Aa}	-0.35 ± 0.05^{Aa}
	P_N [µmol (CO_2) $m^{-2}\ s^{-1}$]	13.20 ± 2.10^{Aa}	5.72 ± 1.44^{Ba}	2.37 ± 1.26^{Ba}	0.47 ± 0.29^{Ca}	11.50 ± 0.39^{Aa}	12.99 ± 1.08^{Aa}
	g_s [mmol (H_2O) $m^{-2}\ s^{-1}$]	219.6 ± 17.6^{Aa}	41.0 ± 3.9^{Cb}	13.5 ± 1.3^{Db}	5.5 ± 0.4^{Eb}	185.7 ± 8.2^{Ba}	196.1 ± 11.2^{Aa}
	F_v/F_m	0.77 ± 0.06^{Aa}	0.75 ± 0.08^{Aa}	0.40 ± 0.04^{Ba}	0.43 ± 0.02^{Ba}	0.74 ± 0.08^{Aa}	0.79 ± 0.02^{Aa}
	Φ_{PSII}	0.19 ± 0.02^{Aa}	0.14 ± 0.01^{Ba}	0.10 ± 0.01^{Ca}	0.08 ± 0.01^{Ca}	0.15 ± 0.01^{Ba}	0.19 ± 0.03^{Aa}

Table 2. Pre-dawn leaf water potential (Ψ_w), net photosynthetic rate (P_N), 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 cultivar Biancolilla during drought stress and rewatering periods. Statistics as in Table 1.

| | | Drought stress | | | | Rewatering | |
		July 11	July 20	July 27	Aug 2	Aug 10	Aug 26
Exposed	Ψ_w [MPa]	-0.40 ± 0.02^{Aa}	-1.60 ± 0.11^{Ba}	-3.69 ± 0.12^{Ca}	-6.72 ± 0.09^{Da}	-0.60 ± 0.03^{Aa}	-0.40 ± 0.03^{Aa}
	P_N [μmol (CO_2) m^{-2} s^{-1}]	11.76 ± 0.45^{Aa}	4.53 ± 1.19^{Ba}	2.97 ± 0.86^{Ca}	0.06 ± 0.03^{Db}	6.09 ± 0.36^{Ba}	8.85 ± 1.28^{Bb}
	g_s [mmol (H_2O) m^{-2} s^{-1}]	153.5 ± 16.9^{Aa}	41.2 ± 5.9^{Ca}	35.4 ± 2.9^{Ca}	30.0 ± 2.2^{Da}	54.22 ± 5.2^{Cb}	105.0 ± 14.7^{Bb}
	F_v/F_m	0.72 ± 0.06^{Aa}	0.69 ± 0.06^{Aa}	0.53 ± 0.02^{Bb}	0.39 ± 0.03^{Cb}	0.49 ± 0.06^{Bb}	0.54 ± 0.02^{Bb}
	Φ_{PSII}	0.23 ± 0.03^{Aa}	0.12 ± 0.01^{Ba}	0.08 ± 0.00^{Cb}	0.06 ± 0.01^{Cb}	0.11 ± 0.03^{Bb}	0.10 ± 0.02^{Bb}
Shaded	Ψ_w [MPa]	-0.40 ± 0.02^{Aa}	-1.63 ± 0.08^{Ba}	-3.69 ± 0.08^{Ca}	-6.55 ± 0.05^{Da}	-0.50 ± 0.05^{Aa}	-0.30 ± 0.08^{Aa}
	P_N [μmol (CO_2) m^{-2} s^{-1}]	11.08 ± 1.71^{Aa}	4.49 ± 0.75^{Ca}	2.90 ± 0.23^{Ca}	0.26 ± 0.02^{Da}	7.62 ± 0.77^{Ba}	12.03 ± 1.15^{Aa}
	g_s [mmol (H_2O) m^{-2} s^{-1}]	149.6 ± 16.0^{Aa}	47.2 ± 2.8^{Ca}	26.6 ± 1.4^{Db}	21.7 ± 1.5^{Db}	69.4 ± 9.7^{Ba}	153.7 ± 10.1^{Aa}
	F_v/F_m	0.71 ± 0.06^{Aa}	0.72 ± 0.04^{Aa}	0.73 ± 0.03^{Aa}	0.62 ± 0.02^{Ba}	0.76 ± 0.01^{Aa}	0.77 ± 0.02^{Aa}
	Φ_{PSII}	0.25 ± 0.02^{Aa}	0.14 ± 0.01^{Ba}	0.15 ± 0.02^{Ba}	0.11 ± 0.01^{Ba}	0.25 ± 0.01^{Aa}	0.26 ± 0.02^{Aa}
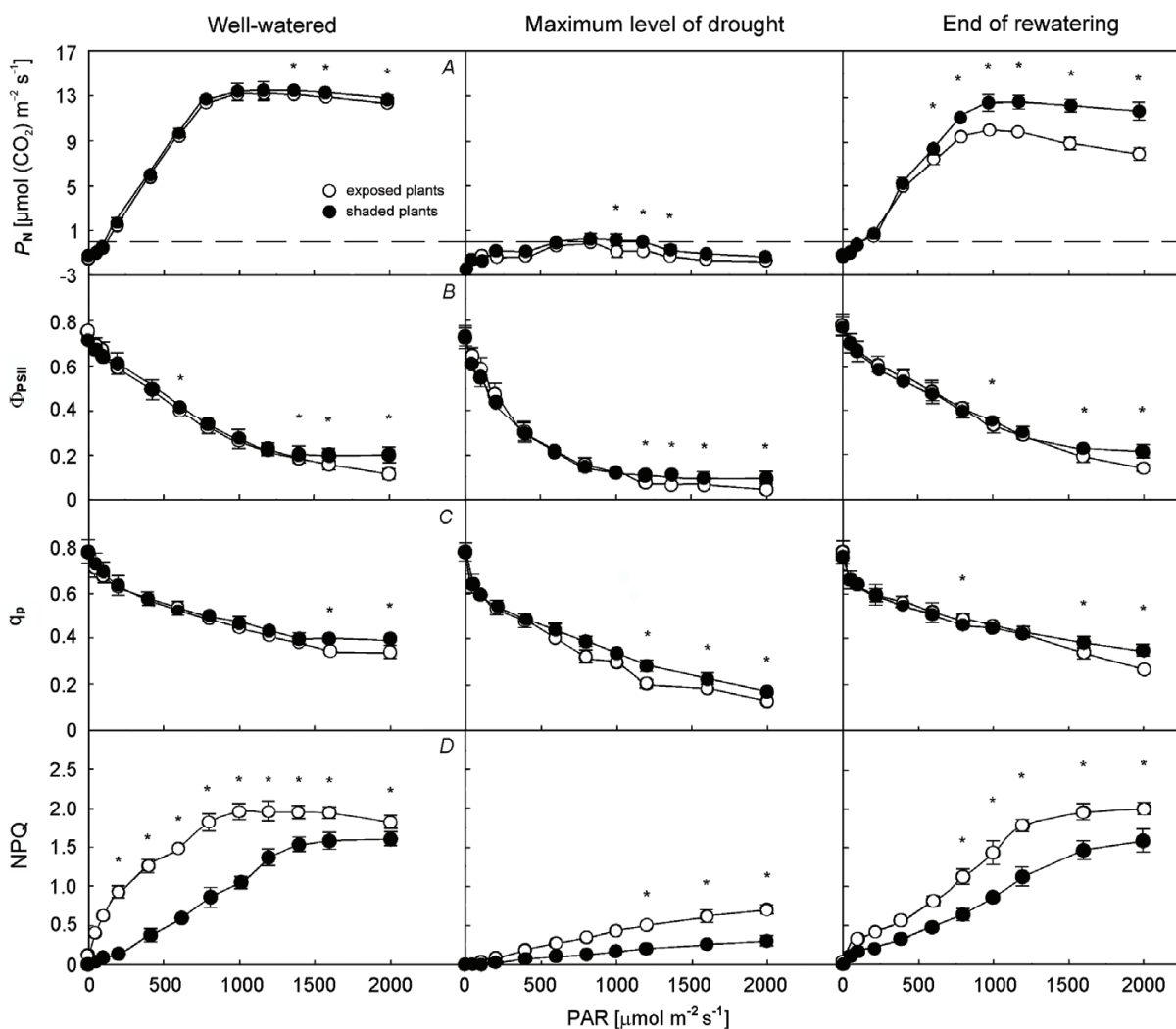
Fig. 1. (*A*) Net photosynthetic rate (P_N) and light-response curves of (*B*) quantum yield of PSII (Φ_{PSII}), (*C*) photochemical quenching (q_P) and (*D*) nonphotochemical quenching (NPQ) measured in exposed (*black symbols*) and shaded (*white symbols*) olive plants of cultivar Coratina in well-watering conditions, at the maximum level of drought stress and at the end of the rewatering period. Each value represents the mean of three measurements ($\pm$ SE) 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).

but, in particular in EP, they also showed a lower recovery (Figs. 1*A*, 2*A*). Well-watered, drought-stressed and rewatered plants of both cultivars showed a rapid initial decline in Φ_{PSII} at low levels of PAR (500-1000 μmol m^{-2} s^{-1}) (Figs. 1*B*, 2*B*). At higher levels of PAR (1000–2000 μmol m^{-2} s^{-1}), the curves of Φ_{PSII} flattened out giving less differences with increasing PAR and this behavior was more evident in SP than in EP (Figs. 1*B* and 2*B*). The values of quantum yield (Φ_{PSII}) at high light levels were significantly higher in SP than in EP of both cultivars (Figs. 2*B* and 3*B*), indicating the presence of photoinhibition in EP.
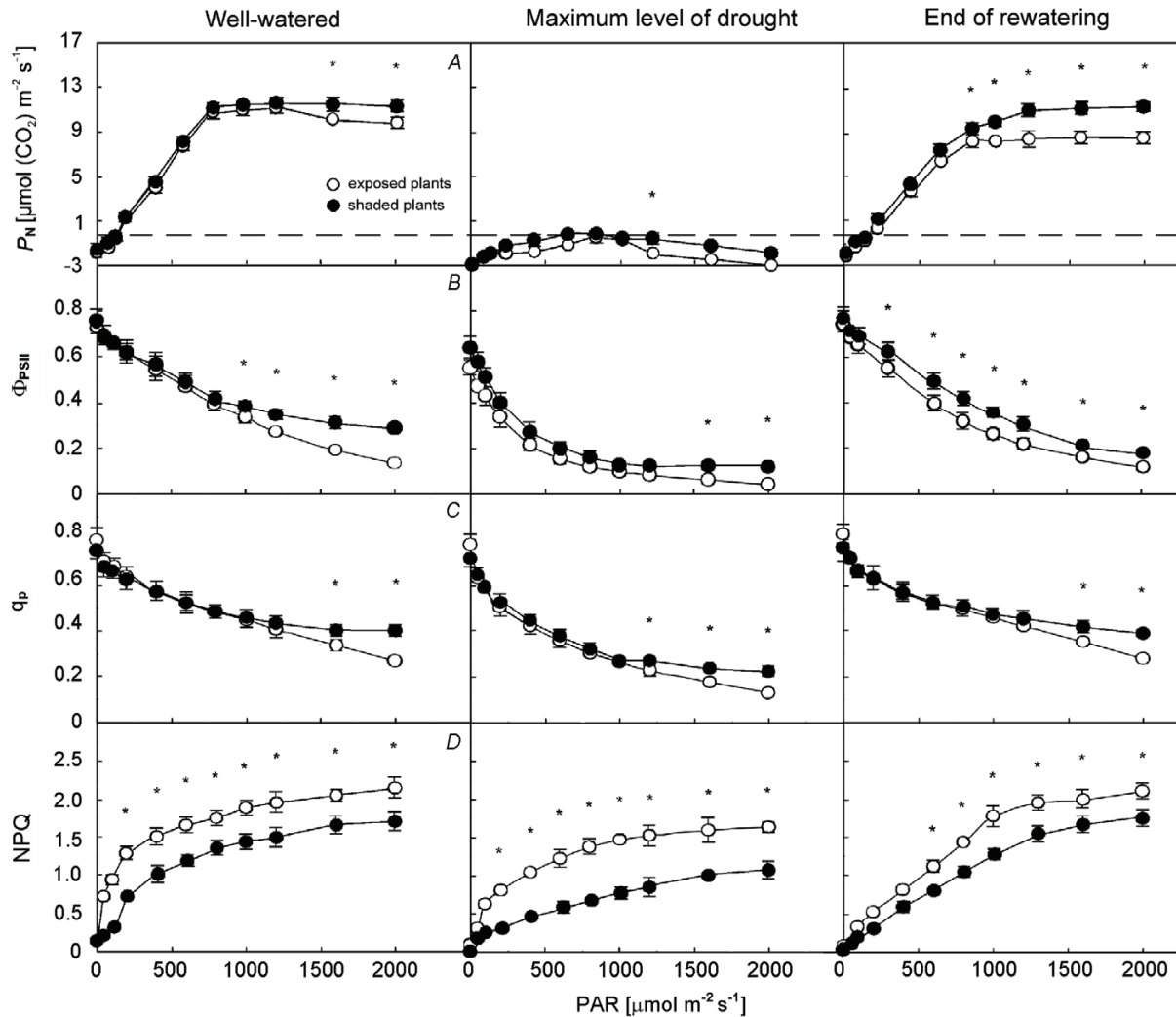

Fig. 2. (*A*) Net photosynthetic rate (P_N), light-response curves of (*B*) quantum yield of PSII (Φ_{PSII}), (*C*) photochemical quenching (q$_P$) and (*D*) nonphotochemical quenching (NPQ) measured in exposed (*white symbols*) and shaded (*black symbols*) olive plants of cultivar Biancolilla in well-watering conditions, at the maximum level of drought stress and at the end of the rewatering period. Each value represents the mean of three measurements (± SE) from three plants having a similar Ψ_w. Statistics as in Fig. 1.

q$_P$ had a decreasing trend with increasing PAR and was different between well-watered and drought-stressed plants (Figs. 1*C*, 2*C*). In drought stress conditions and at the end of rewatering, the values of q$_P$ at high light levels in EP of both cultivars were significantly higher than in SP (Figs. 1*C*, 2*C*). Our data also show marked differences among Coratina and Biancolilla plants in the capacity for NPQ (Figs. 1*D*, 2*D*). In Biancolilla, NPQ of drought-stressed plants was much higher than in Coratina

(Figs. 1*D*, 2*D*). In both cultivars, a more rapid rise in NPQ at lower PAR in EP than in SP was observed (Figs. 1*D*, 2*D*).

The coefficients of Φ_{PSII}/NPQ correlation (R^2) were different between the two cultivars, showing values of 0.87 and 0.74 for Coratina EP and SP, respectively, and 0.94 and 0.79 for Biancolilla EP and SP, respectively (Fig. 3).

Discussion

In this study, olive plants of both cultivars were influenced by the different light level. In fact, the higher light intensity, intensified by the contemporary application of drought stress, affected PSII efficiency and caused significant reductions in the values of P_N, Φ_{PSII} and F_v/F_m (Tables 1, 2). The higher values of photosynthetic
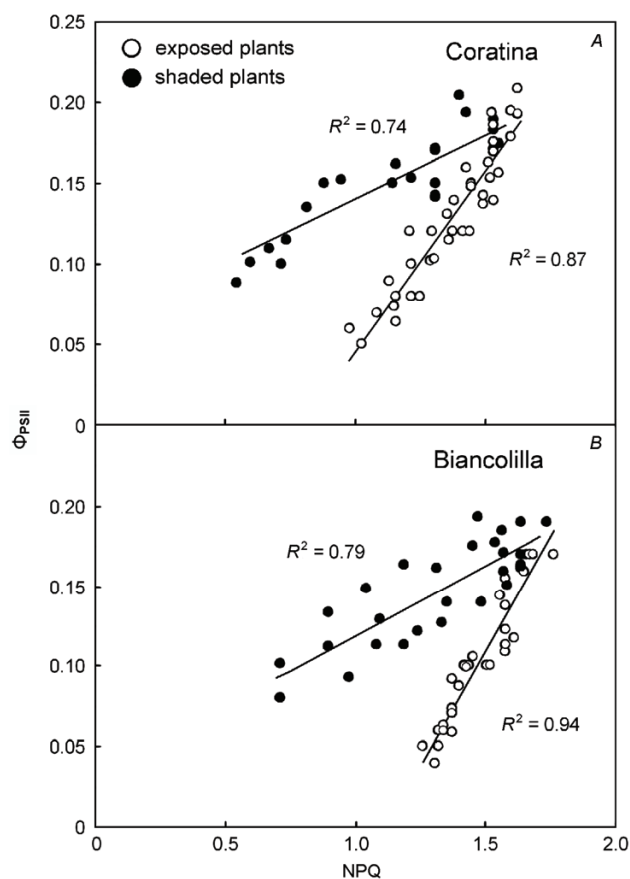

Fig. 3. Relationship between the quantum yield of PSII (Φ_{PSII}) and the nonphotochemical quenching (NPQ) measured in exposed (*white symbols*) and shaded (*black symbols*) olive plants of cultivar Coratina (*A*) and Biancolilla (*B*) during the drought stress period. Values represent individual measurements.

parameters in shaded plants (SP) (Tables 1 and 2) likely occurred because in SP a large proportion of the absorbed light is used in photochemistry and not dissipated through nonphotochemical processes as thermal dissipation (Demmig-Adams *et al.* 1995, Maxwell and Johnson 2000). This 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 and Grace 1992, Krause *et al.* 2001) but it is not so common in cultivated tree crops, with few exceptions (Gamon and Pearcy 1989).

The response of P_N and Φ_{PSII} to light from light response curves (Figs. 1*A*, 2*A*) and the values of P_N (Tables 1, 2) indicate that Coratina plants had higher photosynthetic 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 (Table 1, Fig. 1*A*). By contrary, Biancolilla presented lower values of P_N in well-watered conditions, a less marked photosynthesis decline during drought, and a considerable resilience during rewatering (Table 2, Fig. 2*A*).

The significant decreases in g_s found both in EP and SP with increasing drought (Tables 1, 2) indicate that the reduced PSII efficiency is not the only limiting factor for photosynthesis in olive tree (Angelopoulos *et al.* 1997) but stomatal regulation mechanisms are likely involved (Tables 1, 2). During the rewatering period, SP of both cultivars recovered both PSII efficiency and *A*, while in EP they remained depressed (Tables 1, 2). 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 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 overexcitation of photosynthetic apparatus may have photoinihibitory consequence (Ruban and Horton 1995). In this study, light response curves highlight that the fluctuations of NPQ between EP and SP were wider than those of q_P (Figs. 1*C,D*, 2*C,D*). The values of NPQ in EP at the end of rewatering are comparable to those of well-watered plants (Figs. 1*D*, 2*D*), indicating that in EP the mechanisms of energy dissipation by xantophyll cycle remained active even during the rewatering period. The light-dependent regulation of NPQ observed here for 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 q_P whereas the regulation of thermal dissipation by NPQ is negligible.

Generally, at severe drought stress, the capacity of NPQ in cultivar Biancolilla was higher than in Coratina both in EP and SP (Figs. 1*D*, 2*D*). Moreover, the higher coefficients of Φ_{PSII}/NPQ correlation (R^2) found in EP (Fig. 3) indicate that Biancolilla was better able to regulate nonphotochemical energy dissipation during drought stress. These results can justify the higher sensitivity of cultivar Coratina to high light and drought stress and also show 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 to other tree species (Lo Gullo and Salleo 1988, Bacelar *et al.* 2007), our results confirm that photoinhibition 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 stress conditions of semi-arid environments, characterized by high light intensity and severe water deficit.

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