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Inhibition of photosynthesis in olive trees (*Olea europaea* L.) during water stress and rewatering

K. Angelopoulos[1,3], B. Dichio[2] and C. Xiloyannis[2]

[1] *Laboratory of Plant Physiology, Department of Biology, University of Patras, Greece*

[2] *Dipartimento di Produzione Vegetale, Universita degli Studi della Basilicata, Italy*

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Abstract

The effect of high levels of natural light on leaf photosynthesis in olive trees (*Olea europaea* L. var. Coratina), grown in pots outdoors in the summer and subjected to water stress, was studied. Net photosynthetic rates reached maximum values early in the morning in both control and stressed plants and subsequently declined gradually. This inactivation of photosynthetic activity was accompanied by changes in the fluorescence characteristics of the upper intact leaf surface. The maximum fluorescence yield (*Fp*) and the ratio *Fv/Fp* decreased at midday especially in water-stressed plants, but the initial fluorescence (*Fo*) rose to a maximum value at midday and declined again in the afternoon. In control plants the values of maximum fluorescence *Fp* and the ratio *Fv/Fp* increased again in the afternoon and had recovered almost completely by 8 p.m. as the leaf water potential recovered. In stressed plants this diurnal recovery was not complete, so that the photosynthetic rates and the ratio *Fv/Fp* declined gradually during the development of water stress. These results indicate that in olive trees subjected to severe water stress the non-stomatal component of photosynthesis was affected and perhaps a light-dependent inactivation of the primary photochemistry associated with photosystem II (PSII) occurred. Four to five days after rewatering severely stressed plants, the predawn leaf water potential, net photosynthetic rates and chlorophyll fluorescence indices recovered only partially.

Key words: *Olea europaea*, photosynthesis, water stress, chlorophyll *a* fluorescence, inhibition of photosynthesis.

Introduction

In Mediterranean ecosystems, the summer months are characterized by high temperatures, high light levels, high vapour pressure deficits, and lack of precipitation. Limited water availability induces stomatal closure and a reduction of photosynthetic rates. Under these conditions, olive trees often suffer from drought combined with stress from high temperatures and high light levels.

Stomatal regulation of leaf gas exchange, under drought conditions, has been well documented for drought adapted species (Tenhunen *et al.*, 1987). It has also been reported that the inactivation of photosynthetic activity could be largely ascribed not only to stomatal restrictions on the supply of CO_2 to the leaf, but also to non-stomatal effects related to the inhibition of primary photochemistry and of electron transport in chloroplasts (Boyer *et al.*, 1987). In contrast Genty *et al.* (1987) supported the finding that the primary photochemical reactions and electron transport in cotton leaves do not appear to be much affected by low water potential. Kaiser (1987) also reported that photosynthesis was rather insensitive to dehydration down to 50–70% relative water content, but under long-term severe water stress coupled with full sunlight photoinhibition of photosynthesis is induced. Recent studies have emphasized that changes in PSII fluorescence may result from damage in the reaction centre or from regulatory processes external to the reaction centre, including non-radiative dissipation or increased excitation transfer to PSI (Demmig-Adams, 1990). Björkman and Powles (1984) showed that in *N. oleander* L. full natural light and water stress caused photoinhibitory damage in the photosynthetic system and that water stress predisposed the leaves to photoinhibition. Ludlow and Björkman (1984) found a parahelio-

[3] To whom correspondence should be addressed.

tropic leaf movement in Siratro (*Macroptilium atropurpureum*) as a protective mechanism against drought-induced damage. They also showed that water stress predisposes the photosynthetic system to photoinhibition and high leaf temperature exacerbates this photoinhibitory damage in the absence of paraheliotropic leaf movement. Gamon and Pearcy (1990) found that when leaves of California wild grape, *Vitis californica* Benth., were exposed to a combination of high *PFD* and high temperature, both photoinhibition of PSII and a decrease of net CO_2 uptake occurred. They also hypothesized an interaction of multiple, temperature-dependent processes involving both the regulation of energy distribution and damage to the photosynthetic components. Recently, Cornic *et al.* (1992) reported that leaf photosynthesis is resistant to mild drought stress and that the decline of photochemical yield of PSII is a consequence of an increase in the thermal dissipation of the exciton trapped by PSII. Bongi and Long (1987) found a reduction of 80% of quantum yield of leaf photosynthesis in laboratory-grown olive trees when they were exposed to high light and temperature (38 °C) conditions and supported the finding that photoinhibition during temperature stress is, potentially, a major factor influencing the photosynthetic productivity of olive trees in the field. Olive has been characterized as a drought-tolerant species, developing adaptive reactions (e.g. osmotic adjustment) under drought conditions (Larcher *et al.*, 1981). The effects of water stress on olive photosynthetic rates are well documented (Xiloyannis *et al.*, 1988; Jorba *et al.*, 1985), but there are no data on the effect of water stress on PSII in olive trees grown outdoors in the summer.

Materials and methods

Experimental design

The experiments were conducted at the 'Pantanello' Agricultural Experimental Station in Metaponto, southern Italy (Region of Basilicata) during the summers of 1992 and 1993. Metereological data were monitored all year round by the meterological station on the farm. The trials were carried out using 2-year-old olive trees, of the cultivar 'Coratina' grown in 18 l pots. The pots were arranged in rows in a north–south direction. They were also insulated and covered to avoid evaporation. The consumed water, measured by weighing, was restored to all plants until the end of June, maintaining the soil moisture level at field capacity of around 85%. In July, the amount of water restored to the plants was differentiated so as to create different levels of stress within 8–10 d. Each stress level, defined on the basis of predawn leaf water potentials, was represented by two plants.

Leaf water potentials

Leaf water potentials were measured predawn and at different times over several days using four fully expanded leaves of similar age and position in the canopy for each treatment. All measurements were carried out using the pressure chamber technique according to the procedure recommended by Turner (1981).

Leaf gas exchange and chlorophyll a fluorescence

Three mature leaves from different stems of two olive trees per stress treatment were selected and marked at the beginning of the experiment. Net photosynthetic rates (A) were determined in these intact leaves using the portable photosynthetic system (ADC, UK) and the Parkinson Leaf Chamber LCA-2 operated at 450–500 ml min^{-1} flow rate, under natural climate and irradiance and expressed on a leaf area basis by a computer program (Moon and Flore, 1986).

Chlorophyll *a* fluorescence from PSII was recorded at 650 nm on three leaves on the plant stems, marked at the beginning of the experiment, by using the time-resolving portable fluorimeter (Plant Efficiency Analyser, PEA, Hansatech Instrument Ltd., UK). Before each measurement leaf samples were darkened for 30 min under properly constructed plastic leafclips. The sensor unit, connected to the main control box by a cable, housed an optical assembly which provided powerfull illumination (actinic light beam) to the leaf and detected the consequent fluorescence signals. The sensor was placed over the leafclip so that daylight was excluded. Illumination was provided by an array of six high-intensity light-emitting diodes (LED) which were focused on the leaf surface (about 12.56 mm^2). An optical feedback circuit monitored and corrected changes in the output intensity of the LEDs, caused by internal heat produced in the LEDs. It also compensated for intensity changes caused by the variation in ambient temperature. The detector is a high performance pin photodiode associated with an amplifier circuit. The initial fast rise in the fluorescence signal was digitized at a rate of 100 000 readings s^{-1} in order to give good resolution of *Fo* values. The fluorescence indices *Fo*, *Fp*, *Fv*, and *Fv/Fp* are automatically calculated and displayed. *Fo* is the initial fluorescence (all PSII reaction centres are oxidized) and *Fp* the maximum fluorescence at P level without saturation (complete reduction) of PSII reaction centres according to the nomenclature referred to by van Kooten and Snell (1990). As samples were used, the 4th, 5th and 6th leaves on the stems were used. An illumination intensity was selected at 900 μE m^{-2} s^{-1} for the light pulses to induce *Fp*. In preliminary experiments, it was found that this intensity was sufficient to reduce all *Qa* molecules in severely stressed plants.

Results

Climate conditions and leaf characteristics

Diurnal changes of temperature (*Ta*), vapour pressure deficits (*VPD*) and global radiation (*Rg*) changed during the time-course of the experiments and constituted the climatic conditions in which the olive plants were grown. The data of 16 July 1993 given in Fig. 5A show that global radiation over the canopy reached its maximum of 1750 μE m^{-2} s^{-1} in *PAR* at midday, while the maximum *VPD* value, around 2.9 kPa, was reached between 9 a.m. and 4 p.m. Maximum air temperatures during the trials ranged from 31–34 °C. Leaf temperature was not monitored during the experiments, but some measurements of leaf temperature by an infrared remote-sensing instrument on leaves exposed to direct sunlight in stress plants, showed that these were 4–5 °C greater than air temperature at midday. Leaf angle in olive trees varies between 30–45°. The optical properties of the leaves are

dependent on their water and chlorophyll contents (Baret *et al.*, 1988). Bongi and Long (1987) found small differences in the absorptance of olive leaves with relative water contents of 0.853 and 0.733.

Diurnal changes of leaf water potential

Leaf water potential in control plants decreased from around −0.45 MPa predawn to a minimum of about −2 MPa at midday when stomata closed partially and transpiration decreased for some hours. Leaf water potential recovered partially during the subsequent hours, but complete recovery was only reached during the night. Stress plants separated into three stress levels defined by predawn leaf water potentials (level (I) −1.2 MPa; level (II) −4.25 MPa; level (III) −5.7 MPa). Leaf water potential in stressed plants declined during the day without any recovery during the afternoon or at night. In severe stress level (III) plants, leaf water potential reached −7 MPa in the afternoon (Fig. 1).

Diurnal course of stomatal conductance and photosynthetic rates

At about 8 a.m. local time during sunshine, net photosynthetic rates (A) increased and reached daily maximal values of 22.2, 21.75, 13.56, and 6.32 μmol CO_2 m^{-2} s^{-1} for control and for the different stress levels plants (Fig. 2). During measurements, the light intensity varied between 1300–1800 μE m^{-2} s^{-1} and leaf temperature between 23–34 °C. Under these conditions maximum net photosynthetic rates were attained. During the next 2–3 h, as leaf water potential dropped and sunlight reached 1800 μE m^{-2} s^{-1}, stomatal conductance reduced and a depression in photosynthesis occurred (Fig. 3). Net photosynthetic rates decreased to about 14.26, 6.68, 2.27, and 0.2 μmol CO_2 m^{-2} s^{-1} in control plants and the different stress levels, respectively (Fig. 2). In control and stress level (I) plants, net photosynthetic rates remained relatively stable during the rest of the day. In stress level (III) plants, the photosynthetic rate reached the minimum value at 11 a.m. The corellation between stomatal conductance and maximum photosynthetic rates is linear for control plants, but not linear for all the stressed plants (Fig. 4).

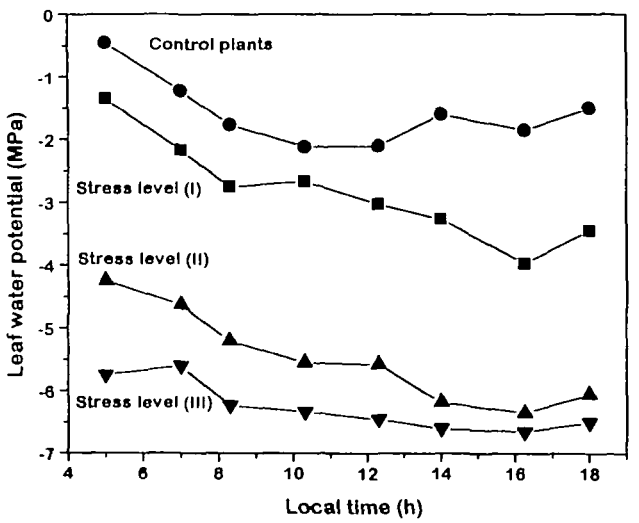

Fig. 1. Diurnal changes of leaf water potential in control and stress plants. Three levels of stress were selected defined on the basis of predawn leaf water potentials. Stress level (I): predawn wp = −1.2 MPa, stress level (II): predawn wp = −4.5 MPa, stress level (III): predawn wp = −5.7 MPa.

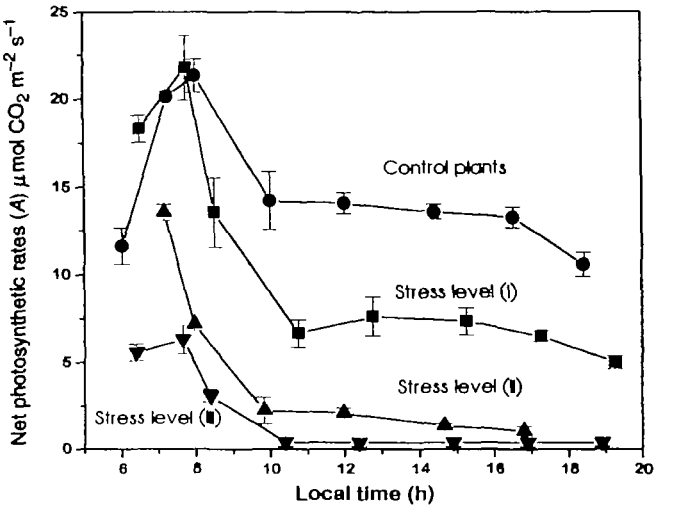

Fig. 2. Diurnal course of net photosynthetic rates in control plants (-●-) and in different stress level plants (-■-) stress level (I), (-▲-) stress level (II), (-▼-) stress level (III).

Diurnal course of chlorophyll a fluorescence

In both control and stress level (III) plants, Fp from PSII and the ratio Fv/Fp declined to minimum values at midday

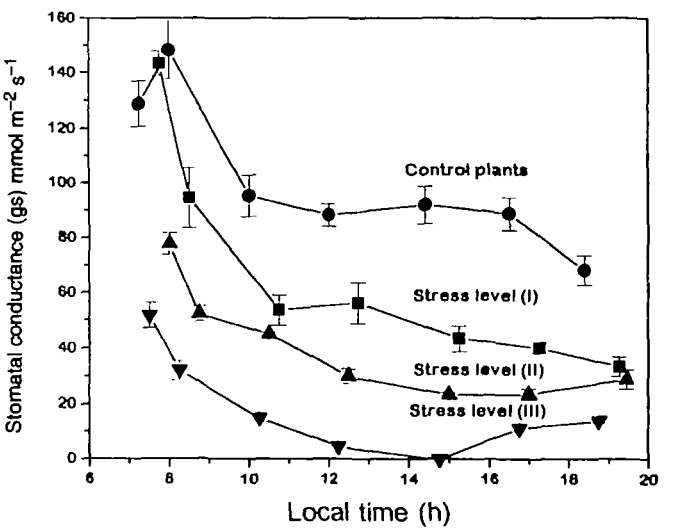

Fig. 3. Diurnal course of stomatal conductance in control and stressed plants (Symbols as in Fig. 2).

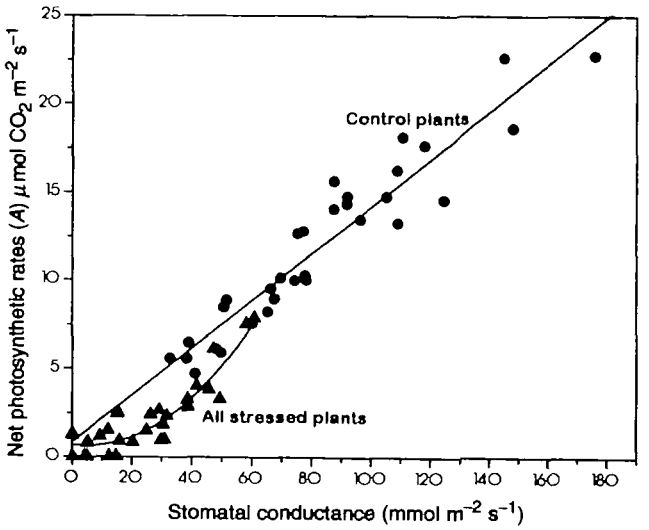

Fig. 4. Correlation between maximal net photosynthetic rates and stomatal conductance in control plants (—●—) and (--▲—) in all stressed plants.

and increased again in the afternoon. The rate and extent of the decrease was greater in stressed plants. *Fp* diminished by about 13% in control plants and 30% in stress level (III) plants, while the ratio *Fv/Fp* decreased by 10% and 20%, respectively. At 8 p.m. recovery was complete in control plants, but not in stressed plants, so during the development of water stress, the initial values of these indices measured in the morning were different (Fig. 5E, F). In contrast, the initial chlorophyll fluorescence, *Fo*, increased to a maximum value at midday and declined in the afternoon in both control and stressed plants (an increase of 18% and 24%, respectively). At 8 p.m. *Fo* values recovered completely in control plants, but not in stress level (III) plants (Fig. 5D). When control and stressed olive trees were moved under shade (about 150–200 μE m^{-2} s^{-1}), chlorophyll *a* fluorescence indices did not change during the diurnal course (data not shown).

Changes of photosynthetic rates and chlorophyll a fluorescence indices during the development of water stress

As leaf water potential in stressed plants was declining during the diurnal course, the values of chlorophyll fluorescence indices measured early each morning (6.30–7.30 a.m.) recovered only partially upon darkening of the leaves, so that during the development of water stress a gradual decline of the ratio *Fv/Fp* occurred. A curvilinear correlation between predawn leaf water potential and the corresponding changes of the ratio *Fv/Fp* were obtained. The changes of *Fv/Fp* were very slow up to −2.5 MPa, but became faster as leaf water potential declined further (Fig. 6B). Net photosynthetic rates also declined during the development of water stress (Fig. 6A).

Time-course of the recovery of chlorophyll a fluorescence characteristics upon rewatering

On rewatering stressed plants, the predawn leaf water potential, the net photosynthetic rates and fluorescence indices were measured early in the morning. Predawn leaf water potential increased to about −0.8 MPa within the next 4 d, followed by a slow but continuous increase of net photosynthetic rates, an increase of fluorescence indices *Fp* and *Fv/Fp*, and a decrease of *Fo*. Five days after rewatering, fluorescence indices reached control values, although the recovery was not complete. Net photosynthetic rates recovered only partially (about 50%) over the same time (Table 1).

In plants with a lower level of water stress (predawn leaf water potential −4.25 MPa), the recovery of fluorescence indices was obtained within 3–4 d after rewatering and photosynthetic rates reached about 65% those of control plants (data not shown).

Discussion and conclusions

Diurnal changes of leaf water potentials

The ranges of leaf water potential used to define drought stress levels ('mild' stress from 0 to −1 MPa, 'moderate' stress from −1 to −2 MPa, and 'severe' stress for leaf water potentials greater than −2 MPa) are usually approximate and depend on plant species and growth conditions (Lawlor, 1983). In the case of olive trees the previous ranges are inadequate to describe their drought stress levels, as the leaf water potential of well-watered plants (control plants) usually reaches −2 MPa at

Table 1. *Evolution in chlorophyll fluorescence indices, net photosynthetic rates (daily maximum) measured in the early morning and predawn leaf water potential during the recovery of severely stressed plants after rewatering*

Date	*Fo*	*Fm*	*Fv/Fm*	*A* (μmol CO_2 m^{-2} s^{-1})	ψ_w(−MPa)
18 July	0.169±0.0071	0.476±0.039	0.643±0.081	6.6±0.78	6.50
19 July	0.142±0.0064	0.550±0.052	0.742±0.043	7.8±1.12	1.30
20 July	0.134±0.0053	0.588±0.041	0.772±0.063	9.4±1.01	0.85
21 July	0.126±0.0078	0.599±0.063	0.789±0.045	11.1±1.2	0.80
22 July	0.135±0.0063	0.645±0.081	0.798±0.054	9 7±1.1	0.80
Control	0.135±0.0055	0.710±0.037	0.816±0.036	22.1±0.95	0.45

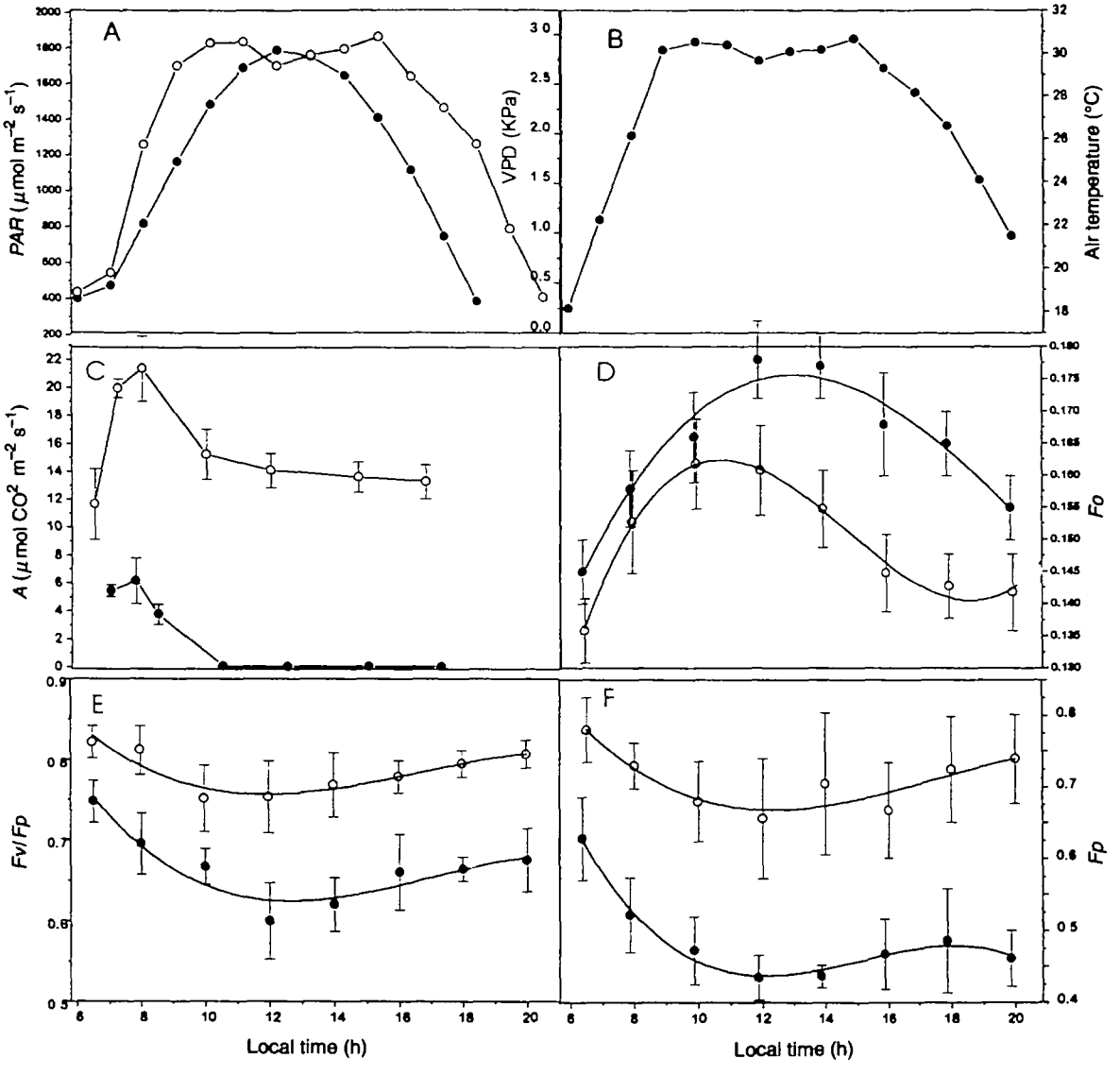

Fig. 5. Diurnal changes of *PAR* (-●-) and vapour pressure deficits (*VPD*) (-○-) (A), air temperature (B), Net photosynthetic rates, *A*, (C), initial chlorophyll fluorescence (*Fo*) (D), (*Fv/Fp*) (E), and maximum chlorophyll fluorescence (*Fp*) (F) in control (-○-), and stress level (III) plants (-●-). The points are means of six measurements from two plants on 16 July 1993.

midday. Plants with predawn leaf water potential of −1.2 MPa reach −3 or −3.5 MPa at midday.

Diurnal course of stomatal conductance, photosynthetic rates and chlorophyll a fluorescence indices

As temperature and *PAR* increased during the diurnal course, net photosynthetic rates (*A*) for control plants also increased to maximum values early in the morning and then decreased at midday to a value, about 64.2% of the morning maximum net photosynthetic rate. In stress level (II) and (III) plants, the midday depression in net photosynthetic rates was greater (about 17% and 3% of the maximum, respectively). A midday depression in stomatal conductance and in the rate of net CO_2 uptake were often observed during warm, dry and cloudless summer days in various species of annual cultivated plants (Vadell *et al.*, 1992), mesophytic or xerophytic shrubs and trees (Tenhunen *et al.*, 1987; Epron *et al.*, 1992), grapevines (Correira *et al.*, 1990) and fruit trees (Faust, 1989). Olive, as a sclerophyllous drought-tolerant plant, can retain sufficient photosynthetic rates (maximum values about 30% those of control plants) under long-term water stress conditions even with a predawn leaf water potential of about −5.7 MPa. This maximum was observed early in the morning when temperature was low, light was at suturating level intensities and *VPD* relatively low. The results confirm the view that the photosynthetic apparatus in olive trees is very resistant to mild and moderate water stress and that stomata are the main limiting factor to carbon uptake (Cornic *et al.*, 1992;

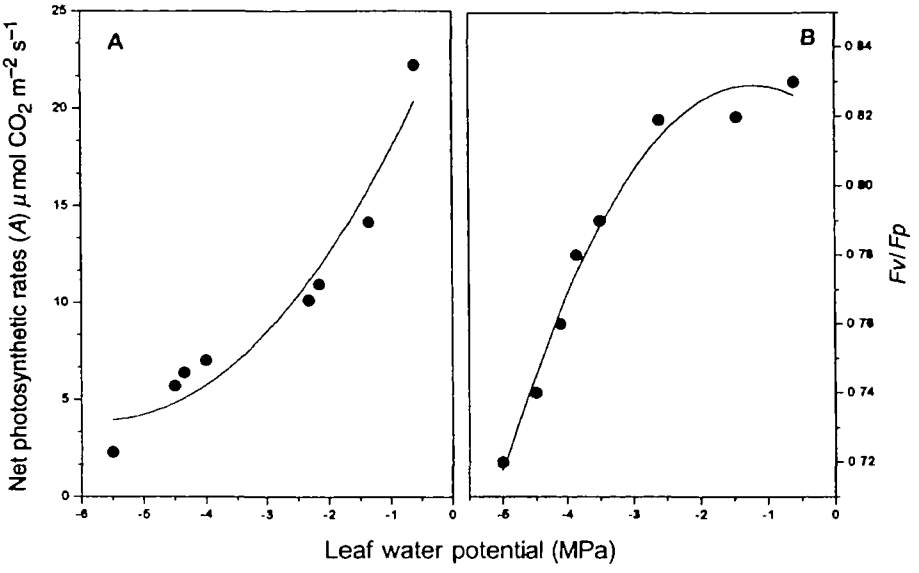

Fig. 6. Correlation between predawn leaf water potential net photosynthetic rates (A), and PSII photochemical efficiency *Fv/Fp*, (B). The values have been measured each day during the development of water stress.

Quick *et al.*, 1992; Kaiser, 1987). However, under severe long-term drought stress accompanied by high temperatures and light intensities greater than 1300 μE m^{-2} s^{-1}, severe limitation of net CO_2 uptake may promote an imbalance between the photochemical activity of PSII and the electron requirement for photosynthesis, leading to an over-excitation and, subsequently, photoinhibitory phenomena (Epron *et al.*, 1992). It is also suggested that the non-linearity in the correllation between A_{max} and g_s (at A_{max}) of stressed plants can be an indication that a non-stomatal factor is responsible for the decline of net photosynthetic rates, in addition to stomatal closure. The diurnal changes of chlorophyll *a* fluorescence indices *Fo*, *Fp* and *Fv/Fp* computed from the time-resolving fluorimeter, can be another indication that high light intensities combined with water stress can cause an inhibition of net photosynthetic rates. These phenomena can include, on the one hand, an avoidance of over-excitation of the PSII reaction centre by decreased light absorption and, on the other hand, an internal increase of thermal dissipation of excitation energy, associated or not with xanthophyll cycle activity. The induction and increase of thermal energy dissipation is associated with a down-regulation of photosynthesis and it has been considered as a photoprotective process. It is characterized by a sustainable quenching of fluorescence yield (*Fo*, *Fm*, *Fv/Fm*, *qE*) and an increase in the rate constant for radiationless energy dissipation in the chlorophyll pigment bed. In some cases light-dependent inactivation of PSII reaction centres is associated with a decline in both *Fm* and *Fv/Fm* and with an increase of initial fluorescence yield, *Fo* (Demmig-Adams and Adams, 1992; Long and Humphries, 1994). According to the Butler model an increase in *Fo* can result from a decrease in the rate constant for photochemistry (*kp*) or from a decrease in the rate constant for energy transfer to PSI (k_T) (Demmig-Adams, 1990). In olive trees the diurnal decrease in *Fp* and *Fv/Fp* and the increase in *Fo* in both control and stressed plants can also be indications that light-dependent inactivation of PSII occurred. The question is whether these variations in chlorophyll fluorescence indices are artefacts or reflect real changes in the properties of the olive photosynthetic system. *Fo* depends on the size of PSII chlorophyll antenna and on the integrity of PSII reaction centres (Krause and Weis, 1991). It may be affected by high leaf temperature. Tergazhi *et al.* (1989) showed in different tropical and temperate species that temperatures greater than 40 °C caused increases in *Fo*. It is also known that high temperature causes thermal damage and, subsequently, an increase in *Fo* (Berry and Björkman, 1980; Schreiber and Berry, 1977; Ludlow and Björkman, 1984). Leaf temperature of stressed plants did not exceed 38–39 °C and a difference of 4–5 °C in leaf temperature between control and stress level (III) plants was observed at midday. It was considered that these temperatures did not cause thermal damage or the subsequently observed increase of *Fo*. High temperatures may also lead to direct inhibition of the Calvin cycle which could, in turn, cause secondary declines in PSII activity (Weis, 1981; Weis and Berry, 1988; Gamon and Pearcy, 1990).

Both *Fo* and *Fp* may also be influenced by the differences in optical properties between leaves of control and stressed plants, and such effects could influence the results to an unknown extent. The same effect of water stress on chlorophyll *a* fluorescence indices has been observed in *Nerium oleander* (Demmig *et al.*, 1988). Further laboratory studies on detached olive leaves are needed in order

to ascertain previous effects on fluorescence yields, and the influence of water stress on optical properties of olive leaves as well as on non-photochemical fluorescence quenching (NPQ).

In contrast to the absolute yields of *Fo* and *Fp*, the ratio *Fv/Fp* is independent of the above artefacts and can be used as an indication for photoinhibition of photosynthesis. Ögren and Öquist (1988), screening for photoinhibition of photosynthesis in the field, found a linear relationship between the ratio *Fv/Fp* measured as previously referred and the ratio *Fv/Fm* measured at 77 K. They also found a linear relationship between inhibition of the quantum yield of O_2 evolution and the inhibition of the *Fv/Fp*. So it is suggested that changes in the ratio *Fv/Fp* can be a measure of changes in quantum yield of PSII. The parallel decline of net photosynthetic rates and *Fv/Fp*, as a measure of quantum yield of PSII under high light intensities, high temperatures and *VPD* in both control and stress groups of olive leaves, are indications that photoinhibitory phenomena may occur. High light intensities and leaf temperatures may promote an imbalance between inactivation and the repair cycle of PSII reaction centres. In control and stress level (I) plants, the balance was restored and the chlorophyll fluorescence characteristics recovered during the afternoon or at night. In contrast, in stress levels (II) and (III) plants, severe water deficits caused irreversible changes in PSII reactions centres. During the development of water stress, the observed changes in *Fv/Fp* are a composite of the development of irreversible photoinhibition and changes which were induced during the early morning hours. These data confirm the view of Björkman and Powles (1984) that water stress predisposes the photosynthetic system to photoinhibition in olive trees.

It is difficult to deduce any clear statement about the state of PSII from the decline of *Fv/Fp* only, as this ratio does not depend on the absolute amount of PSII reaction centres in a given leaf area, but on the proportion of damaged PSII which is not yet degraded.

The amount of functional PSII reaction centres in a given leaf area is the result of the rates of damage and degradation and of repair of PSII. Recently, it has been demonstrated that, at the molecular level, the light-dependent inactivation and repair of PSII is accompanied by damage and degradation of 32 kDa D1 protein and replacement of this protein in the thylakoid membrane by one newly synthesized (Adir *et al.*, 1990; Barber and Andersson, 1992). Damaged D1 protein migrates out of granal thylakoids without their light-harvesting complex (LHC-II) and is replaced by an undamaged protein, probably inactive. A model has been proposed, according to which, during photoinhibition, PSII is in a steady state between 'damage' and 'repair' and that this turnover of proteins in the light is critically dependent on protein synthesis (Rhodes, 1987; Baker, 1994). This D1 protein turnover is affected by light and temperature. Light stimulates protein turnover while high temperatures may cause a separation of PSII from LHC-II (Demmig-Adams and Adams, 1992; Armond *et al.*, 1980). It is also possible that severe water stress not only predisposes plants to photoinhibition, but also inhibits the turnover of the protein complex in PSII by inhibition of protein synthesis in chloroplasts. Baker (1993) reported that under severe water deficits it is possible that electron transport to O_2 and down-regulation will be unable to dissipate the excitation energy in PSII and, consequently, photodamage and loss of the D1 protein of PSII reaction centres can result.

Time-course of the recovery of chlorophyll a fluorescence characteristics upon rewatering

Although the recovery of severely water-stressed plants (−6.5 MPa) was not complete 5 d after rewatering, it was quite fast in relation to other plants such as *Nerium*, in which partial recovery occurred 8 d after rewatering (Björkman and Powles, 1984). This is further evidence that olive trees are drought-tolerant and have a strong mechanism for PSII repair after long-term photoinhibition and water stress. The results described require verification by studying the effects of environmental parameters separately in detached leaf discs in order to evaluate all the effects of these photoinhibition phenomena on olive plants grown in the field.

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References

Adir N, Schochat S, Inoue Y, Ohad I. 1990. Mechanism of the light-dependent turnover of D1 protein. In: Baltscheffsky M, ed. *Curent research in photosynthesis*, Vol. II. Dordrecht: Kluwer Academic Press, 490–513.

Armond UP, Björkman O, Staehelin A. 1980. Dissociation of supramolecular complexes in chloroplast membranes: a manifestation of heat damage to the photosynthetic apparatus. *Biochimica et Biophysica Acta* **601,** 433–42.

Baker NR. 1994. Light-use efficiency and photoinhibition of photosynthesis in plants under environmental stress. In: Smith JAC, Griffiths H, eds. *Water deficits. Plant responses from cell to community.* Oxford, UK: BIOS Scientific Publishers, 221–33.

Barber J, Andersson B. 1992. Too much of a good thing: light can be bad for photosynthesis. *Trends in Biochemical Science* **17,** 61–6.

Baret F, Andrieu B, Guyot G. 1988. A simple model for leaf optical properties in visible and near infrared: application to the analysis of spectral shifts determinism. In: Lichtenthaler K, ed. *Applications of chlorophyll fluorescence.* Dordrecht: Kluwer Academic Publishers, 345–51.

Berry J, Björkman O. 1980. Photosynthetic responses and adaptation to temperature in higher plants. *Annual Review of Plant Physiology* **31,** 491–543.

Björkman O, Powles SB. 1984. Inhibition of photosynthetic reactions under water stress: interaction with light level. *Planta* **161,** 490–504.

Bongi G, Long SP. 1987. Light-dependent damage to photosynthesis in olive leaves during chilling and high temperature stress. *Plant, Cell and Environment* **10,** 241–9.

Boyer JS, Armond PA, Sharp RE. 1987. Light stress and leaf water relations. In: Kyle DJ, Osmond CD, Arntzen CJ, eds. *Photoinhibition. topics in photosynthesis*, Vol. 9. Amsterdam: Elsevier, 111–22.

Correira MJ, Chaves MMC, Pereira JS. 1990. Afternoon depression in photosynthesis in grapevine leaves. Evidence for a high light stress effect. *Journal of Experimental Botany* **41,** 417–26.

Cornic G, Ghashghaie J, Genty B, Briantais JM. 1992. Leaf photosynthesis is resistant to a mild drought stress. *Photosynthetica* **27(3),** 295–309.

Demmig-Adams B. 1990. Carotenoids and photoprotection in plants: a role for the xanthophyll zeaxanthin. *Biochimica et Biophysica Acta* **1020,** 1–24.

Demmig B, Winter K, Kruger A, Czygan FC. 1988. Zeaxanthin and the heat dissipation of excess light energy in *Nerium oleander* exposed to a combination of high light and water stress. *Plant Physiology* **87,** 17–24.

Demmig-Adams B, Adams III WW. 1992. Photoprotection and other responses of plants to high light stress. *Annual Review of Plant Physiology and Plant Molecular Biology* **43,** 399–426.

Epron D, Dreyer E, Brenda N. 1992. Photosynthesis of oak [*Quercus petrea* (Matt) Liebl.] during drought under field conditions: diurnal course of net CO_2 assimilation and photochemical efficiency of photosystem II. *Plant, Cell and Environment* **15,** 809–20.

Faust M. 1989. *Physiology of temperate zone fruit trees.* New York: John Willey & Sons.

Gamon JA, Pearcy RW. 1990. Photoinhibition in *Vitis californica.* The role of temperature during high light treatment. *Plant Physiology* **92,** 487–94.

Genty B, Briantais JM, Da Silva JBV. 1987. Effects of drought on primary photosynthetic processes of cotton leaves. *Plant Physiology* **83,** 360–4.

Jorba J, Tapia L, Sant D. 1985. Photosynthesis, leaf water potential, and stomatal conductance in *Olea europaea* under wet and drought condition. *Acta Horticulturae* **171,** 237–46.

Kaiser WM. 1987. Effects of water deficit on photosynthetic capacity. *Physiologia Plantarum* **71,** 142–9.

Krause GH, Weis E. 1991. Chlorophyll fluorescence and photosynthesis: the basics. *Annual Review of Plant Physiology and Plant Molecular Biology* **42,** 313–49.

Larcher W, De Morales JAPV, Bauer H. 1981. Adaptive responses of leaf water potential, CO_2 gas exchange and water use efficiency of *Olea europaea* during drying and rewatering. In: Margaris NS, Mooney HA, eds. *Components of productivity of Mediterranean climate regions. Basic and applied aspects.* The Hague: W. Junk Publishers, 77–84.

Lawlor DW. 1983. Integration of biochemical processes in the physiology of water-stressed plants. In: Marelle R, Clijsters H, van Poucke M, eds. *Effects of stress on photosynthesis.* London: W. Junk Publishers, 35–44.

Long SP, Humphries S. 1994. Photoihibition of photosynthesis in nature. *Annual Review of Plant Physiology and Plant Molecular Biology* **45,** 633–62.

Ludlow MM, Björkman O. 1984. Paraheliotropic leaf movement in Siratro as a protective mechanism against drought-induced damage to primary photosynthetic reactions: damage by excessive light and heat. *Planta* **161,** 505–18.

Moon JW, Flore JA. 1986. A basic computer program for calculation of photosynthesis, stomatal conductance and related parameters in an open gas exchange system. *Photosynthesis Research* **7,** 269–79.

Ögren E, Öquist G. 1988. Screening for photoihibition of photosynthesis in the field using a portable fluorimeter. In: Lichtenthaler K, ed. *Applications of chlorophyll fluorescence.* Dordrecht: Kluwer Academic Publishers, 165–72.

Quick WP, Chaves MM, Wedler R, David M, Rodrigues ML, Passarino JA, Pereira JS, Adcock MD, Leegood RC, Stitt M. 1992. The effect of water stress on photosynthetic carbon metabolism in four species grown under field conditions. *Plant, Cell and Environment* **15,** 25–35.

Rhodes D. 1987. Metabolic responses to stress. In: Davies DD, ed. *The biochemistry of plants. A comprehensive treatise*, Vol. 12. New York: Academic Press, Inc, 201–41.

Schreiber U, Berry JA. 1977. Heat-induced changes of chlorophyll fluorescence in intact leaves correlated with damage of the photosynthetic apparatus. *Planta* **136,** 233–8.

Tenhunen JD, Pearcy RW, Lange OL. 1987. Diurnal variation in leaf conductance and gas exchange in natural environments. In: Zeiger E, Farquhar GD, Cowan IR, eds. *Stomatal function.* Stanford University Press, 323–51.

Tergazhi WB, Fork DC, Berry JA, Field CB. 1989. Low and high temperature limits to PSII. A survey using trans-Parinaric acid, delayed light emission, and *Fo* chlorophyll fluorescence. *Plant Physiology* **91,** 1494–1500.

Turner NC. 1981. Techniques and experimental approaches for the measurement of plant water status. *Plant and Soil* **58,** 339–66.

Weis E. 1981. Reversible heat inactivation of the Calvin cycle: a possible mechanism of the temperature regulation of photosynthesis. *Planta* **151,** 33–9.

Weis E, Berry JA. 1988. Plants and high temperature stress. *Symposia of the Society for Experimental Biology* **42,** 329–6.

Vadell J, Cabot C, Medrano H. 1992. Diurnal courses of leaf gas exchange rates and related parameters in well-watered and water-stressed plants of subterranean clover growing under field conditions. In: Barber J, Guerrero MG, Medrano H, eds. *Trends in photosynthesis research.* Hampshire: Intercept, 371–81.

van Kooten O, Snell JFH. 1990. The use of chlorophyll fluorescence nomenclature in plant stress physiology. *Photosynthesis Research* **25,** 147–50.

Xiloyannis C, Pezzarossa J, Jorba J, Angelini P. 1988. Effect of soil water content on gas exchange in olive trees. *Advances in Horticultural Science* **2,** 58–63.