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Leaf-level responses of olive trees (*Olea europaea*) to the suspension of irrigation during the winter in an arid region of Argentina

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Abstract

Irrigation is normally suspended during the winter months in the Mediterranean where olive is traditionally cultivated because rainfall is high and reference evapotranspiration (ETo) is low under the fairly cold and cloudy winter conditions in this region. In contrast, the semi-arid and arid provinces of northwestern Argentina receive little, if any, winter precipitation and daily values of ETo are higher than in the Mediterranean. To evaluate the range of winter irrigation strategies currently employed in northwestern Argentina, we assessed leaf-level responses of olive trees to two very contrasting irrigation regimes, no irrigation versus a highly irrigated regime (crop coefficient >1.0), in La Rioja, Argentina. After 15 d, both soil volumetric water content and leaf water potential were substantially lower in the unirrigated treatment. These differences in leaf water potential were consistent through to the end of the 40 d experiment with recovery occurring within a week of rewatering. Only small reductions in leaf gas exchange parameters including transpiration and leaf conductance (g_l) were observed after 40 d without irrigation. Independent of the irrigation level, there was a strong relationship between g_l and atmospheric vapor pressure deficit (VPD), with g_l decreasing in an apparently curvilinear manner as VPD increased. Quantum efficiency of Photosystem II was only reduced by irrigation suspension on 1 d of measurement. These preliminary results suggest that only mild water stress occurred during the winter in trees that were not irrigated for 6–7 weeks in arid La Rioja, Argentina although further research over several years is needed to determine a crop coefficient for the winter months.

Keywords: Olive; Irrigation; Gas exchange; Leaf water potential; Chlorophyll fluorescence; Argentina

1. Introduction

Olive production expanded greatly in Argentina from 30,000 to more than 70,000 ha during the 1990s and the country is now emerging as an important exporter of table olives (SAGPyA, 2004). These new plantations are located at subtropical latitudes under semi-arid or arid climatic conditions that differ markedly from those of the Mediterranean where most olive varieties originated. The agricultural practices of the new plantations include high-tree density (200–600 trees ha^{-1}) and modern technologies such as drip irrigation that were not employed in traditional orchards. Currently, water scheduling is based on studies conducted in the Mediterranean basin or in California (USA) without considering the potential influence of local soil and climatic differences. Because water supply is limited, it is critical that an efficient and sustainable use of this resource be achieved (Boland et al., 2006; Fereres and Evans, 2006).

Olive has long been a successful crop in the Mediterranean region because it can tolerate severe summer drought and still produce an acceptable yield under rain-fed conditions (see review by Connor and Fereres, 2005). To assess this tolerance to water deficit, water potential and leaf gas exchange have been measured under a variety of experimental conditions (e.g., Larcher et al., 1981; Goldhamer et al., 1993; Angelopoulos et al., 1996; Moriana et al., 2002; Dichio et al., 2005). It has been observed that olive can survive very low water potentials (i.e., −5 to −8 MPa) due to osmotic adjustment, changes in cell wall elasticity, and other adaptations (Moriana et al., 2002; Dichio et al., 2003). Decreases in stomatal conductance and net photosynthetic rate under moderate and severe water stress are common in both outdoor pot and field experiments as discussed by several authors (Fernández and Moreno, 1999; Connor and Fereres, 2005). These decreases appear mostly due to stomatal limitations although there are suggestions that photoinhibition

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of Photosystem II may also be important (Angelopoulos et al., 1996). In addition to a stomatal response to soil drying (Giorio et al., 1999), a strong relationship between stomatal conductance and atmospheric vapor pressure deficit (VPD) has been observed under well watered and moderate water stress conditions in some studies (Fernández et al., 1997; Moriana et al., 2002). Thus, soil drying and VPD likely both affect stomatal conductance to varying degrees depending on crop management, climatic conditions, and stress severity.

In the Mediterranean, irrigation is normally suspended during the winter months because fairly cold and cloudy conditions lead to low values of reference evapotranspiration (ETo) and rainfall is high (Civantos, 2001). Crop coefficients (K_c) greater than one have been estimated for Cordoba, Spain, during the winter due in large part to evaporation of rainfall intercepted by foliage (Testi et al., 2006). However, absolute daily values of crop evapotranspiration are very low (1–1.5 mm d^{-1}; Pavel and Fereres, 1998). In contrast, many arid olive growing regions within the provinces of La Rioja and Catamarca in northwestern Argentina receive almost no monthly winter precipitation (<5 mm) and have higher average daily values of ETo (1.6–2.6 mm d^{-1}) due to clear skies, relatively high-midday temperatures (17–23 °C) and moderate daily values of relative humidity (53–64%) (http://www.fao.org/landandwater/aglw/climwat.stm).

These climatic differences with Europe during the winter months along with lack of local knowledge have led to a range of water scheduling strategies from the complete suspension of irrigation to the use of crop coefficients estimated for the Mediterranean during the growing season (K_c = 0.5–1.0). Additionally, insufficient technical information often results in the misapplication of desired irrigation strategies. For example, most of the automated weather stations used in the commercial orchards are situated over bare soil rather than grass and often calculate potential evapotranspiration based on the modified Penman equation (Doorenbos and Pruitt, 1977). Both factors tend to overestimate potential evapotranspiration compared to the Penman–Monteith reference ET method (Allen et al., 1998), which may lead to over-irrigation when using a specific K_c. Misuse of the coefficient of reduction (K_r) associated with percentage crop cover (Fereres and Castel, 1981) is also common.

The primary objective of this study was to assess leaf-level responses of olive trees to the suspension of irrigation during the winter in arid, La Rioja, Argentina. Leaf water potential, gas exchange, and the quantum efficiency of Photosystem II were measured. In addition, crop yield was evaluated the summer following the experiment to evaluate potential longer-term effects.

2. Materials and methods

The experiment was conducted from 20 July to 31 August 2004, using 9-year-old olive trees (*Olea europaea* L. cv. Manzanilla) in a commercial orchard located 10 km east of Aimogasta in the province of La Rioja, Argentina (28°33′S, 66°49′W, 800 m altitude). Tree spacing was 4 m × 8 m with a north–south row orientation and orchard cover was 37% with 3.5–4.0 m tree height. Irrigation was supplied by two drip lines located 0.6 m on either side of the tree row with 2.5 l h^{-1} drip emitters providing a total of 20 l h^{-1} per tree. Two irrigation strategies were employed including an unirrigated treatment where irrigation was suspended and an irrigated treatment where irrigation was applied for 21–23 h each week (approximately 440 l per tree) in 1–3 irrigation events. Although the grower/cooperator intended a K_c of 0.7–0.8 during the winter months in this orchard, the K_c was actually 1.3 for the amount irrigated when the calculations were performed using the Penman–Monteith equation (Allen et al., 1998) and the proper crop cover percentage (37%) was used to determine the coefficient of reduction rather than the 50% cover estimated by the grower. The standard formula for crop evapotranspiration ($ETc = ETo \times K_c \times K_r$) was used. Here, ETo is the Penman–Monteith reference (i.e., grass) evapotranspiration, K_c is the crop coefficient, and K_r is the coefficient of reduction associated with percentage crop cover (Fereres and Castel, 1981). A K_r of 0.74 was used for the 37% cover.

The experimental design was a completely randomized block with four replicates. Each block (i.e., a tree row) contained one plot of each treatment with four adjacent trees. Measurements were performed only on the two central trees within each plot. Meteorological data were collected from an automated weather station (Metos, Pessl Instruments, Austria) located 5 km from the experimental orchard. The station was situated over bare soil and ET values were adjusted to reference conditions over grass using Annex 6 of Allen et al. (1998).

Volumetric soil water content was measured hourly using 20 cm long, dielectric soil probes (ECH$_2$O-20, Decagon Devices Inc., Pullman, WA) connected to an eight-channel data logger (Cavadevices, Buenos Aires). Three probes per treatment were installed 20 cm from the drip emitters and at a soil depth of 20–40 cm. This distance and soil depth were chosen due to the high root length density at a depth of 10–50 cm below the drip line (P.S. Searles, unpublished data). Soil water content was also measured weekly using a soil auger at the same distance from the emitters but including two soil depths (20–40 and 70–90 cm). Soil samples were immediately placed in plastic bags and transported to the laboratory where initial and dried (72 h at 80 °C) weights were recorded. Soil bulk density was approximately 1.2 g cm^{-3}. Field capacity was estimated at the 20–40 cm depth as the soil water content 24 h after irrigation using the dielectric probes, while the permanent wilting point (%) was approximated as the point at which soil water content was no longer changing at 20–40 cm depth in the unirrigated plots.

Leaf water potential was measured using a Scholander-type pressure chamber (Biocontrol, Model 0–8 MPa, Buenos Aires) on short terminal branches with two fully expanded leaf pairs sampled at breast height. These measurements were performed around solar noon and the following pre-dawn every 2 weeks starting with the initiation of the experimental treatments (20 July). There were two subsamples per block from each irrigation treatment for all measurement dates. On the last day (30 August) before rewatering the unirrigated treatment, measurements were also made at mid-morning and mid-afternoon. To assess recovery of leaf water potential, further values were obtained on 6 September, 1 week after rewatering.

Net photosynthetic rate (A), transpiration (E), and leaf conductance (g_l) were measured on mature, fully expanded leaves using a portable gas exchange system (CID Inc., model CI-310, Vancouver, WA) in open-system mode with a flow rate of 0.4 l min^{-1} and leaf temperature within 2–3 °C of ambient air temperature. Photosynthetic photon flux density (PPFD) was always greater than 1300 $\mu mol\ m^{-2}\ s^{-1}$ during the measurements. Leaf area was estimated for each leaf by applying a previously established formula that used measurements of leaf length and width ($r^2 = 0.88$). The gas exchange measurements were performed on the same days as leaf water potential although measurements were not performed on 6 September during the recovery stage. Two to four leaves per block from each irrigation treatment were measured.

A modulated portable fluorometer (Hansatech, FMS2, Norfolk, Great Britain) was used to measure chlorophyll fluorescence on six fully expanded leaves per block from each irrigation treatment at midday and the following pre-dawn. For midday measurements, the quantum efficiency of linear electron transport through Photosystem II (ϕ_{PSII}) was calculated as $(F'_m - F_s)/F'_m$ according to Genty et al. (1989). The F_s represents steady-state fluorescence, and F'_m is the maximum fluorescence under light-adapted conditions. Pre-dawn ratios of variable-to-maximal fluorescence (F_v/F_m) were determined as $(F_m - F_0)/F_m$ where F_0 and F_m are the minimum and maximum fluorescence of dark-adapted leaves, respectively. Measurements were performed on the same dates as leaf gas exchange.

On 4 February 2005, the green fruit of the two central trees of each plot were harvested for table olives to assess the potential effect of suspended winter irrigation on the yield of the following season. For all of the measurements during the study, statistical comparisons of means between the irrigated and unirrigated treatments were performed using a one-way analysis of variance for a completely randomized block design with four replicates in SAS (Statistical Analysis Software, Cary, NC). The non-linear, hyperbolic relationship between g_l and VPD was fitted using GraphPad Prism software (San Diego, CA).

3. Results

3.1. Meteorological conditions and soil water content

Daily air temperature averaged 13 °C during the treatment period (July 20–August 31) with maximum values above 30 °C at the end of August (Fig. 1A). Average potential evapotranspiration using the Penman–Monteith equation (Allen et al., 1998) was 2.72 mm d^{-1} under the non-standard conditions (i.e., over bare soil) of the meteorological station and was 2.52 when adjusted to reference conditions. Peak values of ETo greater than 5 mm d^{-1} were associated with warm, dry air masses during the middle of August and beginning of September (Fig. 1B and C). Daily average ETo values would be 18% higher over the experimental period if calculated using the modified Penman equation (Doorenbos and Pruitt, 1977) (data not shown).

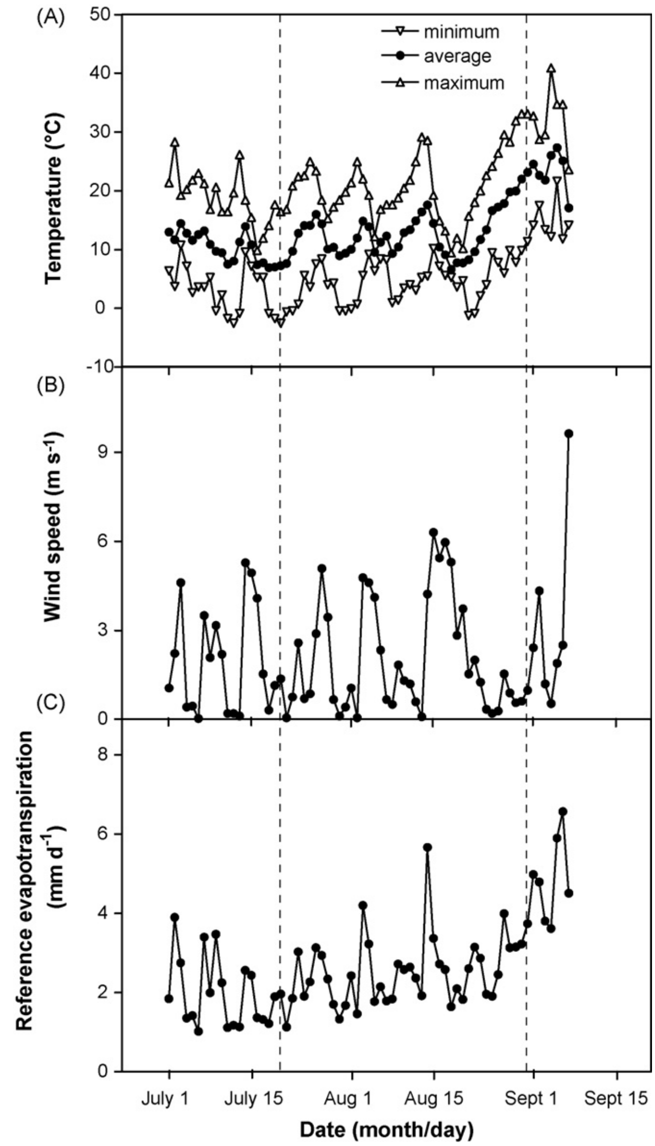

Fig. 1. Temperature, wind speed, and Penman–Monteith reference evapotranspiration (ETo) during the winter months at Aimogasta, La Rioja (Argentina). The dotted lines indicate the beginning and end of irrigation suspension. The last date shown (September 7) coincides with leaf water potential measurements following rewatering of the unirrigated treatment.

On most occasions, dielectric soil probes and extraction by auger provided soil water content values (%) within 1% of each other at the 20–40 cm soil depth (Fig. 2). Any observed differences (>1%) between the methods may have resulted from soil heterogeneity or micro-topographic anomalies around the drip emitters. In the irrigated plots ($K_c = 1.3$), soil moisture at 20–40 cm depth remained near the estimated field capacity (i.e., 12%) throughout the experiment. A slight peak in soil moisture content in the unirrigated treatment occurred at the start of irrigation suspension due to leaks in the irrigation line, but was quickly rectified. Thereafter, the soil water content in this treatment gradually decreased to approach the estimated

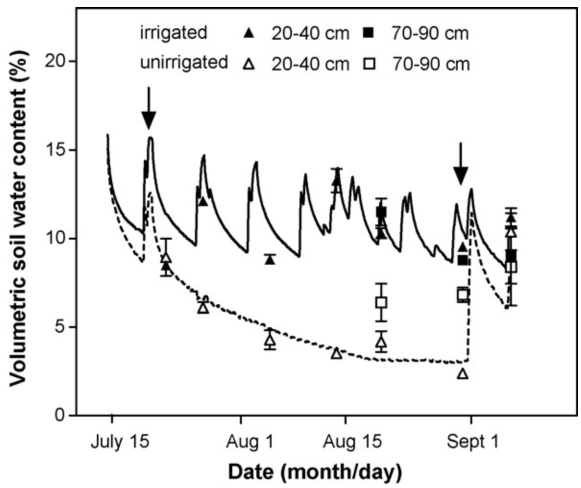

Fig. 2. Volumetric soil water content (%) under irrigated and unirrigated conditions at two soil depths (20–40 and 70–90 cm). Solid and dashed lines indicate the irrigated and unirrigated treatments, respectively, as measured with dielectric soil probes. Values for the 70–90 cm soil depth were only obtained from soil cores during the latter stages of the experiment. Arrows indicate the beginning and end of irrigation suspension. $N = 3$ replicates per irrigation level with means ± S.E.

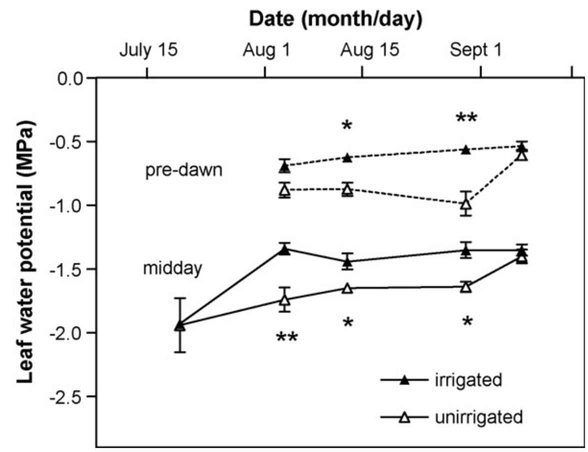

Fig. 3. Pre-dawn and midday leaf water potentials under irrigated and unirrigated conditions. $N = 4$ replicates per irrigation level with means ± S.E. $^{*}P < 0.05$, $^{**}P < 0.01$.

permanent wilting point (3%) 1 month after irrigation suspension. The difference between treatments was smaller at the 70–90 cm depth where the irrigated treatment remained near field capacity (12%) while the unirrigated treatment decreased to only 6–7% after 40 d without irrigation (Fig. 2). One week after the single irrigation event that reinitiated irrigation, soil water content was similar between irrigated and unirrigated plots at both measured depths.

3.2. Leaf water status

Midday leaf water potentials were similar in the irrigated and unirrigated plots on July 20 just prior to the suspension of irrigation (Fig. 3). Some increase in the midday values for the irrigated plots occurred between July 20 and early August, but the values remained steady at about −1.4 MPa throughout the rest of the experiment. Midday values of the unirrigated treatment were 30% lower than under irrigated conditions by early August after 15 d of treatment ($P < 0.05$) and remained around −1.7 MPa until rewatering at the end of August. Similarly, pre-dawn leaf water potentials were significantly lower than the irrigated values after 24 d ($P < 0.05$) and differences between treatments continued to the end of irrigation suspension. Before reinitiating irrigation, the pre-dawn values of the irrigated and unirrigated treatments were −0.6 and −1.0 MPa, respectively. Once irrigation was reestablished, both midday and pre-dawn leaf water potentials of the unirrigated treatment increased within 7 d to values similar to those of the irrigated treatment.

3.3. Leaf gas exchange and chlorophyll fluorescence

Net photosynthetic rate (A), transpiration (E), and leaf conductance (g_l) were similar between irrigated and unirrigated trees during most of the experiment ($P > 0.05$; Table 1). Midday A was around 15 μmol m^{-2} s^{-1} under ambient conditions during the first three measurement dates and decreased to 7.5 μmol m^{-2} s^{-1} on the last date (August 30) likely due to conditions of elevated temperature (28–33 °C) and low humidity (15–20%). The only indication of a decrease in leaf gas exchange due to irrigation suspension occurred on August 30 during mid-afternoon when g_l and E in the unirrigated trees were significantly lower than in irrigated trees by 31 and 33%, respectively ($P < 0.05$; Fig. 4B and C). The values of A were also lower on a percentage basis (44%), but a significant difference could not be detected ($P = 0.12$). No

Table 1
Midday leaf gas exchange parameters and quantum efficiency of Photosystem II under irrigated (I) and unirrigated (UI) conditions

Date	Irrigation treatment	A (μmol m^{-2} s^{-1})	E (mmol m^{-2} s^{-1})	g_l (mmol m^{-2} s^{-1})	WUE (A/E)	Φ_{PSII} $((F'_m - F'_0)/F'_m$
July 20	I	13.9 ± 0.9	2.4 ± 0.2	117 ± 11	5.8 ± 0.1	0.26 ± 0.03
	UI	16.6 ± 2.9	2.4 ± 0.5	128 ± 37	5.8 ± 0.3	0.23 ± 0.03
August 4	I	16.9 ± 0.7	2.5 ± 0.2	159 ± 16	6.8 ± 0.6	0.31 ± 0.01
	UI	14.6 ± 1.4	2.8 ± 0.2	186 ± 41	5.3 ± 0.2*	0.27 ± 0.03
August 13	I	14.9 ± 1.5	3.0 ± 0.3	117 ± 18	4.9 ± 0.3	0.30 ± 0.02
	UI	14.4 ± 1.4	2.8 ± 0.4	100 ± 10	5.4 ± 0.2	0.21 ± 0.02*
August 30	I	8.0 ± 1.2	3.6 ± 0.4	90 ± 4.2	2.2 ± 0.3	0.30 ± 0.02
	UI	7.0 ± 1.3	3.5 ± 0.4	78 ± 10	2.4 ± 0.4	0.27 ± 0.02

$N = 4$ replicates per irrigation level with means ± S.E.
* Significant differences at $P < 0.05$.

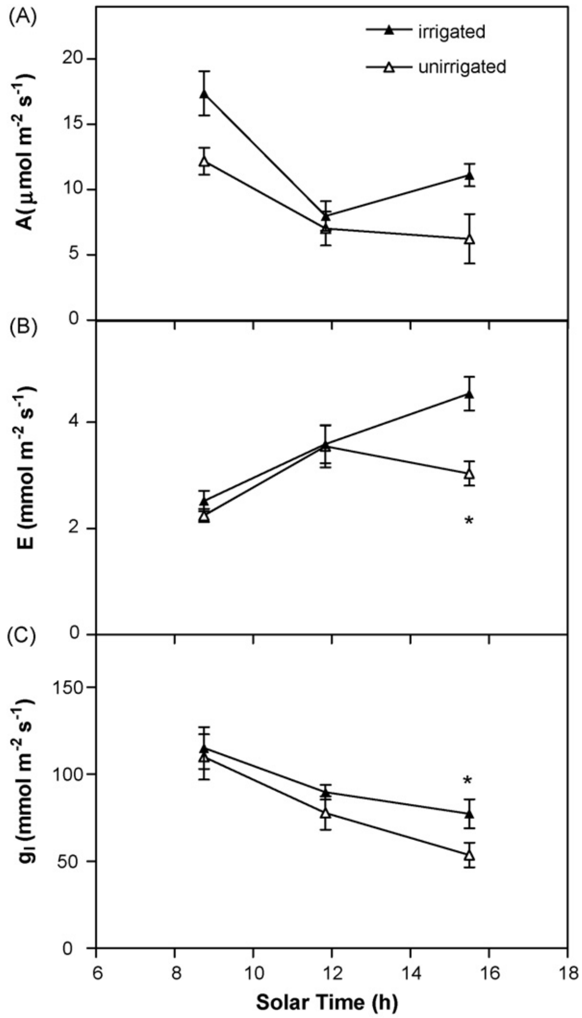

Fig. 4. Leaf gas exchange parameters including net photosynthetic rate (A), transpiration (E), and leaf conductance (g_l) under irrigated and unirrigated conditions. $N = 4$ replicates per irrigation level with means ± S.E. $^*P < 0.05$.

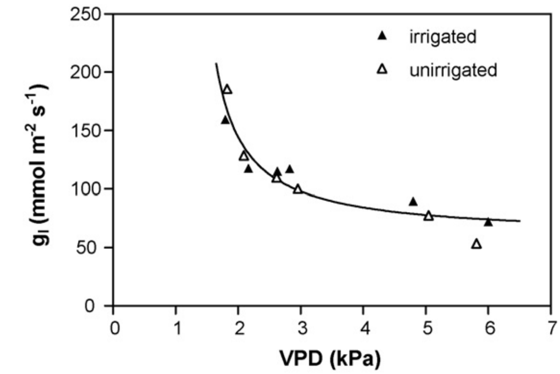

Fig. 5. Leaf conductance (g_l) vs. atmospheric vapor pressure deficit (VPD) under irrigated and unirrigated conditions. Midday mean values from both treatments were pooled for all measurement dates along with average morning and afternoon values from August 30 and fitted to the same hyperbolic function ($r^2 = 0.94$).

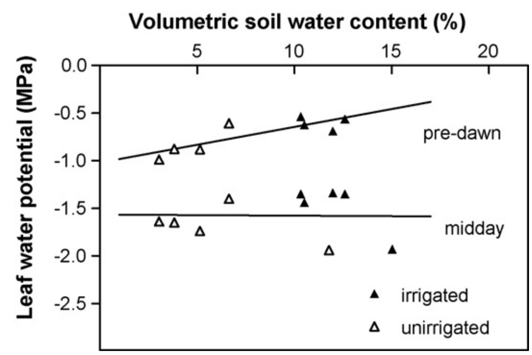

Fig. 6. Pre-dawn and midday leaf water potential vs. volumetric soil water content (%) under irrigated and unirrigated conditions. Mean values of pre-dawn leaf water potential for both treatments were pooled to obtain a single regression line at pre-dawn ($r^2 = 0.70$; $P < 0.01$). The same was done for midday.

consistent differences in water use efficiency (WUE) were apparent, although WUE was lower under the unirrigated than the irrigated treatment on one measurement date (Table 1).

Quantum efficiency of Photosystem II (Φ_{PSII}) measured at midday under high PPFD was significantly lower under unirrigated conditions on August 13 ($P < 0.05$), but not on other days of measurement (Table 1). Pre-dawn measurements of F_v/F_m did not show any differences and values near 0.8 were recorded indicating no chronic photoinhibition under either of the irrigation conditions (data not shown).

Leaf conductance showed a negative curvilinear relationship with atmospheric VPD (Fig. 5) when analyzing midday data from all measurement dates along with morning and afternoon values from August 30, but did not show any correlation with leaf water potential or soil water content (data not shown). The relationship between g_l and VPD indicated a pronounced decrease of g_l for VPDs between 1.5 and 3 kPa, while further increases in VPD were only associated with minimum changes in g_l. The r^2 value was 0.94 when pooling data from the two irrigation treatments. Lastly, pre-dawn leaf water potential displayed a positive linear relationship with volumetric soil water content ($r^2 = 0.70$; $P < 0.01$), but midday leaf water potential did not (Fig. 6).

3.4. Yield per tree

When the crop was harvested for green table olives on February 4, 2005 during the following summer, the yield per tree was not significantly different between the unirrigated (16.5 ± 2.3 kg tree^{-1}) and irrigated (21.1 ± 2.9 kg tree^{-1}) treatments ($P = 0.33$). Although the yield in the unirrigated trees was 20% less than the irrigated trees, it is difficult to evaluate whether this is related to variation among trees or whether suspension of irrigation during the winter months actually leads to somewhat lower yields.

4. Discussion

The suspension of irrigation during the winter is a common agricultural practice in olive plantations under Mediterranean climate conditions, but irrigation strategies are wide ranging in arid Argentina where evapotranspiration is higher and rainfall is minimal. Without irrigating for 6–7 weeks in a sandy soil in La Rioja (Argentina), volumetric soil water content at 20–40 cm depth decreased to less than 20% of available soil water after only 15 d although available soil water remained greater than 25% at the 70–90 cm depth even after 40 d without irrigation. This difference presumably reflects greater root water uptake at 20–40 cm due to much higher root length density at this depth than at 70–90 cm (unpublished data). The decrease in soil water content was sufficient after 15 d to reduce pre-dawn and midday leaf water potential by about 30% with respect to the irrigated treatment. Nevertheless, leaf water potentials without irrigation were not lower than −1.0 MPa at pre-dawn and −1.9 MPa at midday indicating that the trees were not severely stressed. It might be asserted that the high-irrigation level ($K_c > 1$) used by the grower/cooperator may have caused some decrease in physiological leaf function. However, the pre-dawn leaf water potentials (−0.55 MPa) during the latter half of the experiment at this K_c were very similar to those reported by Fernández et al. (1997) under well irrigated conditions (−0.46 MPa) during the spring and summer in Spain, and the sandy (80–90%) texture of the soil likely facilitated drainage.

A more direct comparison of our winter leaf water potentials under arid conditions in Argentina to other studies is difficult because winter rainfall in the Mediterranean generally precludes the need for irrigation studies. In one study, Pavel and Fereres (1998) determined that soil temperatures of 4–6 °C during the winter in Spain lowered midday leaf water potentials sharply from −1 to −3.5 MPa relative to a control of 9–12 °C even when soil moisture was not limiting. In the present study, however, soil temperature at 30 cm depth did not fall below 10 °C. During the spring under a Mediterranean climate, 1 month without irrigation is often not sufficient to reduce leaf or stem water potential compared to irrigated controls (Giorio et al., 1999; Moriana and Fereres, 2002). Here, the relatively fast response of leaf water potential after only 15 d may be related to the low available soil water in these coarse-textured soils and the restricted soil volume explored by roots due to year-round drip irrigation and low precipitation. In contrast, trees in many olive producing regions in Spain and Italy have access to greater available soil water due to finer-textured soils (e.g., Giorio et al., 1999; Moriana and Fereres, 2002) and soil volume explored by roots is likely greater with increasing precipitation.

In many studies of olive photosynthesis, large reductions in *A* are often associated with large differences (>1 MPa) in pre-dawn or midday leaf or stem water potential between irrigation treatments (Angelopoulos et al., 1996; Fernández et al., 1997; Giorio et al., 1999; Moriana et al., 2002). With smaller differences in stem water potential (0.6 MPa), reductions in *A* of only 1–2 μmol CO_2 m^{-2} s^{-1} could be detected towards the end of a 1 month long drought in mid-summer in Spain (Moriana and Fereres, 2002). In our study, differences in leaf water potential never exceeded 0.5 MPa and statistically significant reductions in *A* were not detected possibly due to the low number of replicates ($n = 4$) employed. However, there was some tendency for a decrease in gas exchange parameters due to irrigation suspension for the last measurement date under unseasonably warm temperatures (33 °C) and high VPD (>4 kPa). Osmotic adjustment of leaves and roots may contribute to the ability of olive to maintain photosynthesis under mild water stress (Dichio et al., 2005).

Irrespective of the irrigation regime, a strong curvilinear relationship between leaf conductance (g_l) and VPD was apparent with g_l decreasing sharply between a VPD of 1.5–3 kPa and considerably less at greater values. Similarly, under well watered and moderate water stress, Fernández et al. (1997) proposed that g_l decreased with increasing VPD to 3.5 kPa and was then relatively insensitive to higher values. Moriana et al. (2002) tended to show a negative linear relationship between g_l and VPD over a wide range of VPD values under mild water stress. In contrast, Giorio et al. (1999) found a good correlation between g_l and soil water content and between g_l and midday leaf water potential, but not with VPD. No relationship between g_l and these other variables was found in our study, which suggests that VPD was the most important driving variable for g_l under our experimental conditions in arid Argentina. Lastly, we found a positive correlation between pre-dawn leaf water potential and volumetric soil water content. This linear relation is similar to the one observed by Tognetti et al. (2004) although Moriana et al. (2002) found an exponential response with available soil water and Fernández et al. (1997) did not observe a significant relationship.

In the past decade, large commercial olive orchards (>100 ha) have become common in arid, subtropical Argentina. This expansion has lead to the rapid incorporation of drip irrigation and other modern technologies. However, a local knowledge base for crop management is only starting to develop. In this current study, the normal irrigation employed by the grower/cooperator during these winter months was found to be equivalent to a K_c of 1.3 when the Penman–Monteith ETo equation (Allen et al., 1998) was employed and percentage crop cover was accurately assessed. Crop coefficient values greater than one have been estimated for Spain during the winter due to high evaporation of rainfall from leaf surfaces (Testi et al., 2006), but irrigation is normally suspended during the winter due to the high precipitation. The preliminary results presented here indicate that only mild water stress developed in trees that were unirrigated for almost 7 weeks during the winter without rainfall, and that recovery occurred rapidly upon irrigation. Thus, a fairly low K_c appears appropriate for this region during the winter although further research over several years is necessary using intermediate irrigation regimes or sap flow measurements to estimate K_c for the winter months.

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