Diurnal variations in water relations of deficit irrigated lemon trees during fruit growth period

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Abstract

Field-grown lemon trees [*Citrus limon* (L.) Burm. fil. cv. Fino] were subjected to different drip irrigation treatments: a control treatment, irrigated daily above crop water requirements in order to obtain non-limiting soil water conditions and two deficit irrigation treatments, reducing the water applied according to the maximum daily trunk shrinkage (MDS) signal intensity (actual MDS/control treatment MDS) threshold values of 1.25 (T1 treatment) and 1.35 (T2 treatment), which induced two different drought stress levels. Daily variations in leaf (Ψ_{leaf}) and stem (Ψ_{stem}) water potentials, leaf conductance, net photosynthesis, sap flow (SF) and trunk diameter fluctuations were studied on four occasions during the lemon fruit growth period. Ψ_{stem} and Ψ_{leaf} revealed a diurnal pattern in response to changes in evaporative demand of the atmosphere. Both water potentials decreased in response to water deficits, which were more pronounced in the T2 treatment. Ψ_{stem} was seen to be a better plant water status indicator than Ψ_{leaf}. The difference between the two values of Ψ ($\Psi_{stem}-\Psi_{leaf} = \Delta\Psi$) was closely correlated with sap flow, making it a suitable measure of leaf transpiration. Using the slope of this relationship, the canopy hydraulic conductance (K_C) was estimated. When other continuously recorded plant-based indicators are not accessible, the concurrent measurement of leaf and stem water potentials at midday, which are relatively inexpensive to measure and user-friendly, act as sufficiently good indicators of the plant water status in field grown Fino lemon trees.

Additional key words: *Citrus limon;* leaf conductance; leaf water potential; maximum daily trunk shrinkage; net photosynthesis; sap flow; stem water potential.

Introduction

The increasing demand for water and the scarcity of water sources are creating pressure to improve water use productivity in agriculture (Fereres & Soriano, 2007). The need to improve our understanding of the dynamics of water use by plants is well recognized in order to develop efficient irrigation practices (Fernández *et al.,* 2008). To this end great efforts have been made to identify representative indicators of plant water status. In citrus and fruit trees leaf water potential and its components, as well as leaf conductance (g_l), are good water status indicators (Harrison *et al.,* 1989; McCutchan & Shackel, 1992; Domingo *et al.,* 1996; Ferreira *et al.,* 1997; Girona *et al.,* 2006; Ruiz-Sánchez *et al.,* 2007). However, more recently, new methods for measuring and recording the changes in the water status in woody plants such as stem psychrometers (Yakushiji *et al*., 1996), stem TDR probes (Nadler & Tyree, 2008; Nadler *et al.,* 2008), leaf clamps (Zimmermann *et al.,* 2008; Fernández *et al.,* 2011) and ultrasonics (Álvarez-Arenas *et al.,* 2009; Sancho-Knapik *et al.,* 2010), among others, have been developed.

Specifically, in citrus trees, continuous indicators such as sap flow and maximum daily shrinkage of the trunk (MDS), that is, the difference between the maximum diameter of the trunk in the early hours of the

Abbreviations used: Ψ_{leaf} (leaf water potential); Ψ_{stem} (stem water potential); $\Delta\Psi$ (leaf and stem water potential difference); ETc (crop evapotranspiration); ET_0 (crop reference evapotranspiration); g_l (leaf conductance); K_C (canopy hydraulic conductance); MDS (maximum daily trunk shrinkage); P_n (net photosynthesis); SF (sap flow); VPD (air vapour pressure deficit).

morning and the minimum trunk diameter in the early evening, have proven to be the most sensitive of the continuously measured plant-based water stress indicators (Ginestar & Castel, 1996; Ortuño *et al.,* 2006).

Such indicators can be very useful for irrigation scheduling (Goldhamer & Fereres, 2001; Goldhamer *et al.,* 2003) and, under deficit irrigation conditions, the continuous control of the plant water status may be crucial for preventing a moderate, potentially beneficial, water stress from becoming too severe, which would result in a reduction of yield (Domingo *et al.,* 1996; Johnson & Handley, 2000; Ortuño *et al.,* 2009b).

Water transport from the plant stem to the sites of evaporation in the leaf is critical for maintaining the leaf water balance and for allowing stomata to stay open, resulting in carbon capture (Brodribb & Holbrook, 2003; Oyarzún *et al.,* 2010). However, water transport in the leaf is vulnerable to water stress, leading to reductions in total hydraulic conductance of the leaf canopy (K_C). The linear relationship between leaf and stem water potential difference and transpiration permits canopy hydraulic conductance to be estimated (Schulze *et al.*, 1985; Alarcón *et al.*, 2000, 2003).

Irrigation scheduling based on the signal intensity of MDS (MDS SI) has been carried out in adult lemon trees (García-Orellana *et al.,* 2007) following the model suggested by Goldhamer & Fereres (2001). Ortuño *et al.* (2009a) indicated that by maintaining MDS SI values close to unity, and avoiding drainage, the irrigation water applied can be considered as an estimate of actual water requirements of lemon trees.

Apart from the above mentioned studies, lemon plant water relations research papers point to the absence of leaf osmotic adjustment and an enhancement of cell wall elasticity in response to water deficit (Ruiz Sánchez *et al.,* 1997). But few studies have examined daily variations in the water relations of lemon plants irrigated on the basis of their MDS SI values. For this reason, the aim of this study was to evaluate the response of the main indicators of plant water status, on a diurnal basis, in deficit irrigated field grown adult lemon trees during the fruit growth period. The results also lead us to propose the difference between stem and leaf water potential values as an estimate of leaf transpiration.

Material and methods

The study was performed from June to November 2005 at the CEBAS-CSIC experimental station in Murcia (Spain) (38° 6' 14" N, 1° 1' 59" W) with 31-year-old lemon trees [*Citrus limon* (L.) Burm. fil.] cv. Fino grafted on sour orange (*C. aurantium* L.) rootstocks. Tree spacing was 6 m × 6 m, with an average ground cover of about 65%. The soil was a Paralithic mollic-calciorthid, and the profile showed only a slight differentiation between horizons (an ochric epipedon on a C horizon). The soil was very stony (43%, w/w), with a clay loam texture. Available soil water and bulk density were 106 mm m^{-1} and 1.5 mg m^{-3}, respectively. The volumetric soil water content at saturation and field capacity were 18.9 and 10.6%, respectively. Saturated hydraulic conductivity was 80 mm h^{-1}. In the main root zone (upper 0.6 m), analytical data showed: 460 g kg^{-1} lime content, 0.25 g kg^{-1} available potassium, 35 mg kg^{-1} available phosphorus and 20.5 g kg^{-1} organic matter content.

From 12 April 2005 (day of year (DOY) 102) plants were irrigated daily above the estimated crop evapotranspiration level (140% ETc) in order to obtain non-limiting soil water conditions. Plant irrigation requirements (ETc) were determined according to the reference evapotranspiration (ET$_0$), calculated using the Penman-Monteith equation (Allen *et al.,* 1998), a crop factor based on the time of the year and the percent of ground area shaded by the tree canopy (Domingo *et al.,* 1996).

From 15 May (DOY 135) irrigation in T1 and T2 treatments was progressively reduced to achieve maximum daily trunk shrinkage signal intensity (MDS SI) (actual MDS/control treatment MDS) threshold values below, but in the vicinity, of 1.25 (T1 treatment) and 1.35 (T2 treatment). In both treatments irrigation scheduling began to maintain MDS signal intensity at around these threshold values on 16 June (DOY 167). These MDS SI threshold values (1.25 and 1.35) were adopted because, according to Ortuño *et al.* (2006), they induced two different water stress levels.

The irrigation protocol followed was that proposed by Goldhamer & Fereres (2001). The irrigation rate was decreased by 10% when MDS SI on at least two of three consecutive days did not exceed the MDS SI threshold value. The irrigation rate was increased by 10% when the MDS SI on at least two of three consecutive days exceeded the threshold value.

For all three treatments, irrigation was carried out during the night using a drip irrigation system with one lateral pipe per trees row. T1 and T2 treatments were provided by six emitters (each delivering 4 L h^{-1}) per plant, and control (T0) plants were irrigated by twelve emitters (six delivering 2 L h^{-1} each and six delivering

4 L h^{-1} each) per plant. Total water amounts applied to each treatment were measured with in-line water meters.

Micrometeorological (30 min) data were collected by an automatic weather station located some 100 m from the experimental site. The soil volumetric water content (θ_v) of the top 150 mm of the soil profile was measured with a time domain reflectometer (Model 1502C, Tektronix Inc., OR, USA). The θ_v of the soil from 0.2 m down to a maximum depth of 0.8 m was measured every 0.1 m with a neutron probe (Model 4300, Troxler Electronic Laboratories, NC, USA), in access tubes installed 1.0 m away from the tree trunks and beside the emitter. Measurements (four replications per treatment) were taken in the morning hours (8:00-10:00 am).

Leaf water potential (Ψ_{leaf}), stem water potential (Ψ_{stem}), leaf conductance (g_l) and net photosynthesis (P_n) were measured from predawn to sunset at 2-hourly intervals on cloudless days: 30th June (DOY 181), 4th August (DOY 216), 15th September (DOY 258) and 27th October (DOY 300). Ψ_{leaf} and Ψ_{stem} were measured in two mature leaves per tree and four trees per treatment, using a pressure chamber (Soil Moisture Equip. Corp, Santa Barbara, CA, USA model 3000), following the recommendations of Turner (1988). Ψ_{leaf} leaves were located on the south facing side, from the middle third of the tree, whereas leaves for Ψ_{stem} were taken from close to the tree trunk on the north facing side and were covered with aluminium foil for at least 2 h before measurements. Leaf conductance (g_l) and net photosynthesis (P_n) were measured on a similar number and type of leaves as used for Ψ_{leaf}, using a field-portable and closed gas exchange system (LI-6400, LI-COR., Lincoln, NE, USA) equipped with a transparent 6 cm^2 leaf chamber.

The micrometric trunk diameter fluctuations were measured throughout the experimental period in four trees per treatment, using a set of linear variable displacement transducers (LVDT) (model DF $\pm$ 2.5 mm, accuracy $\pm$ 10 μm, Solartron Metrology, Bognor Regis, UK) attached to the trunk about 0.5 m from the soil with a special bracket made of Invar and aluminium. Sensors were located on the north side of each tree and were covered with silver thermo protected foil to prevent heating and wetting of the device. Measurements were taken every 10 s and the datalogger (model CR10X with AM 416 multiplexer, Campbell Scientific, Logan, UT, USA) was programmed to report 30 min means. Maximum daily trunk shrinkage (MDS) was computed as the difference between the maximum diameter of

the trunk in the early hours of the morning and the minimum trunk diameter in the early evening.

Sap flow (SF) was measured in the control treatment using the compensation heat-pulse technique (Swanson & Whitfield, 1981) from June to September in the same trees as used for the MDS measurements. One set of heat-pulse probes was located above the LVDT sensors on each tree. Each set consisted of a heater needle of 1.8 mm diameter and two temperature probes also of 1.8 mm diameter installed in parallel holes drilled radially in the tree trunks. Each heat-pulse probe had four thermocouple sensors to monitor the sap velocity profile over a radial depth. Sap velocity was measured following the procedure of Green & Clothier (1988), using the theoretical calibrations of Swanson & Whitfield (1981) to account for the probe-induced effects of wounding. The temperature signals and the corresponding heat pulse velocities were recorded at 30 min intervals using heat-pulse instrumentation (MITRA 3.1, Polytechnic University of Cartagena, Spain) controlled by a data logger (CR10, Campbell Scientific Ltd., Logan, UT, USA).

Canopy hydraulic conductance (K_C) was determined from the Ohm's Law electrical analogue: $K_C = T \cdot \Delta\Psi^{-1}$, where T is the plant transpiration (mmol s^{-1}), as measured by sap flow technique, and $\Delta\Psi$ is the water potential gradient (MPa) across the stem-leaf pathway (Ψ_{stem}-Ψ_{leaf}).

The design of the experiment was completely randomized with four replications, each replication consisting of three adjacent tree rows, each with five trees. Measurements were taken in the inner tree of the central row of each replicate, and the other trees served as border trees. Relationships between parameters were fitted to linear regressions using SPSS v. 17.0 software (SPSS, 2002).

Results

During the period of measurements, which coincided with stage II of lemon fruit growth, total ETc was 347 mm and ET$_0$ 533 mm, the daily ET$_0$ values remaining high until late July (DOY 210) and decreasing gradually thereafter. Rainfall, which was low (57 mm), occurred during early September and mid-October (DOY 229-300). The irrigation water applied was 480, 286 and 148 mm for T0, T1 and T2 treatments, respectively.

Deficit irrigation in T1 and T2 treatments decreased the soil (Fig. 1) and plant (Fig. 2) water status. Volumetric soil water content values in the control treat-
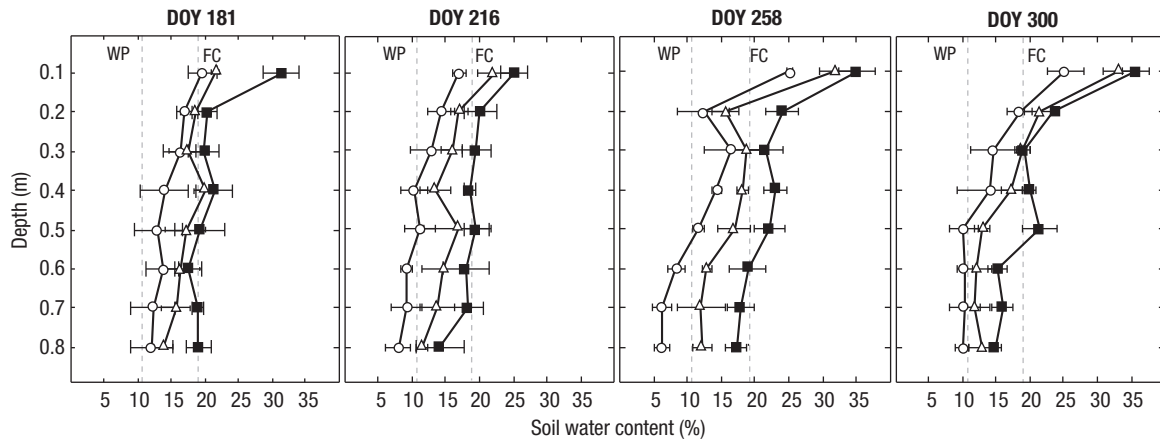
Figure 1. Volumetric water content in the soil profile (0-0.8 m) in the different irrigation treatments: T0 (■), T1 (Δ) and T2 (○) at four times during the fruit growing season. Vertical lines represent permanent wilting point (WP) and field capacity (FC). Horizontal bars are ± S.E. of the mean (not shown when smaller than the symbols) (n = 4).
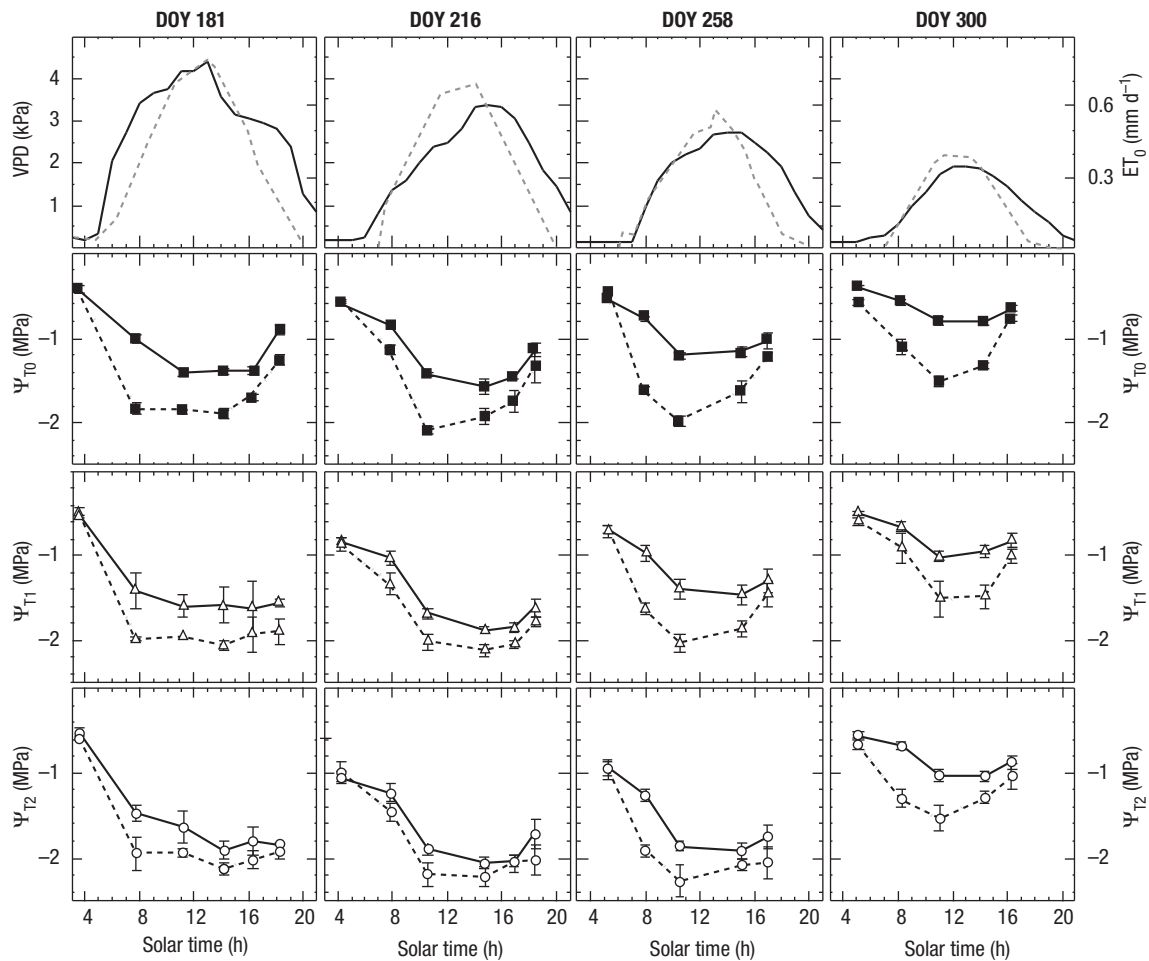
Figure 2. Diurnal course of vapour pressure deficit (VPD, solid line), crop reference evapotranspiration (ET_0, dotted line), stem water potential (Ψ_{stem}, solid line) and leaf water potential (Ψ_{leaf}, dotted line) in the different irrigation treatments: T0 (Ψ_{T0}, ■), T1 (Ψ_{T1}, Δ) and T2 (Ψ_{T2}, ○) at four times during the fruit growing season. Vertical bars are ± S.E. of the mean (not shown when smaller than the symbols) (n = 4).

ment were slightly above field capacity throughout the soil profile, whereas those in the deficit irrigated treatments were lower, especially in T2, in which the soil water content was close to wilting point below a depth of 0.5 m during most of the experimental period (Fig. 1). Higher values were observed in the October sampling date due to the rainfall.

The diurnal time course of both water potentials, leaf (Ψ_{leaf}) and stem (Ψ_{stem}), at the four measuring times, showed similar behaviour, with maximum values reached at predawn, followed by a sharp decrease in the morning, regardless of the irrigation treatment (Fig. 2), while minimum values were reached around solar noon. In deficit irrigated trees, water potentials (Ψ_{leaf} and Ψ_{stem}) were lower than the control values on all the measurement dates, although the differences observed in October (DOY 300) were less pronounced (Fig. 2).

The greatest differences in leaf water potentials between treatments were observed before dawn, while differences in stem water potentials were greatest at noon (Fig. 2). It is important to note that differences between control and deficit treatments were higher for Ψ_{stem} values than those of Ψ_{leaf} (Fig. 2). In addition, higher correlation coefficients were found in the regression Ψ_{leaf} *vs.* VPD ($r = 0.7537^{***}$) than that for Ψ_{stem} *vs.* VPD ($r = 0.6878^{**}$) (data not shown).

Despite the low values, the daily dynamics of leaf conductance (g_l) pointed to a maximum opening of stomata early in the morning in all the irrigation treatments, followed by a gradual decline as radiation increased, with a plateau from midday to sunset (Fig. 3). Net photosynthesis (P_n) followed a similar pattern to that of g_l, with maximum values early in the morning, the values increasing from June to October, when maximum values of P_n were observed (Fig. 3). Deficit irrigation induced slight differences in the values of gas exchange parameters (g_l and P_n) with respect to the control treatment values (Fig. 3). The high evaporative demand conditions recorded in June, with maximum values of VPD and ET_0 (Fig. 2), induced the lowest rates of gas exchange parameters of the experimental period (Fig. 3).

Midday water potential (leaf or stem) and leaf conductance values were weakly correlated (data not shown); however, when minimum water potentials (at midday) and maximum g_l (occurring in the early hours of the morning) were considered, high and significant correlation coefficients were found ($r = 0.89^{***}$ and 0.93^{***}, for Ψ_{leaf} and Ψ_{stem}, respectively) (data not shown).

Considering each treatment separately, the differen-
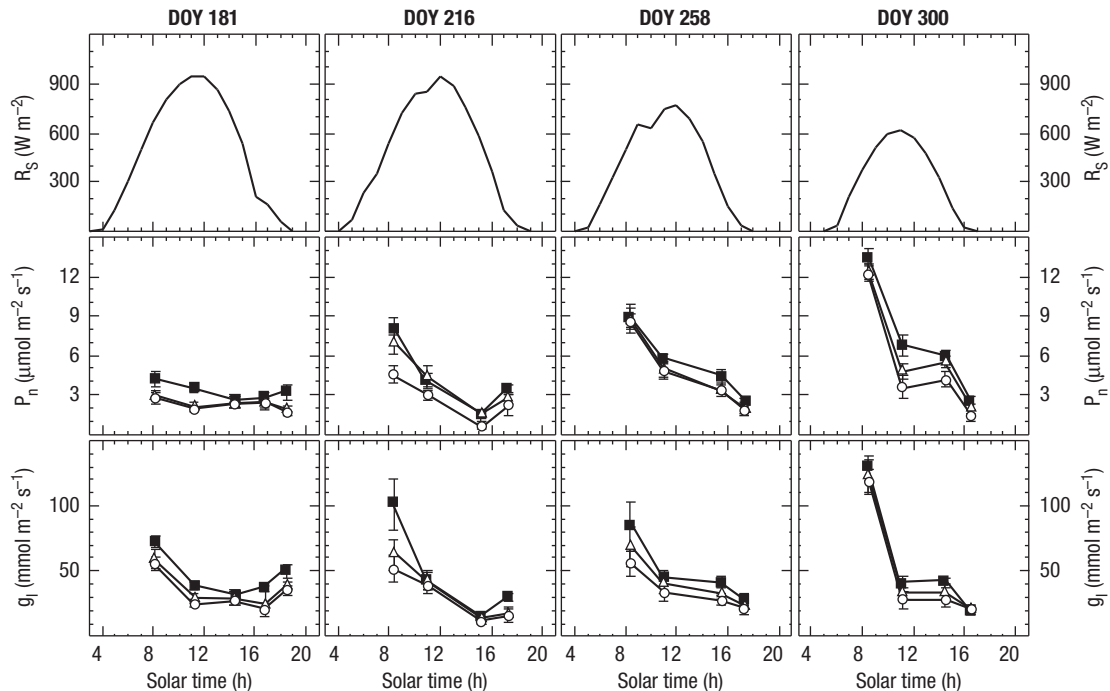
Figure 3. Diurnal course of solar radiation (R_s), net photosynthesis (P_n) and leaf conductance (g_l) in the different irrigation treatments: T0 (■), T1 (△) and T2 (○) at four times during the fruit growing season. Vertical bars are ± S.E. of the mean (not shown when smaller than the symbols) (n = 4).
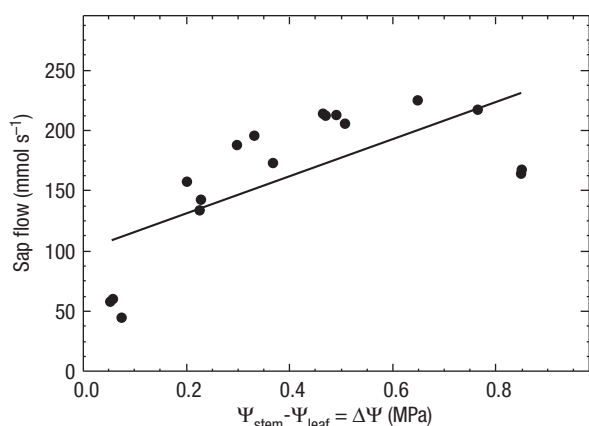
Figure 4. Relationship between hourly sap flow (SF) and the difference between stem and leaf water potentials (Ψ_{stem}-Ψ_{leaf} = $\Delta\Psi$) in control treatment during the fruit growing season. Each point is the mean of four replications. Regression equation of fitted line: SF = 99.12 + 155.54 $\Delta\Psi$, r = 0.69**.

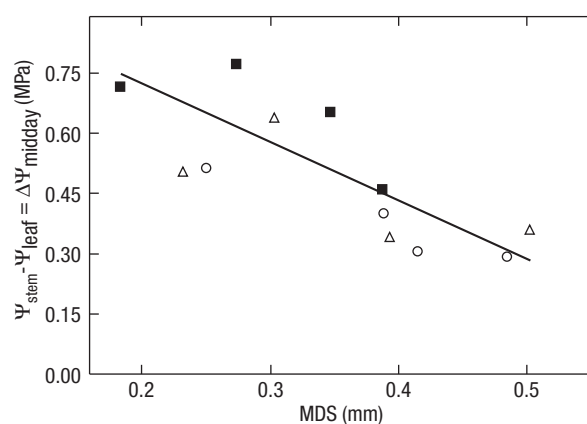**Figure 5.** Relationship between the difference between stem and leaf water potentials (Ψ_{stem}-Ψ_{leaf} = $\Delta\Psi$) at midday and maximum daily trunk shrinkage (MDS) in the different irrigation treatments: T0 (■), T1 (△) and T2 (○) during the fruit growing season. Each point is the mean of four replications. Regression equation of fitted line: $\Delta\Psi_{midday}$ = 0.59 − 0.47 MDS, r = 0.83***.

ces between the two water potential values (Ψ_{stem}-Ψ_{leaf} = $\Delta\Psi$) were minimal, and in some cases nil, at dawn and in the evening hours, with maximum differences being observed at midday, coinciding with the highest evaporative demand of the atmosphere (Fig. 2). In addition, $\Delta\Psi$ values were higher in the control treatment than in either deficit treatment during most of the day (Fig. 2).

Linear regression between sap flow and the corresponding gradient in water potentials measured in trees from the control treatment (Fig. 4) allows the total hydraulic conductance of the leaf canopy (K_C) to be estimated. Similar K_C values were registered for the different diurnal cycles (data not shown), so that the data were mixed in Fig. 4. Although with a slight degree of hysteresis, a significant linear correlation coefficient was found (r = 0.69**), yielding a value of 155 mmol MPa^{-1} s^{-1}.

On the days on which $\Delta\Psi$ was measured a clear relationship between values of $\Delta\Psi$ at midday, and MDS was evident (Fig. 5). The relationship indicated that higher water deficit levels, reflected by lower $\Delta\Psi$ values in the deficit irrigated treatments, were associated with higher MDS values (Fig. 5).

Discussion

Both leaf and stem water potentials followed a circadian rhythm parallel to the evaporative demand of the atmosphere (VPD and ET_0 values, Fig. 2) on all measurement dates and independently of the irrigation treatment, which is typical of most cultivated plants

(Tenhunen *et al.,* 1982; Torrecillas *et al.,* 1988; Sánchez-Blanco *et al.,* 1990; Ruiz-Sánchez *et al.,* 2007). The higher correlation coefficients found in the regression Ψ_{leaf} *vs.* VPD compared with Ψ_{stem} *vs.* VPD pointed to the greater dependence of Ψ_{leaf} on the prevailing weather conditions. These results coincide with those of Remorini & Massai (2003) in peach [*Prunus persica* (L.) Batch] trees, who suggested that the Ψ_{stem} value at noon is a better indicator of plant water status than Ψ_{leaf}. In this sense, it must be indicated that both Ψ_{stem} and Ψ_{leaf} were reduced by deficit irrigation during the experimental period, the decrease being more pronounced in Ψ_{stem} (Fig. 2).

Low values were recorded for the gas exchange parameters g_l and P_n (Fig. 3), which is characteristic of citrus trees (Domingo *et al.,* 1996). A feedback effect of the fruits on leaf photosynthesis (Layne & Flore, 1993; Ben-Mimoun *et al.,* 1996) was observed, with values increasing from June to October, when maximum values of P_n were observed (Fig. 3), coinciding with maximum lemon fruit growth rates (García-Orellana *et al.,* 2007), and just before harvesting.

The fact that leaf and stem water potentials were better correlated with g_l values when taken in the early hours of the morning (at their maximum levels) than at midday suggests that, under deficit irrigation conditions, the optimal time for gas exchange measurements in field-grown lemon trees coincides with the first hours of the morning, when maximum stomatal opening is observed (Fig. 3).

The differences between the two water potential

values (Ψ_{stem}-Ψ_{leaf} = $\Delta\Psi$) were most pronounced at midday (Fig. 2), reflecting higher leaf transpiration values at the time of the highest evaporative demand of the atmosphere (Garnier & Berger, 1985). From data in Fig. 4, it was clear that $\Delta\Psi$ correlated closely with sap flow values, which are related with daily tree transpiration (Moreno *et al.,* 1996; Ortuño *et al.,* 2005); low sap flow values being associated with zero or small differences between stem and leaf water potential values (Fig. 4). For this reason, $\Delta\Psi$ was seen to be a good measure of leaf transpiration in lemon trees. Similarly, Torrecillas *et al.* (1989) established a good correlation between $\Delta\Psi$ and leaf transpiration, measured gravimetrically, in almond trees.

The physiological understanding of the pressure drop in transpiring leaves has been a matter of discussion since the time the concept "frictional water potential gradient" was proposed by Richter (1973). Water moves through the plant-xylem conducting system in proportion to the driving force ($\Delta\Psi$) and the proportionality "constant" is referred to as the hydraulic conductance (Camacho *et al.,* 1974; Elfving *et al.,* 1972). When the soil water potential is high [as in control treatment (Fig. 1)], canopy hydraulic conductance may then be deduced, following Ohm's Law electrical analogue, from the relationship between plant transpiration and the gradient between the upstream source in the trunk (Ψ_{stem}) and the downstream sink corresponding to the leaf (Ψ_{leaf}) ($\Delta\Psi$). This holds true as long as there are negligible changes to the water storage capacitance of the tree (Alarcón *et al.,* 2003). The slope of this regression did not change at any time during the fruit growing period and the estimated K_C value (Fig. 4) was similar in magnitude to that observed in other woody tree species with a similar daily water use, such as field grown mature apricot trees (Alarcón *et al.,* 2003).

Low $\Delta\Psi$ values in deficit irrigated treatments were associated with higher values of MDS of tree trunk (Fig. 5), which, in turns, has been found to be a robust and very suitable plant water status indicator for many woody crops (Fernández & Cuevas, 2010; Ortuño *et al.,* 2010).

In conclusion, stem water potential is a better indicator of plant water status in lemon trees than leaf water potential, since greater differences between irrigation treatments were found in the measurement of Ψ_{stem}, which was also less dependent on weather conditions than Ψ_{leaf}. While sap flow and maximum daily shrinkage were found to be immediate and sensitive water stress

indicators in lemon trees (Ortuño *et al.,* 2006), our results also indicate that when such continuously recorded plant-based indicators are not available, the concurrent measurement of leaf and stem water potentials at midday, which are relatively inexpensive to measure and user-friendly, act as sufficiently good indicators of the plant water status in field grown Fino lemon trees. Moreover, the difference between the two values of Ψ ($\Delta\Psi$) provides an estimate of leaf transpiration, besides allowing canopy hydraulic conductance to be estimated.

Acknowledgements

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