

Daily variations in water relations of apricot trees under different irrigation regimes

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Abstract

Mature apricot (*Prunus armeniaca* L. cv. Búlida) trees, growing under field conditions, were submitted to two drip irrigation treatments: a control (T1), irrigated to 100 % of seasonal crop evapotranspiration (ETc), and a continuous deficit (T2), irrigated to 50 % of the control throughout the year. The behaviour of leaf water potential and its components, leaf conductance and net photosynthesis were studied at three different times during the growing season, when they revealed a diurnal and seasonal pattern in response to water stress, evaporative demand of the atmosphere and leaf age. The deficit-irrigated trees showed, among other effects, a pronounced decrease in leaf water potential (ψ_w), decreased in leaf conductance (g_s) and no osmotic adjustment. For this reason, g_s and ψ_w can be considered good indicators of mature apricot tree water status and can therefore be used for irrigation scheduling.

Additional key words: leaf stomatal conductance, leaf water potential, net photosynthesis, *Prunus armeniaca* L., water deficit.

Introduction

In Mediterranean agro-systems, as in many other semi-arid zones in the world, water has become a precious resource due to its scarcity. There is, therefore, a constant need to improve water use efficiency by means of accurate irrigation scheduling based on physiological indicators which show information on crop water status (Naor and Cohen 2003). However, there is no general agreement on the most suitable indicator (Katerji *et al.* 1988).

The most widely used approach for evaluating plant water status has been to determine leaf water potential, either as predawn readings (Domingo *et al.* 1996, Ferreira *et al.* 1997), or midday readings (Girona *et al.* 2006), as well as stem water potential (McCutchan and Shackel 1992). Gas exchange parameters, such as variations in

stomatal conductance, have also been used as water status indicators (Harrison *et al.* 1989). More recently, some sensors used to measure sap flow and trunk diameter fluctuation have provided useful information about water status because of the continuous nature of the measurements; they have also proved to be very robust (Goldhamer *et al.* 1999, Remorini and Massai 2003, Ohashi *et al.* 2006, Ortúñu *et al.* 2006).

Our knowledge of the water transport through the soil-plant-atmosphere continuum for apricot plants is limited, since studies on drought resistance mechanisms have focus on young plants during short-time water stress periods (Torrecillas *et al.* 1999, Ruiz-Sánchez *et al.* 2000). Consequently, more comprehensive information of water relations in mature trees growing in a field is

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Abbreviations: c_i - internal CO_2 concentration; ETc - crop evapotranspiration; ETo - reference evapotranspiration; g_s - leaf stomatal conductance; LM/LA - leaf mass/leaf area ratio; PAR - photosynthetically active radiation; P_N - net photosynthetic rate; SM/DM - water saturated mass/dry mass ratio; T_l - leaf temperature; VPD - vapour pressure deficit; ψ_o - leaf osmotic potential; ψ_{os} - leaf osmotic potential at full saturation; ψ_p - leaf pressure potential; ψ_w - leaf water potential.

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needed if we wish to optimise both water use and orchard management.

For these reasons, the aim of this paper was to study plant-water relations (leaf water potentials and leaf gas-

exchange) throughout a growing season in mature apricot trees growing in a orchard. The physiological basis of diurnal and seasonal variations and the sensitivity of these parameters to water deficits are discussed.

Materials and methods

The experiment was performed during 1997, in a 20 000 m² plot of a commercial orchard, located in Mula valley, Murcia, Spain (37°57' N, 1°25' E, 350 m above sea level). The soil is loam-textured (sand: 29.85 %; silt: 42.92 %; clay: 27.21 %) and classified as a Xeric Torriorthent. It is highly calcareous, has a pH of 7.8, and a low organic matter content and cationic exchange capacity. The available water capacity is about 0.15 cm³ cm⁻³. The climate is semiarid Mediterranean with hot and dry summers; annual evaporation and rainfall for the experimental period was 1470 and 436 mm, respectively.

The plant material consisted of mature apricot trees (*Prunus armeniaca* L. cv. Búlida, on Real Fino apricot rootstock), spaced 8 × 8 m, with an average ground cover of 52 %. Trees were drip irrigated using one drip irrigation line per row, with seven emitters per tree, each with a flow rate of 4 dm³ h⁻¹. The irrigation water had low electrical conductivity (0.6 dS m⁻¹).

Two irrigation treatments were considered: a control, irrigated at 100 % of seasonal ET_c (685.4 mm year⁻¹) and a continuous water deficit treatment, irrigated at 50 % of the control treatment all year. Irrigation amounts were scheduled on weekly based on crop coefficients (Abrisqueta *et al.* 2001), reference crop evapotranspiration (ET₀), as determined from data collected the previous week in a U.S. Weather Bureau class A pan (on bare soil and located on a weather station in the orchard), and the estimated application efficiency (95 %). Treatments were distributed in a completely randomised block design, with four blocks. Each block consisted of two rows of seven trees. Other details concerning the tree, irrigation and climate characteristics have been described in Pérez-Pastor *et al.* (2004).

Leaf water potentials, gas-exchange parameters and environmental conditions (air temperature, relative air humidity) were measured from predawn to sunset at 2-h intervals and on three clear days representatives of the growing season: 18th March (spring), 24th July (summer), 28th October (autumn). Climatic conditions were measured by an automatic weather station located in the orchard.

Leaf water potential (ψ_w) was measured in mature leaves located on the south facing side, from the middle third of the tree (two leaves per tree and four trees per

treatment), with a pressure chamber (model 3000, *Soil Moisture Equipment Corporation*, Santa Barbara, CA, USA) following the recommendations of Turner (1988). After measuring ψ_w , the leaves were frozen in liquid nitrogen and osmotic potential (ψ_o) was measured after thawing the samples and extracting the sap, using a *Wescor 5500* (Logan, USA) vapour pressure osmometer. Leaf pressure potential (ψ_p) was derived as the difference between leaf osmotic and water potentials. Osmotic potential at full saturation (ψ_{os}) was measured on leaves adjacent to those used to measure predawn leaf water potential. Eight leaves per treatment were allowed to reach full ψ_p by dipping their petioles in distilled water for 24 h in darkness at 8 °C (Yoon and Richter 1990). The rehydrated leaves were weighed (water saturated mass) and frozen in liquid nitrogen, and then ψ_{os} was measured following the same methodology as for ψ_o . Osmotic adjustment was estimated as the difference between the ψ_{os} of deficit and control plants.

Leaf conductance (g_s) and net photosynthetic rate (P_N) were measured in a similar number of leaves, using a field-portable, closed gas-exchange photosynthesis system (*LI-6200, LI-COR*, Lincoln, USA) incorporating IRGA (*LI-6250*). Each leaf was enclosed within a fan-stirred one-litre chamber. The mean return flow rates of air circulating within the closed system and the leaf to air vapour pressure deficit for all measurements were around 450 mmol s⁻¹ and 2 kPa, respectively. The CO₂ analyser was calibrated daily with two standard CO₂/air mixtures. Leaf temperature was measured using a portable infrared thermometer (*Everest Interscience*, Fullerton, USA) with 0.5 °C accuracy and 0.1 °C resolution. Five measurements were taken on four trees per treatment, ensuring that the entire area detected by the sensor was totally occupied by a single leaf in full sunlight.

Volumetric soil water content (θ_v) was determined using a neutron probe (Troxler mod 4300) that had previously been calibrated for the site. Four 1.4 m access tubes were located in each treatment (one per block) in the wetted area close to the second emitter from the tree trunk. Soil moisture was determined at 10 cm intervals. Soil moisture at 10 cm was determined gravimetrically.

Results and discussion

Leaf water potential (ψ_w) at the three measuring times showed a similar circadian rhythm (Fig. 1). It decreased very quickly early in the morning, regardless of the irrigation regime, reaching a minimum at about midday, followed by a sharp recovery in the afternoon, which can be regarded as typical behaviour in cultivated plants (Tenhunen *et al.* 1982, Torrecillas *et al.* 1988, Sánchez-Blanco *et al.* 1990).

In well irrigated plants, predawn ψ_w values remained quite stable throughout the season (above -0.5 MPa), and the midday decrease was more pronounced in July (Fig. 1), which indicates the close dependence of this parameter on the evaporative demand of the atmosphere, as demonstrated by the high correlation coefficient values between ψ_w and the vapour pressure deficit (VPD) (Table 1; Fig. 2). The increase from March to October of both the slope and the intercept of the regression curve of

this relation (Fig. 2) can be attributed to the decrease of plant hydraulic conductance in the xylem as a result of leaf ageing (Rudich *et al.* 1981). A slight stabilization of leaf water potential values around midday can be observed (Fig. 1), which suggests that the water stored in trunk tissues is easily released to the transpiration stream (Davies and Lakso 1979).

The diurnal time course of ψ_w showed similar pattern in the control and deficit treatments early in the season (Fig. 1) when the soil water moisture level was still sufficient to prevent water stress, and evaporative demand was still low (data not shown). In July, the ψ_w in the deficit treatment was 0.3 - 0.4 MPa lower than in the control plants during the most of the day (Fig. 1), the soil showing a low volumetric water content throughout the profile (data not shown). In October, the water stress led to a more pronounced decrease in ψ_w , both at predawn

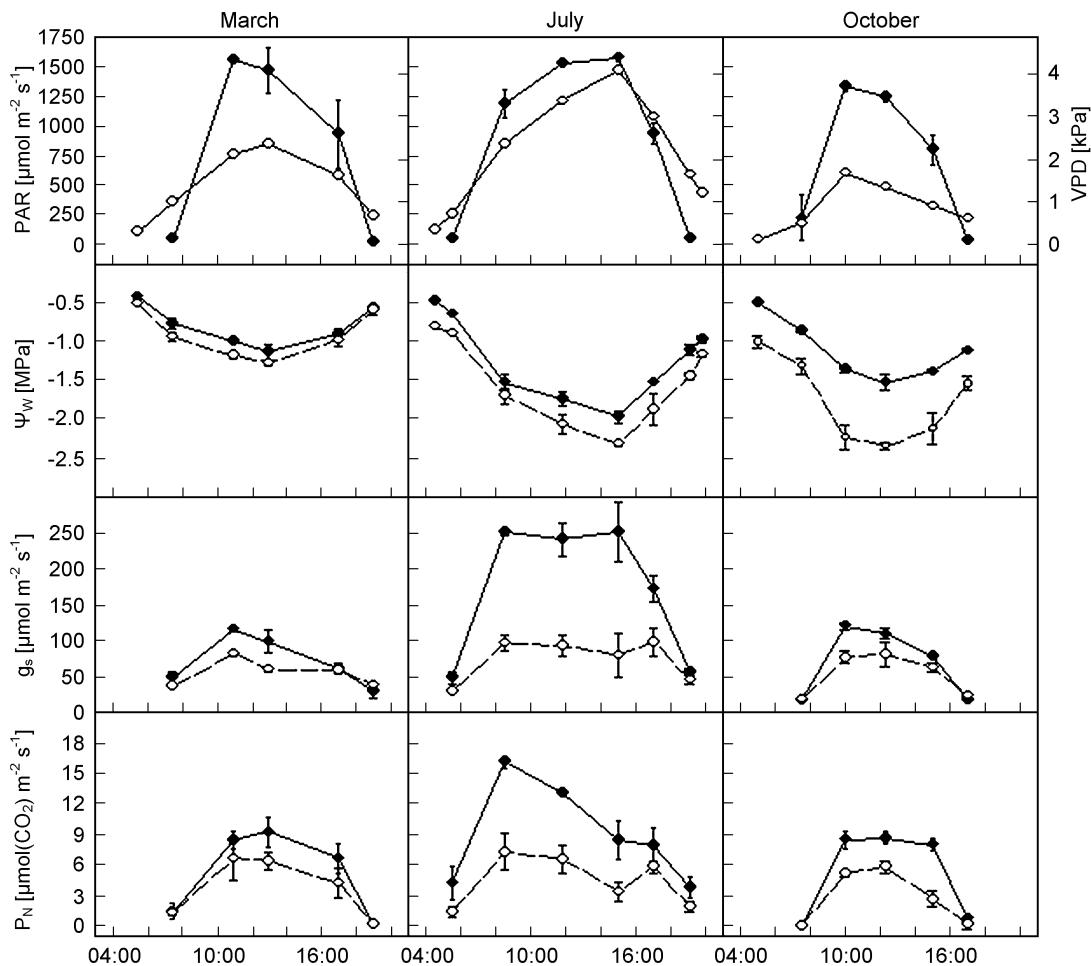


Fig. 1. Diurnal course of photosynthetically active radiation (PAR, *closed circles*), vapour pressure deficit (VPD, *open circles*), leaf water potential (ψ_w), leaf stomatal conductance (g_s) and net photosynthetic rate (P_N) in control (*closed circles*) and deficit (*open circles*) treatment at three times during the growing season. Each point is the mean of four replications. Vertical bars are \pm SE of the means for physiological parameters (not shown when smaller than the symbols).

Table 1. Pearson's correlation coefficients between climatic and leaf water relations parameters in control (C) and deficit (D) treatments during the growing season: March (M), July (J) and October (O). *, ** - significant at 0.05 and 0.01 level, respectively.

	PAR	Ψ_w	P_N	g_s	T_l						
	C	D	C	D	C	D					
VPD	M	0.98**	0.98**	-0.98**	-0.97**	0.99**	0.99**	0.94*	0.83	0.86*	0.93*
	J	0.91**	0.91**	-0.99**	-0.99**	0.47	0.53	0.84*	0.77*	0.92*	0.82
	O	0.95*	0.95*	-0.87*	-0.93**	0.86	0.94*	0.96**	0.91*		
PAR	M		-0.91*	-0.87	0.98**	0.99**	0.95*	0.93*	0.89*	0.95*	
	J		-0.94**	-0.90**	0.75	0.72	0.98**	0.84*	0.80	0.65	
	O		-0.82	-0.93*	0.94*	0.98**	0.99**	0.97**			
Ψ_w	M			-0.95*	-0.92*	-0.88*	-0.72	-0.88*	-0.93*		
	J			-0.60	-0.55	-0.87*	-0.78*	-0.89*	-0.79		
	O			-0.93*	-0.94*	-0.91**	-0.99**				
P_N	M				0.91*	0.91*	0.93*	0.96*			
	J				0.85*	0.93**	0.41	0.17			
	O				0.96**	0.98**					
g_s	M						0.80	0.99*			
	J						0.82	0.55			
	O										

and midday (Fig. 1), even though some recovery in the soil water content was noted in the most superficial horizons (data not shown).

The decrease in leaf osmotic potential at full saturation (ψ_{os}) from March to October (Table 2) can be attributed to the accumulation of osmotically active solutes with ageing, a characteristic of deciduous trees (Lakso *et al.* 1984, Yoon and Richter 1990), and supported by the seasonal decrease in the values of the water saturated mass/dry mass ratio (Table 2). No significant differences were observed in ψ_{os} values between the control and deficit treatments, because plant water deficits must be severe ($\psi_w < -1.5$ MPa at predawn)

Table 2. Leaf osmotic potential at full saturation (ψ_{os}), leaf pressure potential (ψ_p), water saturated mass/dry mass ratio (SM/DM) leaf mass/leaf area ratio (LM/LA) at predawn, and midday leaf temperature (T_l) at three times during the growing season in control (C) and deficit (D) treatments. Means \pm SE followed by different letters for a given row (upper case) or a column (lower case) were significantly different according to Duncan's multiple range test at 0.05 level (n.d. - not detected).

Parameter	March	July	October
ψ_{os} [MPa]	C -1.40 \pm 0.12aA	-1.50 \pm 0.04aA	-1.81 \pm 0.07aB
ψ_p [MPa]	D -1.30 \pm 0.08aA	-1.58 \pm 0.06aA	-1.84 \pm 0.04aB
SM/DM	C 4.10 \pm 0.23aA	3.70 \pm 0.21aB	3.03 \pm 0.05aC
LM/LA [mg cm ⁻²]	D 4.25 \pm 0.25aA	3.65 \pm 0.17aB	3.00 \pm 0.12aC
T_l [°C]	C 4.23 \pm 0.37aA	7.00 \pm 0.81aB	8.36 \pm 0.80aC
	D 4.35 \pm 0.20aA	6.72 \pm 0.67aB	8.45 \pm 0.82aC
	C 22.20 \pm 0.42aA	29.63 \pm 0.62aB	n.d.
	D 24.33 \pm 0.55bA	34.51 \pm 0.70bB	n.d.

for development of osmotic adjustment in apricot plants, as indicated by Ruiz-Sánchez *et al.* (2000) in young potted apricot plants.

The moderate water deficit applied may also be the cause of the absence of any change in leaf pressure potential (ψ_p) in the deficit treatment until late in the season, when water stress induced a significant decrease in ψ_p (Table 2). This implies that the fall in ψ_o (data not shown) was not sufficient to maintain ψ_p at the same levels as in well irrigated plants.

At sunrise, the increase in radiation induces stomata opening and photosynthesis begins; stomatal conductance (g_s) and net photosynthetic rate (P_N), increased, following a similar trend to photosynthetically active radiation (PAR) (Fig. 1). In March, low values were found in young leaves with immature stomata and low chlorophyll contents as described Sams and Flore (1983) and Schubert *et al.* (1996).

In deficit-irrigated plants, the duration of maximum stomatal opening was shortened, as a response to water deficit (Henson *et al.* 1982, Torrecillas *et al.* 1988). Water conservation mechanisms developed in stressed plant (Torrecillas *et al.* 1999) during the period of high evaporative demand (July), when very low g_s values were registered during most of the day (Fig. 1).

As in other woody plants, the values of gas exchange parameters (Fig. 1) increased from March to July and fell at the end of the season (Kriedeman *et al.* 1970, Aslam *et al.* 1977, Torrecillas *et al.* 1988). The decrease P_N with leaf ageing is related not only to stomatal factors but also to the hormonal imbalance and the other ontogenetic changes which take place in leaves (Evans 1983, Ruiz-Sánchez *et al.* 1988). These changes also include thickening of cell walls (Jensen and Henson 1990, Ruiz-Sánchez *et al.* 1997), as revealed by the seasonal increase

in the leaf mass/leaf area ratio in the control plants (Table 2).

The relation between gas exchange parameters and photosynthetically active radiation meant that from 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR, maximum values of g_s and P_N were reached in well irrigated apricot plants (Fig. 3), similar to what can be observed in light-response curves for citrus trees (Vu *et al.* 1986).

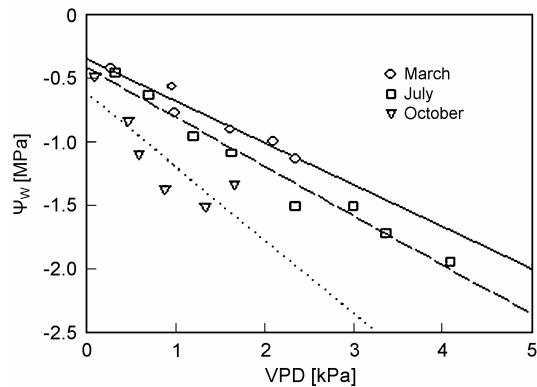


Fig. 2. Relationship between leaf water potential (ψ_w) and vapour pressure deficit of the atmosphere (VPD) in control treatment. Each point is the mean of 4 replications. Regression equations were March: $y = -0.35 - 0.33 x$, $r = 0.99^{***}$, July: $y = -0.42 - 0.39 x$, $r = 0.98^{***}$, and October: $y = -0.62 - 0.58 x$, $r = 0.87^*$.

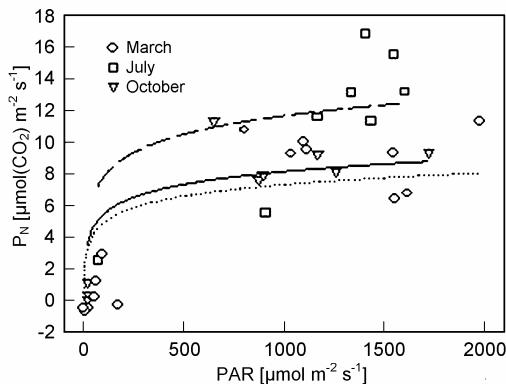


Fig. 3. Relationship between net photosynthetic rate (P_N) and photosynthetically active radiation (PAR) in control treatment for March, July and October. Each point is the mean of four replications.

The highest correlation coefficient values in the relation between ψ_w and g_s were recorded in October in

both treatments (Table 1). This can be attributed to the dominant role of leaf water status in controlling stomata behaviour as the season progresses (Torrecillas *et al.* 1988, Sánchez-Blanco *et al.* 1991).

Among the physiological mechanisms involved in the response of mature field-grown apricot plants to water stress, stomatal regulation of gas exchange (Fig. 1) is an avoidance mechanisms recognised as an important adaptive response to drought, which reduces water loss (Ruiz-Sánchez *et al.* 2000). However, stomatal closure induced an increase in leaf temperature (T_l), T_l of stressed plants being 2 - 5 °C above that of the control, with maximum differences at midday (Table 2). It has been proposed that T_l increases progressively when soil moisture is a limiting factor, for which reason it can be used as an index of plant water status (Ehrler 1973). In contrast, Remorini and Massai (2003) thought that T_l showed poor sensitivity for estimating peach tree water status.

P_N and g_s were linearly correlated, which suggested a stomatal limitation to photosynthesis under mild water stress conditions (Wong *et al.* 1979); it also suggested that an efficient co-ordination of stomatal behaviour and photosynthetic activity occurred in apricot plants, as has been found in other *Prunus* species (Harrison *et al.* 1989, Yoon and Richter 1990).

It should be mentioned that the difference between treatments were lower for P_N than for g_s (Fig. 1), which might imply that the main role of stomata under water stress is to optimise the balance between CO_2 uptake and water loss *via* transpiration; this fact could also be considered as a mechanism for maintaining productivity of photosynthates due to remaining leaf water content (Farquhar and Sharkey 1982, Gebre and Kuhns 1993).

It should be noted that the measurement of leaf water potential in non-transpiring leaves (stem water potential) will almost certainly produce a more intense signal than that observed in sun-exposed transpiring leaves (Goldhamer *et al.* 1999, Ortúñoz *et al.* 2006). More research is needed before we can confirm what is the best plant water stress indicator for adult apricot trees. However, until such information is available, measurements of leaf water potential and leaf conductance can be considered as sufficiently good indicators of apricot tree water status and can be used for irrigation scheduling, as Hutmacher *et al.* (1990) suggested.

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