Vine and soil-based measures of water status in a Tempranillo vineyard

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Summary

Seasonal changes of leaf and stem water potential and midday stomatal conductance (gs) of Tempranillo grapevines were determined in irrigated and non-irrigated vines in 2003 and 2004. Leaf water potential was measured at pre-dawn (Ψ_{pd}) and at midday (Ψ_l^{md}), while stem water potential was measured in the early morning (Ψ_s^{em}) and at midday (Ψ_s^{md}). At Ψ_{pd} to -0.54 MPa rain-fed and irrigated vines had similar midday Ψ_l and Ψ_s. This was due to both, stomatal closure and reduction of leaf area. Under these conditions, Ψ_{pd} and Ψ_s^{em} were better water stress indicators than midday Ψ. In both years a close correlation was found between Ψ_{pd} and Ψ_s^{em}. However, for a given Ψ_{pd}, Ψ_s^{em} of vines was lower in 2004 than in 2003. This was probably due to the larger leaf area developed by vines in 2004. Stomatal conductance reflected reasonably well differences in the vine water status but its variability was much higher than that of Ψ. Moreover, the afternoon depression of stomatal conductance observed even in irrigated plots, indicates that measuring gs early in the morning is more convenient when assessing different treatments.

K e y   w o r d s : drip irrigation, leaf and stem water potential, leaf area, stomatal conductance.

Introduction

Some woody plants have developed mechanisms to withstand soil water scarcity. At the cellular level, osmotic or elastic adjustment frequently have been described as strategies to maintain tissue hydration (Düring 1984, Kozlowski and Pallardy 2002).

Water loss of grape can be controlled, to some extent, by reducing vegetative growth or by closing stomatal pores (Winkel and Rambal 1993). This leads to a reduction in total plant carbon gain, thus affecting yield, but may help to survive under drought conditions.

Tempranillo is widely cultivated in Spain and irrigation is known to have a crucial impact on its yield (Medrano et al. 2003) and must quality (Esteban et al. 2002). Thus, it is important to explore physiological responses to drought in order to provide tools for an irrigation management.

Many studies have described short-term effects of soil drought on stomatal conductance and leaf water potential (Naor 1998, Williams and Araujo 2002, de Souza et al.

2005), but there has been less effort to characterize seasonal effects of drought. E.g. on a seasonal basis reduction of leaf area may have a crucial role as a drought adaptative mechanism (Winkel and Rambal 1993).

Our objective was to characterize responses of leaf water relations of cv. Tempranillo to soil drought, by analyzing seasonal changes of various water potential parameters in relation to stomatal conductance. Physiological and practical implications for irrigation are discussed.

Material and Methods

E x p e r i m e n t a l   p l o t   a n d   p l a n t   m a t e r i a l : Experiments were carried out in 2003 and 2004 with Tempranillo (*Vitis vinifera* L.) on the rootstock 161-49 planted in 1991 at a spacing of 2.45 m by 2.45 m (1666 vines ha^{-1}). The vineyard was located near Requena, Valencia, Spain (39º 29'N, 1º 13'W, elevation 750 m). In 2000 a drip-irrigation system had been installed and vines were trained to a vertical trellis on a bilateral cordon system oriented North-South. In both years vines were spur-pruned to about 12 buds per vine. In 2003 the average number of clusters per vine was 10.8 whereas in 2004 it was 21.5. This was due to shoot thinning: in 2003 8 shoots per vine were left, while in 2004 14 shoots were retained.

The soil of the vineyard was a typic Calciorthid with a clay-loam to light clay texture, highly calcareous and of low fertility. Soil depth was >2 m, available water capacity was about 200 mm m^{-1} and the bulk soil density ranged from 1.43 to 1.55 t m^{-3}. The climate in this area is continental and semiarid with an average annual rainfall of 450 mm (about 65 % in winter). During the experiment weather data were taken from an automated meteorological station located in the plot. Experiments were performed in the relatively dry year 2003, with 330 mm of total rainfall, while in 2004 the total rainfall was 520 mm. From June to harvest rainfall was 86 and 113 mm for 2003 and 2004.

I r r i g a t i o n   t r e a t m e n t s : The experimental design consisted of the following three treatments: (1) Rain-fed; (2) I-50, watered at 50 % of estimated crop evapotranspiration (ET$_c$); (3) I-100 watered at 100 % of ET$_c$. Each treatment was replicated 6 times in a randomised block design.

Crop evapotranspiration was estimated as the product of reference evapotranspiration (ET$_o$) and crop coefficient (K$_c$). The ET$_o$ was calculated according to Penman-Monteith (Allen et al. 1998) with hourly values recorded in the plot. Irrigation started in June depending on the soil

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water content and on the rainfall occurring during winter months. K_c was estimated according to results obtained in previous irrigation trials in the same vineyard (Salón *et al.* 2004) and a vineyard nearby planted with cv. Bobal (Salón *et al.* 2005). Crop coefficient varies with the phenological stage and the development of leaf area. From June to July, K_c gradually increased from 0.075 to 0.30. On a seasonal base, irrigation in the more irrigated treatment was 94 and 82 mm in 2003 and 2004, respectively. Taking into account the effective rainfall, this represented an average fraction of ET_o of 0.31 (2003) and 0.36 (2004).

Water was applied on 3-5 d per week with two pressure-compensated emitters (2.4 l h^{-1}) located 60 cm on either side of the vine on a single tube per row.

D e t e r m i n a t i o n s : Soil water content (SWC) in the profile was monitored with capacitance probes (Enviroscan, Sentek, South Australia). Four access tubes per treatment were placed within the vine row approx. 75 cm from the trunk and 25 cm from emitters. The equipment was calibrated *in situ* against the volumetric soil moisture content determined in undisturbed soil samples from each depth down to 100 cm. Due to equipment limitations SWC was only measured in the rain-fed and I-100 treatments.

Leaf and stem water potential were determined with two pressure chambers (Soil Moisture Corp., Santa Barbara, USA) on 4 representative vines per treatment and two leaves per vine. Stem water potential was measured in the early morning, from 0700 to 0800 h (Ψ_s^{em}) and at midday (1130 to 1230 h; Ψ_s^{md}). Leaf water potential (Ψ_l) was measured only at midday (Ψ_l^{md}). Water potential was determined every two weeks. Pre-dawn leaf water potential (Ψ_{pd}) was measured before 0500 h on monthly intervals. All vines were measured in about 30 min at pre-dawn and in the early morning and in about 50 min at midday when leaf and stem water potential were measured.

Stomatal conductance (gs) was determined on the vines used for water potential measurements using three fully expanded, sun-exposed leaves per vine. Measurements were taken at about solar midday using a dynamic diffusion porometer (AP4, Delta-T Devices, Cambridge, UK); determinations were carried out in about 30-40 min.

After veraison when shoot growth had ceased leaf area per vine was estimated from a linear equation relating leaf area (Y, cm^2 per shoot) to total shoot length (main plus laterals; X, cm). In both years this relationship was obtained from samples of about 10 representative shoots. The resulting equation was: $Y_{shoot} = 20.729X_{shoot} + 814.5$; (n = 20, $r^2 = 0.95$, P<0.001).

S t a t i s t i c a l   a n a l y s i s : For each year, simple linear regression analyses were carried out using the 'reg' procedure (SAS Institute 1994) to explore relationships between Ψ_{pd} and the other water potential parameters and between gs and Ψ. If there were no statistically significant differences (*P*>0.05) in slope between years, data from both years were pooled in a unique regression equation. A completely randomised design was used to study the effect of the irrigation on leaf area and water relations. Analysis was based on one-way ANOVA using the 'glm' procedure (SAS Institute 1994) and Dunnett's t-test.

Results

S e a s o n a l   d y n a m i c s   a n d   v e g e t a t i v e   g r o w t h : In both years early in the season SWC was initially higher for the non-irrigated than for the irrigated vines (Fig. 1 A and 1 B). With irrigation SWC increased in the irrigated vines and the trend reversed, differences between irrigated and non-irrigated vines being not statistically significant (*P*>0.05) in most cases. This was presumably due to the high spatial variability of soil moisture. The
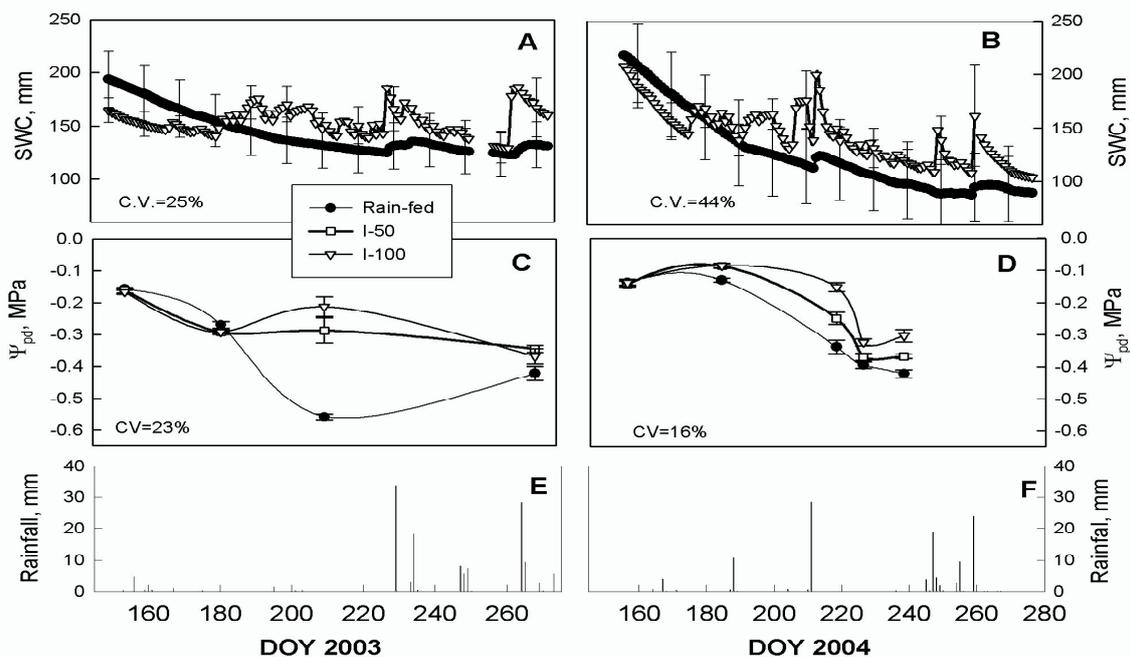
Fig. 1: Seasonal patterns: **A** and **B**) soil water content (SWC) in the soil profile from 10-90 cm depth, **C** and **D**) pre-dawn water potential (Ψ_{pd}), **E** and **F**) rainfall. Values are means and standard error of 4 access tubes and 8 leaves per treatment for SWC and Ψ_{pd}. DOY, day of the year, CV, typical value of the coeficient of variation.

typical coefficient of variation of the SWC readings was about 25 % and 44 % in 2003 and 2004. Differences in Ψ_{pd} between irrigated and rain-fed vines began to enlarge by the end of June and further increased throughout most of the season. Thus, in the more irrigated vines (I-100), Ψ_{pd} remained between -0.15 and -0.3 MPa, whereas in the rain-fed ones minimum values observed by mid-August reached -0.54 MPa in 2003 (Fig 1 C), and -0.4 MPa in 2004 (Fig. 1 D).

Early morning Ψ_s allowed a clear differentiation between the treatments during most of the season and agreed reasonably well with the changes of Ψ_{pd}. Instead, at midday, values of Ψ_s and particularly of Ψ_l were more similar among treatments (Fig. 2).

In both seasons the first determination of gs in early June showed similar values for all treatments and indicated that stomata were open. Throughout the season gs decreased in all treatments. As expected, gs decreased more severely in the non-irrigated vines, very low values indicating almost complete stomatal closure by August. In general, the changes of gs reflected reasonably well differences in irrigation between treatments (Fig. 2 G and 2 H).

In both seasons irrigation led to an increase vigour as indicated by the higher leaf area per vine, which was especially noticeable in the more irrigated treatment (Table). Vine leaf area was higher in 2004 than in 2003 (Table); this was in part due to the higher number of shoots per vine in 2004, but also to increased shoot growth.

Diurnal evolution of water potential and stomatal conductance: From diurnal cycles obtained on August 13 and 24, 2004 (Fig. 3), it is

Table

Effects of irrigation treatments on vine leaf area, m^2 $vine^{-1}$

Year	Rain-fed	I-50	I-100	MSD[a]	Prob[a]
2003	4.8	5.6	6.2	1.4	0.09
2004	8.4	9.4	10.4	1.47	0.03

[a] MSD = Minimum significant difference by Dunnett's t-test at P<0.05. Prob = significance level of treatment effects from ANOVA.
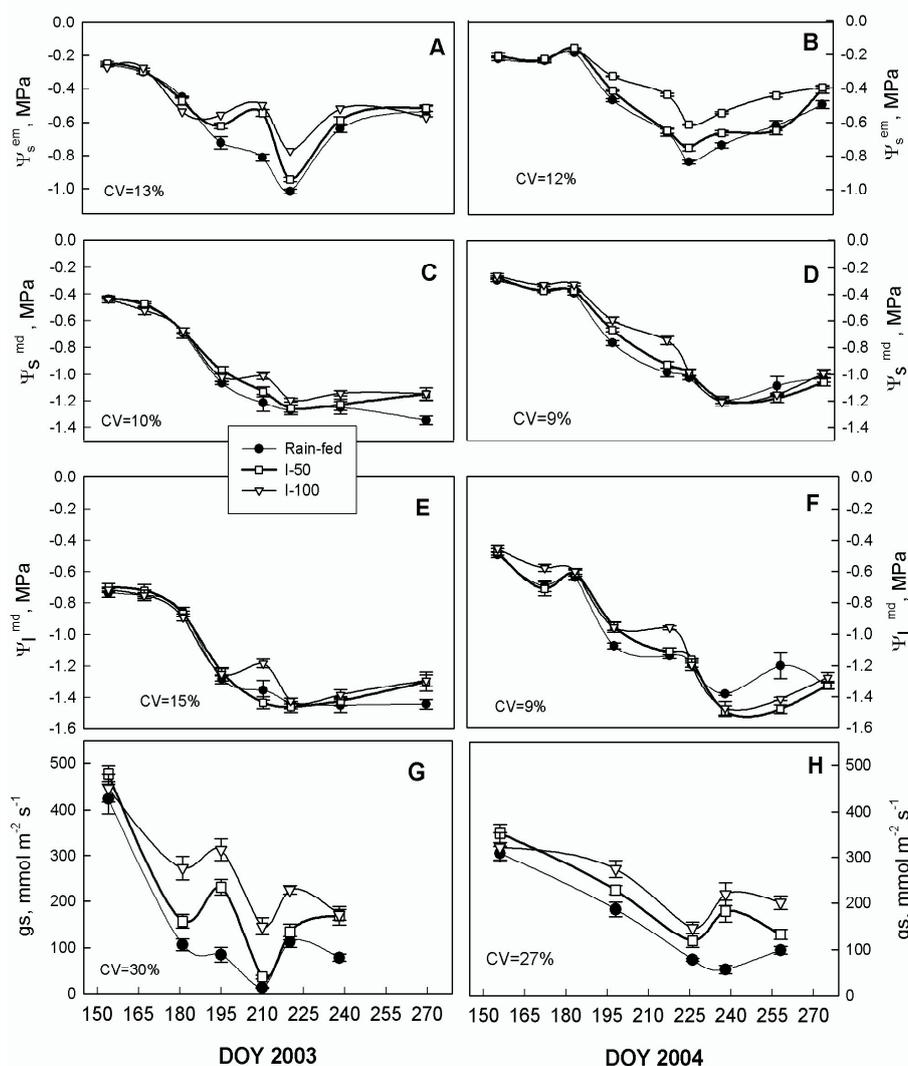
Fig. 2: Seasonal patterns: **A and B**) stem water potential measured in the early morning (7:00- 8:00 solar time; Ψ_s^{em}); **C** and **D**) midday stem water potential (Ψ_s^{md}); **E** and **F**) midday leaf water potential (Ψ_l^{md}), **G** and **H**) midday stomatal conductance (gs). Values are means and standard errors of 8 and 12 determinations of water potential and stomatal conductance. For details see Fig. 1.

evident that before dawn, as well as during the first hour in the morning and the last hour in the afternoon, the non-irrigated vines have lower Ψ_s values than the irrigated vines, while at noon differences are minimal and not significant ($P>0.05$) (Fig. 3 A and 3 C). During the whole day gs values of non-irrigated vines were lower than those of irrigated vines. However, the differences are more evident in the first morning hour than in the afternoon. During the early afternoon of 13 and 24 August with a vapour pressure deficit of 4.0 kPa and 4.2 kPa, respectively, stomatal closure was observed in all treatments (Fig. 3 B and 3 D).

R e l a t i o n s   b e t w e e n   w a t e r   s t a t u s   p a r a m e t e r s : Pooling treatments and years Ψ_s^{em}, Ψ_l^{md} and Ψ_s^{md} were all significantly ($P<0.01$) related with Ψ_{pd} (Fig. 4). Nevertheless, for Ψ_{pd} vs Ψ_s in the early morning, the slope was significantly ($P<0.01$) different between years, while for Ψ_{pd} vs Ψ_s^{md} and Ψ_{pd} vs Ψ_l^{md} differences between years were statistically not significant ($P>0.40$) and ($P>0.18$).

Stomatal conductance was significantly ($P<0.01$) related with all Ψ measurements, although correlations were clearer when related to pre-dawn and early morning Ψ than to Ψ at midday (Fig. 5). The slopes of the linear regression of gs vs Ψ_{pd} and Ψ_s in the early morning were not significantly different between years, ($P>0.44$) and ($P>0.07$); but there were statistically significant differences between years for the relationship of gs with Ψ_s and with Ψ_l measured at midday ($P<0.01$).

Discussion

To predict the effects of soil water deficit on the vine water status and performance the most straightforward strategy may be to directly measure the soil water content or potential. However, this approach has often shown to be unsuccessful (INTRIGLIOLO and CASTEL 2004, NAOR 2004) given the difficulty to obtain a precise estimation of the actual soil water availability at the site of roots (RUSSO and BRESLER 1982). This is mainly due to the large spatial variability of soil parameters and to the three-dimensional gradients of soil water originating from drip irrigation (OR 1995). In our study the variability of SWC often precluded detection of differences between irrigated and non-irrigated vines (Fig. 1 A and 1 B). Besides, the correlations between SWC and vine water potential were not significant, even when the latter was measured at pre-dawn or in the early morning (not shown).

Under our experimental conditions, covering a range of Ψ_{pd} down to -0.54 MPa, which can not be considered as severe drought (Medrano et al. 2003), Tempranillo showed similar values of midday Ψ_l and Ψ_s for irrigated and rainfed vines. This behavior is considered a water saving ability which has been shown to be cultivar-specific (SCHULTZ 2003). Similar trends of midday Ψ_l have been observed in other cultivars (NAOR 1998, CHONÉ et al. 2001, PATAKAS et al. 2005) and for the same cultivar in other areas
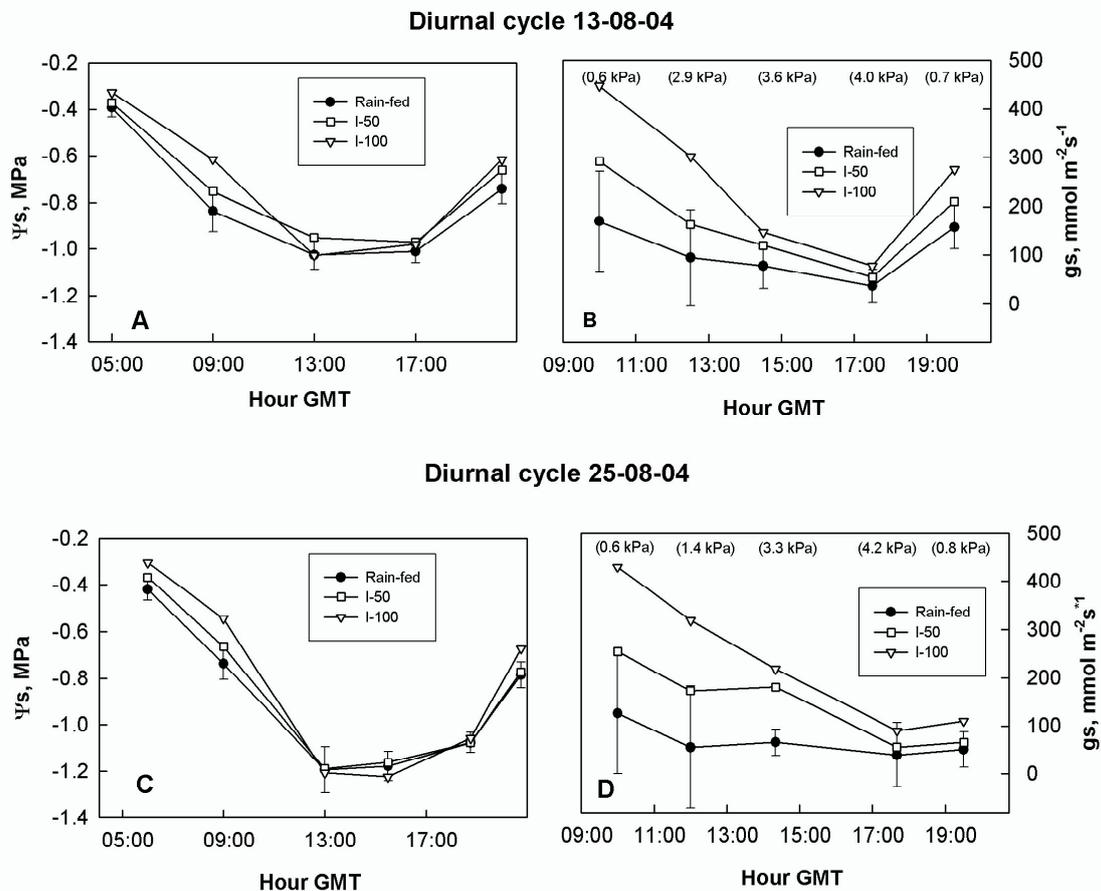
Fig. 3: Diurnal cycles: **A** and **C**) stem water potential (Ψ_s) and **B** and **D**) stomatal conductance (gs) carried out on 13th and 25th August 2004. Bars indicate 5 % minimum significant differences with respect to control (rain-fed) vines. Values are means of 8 and 12 determinations of water potential and stomatal conductance. In B and D values in brackets indicate vapour pressure deficit (VPD).
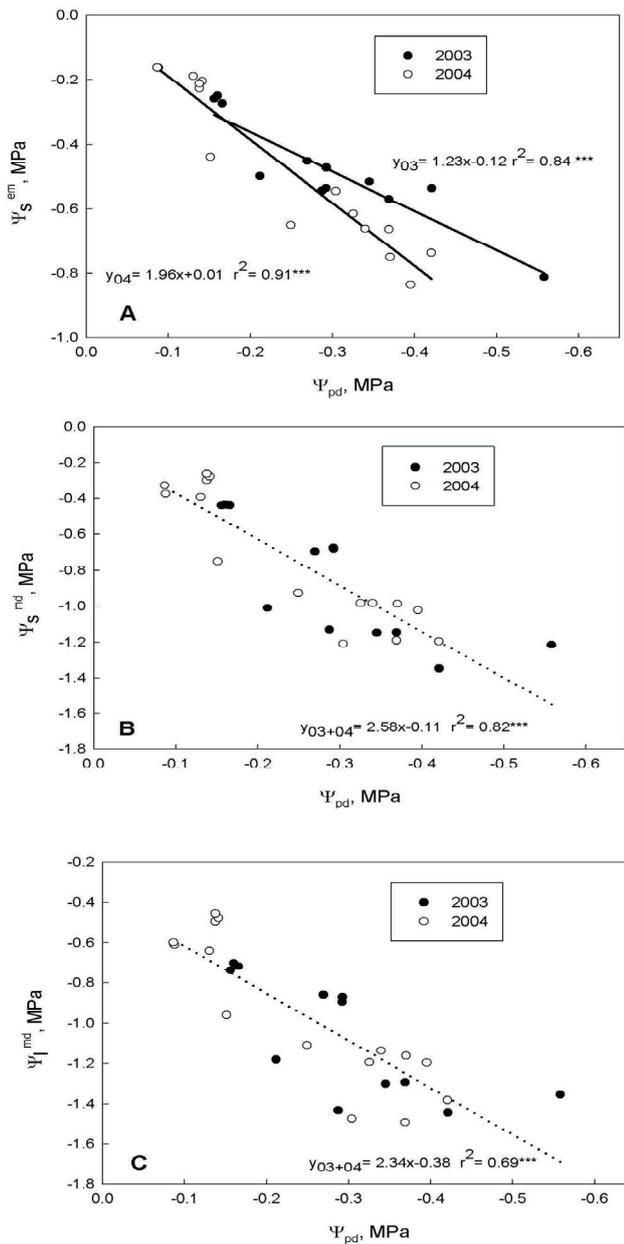
Fig. 4: Relationship between pre-dawn leaf water potential (Ψ_{pd}) and A) early morning stem water potential (Ψ_s^{em}), B) midday stem water potential (Ψ_s^{md}) and C) leaf water potential (Ψ_l^{md}). Values are means of 8 leaves. R^2 values indicate significance at 1 % (***) and at 5 % (**).

Fig. 5: Relationship between midday stomatal conductance (gs) and **A)** pre-dawn leaf water potential (Ψ_{pd}), **B)** early morning stem water potential (Ψ_s^{em}), **C)** midday stem water potential (Ψ_s^{md}) and **D)** leaf water potential (Ψ_l^{md}). Values are means of 8 and 12 determinations of water potentials and stomatal conductance. For details see Fig. 4.

of Spain (Yuste *et al*. 2004). However, in contrast to our results, these midday Ψ_s data reflected clearly the differences between the watering regimes. However, the differences between the present work and previous reports might also be due to the fact that the water stress level reached in our study was more moderate. There is evidence that under severe drought stress conditions, the capacity of vines to maintain their water status collapses (Medrano *et al*. 2003). Therefore under our conditions, Ψ_{pd} and early morning Ψ_s were better indicators of water stress than values measured at midday (Ψ_s^{md} or Ψ_l^{md}). Previous results obtained with cv. Bobal (Salón *et al*. 2005) also showed that Ψ_s determined in the early morning was the best predictor of water stress being correlated closer with yield and wine quality parameters than other Ψ parameters.

In our study the water saving behavior was particularly noticeable by mid-August (Fig. 2), after veraison; when pooled over years, the most irrigated vines had a higher leaf area (+27 %) than the non-irrigated ones (Table). Thus, canopy transpiration of the non-irrigated vines was reduced (1) by a strong stomatal control, being particularly effective in vineyards with aerodynamically rough surfaces and a high boundary layer conductance (Riou *et al*. 1987), and (2) by the significant reduction of leaf area. In cv. Syrah, with an anisohydric behavior (Schultz 2003), the reduction in leaf area caused by water stress was larger than in our experiments with Tempranillo, but stomata were less effective in controlling plant water status (Schultz 2003, Winkel and Rambal 1993). These observations suggest that both features, reduced vegetative growth and stomatal closure, define the water saving behavior.

Although diurnal changes of leaf or stem water potential strongly depend on environmental factors in addition to the soil water status, we found highly significant correlations between Ψ_s^{em}, Ψ_s^{md}, Ψ_l^{md} and Ψ_{pd} (Fig. 4). According to Ohm's law analogy for water flow, in the early morning, when the evaporative demand is still low, the water potential gradients generated by water flow within vines should also be small. Consequently, Ψ_s^{em} may be less dependent on factors affecting transpiration rate than midday Ψ values. In fact, our results show that Ψ_{pd} was better correlated with Ψ_s^{em} than with Ψ_s^{md} or Ψ_l^{md}. The equation reported in Fig. 4A might then be used to estimate Ψ_{pd} from Ψ_s^{em}. However, results reported in Fig. 4 A also show that for a given Ψ_{pd} value the vines had a lower Ψ_s^{em} in 2004 than in 2003. Given that the evaporative demand in both years was similar (not shown), and that stomatal conductance was not higher in 2004 than in 2003 (Fig. 5) this was mainly attributable to the larger vine leaf area in 2004. Thus, differences in leaf area development between seasons, due for instance to different pruning or training systems, might affect the relationship between Ψ_{pd} and the early morning or midday plant water potential.

Stomatal conductance responded reasonably well to different water applications, thus it may be used as a reliable vine water status indicator. However it was much more variable than the Ψ values (Fig. 2). This implies the need for a higher number of determinations of gs to reasonably estimate the vine water status. The higher variability of gs from leaf-to-leaf in grapevines is probably attributable to the important effects of VPD or light exposure (Düring 1976) on stomatal aperture, but perhaps also to stomatal patchiness phenomena (Düring and Loveys 1996).

Midday gs was better related to Ψ_{pd} and Ψ_s^{em} than to midday water potential values (Fig. 5). These results suggest that midday stomatal conductance is dependent on the water status of the soil explored by roots rather than being only a simple response to leaf turgor. This hypothesis may also explain why, in similarity to other reports (Naor 1998, Choné et al. 2001), midday Ψ_s was closer correlated with gs than midday Ψ_l (Fig. 5). It is currently accepted that stomatal closure is also mediated by chemical signalling from roots in response to soil drought (Davies and Zhang 1991) with possible interaction between hydraulic and chemical information controlling gs (Tardieu and Davis 1993). In fact, in some studies the concentration of abscisic acid in xylem vessels has been shown to control gs of grapevines (Loveys 1984, Loveys and Düring 1984). In other cases, however, a clear control has been found only for a single g_s value during the day (Correia et al. 1995).

Our results show that even in the more irrigated plants along with practically no change in soil water content, gs underwent important diurnal fluctuations (Fig. 3). The afternoon depression of gs, associated with increased VPD, is a feature commonly reported in grapevine and other species (Chaves et al. 1987, Tenhunen et al. 1987) and is probably due to a direct response of guard cells to air humidty (Schulze 1986). For practical purposes, gs should be measured early in the morning at low VPD, ensuring light intensity is not limiting gs. Under these conditions

differences in gs between irrigated and non-irrigated vines should be greater.

Acknowledgements

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