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RELATIONSHIPS BETWEEN LEAF WATER POTENTIAL AND PHOTOSYNTHETIC ACTIVITY OF FIELD-GROWN GRAPEVINES UNDER A MEDITERRANEAN ENVIRONMENT

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Abstract

In order to verify the dependence of net assimilation rate (A) and stomatal conductance (g_s) on leaf water potential (ψ), physiological data from a training system and irrigation experiment conducted during 1991 and 1992 are correlated. In 1991, a very hot and dry season caused a high water stress, which induced premature leaf senescence and low photosynthetic rates on the remaining leaves and, consequently, reduced berry sugar accumulation. The irrigation applied in 1992 positively affected grapevine physiology, growth and yield without changing wine quality. In stress conditions, A and g_s measured during the summer on sun leaves at three different periods of the day were highly correlated with predawn leaf water potential (ψ_{pd}). In non-irrigated plants the correlations between the diurnal values of ψ and A or g_s , measured at the same time, were also significant but the coefficients were lower than those found on the correlation with the ψ_{pd} . In the irrigated vines there were no significant correlations between ψ values and A or g_s measured during the photoperiod. Under water stress conditions, ψ_{pd} was a very sensitive indicator of the physiological activity of sun leaves. During the photoperiod, leaf water status was a poor indicator of sun leaf photosynthetic activity and its relative importance decreases with the increase in soil water availability.

1. Introduction

During summer, grapevines in the mediterranean region are often subjected to a soil water deficit combined with high irradiance, high temperature and low air humidity. Grapevines respond to water deficits by stomatal closure restricting transpirational loss during periods of high atmospheric demand. This strategy helps to increase the daily water use efficiency but affects CO_2 uptake and increases leaf temperature, leading to an important reduction on carbon assimilation (Chaves, 1991; Lopes, 1994).

Stomatal conductance decreases with soil water depletion (Downton *et al.*, 1987). In contact with drying soil roots generate chemical compounds that, when transported to the shoots, can restrict stomatal aperture independently of plant water status (Davies and Zhang, 1991). ABA appears to play an important role in this regulation (Correia *et al.*, 1995).

Leaf water potential has commonly been used as a plant water status indicator. When using this indicator it is assumed that there is no osmotic regulation although, when water stress develops, vine leaves have the ability to accumulate solutes, decreasing the osmotic potential and allowing the plant to maintain a positive turgor as water potential becomes more negative (Düring, 1984; Rodrigues *et al.*, 1993).

Predawn leaf water potential is a good estimate of mean soil water potential for the more wetted soil volume explored by roots (Pacheco, 1989). It is a more sensitive indicator of water stress than the diurnal values (Van Zyl, 1987; Castro *et al.*, 1993) as,

during water stress, the increase in stomatal closure can moderate the decrease in leaf water potential. Moreover, diurnal variations in leaf water status are strongly dependent on other environmental factors such as light intensity, air temperature and humidity (Schulze, 1986).

The aim of this study was to examine the dependence of stomatal conductance and net assimilation rate on leaf water potential in order to understand the relative importance of plant water status for photosynthetic activity of a field-grown white portuguese grapevine variety.

2. Materials and methods

Data was collected in a field trial carried out on the experimental vineyard of the Instituto Superior de Agronomia, located at Tapada da Ajuda, Lisbon (39° 10' N; 8° 45' W). The six-year-old vines of the white variety 'Fernão Pires', grafted on R99, were spaced 2.8 m between and 1.1 m along rows and trained on a vertical trellis. The trial compared two pruning systems - *Guyot vs Royat*- and two trunk heights - 45 vs 85 cm - arranged in a 2 x 2 factorial experiment in a randomised complete block with four replications of 18 vines. As a consequence of three consecutive dry seasons, a new factor - irrigation - was added in 1992. A furrow irrigation of 50 mm was applied four times between 29 June (24 days before veraison) and 3 August (11 days after veraison). For a detailed description of methodologies and growing conditions see Lopes (1994).

Leaf water potential (ψ) and photosynthesis (A) measurements were made 3 and 4 times a day, periodically with a pressure chamber and an IRGA (LCA-2, ADC), respectively. Measurements were made on four to six leaves per treatment using different leaves for gas exchange and ψ measurements. Sampled leaves were fully mature, well exposed and dew free. Data were collected on hot sunny days during the 1991 and 1992 seasons between June and August (table 1). As water stress had a major role, data were divided into two main groups - irrigated and non-irrigated - for correlation analysis

3. Results

3.1. Seasonal and diurnal leaf activity

In both seasons, the very low predawn leaf water potential (ψ_{pd}) measured at veraison (-0.4 to -0.5 MPa) indicated a high soil water depletion in the root zone and a severe water stress which induced premature leaf senescence and low photosynthetic rates on the remaining leaves. This stress has negatively affected berry sugar accumulation and plant longevity. The irrigation applied in 1992 affected positively grapevine physiology, growth and yield without changing wine quality (data not shown, Lopes, 1994).

As in precedent season, the ψ_{pd} measured on non-irrigated plants (NI) showed in 1992 a decreasing pattern from middle of June to harvest date (Fig. 1A). In both treatments, the seasonal pattern of A , measured at midday in 1992, showed a decrease from the beginning of July (3 weeks before veraison) to harvest date (Fig. 1B). During all season, irrigated plants presented significantly higher A values showing the positive effects of water availability on the photosynthetic rate.

Figure 2 shows a time-course of ψ and A measured at veraison (23 July 1992). The ψ decreased from morning to midday and then increased slightly in the afternoon (fig. 2A). Both treatments showed a similar pattern although irrigated plants always exhibited a significantly higher ψ . Diurnal pattern of photosynthetic rate showed a similar trend with the highest values in the morning and the lowest ones at noon. The stressed plants showed significantly lower photosynthetic rates during the whole day and a more intense midday depression than irrigated ones (fig. 2B).

3.2. Relationships between leaf water potential and physiological activity

Diurnal values of A presented a strong correlation with stomatal conductance (g_s) (NI: $r = 0.94$; I: $r = 0.77$) showing that fluctuations in A were closely related to alterations in g_s .

In non-irrigated vines, g_s and A were highly and significantly correlated with ψ_{pd} (Fig. 3). This positive dependence was observed at the three measurement times with the highest coefficients of determination (R^2) obtained in the afternoon. At all times of the day the ψ_{pd}/g_s regression lines had a lower R^2 than those found for the ψ_{pd}/A relationship. For both relationships, the highest slope of regression lines was obtained at noon. Plots show that the dependent variables had a higher variability at more positive ψ_{pd} than at lower ones ($\psi_{pd} < -0.5$ MPa), suggesting a non-linear relationship.

In irrigated plants, diurnal fluctuations of g_s and A show a much lower dependence on ψ_{pd} than stressed plants did (Fig. 4). The highest R^2 was observed in the afternoon and the smallest at noon ($R^2 \approx 0$).

Table 2 presents the correlation coefficients between diurnal values of ψ and g_s or A measured at three different periods of the day. In NI plants the correlations are all significant but the coefficients are much lower than those found in correlations with ψ_{pd} . The highest correlation coefficient was observed in the afternoon for NI plants. In irrigated plants no significant correlations were found.

4. Discussion

During conditions of water stress, the highly significant correlations found in ψ_{pd}/g_s and ψ_{pd}/A relationships show that predawn leaf water potential can be a very sensitive indicator of sun leaf physiological activity. However, when the root zone is well watered, shown by high ψ_{pd} values of > -0.25 MPa, the relative importance of this indicator decreases. This could be a result of the absence of a root signal in wetted soil (Davies and Zhang, 1991) and, consequently, stomatal conductance and photosynthetic fluctuations were mainly dependent on atmospheric conditions (Schulze, 1986).

Despite the significant correlations found in diurnal ψ/g_s and ψ/A relationships the low correlation coefficients indicate that, in stress conditions, diurnal leaf water status explains only a small part of diurnal variations on stomatal conductance and photosynthetic activity of sun leaves. In irrigated plants this relative dependence decreases almost to zero. This lack of correlation shows that during the photoperiod combined effects of high light, high temperature and vapour pressure deficits and other photosynthetic limitations (Chaves, 1991) can override the effects of leaf water status on diurnal fluctuations of net CO_2 assimilation.

The results shown in this study underline the great importance of predawn leaf water potential as a sensitive indicator of photosynthetic activity of field-grown grapevines under stress conditions.

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Table 1. Data collection dates and atmospheric conditions. (PPFD – Photosynthetic photon flux density).

Year/ Date	Days After veraison ⁽¹⁾	Average PPFD at leaf surface ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$)			Air temperature (°C)		
		10:00 h ⁽²⁾	14:00 h	18:00 h	10:00 h	14:00 h	18:00 h
1991							
25 June	-28	1624	1617	1226	31	30	28
25 July	+2	1472	1758	1299	25	31	27
13 August	+21	1018	1430	1077	30	37	35
1992							
16 June	-34	1181	1550	1177	22	24	23
7 July	-13	1633	1807	1483	27	27	27
23 July	+3	1820	1893	1744	27	29	26
6 August	+14	1510	1066	1011	31	35	31

(1)-Veraison: 1991 – 23 July; 1992 – 20 July. (2) Local time.

Table 2. Correlation coefficients (r) between daily leaf water potential (ψ) and stomatal conductance (g_s) or net assimilation rate (A) measured during the 1991 and 1992 seasons. Non-irrigated: n= 56; Irrigated: n= 24.

	MORNING (10 h)		MIDDAY (14 h)		AFTERNOON (18 h)	
	Non Irrigated	Irrigated	Non Irrigated	Irrigated	Non Irrigated	Irrigated
g_s	0.43 **	0.30	0.46 ***	0.10	0.77 ***	0.41
A	0.46 ***	0.05	0.36 **	0.12	0.75 ***	0.05

, * - significant at 1% and 0.1% levels, respectively.

Figure 1. Seasonal patterns of predawn leaf water potential (Ψ_{pd}) and net assimilation rate (A) measured at midday in 1992. Average $\pm$ standard error of 16 adult sun leaves. NI- non-irrigated; I - irrigated. Arrows indicate irrigation dates.

Figure 2. Diurnal time-course of leaf water potential (Ψ) and net assimilation rate (A) measured at veraison (23 July 1992). Average $\pm$ standard error of 16 adult grapevine sun leaves. NI- non-irrigated; I - irrigated.

Figure 3. Dependence of stomatal conductance and net assimilation rate on predawn leaf water potential measured during the 1991 and 1992 seasons in non-irrigated 'Fernão Pires' grapevines. Regression lines are plotted for morning (solid line), midday (dashed line) and afternoon (solid bold line). $n=56$; *** - significant at 0.1% level.

Figure 4. Dependence of stomatal conductance and net assimilation rate on predawn leaf water potential measured during 1992 in irrigated 'Fernão Pires' grapevines. $n=23$; *, ** - significant at 5% and 1% levels, respectively. Regression line is plotted only for afternoon data.