

## Water-stress induced physiological changes in leaves of four container-grown grapevine cultivars (*Vitis vinifera* L.)

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### Summary

**Predawn leaf water potential, night respiration, stomatal conductance, transpiration, and photosynthesis of 4 grapevine cultivars were assessed under irrigated and non-irrigated conditions in July, August and September 1994. Predawn leaf water potential was not significantly related to either stomatal conductance or photosynthesis. Water stress induced distinct stomatal closure in all cultivars at 11 a.m. For a given stomatal conductance rate, photosynthesis of stressed vines was lower than that of non-stressed vines. At similar stomatal conductance rate, photosynthesis was lower in cv. Chardonnay than in any other cultivar. Photosynthesis was the physiological parameter mostly affected by water stress. Dry matter production was linearly related to stomatal conductance, photosynthesis, and the night respiration to photosynthesis ratio for all vines pooled together. In contrast, under stress conditions dry matter production was not related to any physiological parameter.**

**Key words:** Dry matter, drought, night respiration, photosynthesis, stomatal conductance, transpiration, *Vitaceae*, water stress.

**Abbreviations:** A = photosynthesis, ABA = abscisic acid, E = transpiration,  $g_s$  = stomatal conductance, NR = night respiration, NS = non-stressed, S = drought-stressed,  $\psi_{PD}$  = predawn leaf water potential.

### Introduction

Drought is one of the leading environmental stresses causing decreases of plant production in the Mediterranean area. Most higher plants have mechanisms to avoid or to endure water stress, and they have also developed mechanisms to increase their water use efficiency (JONES 1983).

Mechanisms like drought avoidance by reducing leaf surface area (WINKEL and RAMBAL 1993), a high degree of succulence (DÜRING and SCIENZA 1980), a high leaf water storage capacity (DÜRING and SCIENZA 1980, SCHULTZ 1996), high stomatal density (DÜRING 1980), lowered stomatal conductance (KLIEWER *et al.* 1985, WILLIAMS *et al.* 1994, DÜRING *et al.* 1996, SCHULTZ 1996, SPRING 1997, FLEXAS *et al.* 1998) have all been observed in *Vitis vinifera* L. In addition, drought tolerance, *e.g.* by osmoregulation (DÜRING 1984,

GRIMES and WILLIAMS 1990, SCHULTZ and MATTHEWS 1993) and diminished water reserves in the apoplast to preserve metabolic functions (SCHULTZ 1996), have also been documented.

Grapevine cultivars have been deemed to be adapted to arid conditions if they survive and, in addition, produce high yield and quality under non-optimal conditions (DÜRING and SCIENZA 1980, ALBUQUERQUE-REGINA 1993). SCHULTZ (1996) concluded that grapevine cultivars avoiding water stress deployed a range of physiological mechanisms in response to stress, whereas drought tolerant cultivars did not undergo adaptive changes of any kind.

The object of the present experiment was to study effects of water stress in leaves of 4 grapevine cultivars originating from ecologically different regions, namely Garnacha tinta, grown in arid parts of Aragón (Spain); Tempranillo, regarded to have its origin in La Rioja (Spain); Chardonnay, from temperate Burgundy (France); Airén, grown in the hot, dry La Mancha region (Spain).

### Material and Methods

The experiment was carried out at the Madrid Polytechnic University in Spain in 1994. Two-year-old grapevines were grown in 35 l weighing lysimeters covered with a plastic film to prevent evaporation and infiltration of rainfall. Excess water from irrigation was allowed to drain into a separate container for quantification. The lysimeters were filled with a mixture of peat, sand, and organic soil (63:25:12). Vines had only one annual shoot. Before starting the experiment, 5 vines per cultivar were used to determine total dry matter of vines. The experiment was completely randomized and included 5 single-vine replications per cultivar and water availability treatment. Two factors were analysed: cultivar and water availability. The cultivars, Garnacha tinta, Tempranillo, Chardonnay, and Airén, were grafted to 1103 Paulsen. The water availability treatments were drought stressed (S) and non-stressed (NS).

The leaf area per vine was measured biweekly. Using a second order polynomial equation, vein length was related to leaf area for each cultivar.

NS grapevines were irrigated to maintain the potting medium close to field capacity. Each week the amount of water the vines had absorbed the week before was supplied. Water consumption was determined gravimetrically, making allowance for drainage. In the S treatment grapevines re-

ceived 50 % of the water consumed by the NS vines; the amount of water was corrected according to the ratio of leaf area produced under each of the water availability conditions as follows:

$$W_S = 0.5 \cdot W_{NS} \cdot LA_S \cdot LA_{NS}^{-1}$$

where  $W_S$  = water supplied to the stressed vines,  $W_{NS}$  = water supplied to the non-stressed vines,  $LA_S$  = leaf area of the stressed vines, and  $LA_{NS}$  = leaf area of the non-stressed vines.

Stomatal conductance ( $g_s$ ), transpiration (E), photosynthetic activity (A), night respiration (NR), and predawn leaf water potential ( $\psi_{PD}$ ) were measured, on healthy mature leaves on three dates: 6 July, 7 August and 5 September. For each cultivar per irrigation treatment, a single leaf was measured on each of the 5 replicates to obtain mean values of each cultivar. At 11 a.m. (approximately 9 a.m. solar time)  $g_s$ , E and A were determined on the same sun-exposed leaf. On the days gas exchange was measured, mean solar radiation values were 1732, 1745, and 1704  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , respectively; the corresponding leaf temperature was 30.2; 25.4, and 24.6 °C, respectively; relative humidity was 16.2; 30.9, and 32.3 %, respectively. On August 7, stomatal conductance measurements were also taken at 8 a.m., 2 p.m., 5 p.m., and 8 p.m. local time. Predawn leaf temperature was 19.0, 17.2 and 14.6 °C on 6 July, 7 August and 5 September, respectively.  $g_s$  and E were determined using a steady state porometer (Li-1600, Li-Cor, Lincoln, NE, USA). A and NR were measured using a portable infrared gas analyser system (LI 6200, Li-Cor, Lincoln, NE, USA).  $\psi_{PD}$  was measured using a pressure chamber (Soil Moisture Co., Santa Barbara, CA, USA).

At the onset of the experiment, total dry matter of 5 vines was determined, tissues being dried at 80 °C until weight was constant. At the end of the experiment, total dry matter of 5 vines of each cultivar and irrigation treatment was determined again.

The analysis of variance was performed using the statistical software MSTAT-C (University of Michigan, USA).

## Results and Discussion

**Predawn leaf water potential:** Predawn leaf water potential ( $\psi_{PD}$ ) was used as an indicator of soil moisture levels (WILLIAMS *et al.* 1994), assuming that the water status of vine and soil are balanced (VAN ZYL 1987). Cultivars and the water availability (irrigation treatment) affected the  $\psi_{PD}$  significantly on all three dates of measurement (Tab. 1). The method used to establish the amount of irrigation for stressed vines was designed to achieve a similar level of stress for each cultivar irrespective of the leaf area formation and thus to cancel out the interaction between water availability and cultivar, assuming that leaf area is the most important component of total vine transpiration. On the first date of measurement water stress significantly reduced  $\psi_{PD}$  of Garnacha tinta and Tempranillo but not of Chardonnay and Airén. At the onset of experiments, lysimeters had been watered to field capacity, thus at that time no significant differences in the water potential between the irrigation treatments were perceptible. As the growing season progressed, the differences in  $\psi_{PD}$  between the irrigation treatments be-

Table 1

Predawn leaf water status (MPa) in two-year-old Garnacha tinta (G), Tempranillo (T), Chardonnay (C), and Airén (A) grapevines grown under water stress (S) and not stressed (NS) on three days during the growing season. Factorial analysis of variance, CUL = cultivar, IT = irrigation treatment, CUL·IT = interaction

	6 July	7 August	5 September
CUL	**x	**	**
IT	**	**	**
CUL·IT	ns	ns	**
G-NS vs. G-S	*	**	**
T-NS vs. T-S	*	**	**
C-NS vs. C-S	ns	**	**
A-NS vs. A-S	ns	**	**
G-NS	-0.31 b <sup>y</sup>	-0.34 b	-0.17 b
T-NS	-0.35 b	-0.32 b	-0.19 b
C-NS	-0.22 a	-0.23 a	-0.16 b
A-NS	-0.25 a	-0.24 a	-0.11 a
G-S	-0.45 b	-0.46	-0.50 c
T-S	-0.49 b	-0.49	-0.31 ab
C-S	-0.32 a	-0.40	-0.28 a
A-S	-0.36 a	-0.46	-0.38 b

x ns, \*, \*\*: non-significant, significant at P = 0.05 or 0.01, respectively. <sup>y</sup> Mean separation by Duncan's multiple range test at P = 0.05.

came significant. On the three dates of measurement the average  $\psi_{PD}$  in S vines compared with the NS vines was lowered by 44, 64, and 144 %, respectively. The mean value for the NS vines was -0.24 MPa, that of S vines -0.41 MPa. According to CARBONNEAU (1998),  $\psi_{PD}$  values between -0.2 and -0.4 MPa indicate that vines are suffering slightly, while values between -0.4 and -0.6 MPa indicate severe stress.

The cultivars exhibited significantly different  $\psi_{PD}$  values for each of the irrigation treatments, except for stressed vines on August 7. Among the NS grapevines cv. Airén had highest  $\psi_{PD}$  values on all dates but did not show higher stomatal conductance values at 11 a.m. (Tab. 2). Of the S grapevines Garnacha tinta had the lowest values on all three dates, differences between cultivars being significant. Significant  $\psi_{PD}$  differences between cultivars under non-irrigated conditions have been observed by BOTA *et al.* (2001), MEDRANO *et al.* (2003), but not by SPRING (1997).

**Stomatal conductance:** An increase in stomatal conductance ( $g_s$ ) was observed for both irrigation treatments on August 7 from dawn to 11 a.m. The value increased from dawn to peak at 11 a.m. in the cvs Airén and Tempranillo and at 2 p.m. in cvs Chardonnay and Garnacha tinta under NS conditions (Fig. 1). The increase during the morning was apparently due to increasing light intensity and was followed by a decrease in  $g_s$  possibly due to greater stomatal sensitivity to the partial pressure of intercellular CO<sub>2</sub> in the afternoon and due to an increase of abscisic acid (ABA) (DURING and LOVEYS 1996). Values were significantly higher at 11 a.m. in NS Airén vines (Tab. 4). The trend of  $g_s$  in S vines differed from that of NS vines on August 7 (Fig. 1),

Table 2

Gas exchange rates of leaves of 4 cultivars at 11 a.m. on three days. Factorial analysis of variance. For details: Tab. 1

	Stomatal conductance (mmol H <sub>2</sub> O·m <sup>-2</sup> ·s <sup>-1</sup> )			Transpiration (mmol H <sub>2</sub> O·m <sup>-2</sup> ·s <sup>-1</sup> )			Net CO <sub>2</sub> assimilation rate (μmol CO <sub>2</sub> ·m <sup>-2</sup> ·s <sup>-1</sup> )		
	6 July	7 August	5 Sept.	6 July	7 August	5 Sept.	6 July	7 August	5 Sept.
CUL	* x	ns	**	*	ns	**	**	ns	**
IT	**	**	**	**	**	**	**	*	**
CUL·IT	ns	*	**	ns	ns	**	ns	ns	**
G-NS vs. G-S	**	ns	**	**	ns	**	*	ns	**
T-NS vs. T-S	**	ns	ns	**	ns	ns	**	ns	ns
C-NS vs. C-S	*	ns	ns	*	ns	ns	**	ns	ns
A-NS vs. A-S	**	**	**	**	**	*	**	*	**
G-NS	109	211 b <sup>y</sup>	102	4.3	5.2	2.4	8.2 bc	12.4	8.5
T-NS	137	218 b	112	5.4	5.2	2.5	11.9 a	10.2	9.4
C-NS	103	194 b	104	4.1	4.5	2.6	6.4 c	9.0	7.9
A-NS	113	277 a	110	4.5	6.5	2.6	9.1 b	12.0	7.5
G-S	60	195	29 c	2.4	4.7	0.7 c	3.7	9.8	2.4 c
T-S	84	188	121 a	3.4	4.7	2.9 a	4.9	9.8	9.5 a
C-S	72	170	110 a	2.9	4.0	2.6 a	3.2	8.3	6.1 b
A-S	67	170	75 b	2.7	4.0	1.8 b	5.4	8.3	3.2 c

x ns, \*, \*\*: non-significant, significant at P = 0.05 or 0.01, respectively.

y Mean separation by Duncan's multiple range test at P = 0.05.

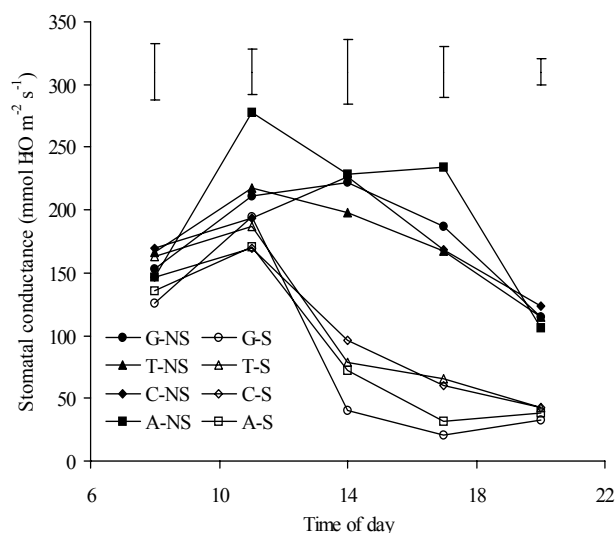


Fig. 1: Diurnal changes of stomatal conductance in two-year-old Garnacha tinta (G), Tempranillo (T), Chardonnay (C), and Airén (A) grapevines grown under water stress (S) and not stressed (NS) on August 7. Bars represent coefficient of variation.

values peaking at 11 a.m. but at a lower level than in NS vines. Subsequently the  $g_s$  values dropped, Garnacha tinta vines having lowest values at 2 p.m. SCHULTZ (1996) found this cultivar to be more sensitive to water stress than cv. Shiraz grapevines. Similar differences in the pattern of daily stomatal conductance in the field between irrigated and water-stressed grapevines were observed for cv. Carignane by KLIEWER *et al.* (1983).

No major differences in the patterns of daily stomatal conductance were observed among the cultivars within each irrigation treatment; this agrees with the findings of SCHULTZ

(1996). In contrast, SPRING (1997) reported that under conditions of water stress  $g_s$  decreased distinctly in some cultivars before noon compared to smaller decreases in some other cultivar.

The critical leaf water potential at which stomata close depends on various factors, *e.g.* environmental conditions, leaf position and age, vine prehistory (SMART and COOMBE 1983). On the other hand, it appears that stomatal closure does not occur in response to hormonal signals from the roots in all cultivars (SCHULTZ 1996). In our experiment water stress lowered  $g_s$  significantly on all three dates (Tab. 2), the mean decrease being 33 % even though  $\psi_{PD}$  values did not differ significantly between the NS and S treatments in cvs. Chardonnay and Airén (Tab. 1).

For both irrigation treatments peak values of  $g_s$  were recorded in August. FANIZZA and RICIARDI (1990) reported that as the growing season advanced stomatal resistance (the inverse of  $g_s$ ) tended to increase under S conditions but to remain constant under NS conditions. However, as BARTOLOMÉ (1993) pointed out for unirrigated Tempranillo grapevines in the field, at the end of the season leaf senescence may lower  $g_s$  values. The effect of water stress on the last date was smaller than on the other dates, the mean reduction in  $g_s$  caused by water stress being 39 %, 38 %, and 22 % on July 6, August 7, and September 5, respectively. Other studies have reported larger differences in  $g_s$  between irrigation treatments (BARTOLOMÉ 1993, PEREIRA and CHAVES 1993), possibly due to different degrees of water stress.

At the end of the season  $g_s$  differed significantly among stressed cultivars, the lowest values were recorded for Garnacha tinta, followed by Airén (Tab. 2) possibly due to their low  $\psi_{PD}$  values (Tab. 1). Irrigated Airén vines exhibited significant differences in  $g_s$  at all three dates. Tempranillo

and Chardonnay vines displayed the lowest changes of  $g_s$  which did not differ significantly between S and NS vines despite significant differences of  $\psi_{PD}$  between the treatments; they showed significantly highest values under S conditions. Tempranillo and Chardonnay may be classified “luxurious”, and Garnacha tinta and Airén “alarmist” cultivars following the classification proposed by BOTA *et al.* (2001). The cultivars displayed differing stomatal sensitivity to water stress, cultivars with the lowest stomatal conductance values being able to tolerate low water availability and hence being most drought-resistant (DÜRING and SCIENZA 1980, KLIEWER *et al.* 1985, DÜRING 1990, SCHULTZ 1996, SPRING 1997, BOTA *et al.* 2001). These varietal differences in stomatal sensitivity to water stress are possibly related to differences in ABA levels (FREGONI *et al.* 1977, DÜRING and BROQUEDIS 1980) or to different thresholds of sensitivity to ABA (LOVEYS and DÜRING 1984). But  $g_s$  seems to be regulated by leaf hydraulic conductance as well (SCHULTZ 2003). Stomatal closure may be induced by ABA and hydraulic signals acting independently (LOVISOLO *et al.* 2002).

**Stomatal control of photosynthesis and transpiration:** Photosynthesis seems to be closer related to stomatal conductance than to the leaf water status (MEDRANO *et al.* 2002). Stomatal closure is not related linearly with photosynthesis (LAKSO 1985, WILLIAMS *et al.* 1994, DÜRING *et al.* 1996, FLEXAS *et al.* 1998). For  $g_s$  values below  $100 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ , there was a sharp drop in photosynthesis, whereas above  $100 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$  there was only a slight increase (Fig. 2). Water stress significantly modified the regression between  $g_s$  and photosynthesis (statistical analysis not shown). For a given value of  $g_s$ , photosynthesis was higher in NS than in S vines even at low values of  $g_s$ . This indicates that under water stress photosynthesis may be affected by non-stomatal factors such as air humidity, carbohydrate accumulation or photoinhibition (DÜRING 1991). Moreover non-stomatal limitation of photosynthesis seems to be related to decayed electron transport rates and reduced Ribulose-1,5-biphosphate regeneration (MEDRANO *et al.* 2003). Stomatal closure is the main limitation of photosynthesis under mild water stress ( $g_s > 150 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ), when  $g_s$  arrives at  $50 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$  diffusional limitations are the main factor limiting photosynthesis (FLEXAS *et al.* 2002). The relationship between  $g_s$  and photosynthesis differed among cultivars (Fig. 2). For a given value of  $g_s$ , Garnacha tinta and Tempranillo vines had higher photosynthetic rates, while Chardonnay vines had lowest values. DÜRING (1987) also observed differences in the relationship between photosynthesis and stomatal conductance between cultivars.

Of the gas exchange parameters photosynthesis was mostly affected by water stress, as was reported by KRIEDEMANN and SMART (1971), CHAVES *et al.* (1987), and SCHULTZ (1996). On July 6 photosynthesis of stressed vines was 51 % lower, and there were significant differences between the NS and S vines for all the cultivars (Tab. 2). On August 7 the reduction of photosynthesis due to water stress was 16 %, on September 5 38 %, but not all stressed cultivars had lower photosynthetic activity on these dates. The differences between the cultivars were significant for NS vines on the first date and for the S vines on the last date. Values

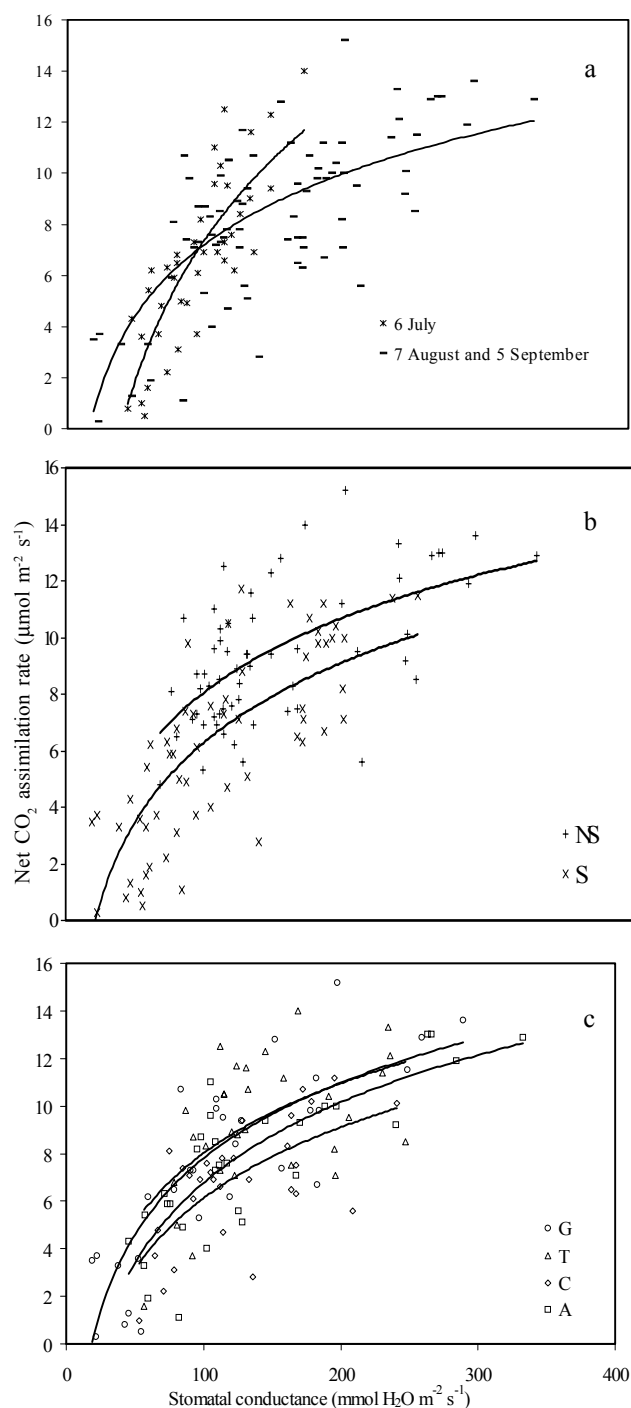


Fig. 2: Relationship between stomatal conductance and net  $\text{CO}_2$  assimilation rate of 4 cvs on July 6, August 7, and September 5. **a:** Regression for 6 July:  $Y = 7.8 \ln(X) - 28.4$  ( $R^2 = 0.68$ ); regression for 7 August and 5 September:  $Y = 4.0 \ln(X) - 10.9$  ( $R^2 = 0.51$ ). **b:** Regression for NS:  $Y = 3.8 \ln(X) - 9.3$  ( $R^2 = 0.36$ ); regression for S:  $Y = 4.1 \ln(X) - 12.4$  ( $R^2 = 0.57$ ). **c:** Regression for Garnacha tinta (G):  $Y = 4.6 \ln(X) - 13.4$  ( $R^2 = 0.70$ ); regression for Tempranillo (T):  $Y = 4.2 \ln(X) - 11.5$  ( $R^2 = 0.32$ ); regression for Chardonnay (C):  $Y = 4.3 \ln(X) - 13.7$  ( $R^2 = 0.43$ ); regression for Airén (A):  $Y = 4.9 \ln(X) - 15.7$  ( $R^2 = 0.65$ ). For details: Fig. 1.

on these days were higher for Tempranillo than for the other cultivars under both irrigation treatments (Tab. 2). BRAVDO *et al.* (1972) likewise did not find significant differences among cultivars, while ALBUQUERQUE-REGINA (1993), CHAVES (1986) and BOTA *et al.* (2001) did. Stomatal closure led to a

linear decrease of the transpiration rate (Fig. 3), as was previously observed by LAKSO (1985) and DÜRING (1987, 1990). The linear regression between  $g_s$  and transpiration were significantly different under NS and S conditions (statistical analysis not shown). This resulted in slightly higher transpiration rates in NS vines than in the S vines for a given value of  $g_s$ . The regression for measurements taken on the first day were significantly different from the two others (statistical analysis not shown). The slope of the regression line of the first day was 5 times higher than that on the two other days, *i.e.* at a given stomatal conductance, transpiration rates of young leaves were higher than those of mature leaves. This may be explained by the fact that during the first day leaf temperature was higher and relative humidity was lower than during the two others.

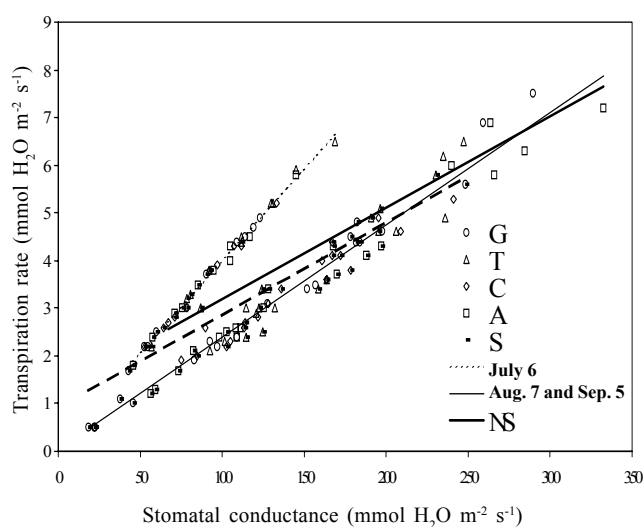


Fig. 3: Relationship between stomatal conductance and transpiration rate of 4 cvs on July 6, August 7, and September 5. Regression for NS:  $Y=0.02X+1.3$  ( $R^2=0.64$ ); regression for S:  $Y=0.02X+0.8$  ( $R^2=0.79$ ); regression for 6 July:  $Y=0.04X+0.1$  ( $R^2=0.99$ ); regression for 7 August and 5 September:  $Y=0.02X+0.03$  ( $R^2=0.96$ ). For details: Fig. 3.

**Night respiration:** On the first two dates night respiration was affected by water availability; night respiration was different between cvs (Tab. 3). The effect of water stress on night respiration was not constant during the growing season. On the first date night respiration increased significantly due to water stress in Chardonnay vines, whereas on the second date it was significantly lower in Airén vines; no significant differences were recorded between the irrigation treatments for the other cultivars. Our results do not corroborate a decrease of dark respiration at moderate or severe stress as reported by HSIAO (1973). Rather, as BEGG and TURNER (1976) observed, the decrease in night respiration was less than that of photosynthesis, and there was no reduction in night respiration until water stress had caused stomatal closure and restriction of photosynthesis.

Mean night respiration values were higher at the first date and decreased thereafter, possibly they were related to temperature (AMTHOR 1989). Night respiration influenced photosynthesis, an increment in night temperature produced an increment in respiration and in photosynthesis the day

after, due to the reduction of carbohydrates in leaves (TURNBULL *et al.* 2002). Night respiration values for NS vines peaked at the second date coinciding with maximum rates of photosynthesis and stomatal conductance (Tab. 2). In contrast, except for Airén, a decline in night respiration was observed in S vines as the season progressed. Under field conditions SCHULTZ (1996) also reported that night respiration decreased with increasing drought. For both irrigation treatments, night respiration values for Airén were among the lowest, the difference being statistically significant.

**Water use efficiency (A/E):** The ratio of photosynthesis to transpiration (A/E) is an indicator of the water use efficiency of leaves (DÜRING 1990). A/E is reported to be affected by irrigation treatments (EIBACH and ALLEWELDT 1984) and differs between cultivars (DÜRING 1987, 1990); in the present experiment the only significant differences between the irrigation treatments were those between Tempranillo and Chardonnay on the first date (Tab. 3). There were no significant differences between cultivars on any other date for either irrigation treatment. Similarly, SPRING (1997) did not observe differences in the ratio A/E among cultivars.

**Night respiration/photosynthesis (NR/A):** Night respiration was 17 % of net photosynthesis at 11 a.m. Values ranged between 8 % and 37 %, except for stressed Chardonnay vines on the first date (62 %) (Tab. 3). ALBRIZIO and STEDUTO (2003) report values of 60 % (sunflower) and 30 % (wheat).

Water stress caused a significant increase in the NR/A ratio. S vines of Garnacha tinta, Tempranillo, and Chardonnay exhibited significantly higher values than NS vines on July 6, as was the case for the Airén vines on September 5.

NR/A was different between cvs on the first two dates at temperatures of 19.0 °C and 17.2 °C respectively, while on the last date temperature was 14.6 °C. Values for Chardonnay were significantly higher on all dates compared to Airén and Tempranillo.

**Dry matter production and leaf physiological activity:** Dry matter production over the growing season was linear when related to mean  $g_s$  and to mean photosynthesis, both on a single cultivar basis and based on the average of cultivars (Tab. 4), such that dry matter production increased with  $g_s$  and A.

On the other hand, considering S vines only, dry matter production was not linearly related neither to stomatal conductance nor to photosynthesis. The relationship between dry matter production and net photosynthesis was significant for NS vines. Stomatal conductance and net photosynthesis may be regarded as indicators of vine productivity as long as vines of the same cultivar are compared.

Dry matter production of NS vines was linearly related to night respiration, but the regression were not significant for any cultivar investigated or for S vines (Tab. 4).

In no case the relationship between dry matter production and A/E was significant (Tab. 5).

The relationship between dry matter production and NR/A was linear for Garnacha tinta, Chardonnay, and Airén and for all the NS vines pooled (Tab. 5).

There was no linear relation between dry matter production and leaf physiological parameters or the ratios between

Table 3

Night respiration, water use efficiency (A/E) and night respiration/photosynthesis ratio of leaves of 4 cultivars on three days. Factorial analysis of variance. For details: Tab. 1

	Night respiration ( $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ )			A/E ( $\text{mmol CO}_2 / \text{mol H}_2\text{O}$ )			Night respiration (%)		
	6 July	7 August	5 Sept.	6 July	7 August	5 Sept.	6 July	7 August	5 Sept.
CUL	** x	**	ns	ns	ns	ns	**	**	ns
IT	*	**	ns	**	ns	ns	**	ns	*
CUL:IT	ns	ns	ns	ns	ns	ns	**	ns	ns
G-NS vs. G-S	ns	ns	ns	ns	ns	ns	*	ns	ns
T-NS vs. T-S	ns	ns	ns	*	ns	ns	*	ns	ns
C-NS vs. C-S	*	ns	ns	*	ns	ns	**	ns	ns
A-NS vs. A-S	ns	*	ns	ns	ns	ns	ns	ns	*
G-NS	1.183	1.547 a	1.133	1.925	2.569	3.639	14.3 bc	13.2	13.9
T-NS	1.024	0.934 b	0.883	2.200	2.007	3.565	9.3 a	9.14	8.8
C-NS	1.325	1.413 a	1.062	1.605	2.028	3.168	21.2 c	16.20	13.8
A-NS	0.770	0.938 b	0.535	2.081	1.864	2.913	8.4 b	7.9	6.9
G-S	1598 a <sup>y</sup>	1.042	0.926	1.386	2.086	3.759	24.8 b	11.0 ab	33.9
T-S	1.520 a	0.807	0.802	1.400	2.150	3.340	21.8 b	8.34 b	8.1
C-S	2.262 a	1.150	0.829	1.045	2.074	2.555	62.0 a	13.0 a	15.6
A-S	0.581 b	0.591	0.900	2.055	2.081	1.950	10.7 b	7.1 b	37.0

<sup>x</sup> ns, \*, \*\*: non-significant, significant at P = 0.05 or 0.01, respectively.

<sup>y</sup> Mean separation by Duncan's multiple range test at P = 0.05.

Table 4

Relationship between dry matter production per vine and gas exchange parameters. For details: Tab. 1

	Stomatal conductance ( $\text{mmol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ )		Net photosynthesis ( $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ )		Night respiration ( $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ )	
G	y = 2.7 x + 123	**	y = 39 x - 45	**	y = 230 x - 3	ns
T	y = 3.7 x - 289	*	y = 39 x - 118	*	y = -28 x + 271	ns
C	y = 4.6 x - 340	*	y = 32 x + 25	*	y = -88 x + 357	ns
A	y = 3.0 x - 142	**	y = 45 x - 80	**	y = 303 x + 45	ns
NS	y = 0.2 x + 308	ns	y = 10 x + 250	*	y = -35 x + 379	*
S	y = 0.3 x + 123	ns	y = - x + 158	ns	y = 7 x + 147	ns
Total	y = 2.7 x - 99	**	y = 33 x - 6	**	y = -18 x + 267	ns

ns, \*, \*\*: non-significant, significant at P = 0.05 or 0.01, respectively.

Table 5

Relationship between dry matter production per vine and the water use efficiency (A/E) and night respiration/photosynthesis ratio. For details: Tab. 1

	A/E ( $\mu\text{mol CO}_2 / \text{mmol H}_2\text{O}$ )		Night respiration/A (%)	
G	y = 23 x + 187	ns	y = -1185 x + 462	**
T	y = 76 x + 57	ns	y = -847 x + 337	ns
C	y = 78 x + 77	ns	y = -675 x + 381	*
A	y = 110 x + 25	ns	y = -2020 x + 471	*
NS	y = 24 x + 281	ns	y = -330 x + 380	**
S	y = -7 x + 170	ns	y = 15 x + 152	ns
Total	y = 41 x + 153	ns	y = -655 x + 347	**

ns, \*, \*\*: non-significant, significant at P = 0.05 or 0.01, respectively.

them in the case of the S vines (Tabs 4 and 5). This demonstrates that analysis of the physiological parameters in our trials was insufficient to explain vine productivity under conditions of water stress.

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