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# Effect of previous water conditions on vine response to rewatering

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## Summary

**A comparative study of stomatal responses to rewatering was conducted on grapevines previously subjected to conditions of water stress and no water stress. Two cultivars were grown in 35 L lysimeters: 'Airén', from the dry zone of La Mancha, and 'Chardonnay', from the humid zone of Burgundy. The day after rewatering no significant differences in soil water content were found between water treatments or cultivars. However, predawn leaf water potential was significantly higher under non-stress than under stressed conditions, differences between cultivars were also found. Water consumption during the 5 d after rewatering was directly related to vine leaf area development. Vines grown under water stress conditions showed more uniform stomatal behaviour after rewatering. One day after rewatering rates of leaf conductance, transpiration and net photosynthesis were significantly higher in non-stressed vines, while 3 d after rewatering leaf conductance and transpiration were significantly higher in vines previously subjected to water stress. Net photosynthesis was significantly higher in water-stressed vines 5 d after rewatering. No differences were found between cultivars with regard to leaf conductance. The differences in the relationship between net photosynthesis and leaf conductance between stressed and non-stressed vines before rewatering were not found after rewatering. The only permanent adaptation mechanism to water stress was a lowering of leaf area development, which allowed water-stressed vines to consume less water to maintain a higher water availability and high or constant stomatal conductance.**

A b b r e v i a t i o n s : $\Psi_{PD}$ - predawn leaf water potential; A - net photosynthesis; $g_l$ - leaf conductance; E – transpiration; NS - no water stress; S - water stress.

K e y  w o r d s : *Vitis vinifera* L., cv. Airén, cv. Chardonnay, predawn leaf water potential, photosynthesis, leaf conductance, transpiration.

## Introduction

Under mediterranean climatic conditions, soil moisture content slowly decreases from the beginning of spring to summer. In some years intermittent rainfall is common throughout summer. Plant growth and survival after these rains depend on the plant's capacity to use available water efficiently and its response to the following drought period.

During the season it is difficult to determine the efficiency of water use due to variations of weather. On the one hand, an 'optimistic' plant will produce a large leaf area, although in very dry years rainfall may be low or even zero so that the plant's survival is threatened. On the other hand, a 'pessimistic' plant ensures its survival and production. In general, an 'optimistic' behaviour, with high stomatal conductance values, is more productive, while a 'pessimistic' attitude with lower stomatal conductance values is more suitable in dry years (Jones 1983).

Other authors have studied seasonal water consumption or vine responses to soil water availability (Bota *et al.* 2001, Deloire *et al.* 2004, Medrano *et al.* 2003). However, little is known about the vine water use after a period of water stress or the response of vines grown either under high or low water availability conditions to water stress. In this work we studied responses of two cultivars to watering previously being subjected to water stress. For this study two cultivars originating from different climatic zones were used: 'Airén' from the dry zone of La Mancha and 'Chardonnay' from the humid zone of Burgundy.

## Material and Methods

This experiment was carried out at the Universidad Politécnica de Madrid in Spain (40º26'36"N, 3º44'18"W, 590 m a.s.l.). Three-year-old grapevines were grown in 35 L lysimeters with a mixture of peat, sand and organic soil (63:25:12) and covered with a plastic film to eliminate evaporation and the infiltration of rainfall. The vines were grown open air in full sun. Drainage was measured in a second container. A 0.2 m TDR soil moisture probe (Trase Soil Moisture, Santa Barbara, CA, USA) was installed in each lysimeter. Each vine was restricted to two shoots. This experiment was completely randomised with 5 single vine repetitions. Two factors were analysed: cultivar and irrigation. The cultivars were 'Chardonnay' and 'Airén' grafted onto '1103 Paulsen'. Irrigation treatments started on May 8.

In the non stress irrigation treatment (NS) the potting medium was kept close to field capacity by applying throughout one week the amount of water the vines had consumed the previous week. Water consumption was determined gravimetrically by allowing drainage. In the stress treatment (S) we applied 50 % of the water consumed by NS vines for each cultivar with corrections for differences in leaf area between treatments, calculated by the following formula:

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

Where $W_S$ = water applied to stressed vines, $W_{NS}$ = water applied to non-stressed vines, $LA_S$ = leaf area of stressed

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vines and $LA_{NS}$ = leaf area of non-stressed vines. Leaf area per vine was measured biweekly. Leaf area was estimated by developing a second order polynomial equation, relating main vein length to leaf area of 30 leaves of each cultivar, as proposed by Carbonneau (1976).

On July 31 all experimental vines were watered to reach field capacity. No additional water was applied for the next 6 d. On August 1, 3 and 5, water consumption of 3 vines of each cultivar was evaluated in each irrigation treatment. Soil moisture content was measured on 5 vines of each cultivar and irrigation treatment. On July 26 and August 1 predawn leaf water potential ($\Psi_{PD}$) of three vines of each cultivar was measured in both irrigation treatments. Before rewatering (July 26) and 1, 3 and 5 d after rewatering (August 1, 3 and 5) leaf conductance ($g_l$), transpiration (E), and net photosynthesis rate (A) were measured at 11 a.m. (9:00 solar hour aprox.) using healthy, mature sun-exposed leaves. On July 26, August 1, 3 and 5 at 11 a.m. relative humidity was 24.5, 35.3, 32.4, 28.3% and temperature was 28.1, 28.7, 24.3, 24.8 ºC. Predawn leaf water potential was measured with a pressure chamber (Soil Moisture Equipment, Santa Barbara, CA, USA). Transpiration (E) and leaf conductance ($g_l$) were measured using a steady state porometer (Li-1600, Li-COR, Lincoln, NE, USA). Net photosynthesis was measured with a portable IRGA system (Li 6200, Li-COR, Lincoln, NB, USA) on leaves fully exposed to solar radiation.

Variance analyses were carried out using the software package MSTAT-C (University of Michigan).

## Results and Discussion

Water consumption: One day after rewatering (August 1) the soil water content did not differ significantly between treatments or cultivars (Tab. 1). However, 3 and 5 d after rewatering soil water content was significantly higher in water-stressed vines than in non stressed vines and 'Chardonnay' had higher values than 'Airén'.

Table 1

Predawn leaf water potential ($\Psi_{PD}$) the day after rewatering (August 1) and water content 1, 3 and 5 d after rewatering for 'Airén' (A) and 'Chardonnay' (C) grapevines cultivated without water stress (NS) and under water stress (S) before rewatering. Factorial analysis of variance (CV = cultivar, IT = irrigation treatment, CUL·IT = interaction)

| | $\Psi_{PD}$ (MPa) August 1 | Water content % (v/v) | | |
|---|---|---|---|---|
| | | August 1 | August 3 | August 5 |
| C-NS | -0.20 | 25.3 | 9.5 | 7.5 |
| A-NS | -0.17 | 25.1 | 9.5 | 4.3 |
| C-S | -0.35 | 30.3 | 29.3 | 16.8 |
| A-S | -0.25 | 26.9 | 21.3 | 10.2 |
| CV | * | ns | * | ** |
| IT | ** | ns | ** | ** |
| CV-IT | ns | ns | * | ns |

ns,**, *, non-significant, significant at P = 0.01 and P = 0.05, respectively.

Water consumption during the 5 d after rewatering was directly related to vine leaf area (Fig. 1); no significant differences were found between cultivars or treatments (statistical analysis not shown). Unstressed 'Airén' vines ('Airén' NS), which developed a larger leaf area before rewatering, consumed more water than those that had developed a smaller leaf area ('Chardonnay' S). In the NS and S treatments leaf area development was greater in 'Airén' than in 'Chardonnay'. The leaf area of non-stressed vines was 3 and 2 times greater than that of stressed vines in 'Chardonnay' and 'Airén' respectively. In stressed vines leaf area developed from budburst to fruit set in both cultivars. In NS vines however, leaf area developed from budburst to veraison (Gómez del Campo et al. 2002).

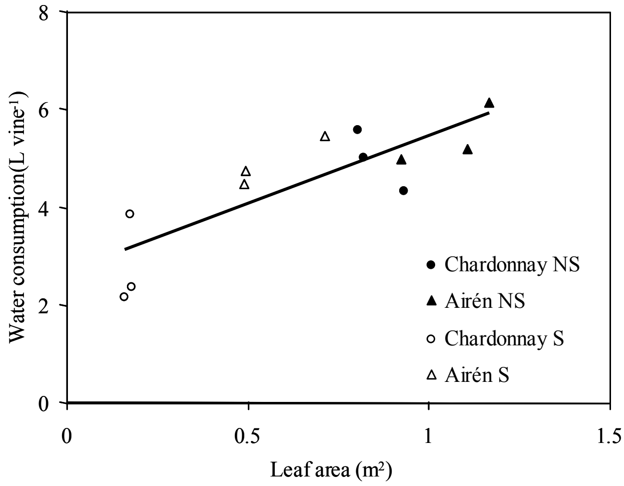


Fig. 1: Water consumption during 5 d after rewatering as a function of vine leaf area ($Y = 2.78x+2.68$, $R^2 = 0.68$*) for 'Airén' and 'Chardonnay' grapevines cultivated without water stress (NS) and under water stress (S) before rewatering.

Predawn leaf water potential ($\Psi_{PD}$): Although the amount of water available to vines after rewatering was not significantly different, significant differences in $\Psi_{PD}$ were found between treatments and cultivars the night after rewatering (Tab. 1). Significantly higher $\Psi_{PD}$ values were obtained in NS vines than in S vines. 'Airén' showed significantly higher $\Psi_{PD}$ values than 'Chardonnay' in both treatments. Higher $\Psi_{PD}$ in NS indicate that, although soil water availability after rewatering was the same in both irrigation treatments (Tab. 1), vines subjected to water stress before rewatering are unable to reach the hydration levels of non-water stressed vines. Sap cavitation in xylem may have prevented total hydration of the water-stressed tissues, thereby causing differences between cultivars as was observed by Schultz (2003). Moreover, the lower development of the root system of water-stressed vines (Gómez del Campo et al. 2005) may explain the lower rehydration capacity. Other authors have also observed that the recovery of vines after rewatering is not immediate. In vines cultivated in pots under water stress conditions, $\Psi_{PD}$ recovered 2 d after rewatering (Hardie and Considine 1976). In a field study Schultz (1996) observed that $\Psi_{PD}$ only slowly recovered after a prolonged period of drought and one precipitation event.

Cultivar differences in rehydration during the night have been shown by Bota *et al.* (2001), Medrano *et al.* (2003) and Gómez-del-Campo *et al.* (2004). Schultz (1996) found that $\Psi_{PD}$ of different cultivars responded differently to one precipitation event after a prolonged period of drought. Schultz (2003) attributed these cultivar differences to differences in the hydraulic conductance of stems and particularly petioles. He obtained different cavitation rates between grapevine cultivars and reported that these differences were related to vine responses to water stress; cultivars with greater hydraulic conductance were more sensitive to cavitation which induced stomatal closure. Besides the hydraulic control of stomatal action there is strong evidence for a hormonal control, mainly by ABA, (Correia *et al.* 1995, Lovisolo *et al.* 2002).

S t o m a t a l  b e h a v i o u r : Before rewatering $g_l$, E and A values of unstressed vines were three times greater than those of the S treatment (Tab. 2). After rewatering leaf conductance increased in both irrigation treatments, 1.7 times in NS and 3.7 in S vines. The high value in NS vines on August 1 compared to June 26 may be due to relative humidity which increased from 24.5 to 35.3 %. One day after rewatering $g_l$ was significantly higher in NS vines (Tab. 2). However, no significant differences were found between treatments in any of the forthcoming measurements. Three d after rewatering a sharp decrease in $g_l$ was observed in the NS vines, nevertheless S vines maintained similar $g_l$ values during the 1, 3 and 5 d after rewatering. This response of $g_l$ in NS vines to a punctual rewatering followed by 6 d without irrigation was related to the high water consumption between August 1 and 3 (Tab. 1) due to the high leaf area which had developed due to the previous water availability (Fig. 1). Stressed vines had more stable $g_l$ values after rewatering (Tab. 2). During the 6 d without irrigation, $g_l$ values were not as low as those of S vines before rewatering (on July 26). At 11 a.m. E values were significantly different between treatments at the first two measurements after rewatering (Tab. 2). One day after rewatering the NS treatment had significantly higher E values, while the S treatment had significantly higher values 3 d after rewatering. One and 5 d after rewatering A values were different between treatments (Tab. 2). One day after rewatering unstressed vines had significantly higher values, while these values were significantly lower 5 d after rewatering. Other authors have also observed that the recovery of $g_l$, E and A after rewatering of stressed vines was not immediate (Kliewer *et al.* 1985, Loveys and Kriedemann 1973, Poni *et al.* 1993), although these values recovered more rapidly than $\Psi_{PD}$ (Schultz 1996). Previous to rewatering S vines were subject to severe stress, after rewatering, the experimental vines were subject to mild stress considering that $g_l$ was higher than or close to 150 $mmol \cdot m^{-2} \cdot s^{-1}$ (Cifre *et al.* 2005).

$g_l$, E and A were not significantly different between cultivars during the experiment (Tab. 2).

Therefore, the lower hydration of vines subjected to water stress before rewatering (Tab. 1) allowed these vines to maintain constant $g_l$ and A rates after rehydration as well as significantly higher A rates 5 d after rewatering (Tab. 2).

R e l a t i o n s h i p  b e t w e e n  $g_l$  a n d  A : Significant differences in the relationship between $g_l$ and A were found between water treatments before rewatering (Fig. 2). Related to $g_l$, A values were higher in the NS treatment, which confirms results of Chaves (1986), Bota *et al.* (2001), Gómez-del-Campo *et al.* (2004). After rewatering however the relationship between A and $g_l$ was not significantly affected by previous water conditions (Fig. 3). This seems to indicate that the relationship between A and $g_l$ is dependent on the water availability. Differences in the adjustment of A to $g_l$ seem to be a specific response to a specific situation of water availability and should not be considered a permanent adaptation mechanism.

After rewatering, the water use efficiency ($A/g_l$) was not significantly different between treatments or cultivars (Tab. 3). This confirms that it is preferable to use the term 'drought tolerant' rather than 'drought resistant' to describe the mechanisms allowing plant survival or productivity under drought conditions (Jones, 1983).

T a b l e 2

Leaf conductance, transpiration and net photosynthesis at 11 a. m. before rewatering (July 26), 1, 3 and 5 d after rewatering for 'Airén' (A) and 'Chardonnay' (C) grapevines cultivated without water stress (NS) and under water stress (S) before rewatering. Factorial analysis of variance (CV= cultivar, IT = irrigation treatment, CUL·IT = interaction)

| | July 26 | August 1 | August 3 | August 5 |
|---|---|---|---|---|
| Leaf conductance (mmol $H_2O \cdot m^{-2} \cdot s^{-1}$) | | | | |
| C-NS | 123.6 | 267.6 | 83.8 | 129.2 |
| A-NS | 179.4 | 229.2 | 92.1 | 108.7 |
| C-S | 51.0 | 180.2 | 149.8 | 134.7 |
| A-S | 37.5 | 146.4 | 167.5 | 163.2 |
| CV | ns | ns | ns | ns |
| IT | ** | ** | ns | ns |
| CV-IT | * | ns | ns | ns |
| Transpiration (mmol $H_2O \cdot m^{-2} \cdot s^{-1}$) | | | | |
| C-NS | 4.03 | 7.08 | 1.72 | 3.37 |
| A-NS | 5.58 | 6.44 | 2.11 | 2.85 |
| C-S | 1.86 | 5.55 | 3.38 | 3.21 |
| A-S | 1.46 | 4.47 | 3.65 | 3.86 |
| CV | ns | ns | ns | ns |
| IT | ** | * | * | ns |
| CV-IT | * | ns | ns | ns |
| Net photosynthesis (µmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) | | | | |
| C-NS | 11.8 | 15.4 | 9.8 | 8.7 |
| A-NS | 11.8 | 14.5 | 9.0 | 4.5 |
| C-S | 4.8 | 11.5 | 10.7 | 11.7 |
| A-S | 3.7 | 10.6 | 11.3 | 12.3 |
| CV | ns | ns | ns | ns |
| IT | ** | ** | ns | * |
| CV-IT | ns | ns | ns | ns |

ns,**, *, non-significant, significant at P = 0.01 and P = 0.05, respectively.

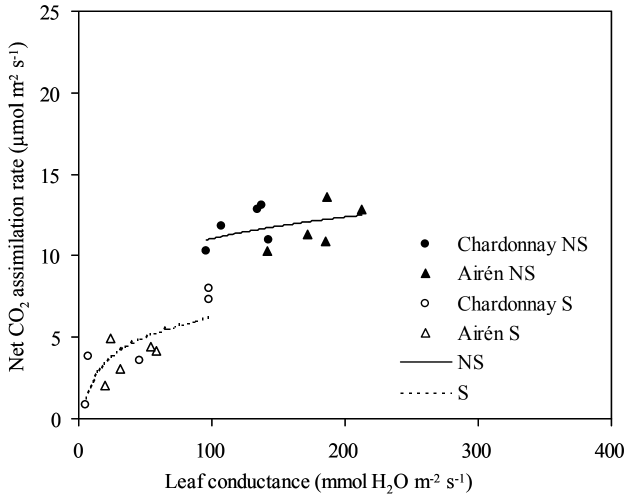


Fig. 2: Net photosynthesis as a function of leaf conductance at 11 a.m. before rewatering of 'Airén' and 'Chardonnay' grapevines cultivated without water stress (NS) and under water stress (S) before rewatering. NS: Y = 1.9 Ln(x) +2.2 $R^2$ = 0.15; S: Y = 1.7 Ln(x) +1.6 $R^2$ =0 .60**.

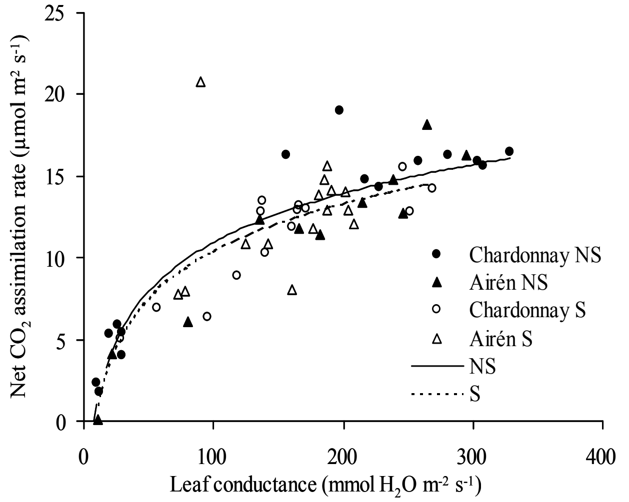


Fig. 3: Net photosynthesis as a function of leaf conductance at 11 a.m. 1, 3 and 5 d after rewatering of 'Airén and 'Chardonnay' grapevines cultivated without water stress (NS) and under water stress (S) before rewatering. NS: Y = 4.3 Ln(x) -9.0 $R^2$ = 0.90**; S: Y = 4.4 Ln(x) -9.7 $R^2$ = 0.58**.

## Conclusions

The only permanent adaptation mechanism to water stress observed in this assay was the lower leaf area development in S vines which allowed to use less water and to maintain higher water availability levels than NS vines. After rewatering S vines did not rehydrate like NS vines possibly due to cavitation and/or lower root development. As a result of lower leaf area and lower hydration, stomatal conductance in S vines remained fairly constant and 5 d after rewatering A was higher than in NS vines.

The use of $\Psi_{PD}$ as an indicator for grapevine irrigation management proposed by CARBONNEAU (1998) should not only consider phenological stages (DELOIRE *et al.* 2004) and cultivars (BOTA *et al.* 2001, MEDRANO *et al.* 2003, SCHULTZ

Table 3

Water use efficiency ($A/g_l$) at 11 a.m. 1, 3 and 5 d after rewatering on July 31 for 'Airén' (A) and 'Chardonnay' (C) grapevines cultivated without water stress (NS) and under water stress (S) before rewatering. Factorial analysis of variance (CV= cultivar, IT = irrigation treatment, CUL·IT = interaction)

| | A/g (µmol $CO_2$·m$^{-2}$·s$^{-1}$ / mmol $H_2O$·m$^{-2}$·s$^{-1}$) | | |
|---|---|---|---|
| | August 1 | August 3 | August 5 |
| C-NS | 0.058 | 0.168 | 0.135 |
| A-NS | 0.064 | 0.332 | 0.010 |
| C-S | 0.072 | 0.081 | 0.300 |
| A-S | 0.073 | 0.071 | 0.076 |
| CV | ns | ns | ns |
| IT | ns | ns | ns |
| CV-IT | ns | ns | ns |

ns, non-significant at P = 0.05.

2003, GÓMEZ-DEL-CAMPO *et al.* 2004), but also previous water conditions of the vine.

In spite of the significant differences in $\Psi_{PD}$ found between cultivars after rewatering, $g_l$, E and A values were found not to be cultivar specific. Due to its stomatal behaviour under conditions of prolonged water stress, 'Chardonnay' can be considered 'luxurious' while 'Airén' could be considered 'pessimistic' (GÓMEZ-DEL-CAMPO *et al.* 2004) according to the classification of BOTA *et al.* (2001), or they could be considered 'isohydric' and 'anisohydric', respectively, terms suggested by SCHULTZ (2003). These genetic differences in stomatal behaviour however, disappeared after rewatering. Likewise, the relationship between A and $g_l$ was not significantly different between treatments after rewatering.

Vines subjected to high water availability experience a sharp decrease in A when irrigation is stopped due to the high water consumption by the great leaf area and high hydration capacity. These results could help to develop irrigation scheduling under conditions of water shortage. Long irrigation intervals with application of high amount of water will cause lower levels of A when vines have consumed the available water than applying low amount of water frequently, because it will induce adaptation of the leaf area development to the available water, thereby improving water use efficiency.

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