

Vitis 46 (1), 1–6 (2007)

Water relations and vulnerability to embolism are not related: Experiments with eight grapevine cultivars

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Summary

Drought tolerance mechanisms at the leaf level have been reported for grapevines but less is known about their vulnerability to embolism caused by water stress. The objective of this experiment was to determine if there is a relationship between xylem hydraulic characteristics and drought resistance mechanisms at the leaf level. The experiment was carried out on 10-year-old plants of 8 *V. vinifera* cvs: 'Sauvignon Blanc', 'Chardonnay', 'Cabernet Sauvignon', 'White Grenache', 'Black Grenache', 'Alicante Bouschet', 'Tempranillo', and 'Parellada' grown under field conditions without irrigation under Mediterranean climatic conditions. Embolism vulnerability curves were drawn for each cultivar. Values of the osmotic potential at full turgor, and at the turgor loss point, and the leaf bulk modulus of elasticity were obtained from pressure-volume curves on 4 different dates, from berries at pea size until harvest. All cultivars except 'Chardonnay', which showed elastic adjustment, showed osmoregulation but different patterns in vulnerability curves were found for each cultivar. While 'Parellada', 'Tempranillo' and 'Black Grenache' proved to have the most vulnerable xylem, 'Chardonnay' and 'Sauvignon Blanc' were shown to have the least vulnerable xylem to embolism. There was no relationship between the level of vulnerability to embolism for each cultivar and the drought tolerance mechanisms at the leaf level under the environmental conditions of this experiment.

Key words: grapevine, drought, vulnerability curves, hydraulic conductivity, water potential, osmoregulation, elastic adjustment.

Abbreviations: AB - Alicante Bouschet, BG - Black Grenache, WG - White Grenache, CH - Chardonnay, CS - Cabernet Sauvignon, PA - Parellada, SB - Sauvignon Blanc, TP - Tempranillo, K - Hydraulic conductance, K_0 - Initial hydraulic conductance, K_{max} - Maximum hydraulic conductance, PCL - Percentage of hydraulic conductivity loss, PV curves - Pressure-volume curves, RWC - Relative water content, VC - Embolism vulnerability curves, ϵ - Leaf bulk modulus of elasticity, Ψ - Leaf water potential, $\Psi_{\pi 0}$ - Osmotic potential at zero turgor, $\Psi_{\pi 100}$ - Osmotic potential at full turgor, Ψ_{50} - Leaf water potential when PCL = 50 %, Ψ_{crit} - Leaf water potential at PCL = 100 %.

Introduction

Summer drought causes periods of water stress, to which certain species adapt by using strategies to maintain

growth and reproductive processes. One of these strategies is the evolution of resilient xylem structures that favor non-interruptible water transport. It has been shown that xylem embolism is a significant factor in reducing plant productivity for plants exposed to abiotic (drought, cold, freeze) or biotic (tracheomycoses, fungus, nematodes) stresses (SPERRY 1995).

Under water stress conditions plants have developed several functional and/or structural solutions in order to avoid and/or reduce this problem. Xylem vessel dimensions are positively related to vulnerability to embolism of the system; short and narrow xylem vessels are advantageous to plants when exposed to xylem embolism; however, this is associated with a lower efficiency of water conduction (TYREE and ZIMMERMAN 2002). On the contrary, plants with wider xylem vessels develop cavitation at higher water potentials than plants with narrow ones (TYREE and DIXON 1986). On the other hand, there is evidence that the pit-membrane pore diameter determines the vulnerability to drought embolism rather than the vessel diameter (LO GULLO and SALLESO 1993, TYREE and ZIMMERMANN 2002). From an ecological point of view, each species or cultivar should develop a xylem structure that permits a proper balance between conductive efficiency and embolism vulnerability depending on the environmental conditions during growth.

We also must take into account the ability of plants to recover from stress (LEVITT 1980). Frequent embolisms may permanently damage xylem vessels, thereby increasing the rate of embolism and decreasing the xylem's capacity to recover. LO GULLO and SALLESO (1993) observed that as the ratio of the minimum diurnal leaf water potential to the leaf water potential at the turgor loss point increased from 0.9 to 1.3 in *Quercus*, the PCL due to summer drought embolism increased from 30 % to 85 % and the xylem's capability to recover from embolism decreased dramatically.

The main objectives of this study are to determine the relationship between xylem hydraulic characteristics and the leaf drought resistance mechanisms of 8 grapevine cultivars.

Material and Methods

Eight *Vitis vinifera* cultivars, 'Sauvignon Blanc' (SB), 'Chardonnay' (CH), 'Cabernet Sauvignon' (CS), 'White Grenache' (WG), 'Black Grenache' (BG), 'Alicante Bouschet' (AB), 'Tempranillo' (TP) and 'Parellada' (PA), all 10 years old, were grown under field conditions without irrigation in a commercial plot in Alt Penedès (latitude =

41° 23' N, longitude = 001° 38' E), Barcelona area, Spain. Average rainfall is 547 mm a year concentrated in autumn. Summer rainfall comprises only 16 % of the total precipitation per year. The average minimum temperature in winter is 1 °C and the average maximum temperature in summer is 32 °C (data collected from the weather station in the experimental plot 6 years prior to the experiment). The soil in the vineyard is alluvial with a silt-clay-loam texture.

S a m p l i n g d a t e s i n 2 0 0 1 : Date I: berries at the stage of pea size (last week of May), date II: veraison (1st week in July), date III during maturation (1st week of August) and date IV was just after harvest (last week of September).

P r e s s u r e - v o l u m e c u r v e s : For each of the 4 sampling dates, mature leaves (10th leaf from the apex) were randomly selected at 10 a.m. from each of the plots. On each of the dates we collected 5 leaves per cultivar to obtain pressure-volume curves (PV curves) (TYREE and RICHTER 1981, SAVÉ *et al.* 1993, 1994.). Osmotic potential at full turgor ($\Psi_{\pi 100}$), zero turgor ($\Psi_{\pi 0}$), and the leaf bulk modulus of elasticity (ϵ) were obtained from the PV curves (TURNER 1988). Leaves were excised, immediately sealed in plastic bags containing water, and transported to the laboratory. Petioles were put in water-filled beakers, re-cut under water and then the beaker was enclosed by a plastic bag to rehydrate the leaf for 24 h at 5 °C in the dark. Five water-saturated leaves of each treatment were measured. Each leaf was weighed and allowed to dehydrate at 23 °C for a period during which they were repeatedly placed in a pressure chamber (Soilmoisture 3005) to determine leaf water potential (Ψ) (KIKUTA and RICHTER 1986). Data for initial saturated weight, intermediate fresh weight corresponding to values of Ψ , and final dry weight were used to calculate the relative water content (RWC). The RWC and the corresponding Ψ were plotted as a "Type II" (Ψ^{-1} x RWC) transformation (TYREE and RICHTER 1981, 1982).

E m b o l i s m v u l n e r a b i l i t y c u r v e s : In embolism vulnerability curves (VC) Ψ is related to the percent of conductivity loss (PCL) (SPERRY *et al.* 1988, COCHARD *et al.* 1992).

Between June and October shoots were sampled several times. The shoots cut off from the plants at the field were rehydrated for 4 d; the cut end of the whole shoot with leaves, was submerged in water and placed in a dark chamber at 4 °C. Water-saturated shoots were introduced in a 10 l plastic container filled with water; during this transfer, the cut end of the shoots was always kept submerged in water to avoid any contact of the cut surface with air. The internodal segments were then cut under water. Immediately before cutting segments, the Ψ of leaves of correspondent nodes were measured in a Scholander chamber. In order to avoid embolism caused by air entering into the cut vessels, the remaining shoot was taken out of the water with its cut end sealed with vaseline. In preliminary experiments we observed that vaseline was sufficiently isolating. The sealed shoots were allowed to dehydrate for some time. The water potential of each stem was measured during the dehydration period.

The initial hydraulic conductance (K_0) of each segment was measured gravimetrically by connecting the

xylem segment to a low-pressure water source (approximately 0.005 MPa) and registering the weight of the exuding water every second on a balance until a steady state was reached. The low-pressure water source consisted of a glass container situated at a height of 1 m. Then embolisms were flushed out using a 0.15 MPa water flow, originating from a compressed air tank, and the hydraulic conductance (K) was measured again. This process was repeated until K no longer changed after flushing, and this point was registered as the maximum conductance (K_{max}).

Finally, the percentage of hydraulic conductivity loss (PCL) was calculated for each Ψ value, from K_0 and K_{max} of the corresponding segment.

Vulnerability curves were obtained for each data set: according to PAMMENTER and VANDER WILLIGEN (1988) Ψ (x-axis) is related to the percentage of hydraulic conductivity loss (y-axis) using the expression:

$$\text{PCL \%} = \frac{100}{1 + e^{a(\Psi-b)}} \quad (1)$$

We obtained coefficients a and b from a linearized form of the expression (1), a corresponds to the slope of the sigmoid curve and b to the position of the curve on the x-axis. From the VC, we obtained Ψ_{50} for each cultivar. Ψ_{50} corresponds to Ψ at which the xylem has lost the 50 % of K_{max} due to embolism; it is the value of the b coefficient in expression (1). From the VC equations, Ψ_{crit} was calculated for each cultivar. Ψ_{crit} is the Ψ corresponding to PCL = 100 % (SPERRY 2004).

S t a t i s t i c a l a n a l y s i s : An analysis of variance on data obtained from the PV curves was performed to detect differences between cultivars. We then performed a Duncan's multiple range test ($\alpha \leq 0.05$) on the significant parameters to find out statistically significant differences between cultivars.

For VC we calculated R^2 and the statistical significance ($\alpha = 0.05$) of the linear regressions made to obtain the sigmoid parameters a and b (PAMMENTER and VANDER WILLIGEN 1998). The SAS reg procedure was used to check the fit of the significant sigmoid regression to the original data. We forced values a and b to the calculated values in the linear regressions. Then, for each pair of parameters corresponding to each cultivar we checked the fit ($\alpha \leq 0.05$) of the sigmoid regression using the original data.

Finally, we performed a Tukey-Kramer test for unplanned comparisons among a set of regression coefficients ($\alpha \leq 0.05$) to compare the a parameter in the 8 linear regressions (SOKAL and ROHLF 1995).

Results

PV curves for AB and WG showed constant and significant decreases in $\Psi_{\pi 100}$ throughout the season (Table). $\Psi_{\pi 100}$ was not significantly different for CH, CS, SB and PA during dates I, II and III, but decreased significantly between date III and IV. For WG, BG and TP the decrease in $\Psi_{\pi 100}$ between date I and III was significant. For date I and IV the difference between $\Psi_{\pi 100}$ was significant for all cultivars except CH and AB. Finally, between dates II

Table

Osmotic potential at full turgor ($\Psi_{\pi 100}$), osmotic potential at the turgor loss point ($\Psi_{\pi 0}$) and bulk modulus of elasticity (ϵ) of leaves of 'Sauvignon Blanc' (SB), 'Chardonnay' (CH), 'Cabernet Sauvignon' (CS), 'White Grenache' (WG), 'Black Grenache' (BG), 'Alicante Bouschet' (AB), 'Tempranillo' (TP) and 'Parellada' (PA) at 4 sampling dates: I: grape at pea size (May, last week), II: veraison (1st week in July), III: during maturation (1st week in August), IV: just after harvest (last week in September). Different letters within each row mean significant differences between dates for each cultivar (Duncan's Multiple Test ($\alpha \leq 0.05$))

Cultivar	Osmotic potential at full turgor $\Psi_{\pi 100}$ (MPa)			
	I	II	III	IV
AB		-0.64 ± 0.05 a	-0.90 ± 0.11 b	-1.57 ± 0.07 c
CH		-0.98 ± 0.11 a	-0.74 ± 0.18 a	-1.85 ± 0.10 b
CS	-0.83 ± 0.06 a	-1.06 ± 0.08 a	-1.12 ± 0.15 a	-1.97 ± 0.11 b
SB	-0.77 ± 0.29 a	-1.01 ± 0.02 a	-1.08 ± 0.05 a	-1.67 ± 0.15 b
PA	-1.17 ± 0.09 a	-1.21 ± 0.07 a	-1.45 ± 0.17 a	-1.89 ± 0.17 b
WG	-0.65 ± 0.06 a	-1.25 ± 0.04 a	-1.43 ± 0.16 b	-1.90 ± 0.12 c
BG	-0.51 ± 0.07 a	-1.12 ± 0.13 ab	-1.36 ± 0.18 bc	-2.00 ± 0.39 c
TP	-0.92 ± 0.10 a	-1.42 ± 0.19 ab	-1.53 ± 0.14 b	-2.01 ± 0.29 b
Osmotic potential at zero turgor $\Psi_{\pi 0}$ (MPa)				
AB		-1.08 ± 0.09 a	-1.60 ± 0.05 b	-2.11 ± 0.04 c
CH		-1.36 ± 0.10 b	-0.92 ± 0.19 a	-2.33 ± 0.09 c
CS	-1.21 ± 0.12 a	-1.63 ± 0.04 b	-1.67 ± 0.16 b	-2.31 ± 0.12 c
SB	-0.95 ± 0.26 a	-1.50 ± 0.05 b	-1.77 ± 0.07 b	-2.26 ± 0.15 c
PA	-1.62 ± 0.10 a	-1.08 ± 0.10 a	-2.00 ± 0.16 a	-2.57 ± 0.22 b
WG	-1.33 ± 0.15 a	-1.36 ± 0.08 b	-1.82 ± 0.08 b	-2.45 ± 0.17 c
BG	-1.11 ± 0.04 a	-1.63 ± 0.12 ab	-1.78 ± 0.17 b	-2.21 ± 0.14 c
TP	-1.59 ± 0.11 a	-1.50 ± 0.18 a	-1.99 ± 0.15 a	-2.53 ± 0.16 b
Bulk modulus of elasticity ϵ (MPa)				
AB		5.02 ± 2.23 a	4.78 ± 2.23 a	5.67 ± 1.72 a
CH		11.33 ± 0.93 a	7.41 ± 0.93 b	8.01 ± 0.77 ab
CS	4.30 ± 0.94 b	5.66 ± 0.82 b	6.53 ± 0.82 ab	10.33 ± 1.55 a
SB	4.83 ± 1.79 b	9.68 ± 1.14 a	8.38 ± 0.95 ab	7.93 ± 0.31 ab
PA	7.95 ± 2.23 a	9.67 ± 0.66 a	9.67 ± 0.62 a	9.87 ± 0.43 a
WG	2.07 ± 0.44 b	9.23 ± 0.71 a	9.23 ± 1.47 a	10.69 ± 0.94 a
BG	3.36 ± 0.54 b	8.34 ± 1.26 a	8.34 ± 0.92 a	8.35 ± 1.22 a
TP	3.44 ± 0.61 b	10.54 ± 1.66 a	10.54 ± 0.96 a	8.89 ± 1.15 a

and III significant decreases in $\Psi_{\pi 100}$ were found for all cultivars except TP. The $\Psi_{\pi 0}$ decreased throughout the season in all cultivars except in CH, PA and TP where it decreased significantly only between dates III and IV (Table).

In general, increases in ϵ were found during the whole season and for the 8 cultivars except for CH which showed a significant decrease in ϵ between dates II and III (Table).

Embolism vulnerability curves (Fig. 1) showed slopes ranging from 1.98 (PA) to 0.53 (SB). Sigmoid curves for PA and BG had significantly higher slopes than SB, CH ($\alpha = 0.05$) and CS ($\alpha = 0.1$). The remaining cultivars had vulnerability curves with intermediate slopes, ranging from 0.89 for CS to 1.22 for WG.

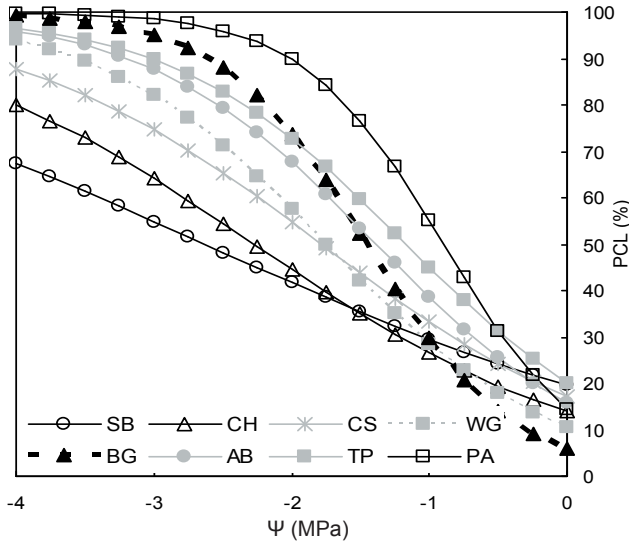
From the values of the constant b in the sigmoid expression for each cultivar, the Ψ_{50} in SB was the lowest among the 8 cultivars with a value of -2.63 MPa while the highest value corresponded to PA with $\Psi_{50} = -0.90$ MPa. All other cultivars showed Ψ_{50} values ranging from -1.17 MPa for TP to -2.27 MPa for CH.

The PCL at $\Psi_{\pi 0}$ increased for all cultivars during the season with AB and BG showing the greatest increase (Fig. 2). We observed that PA and TP had a higher PCL

at $\Psi_{\pi 0}$ than all other cultivars from the beginning of the experiment until the end when it reached values of 80 and 95 %, respectively. The other cultivars showed values of PCL around 40 % at date I and increased to values of 80 % (BG), 60-70 % (AB, CS, WG) and 40-50 % (CH, SB) at date IV. No correlation was found between the $\Psi_{\pi 0}$ and Ψ_{crit} .

Discussion

Our results show that during the growing season $\Psi_{\pi 100}$ decreased together with constant or increasing values of ϵ for all cultivars, except CH. These changes at the leaf level signal osmotic adjustment in response to summer drought stress and can be considered a drought tolerance mechanism (MORGAN 1984, LEVITT 1980). On the contrary, CH showed an increase of elasticity of cellular walls (*i.e.* decrease in ϵ) during that period. It can be concluded that this cultivar developed elastic adjustment to tolerate water stress (ROBICHAUX *et al.* 1986). With regard to the vulnerability curves we can focus on two parameters to classify



	SB	CH	CS	WG	BG	AB	TP	PA
SB					**			**
CH					**			**
CS					*			*
WG								
BG	**	**	*					
AB								
TP								
PA	**	**	*					

** $\alpha = 0.05$ * $\alpha = 0.1$

Fig. 1: Embolism vulnerability curves of 8 cultivars. Ψ_l : leaf water potential, PCL: percent conductivity loss. Each curve is adjusted significantly ($\alpha \leq 0.01$) to a set of 18-20 pair of values (Ψ_l , PCL). Asterisks in the table indicate significant differences among CV curves of the 8 cultivars. For abbreviations and details see the Table.

cultivars with regard to their vulnerability to embolism. Ψ_{50} is usually taken as a reference to classify the vulnerability to embolism of different species (TYREE and ZIMMERMANN 2002). According to this classification method, the most vulnerable cultivar among those studied here is PA followed by TP, AB and BG, while the least vulnerable are SB and CH. The second important parameter is the slope of the curve, which is a function of a in the curve equation (PAMMENTER and VANDER WILLIGEN 1998). A steep slope of the VC indicates a large volume of air-blocked vessels per unit of change in Ψ . Using this classification method it is possible to group cultivars differently than previously was considered. While CH, SB and PA are classified the same BG now is classified as being more vulnerable than TP and AB (Fig. 1). Xylem structure is responsible for cavitation in vessels when tension is increasing; so the differences in the slopes found among the 8 cultivars indicate that their xylem structure is different. Ψ_{50} and the slope of the curve have to be taken into account together when we study vulnerability to embolism. In our results, 50 % of xylem vessels in BG became embolized at a Ψ closer to 0 than in AB,

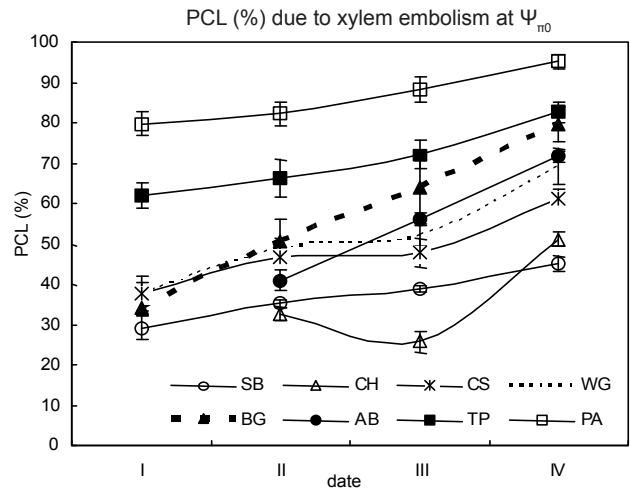


Fig. 2: PCL, percent conductivity loss due to xylem embolism of 8 cultivars when leaf water potentials corresponded to the turgor loss point at 4 sampling dates. For abbreviations and details see the Table.

but as Ψ declined the number of embolized vessels per unit of change in Ψ was greater in this cultivar than in AB. Despite Ψ_{50} values, under water deficit conditions BG would be superior to conduct water to leaves when Ψ decreases.

Osmotic adjustment leads to the development of high tensions in xylem in order to extract more water from the soil under water shortage conditions (LEVITT 1980, SAVÉ *et al.* 1993). An increasing tension would be deleterious if xylem structure could not adapt to maintain vessel function avoiding cavitation. Thus it seems that osmoregulation correlates with lower vulnerability to embolism.

Ψ_{π_0} is the leaf water potential at the turgor loss point, it is considered to coincide with stomatal closure (JONES and TURNER 1978), *i.e.* stomatal conductance will be near zero and xylem flow stops. In SB and CH, Ψ_{π_0} is much more positive than Ψ_{50} while for TP, AB and BG Ψ_{50} is closer to 0 than Ψ_{π_0} . This means that during water stress, despite drought tolerance mechanisms at the leaf level and assuming all turgor dependant processes to continue, water flow to leaves would be reduced by half and would limit stomatal conductance. Thus this reduction in water flow would act as a hydraulic signal to close stomata. In cultivars with intermediate vulnerability to embolism, the margin between Ψ_{50} and Ψ_{π_0} is reduced as the season advances and Ψ_{π_0} decreases due to water deficit conditions in Mediterranean summer.

During the season, 80 % of xylem vessels in PA and 60-70 % in TP are blocked when stomata are fully closed, despite osmoregulation enabling the extraction of water from soil, xylem is near total failure (Table and Fig. 2). In these cultivars embolism is limiting because turgor dependant processes must proceed despite of PCL being >60 %. TP and PA seem to suffer from a severe embolism (CRUIZIAT *et al.* 2002) during the whole season, as they are operating near the point of xylem dysfunction. For BG the high slope in the VC for BG produces also a PCL of 80 % at Ψ_{π_0} at the end of the season although this cultivar shows 40-50 % of functional xylem at the beginning. When stomata are completely closed (Fig. 2), PCL never exceeds

70 % for all cultivars, except for PA, BG and TP. These results represent wide safety margins from water potential at stomatal closure to Ψ_{crit} as 30-70 % of vessels, depending on the date and the cultivar, are still filled with water when stomata close. This means that, under dry environmental conditions, in all these cultivars xylem is hydraulically overdimensioned; they have more conductive area than necessary to cope with water loss through stomata, and thus embolism should not be a limiting factor for growth. Furthermore, the fraction of xylem that is still filled with water at Ψ_{π_0} may help in xylem recovery after embolism. The most vulnerable cultivars, PA, BG and TP, show a narrow safety margin mainly after harvest (date IV), for PA this margin even disappears. When xylem is near total dysfunction, these cultivars will have less recovery capacity after cavitation. On the other hand, having low vulnerability to embolism would help to restore cell turgor in CH faster than in the other cultivars because, despite the environmental conditions, the xylem remains almost filled with water (Fig. 2).

CH is the only cultivar that showed elastic adjustment and it is one of the two cultivars, which showed less vulnerability to embolism (Fig. 1). Thus, this cultivar has an overdimensioned xylem system in relation to its poor adaptation of turgor dependant processes at the leaf level. Similarly SB has high embolism resistance but showed osmoregulation. It seems that despite having a low vulnerability to embolism, these cultivars would not adapt well to drought environments due to the limitations in all turgor dependant processes. Our results agree with those published by JONES *et al.* (2004) where CH and SB were classified as well adapted to cool or intermediate climates and TP, CS and BG to warm climates.

The regulation of stomatal water loss is, amongst others, controlled by hydraulic and hormonal signals (TARDIEU 1996). At the turgor loss point, these signals have induced stomatal closure, thus the contribution of the hydraulic regulation at this point may be related to the PCL. PA and TP show the highest hydraulic contribution to stomatal control. In TP this contribution changes between 60 % in date I to 75 % in date IV, for PA from 80 % at date I to 100 % at date IV (Fig. 2). So, in these cultivars, hydraulic signals seem to have great influence on stomatal closure independently from osmoregulation.

From all these results we can conclude that there is no relationship among the level of vulnerability to embolism and the drought tolerance mechanisms at the leaf level; they seem to be independent mechanisms. We were unable to find a relationship between Ψ_{π_0} and Ψ_{crit} (Fig. 3) which supports our conclusion. Vine cultivars and rootstocks used for grape production have been mainly selected to improve yield and quality (HARVEY *et al.* 2003, 2004) or to increase fungus tolerance, while less breeding efforts has been spent on environmental adaptation (POSSINGHAM *et al.* 1990). Possibly this explains the uncoupling of drought tolerance at the leaf level from the vulnerability to embolism in the 8 studied cultivars. Osmoregulation has been widely reported for grapevines (DÜRING 1984, PATAKAS and NOISTSTAKIS 1999 a, b) and in this experiment we have reported different levels of vulnerability to embolism among

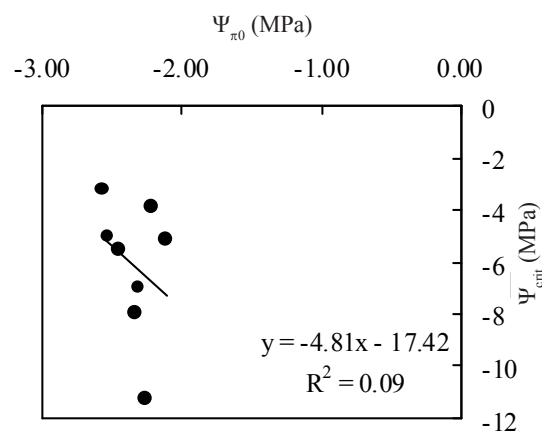


Fig. 3: Correlation between the critical leaf water potential (Ψ_{crit}) obtained from the embolism vulnerability curves and the osmotic water potential at the turgor loss point (Ψ_{π_0}) obtained from the PV curves for 8 cultivars.

cultivars. There is a need to breed cultivars with increased osmoregulatory capacity at the leaf level and with a xylem structure with withstands the drought conditions of Mediterranean summers.

Acknowledgements

This work was funded by Miguel Torres S.A. The authors thank the company for the permission to publish these results and for the helpful assistance of their Viticulture Department. The authors want to thank T. STOCKERT and A. BREAZEALE for their help to improve English language.

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Received April 6, 2006