CHARACTERIZATION OF GRAPEVINE (*VITIS VINIFERA* L.) VARIETIES BASED ON DROUGHT INDUCED ACCLIMATION MECHANISMS

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Different impacts of water deficiency on water relation and CO_2 gas exchange in grapevine leaves were studied on two varieties belonging to two different ecogeographical groups. Fourteen-year-old vines of ***Vitis vinifera*** L. varieties 'Furmint' (autochthonous) and 'Sauvignon blanc' - were investigated in a non-irrigated vineyard on the Mecsek Hills in Hungary (latitude: 46°07' N; longitude: 18°17' E, 230 m a.s.l.). The varieties were studied under drought conditions and well-watered status in the year 2013. In practice, it was well known that drought tolerance of 'Furmint' is weaker compared to other varieties. According to pressure-volume analysis, osmotic potential at full turgor II_{100}) in stressed 'Sauvignon blanc' vines was lower compared to the control variants. Drought stress resulted in increasing 'ε' values ('ε'> 9 MPa) with 'Furmint', indicating decreased cell wall elasticity. Values of C_i and P_N showed a positive exponential correlation; C_i values increased parallel with increasing net CO_2 assimilation in well-watered and stressed vines. In each variety, intrinsic water use efficiency (WUE_i) increased at reduced stomatal conductance. WUE_i was significantly ($P<0.05$) higher in drought stressed vines compared to the control variants in both varieties irrespective of the different ecogeographical origins.
Keywords: water deficit, osmotic adjustment, leaf water potential, net CO_2 assimilation, water use efficiency

Charakterisierung von Rebsorten (*Vitis vinifera* L.) basierend auf durch Trockenstress induzierten Akklimatisierungsmechanismen. Die durch Wassermangel bedingten Veränderungen des Wasserhaushaltes und der CO_2-Assimilation (P_N) von zwei Rebsorten mit unterschiedlicher ökogeografischer Herkunft ('Furmint' (autochthone Sorte) und 'Sauvignon blanc') wurden 2013 an 14 Jahre alten Weinreben unter unbewässerten Bedingungen in einem Weingarten im Mecsek-Gebirge (Ungarn)untersucht. Die Sorten wurden unter trockenen Bedingungen bzw. im gut bewässerten Zustand untersucht. Aus der Praxis war bekannt, dass 'Furmint' im Vergleich zu anderen Sorten weniger trockenheitsresistent ist. Laut Druck-Volumen-Analyse war das in voller Turgeszenz bestimmte osmotische Potenzial (II_{100}) beim 'Sauvignon blanc' unter Trockenstress im Vergleich zur Kontrolle niedriger. Der Trockenstress bewirkte steigende 'ε-Werte' bei ‚Furmint ('ε'>9 MPa), die auf abnehmende Elastizität der Zellwände hinweisen. Die C_i- und P_N-Werte zeigten eine positive exponentielle Korrelation; die C_i- Werte stiegen parallel zu der Fotosyntheserate bei Reben in günstigem Pflanzenwasserzustand und unter Trockenstress. Bei beiden Sorten konnte die Erhöhung der internen Wassernutzungseffizienz (WUE_i) bei paralleler Senkung der Werte der Stomata-Konduktanz beobachtet werden. Der WUE_i-Wert war bei Reben beider Sorten unter Trockenstress signifikant höher ($P<0.05$) als bei der Kontrolle, unabhängig von der unterschiedlichen ökogeografischen Herkunft.
Schlagwörter: Wassermangel, Osmoregulation, Wasserpotenzial, Fotosyntheserate, Wassernutzungseffizienz

It is well known that different grapevine varieties have been classified as plants with high drought tolerance, most of the varieties can produce sufficient yield and good quality despite suboptimal water conditions (Düring and Scienza, 1980). However, several varieties and hybrids have different tolerance levels to drought. Varieties with sensitive stomatal closure (greater drought tolerant) can reduce water loss, but it has an adverse effect on photosynthesis and carbon accumulation. Acclimation mechanisms to drought result in low leaf area, almost full stomatal closure, low assimilation, but a fluctuating level of osmotic adjustment and cell wall elasticity for turgor maintenance, greater soil water conservation and survival in some varieties (Schultz, 1996). Mechanisms by which plants can stabilize their internal water content against a changing external water regime (e.g. in the soil) have great significance in acclimation and adaptation, too. The relationship between the water potential of leaf tissue and the water content of that tissue is fundamental to study plant water relations with the so-called pressure-volume analysis (Pallardy et al., 1991). This analysis provides an opportunity to study water responses of plant cells and tissues in different grapevine varieties within a single methodology (Alsina et al., 2007). Climatic scenarios are predicted to lead to increasing atmospheric CO_2 concentration and reduction in soil moisture (Ipcc, 2007). Based on these scenarios a higher frequency of drought events during the growing season can be expected. During moderate or intense drought periods yield and berry quality of different varieties mainly depend on their acclimation characteristics (e. g. isohydric or anisohydric type).

The classification into isohydric and anisohydric plants applies to different *Vitis vinifera* L. varieties (different genetic origin with varied presence of responses) (Schultz, 2003). Isohydric and anisohydric behaviour of varieties is not widely known and there is no information about autochthonous Hungarian varieties. Isohydric plants reduce stomatal conductance (g_s) as soil water content decreases, maintaining a relatively constant leaf water potential (LWP) regardless of drought conditions (Tardieu and Simonneau, 1998). Anisohydric plants maintain higher gs for a given LWP, effectively allowing LWP to decline with decreasing soil water content (Schultz, 2003; Tardieu and Simonneau, 1998). The two types of stomatal control in isohydric and anisohydric varieties depend on differences in the perception of abscisic acid (plant hormone), which is a chemical signal coming from the roots and inducing stomatal closure of leaves (Tardieu and Simonneau, 1998).

In knowledge of different acclimation mechanisms we can contribute to the selection among varieties for plantations. These mechanisms of hydraulic regulation in different grapevine varieties are closely related to the intrinsic water use efficiency (WUE_i) of vines. WUE_i is defined as a ratio of net CO_2 assimilation (P_N) to gs ($WUE_i = P_N/g_s$). In general, values of WUE_i are significantly higher in drought stressed vines compared to the plants growing under well-watered conditions. WUE_i range from 40 to 110 (µmol CO_2/ mol H_2O), high values of WUE_i indicate also low gs (strong stomatal closure) of leaves (Medrano et al., 2006).

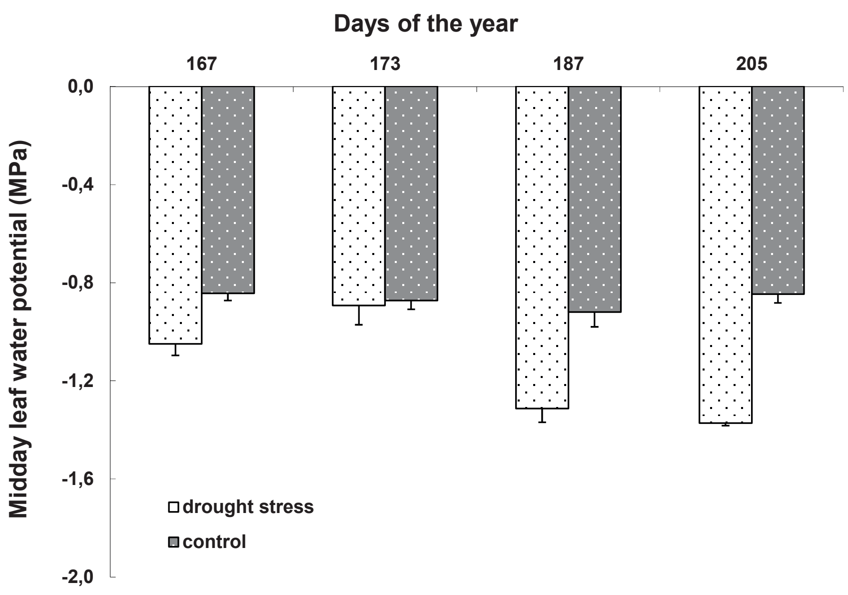
Grapevine varieties and hybrids have different tolerance levels to drought, such as the differences in stomatal control of transpiration (Düring and Scienza, 1980; Rodrigues et al., 1993). In the light of different acclimation mechanisms we can contribute to the selection among varieties for plantations. The climate change-related effects cause significant alterations in phenological phases of grapevine. The beginning of developmental stages and growing seasons is getting earlier; some developmental stages are shortened depending on meso- and microclimatic conditions. Growing areas of cool climate regions will become more favourable, because of global temperature rising. The most vulnerable areas, which have been affected by climate change, are the Mediterranean-type vineyards and 'steep slope' viticulture (Schultz, 2007). Mediterranean-type vineyards are characterised by a typical Mediterranean type of climate (with maximum temperatures ranging from 30 to 35 °C during the growing season, and with annual precipitation varying from 300 to 400 mm, concentrated in the winter season. These types have put in a risk not only increasing frequency of drought periods, but also because of unequal distribution of precipitation events, which increase erosion damages and reduce the amount of utilizable water through rainfalls with large quantities. In case of steep slopes it will be most important to use irrigation techniques (or additional water saving management). These characteristics of vineyards generate a much stronger differentiation of the terroir effects. As hitherto, there were vintages with high-quality both in wet and droughty years, however, degree of drought and vintage quality show a significant negative correlation (Pieri and Gaudilerre, 2005). The frequency of extreme weather-events is likely to increase, and therefore an enhanced appearance of extremes (e.g. severe drought) may be expected. The aim of this study was to describe potential acclimation ability of two different varieties (well-known and autochthonous) and demonstrate some important relationship among the studied physiological characteristics.

MATERIALS AND METHODS

PLANT MATERIAL AND EXPERIMENTAL SITE

The study was carried out in the Szentmiklós vineyard of the Research Institute for Viticulture and Oenology Pécs, Hungary. We studied two grapevine varieties: 'Furmint' (clone P.51) (convar. *pontica*), 'Sauvignon blanc' (clone P.167) (convar. *occidentalis*) by the ampelographic taxonomy (NÉMETH, 1967). Fourteen-year-old vines (grafted on V. *berlandieri x V. riparia* 'Teleki 5C' rootstocks) were grown on the south-facing slopes of the Mecsek Hills (latitude: 46º07' N, longitude: 18º17' E, 180 to 200 m a.s.l.) in non-irrigated field conditions. The soil was a Ramann-type brown forest soil mixed with clay formed on red sandstone covered by Pannonian sediment. Vines were grown with 2.2 x 0.8 m vine spacing with North-South row direction. The studied vineyard was characterized as a severely eroded site with shallow soil layer and with a maximum slope angle of 35 % . The representative leaf samples and executed measurements originated from homogeneous plantations with 150 vines of each variety. Weather conditions, i.e. global radiation, precipitation, air temperature and relative humidity, were registered by means of an automatic weather station (Lufft WS600, Fellbach, Germany) in the experimental vineyard. The site is situated within the *Praeillyricum* (plant geographical district), which on average receives 782 mm of precipitation per year, 2021 hours of sunshine annually, with an annual mean temperature of 11.6 °C. However, the mesoclimatic characteristics of the site show significant extremes in precipitation events (344 to 1140 mm), in amount of sunshine hours (1986 to 2548 hours) and in annual mean temperature (9.3 to 14.0 °C) according to meteorological data collected between 1950 and 2013 in our research station (RIVO, 2014). There was a progressed drought period between July and August in 2013 in most Hungarian vineyards; we recorded a strong decrease in the amount of monthly precipitation. Average monthly precipitation was lower by 60 % in June, by 25% in July and by 50% in August compared to the long-term average between 1950 and 2011 (RIVO, 2014). The increasing water deficit generated moderate drought stress conditions in August, which were detected by measurements of leaf water potentials (Fig. 1).

Fig. 1: Seasonal variation of midday leaf water potentials of 'Sauvignon blanc' under drought stress and well-watered (control) conditions between June and August in 2013. Days of the year numbered by 167, 173, 187 and 205 were 16.06., 22.06., 06.07. and 24.07.



PHYSIOLOGICAL MEASUREMENTS

LEAF WATER POTENTIAL MEASUREMENTS

Leaf water potentials (LWP) were determined according to Scholander et al. (1965) using a pressure chamber Water Status Console 3000 (Soilmoisture Corp., Santa Barbara, USA). Predawn leaf water potential (LWP_{PD}) was measured at the end of the night between 0200 h and 0300 h (local time) on mature leaves from flowering till post-harvest period (4 recordings of the growing season) in five replications. Values of LWP_{PD} are well related to the soil water potential (Lebon et al., 2003). Midday leaf water potentials (LWP_{MD}) of healthy mature leaves (exposed to direct sunlight) were measured simultaneously (on the same day) to the LWP_{PD}. The level of drought stress was determined on the basis of meteorological data and changing of LWP_{PD}. We investigated each variety simultaneously on drought stressed exposition of steep slopes and on terraces with deeper soil layer and well-watered conditions in the same vineyard.

PRESSURE-VOLUME ANALYSIS

Fully expanded, healthy sun-adapted detached leaves were used from the selected vines. Samples (5 leaves per treated and control variant in both varieties) were collected from five different vines in polyethylene bags from the 8th to 12th nodes once during the growing season at ripening phenological stage. Leaf water potential (Ψ) (pressure) and leaf weight (volume) were determined 10 times in each leaf under continuous dehydration with a pressure chamber and analytical balance (± 0.1 mg). At the end of this procedure, leaves were completely dried in a drying oven (at 105 °C) and weighed to determine dry mass. The relative water content (RWC) in each leaf was calculated according to the following formula: RWC(%)= (FW – DW) ÷ (TW – DW) × 100, where FW = fresh weight from the first measurement before full saturation, DW = dry weight and TW = turgid weight, followed by actual water potential measurement. Linear regression of data ($1/\Psi$, RWC) was carried out using Excel® (Microsoft Corp., Redmond, USA). The turgor loss point (RWC_{TLP}), osmotic potential at full turgor (II_{100}), apoplastic water fraction at full turgor (A_{WSD}%) and cell wall elasticity (ε) were derived from the PV curves (Pallardy et al., 1991). In general, RWC and osmotic potential of grapevine leaves decrease during a progressed drought period (Alsina et al., 2007).

LEAF GAS EXCHANGE MEASUREMENTS

The gas exchange measurement was conducted on attached leaves using an infrared open-system portable gas analyser (LCA-4, ADC BioScientific Ltd., Great Amwell, UK) in five vines per sampling four times during the growing season. The analysed leaves were fully mature, sound and sun-adapted leaves from 8 to 12 leaf levels. Measurements were carried out under the maximum photosynthetic activity of leaves, between 1000 and 1130 hours at local time, at 1500 to 1800 µmol m^2/s PPFD (photosynthetic photon flux density or photosynthetically active radiation) under normal atmospheric CO_2 concentration, at 25 to 28 °C leaf surface temperature under 0.21 to 0.43 kPa vapour pressure deficit. We determined the net CO_2 assimilation rate (P_N), the rate of transpiration (E), the stomatal conductance (gs), the value of partial pressure of intercellular CO_2 (mesophyll conductance) (C_i) and WUE_i (P_N/g_s). The PPFD incident on the leaves was always higher than 1500 µmol m^2/s, which is above photosynthesis saturation considered in the grapevine (Flexas et al., 2002). The PN/gs ratio was used as intrinsic water use efficiency (WUE_i), according to Iacono et al. (1998).

STATISTICAL ANALYSIS

Statistical analysis was carried out using Excel® (Microsoft Corp., Redmond, USA). Paired sample t-tests (Student‘s t-test) were performed on data sets with 99 % confidence interval (Tab. 1, Tab. 2, Fig. 1). In the case of Fig. 1 error bars show the standard deviations of data set. Correlation analysis with scatter diagram was performed between leaf water potential at turgor loss point (LWP_{TLP}) and relative water content at turgor loss point (RWC_{TLP}) using Excel® (Fig. 3).

RESULTS AND DISCUSSION

Analysis of the meteorological data set showed that 2013 was an average year in Hungary. The high precipitation quantities of winter and spring periods caused favourable water status during bud-break, bloom and berry set. However, the studied site received less precipitation in July and in August compared to the long-term average (from 1951 to 2011). Increasing soil water deficits (based on LWP_{PD}) and general drought effects (high temperature, low relative humidity) induced significant responses of varieties (Tab. 1). In the case of both varieties significantly lower LWP_{PD} values were recorded compared to the earlier well-watered period. ‘Sauvignon blanc‘ showed 56 % decrease of LWP_{PD} contrary to

Fig. 2: Diurnal course of net CO_2 assimilation in 'Furmint' and 'Sauvignon blanc' under drought stress and well-watered conditions in 2013

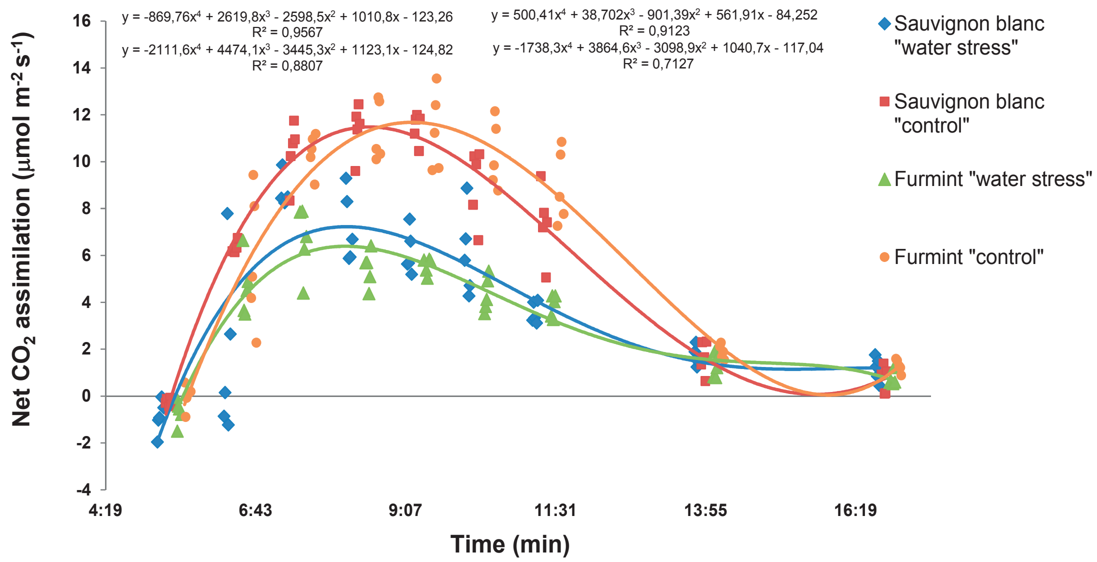
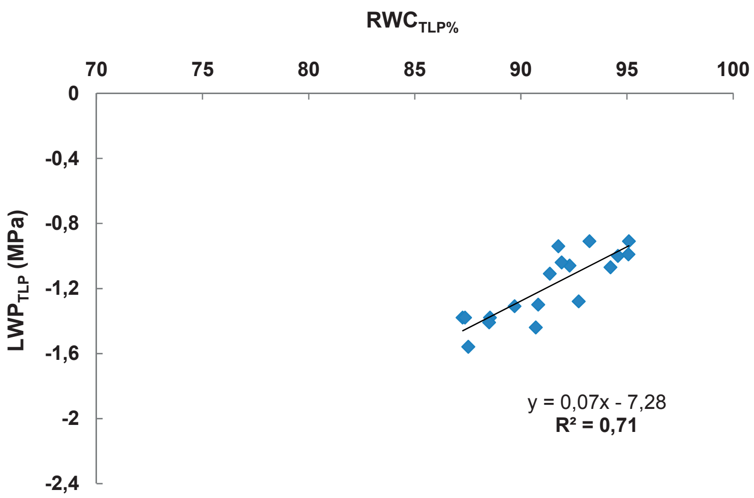


Fig. 3: Leaf water potential at turgor loss point (LWP_{TLP}) in relation to relative water content at turgor loss point (RWC_{TLP}) in leaves of 'Sauvignon blanc'. Correlation analysis of scatter diagram shows significant relationships at or above: $r_{0.5} = 0.57$ ($R^2 = 0.32$). There is a negative linear correlation between RWC_{TLP} and LWP_{TLP}.



Tab. 1: Predawn leaf water potential (LWP_{PD}) of 'Furmint' and 'Sauvignon blanc' under drought stress condition on N-S directed steep slope with eroded shallow soil layer in 2013. Based on Student's t-test asterisks indicate significant differences between drought stress and well-watered conditions at p<0.01 (**) levels (n = 5).

Varieties LWP_{PD} (MPa)	'Furmint'	'Sauvignon blanc'
drought stress	-0.57 ±0.03	-0.54 ±0.06
control	-0.37 ** ±0.05	-0.24 ** ±0.02

Tab. 2: Differences between intrinsic water use efficiency (WUE_i) of 'Furmint' and 'Sauvignon blanc' under drought stress and well-watered conditions in 2013. Based on Student's t-test asterisks indicate significant differences between drought stress and well-watered conditions at p<0.001 (***) levels (n = 5).

Varieties	'Furmint' drought stress	'Furmint' control	'Sauvignon blanc' drought stress	'Sauvignon blanc' control
WUE_i	61.85 ±13.65	58.95 ±8.45	99.08*** ±26.02	57.70 ±11.37

'Furmint', which indicated smaller reduction of LWP_{PD} values (with 35 %) compared to the well-watered status. The LWP_{PD} values between -0.2 MPa and -0.5 MPa indicated significant differences in water-status altered by moderate drought stress in each variety (Tab. 1). High LWP_{PD} values (less negative) indicate favourable plant water status in most of the varieties (Van Zyl, 1987; Gomez del Campo et al., 2007).

Based on changes of LWP we can hypothesize that isohydric and anisohydric regulation of water status can be found with the two analysed varieties. 'Sauvignon blanc' showed significantly decreasing LWP under water stress conditions compared to the stable LWP in control leaves (Fig. 1). In the case of 'Furmint' LWP_{MD} values decreased gradually parallel to enhance of drought stress (data not shown). 'Furmint' had lower levels of control hydraulic conductance, but it is assumed that these properties of variety did not result from the hypothesized deficiency of sensitive stomatal closure (Teszlák, 2008). Results of present experiments about water relations in 'Furmint' are supported by previous results from physiological pilot measurements (seasonal variability of LWP_{PD} and LWP_{MD}), which has already been published (Teszlák et al., 2004). This earlier investigation showed that midday leaf water potential of 'Furmint' decreased with the progressing drought stress conditions during the growing season. Based on decreasing values of LWP_{MD} without significant changes of transpiration rate or stomatal conductance we hypothesized that'Furmint' might be rather an anisohydric grapevine variety.

The net CO_2 assimilation rate (P_N) showed significant differences between drought stressed and control vines in both varieties during the diurnal changes (Fig. 2). We measured the highest net CO_2 assimilation rate in 'Furmint' leaves, which indicated less stomatal sensitivity to moderate drought. Deficiency of stomatal closure caused higher photosynthetic activity with higher transpiration rate (more water loss through stomata) of 'Furmint' leaves compared to the other variety. For this reason 'Furmint' had lower acclimation ability during water deficit than 'Sauvignon blanc'. From comparison of the two varieties 'Sauvignon blanc' had sensitive stomatal response to the moderate drought on steep slopes (intense stomatal closure with 0.03 mol m^2/s of g_s); this variety had the highest fluctuation ability of stomatal movement between moderate water stress and well-watered conditions (Teszlák et al., unpublished).

Significant differences were recorded between the drought stressed and control vines of each variety according to diurnal course of net CO_2 assimilation. 'Furmint' and 'Sauvignon blanc' showed maximal values of photosynthetic rate at 10.00 a.m. in the morning; after this time P_N decreased sharply till the end of the daily photoperiod. In the case of drought stressed vines P_N values indicated earlier photosynthetic depression compared to the control plants during the diurnal changes (Fig. 2).

Pressure-volume analysis showed that loss of turgor in 'Furmint' leaves occurred only at lower RWC compared to the other variety. 'Sauvignon blanc' had a closer relationship between LWP and RWC at turgor loss point (Fig. 3). The analysis was performed under drought conditions and also well-watered status. It was well known (in practice) that drought tolerance of 'Furmint' is weaker compared to the other varieties. Drought stress resulted in increasing cell wall rigidity in both varieties and affected the linear correlation between elasticity modulus ('ε') and relative water content at the turgor loss point (RWC_{TLP}).
Values of C_i and P_N showed a positive exponential correlation; C_i values increased parallel with increasing net CO_2 assimilation in a range between 18 to 27 Pa of C_i both in well watered and stressed vines (data not shown). In each variety, intrinsic water use efficiency (WUE_i) increased at reduced stomatal conductance (g_s). WUE_i was significantly higher in drought stressed vines compared to the controls in both varieties (Tab. 2) irrespective of the different ecogeographical origins. Our results were in agreement with other independent studies about autochthonous grapevine varieties (Flexas et al., 2002; Medrano et al., 2006), which concluded close relationship between stomatal conductance and net CO_2 assimilation. If grapevines are subjected to moderate drought stress, values of WUE_i may be maximized (Medrano et al., 2006). ,Sauvignon blanc' presented higher

WUE_i than 'Furmint' under drought stress conditions at the given water potential range, confirmed its reputation as a more drought tolerant variety (Tab. 2). These results show that WUE_i estimated by P_N/g_s represents differences between the two varieties, which could be contributed to improve our knowledge about physiological performance of different grapevine varieties.

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