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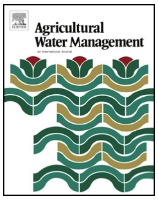

Differences among grapevine cultivars in their stomatal behavior and water use efficiency under progressive water stress

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ABSTRACT

Evaluation of different mechanisms adopted by grapevine cultivars to deal with drought is of major importance to carry out more efficient cultivar selection. In this report, 23 cultivars, including local and foreign grape cultivars, were studied under field conditions in order to identify the different behaviors in response to water deficit, and how it can affect water use efficiency (WUE) at leaf level (intrinsic water use efficiency (WUE$_i$) and leaf carbon isotope composition (δ^{13}C)). Ψ_{stem} was used to assess plant water status. Under a common environment, a high variability was found in photosynthetic parameters, stomatal response, WUE$_i$ and leaf δ^{13}C. This large variability observed represents an opportunity for genotype selection. Using different physiological traits we were able to select suitable cultivars for current and future viticulture. Under non-water stress situation the cultivar Escursac combined high rates of net photosynthesis with low stomatal conductance, resulting in high WUE$_i$. In response to drought, strong, and moderate water saving behavior of local cultivars Manto Negro, Giró Ros, Argamussa and Vinater Negre resulted in higher WUE$_i$. Long-term WUE (leaf δ^{13}C) corroborate these cultivars as high water use efficient.

1. Introduction

Soil water deficit is the main environmental constraint for viticulture in Mediterranean regions (Cifre et al., 2005; Chaves et al., 2007). In this geographical area, the drought periods coincide with the highest plant growth, leading to the reduction and inhibition of vegetative development and final net production. Moreover, as a consequence of climate change, medium (4–6 month) or long (>12 month) drought periods are forecast to be 3–8 times more frequent than nowadays (Sheffield and Wood, 2008). These changes will affect grapevine phenology, grape composition and, of course, increase of plant water consumption. In order to mitigate the negative impact of those changes on grape growth and quality, some adaptation of future viticulture is needed. This new viticulture implies to adapt agronomical practices and cultivar selection strategies to obtain or identify genotypes more adapted to the new environmental conditions. Grapevine breeding is a slow and expensive process. A new crossing may take over 25 years before being released as a new cultivar (Regner et al., 2004). For this reason, to explore the existing genetic variability in search of more water-efficient genotypes seems a good alternative. Thousands of grapevine cultivars have been described around the world (This et al., 2006; OIV, 2009) showing an impressive genetic variability and plasticity of the grapevine genome. In fact, genotype related differences have been described in the responses to drought, in terms of their photosynthesis, stomatal conductance and water use efficiency (WUE) (Bota et al., 2001; Escalona et al., 1999, 2003; Soar et al., 2006; Tomás et al., 2012, 2014; Costa et al., 2012; Gibberd et al., 2001; Prieto et al., 2010; Souza et al., 2005; Zsófi et al., 2009; Chaves et al., 2010). The research emphasis to understand these physiological and molecular bases of grapevine responses to water deficits was deep undertaken in the last decade (Chaves et al., 2010). Regarding stomatal regulation, it is well described that gas exchange control by the stomata is the crucial issue for grapevine drought response and water use efficiency (WUE) (Bota et al., 2001; Schultz, 2003; Rogiers et al., 2009, 2012; Costa et al., 2012; Tomás et al., 2014; Martorell et al., 2015). Different stomatal behaviors under drought conditions have been well described in grapevines; some genotypes have better stomatal control under water stress than others and were classified as isohydric (“pessimistic”). Other genotypes, in turn, have a less marked stomatal regulation under drought and were classified as anisohydric (“optimistic”) (Schultz, 2003; Soar et al., 2006). However, this classification of cultivars in two different categories, iso- and anisohydric behaviors, are not always clearly identified in each cultivar, and consequently, is not

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Table 1
Climatic parameters measured during the experimental periods in 2009, 2010, and 2011. The values are daily mean temperature (mean T) ± SD, rainfall, reference monthly evapotranspiration (ET_0) and irradiance (I) ± SD. Data were averaged (T and I) or integrated (rainfall and ET_0) over each experimental month.

		Mean T (°C)	Rainfall (mm)	ET_0 (mm)	I (MJ m^{-2} day^{-1})
2009	June	23.35 ± 0.34	1.40	166.05	26.13 ± 0.48
	July	26.13 ± 0.24	0.00	176.46	25.00 ± 0.48
	August	26.17 ± 0.14	7.20	148.11	21.29 ± 0.70
	Accumulated values		8.60	490.62	
2010	June	21.34 ± 0.25	15.20	146.70	26.63 ± 1.09
	July	25.92 ± 0.18	1.20	179.10	27.11 ± 0.68
	August	25.12 ± 0.26	3.80	147.79	22.48 ± 0.76
	Accumulated values		20.20	473.59	
2011	June	21.52 ± 0.55	25.80	149.67	24.88 ± 1.09
	July	24.40 ± 0.28	17.20	160.86	23.81 ± 0.91
	August	25.83 ± 0.28	0.00	156.45	23.26 ± 0.44
	Accumulated values		43.00	466.98	

always applicable (Chaves et al., 2010; Pou et al., 2012; Tomás et al., 2014). Genotypes behave differently according to the growing conditions (e.g., field versus greenhouse or potted plants versus field plants) and the degree of stress imposed to the vines (Chaves et al., 2010; Lovisolo et al., 2010). A wider study of varietal responses to drought under common conditions is still needed. The proper characterization and the evaluation of cultivar responses to drought will help to carry out more efficient selection. The major aims of this study were to evaluate the stomatal behavior of a wide number of *Vitis vinifera* L. cultivars in response to progressive drought and to identify those genotypes with better water use efficiency. For this purpose, stomatal response to stem water potential, intrinsic water use efficiency (WUE_i) and leaf carbon isotope composition ($\delta^{13}C$), were evaluated in 23 cultivars under field conditions during three consecutive years.

2. Material and methods

2.1. Location and climate

The study was carried out in 2009, 2010, and 2011, in an experimental vineyard located in Palma de Mallorca (39°35′N, 2°39′E) (Balearic Islands, Spain). The climate is Mediterranean with hot and dry summers and precipitations during autumn and winter. Environmental conditions were monitored during the experiments with a meteorological station (Meteodata 3000, Geónica SA, Madrid, Spain) installed in the experimental field. In general, the climatic conditions registered in 2009, 2010, and 2011 were quite similar, except accumulated precipitation (Table 1). Nevertheless, in order to start with similar water availability, at the beginning of the season the experimental plots were generously irrigated (see next section for details).

The soil presents a loamy texture with alkaline pH due to the high concentration of active limestone and carbonates, as is typical on the island. The average characteristics of the soil are: clay 23%; silt 41%; sand 36%; organic matter 1.25%; pH 8.5.

2.2. Plant material and treatments

A total of 23 grapevine cultivars (16 local cultivars and 7 widely cropped ones) were chosen to perform the present study (Table 2). The plants were 10 years old grafted in 99-Richter rootstock. They were placed in rows, spaced 2.5 × 1.0 m and trained on bilateral Royat Cordon system. All vines were uniformly pruned to 12 nodes per vine. Ten plants per cultivar were used for the experiment.

Plants were well watered at the beginning of flowering in each experimental period (around 30 mm applied). Afterwards, no irrigation was applied. The decrease in water availability was monitored in 2009 by the measurement of soil matricial potential by psycrometers (Wescor Sci. Inc., USA), in different points of the plot, at 30 and 60 cm depth of soil from June to the end of August every two weeks. Soil water availability was declining over the summer, especially in first 30 cm depth when soil matricial potential decreased from −0.1 to −1.7 MPa. In 60 cm depth soil matricial potential arrived around −1.0 MPa.

Table 2
List of 23 studied grapevine cultivars.

	Cultivar	Berry color
Local cultivars	Argamussa	White
	Callet	Black
	Callet Blanc	White
	Escursac	Black
	Esperó de Gall	Black
	Galmeter	Black
	Giró Ros	White
	Gorgollasa	Black
	Malvasia de Banyalbufar	White
	Manto Negro	Black
	Moll	White
	Sabater	Black
	Valent Blanc	White
	Valent Negre	Black
	Vinater Blanc	White
	Vinater Negre	Black
Wide distributed cultivars	Cabernet Sauvignon	Black
	Chardonnay	White
	Grenache	Black
	Macabeo	White
	Merlot	Black
	Syrah	Black
	Tempranillo	Black

2.3. Plant water status

The plant water status was estimated by midday stem water potential (Ystem) measurements, with a Scholander pressure chamber (Soil moisture Equipment Corp., Santa Barbara, California, USA). Ψ_{stem} was measured on non-transpiring leaves that had been bagged with both plastic sheet and aluminium foil at least 1 h before measurement. Bagging prevented leaf transpiration, so leaf water potential equaled stem water potential (Begg and Turner, 1970). Ψ_{stem} was measured on one leaf per plant in four plants per cultivar in three different moments through the season: veraison (M1), ripening (M2) and harvest (M3).

2.4. Gas exchange measurements

Leaf net photosynthesis (A_N), stomatal conductance (g_s), and transpiration rate (E) were measured in six leaves per cultivar in the same days of plant water status measurements. Measurements were done between 10:00 and 12:00 h (local time) using an infrared open gas exchange system (Li-6400, Li-cor Inc.,

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