Rootstock effects on the adaptive strategies of grapevine (*Vitis vinifera* L. cv. Cabernet–Sauvignon) under contrasting water status: Leaf physiological and structural responses

Stefanos Koundouras [a,*], Ioannis T. Tsialtas [b], Eleftheria Zioziou [a], Nikolaos Nikolaou [a]

[a] *Laboratory of Viticulture, School of Agriculture, Aristotle University of Thessaloniki, 541 24 Thessaloniki, Greece*
[b] *Hellenic Sugar Industry SA, Larissa Factory, Department of Experimentation, 411 10 Larissa, Greece*

ABSTRACT

The effects of two rootstocks (1103P and SO4) on water status, gas exchange, leaf structural characteristics and vine growth were studied in a factorial experiment over 2 years (2005–2006), in field-grown grapevines of cv. Cabernet–Sauvignon (*Vitis vinifera* L.), subjected to three irrigation levels (FI: 100% of evapotranspiration, DI: 50% of evapotranspiration and NI: not irrigated). The experiment was conducted on 10-year-old vines, grown under the semi-arid conditions of central Greece. There was a significant depressive effect in water status (estimated by midday stem water potential, Ψ_s) and net assimilation rate (A) of Cabernet–Sauvignon with decreasing water supply, on both rootstocks. The down regulation of A was mainly due to decreases in stomatal conductance (g_s). NI treatment showed significantly higher intrinsic water use efficiency (A/g_s) and lower leaf carbon isotope discrimination (Δ) compared to irrigated treatments. Leaf area index (LAI) and pruning weight (PW) were found to be higher under FI treatment but this effect was more pronounced on the 1103P-grafted vines. Canopy growth was strongly controlled by rootstock, being significantly higher on 1103P, presumably due to its higher capacity to access soil water. Rootstock genotype affected scion water status via its effect on whole-vine transpiration. Cabernet–Sauvignon photosynthesis response to water status was not altered by rootstock. The only apparent difference between rootstocks was the higher A of SO4-grafted vines under NI treatment, associated with higher Ψ_s. A/g_s and Δ were only altered under FI treatment, with 1103P showing more efficient use of available soil water than SO4. Vines on SO4 had a lower specific leaf area (SLA) as a result of lower growth rate than 1103P, which possibly provided a supplemental mechanism to maintain leaf water status and gas exchange.

Concluding, SO4 could be better adapted on fertile soils under non-limiting water supply due to its capacity to achieve a balanced vegetative and reproductive growth while 1103P, a more water efficient rootstock, would be better to grow in semi-arid regions where water limitation occurs.

© 2008 Elsevier B.V. All rights reserved.

1. Introduction

Drought is the major abiotic constraint of plant growth and yield in the Mediterranean region. Grapevines (*Vitis vinifera* L.) have developed various physiological and morphological mechanisms in order to sustain growth and productivity under water-limited conditions. One of the first vine responses to drought is the reduction of leaf stomatal conductance (g_s) associated with an optimization of water use efficiency [WUE, the ratio of net assimilation (A) to stomatal conductance (g_s)], an indicator of long-term regulation of carbon assimilation under drought (Bota et al.,

2001; Cifre et al., 2005). In C_3 species, g_s is also related with carbon isotope discrimination (Δ, a measure of the $^{13}C/^{12}C$ ratio in plant tissues compared with the air) via its effect on C_i/C_a ratio (the ratio between intercellular and atmospheric concentration of CO_2) (Farquhar et al., 1989). Higher C_i/C_a ratio is positively related with Δ which is a reliable, long-term assessment of WUE in C_3 species (Turner, 1997), grapevines included (Gibberd et al., 2001; van Leeuwen et al., 2001).

Grapevine cultivars have also been reported to adapt to water deficit by modifications of their morphological and anatomical characteristics, such as alterations in leaf area (Gómez del Campo et al., 2003), root/shoot ratio (Toumi et al., 2007) and xylem vessel size and conductivity (Lovisolo and Schubert, 1998). Leaf structural adjustments to water limitation are rather less explored compared to physiological ones (Manoj et al., 2007). It is commonly accepted

---

that increased density of the foliar tissue is a mechanism that enables plants to reduce transpiration by withholding water in the mesophyll (Lo Gullo and Salleo, 1988).

Rootstocks have been reported to modify *Vitis vinifera* varieties' water status and gas exchange in pot (Iacono et al., 1998) and field conditions (Candolfi-Vasconcelos et al., 1994). Rootstock effects on gas exchange characteristics are scion-specific and vary among scion-rootstock combinations (Düring, 1994; Novello and de Palma, 1997; Padget-Johnson et al., 2000). However, the exact mechanisms underlying rootstock effects are difficult to be defined since rootstock affects numerous vegetative and reproductive parameters of the scion, such as canopy growth (Ezzahouani and Williams, 1995) and yield (Ezzahouani and Williams, 2005) which interfere with the scion's physiological processes (Paranychianakis et al., 2004).

Soar et al. (2006) reported that rootstock effect on gas exchange of field-grown grapevines is most likely due to differences in the relative capacity of rootstocks to extract and provide scions with water. Rootstocks have been reported to affect the efficiency of water transport to the shoots via conductivity constrains imposed by the anatomy of xylem vessels (de Herralde et al., 2006). Most importantly, rootstock genotype has a major influence on root density (Southey and Archer, 1988; Williams and Smith, 1991) even though the distribution of grapevine roots is significantly dependent on both edaphic conditions (Smart et al., 2006) and vine spacing (with narrower plantings being associated with denser root systems; Archer and Strauss, 1985). Moreover, grapevine root growth depends on the interaction of a given rootstock genotype with environment, i.e. its suitability to soil factors such as soil texture and bulk density (Morlat and Jacquet, 2003), water and nitrogen availability (van Zyl, 1988), pH (Conradie, 1988) and salinity (Southey and Archer, 1988).

Although grape growing requires less water per value of crop than most plants, the predicted climatic change (i.e. reduced rainfall and increased evapotraspiration rates) will intensify water stress on vines, especially in water-limited regions such as Greece, affecting the ability of existing varieties to ripen fruit (Jones et al., 2005). To facilitate adaptation to conditions of limited rainfall and less irrigation water, rootstock selection could provide an alternative means to control grapevine response to irrigation with maximum WUE. Existing rankings of commercial rootstocks with regard to their drought tolerance were conducted on potted vines (Carbonneau, 1985) or on ungrafted *Vitis* species (Padget-Johnson et al., 2003) while there is limited knowledge on the pedoclimatic adaptation of specific scion-rootstock combinations in the field, especially under drought conditions.

In this study, two rootstock cultivars widely grown in Greece and characterised by different reported tolerance to dry conditions were used: 1103 Paulsen, qualified as drought tolerant, and SO4 which is reported as less adapted to limited water conditions (Winkel and Rambal, 1993). The aim of the study was to evaluate the effects of rootstock genotype on drought adaptation of field-grown *V. vinifera* cv. Cabernet–Sauvignon vines by studying leaf and whole-vine physiological and structural characteristics.

2. Materials and methods

2.1. Plant material and experimental conditions

A field trial was conducted during 2 consecutive years (2005–2006) in a 10-year-old commercial vineyard in Larissa, central Greece (39° 48′ N, 22° 27′ E, 190 m), planted with cv. Cabernet–Sauvignon (*Vitis vinifera* L.) at 3200 vines per ha (1.3 m × 2.4 m). The vineyard was located on a deep loamy soil (44% sand, 31% silt and 25% clay). Vines were trained on a vertical trellis with three fixed wires and spur-pruned on a bilateral cordon system to 12–14

nodes per vine. The region has a semi-arid climate with less than 60 mm of summer rainfall. The average midday temperature and air humidity during the summer months were 32.2 °C and 35%, respectively. Comparing the 2 years of the study, 2005 had an average temperature of the growth period (April to September) of 21.8 °C, compared to 21.0 °C in 2006.

The experiment was arranged as a 2 × 3 factorial design with two rootstocks [1103 Paulsen (*V. rupestris* × *V. berlandieri*) and SO4 (*V. riparia* × *V. berlandieri*)] and three irrigation treatments [full irrigation (FI): 100% of crop evapotranspiration (ET_c), deficit irrigation (DI): 50% ET_c and not-irrigated (NI)]. ET_c was estimated from potential evapotranspiration (calculated by the Penmann–Monteith method) and crop coefficients were adapted from Williams et al. (2003). Irrigation was scheduled on a weekly basis starting at berry set (E-L 27 according to Eichhorn and Lorenz, 1977) through harvest (E-L 38), according to climatic data recorded on a Vantage Pro2 automatic weather station (Davis Instruments Corp., Hayward, CA, USA) located inside the vineyard. Water was supplied by a drip irrigation system with two 4 L h^{-1} emitters per vine on either side of the trunk, positioned at regular intervals along the pipe. The total amount of applied water for the season was approximately 300 mm for the FI treatment and 150 mm for DI. The six treatments were replicated three times in randomized blocks, with three rows per replication. In each plot, only the central four vines of the middle row were used for measurements and the other rows served as borders.

2.2. Parameters measured

2.2.1. Water status

Vine water status was estimated by measurements of stem water potential (Ψ_s) using a pressure chamber (Scholander et al., 1965), according to Choné et al. (2001). In each measurement set, four leaves of the inside part of the canopy were enclosed in plastic bags and covered with aluminium foil for at least 90 min before measurement, to allow equilibration of Ψ_s. Measurement of Ψ_s was performed at solar noon (12 h 30 to 13 h 30), on cloudless days corresponding to the stages of bunch closure (d1: E-L 33, approximately 15 days after the beginning of irrigation), veraison (d2: E-L 35) and harvest (d3: E-L 38).

2.2.2. Leaf gas exchange

Net assimilation rate (A), stomatal conductance (g_s), evaporation (E), intercellular CO_2 concentration (C_i) and leaf-to-air temperature difference ($T_1 - T_a$) were recorded at midday, simultaneously with Ψ_s measurements, using the LC_i portable gas exchange system (ADC BioScientific Ltd, Hoddesdon, UK). Measurements were taken on four fully expanded, recently matured, sun-lit leaves per plot (photosynthetic photon flux density > 1200 µmol m^{-2} s^{-1}) and adjacent to those used for Ψ_s determination. Intrinsic WUE was calculated as the A/g_s ratio. Gas exchange measurements were conducted at midday in order to obtain an accurate indication of grapevine response to environmental stress (Medrano et al., 2003).

2.2.3. Leaf structure

In each plot, structural parameters were measured on the four leaves collected for Ψ_s measurements. Individual leaf area (LA, cm^2) was determined using the WinDias image analysis system (Delta-T Devices Ltd., Cambridge, UK), the fresh mass was weighed (FM) and the dry mass (DM) was estimated after oven-drying at 75 °C for 48 h. Specific leaf area (SLA, cm^2 g^{-1}) was determined as the ratio of LA to DM of the four leaves per plot. To estimate the relative importance of leaf structural traits in the variation of SLA, leaf thickness (LT) was calculated as the ratio of FM to LA (de