The effect of rootstock on water relations and gas exchange of *Vitis vinifera* cv. Xinomavro

Effet du porte-greffe sur le régime hydrique et les échanges gazeux de *Vitis vinifera* cv. Xinomavro

Stefanos KOUNDOURAS[1*], Eleftheria ZIOZIOU[1],
Nikolaos NIKOLAOU[1] and Konstantinos ANGELOPOULOS[2]

1: Laboratory of Viticulture, School of Agriculture, Aristotle University of Thessaloniki, 54124, Thessaloniki, Greece
2: Laboratory of Plant Physiology, Department of Biology, University of Patras, 26500, Patras, Greece
Tel: +30 26 10 99 72 28, Fax: +30 26 10 99 16 06, e-mail: agelop@upatras.gr
*Corresponding author: Tel: +30 23 10 99 86 50, Fax: +30 23 10 99 86 19, skoundou@agro.auth.gr

Abstract: The effect of two rootstocks of different drought tolerance (1103 Paulsen and 3309 Couderc) on sap flow, water relations and gas exchange of cv. Xinomavro (*Vitis vinifera* L.) was investigated during the 2005 season in Naoussa, Greece. Soil was maintained at field capacity for both rootstock treatments until mid July when a restricted water regime was applied by irrigation cutoff. Sap flow diurnals for the Xinomavro-1103P combination showed a rapid decrease of flow after midday, under water stress conditions. On the contrary, vines grafted on 3309C maintained the transpiratory flux during the day, despite conditions of limited water availability. Vines grafted onto 1103P had significantly higher (less negative) values of late afternoon (16h00) stem water potential, compared to those grafted on 3309C. Simultaneous assimilation and stomatal conductance values were significantly lower for the Xinomavro-1103P combination compared to Xinomavro on 3309C. These results support the possibility of a more sensitive drought avoidance mechanism for vines grafted on 1103P based on stomatal control. On the contrary, 3309C allowed this cultivar to maintain higher stomatal conductance and water uptake under water deficit. Grapes from the Xinomavro-3309C combination exhibited significantly superior sugar content at harvest, expressed on a per g of fresh berry weight basis. Since growth and yield parameters were similar among treatments, this finding is likely to be related to the higher afternoon photosynthetic rate of 3309C-grafted vines, prior to harvest.

Key words: rootstock, drought tolerance, sap flow, stem water potential, gas exchange

Introduction

Water is the most limiting resource for viticulture in the Mediterranean region where vines are often exposed to extreme water deficits during the growth period. Grapevines (*Vitis vinifera* L.) respond to water stress with a variety of physiological and molecular mechanisms. Among the first responses to drought is a reduction of the conductivity to water flow along the soil-plant-atmosphere system, mainly regulated by stomatal control (Cifre *et al.*, 2005). One of the primary processes affected by drought is photosynthesis, a fact primarily due to stomatal closure (Escalona *et al.*, 2002). Thus, under semi-arid conditions, water management is of major importance in reducing drought impacts on grape yield and quality.

In dry-farmed areas, both scion and rootstock cultivar can have a strong influence on vine performance under stress conditions. Recent studies indicated differential stomatal sensitivity to water stress conditions between near-isohydric and anisohydric *Vitis vinifera* cultivars (Schultz, 2003). However, there are also reports that rootstocks can modify a grape scion's water status and gas exchange. Padgett-Johnson *et al.* (2000) found that grafted Carignan grapevines exhibited stomatal behaviour similar to that of the rootstock. Düring (1994) showed that photosynthesis and stomatal conductance are affected by the rootstock and that this effect is scion-specific. The reasons for these effects remain obscure due to rootstock influence on root distribution, vegetative growth pattern and productivity, which may also affect gas exchange parameters by altering source-sink relations (Paranychianakis *et al.*, 2004).

Rootstocks have been classified with regard to their resistance to water stress conditions (Carbonneau, 1985) but relatively few studies exist on the pedoclimatic adaptation of scion-rootstock combinations in the field. Especially under dry cultivation, the interaction between scion and rootstock with regard to production performance under water deficits may be an important consideration in vineyard planting strategies. 1103 Paulsen, currently the fastest developing rootstock in Greece in terms of new plantations, is qualified as drought resistant. On the contrary, 3309 Couderc has never been introduced to Greek vineyards because of its reported low adaptation to dry-land conditions. The aim of this study was to evaluate drought adaptation processes for the two scion-rootstock combinations under field conditions, using sap flow sensors combined with measurements of water relations and gas exchange parameters. Results presented in this paper summarize data of the first year of the experiment.

Materials and methods

The experiment was conducted in a commercial vineyard in Naoussa A.O.C. area in Northern Greece (40°65'N, 22°11'E) in the summer of 2005. Grapevines of the dominant red cultivar of the region Xinomavro (*Vitis vinifera* L.) were used, grafted on two rootstocks, respectively 1103 Paulsen (*V. berlandieri* × *V. rupestris*), which is termed to be drought resistant and 3309 Couderc (*V. riparia* × *V. rupestris*) which is of intermediate or low resistance to drought (Carbonneau, 1985). Treatments consisted of two adjacent groups of five years old vines per rootstock, trained to a bilateral cordon system and spur-pruned to 10-12 nodes per vine. The soil was a deep clay loam. The climate is Mediterranean continental, with hot and dry summers. From the beginning of summer (June 2005), soil was maintained at field capacity by periodic irrigation for both rootstock treatments. At mid July, a restricted water regime was applied by withholding irrigation.

In order to estimate the transpiration flux of grapevines, sap flow was measured continuously using the Granier system, according to Braun and Schmid (1997). Two cylindrical probes with a diameter of 2 mm and a length of 15 mm were installed radically into the trunk at a vertical distance of 15 cm, on two adjacent plants per treatment. Measurements were stored on a data logger every 15 min. Sap flow data were expressed on a leaf area basis. Primary and secondary leaf area per vine was calculated in a non-destructive way, using a model with four variables – shoot length, leaf number, area of the largest leaf and area of the smallest leaf – as described by Lopes and Pinto (2000). Vapor pressure deficit (*VPD*) was calculated from air temperature and relative humidity data, recorded continuously using a HOBO H8 data logger (Onset Computer Corporation, MA, USA).

Stomatal conductance (g_s) and net CO_2 assimilation rate (A) were measured on six mature leaves of the outside part of the canopy per rootstock, selected on the vines closest to the plants were xylem sap flow was assessed. Leaf gas exchange measurements were taken at 10.00 h, 13.00 h and 16.00 h on two separate days at the end of the water stress period, respectively August 25 (DOY 237) and August 31 (DOY 243), using a portable gas exchange system Li-6200 (Li-Cor Inc., NE, USA).

Water relations were estimated by daily measurements of stem water potential (Ψ_s) every 2 h starting at 8.00 h, with a Scholander-type pressure chamber, according to the method described by Choné *et al.* (2001). Measurements were performed on fully-expanded leaves of the inside part of the canopy, selected on the vines closest to the plants were xylem sap flow was assessed, on four separate days, from irrigation cutoff through harvest (DOY 207, 219, 237 and 258).

Grapes were harvested on the 20 September 2005 for both scion-rootstock combinations. Grape yield parameters (number and weight of clusters per plant) were determined in all vines per rootstock. 100 berries were randomly taken from a total pool of ten selected clusters per treatment and total soluble solids were determined on the extracted juice. Sampling was done in triplicate. Finally, pruning mass and cane number per vine were recorded in all vines per treatment during the following winter.

All values were compared by one-way ANOVA test and mean differences were determined using Duncan's multiple range test by SPSS software (version 12.0, SPSS Inc., IL, USA).

Results and discussion

Figure 1 shows the diurnal course of sap flow on two typical summer days at the end of the stress period, respectively the 25 and 31 of August 2005. Sap flow measurements revealed a striking difference in the general pattern of flow between the two rootstock treatments. Sap flow of the vines grafted on 1103P increased during the day, reaching maximum values early in the morning (8.00 h) and decreased thereafter. On the contrary, in vines on 3309C, sap flow remained at near maximum levels between 11.00 h and 17.00 h, even though values were still very low which is consistent with the increased xylem cavitation reported in water-stressed grapevines (Lovisolo and Schubert, 1998). The lower sap flow rates in 1103P than in 3309C suggest a stronger reduction of stomatal conductance in the case of Xinomavro on 1103P, presumably as a result of the production of chemical signals (i.e. ABA) in dehydrating roots (Stoll *et al*., 2000).

Our data also allow us to distinguish between the two rootstocks regarding the relationship of sap flow with vapor pressure deficit (*VPD*) which integrates a large range of environmental conditions and it is related to stomatal opening. Sap flow in the 3309C treatment responded to VPD linearly whereas no relationship was found in the case of 1103P (figure 2). It can be assumed that, since stomatal function of 3309C-grafted plants was less sensitive to decreasing water status, water flow followed a concomitant evolution with VPD. The correlation was better with whole day averages of VPD, presumably because grapevines maintained during the night up to 30% of the peak flow rate of day, fact that is in accordance with the observations of Braun and Schmid (1997).

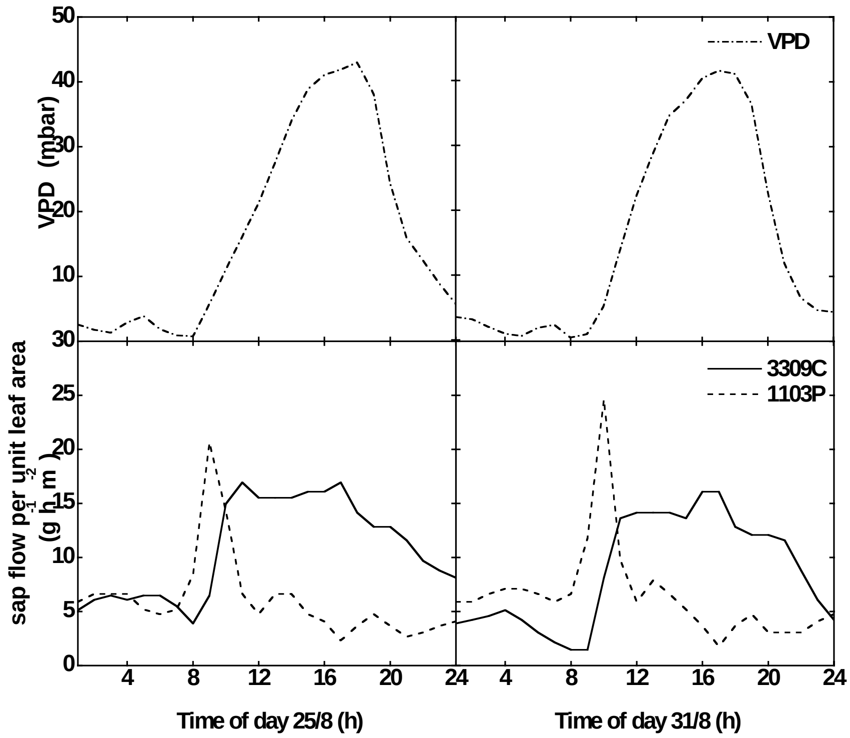

Figure 1 - Daily time course of air vapor pressure deficit and sap flow per unit leaf area for the two scion-rootstock combinations, on two selected days at the end of the drought period (25 and 31 August 2005).

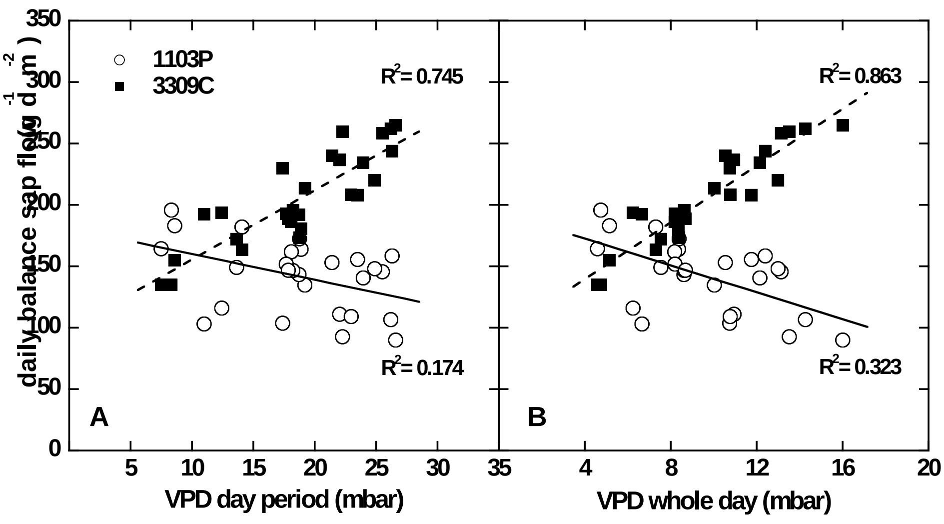

Figure 2 - Relationship between daily balance sap flow per unit leaf area and air vapor pressure deficit (VPD) for the two scion-rootstock combinations over the water deficit period.

VPD data are averages of day period 08 h 00 -20 h 00 (A) or whole day (B) from August 18 to September 11, 2005. Sap flow data correspond to daily sums of hourly values.

The results of sap flow data are supported by gas exchange measurements on the same two days (figure 3). On both days, the course of photosynthesis (*A*) and stomatal conductance (g_s) was similar until midday for the two rootstocks, yet in the late afternoon in the diurnal course, both parameters became significantly higher in the vines grafted on 3309C, compared to those on 1103P. These results suggest a higher desiccation tolerance for vines on 3309C, in spite of the same soil water supply, which allows the maintenance of transpiration and stomatal conductance at higher levels. On the contrary, A and g_s were more sensitive to water deficit in the Xinomavro-1103P combination, resulting in an inferior assimilation rate after midday.

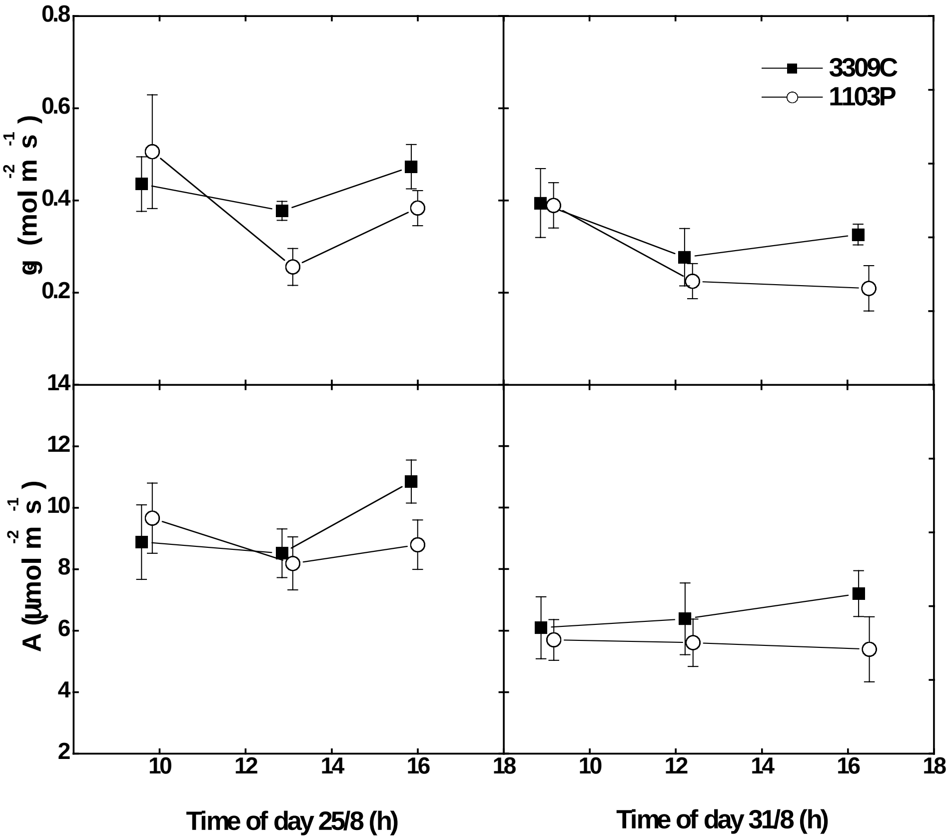

Figure 3 - Influence of rootstock on the diurnal variation of stomatal conductance (g_s) and assimilation rate (A) of cv. Xinomavro vines on two selected days at the end of the drought period (25 and 31 August 2005).
Each point represents the mean of six replicates. Vertical bars represent ± S.E.

Stem water potential (Ψ_s) indicates the capacity of grapevines to conduct water from the soil to the atmosphere and it is shown to be well correlated with the transpiration flow and stomatal conductance (Choné *et al.*, 2001). The two rootstocks showed similar seasonal decrease of morning and midday stem water potential in relation to decreasing soil water availability (figure 4). However, late afternoon Ψ_s values of vines on 1103P were significantly higher (i.e. less negative) compared to those on 3309C, in all measurement days (except for the 25 August). This observation indicates that the tightest late afternoon stomatal closure of vines grafted on 1103P could maintain vine water status at more favorable levels. Such stomatal regulation of transpiration in order to prevent water potential decrease and avoid leaf damage is typical of the isohydric behavior of grapevines (Escalona *et al.*, 2002). In the case of 3309C, this adaptation process to water stress was less evident since stomata remained more open and water loss continued leading to a greater decrease in Ψ_s during the day. Nevertheless, this type of functioning has the advantage of allowing vines to maintain water uptake and to explore a greater volume of soil (Turner, 1986), fact that could explain the higher sap flow rates of 3309C. The observed differences in the physiological responses of the two scion-rootstock combinations could presumably increase in the case of a longer drought period.

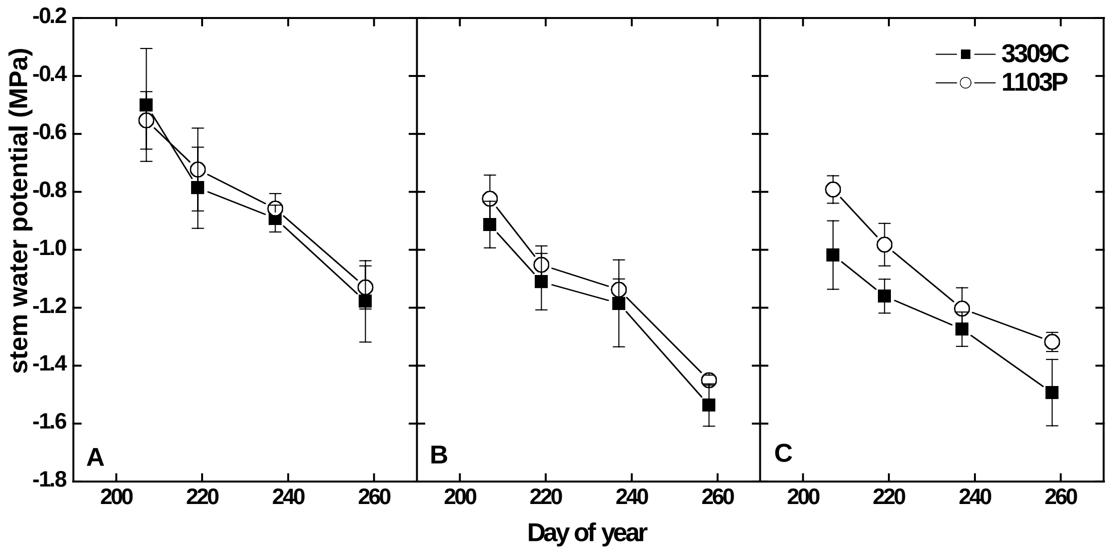

Figure 4 - Influence of rootstock on the seasonal variation of morning (A), midday (B) and afternoon (C) stem water potential of cv. Xinomavro vines, from irrigation cutoff through harvest.
Each point represents the mean of six replicates. Vertical bars represent ± S.E.

Vines on 3309C exhibited lower vigor parameters (leaf area, total pruning weight and mean cane weight) but the differences were not significant (table 1). Ludlow (1980) stated that tolerance to dehydratation (such as in the case of 3309C rootstock) is usually associated with slower rates of growth. Rootstock effect on yield and individual cluster weight was not significant, although values were more reduced in the 3309C treatment. Both scion-rootstock combinations matured fruit to similar sugar concentration in the juice. However, when total soluble solids were expressed on a per g of fresh fruit weight basis, grapes from the Xinomavro-3309C combination exhibited significantly higher values. Since mean crop load was similar for the two treatments (1.90 and 1.97 clusters per shoot respectively), this finding is likely to be related to the higher afternoon photosynthetic activity of the vines grafted on 3309C, at the end of the ripening period. According to Wang *et al.* (2003), water stress applied to vines appears to inhibit sugar accumulation in berries during the day, mainly after 13.00 h (and in a more pronounced way after 15.00 h), in relation to a significant reduction in assimilation rates.

Table 1 - Mean values of growth, yield and quality parameters of Xinomavro grapevines for the two scion-rootstock combinations.
Statistically significant differences by Duncan test (0.05) are indicated by different letters.

Characteristic	1103 P	3309 C
Total leaf area (m^2 $vine^{-1}$)	3.52 a	2.94 a
Total pruning mass (kg $vine^{-1}$)	1.32 a	1.18 a
Cane weight (g $cane^{-1}$)	132 a	126 a
Yield (kg $vine^{-1}$)	5.96 a	4.69 a
Cluster weight (g $cluster^{-1}$)	302 a	265 a
Berry weight (g $berry^{-1}$)	1.99 a	2.02 a
Sugar (g l^{-1} juice)	200 a	202 a
Sugar (μg g^{-1} of berry f. wt)	17.3 a	22.2 b

Conclusion

Photosynthetic performance of grapevines under dry-land conditions is ultimately related to their capacity to assimilate under high water deficits. Our results showed that rootstock can strongly influence plant response to low soil moisture in terms of xylem sap flow, stomatal conductance and photosynthesis of *Vitis vinifera* cv. Xinomavro. This finding may be of great relevance in increasing potential net photosynthesis of grapevines and therefore it should be taken into account in genotypic selection of rootstocks in order to evaluate their suitability for dry cultivation.

Our results suggest that vines grafted on 1103P modified their physiology in order to conserve water resources, thus 1103C could be considered as a drought avoiding rootstock. On the other hand, vines on 3309C seemed to better endure dehydratation and adapted less to stress, thus 3309C rootstock could be characterized as more drought tolerant. Data presented also showed that the 3309C-scion combination achieved better fruit maturity, most likely by permitting better assimilation under limited soil water availability. From an enological point of view, 3309C might be viewed as more advantageous. However, since stress responses could be carried over from year to year, possible implications on vine survival must be taken into consideration.

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