EFFECTS OF ROOTSTOCK AND IRRIGATION REGIME ON HYDRAULIC ARCHITECTURE OF *VITIS VINIFERA* L. CV. TEMPRANILLO

EFFETS DES PORTE-GREFFES ET DEUX NIVEAUX D'IRRIGATION SUR L'ARCHITECTURE HYDRAULIQUE DE *VITIS VINIFERA* L. CV. TEMPRANILLO

Felicidad de HERRALDE, Maria del MAR ALSINA, X. ARANDA,
R. SAVE and Carme BIEL

Departament de Tecnologia Hortícola, Institut de Recerca i Tecnologia Agroalimentàries (IRTA), Carretera de Cabrils s/n, 08348 Cabrils Barcelona, Spain

Abstract: Rootstock hydraulic properties are probably the keys to drought or waterlogging resistance. This work evaluates the effects of two rootstocks (110R, SO4) and two irrigation levels (ET0, 0,5 ·ET0) on the hydraulic architecture of Tempranillo. The experiment was carried out on potted plants near Barcelona (Spain). Hydraulic resistance in trunks was measured by low pressure method and using a High Pressure Flow Meter (HPFM). The trunks of Tempranillo grafted onto 110R showed a lower resistance than the ones grafted onto SO4. The grafting point showed a higher resistance than the cultivar segment and the rootstock segment. HPFM results were more consistent than low-pressure measurements.

Résumé : Le porte-greffe détermine en partie la résistance de la vigne à la sécheresse et à l'asphyxie racinaire. Mais la raison pour laquelle un porte-greffe déterminé confère cette résistance reste inconnue. Les propriétés hydrauliques des racines et le transport de l'eau de celles-ci vers les feuilles sont probablement des éléments - clefs. L'objectif de ce travail a été d'évaluer l'effet de deux porte-greffes et de deux niveaux d'irrigation sur les caractéristiques hydrauliques de *Vitis vinifera* cv. Tempranillo. L'expérience a été réalisée sur des plantes en pot, âgées de quatre ans à Cabrils, dans la région de Barcelone, en Espagne. Le cépage Tempranillo était greffé sur deux hybrides (110R et SO4) soumis à deux doses d'irrigation, correspondant à 50 et à 100 % de l'ET0, au cours de trois saisons. La résistance hydraulique au passage de l'eau dans les troncs a été évaluée par la méthode à basse pression, et par la mesure du flux à haute pression « High Pressure Flow Meter (HPFM) ». En général, les troncs des vignes greffés sur 110R présentent une résistance plus faible que ceux greffés sur SO4. Les caractéristiques hydrauliques des différentes parties des troncs (au-dessus du point de greffe, au niveau du point de greffe et au-dessous du point de greffe) ont été mesurées et analysées séparément. Le point de greffe a présenté la plus grande résistance au transfert de l'eau. Les résultats obtenus avec la technique HPFM ont été plus homogènes et répétables que ceux obtenus avec la méthode à basse pression pour tous les traitements et pour tous les fragments de la plante. Les résultats sont discutés afin d'expliquer les réponses écophysiologiques de ces plantes et les implications agronomiques de ces résultats.

Key words: grapevine, hydraulic resistance, rootstock, grafting point

Mots clés : vigne, resistance hydraulique, porte-greffe, point de greffe

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*Corresponding author:tmp2104@irta.es

INTRODUCTION

Roots are the interface between plant and soil. Plants grow and develop from nutrient and water uptake in the soil. Then root characteristics play an important role in the way plants adapt to the environmental conditions and develop the aerial parts. Grapevines, especially in Europe, are grown grafted onto rootstocks. Rootstock selection is one of the most important factors when a new vineyard is planned. It would depend on many factors such as cultivar affinity for the rootstock, pests' resistance, and adaptation to soil conditions of drought, salinity or waterlogging, all depending on the geographical situation of the vineyard and the climatic conditions. Due to the difficulties of working with root systems the knowledge on root is scarce. Frequently, rootstock characteristics have been established more or less empirically, working with whole vines in the vineyard. Therefore a lot of work has to be done to improve the background on the root functions. Most of the studies on root systems have been performed in order to describe root growth and turnover (Mullins *et al.*, 1992). Those studies show how roots basically grow from just before spring sprout up to anthesis and in a second moment, after harvest and up to leaf fall (Araujo and Williams, 1988). Root density and distribution depends on the combination of rootstock and cultivar and on the edaphoclimatic conditions (Southey and Archer, 1988 ; Swanpoel and Southey, 1989 ; Williams and Smith, 1991). The relationship among growth rates and water uptake has not been directly described, but is clear that soil type, water availability and vineyard management affect root distribution and therefore water uptake. Root and xylem hydraulic conductivity also play a key role in plant water use efficiency. Plant conductivity is the result of xylem anatomy and a combination of three different water pathways: apoplastic transport (Tyree 2003), simplastic transport, and the transcellular pathway trough aquaporins (Tyerman *et al.*, 2002). In some experiments the conductance of the whole root in vines (Peterlunger *et al.*, 1990) or other species (Ramos and Kaufmann, 1979) have been measured with the pressure chamber method, but few of them have been performed using the HPFM (Basile *et al.*, 2003). HPFM offers advantages in front of the pressure chamber method: with the HPFM whole root systems can be measured faster than with the pressure chamber method, while they are still within the soil, with independence of their size and without disturbing them. In the last years some of the knowledge about water transport has been described for grapevines (Sperry *et al.*, 1988 ; Schultz, 2003 ; Tyree, 2003 ; Schubert and Lovisolo, 2004). In particular, root hydraulic conductance has been correlated to vigour, growth and water use efficiency (Peterlunger *et al.*, 1990). Xylem anatomy (i.e. vessel length, diameter and distribution) is a key point for hydraulic conductance (Tyree and Zimmermann, 2002). In grapevines, leaf specific conductivity is lower in nodal segments than in internodal segments of shoots. The nodes could thus be regarded as hydraulic constriction zones in the stem (Salleo *et al.*, 1982). Grafting often can have lower hydraulic conductance than the cultivar thus, it can reduce the whole hydraulic conductance, as it happens in grapevine (Bavaresco and Lovisolo, 2000) or apple (Atkinson *et al.*, 2003).

110R and SO4 are two widely used rootstocks with different drought resistance, in general 110R has been classified as drought tolerant while SO4 has been classified among the less drought resistant rootstocks (Martínez *et al.*, 1990 ; Pongrácz, 1983). Although, Carbonneau (1985) classified a group of 26 vine rootstocks depending on their drought tolerance, using the values of stomatal conductance multiplied by the total leaf area, and in that experiment he ascribed to SO4 a 73 % of the 110R values while the less drought tolerant rootstocks had values only the 36 % of 110R, thus, he classified the SO4 as intermediate drought tolerant rootstock.

The aim of this work was to compare the effect of 110R and SO4 on the hydraulic resistance of whole vines, submitted to two different water regimes. The experimental efforts were focused in the relationship between rootstock and cultivar and on the effect of the grafting point as a bottleneck in this transport.

MATERIALS AND METHODS

The experiment was carried out during year 2004, in IRTA Cabrils (41.5ºN, 2.38ºE, 82 meters high from sea level). We studied four years old vines (*Vitis vinifera* cv. 'Tempranillo') grafted on 110R and SO4 and grown in 50L containers. During 2002, 2003 and 2004, the plants had been submitted to two different irrigation doses (corresponding to 50 % and the 100 % of the calculated balance ET0 - rainfall) from full bloom to harvest. During the rest of the year, the irrigation corresponded to the 100 % of the same balance for all plants. The doses were updated every three days from Cabrils weather station data. 7 to 8 potted plants of each treatment (rootstock x irrigation dose) were taken to the lab. Each plant was cut 10 to 15 cm below the graft. Immediately, root system was connected to a High Pressure Flow Meter (HPFM) (Dynamax Inc. Houston TX, USA). We performed a transient measurement of whole root system hydraulic conductance (K_R) with the HFPM technique (Tyree *et al.*, 1995) (see figure 1 for details). Then, trunk was cut 10 to 15 cm above the graft and we performed transient measurements of the whole trunk hydraulic conductance, which is the parallel sum of the conductance of trunk below the grafting point (K_{RT}), the grafting point (K_{GP}), and the segment of cultivar trunk over the grafting point (K_{CT}) or the series sum of the resistances of the trunk below the grafting point

(R_{RT}), the grafting point (R_{GP}), and the segment of cultivar trunk over the grafting point (R_{CT}). Just after this, the same whole trunk was measured with the low pressure method (LPFM) (Sperry *et al.*, 1988). After this measurement, the segment of cultivar trunk above the grafting point was cut away and we performed a transient measurement of the conductance of the remaining portion (the K_{RT} plus the K_{GP}). Finally the grafting union was removed and the KRT was measured with both methods. Once all measurements were obtained, we calculated the inverse of K values to obtain the resistances (R_T: trunk resistance, R_{RT}: rootstock trunk resistance, R_{GP}: grafting point resistance and R_{CT}: cultivar trunk resistance ($MPa.s.Kg^{-1}$)) and since R_T is the sum of the resistance of the different segments in series ($R_T = R_{RT} + R_{GP} + R_{CT}$) we could calculate each single resistance for both methods.

HPFM and LPM are both methods used for measuring xylem hydraulic conductance. With HPFM water is flushed into the sample with the pressure increasing at a constant rate from 0 to 500 kPa; water flows into the sample and the applied pressure is measured every two seconds. K is then calculated as the slope of the plot of the water flow (ϕ) versus the pressure (P),

$$K = \frac{d\Phi}{dP}(Kg \cdot s^{-1} \cdot MPa^{-1})$$

On the other hand, LPFM measures K at very low pressure (5 kPa) and water circulating through xylem is measured gravimetrically. HPFM provides a quick measurement of the K and whole root systems or whole plants can be measured with this method, which is not possible with the LPFM. Also, the HPFM minimizes the effects of shoots and roots capacitance and the effects of changes osmotic water potential in roots (Tsuda and Tyree, 2000). LPFM, though, is more suitable for measuring embolism. In the case of trunk segments both methods can be used and then compared. From the roots to the cultivar trunk, the conductance of the measured vine fragments (root, rootstock trunk, grafting union and cultivar trunk) are arranged in parallel while resistances are in series so we expressed all results in terms of resistance to simplify the calculations.

On 27th of August the root biomass of 4 plants per treatment was measured. It was determined washing the roots carefully with tap water and weighting after drying them at 65 ºC in an oven for a week. Harvest was on the 13th of September, in that moment we obtained yield per vine ($kg \cdot vine^{-1}$) in 4 randomly chosen plants. Leaf area was measured using a DIAS (Delta-T Devices). The statistical analysis of data was conducted using the proc GLM of the SAS System for Windows 8.02. Analysis of variance was used to test rootstock and irrigation effects. Mean separations were calculated using a Duncan's multiple range test, $P \leq 0.05$, when appropriate.

RESULTS

Root hydraulic resistance measured with HPFM showed significant differences between rootstocks, but not between water regimes, with 110R offering the highest resistance to water flow (figure 2). We have found no influence of the irrigation dose in root resistance.

On the contrary to what happened with the root system, RT was lower in 110R than SO4 (figure 3). Again, there were no significant differences between water regimes. Absolute values of R_T and R_R cannot be compared because we did not measure the whole shoot, only the trunk portion (figure 1), as a comparison with the whole root system, but in terms of general behavior they can be compared and contrasted.

From the three segments of the trunk that we measured, no significant differences between rootstocks nor

Table I - Root biomass (g) and leaf area (m^2) on August 27th, and yield ($kg \cdot vine^{-1}$) the day of harvest for the four treatments: rootstock (110R and SO4) x irrigation dose (100% and 50% ET0).

Each value is the mean of 4 samples ± S.E. Different letters in the same column represent statistical differences (Duncan's multiple range test, $P \leq 0.05$)

Biomasse de la racine (g) et surface de feuilles (m^2) le 27 août 2004 et rendement ($kg \cdot vine^{-1}$) le jour de vendange pour chaque traitement: porte-greffe (110R et SO4) x dose d'irrigation (100 % et 50 % ET0).

Chaque valeur est la moyenne de 4 échantillons ± S.E. Les différentes lettres dans la même colonne représentent les différences statistiques.

Rootstock	Irrigation dose	Root biomass (g)	Leaf area (m^2)	Yield ($kg \cdot vine^{-1}$)
110R	50%	580.72±52.11a	2.35±0.10c	1.18±0.32b
	100%	617.74±59.26a	3.12±0.03a	3.50±0.18a
SO4	50%	450.73±59.98b	2.18±0.06c	1.69±0.25b
	100%	453.65±25.65b	2.81±0.06b	4.10±0.6a

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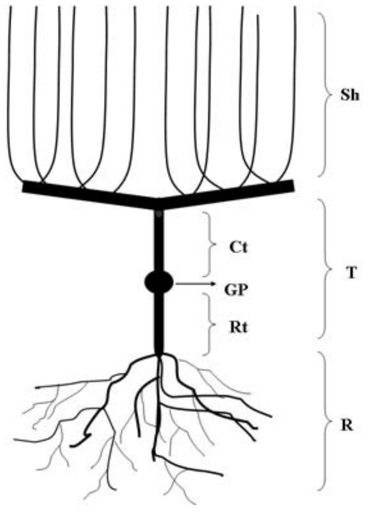

Figure 1 - Drawing representing the organs of vine where hydraulic resistance was measured.
Sh: shoot; T: trunk; Ct: cultivar trunk; GP: grafting point; Rt: rootstock trunk; R: root.

Dessin représentant les organes de la vigne où on a mesuré la résistance hydraulique.
Sh : branches et sarments ; T : tronc ; Ct : tronc du cultivar ; GP : point de greffage ; Rt : tronc des racines ; R : racines.

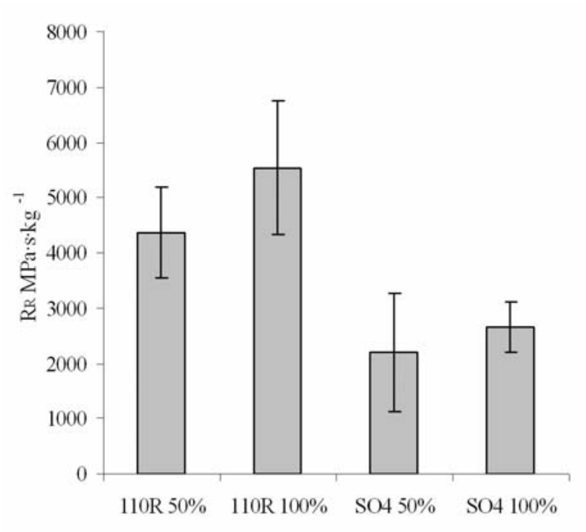

Figure 2 - Root hydraulic resistance RR (MPa·s[1]·kg[1]) for the four treatments: rootstock. (110R and SO4) x irrigation dose (100% and 50% ET0).
Each value is the mean of 7-8 samples and the bars represent the standard error.

Résistance hydraulique des racines RR (MPa·s[1]·kg[1]) de chaque traitement: porte-greffe (110R et SO4) x dose d'irrigation (100 % et 50 % ET0).
Chaque valeur est la moyenne de 7-8 échantillons. Les barres représentent l'écart-type.

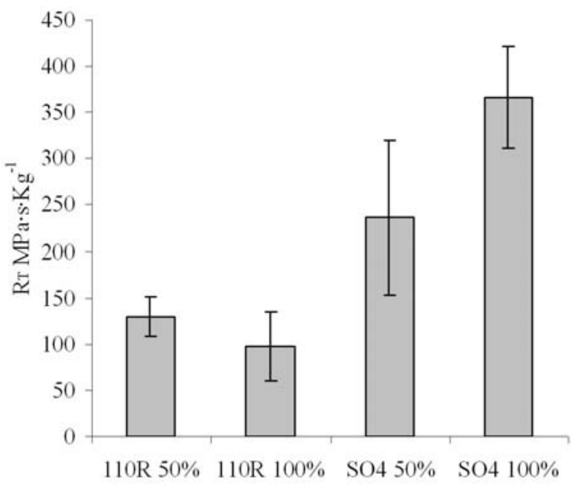

Figure 3 - Trunk hydraulic resistance, RT (MPa·s[1]·kg[1]) for the four treatments: rootstock (110R and SO4) x irrigation dose (100 % and 50 % ET0).
Values are mean of 5-8 values for each treatment (rootstock x irrigation dose) and the bars represent standard error.

Résistance hydraulique du tronc, RT (MPa·s[1]·kg[1]) de chaque traitement : porte-greffe (110R et SO4) x dose d'irrigation (100 % et 50 % ET0).
Les valeurs sont la moyenne de 5 - 8 échantillons par traitement (porte-greffe x irrigation) et les barres représentent l'erreur standard.

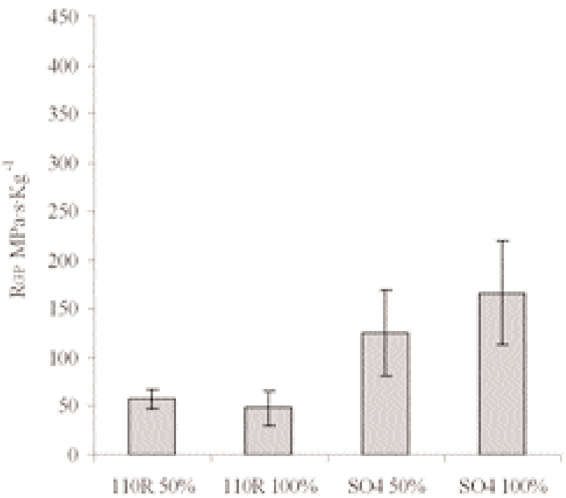

Figure 4 - Grafting point hydraulic resistance, RGP (MPa·s[1]·kg[1]) for the four treatments: rootstock (110R and SO4) x irrigation dose (100 % and 50 % ET0).
Values are mean of 5-8 values for each treatment (rootstock x irrigation dose), and the bars represent standard error.

Résistance hydraulique du point de greffage RGP (MPa·s[1]·kg[1]) de chaque traitement: porte-greffe (110R et SO4) x dose d'irrigation (100 % et 50 % ET0).
Les valeurs sont la moyenne de 5-8 échantillons par traitement (porte-greffe x irrigation), et les barres représentent l'erreur standard.

Table II - Coefficient of variation (% CV) of the resistance values of trunk (T), grafting point (GP), and cultivar trunk (CT) measured with HPFM or LPFM on the same segments.

Coefficient de variation (% CV) de la résistance moyenne du cultivar tronc (CT), le point de greffage (GP) et le tronc (T) obtenus par HPFM et LPFM.

Rootstock	Irrigation dose	Plant fraction	LPFM	HPFM
110 R	50%	CT	49.7	57
		GP	46.1	32.7
		T	38.1	37.6
	100%	CT	42.1	20.6
		GP	21.8	26.4
		T	22.1	18.2
SO4	50%	CT	69.4	104.9
		GP	60.9	23.6
		T	58.6	34.5
	100%	CT	111	5.6
		GP	93.8	44.2
		T	90.9	29.5

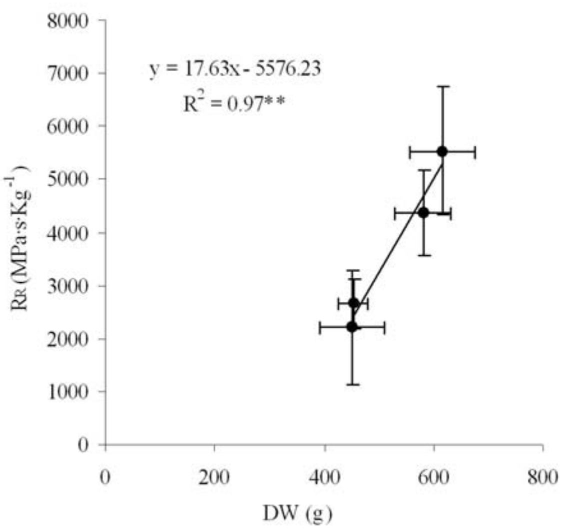

Figure 5 - Lineal relationships of root biomass (DW (g)) vs. root hydraulic resistance RR ($MPa{\cdot}s^{1}{\cdot}kg^{1}$) for the four treatments: rootstock. (110R and SO4) x irrigation dose (100% and 50% ET0).
Each value is the mean of 7-8 samples and the bars represent the standard error. The straight line represents the linear regression between the two parameters.

Corrélation linéale entre la biomasse des racines et sa résistance hydraulique (RR) ($MPa{\cdot}s^{1}{\cdot}kg^{1}$) de chaque traitement : porte-greffe (110R et SO4) x dose d'irrigation (100% et 50% ET0).
Chaque valeur est la moyenne de 7-8 échantillons. Les barres représentent l'erreur standard. La droite représente la regression linéraire entre les deux variables.

water regimes were observed in RCT or RRT, whereas grafting point resistance RGP was significantly lower in 110R than in SO4 (figure 4).

Leaf area at the end of season and yield at harvest were both significantly affected by the irrigation dose, being always bigger the values corresponding to the highest irrigation dose. Besides this, leaf area for plants grafted on 110R and sumited to the highest irrigation regime was significantly higher than those in the rest of treatments (table I). On the other hand, root biomass was not affected by the irrigation regime but for the rootstock effect; roots of 110R were significantly higher than roots of SO4 (table I).

We observed a significant positive correlation ($P \leq 0.05$) between root biomass and whole root hydraulic resistance measured with the HPFM (figure 5).

Hydraulic resistance of plant segments measured with the HPFM and with the LPFM showed a significative correlation ($P \leq 0.05$) (figure 6). In order to compare the accuracy of the methods, we calculated the coefficient of variation (CV) for the results obtained in several sets of samples with both methods (table II).

DISCUSSION

In our experiment, 110R was the rootstock which offered the highest root hydraulic resistance (figure 2). According to literature (Martínez *et al.*, 1990, Pongrácz, 1983), 110R confers to the grafted cultivar better resistance to water shortage than SO4. Galet (1985) also mentioned the 110R drought resistance, and Carbonneau (1985) stated a better drought resistance to drought in 110R than SO4, but being the latter quite tolerant. Higher hydraulic resistance may represent an advantage under water deficit condition, allowing water saving, whereas a lower resistance can mean faster water depletion. This adaptation mechanism allows plants to survive drought (Sperry, 2000 ; Comstock, 2002 ; Domec *et al.*, 2004 ; Trifilo *et al.*, 2004). Xylem anatomy is partially determined by constitutive traits (genetics) and partially as a response to environment. Since we did not found influences of the irrigation dose in root or trunk resistances, but we did found differences due to rootstock (figs. 2 and 3), we think that changes in xylem structure due to water stress have not occurred during the three years of treatment. On the other hand, we found significant differences between treatments in grape production and total leaf area, being always bigger for the biggest irrigation dose (table I). Irrigation dose affected the development of leaves and grapes but it did not affect root and trunk xylem structure. 'Tempranillo', under mild drought conditions showed a mechanistic response, reducing growth and yield, but the imposed stress was not enough to modify xylem vessel characteristics. We observed that

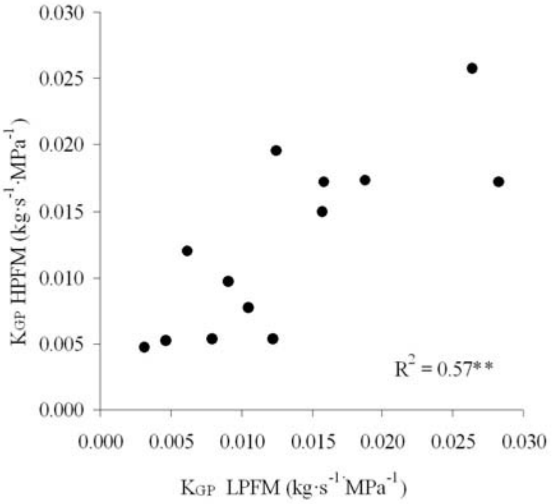

Figure 6 - Relationship between the hydraulic resistance of the grafting point (RGP) ($MPa \cdot s^{1} \cdot kg^{1}$) measured by both methods: High Pressure Flow Meter (HPFM) and Low Pressure Method (LPM).
Each point in the graphic corresponds to the same sample measured with both methods.

Relation entre la résistance hydraulique mesurée au niveau du point de greffe (RGP) ($MPa \cdot s^{1} \cdot kg^{1}$) par les deux methods: High Pressure Flow Meter (HPFM) et Low Pressure Method (LPM).
Chaque point c'est le valeur pour la même échantillon mesuré avec les deux méthodes.

for these two rootstocks the bigger is the root the more resistance it offers to water flow (figure 5). Hence, the increase in hydraulic resistance is explained mainly by the development of bigger roots, even when their growth is restricted by the container. As it has been exposed before, the higher drought resistance known for 110R may be due to a higher R_R. This higher resistance in combination with a bigger root volume (May, 1994) may explore bigger soil volumes and give an advantageous adaptation to the plant under dry soil conditions. This idea is also reinforced by the fact that *V. berlandieri* x *V. rupestris* crosses, 100R among them, are strong and deep growing and in opposition to this, the SO4 is known to have a shallow root system and to not adapt well to deep and dry soil (Shaffer *et al.*, 2004).

The absence of significant differences among 110R and SO4 in RCT or RRT leads us to the conclusion that the R_{GP} is the responsible for the difference in R_T between rootstocks. The grafting point is a bottleneck in the water transport from roots to shoots. It means that this structure anatomy reduces the water flow from roots to stem, which both have lower hydraulic resistance, as it has been described by Bavaresco and Lovisolo (2000) and Atkinson *et al.* (2003). In some cases is known that the callus that is formed in the grafting point may promote the strangulation of the cultivar along the three first years after the plant. So the study of this structure is a key point for a better knowledge of water transport in grafted cultivated species.

The LPFM method is widely used in measures of embolism in shoots of different species (Tognetti *et al.*, 1998 ; Lovisolo *et al.*, 2002 ; Vilagrossa *et al.*, 2003). As the correlation among the K measured with the HPFM and with the LPFM is significative, we consider that HPFM values are acceptable to measure the K, even the HPFM lightly underestimate the values of K in comparison to those obtained with the LPFM (figure 6).

In general, coefficient of variation is higher in the results obtained with LPFM than in those obtained with HPFM for the same group of samples. The variability due to plant material must be the same in both set of results, as the samples measured are the same; then, the difference in the CV among methods must be due to the accuracy of the method. This indicates that HPFM method produces less experimental variability than LPFM method (table II).

CONCLUSIONS

From all these results we concluded that root hydraulic resistance is a very important and determinant point for the regulation of vine water relations. Grafting point offers a high resistance to water flow from roots to cultivar that can be a bottleneck to evapotranspirative flow. In this way we go on working to increase the knowledge about the effects of interactive actions among hydraulic resistance, biomass and other root properties and mechanisms with vine water balance, and the effects of grafting point over all this parameters.

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REFERENCES

ARAUJO F.J. and WILLIAMS L.E., 1988. Dry matter and nitrogen partitioning and root growth of young 'Thompson Seedless' grapevines grown in the field. *Vitis*, **27**, 21-32.

ATKINSON C.J., ELSE M.A., TAYLOR L. and DOVER C.J., 2003. Root and stem hydraulic conductivity as determinants of growth potential in grafted trees of apple (*Malus pumila* Mill.). *J. Exp. Bot.* **54**, 1221-1229.

BASILE B., MARSAL J., SOLARI L.I., TYREE M.T., BRYLA D.R. and DEJONG T.M., 2003. Hydraulic conductance of peach trees grafted on rootstocks with differing size-controlling potentials. *J. Hort. Sci. Biotech.*, **78**, 768-774.

BAVARESCO L. and LOVISOLOC., 2000. Effects of grafting on grapevine chlorosis and hydraulic conductivity. *Vitis,* **39**, 89-92.

CARBONNEAU A., 1985. The early selection of grapevine rootstocks for resistance to drought conditions. *Am. J. Enol. Vitic.,* **36**, 195-198.

COMSTOCK J.P., 2002. Hydraulic and chemical signalling in the control of stomatal conductance and transpiration. *J. Exp. Bot*., **53**, 195-200.

DOMEC J.C., WARREN J.M., MEINZER F.C., BROOKS J.R. and COULOMBE R., 2004. Native root xylem embolism and stomatal closure in stands of Douglas-fir and ponderosa pine: mitigation by hydraulic redistribution. *Oecologia*, 141, 7-16.

GALET P., 1985. *Précis d'ampélographie pratique*. Ed. Charles Dehan. Montpellier, France.

LOVISOLO C., HARTUNG W. and SCHUBERT A., 2002. Whole-plant hydraulic conductance and root to shoot flow of abscisic acid are independently affected by water stress in grapevines. *Funct. Plant. Biol*., **29**, 1349-1356.

MARTINEZ A., CARREÑO J., ERENA M. and FERNÁNDEZ J., 1990. *Patrones de la vid. ed. Consejería de Agricultura*, Ganadería y Pesca de la Región de Murcia. España.

MAY P., 1994. Using grapevine rootstocks, the Australian perspective. *Winetitles*, 62 p. Cowandilla. Australia.

MULLINS M.G., BOUQUET A. and WILLIAMS L.E., 1992. *Biology of the grapevine*. Cambridge University Press. UK.

PETERLUNGER E., MARANGONI B. and CIPRIANI G., 1990. Root hydraulic conductivity of grapevine rootstocks. *Vignevini,* **17**, 43-46.

PONGRÁCZ D.P., 1983. *Rootstocks for grape-vines*. Ed. David Philip. Cape Town. South Africa.

RAMOS C. and KAUFMANN M.R., 1979. Hydraulic resistance of rough lemon roots. *Physiol. Plant.,* **45**, 311-314.

SALLEO S., ROSSO R. and LO GULLO M.A., 1982. Hydraulic architecture of *Vitis vinifera* L. and Populus deltoides Bartr. 1-year-old twigs: I. Hydraulic conductivity (LSC) and water potential gradients. *Giorn. Bot. Ital*., **116**, 15-27.

SCHUBERT A. and LOVISOLO C., 2004. Aquaporin mediated transcellular water transport in grape under stress and rehydration. *In: Workshop on Water Transport ans Aquaporins in Grapevines*. Cost Action 858. Alcúdia, Mallorca.

SCHULTZ H.R., 2003. Differences in hydraulic architecture account for near-isohydric and anisohydric behaviour of two field-grown *Vitis vinifera* L. cultivars during drought. *Plant. Cell. and environ.*, 26, 1393-1405.

SHAFFER R., SAMPAIO T.L., PINKERTON J. and VASCONCELOS M.C., 2004. *Grapevine rootstocks for oregon vineyards*. Ed. OSU extension publications. EM 8882.

SOUTHEY J.M. and ARCHER E., 1988. The influence of rootstock cultivar on grapevine root distribution and density. *In: The grapevine root and its environment*. Ed. J.L. van Zyl (Department of Agriculture and Water Supply), South Africa.

SPERRY J.S., 2000. Hydraulic constraints on plant gas exchange. *Agric. For. Meteor*., **104**, 13-23.

SPERRY J.S., DONELLY J.R. and TYREE M.T., 1988. A method for measuring hydraulic conductivity and embolism in xylem. *Plant, cell and environ.,* **11**, 35-40.

SWANPOEL J.J. and SOUTHEY J.M., 1989. The influence of rootstock on the rooting pattern of the grapevine. *S. Afr. J Enol. Vitic.*, **10**, 23-28.

TOGNETTI R., LONGOBUCCO A. and RASCHI A., 1998. Vulnerability of xylem to embolism in relation to plant hydraulic resistance in *Quercus pubescens* and *Quercus ilex* co-occurring in a Mediterranean coppice stand in central Italy. *New Phytol*., **139**, 437-447.

TRIFILO P., RAIMONDO F., NARDINI A., GULLO M. A. LO, SALLEO S., 2004. Drought resistance of Ailanthus altissima: root hydraulics and water relations. *Tree Physiol*., **24**, 107-114.

TSUDA M. and TYREE M., 2000. Plant hydraulic conductance measured with the high pressure flow meter in crop plants. *J. Exp Bot*., **51**, 823-828.

TYERMAN S.D., NIEMIETZ C.M. and BRAMLEY H., 2002. Plant aquaporins: multifunctional water and solute channels with expanding roles. *Plant. Cell Environ*., **25**, 173-194.

TYREE M.T., 2003. Hydraulic properties of roots, 125-150. *In: Root Ecology. ed. de Kroon*, H. and Visser, J.W. Springer, Berlin 394p.

TYREE M.T., PATIÑO S., BENINK J. and ALEXANDER J., 1995. Dynamic measurements of root hydraulic conductance using a high-pressure flowmeter in the laboratory and field. *J. Exp. Bot*., **46**, 83 - 94.

TYREE M.T. and ZIMMERMANN M.H., 2002. *Xylem Structure and the Ascent of Sap*, 2nd ed. Springer, Berlin.

VILAGROSA A., BELLOT J., VALLEJO V.R., GIL-PELEGRÍN E., 2003. Cavitation, stomatal conductance, and leaf dieback in seedlings of two co-ocurrin Medirterranean shrubs during an intense drought. *J. Exp. Bot.*, **54**, 2015-2004.

WILLIAMS L.E. and SMITH R.J., 1991. Partitioning of dry weight, nitrogen and potassium and root distribution on Cabernet Sauvignon grapevines grafted on three different rootstocks. *Am. J. Enol. Vitic*., **42**,118-122.

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