ROOT HYDRAULIC CONDUCTIVITY IN THREE SELF-ROOTED AND GRAFTED TABLE GRAPE CULTIVARS

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Abstract

Aim : Root hydraulic conductivity is one of the main factors that control water flow in the soil-plant system and ultimately affect crop irrigation requirements. This work sets out to estimate root water conductivity for three self-rooted or grafted table grape cultivars.

Methods and results : We evaluated root water conductivity of the cultivars 'Black Magic', 'Matilde' and 'Victoria' grafted onto 1103 Paulsen rootstock or self-rooted. Measurements were performed on two-year-old table grapes grown in pots filled with pumice. Root water conductivity was determined by placing the pots in a pressure chamber and increasing pressures from 0.05 to 0.30 MPa, at intervals of 0.05 MPa. Plant growth in terms of shoot and root dry matter was also evaluated, as well as leaf and root area.

Conclusion : Root water conductivity differed according to cultivar and grafting. The 'Victoria' cultivar had higher root water conductivity than the other two, which differed little between them. The grafted plants showed higher root water conductivity than the self-rooted plants, except the plants of the cultivar 'Matilde', whose root water conductivity for the grafted and self-rooted plants was almost the same. It was also observed that the higher root water conductivity in relation to cultivar and grafting changed with increasing water flux and was constant for high water flux.

Significance and impact of the study : Estimation of root hydraulic conductivity helps to determine the water consumption of the cultivars investigated, whether self-rooted or grafted, as well as the amount of irrigation water to apply to vineyards.

Key words : root hydraulic conductivity, roots, soilless, table grape, 1103 Paulsen

Résumé

Objectif : La conductivité hydraulique des racines est un des principaux facteurs qui contrôlent l'écoulement de l'eau dans le système sol-plante. Le but de cette étude était d'évaluer la conductivité hydraulique racinaire de trois variétés de raisins de table auto-enracinées ou greffées.

Méthodes et résultats : On a mesuré la conductivité hydraulique des racines des cépages 'Matilde', 'Black Magic' et 'Victoria' greffés sur porte-greffe 1103 Paulsen ou auto-enracinés. Les mesures ont été effectuées sur des plantes âgées de deux ans cultivées dans des vases contenant de la pierre ponce comme substrat. La conductivité hydraulique des racines a été déterminée en mettant les vases dans une chambre à pression et en augmentant la pression tous les 0.05 MPa, de 0.05 à 0.30 MPa. La croissance de la plante a été évaluée en fonction de la matière sèche des sarments et des racines, de même que de la surface des feuilles et des racines.

Conclusion : La conductivité hydraulique des racines varie selon la variété et la greffe. La variété 'Victoria' détient la plus haute conductivité hydraulique racinaire par rapport aux deux autres qui montrent de légères différences entre elles. Les plantes greffées révèlent la plus haute conductivité hydraulique racinaire par rapport aux plantes enracinées, sauf le cépage 'Matilde' dont la conductivité pour les plants greffés et auto-enracinés restait plus ou moins semblable. Par ailleurs, il a été observé que la plus haute conductivité hydraulique par rapport à la variété et à la greffe a pu se modifier suivant la variation de la puissance du flux de l'eau, mais elle est restée constante pour des flux d'eau élevés.

Signification et impact de l'étude : La mesure de la conductivité hydraulique racinaire permet de connaître la consommation d'eau des variétés étudiées, auto-enracinées ou greffées, et de déterminer la quantité d'eau nécessaire pour l'irrigation du vignoble.

Mots clés : conductivité hydraulique radiculaire, racines, hors-sol, raisin de table, 1103 Paulsen

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INTRODUCTION

Root hydraulic conductivity is one of the main factors controlling water flow in the soil-plant system. In tree species there has been little research on the subject and the varying responses, in several cases, may be related to the root anatomy of the different species (Rieger and Litvin, 1999).

Differences in the ability of roots to draw and transport water and mineral nutrients are pronounced for grafted plants where the scion usually differs genetically from the root system. The root system can affect plant vigour (Wutscher, 1979; Atkinson *et al.*, 2003; Radin and Eidenbach, 1984), water relations (Castle and Krezdorn, 1975), frost resistance (Wutscher, 1979), mineral nutrition (Castle and Krezdorn, 1977; Chaplin *et al.*, 1972), water use efficiency (Camacho-B *et al.*, 1974; Crocker *et al.*, 1974), hormonal balance (Steven and Westwood, 1984), yield in terms of quantity and quality (Fallahi *et al.*, 1984; Ezzahouani and Williams, 1995) and shoot growth. Transpiration, CO_2 exchange, N and P content and shoot-root ratio are affected by rootstock (Syvertsen and Graham, 1985; Gonçalves *et al.*, 2005).

However, while the effect of the rootstock system on the scion has been studied (Atkinson *et al.*, 2003), little is known concerning the effect of the scion upon the rootstock. Shoot water transport in the grapevine has been extensively described, while there has been less focus on the root system (Peterlunger *et al.*, 1990; Düring, 1994; Lovisolo and Schubert, 2006; Galmés *et al.*, 2007; Lovisolo *et al.*, 2008) and the effects that the scion should have on root water conductivity (Bavaresco and Lovisolo, 2000).

The importance of these studies is not merely theoretical but also practical, given that there is a correlation between root hydraulic conductivity and transpiration (Vandeleur *et al.*, 2009) via stomatal regulation (Lovisolo and Schubert, 2006), and between the latter and the plant's water status (Flexas and Medrano, 2002). This is important to regulate both water volumes, for crops under irrigation, and water stress level, for rainfed crops or those using the strategy of supplying water to only part of the root zone (Partial rootzone drying, PRD) (Chaves *et al.*, 2010). The use of this technique has led to both an increase in root water conductivity through the activity of aquaporins stimulated by abscisic acid (ABA), and the production of new secondary roots (Kang and Zhang, 2004). In particular, in rainfed crops it has been shown that to avoid stress damage it is more important to regulate root water absorption than regulate the opening of the stomata (Matsuo *et al.*, 2009). Indeed, De Souza *et al.* (2009) established that plant water status is affected more by the rootstock than by the irrigation strategy.

Understanding the physiological and molecular basis that governs root water absorption is thus very important to regulate the balance between vegetative and reproductive development (Chaves *et al.*, 2010; Lovisolo *et al.*, 2010), in order to improve crop water use efficiency (WUE) (Blum, 2009) and to control fruit quality with irrigation deficits (Chaves *et al.*, 2007). A further consideration is the fact that modern irrigation management has shifted from maximisation of production per unit of surface area to maximisation of water productivity (Fereres and Soriano, 2007).

The aim of this paper was to estimate root water conductivity for three table grape cultivars when they are self-rooted or grafted onto the same rootstock.

MATERIALS AND METHODS

1. Plant material

Two-year-old table grape vines were grown in 14 l pots filled with pumice in a cold greenhouse in Victoria (South Italy Lat. 36° 57' N; Long. 14° 32'E). During the growing period the mean temperatures in the greenhouse varied between 15 °C and 45 °C. During the cooler months the maximum temperature at noon was almost 30 °C, while the minimum was never lower than 8 °C. Relative humidity was always higher than 60 %. The photon flux in the greenhouse was almost 44 % of that measured in the field (1180 µmol photon m^{-2} s^{-1}). The soilless technique followed the protocol established by the Tree Crop Department of Palermo University (Di Lorenzo *et al.*, 2003). The following were measured: shoots and roots in terms of weight, leaves and roots in terms of surface area, and root hydraulic conductivity (Lpr). Three *Vitis vinifera* L. table grape cultivars were used in the study: 'Victoria', 'Matilde' and 'Black Magic'. The vines were either self-rooted or grafted onto 1103 Paulsen rootstock. All measurements were made on three plants per treatment per day over three days in July 2004 at the laboratory of the Department of Agricultural Engineering and Agronomy of Naples University Federico II.

2. Root hydraulic conductance

Just after cutting the shoots above the grafting point for grafted plants and at the same height for non-grafted, root hydraulic conductivity was measured by placing the pots containing the vines in a steel chamber and pressuring the pots with air. The pressure in the chamber was increased from 0.05 MPa up to 0.30 MPa. The xylem exudate was collected from the cut shoots above the grafting point by using Eppendorf capsules filled with cotton wool. Pressure application times decreased as the applied pressure increased: 6, 5, 4, 3, 2 and 1 min, respectively, for pressures of 0.05, 0.10, 0.15, 0.20, 0.25 and 0.30 MPa. The measurements were repeated four times per plant and for each pressure, following Rüdinger *et al.* (1994). For a given pressure applied, the exudate volume of the root system was plotted against time.

We calculated the slope of this curve and related it to the root surface of the plant, which gave the water flow (JVr) (m^3 m^{-2} s^{-1}). Lpr was determined by the slope of the regression curve between JVr and applied pressure. As shown by Rüdinger *et al.* (1994), the relation is not linear at low pressures, especially up to a pressure of 0.15 MPa. Thus, Lpr was determined only from the linear part of the slope when the osmotic component of the potential gradient is minimal due to sap dilution. All the measurements, for each variety whether grafted or self-rooted, were conducted on only one day, repeating the experiment three times on three consecutive days.

Once the measurements were completed, the root system was oven-dried at 70 °C, and weighed after separation of the substrate; it was then cut and, on three samples per plant, root length and diameter were measured. Root length was measured using the Newman method (1966). Root diameter was measured with a digital caliper on 20 root segments. Total root length and root surface per vine were calculated. Leaf area per vine was determined with a Li-Cor 3000 leaf area meter ratio.

3. Statistical analysis

All data collected were subjected to analysis of variance (ANOVA) using the SPSS program package (SPSS 7.5.1, SPSS Inc., Chicago, IL) and the means were separated by the Duncan test (P = 0.05) (Duncan, 1955).

RESULTS

1. Plant growth

Dry matter (shoot and root) and area (leaf and root) was similar between the self-rooted and grafted 'Victoria' and 'Matilde' vines (Figures 1 and 2).

Only the cv. 'Black Magic' showed significant differences in the quantity of shoot dry matter between grafted and self-rooted plants (240 g vs 433 g, respectively), as well as with the other two cultivars, whether grafted (240 g for 'Black Magic' vs 326 g for the other two cultivars) or self-rooted (433 g for 'Black Magic' vs 305 g for the other two cultivars) (Figure 1). The aerial part, in terms of

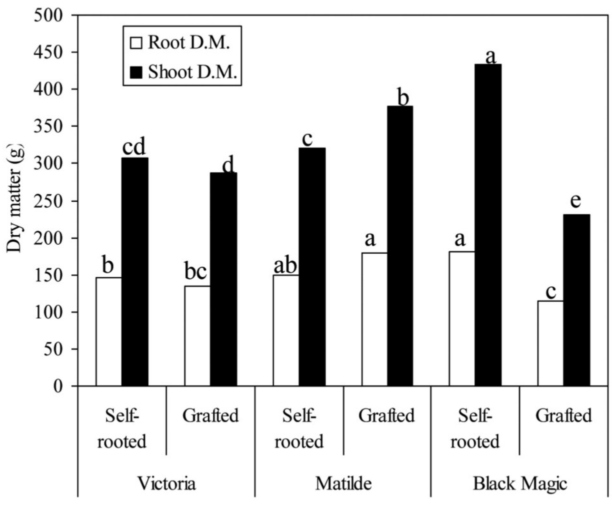

Figure 1 - Mean values of root and shoot dry matter (DM) per plant for the three grafted and self-rooted cultivars. Values with different letters, respectively for root and shoot, are statistically significantly different at the 0.05 P level.

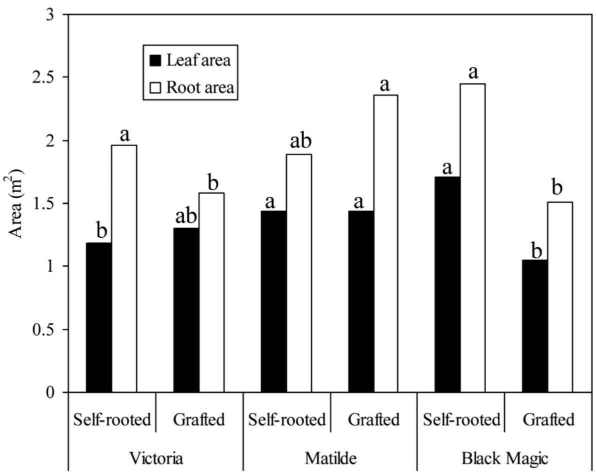

Figure 2 - Mean values of root and leaf area for the three grafted and self-rooted cultivars. Values with different letters, respectively for root and leaf, are statistically significantly different at the 0.05 P level.

weight, was more developed than the root system (326 vs 140 g). However, in terms of area (Figure 2), the roots (average root area of about 2 m^2) exceeded the leaf area (1.35 m^2). The vines underwent green pruning, with the suckers being removed and the leaves thinned. There were no significant differences in root diameter among treatments, with a mean of about 0.22 mm.

2. Water flow pattern

Water flow (JVr) was plotted against applied pressures. Figure 3 reports the mean values for the three self-rooted and grafted cultivars.

The slope of the curve increases as the applied pressure rises. This means that Lpr is low at low pressures and increases as the pressure rises until a pressure of 0.20 MPa. After this pressure the slopes, respectively for each curve, are similar, since the xylem exudate is very diluted and the osmotic component does not contribute greatly to water flow. The highest flows occurred in the cv. 'Victoria' and the lowest in 'Black Magic', in grafted plants compared to self-rooted plants, with the exception of the cv. 'Matilde' where the water flow curve of self-rooted plants overlaps that of grafted plants.

3. Root hydraulic conductivity

The cv. 'Victoria' (Figure 4) recorded a much higher root hydraulic conductivity than the other two, which were both similar.

Grafted plants of the cultivars 'Victoria' and 'Black Magic' showed significantly higher conductivity than their self-rooted counterparts (54 % and 75 % higher, respectively) while in 'Matilde' the differences were not significant.

DISCUSSION AND CONCLUSIONS

Contrary to the widely-held belief that the roots of plants grown in pots may suffer constraints and damage, our values of root hydraulic conductivity are similar to those measured for some rootstocks of grapevine (Peterlunger *et al.*, 1990) or other tree species, with the same method (Steudle, 2000), or with similar methods (Rieger and Motisi, 1990; Rieger and Litvin, 1999), all in soil potted plants.

Our findings highlight the considerable effect of the cultivar and, to a lesser extent, the rootstock, upon root hydraulic conductivity. This subject has received little coverage in the literature. However, for the hybrid *Berlandieri x Rupestris* Lovisolo *et al.* (2008) found root water conductivity over 2.75 times greater than in the hybrid *Berlandieri x Riparia*. Vandeleur *et al.* (2009) report a water conductivity which is twice as high for cv. 'Chardonnay' as for 'Grenache'. For the rootstock 1103 Paulsen, Alsina *et al.* (2011) found in September an almost 4-fold root conductivity compared with that of 101-14 Mgt, even though differences were not noted in June. For some rice cultivars, Matsuo *et al.* (2009) report a 1 to 6.5-fold variability in this parameter. However, a greater quantity of data is reported for transpiration and stomatal conductance. On this point Rogiers *et al.* (2009), on field-grown self-rooted plants, found for cv. 'Semillon' a higher transpiration and stomatal conductance (gs) than the other nine cultivars, especially for stomatal conductance. Also Bota *et al.* (2001) reported, for 22 self-rooted cultivars

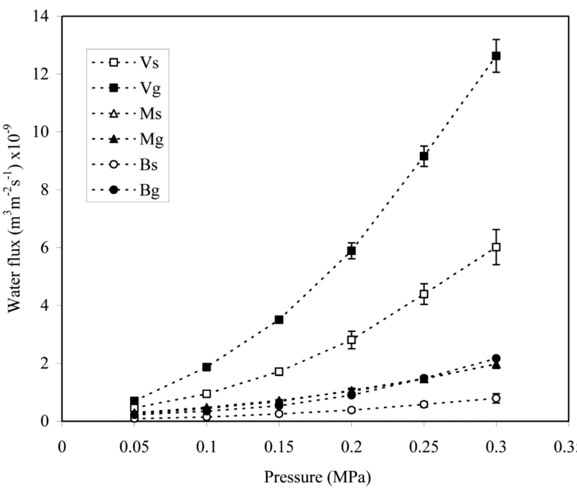

Figure 3 - Mean values (± S.E.) of water flux plotted as a function of pressure for the three grafted and self-rooted cultivars. V = 'Victoria', M = 'Matilde', B = 'Black Magic', s = self-rooted, g = grafted. Vertical bars are LSD at the 0.05 P level.

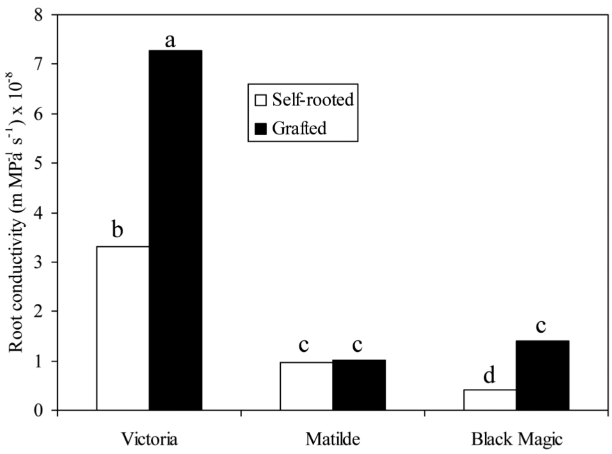

Figure 4 - Mean values of root hydraulic conductivity for the three grafted and self-rooted cultivars. Values with different letters are statistically significantly different at the 0.05 P level.

grown in a pot filled with only peat and fertilised with a natural commercial nutritive solution, a 1 to 3.4-fold variability of stomatal conductance for irrigated plants and a 1 to 42-fold in rainfed crops. Given the correlation between these parameters and root water conductivity, it is legitimate also to expect a considerable variability in the latter.

Roots of grafted plants almost always showed higher hydraulic conductivity than self-rooted plants (on average 105 % higher). In general, 1103 Paulsen is considered a rootstock that is able to confer greater resistance to drought conditions, although in particular cases it did not show such capabilities (Lavrencic *et al.*, 2007). This capability is expressed in higher transpiration flow, resulting from a greater root growth capacity at depth during the summer (Bauerle *et al.*, 2008; Alsina *et al.*, 2011) or from higher leaf water potential (Ezzahouani and Williams, 1995). In particular, Alsina *et al.* (2011) noted that the cv. 'Merlot' on 1103 Paulsen has a 3-fold stomatal conductance compared with the same on 110-14 Mgt.

In our case, rootstock activity is greatly conditioned by the scion. It is commonly believed that grafting reduces water flow (Jones 1974, 1984), although our findings would appear to contradict this hypothesis, given that grafted plants showed a higher root hydraulic conductivity than self-rooted plants. Düring (1994) also failed to find negative effects of grafting on transpiration flow, reporting identical stomatal conductance between self-rooted 'Riesling' and 'Riesling' grafted to 'Riesling'. If Jones's (1984) supposition is valid, it must be granted that the higher root hydraulic conductivity of the rootstock 1103 Paulsen which, of those studied by Peterlunger *et al.* (1990), had the highest root hydraulic conductivity, is such as to overcome any grafting incompatibility. Only in the cv. 'Matilde' were there no differences between the self-rooted and grafted plants, which strongly suggests that the scion has such an effect on the rootstock as to annul that of 1103 Paulsen. Moreover, it is worth bearing in mind that the resistance encountered in the tissues of the scion is axial, whereas the resistance occurring in the roots is radial. In general, axial resistance is believed to be far lower than radial resistance (Klepper, 1983; Amodeo *et al.*, 1999), except in the presence of living cells in the metaxylem (St. Aubin *et al.*, 1986) or that of pathogenic microorganisms in the vascular system (Tyree and Dixon, 1986). The cv. 'Victoria', both in self-rooted and grafted plants, recorded a much higher root hydraulic conductivity than the other two cultivars which, on average, had almost the same value. In the literature, the scion is believed to have less effect than the rootstock rather than vice versa (Tubbs, 1973a, b; Atkinson *et al.*, 2003). Also in this case the data obtained conflict with those reported in the literature, showing the great effect of the scion upon the rootstock.

Plant water balance entails the controlled conductivity of all plant organs that interact in response to environmental stimuli. In recent years it has been observed that aquaporins contribute to this balance (Maurel and Chrispeels, 2001; Luu and Maurel, 2005; Galmés *et al.*, 2007; Cochard *et al.*, 2007; Kaldenhoff *et al.*, 2008; Choat *et al.*, 2009; Vandeleur *et al.*, 2009; Lovisolo *et al.*, 2010). The results obtained for these genotypes may well stem from the differences in quantity and expression of these proteins. For the cv. 'Chardonnay', Choat *et al.* (2009) found changes in xylem water resistance with changes in PIP (plasma membrane intrinsic protein) expression. Also Cochard *et al.* (2007) observed changes in leaf water conductivity in relation to radiation and aquaporin expression. Different aquaporin expression was noted by Galmés *et al.* (2007) both in the leaves and roots in relation to water stress severity. For *Olea europaea*, during drought, a decrease in twig water potential, an increase in twig hydraulic resistance and an increase in the extent of xylem vessel embolisation were observed in parallel with a decrease in aquaporin gene expression. The opposite trends were recorded during rewetting (Secchi *et al.*, 2007). During water stress Vandeleur *et al.* (2009) observed an increase in aquaporin expression for the self-rooted cv. 'Chardonnay' but not with the cv. 'Grenache'. However, Lovisolo *et al.* (2010) pointed out that a strict causal linkage of scion response with root aquaporins occurs only on own-rooted plants.

In conclusion, although the data obtained in this test highlight the considerable influence of variety and rootstock on the hydraulic conductivity of vine roots, for a clearer picture of the matter in question further enquiries are required both in terms of case studies and the factors involved.

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