# Seasonal changes of whole root system conductance by a drought tolerant grape root system.

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**Summary**

- Adjustments of leaf area ($A_L$) to root area ($A_R$) ratios ($A_L$:$A_R$) is a major proposed mechanism for woody perennial plants to tolerate drought by moderating demand versus supply ($A_L$ versus $A_R$), but few investigations have directly observed $A_R$ changes with respect to $A_L$.
- We investigated root proliferation using minirhizotrons, stomatal conductance ($g_s$) and whole root system hydraulic conductance ($k_R$) for a drought tolerant (*Vitis berlandieri* x *V. rupestris* cv 1103P) and non-drought tolerant (*Vitis riparia* x *V. rupestris* cv 101-14 Mgt) grape root system, upon which had been grafted the same drought sensitive clone of *Vitis vinifera* cv Merlot.
- Leaf $g_s$ was more restricted in spring by the drought sensitive root system at somewhat elevated midday leaf water potentials ($\Psi_L$) of -0.8 to -1.0 MPa, but the drought tolerant root system grew more roots at depth and whole root system conductance ($k_R$) increased 2-fold during that same time period of drought and could not be explained by xylem anatomy or conductivity ($K_r$) changes of individual root segments.
- We conclude that the drought tolerant root system improved water supply during the summer drought period by growing new roots at depth.

Key-words: *Vitis vinifera* (grape), root water relations, drought tolerance, root hydraulic conductance, stomatal conductance, root hydraulic conductivity.

Abbreviations: A, net photosynthetic rate (μmoles $CO_2$ $m^{-2}$ $s^{-1}$); $A_L$, leaf area ($m^2$) $A_R$, root area roots ($m^2$); $A_{cr}$ mean cross sectional area of the trunk ($cm^2$); $d_L$ xylem lumen diameter (mm); E, leaf transpiration rate (mmol $H_2O$ $m^{-2}$ $s^{-1}$); $E_c$, canopy transpiration rate (mmol $H_2O$ $vine^{-1}$ $s^{-1}$); $e_a$, ambient vapor pressure (kPa); $e_s$, saturation vapor pressure (kPa); $K_c$, crop coefficient, $g_s$, stomatal conductance to water vapor ,; $g_{max}$, maximum stomatal conductance to water vapor (mmol $m^{-2}$ $s^{-1}$); $k_R$, root hydraulic conductance (kg $MPa^{-1}$ $s^{-1}$); $k_L$, leaf specific root hydraulic conductance (kg $MPa^{-1}$ $s^{-1}$ $m^{-2}$); $K_r$, hydraulic conductivity of excised root segments (kg m $MPa^{-1}$ $s^{-1}$); $L_0$, most common vessel length (m); $L_m$, maximum vessel length (m); $N_L$, number of vessels per cross sectional area of root xylem (no. $mm^{-2}$); $N_R$, number of first order roots (no. $trunk^{-1}$) $N_{sfv}$, number of silicon filled vessels per root cross section; PAW, plant available water (%); Px, frequency distribution of vessels in specific length classes (%); $\psi_{crit}$ stem water potential at which xylem cavitation ensues (MPa); $\psi_{Lmin}$, leaf water potential at which stomata begin to close (MPa); $\psi_{PD}$, pre-dawn leaf water potential (MPa); $\psi_L$, midday leaf water potential (MPa); VPD, air vapor pressure deficit (kPa).

## Introduction

Hydraulic limitations of water supply to leaves of woody plants is still the subject of some debate. At issue is not necessarily where key points of flow restriction occur, as much as the relative role each physical limitation plays in the control of hydraulic conductance through the soil-plant-atmosphere continuum for different species and in diverse environments (Addington et al., 2006, Oren et al., 2001). Models of woody plant hydraulic conductance (Sperry et al., 1998; Sperry et al., 2002, Williams et al., 2001) are consistent with respect to how resistances to water transport in the soil-plant-atmosphere continuum act to optimize water use in a given environment. These models are generally based on stomata acting as the major control point for limiting water loss and thus regulating undesirable negative pressures, while hydraulic resistances at the soil-rhizosphere interface (Newman, 1969), root and stem xylem anatomical properties (Davis et al., 1999, Hacke et al., 2004; Sperry, 1995), and differences in the extent of root surface area versus leaf surface area (Jackson et al., 2000) comprise the main factors that limit water supply versus demand. These modeling exercises predict that adjustment of the ratio of root surface to leaf surface area is one of the major architectural features that can moderate water demand with respect to supply, but empirical data to verify this prediction are not readily available.

There are two generally recognized points of weakness where the hydraulic continuum can more easily break for woody plants. The first concerns loss of contact between the rhizosphere and soil-matrix as soils dry and water potential gradients steepen. The second concerns the cavitation of xylem elements as stem water potentials exceed a critical value ($\psi_{crit}$) (Milburn, 1973). When canopy water demand exceeds that of the integrated capacity of the entire conduction pathway to supply water, or the ability of the hydraulic equipment of the plant to

limit water loss (Sperry *et al.*, 2002), catastrophic or 'runaway' xylem cavitation ensues (Sperry et al., 1988, Tyree & Sperry, 1988), resulting in lethal desiccation. In the short-term, stomata clearly serve to regulate water loss instantaneously (Jones, 1998), and ease negative water potential pressures that would lead to catastrophic xylem cavitation. But many other physiological adjustments (like canopy leaf area modification or leaf orientation) require longer time periods to effectively alter water demand with respect to supply (Givinish, 1986).

A conceptual feature of the above models with respect to longer-term adjustments to moderate water demand with respect to supply is that root system size (or conduction capacity) is often viewed as remaining static during a season while major adjustments may occur at the leaf level (Fordyce et al., 1997, Hacke et al., 2000; Vilagrosa et al., 2003). For example, Sperry and coworkers (Sperry et al., 2002) approach "the thesis that stomatal regulation and longer-term leaf area regulation of gas exchange is necessary to preserve hydraulic continuity of the soil-leaf continuum". Although we do not disagree with the thesis, we simply note that little information exists concerning root response to drying soils. Williams and colleagues (Williams et al., 2001), for example, pointed out that there were "important uncertainties that need to be resolved" with respect to understanding the hydraulic continuum that "concern seasonal dynamics of root growth and rooting depth, especially in response to developing drought…". Root system properties alone may comprise a key element of plant sensitivity to drought stress (Jackson *et al.*, 2000) and reports have indicated that root xylem water potential may often operate near its hydraulic limitation (Alder et al., 1996, Domec et al., 2006; Hacke & Sauter, 1996) In order to examine the hypothesis that root growth dynamics might serve to moderate the water supply and demand equation on a seasonal basis, we examined root growth with depth, root system hydraulic conductance, root anatomical features, and stomatal conductance ($g_s$) for a drought

123 sensitive clone of grape (scion) grafted onto two rootstocks that differ in drought tolerance
124 (Bauerle et al., 2007; Carbonneau, 1985).

125 **Materials and Methods**

126 *Field Site*

127 The experiment was carried out in a 1.05 hectare vineyard situated in Oakville, Napa Valley
128 (California) (38º 25' N 122º 24' W). The Oakville region averages 830 mm of precipitation
129 annually and has a mean annual temperature of 14.3ºC (CIMIS, 2007). The vines (13 year old)
130 were trained to a bilateral cordon with vertical shoot positioning (VSP). Rows were oriented SE
131 to NW, with 2.4 x 2.2 m between and within row vine spacing, respectively. Water was withheld
132 in order to restrict new leaf and leaf area production during the period of fruit growth and
133 veraison (ripening) beginning in 2002. In order to achieve this restriction, irrigation amounts
134 were regulated at 40% of the estimated evapotranspiration demand ($ET_c$) as calculated from the
135 Penmann-Monteith relationship, that was subsequently corrected using a grape crop coefficient
136 ($K_c$) and evaporation from a Class A pan (Prichard, 1992). ETc amounts were calculated and
137 water applied bi-weekly.

138 *Plant Material*

139 We examined two rootstocks that differ in growth dynamics, *Vitis berlandieri* x *V. rupestris*
140 cv (1103P) and *V. riparia* x *V. rupestris* cv (101-14Mgt). Rootstock 101-14Mgt confers lower
141 scion growth (Bauerle et al., 2008b), and is classified as highly drought susceptible (Carbonneau,
142 1985). Rootstock 1103P, on the other hand, confers much higher growth to its scion, and is
143 classified as highly drought resistant (Carbonneau, 1985). Both rootstocks were grafted to the
144 identical drought sensitive clone (scion) of *Vitis vinifera* cv Merlot.

145 *Leaf Area Measurements*

Vine leaf area (LA) was estimated using the specific leaf weight (SLW, area per gram dry mass) of twenty leaves from each of four vines per rootstock that were cut off at the trunk for estimates of root hydraulic resistance on June 21st and September 19th of 2006. All leaves were removed at the petiole base, placed in an ice chest and returned to the laboratory. Leaf area for the 20 leaves was obtained using a planimeter (LI-COR Inc. Model LI-3000, Lincoln Nebraska USA). After leaf area was measured leaves were dried to constant weight at 65ºC, to obtain SLW. All of the remaining leaves were similarly dried to obtain whole canopy dry biomass and thus, an estimate of total leaf area.

*Leaf Gas Exchange Measurements*

Leaf gas-exchange measurements were conducted on mature, fully expanded canopy leaves with an open-path gas-exchange system (LI-COR 6400, Lincoln, Nebraska, USA). Measurements were made on fully exposed leaves just following the phenological stage of pea-size berry development (June 21st), and again just prior to harvest (September 19th). Photosynthetic rate (A), transpiration rate (E) and stomatal conductance ($g_s$) were measured diurnally between sunrise and sunset. Maximum stomatal conductance ($g_{max}$) at ambient $CO_2$ concentration (382ppm) was observed between 10:30 and 12:00h. To obtain an estimate of whole canopy transpiration rate ($E_c$, mmol $H_2O$ $vine^{-1}$ $s^{-1}$) we used a weighted mean average of

$$E_c = \sum_{i=1}^{i=8}(S_i \alpha_i E) \qquad \text{Eqn. 1}$$

where $E$ is the maximum instantaneous leaf transpiration rate measured during the day, $S_i$ is the proportion of leaf area with respect to the vine area in each of eight canopy sectors and $\alpha_i$ is the proportion of $E$ following the approach of Escalona and co-workers (Escalona et al., 2003).

167 *Leaf water status*

168 Predawn ($\psi_{PD}$) and leaf water potential at midday ($\psi_{MD}$) were monitored throughout the
169 growing season (June 7$^{th}$ and 20$^{th}$, July 18$^{th}$, September 11$^{th}$ and Sept 19$^{th}$) with a pressure
170 chamber (Soil Moisture Inc., Santa Barbara, CA). The 4$^{th}$ to 6$^{th}$ leaf was selected on a randomly
171 chosen cane, and the petiole cut free from the cane with a razor blade. The leaf was
172 simultaneously placed in a plastic bag that had been charged to approximately 20,000ppm with
173 anthropogenic derived $CO_2$ to close stomates, and immediately inserted into the pressure
174 chamber. Leaf water potential ($\psi_{PD}$ or $\psi_L$) was measured within 1 to 2 minutes of cutting the
175 leaf from the vine by slowly pressurizing the chamber until sap emerged from the cut end of the
176 petiole.

177 *Root Hydraulic Conductances*

178 The hydraulic resistance of the intact root system was measured using a high pressure flow
179 meter (HPFM, Tyree et al., 1995). Four vines of each rootstock were measured on the 21$^{st}$ of
180 June and five vines were measured on the 19$^{th}$ of September of 2006 between 6:00 and 10:00,
181 solar time. In order to avoid pressure anomalies caused by cavitated xylem, we completely re-
182 hydrated the root during the night by irrigating soils around each vine to field capacity the day
183 before measuring. The trunks were cleanly cut approximately 6 cm above the swelling of the
184 graft union using a pair of razor sharp shears in order to make a quick single cut. The cut trunks
185 were level and did not reveal any signs of crushing or cracking. Bark and the underlying cambial
186 tissue (phloem) were removed to avoid any non xylematic flow to roots during measurements.
187 This also exposed a clean smooth surface that facilitated attaching the HPFM collar quickly and
188 in a manner that precluded any leakage that might interfere with measurements of root hydraulic
189 conductance ($k_r$). Immediately after attaching the HPFM to the cut trunk, the hydraulic

190 resistance of the root was measured using the transient mode of measurement (Bogeat-Triboulot
191 et al., 2002; Tyree *et al.*, 1995). The HPFM system forces distilled and degassed water through
192 the cut trunk into the root system under increasing pressure. Pressure was increased from 0 to
193 500 kPa at a constant rate of 0.5kPa $s^{-1}$. The water flow ($\phi$) was plotted against the pressure (P),
194 and k calculated as the slope of this plot,

195 $$k = \frac{\Delta\phi}{\Delta P} \text{ (Kg } s^{-1} \text{ MPa}^{-1}\text{)} \qquad \text{Eqn. 2}$$

196 Following the first measurement, the HPFM was disconnected, the trunk was cut just below the
197 grafting union, bark and cambium removed, and a new hydraulic resistance measurement was
198 taken. We obtained leaf area specific hydraulic conductance ($k_L$) of the whole root/leaf surface
199 system by expressing the hydraulic conductance of the root system with respect to the leaf
200 surface area of each individual vine ($k_r$ /LA).

201 Upon completion of HPFM measurements, the immediate portion of the root system was
202 excavated and at least two 20 cm segments of each first order root emerging from the trunk was
203 cleanly cut.. Two other root segments of at least 0.5 cm diameter and between 15 and 20cm in
204 length were also cleanly cut from each root system, wrapped in moist paper towels, placed in
205 plastic bags on ice in a cooler where they were transported to the laboratory. Once in the
206 laboratory, we measured the maximum hydraulic conductivity in one root fragment per size
207 category for each excavated root system ($K_r$) using the gravimetric method (Sperry *et al.*, 1988).

208 *Vessel length distribution and morphology*

209 The other root fragments excised were used to define vessel length distribution in root xylem.
210 They were first flushed with deionized water to refill the xylem and avoid the presence of
211 embolisms after which they were vacuum-infused (Rhodorsil RTV-141; Rhodia USA) with a red
212 silicon-based pigment (Silastic LSPRD11; Dow Corning; (André, 1998). Each sample was dried

for 45 min in a 65ºC oven and a thin cross sectional disk of about 2.5 mm thickness was cut every 2 cm along the root fragment. Disks were set out in order starting from the silicon dye injection point to the end of the root fragment. The number of silicon-filled vessels in the initial section ($N_0$) and every two centimeters thereafter ($N_L$) were counted using a dissecting microscope. The fraction of silicon-filled vessels over $N_0$ was calculated, and vessel length distribution for each root sample was calculated using an exponential decay function (Sperry *et al.,* 2005):

$$N_L = N_0 e^{(-\alpha L)} \qquad \text{Eqn. 3}$$

where L is the length of the individual segment and α is a coefficient representing the rate of disappearance (extinction) of dyed cross sectional vessel elements. Data were fitted using the PROC NLIN procedure in SAS 9.1 ($P \leq 0.0001$). The best fit coefficient of extinction (α) (Cohen et al., 2003) was obtained for each silicon-injected sample and mean α value was obtained for each rootstock and data were subjected to one-way ANOVA. The proportion of conduits ($P_{LC}$) between two lengths of root ($L_1$, $L_2$) was obtained as follows (Sperry et al., 2005):

$$P_{LC} = -(1+\alpha L_2)e^{(-\alpha L_2)} + (1+\alpha L_1)e^{(-\alpha L_1)} \qquad \text{Eqn. 4}$$

Finally, the maximum vessel length ($L_m$) and the most common vessel length ($L_0$) were determined for both rootstocks according to Cohen and colleagues (2003):

$$L_m = \frac{\ln N_0}{\alpha} \text{ and } L_0 = \frac{1}{\alpha} \qquad \text{Eqn. 5 and Eqn 6}$$

Leaf, fruit, stem and root biomass was separated and dried at 65ºC in a forced air oven until constant weight was achieved. Dry weight for each fraction was obtained with a precision balance.

*Root Growth Dynamics*

In April of 2002 120 clear cellulose acetate butyrate (CAB) root observation tubes (minirhizotrons) were installed at an angle of 30˚ from the vertical through the drip irrigation zone and a second minirhizotron was placed about 60 cm from the trunk on the opposite side of the vine in an area that was not irrigated. Tubes were 1.5 m in length, 6 cm outside diameter and had a viewing area of 0.0192$m^2$. They were maintained in a light- and watertight condition by plugging the ends of the tubes protruding aboveground and covering it with a white aluminum heat shield. During 2003 to 2006 digital images were acquired every two weeks during the growing season, and once a month after leaf fall and before bud break, using a specially designed digital imaging camera (BTC-2, Bartz Technology, Santa Barbara, CA). Root images were acquired using software designed for root observation capture (ICAP v.4.1; Bartz Technology, Santa Barbara, CA). Images were analyzed using Win RhizoTron MF software (Regents Inc. Quebec, Canada). Root births were estimated by calculating the date midway between the date of observation a root was first observed and the previous date of observation (Comas et al., 2000). Roots transecting more than one minirhizotron observation window were only counted once.

*Data Analysis*

The vines were in a previously established experiment (Bauerle *et al.*, 2007) consisting of a completely randomized block design with three levels of irrigation and two rootstock cultivars within six blocks. Only one irrigation level was used in the present experiment. Four of the six blocks (randomly selected) were used for leaf area, fruit weights and root hydraulic resistance properties on account of the amount of labor involved in acquiring the data. Six blocks were used for gas exchange and water potential measurements. All six blocks were also used for the

root growth investigations. All data were subjected to ANOVA using a randomized complete blocks design with four or six blocks depending on the measurements taken.

## Results

*Root proliferation*

The 1103P root system produced a much larger fraction of new roots during the hot dry season (Fig. 1, Bauerle et al., 2008b). The 101-14Mgt root system on the other hand produced nearly 3-fold more of its new roots during the period of shoot dormancy and of low water stress (season x rootstock interaction: $P = 0.002$, Fig. 1). As summer progressed, root production by the 1103P root system shifted to greater depths where more than 40% of new roots were produced below 60 cm, whereas less than 20% of new roots and less roots overall were produced below 60 cm for the 101-14Mgt rootstock during August.

Twice as much leaf area was produced by *Vitis vinifera* cv Merlot on the 1103P root system, as compared to 101-14Mgt (Fig. 2a). Both canopies had leaf area removed during the summer as a normal management practice. The vines were hedged twice, once in June and once in July, and leaves were manually removed from the fruiting zone in mid-July. The amount of leaf surface area removed from the vines by the above practices during the 2006 growing season were $2.24 \pm 0.24$ $m^2$ per vine for Merlot on 1103P and $0.81 \pm 0.11$ $m^2$ per vine for Merlot on 101-14Mgt. When transpiration rates were normalized to the canopy scale, $E_c$ for Merlot growing on the 1103P rootstock exceeded that of 101-14Mgt by nearly 2-fold in both June and in September (Fig. 3c,f). This occurred in spite of the fact that the canopies on the 1103P rootstock had higher leaf area (Fig. 2a, $P \leq 0.05$ ) and thus a larger fraction of their leaf area in more densely shaded portions of the canopy where transpiration rates were decidedly slower. A difference that emerged between the two rootstocks was that Merlot grafted onto 1103P sustained higher

281 photosynthetic carbon assimilation rates compared to 101-14Mgt during the time period between
282 approximately 9:00 a.m. and 10:00 a.m. when VPD was still below about 2 kPa (Fig. 4, $P \leq$
283 0.05).

284 Patterns of daily stomatal conductance ($g_s$) for Merlot on the two rootstocks differed. In
285 June, stomatal conductance (Fig. 3a) of Merlot on both root systems rose during the early
286 morning hours to rates generally considered to be high (see (Padgett-Johnson et al., 2000). After
287 10:00 a.m., during a time when vapor pressure deficits increased from less than 1 kPa to greater
288 than 5 kPa (Fig. 4), $g_s$ decreased. Stomatal conductance then remained steady throughout the
289 afternoon and was statistically significantly lower for Merlot on the 101-14Mgt rootstock at
290 166.5 ± 24.5 as compared with 260.6 ± 52.4 for Merlot growing on 1103P (Fig. 3a, $P \leq 0.05$).
291 The cost in carbon gain after stomata began to restrict water loss was approximately a 52.2%
292 reduction in photosynthetic carbon assimilation rates on average for Merlot on 101-14Mgt while
293 it was only reduced by 33.9% on average for Merlot growing on the 1103P rootstock (Fig. 3b).

294 *Leaf Water Potential*

295 Leaf water potential ($\psi_L$) was measured throughout the summer on June 6$^{th}$, June 20$^{th}$, July
296 18$^{th}$, September 11$^{th}$ and September 19$^{th}$, (Table 1). We here present diurnal results from the two
297 days that preceded whole root system hydraulic conductance measurements. The measurements
298 are also completely consistent with the other days when $\psi_L$ was measured (since 2002).
299 Predawn leaf water potentials ($\psi_{PD}$) for each rootstock were not statistically significantly
300 different at both time periods and this was true throughout the season ($P = 0.812$ in June and $P =$
301 0.557 in September, Table 1). In June $\psi_L$ dropped gradually during the early morning hours until
302 it went below approximately –0.90 MPa. It subsequently stabilized at approximately -0.99 ±
303 0.08 MPa for Merlot on rootstock 1103P and –1.09 ± 0.08 MPa for Merlot growing on 101-

14Mgt when stomatal conductance became more restricted (Fig. 3a). During the summer as soils dried these levels dropped to -1.44 ± 0.095 MPa and -1.32 ± 0.125 MPa for 1103P and 101-14Mgt rootstocks respectively, in spite of the fact that vines received approximately 40 to 80 liters of irrigation water weekly depending on evapotranspiration demand. These apparent steady-state levels of leaf water potential measured at midday (12:00 to 16:00) differed between the two root systems ($P \leq 0.05$). Thus, in at the beginning of summer (June 20$^{th}$) 1103P sustained midday leaf water potentials of approximately 0.1 to 0.2 MPa less negative than 101-14Mgt, whereas in fall the reverse was true. On Sept 19$^{th}$ $\psi_L$ for Merlot on rootstock 1103P was about -0.2 MPa more negative than 101-14Mgt (Fig. 5b).

*Root Hydraulic Conductance*

In June, whole root hydraulic conductance ($k_r$) was similar for the two rootstocks. Rootstock 101-14Mgt was $2.92 \times 10^{-3} \pm 6.89 \times 10^{-4}$ kg MPa$^{-1}$ s$^{-1}$ (mean ± S.E. n=4) and not statistically significantly different from that of rootstock 1103P at $3.81 \times 10^{-3} \pm 6.23 \times 10^{-4}$ ($P = 0.379$, Fig. 6a). The resistance to water transport for the graft union of 101-14Mgt was 28.1 ± 14.3% as a fraction of the total resistance of the root system plus the graft union, while it was 34.4 ± 11.8% for 1103P. The hydraulic conductance of the graft union did not differ between the two rootstocks in June (at $1.37 \times 10^{-2} \pm 5.85 \times 10^{-3}$ for 101-14Mgt and $1.2 \times 10^{-2} \pm 5.35 \times 10^{-3}$ for 1103P, $P = 0.887$) or in September (at $3.71 \times 10^{-2} \pm 6.00 \times 10^{-3}$ for 101-14Mgt and $2.45 \times 10^{-2} \pm 4.62 \times 10^{-3}$, $P = 0.695$). Thus, while the graft union did represent a relatively large proportion of the total root resistance to water transport ($R_r$), there were no indications that this represented a substantial difference between the two rootstock scion systems. Hydraulic conductance ($k_r$) remained constant during the summer dry season for the 101-14Mgt root system ($P = 0.4082$),

while, in contrast to 101-14Mgt, $k_r$ for the 1103P root system increased more than two-fold during the summer dry period ($P = 0.017$, Fig. 6a).

The leaf area specific hydraulic conductance ($k_L$), here measured with respect to the total leaf area in the canopy (kg $MPa^{-1}$ $s^{-1}$ $m^{-2}$), changed during the summer dry period for Merlot growing on the 1103P root system while it did not change for Merlot on 101-14Mgt (Fig. 6b). In the beginning of summer (June 21st) $k_L$ for 1103P was $0.001 \pm 3.4855 \times 10^{-4}$ not significantly different from that of Merlot on 101-14Mgt at $0.001 \pm 1.762 \times 10^{-4}$ ($P = 0.179$, Fig. 6b). Three months later on September 27th $k_L$ of Merlot on 1103P was nearly two times greater ($P = 0.047$) in spite of the fact that leaf area was sustained at a constant level (Fig. 2a).

The conductivity of root segments ($K_r$) increased from June to September (Fig. 6c). For rootstock 101-14Mgt, it increased from $7.24 \pm 2.19 \times 10^{-4}$ kg m $MPa^{-1}$ $s^{-1}$ (mean SE, n = 15) to $20.92 \pm 5.91 \times 10^{-4}$ kg m $MPa^{-1}$ $s^{-1}$ and for rootstock 1103P it increased from $7.06 \pm 2.60 \times 10^{-4}$ to $19.48 \pm 4.71 \times 10^{-4}$ kg m $MPa^{-1}$ $s^{-1}$. While the increase from June to September was statistically significant ($P < 0.05$), the difference between rootstocks in the same season (month) was not.

*Vessel Length Distribution*

The frequency distribution of vessels (Px) in each of 25 length classes, calculated as the number of vessel-ends in each 2 cm root fragment from the injection point to the end of root segment, differed between 1103P and 101-14Mgt (Fig. 7). For all vessel length classes included in the length intervals between classes 3 through 8 (eg. 6 to 16 cm) and between classes 15 through 25 (eg. 30 to 50 cm), the proportion of vessel-ends expressed as a fraction of the total ($N_0$) was different for 101-14Mgt versus 1103P. In the shorter vessel length interval, a proportion of $0.56 \pm 0.07$ were included for 101-14Mgt, while only $0.37 \pm 0.04$ were detected

between 6 and 16 cm for 1103P. For the proportion of vessels found in the longer length interval of 30 to 50 cm, it was greater for 1103P at 0.25 ± 0.02 as compared with 101-14Mgt at 0.15 ± 0.04 (Fig. 7).

These differences in vessel length distribution (Px) resulted in an estimated most common vessel length ($L_0$) and a maximum vessel length ($L_m$) that were both statistically significantly longer for 1103P than for 101-14Mgt (Table 1). On the one hand, when number of vessels (N) and mean lumen diameter $d_L$ were measured for 1 $mm^2$ of root cross section, no significant differences were found between rootstocks (Table 1). On the other hand, root cross sectional area was significantly higher for 1103P than for 101-14Mgt even though first order root thickness (RT) was the same for both rootstocks. The number of first order roots ($N_R$) was significantly greater in 1103P, at 22.44 ± 2.47 per vine, as compared with 101-14Mgt where it was 15.00 ± 1.26 (Table 1).

## Discussion

Woody plants respond to water stress in a number of important ways. These responses range in temporal scale from being extremely rapid and reversible, like stomatal closure or accumulation and compartmentation of osmotically active solutes, to growth and development of permanent phenotypic structures and hydraulic linkages between them. In the later case, leaf area to root area ratios ($A_L$:$A_R$) that moderate demand for water with respect to supply, and the production of xylem elements less vulnerable to embolism are two responses deemed to have high importance for tolerating more negative water potential gradients or restricted water supply (Sperry *et al.*, 2002). Long term adjustments to root system size with respect to soil water capacity have been reported ((Hacke *et al.*, 2000), and inferences have also been drawn from comparative observations: Jackson and colleagues (Jackson et al., 2000), for example, have shown that differences in rooting depth patterns exist with respect to the World's major plant biomes (Canadell et al., 1996 ), with plants of xeric environments having deeper root depth distributions than plants in more humid environments. But short-term belowground physiological responses to drought stress by woody plants, is less well studied than aboveground responses (Bauerle et al. 2008a). Recent investigations (McCully, 1999; Alder et al., 1996)) demonstrate a high sensitivity of root xylem to embolism and suggest a signaling function (Jackson et al., 2000). Others have indicated internal redistribution of water within the root system of woody perennial plants (xylem refilling) may play an important short-term functional role in drought resistance (Bauerle et al., 2008a; Smart et al., 2005). Nonetheless, we lack information on short-term root responses to drought.

Seasonal adjustments of $A_R$ with respect to $A_L$ may provide information on the relative importance of root system growth during water limitations, but few direct tests of this hypothesis

385 exist to our knowledge. In contrast to $A_L$, direct experimental observation of roots of woody
386 perennials is extremely challenging and limited experimental information exists in this area.
387 During the three years of root observations we conducted in this investigation, we found the
388 drought tolerant root system had an enhanced ability to produce roots at depths greater than 60
389 cm during summer drought, and most of these roots were produced during the summer dry
390 period (Fig. 1). Using the high pressure flow meter (HPFM) approach (Tsuda & Tyree, 2000,
391 Tyree *et al.*, 1995), we found that whole root system water conductance ($k_r$) of this root system
392 increased during this same dry period. The change in $k_r$ we observed for the drought tolerant
393 root system was nearly 2-fold in September compared to June, while $k_r$ remained constant for the
394 drought sensitive root system (Fig. 6a).

395 There are a number of reasons why $k_r$ might change during the period of observation. An
396 increase in conductivity ($K_r$) of individual framework roots, or roots of greater than one year of
397 age, by growing and producing new conduction pathways is one such mechanism. But we found
398 that although $K_r$ increased during the period of investigation, it increased in each root systems by
399 the same magnitude (Fig. 6c). Thus, changes in root hydraulic conductivity measured in root
400 fragments could not explain the difference we observed in root conductance. Second,
401 Zwieniecki and coworkers (Zwieniecki et al. 2003) have shown that root water absorption occurs
402 primarily in the apical ends of roots. Thus, root proliferation should increase conductance to
403 water supply as new roots and their branching connections increase. Conductance of water by
404 the whole root system would also increase (Comstock & Mencuccini, 1998), and this is what we
405 observed.

406 Restriction of stomatal conductance ($g_s$) to maintain a positive balance between carbon
407 uptake and water loss is one of the first responses to water stress in field grown grapevines

(Schultz, 2003). The magnitude of plant $g_s$ depends on the hydraulic conductivity of the entire soil–leaf pathway (Nardini & Salleo, 2003; Sperry & Pockman, 1993), but the signaling mechanisms involved in $g_s$ regulation are still the subject of some debate. Grapevine stomata have been shown to respond to chemical signals like ABA synthesized as soils dry (Tardieu & Simonneau, 1998), as well as to decreasing leaf water potential (Shultz, 2003). We observed diurnal restriction of $g_s$ by Merlot grafted onto both 101-14 Mgt and 1103P rootstocks (Fig. 3) but the degree of control and apparent signal differed. In June, when water was still readily available, the maximum $g_s$ ($g_{max}$) were achieved at mid-morning, and were the same for Merlot on both rootstocks. But corresponding with a decline in $\psi_L$, $g_s$ was more strongly restricted on the 101-14Mgt root system in comparison to 1103P (Fig. 3a). Under the assumption that signal perception by the Merlot clonal tissue grafted onto the two rootstocks is the same, this indicated that signal strength was fundamentally different in nature between the two rootstocks. Measured values of $k_r$ in June were not significantly different for both rootstocks, suggesting that a non-hydraulic signal was strongly acting on stomata in vines on 101-14Mgt. This calls into question the results of Shultz (2003) in as much as the two cultivars he examined (Syrah, anisohydric and Garnacha, isohydric) were apparently grafted onto two different '*V. rupestris*' rootstocks (Schultz, 2003), and our *V. rupestris* rootstocks conferred anisohydric like stomatal behavior on the Merlot clone in one case (1103P), while conferring isohydric like behavior in the other (101-14Mgt).

The significantly greater leaf area of vines grafted onto 1103P in addition to its higher $g_s$, resulted in substantially larger canopy water use ($E_c$) for vines on this root system (Fig. 3c,f). If the low degree of stomatal regulation demonstrated by vines grafted onto 1103P at the beginning of the growing cycle had been maintained throughout the summer drought period from June to

September when no rain, high temperatures (T), net radiation (Rn) and VPD were registered, $\Psi_L$ may have exceeded critical values ($\psi_{crit}$) and suffered severe hydraulic failure. No evidence to support this hypothesis was observed from the current or previous seasons and late in the season vines on 1103P still maintained higher $g_s$ (Fig. 3d) and $E_c$ (Fig. 3f) than vines on 101-14Mgt before midday.

Our data indicated that the increased $k_r$, of 1103P was a consequence of new root production in as much as the change in $k_r$ occurred during the growing season and not as a consequence of root system size gained over the eleven years the vines established permanent root structures in this environment. Thicker first order (framework) roots measured for 1103P (Table 2) will contain more vessels per cross sectional area, resulting in a greater number of parallel water conducting pathways within the root system. From the Ohm's law analogy this would increase $k_r$, since it allows for a higher number of redundant water paths from soil to leaves. The number of first order roots was also statistically significantly higher for 1103P than for 101-14 (Table 1) but this did not result in a greater whole root conductance in June while it was substantially greater for 1103P in September (Fig. 5). Thus, new root production was the most likely reason Merlot on rootstock 1103P maintained better hydraulic supply and thus supported higher evaporature fluxes (Fig. 3c,f).

Vessel-length distribution is a fundamental parameter in determining the hydraulic conductance for long-distance transport elements of plants (Zimmermann & Jeje, 1981). Most common vessel lengths ($L_0$) for roots of 101-14Mgt (at 9 ± 1 cm) and 1103P (at 13 ± 1 cm) were within a range very similar to that estimated for stems of an unidentified cultivar of grape at 13 ± 5 cm (Sperry *et al.*, 2005). This finding indicated that vessel length in stems of grape may, in general, be somewhat conserved in proximal roots, even though we found significant differences

in most common vessel length ($L_0$) and maximum vessel length ($L_m$) for 1103P roots in comparison with 101-14 (Table 1). Hydraulic resistance in xylem conduits, is largely determined by lumen resistance, which is known to increase with length (Zimmermann & Jeje, 1981) and by intervessel hydraulic resistance. The latter has been found to represent approximately 50% of the total conduit resistance (Sperry *et al.*, 2005). A higher proportion of shorter vessels measured for 101-14Mgt, in contrast with 1103P (Fig. 7 and Table 1), would technically decrease $k_r$ in 101-14Mgt as both rootstocks showed the same cross sectional area for a single vessel and the same vessel density in xylem cross sectional area. This may help to explain why 1103P and 101-14Mgt had the same whole root kr in Spring, thus the relative size, or conducting capacity of each root with respect to the major resistances to water transport was the same (Fig. 6c).

*Summary*

We present evidence that adjustments of fine root system growth may play an important role in drought tolerance mechanisms to complement leaf area modification. We documented that a growth invigorating root system (*V. berlandieri* x *V. rupestris* cv 1103P) was able to confer greater drought tolerance upon a drought sensitive clone of grape that was grafted onto it (*V. vinifera* cv Merlot). Leaf water potentials dropped to lower levels in leaves, and $g_s$ was less well regulated by the drought tolerant root system Nonetheless, the drought sensitive clone on the drought tolerant root system was able to maintain a higher evaporative flux throughout the season. Thus, the manner in which drought toleration was conveyed to the drought sensitive clone appeared to arise from deep root proliferation during the hottest and driest part of the season rather than stomatal regulation.

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**Table 1.** Predawn ($\psi_{PD}$) and midday ($\psi_L$) leaf water potentials for plants of *Vitis Vinifera* cv Merlot grafted onto *V. riparia x V. rupestris* cv 101-14Mgt or *V. Berlandieri x V.rupestris* cv 1103P root systems. Shown are the means and standard errors of the mean from 5 plants. Vines were irrigated just prior to the measurements made on July 18th and September 19th 2006.

| | *V. berlandieri* x *V. rupestris* cv 1103P | | *V. riparia* x *V. rupestris* cv 101-14 | |
|---|---|---|---|---|
| | $\psi_{PD}$ | $\psi_L$ | $\psi_{PD}$ | $\psi_L$ |
| June 6th 2006 | -0.065 ± 0.012 | -0.916 ± 0.040 | -0.061 ± 0.011 | -0.913 ± 0.013 |
| June 21st 2006 | -0.075 ± 0.006 | -1.053 ± 0.034 | -0.078 ± 0.009 | -1.065 ± 0.019 |
| July 18th 2006 | – | -0.944 ± 0.055 | – | -1.176 ± 0.052 |
| Sept 11th 2006 | -0.157 ± 0.014 | -1.285± 0.034 | -0.171 ± 0.019 | -1.500 ± 0.016 |
| Sept 19th 2006 | – | -1.260 ± 0.034 | – | -1.052 ± 0.034 |

492 **Table 2.** Most common vessel length $L_0$ (m), maximum vessel length $L_m$ (m), number of vessels
493 per cross sectional area of root xylem ($N_L$, no. $mm^{-2}$), number of first order roots ($N_R$, no. $trunk^{-1}$)
494 and mean cross sectional area of framework roots emerging from the trunk ($A_R$ $cm^2 \cdot root$), and
495 xylem vessel lumen diameter ($d_L$, mm) for plants of *Vitis Vinifera* cv Merlot grafted onto *V.*
496 *riparia x V. rupestris* cv 101-14Mgt or *V. Berlandieri x V.rupestris* cv 1103P root systems.. Each
497 value is the mean from 5 plants for xylem measurements, and 9 plants for root morphology
498 measurements, within the same rootstock and sampling date ± the corresponding standard error.
499 Statistically significant differences between rootstocks are indicated by values within the same
500 row that do not share the same lowercase letter ($P \leq 0.05$).

| | Root System | |
|---|---|---|
| Root Property | *V. riparia* x *V. rupestris* cv 101-14Mgt | *V. berlandieri* x *V. rupestris* cv 1103P |
| $L_0$ (m) | $0.09 \pm 0.01^b$ | $0.13 \pm 0.01^a$ |
| $L_m$ (m) | $0.52 \pm 0.06^b$ | $0.70 \pm 0.04^a$ |
| $N_L$ (number $mm^{-2}$) | $27.92 \pm 3.60^a$ | $27.33 \pm 3.27^a$ |
| $d_L$ (mm) | $0.09 \pm 0.01^a$ | $0.11 \pm 0.02^a$ |
| $N_R$ (number $trunk^{-1}$) | $15.00 \pm 1.26^b$ | $22.44 \pm 2.47^a$ |
| $A_R$ ($cm^2$ $trunk^{-1}$) | $1.80 \pm 0.26^a$ | $1.86 \pm 0.22^a$ |

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504 **Fig. 1:**

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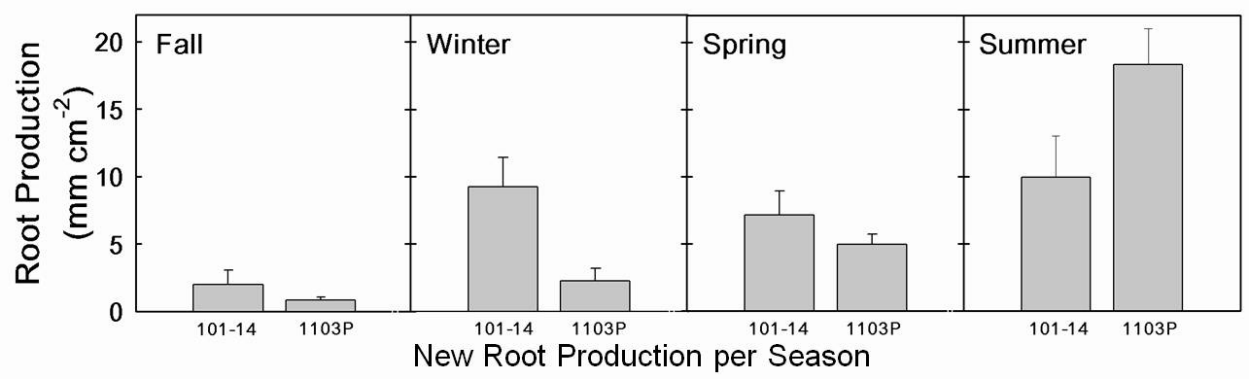


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508 **Fig. 2**

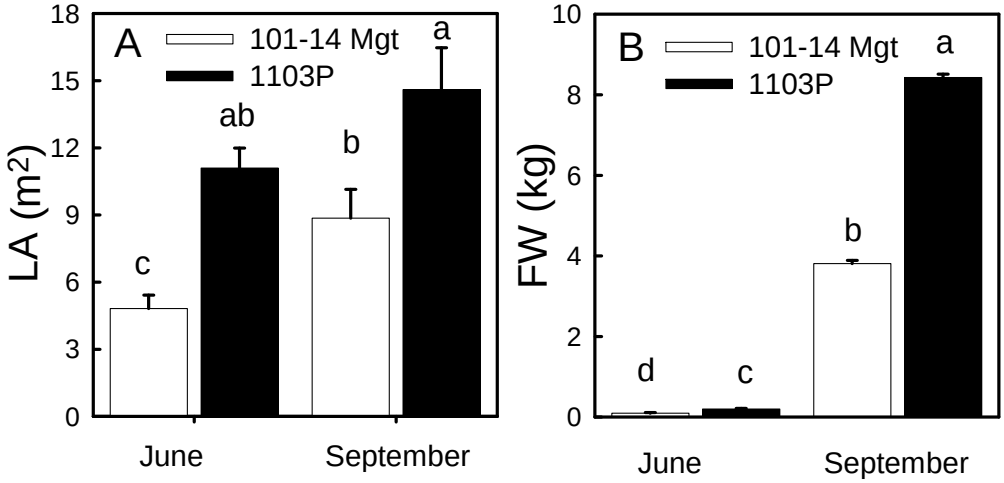


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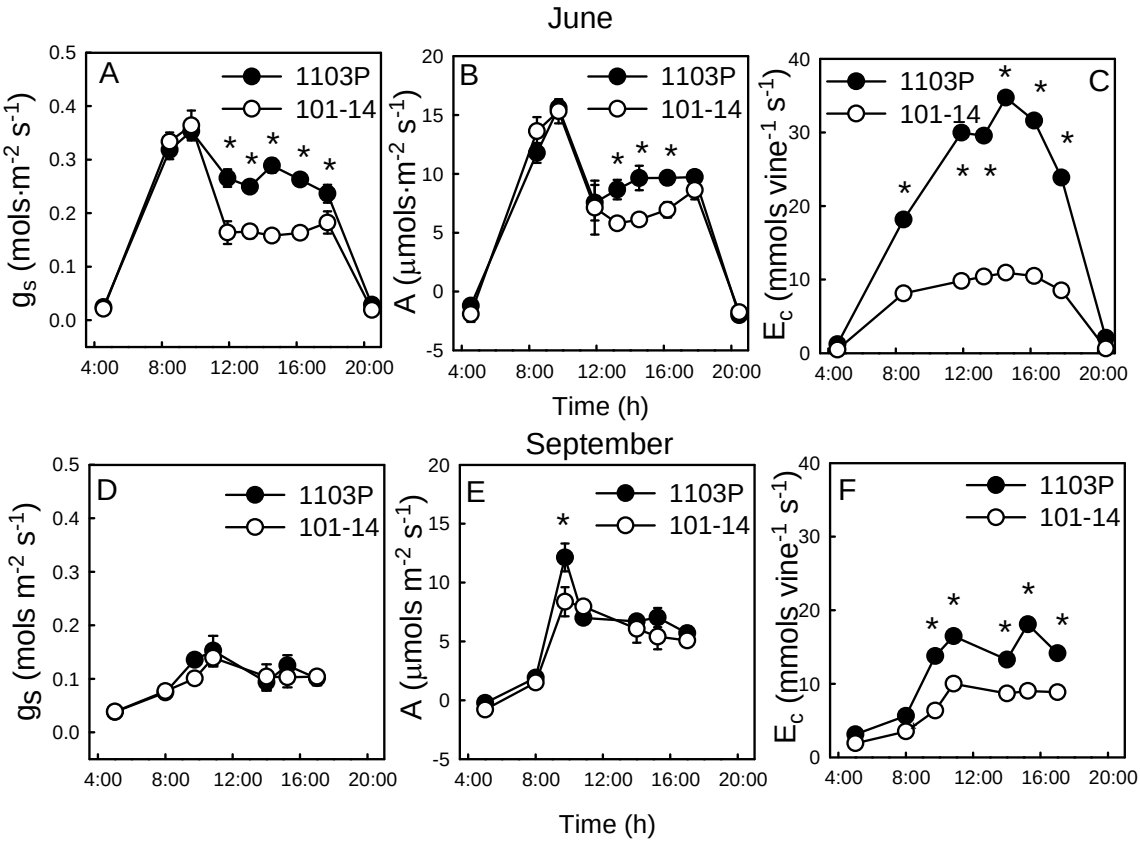
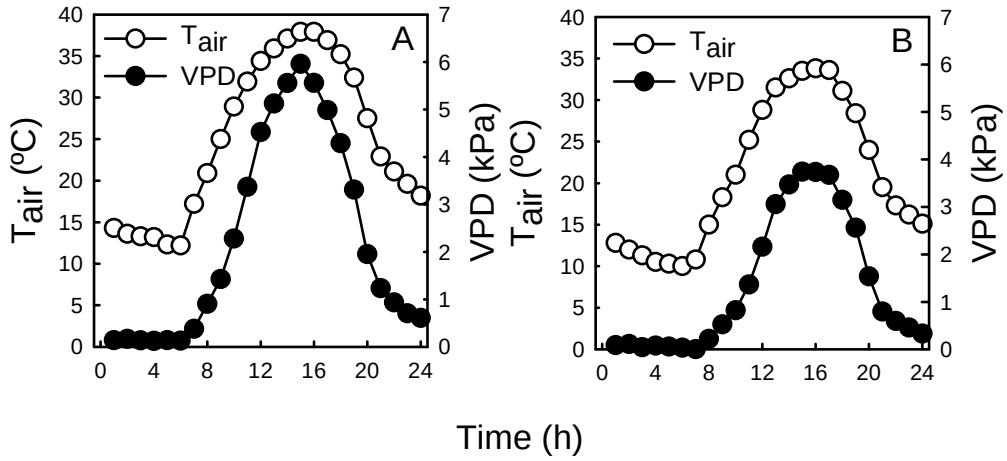
**Fig. 3**


June
A
B
C
1103P
101-14
$g_s$ (mols·m$^{-2}$ s$^{-1}$)
A (µmols·m$^{-2}$ s$^{-1}$)
$E_c$ (mmols vine$^{-1}$ s$^{-1}$)
Time (h)
September
D
E
F
$g_s$ (mols m$^{-2}$ s$^{-1}$)
A (µmols m$^{-2}$ s$^{-1}$)
$E_c$ (mmols vine$^{-1}$ s$^{-1}$)
Time (h)

514 **Fig. 4:**

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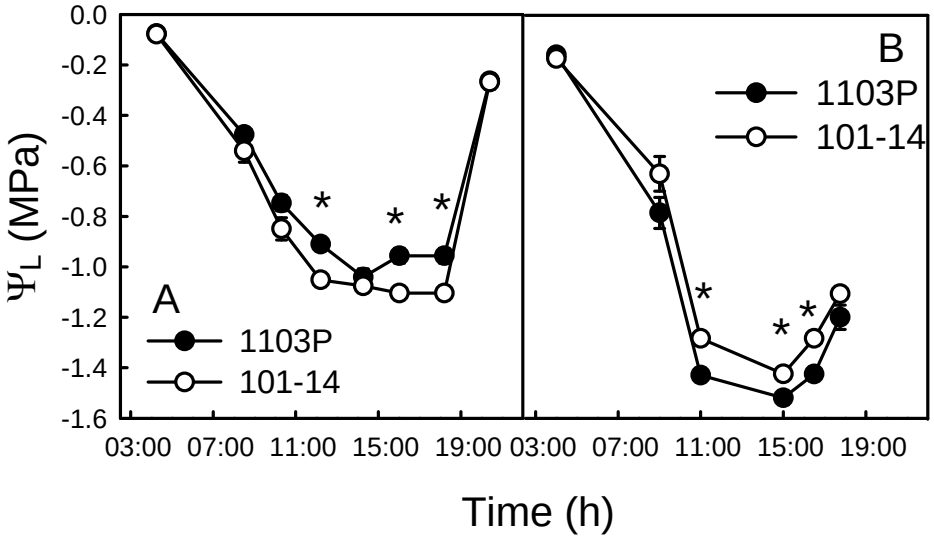
517 **Fig. 5**

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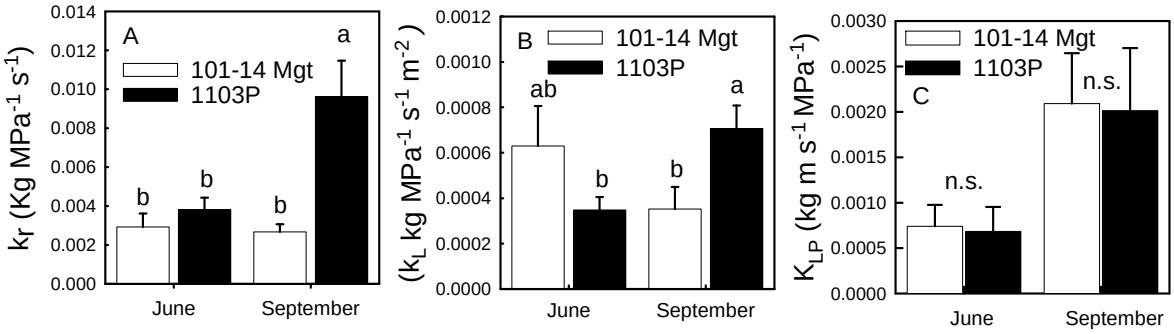
520 **Fig. 6:**

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523 **Fig. 7:**

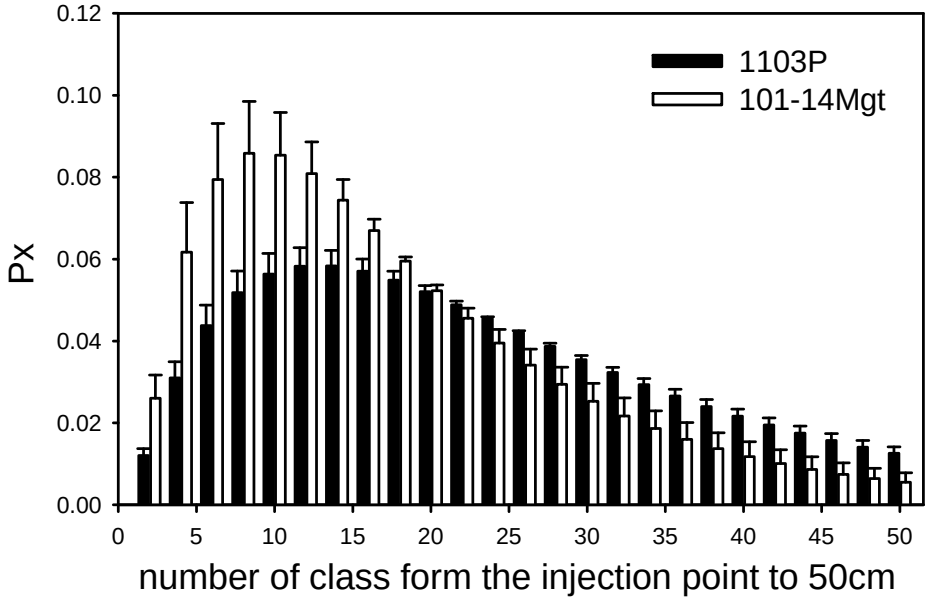


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**Fig. 1.** Seasonal root production (± 1 SE) for root systems of *V. berlandieri x V. rupestris* cv 1103P and *V. riparia* x *V. rupestris* cv 101-14Mgt (season x root system interaction: *P*=0.002). Data represent total root length produced per $cm^{-2}$ of observational window over three months periods for the years, 2003-2005. Each season corresponded to the following months: Fall, Sept-Nov (Significance of difference between 1103P and 101-14Mgt, *P* =0.328); Winter, Dec-Feb (*P* =0.009), Spring, March-May (*P*=0.230); B. Summer, June-Aug (*P* =0.032). Reprinted with the permission of *The New Phytologist* (Chesire England UK).

**Fig. 2.** Shown for spring (June) and fall (Sept) are square meters of leaf area, LA (A) and fruit weight, FW (B) per vine for *Vitis vinifera* cv Merlot grafted onto *V. rupestris* x *V. riparia* cv 101-14Mgt (open bars) and *V. berlandieri* x *V. rupestris* cv 1103P (shaded bars) root systems. Each value is the mean of 5 vines of the same rootstock for each sampling date. Bars represent the standard error. Means that do not share the same lower case letter are significantly different (P≤0.05).

**Fig. 3.** Diurnal courses of leaf stomatal conductance ($g_s$, mmol $m^{-2}$ $s^{-1}$), net photosynthetic rate (A, μmoles $CO_2$ $m^{-2}$ $s^{-1}$) and canopy transpiration rate ($E_c$, mmoles $vine^{-1}$ $s^{-1}$) on June 21$^{st}$ (A, B, C) and Sept 19$^{th}$ (D, E, F) for *V. vinifera* cv Merlot grafted onto *V. berlandieri x V. rupestris* cv 1103P (●) and, *V. riparia x V. rupestris* cv 101-14Mgt (○) rootstocks. Each value is the mean of observations from 6 vines. Vertical bars represent the standard error (P≤0.05) and a * denotes a significant difference (P≤0.05) between rootstocks.

**Fig. 4.** Shown are diurnal courses of air temperature (T, ○) and vapour pressure deficit (VPD, ●) for June 21, 2006 (A) and September 19, right panel (B) for a vineyard in Oakville California, Napa Valley USA.

**Fig. 5.** Diurnal course of leaf water potential ($\psi_L$) for *V. vinifera* cv Merlot growing on *V. berlandieri x V. rupestris* cv 1103P (●) and *V. riparia x V. rupestris* cv 101-14Mgt (○). Shown are the mean values for 6 vines of each rootstock and sampling date, June (A) and September (B). Vertical bars represent the standard error and a * indicates significant differences between rootstocks ($P \leq 0.05$).

**Fig. 6.** (a) Root hydraulic conductance ($k_r$, kg $H_2O$ $MPa^{-1}$ $s^{-1}$), and, (b) canopy specific root hydraulic conductance ($k_L$, kg $H_2O$ $MPa^{-1}$ $s^{-1}$ $m^{-2}$) in spring (June) and fall (September) for *V. vinifera* cv. Merlot grafted onto onto *V. rupestris* x *V. riparia* cv 101-14Mgt (open bars) and *V. berlandieri* x *V. rupestris* cv 1103P (shaded bars). (c) Hydraulic conductivity ($K_r$, kg $H_2O$ m $s^{-1}$ $MPa^{-1}$) for individual root segments. Each value is the mean of 5 vines of each and sampling date. Vertical bars represent the standard error. Different lower case letters indicate statistically significant differences between rootstocks ($P \leq 0.05$).

**Fig. 7.** Frequency distribution of conduits (Px) in each of the 25, 2 cm length classes from a silicon injection point, representing the proximal end with respect to the vine trunk, up to 50cm distal to the trunk for roots of *Vitis vinifera* cv Merlot grafted onto *V. rupestris* x *V. riparia* cv 101-14Mgt (open bars) and *V. berlandieri* x *V. rupestris* cv 1103P (shaded bars).

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