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Impact of soil texture and water availability on the hydraulic control of plant and grape-berry development

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Abstract

Aims: All components of the soil-plant-atmosphere (s-p-a) *continuum* are known to control berry quality in grapevine (*Vitis vinifera* L.) via ecophysiological interactions between water uptake by roots and water loss by leaves. The scope of the present work was to explore how the main hydraulic components of grapevine influence fruit quality through changes in liquid- and gas-phase hydraulic conductance.

Methods: To reach our objectives, determinations of shoot growth, berry size and sugar content, leaf gas exchange, predawn leaf water potential (as a proxy of soil water potential), midday stem water potential and leaf water potential were performed in conjunction with anatomical measurements of shoot xylem. All measurements were conducted in two different cultivars (Cabernet franc and Merlot) and on three different soil types (clayey, gravelly, and sandy).

Results: Shoot xylem morphometric characteristics and whole-plant hydraulic conductance were influenced by cultivar and soil type. Differences in leaf gas exchange parameters and water potentials were determined by soil type significantly more than by cultivar. Between the two extremes (gravelly soil imposing drought conditions and sandy soil with easily accessible water) the clayey soil expressed an intermediate plant water consumption and highest sugar accumulation in berry.

Conclusions: Hydraulic and non hydraulic limitations to vine/berry interactions supported the conclusion that water availability in the soil overrides differences due to cultivar in determining the productive potential of the vineyard. Non hydraulic stomatal control was expected to be an important component on plants grown on the clayey soil, which experienced a moderate water stress. Possible links between hydraulic traits and berry development and quality are discussed.

Key words: *Cabernet franc, grapevine, hydraulic architecture, Merlot, soil type, water deficit*

Abbreviations

101-14 MGt: Millardet et de Grasset 101-14 (an hybrid of *Vitis riparia* × *Vitis rupestris*)

A: assimilation rate

ABA: Abscisic acid

c_i: intercellular CO_2

C soil: clayey soil, characterised by moderate water availability

E: transpiration rate

g_s: stomatal conductance

G soil: gravelly, characterised by high water availability

K_h: hydraulic conductance

K_h Sf_{leaf}: hydraulic conductance of the whole vine plant multiplied for the total canopy area

Riparia Gloire de Montpellier: cultivar of *Vitis riparia*

$R_{soil\text{-}leaf}$, $R_{soil\text{-}stem}$, $R_{stem\text{-}leaf}$ = components of resistance along the s-p-a *continuum*

SO4: Selection Oppenheim 4 (an hybrid of *Vitis riparia* × *Vitis berlandieri*)

S soil: sandy, characterised by unlimited water availability because of the presence of a water table within the reach of the roots

Ψ_{PD}: Predawn leaf water potential

Ψ_{leaf}: Leaf water potential

Ψ_{stem}: Midday stem water potential

Introduction

Vitis vinifera is a species tolerant to (and therefore traditionally grown in) arid and semi-arid conditions, and has developed complex mechanisms to survive in dry soil and under summer drought conditions (Lovisolo et al. 2010). In the meantime, grapevine can adapt to various climatic conditions, expressing high intraspecific variability, from cool temperate to tropical climates

(Schultz 2003; Zufferey et al. 2011). This adaptability, together with the complexity of the grapevine most valuable final product, i.e. wine, makes the study of the mechanisms influencing its productivity and grape composition particularly challenging. Furthermore, the concept of *terroir* straightens the international awareness for the need of further investigation concerning the impact of water relations on wine quality (e.g. Tesic et al. 2001, Tregoat et al. 2002, van Leeuwen and Seguin G 1994, Zsófi et al. 2009). The aim of the present study was to clarify the ecophysiological mechanisms underlying the *terroir* effect by focusing on the hydraulic interactions between plant and soil. In order to understand these interactions, we started our analysis from the observation of the differences in the hydraulic architecture of single plants. The concept of hydraulic architecture applied in this paper follows the definition given by Cochard (1994, unpublished talk; cited in Cruiziat et al. 2002) as "the set of hydraulic characteristics of the conducting tissue of a plant which qualify and quantify the sap flux from roots to leaves". This concept implies the combination of several information to obtain a clear picture of the main driving forces determining plant water transport capacity. The analysis of gas exchanges is strongly correlated to plant water transport: the capacity of the plant to displace water along the soil-root-shoot-leaf-atmosphere pathway impacts on its stomatal conductance and photosynthesis rate (Hubbard et al. 1999). The balance between these two components is the consequence of the tight co-ordination between liquid- and gas-phase water transport, driving simultaneously gas exchange and carbon assimilation (Meinzer 2002). Furthermore, the water movement inside the plant is shaped by the structural characteristics of the xylem: vessels size, number and structure contribute to the xylem conductivity (Tyree and Ewers 1991; Schultz and Matthews 1993; Lovisolo and Schubert 1998) while limiting water supply vs demand in grapevine plants (Lovisolo and Schubert 1998; Alsina et al. 2011). Structural and anatomical plant features are therefore key interpretative elements of the efficiency of the system in displacing water along the soil-plant-atmosphere continuum.

For these reasons, information concerning the xylem architecture of shoots, water potentials and gas exchanges in leaves have been combined and analyzed together as components of the same system, in order to explain differences in conductivity from hydraulic, metabolic and structural perspectives simultaneously.

The aim of the present study is to better understand the main underlying hydraulic mechanisms that could potentially increase plant productivity as well as berry and wine quality. To reach our goal, we investigated grapevine hydraulic characteristics (vine anatomy, ecophysiology, and productive characteristics) between two genotypes on three contrasting soil types present in a vineyard reputed for producing world class wines.

Materials and Methods

Experimental plots

This study was carried out during the spring and summer of 2011, on experimental plots chosen among existing blocks of a commercial rainfed vineyard of the Saint-Émilion region, located approximately 40 km East of Bordeaux, France (44°56'N; 0°11'W).

The studied *Vitis vinifera* L. cultivars were Merlot and Cabernet franc, grown on three different soil types with a density of 6000 vines/ha and grafted on rootstocks inducing low drought resistance (101-14 MGt, Riparia Gloire de Montpellier, and SO4). All vines are over 14 years old and can be considered having a fully expanded root system.

The selected plots are characterized by soils with very different natural water availability conditions, due to the type of soils and root zone profiles, but independent from rootstocks, whose characteristics concerning water stress tolerance are similar. The first plot had a heavy clay subsoil (clay > 60%) between 0.3 and 0.6 m in depth (Albaquic Hapludalf), with a rooting depth of 1.3 m and a soil water-holding capacity of 168 mm. The second plot was a gravelly soil (Arenic Eutrudept; coarse elements > 50%), where soil is mainly composed of sand and rooting depth is limited to 1.2 m by an impermeable layer, with soil water-holding capacity of 40 mm. The third plot was characterized by a sandy soil in the first meter and a sandy-clay texture below 1.0 m. At this plot, the water table was close to the surface, varying from 0.6 m at the end of the winter to 1.6 m at the end of the summer. Considering that rooting depth was 1.35 m, we expected the root system to remain in contact with the capillary zone above the water table throughout the growing season. Hence, water uptake from the water table can be considered unlimited.

Soil water-holding capacities of the different plots were homogeneous inside a given plot but highly distinct between plots, creating a large range of plant water availability conditions (see Vine water status section). Thereafter, the three soil types will be respectively indicated as C soil (clayey, moderate soil water availability), G soil (gravelly, low soil water availability), and S soil (sandy, unlimited soil water availability). The maximum distance between the experimental sites was 500 meters, on flat land, so that climate conditions could be assumed as homogenous. The climate of the region is characterised by moderately dry summers during which evapotranspiration exceeds rainfalls, inducing water deficits. Soil water reserves are replenished during winter, when rainfall is high and evapotranspiration low. Mean annual temperature is 13.7 °C, and mean annual precipitation is 803 mm. Summers are warm and humid, and the growing season mean temperature is 18.2 °C (data from weather station château Cheval Blanc, averages from 1995-2010).

Leaf area

Total leaf area of the selected plants was estimated according to the model proposed by Mabrouk and Carbonneau (1996). The correlation between leaf area and the length of the primary and lateral shoots was established in each plot on 15 shoots, randomly collected from plants (excluding those sample plants selected for water potentials and gas exchange measurements). Leaf area was measured using LI300C area meter (LiCOR, Lincoln, NE, USA) separately for primary and secondary shoots. Equations relating shoot length and leaf area per shoot were calculated and are specific for each cultivar on each soil. By measuring shoot length and applying the equation to convert it to leaf area, this allowed an indirect but non-destructive measurement of the leaf area of each sample plant. Considering that leaf area changed over the growing season, this measurement was repeated twice during the summer (29 June 2011 and 8 August 2011). The shoots used for leaf area determination were used for carrying out the morphometric measurements (See Section 2.7).

Vine vigour and berry ripening

Shoot growth was measured 15 times from May to September of 2011. To prevent accidental trimming by the hedging machine, shoot growth was performed on shoots positioned horizontally on the lowest wire of the trellising system. Berry weight and sugar content were collected 8 times from veraison to ripeness. All the measurements were replicated 4 times during the last sampling date (Fig. 1).

Vine water status

Leaf water status was estimated with a pressure chamber (Scholander et al. 1965; model used: SAM Précis 2000, F-33170 Gradignan, France). Three different water potentials were measured:

i. Predawn leaf water potential (Ψ_{PD}) was determined at the end of the night preceding the day of measurements (from two hours to half an hour before sunrise). Assuming that leaf water potential and soil water potential are in equilibrium at night, this measurement can be used as an indirect indicator of soil water potential (Tardieu and Simonneau 1998). Ψ_{PD} corresponds to the soil water potential of the most humid soil layer explored by the root system, therefore it doesn't provide information concerning the effective water availability for the plant during the day, which has to consider also the evaporation from the soil and the evaporative demand of the plant (Améglio et al. 1999). The plant water availability is more related to the midday stem water potential.

ii. Leaf water potential (Ψ_{leaf}) was measured at the same time as each gas exchange measurement. Leaves on which Ψ_{leaf} was measured were exposed to the sunlight at least one hour before the measurement (PAR ranged between 300 and 2000 µmol m^{-2} s^{-1} during the days of measurement).

iii. Midday stem water potential (Ψ_{stem}) was measured between 14:00 to 16:00, when its value is typically the lowest of the day. Measurements were carried out on leaves at the basal portion of primary shoots, enclosed in a reflective plastic envelope for at least one hour. This time period allowed the water potential in the leaf to reach equilibrium with the water potential in the stem, as transpiration stops in the plastic bag. This measure is considered to be the most representative of the actual level of water deficit of the whole plant (Choné et al. 2001).

All the measurements of water potentials were carried out on fully expanded leaves from primary stems, randomly selected at the moment of the measure. At the end of each day, the following dataset was available from each plant: 1 measurement of Ψ_{PD}, 1 measurement of Ψ_{stem}, and 1 to 6 measurements of Ψ_{leaf}.

The comparison among the six plots during a single day, where a plot is a combination of cultivar and soil, was repeated four times during the summer (1st and 11th of July, 10th and 11th of August corresponding to the respective Julian days 182, 192, 222 and 223).

Additional Ψ_{PD} and midday Ψ_{stem} were collected 7 and 12 times from June to August, averaging 8 measurements on each plot, in order to produce seasonal curves of vine water status (Fig. 2) and to obtain a clear indication of soil water availability and plant water status respectively.

Gas exchange measurements

At the beginning of the data collection, four plants were randomly selected for each plot and two sunlight-exposed fully mature leaves, all approximately attached at the same level on the stem, were identified on each plant. One leaf from each side of the line was sampled in order to have always one leaf fully exposed to the sun independently from the moment of the day. Physiological data on assimilation rate (A), intercellular CO_2 (c_i), stomatal conductance (g_s), transpiration rate (E) were collected always from those same leaves with a portable Gas exchange Fluorescence System (GFS 3000, Walz, Effeltrich, Germany), which measures CO_2-uptake and H_2O-release.

The measurements were conducted by clamping the attached leaves in the leaf chamber, with the following fixed parameters inside the cuvette: carbon dioxide concentration (380 ppm), photosynthetic active radiation, (PAR, 1500 µmol m^{-2} s^{-1}) and temperature (25 °C).

During data collection, a zero-point for CO_2 was set after each displacement of the apparatus between different plots and measurements were taken once the whole set of variables was stabilized.

The data were collected during six days from June through August. The first data set was discarded because of extreme temperatures.

Hydraulic conductance and resistance

In order to measure the hydraulic conductance of the whole plant, we applied the cohesion-tension theory (Dixon and Joly 1894, Angeles et al. 2004) adapted to the Ohm's analogue by van den Honert (1948) and the hydraulic model of the soil-plant-atmosphere *continuum* (Huber 1928; Zimmermann 1983). The hydraulic conductance (K_h; mmol MPa^{-1} s^{-1}) can be expressed as the relationship between the plant water loss, and the water potential drop across a segment of the soil-plant-atmosphere *continuum* ($\Delta\Psi$; MPa; Sperry et al. 1998; Tyree and Zimmermann 2002), assuming a steady state (i.e. neglecting the capacitance effect) water flux (Damour et al. 2010). The water movement through the whole plant corresponds to the total transpiration rate of the plant (E; mmol m^{-2} s^{-1}). This can be obtained from the single-leaf transpiration rate per unit leaf area, multiplied by the specific canopy area of the plant, with an approximation made possible by the low vigour of the studied grapevines and in agreement with Addington et al. (2004).

$$E = \Delta\Psi / R \qquad (1)$$

and,

$$\Delta\Psi = RE = E / K_h \qquad (2)$$

Where R is the resistance.
This simplified approach assumes that the plant acts as a unique pipe (Damour et al. 2010).
The whole-tree hydraulic conductance (K_h):

$$K_h = E / \Delta\Psi \qquad (3)$$

where $\Delta\Psi$ represents the difference in water potential from roots to leaves ($\Delta\Psi = \Psi_{PD} - \Psi_{leaf}$) (Sperry and Pockman 1993).
Conductance and resistance were also partitioned by applying the difference in water potentials between soil and stem, and between stem and leaf, in order to observe their different distribution according to the soil type. In order to quantify the part of R due to the proximal component or to the distal component, the partitioning was quantified as a proportion of the total R (%): the weight of the R proximal component corresponding to $(R_{soil\text{-}stem} / R_{soil\text{-}leaf})*100$ and the weight of the R distal component corresponding to $(R_{stem\text{-}leaf} / R_{soil\text{-}leaf})*100$. The total R was calculated as $R = \Delta\Psi / E$ and not simply by adding together the values of the two segments, in order to obtain an immediate countercheck of the Ohm's law analogy.

Morphometric measurements

Morphometric measurements were conducted at the internode 5 of primary shoots, by cross sectioning midway between the nodes with a hand-held scalpel. All samples were collected on 8 of August. Fresh sections were observed at the same date by means of a stereomicroscope (×100) and pictures taken with a camera (ScopeTek) for a later elaboration.

Shoot, vessel and xylem sectional areas were calculated from the average of two orthogonal measurements of shoot and vessel diameter, and xylem annulus, respectively. Vessel number and diameter were counted and measured within three randomly selected xylem wedges per section (Lovisolo and Schubert 1998). The index of "investment" into xylem development was calculated as the percentage of area occupied by the xylem on the total area of the section.

For a given sampling day, five sections were cut and observed for each combination of soil and cultivar.

Statistical analysis

Plants were randomly chosen for measurements. An analysis of variance (ANOVA) was used, when appropriate, to explain the observed variation. A procedure considering soil × cultivar × date, as well as pair wise interactions, was used to select the best fitting model. Percentages of variance attributable to each of the above-mentioned variables were calculated and the significance of pair wise differences between groups was tested with the Tukey test. The software used was SAS software (version 9.2, SAS 2009).

Results

Vine vigour and berry ripening

The mean shoot length at the end of the growing season differed between the two cultivars on the three soils (Fig. 1.A). The difference in the mean values were statistically significant among soils ($P = <0.001$), without statistically significant interaction between soil and cultivar ($P = 0.066$). Berry weight was low on G, medium on C and high on S soil for both cultivars (Fig. 1.B). Grape sugar at harvest was high on C soil both for Merlot and Cabernet franc (Fig. 1.C). Sugar was low on G and medium on S soil for Cabernet franc. Sugar was slightly lower on S than on G soil for Merlot. For both variables (berry weight and sugar accumulation) statistically significant differences were observed among soils and between cultivars ($P = <0.001$). There was also a significant positive interaction between the two variables ($P = <0.001$).

Water potentials

According to the observed seasonal dynamics of Ψ_{PD} and Ψ_{stem} (Fig. 2), on C soil vines were subjected to mild and stable water stress, on G soil to a stress increasing during the season, on S soil to little or no stress. The comparison of the two Ψ curves on G soil clarifies how low soil water availability (Ψ_{PD}) doesn't necessarily satisfy the evaporative demand of the plant (Ψ_{stem}). The model with the best fit for Ψ_{PD} includes only two independent variables, from which soil contributes alone 87% of the total explained variance (Table 1). The pair wise comparisons between the three soils resulted in a significant difference for the G soil from the other two soils in Ψ_{PD}, Ψ_{stem} and Ψ_{leaf}. The percentage of variance explained by the soil component decreases from Ψ_{PD} to Ψ_{stem} to Ψ_{leaf}, (Table 1).

Gas exchange measurements

Leaf gas exchange measurements such as A, E and g_s were highly related to soil type, while variations in c_i did show a weak correlation with soil and no correlation with cultivar (Table 1). Daily patterns of hydraulic resistance was clearly distinct on G soil (Fig. 3.A), where $R_{soil\text{-}stem}$ and $R_{soil\text{-}leaf}$ increased substantially more than on the other two soils during the whole day. In addition, the distribution of R (Fig. 3.B) differed between soil types, R between soil and stem accounted for more than the 80% of total R on G soil, .from 60 to 80% on C soil , and from 50 to 70% on S soil. When g_s was plotted as a function of Ψ_{PD} (Fig. 4), the distribution of the data points remained clearly clustered for the three soils. On S soil, Ψ_{PD} values were almost all between 0 and -0.2 MPa, with a large range of variation in g_s; C soil showed a larger range for Ψ_{PD} and a lower variability for g_s than G soil; G soil showed the highest range for Ψ_{PD} and the lowest for g_s.

When g_s was plotted against K_h, data points were clustered according to soil type (Fig. 5). On G soil, g_s and K_h were low. On S soil, g_s increased linearly with K_h. On C soil, g_s shows little variation despite a large range of K_h values. Differences between cultivars were also observed: averages for both g_s and K_h were higher for Cabernet franc than for Merlot. This varietal difference is particularly clear on S soil.

Morphometric measurements

Morphometric data (average vessel number /wedge, average vessel size, average wedge number) was compared between cultivars and soils.

The relationship between the average vessel size and number per wedge is presented in Fig. 6. Cabernet franc and Merlot differed significantly ($P < 0.05$) both in terms of vessel number per wedge and vessel size (Fig. 6.A). Cabernet franc had smaller vessels but a higher number of vessels per wedge than Merlot. Differences were also significant ($P < 0.05$) for vessel density and size among soils (Fig. 6.B). For plants grown on G soil, where the Ψ_{stem} are the most negative (Fig. 2.B), vessel size was significantly lower than in plants grown on C and S soils. The value referring to the average number of vessels was significantly higher for vines on S soil than for the other two soils. The proportion of surface occupied by xylem tissues compared to the total surface of the section can be considered as an indicator of the "investment" in the development of the water transport system by the plant (Fig. 7). Cabernet franc showed a significantly higher proportion of the section occupied by xylem than Merlot ($P = < 0.001$; Fig. 7.A). On C soil the "investment" was higher compared to G soil (Fig. 7.B.; $P < 0.05$). From the combination of the average xylem area with the whole vine $K_{h\ soil\text{-}leaf}$ (Sf_{leaf}), grouped for each combination of cultivar and soil, a linear correlation was obtained (Fig. 8). On the G soil, vessel area and K_h Sf_{leaf} were the lowest, while differences between Cabernet franc and Merlot were evident only for K_h Sf_{leaf}. The other four points were clustered around much higher values for the K_h Sf_{leaf} and xylem area, where the differences for K_h Sf_{leaf} between the two cultivars were more evident on C than on S soil and between the two soils for the same cultivar more evident for Cabernet franc than for Merlot.

Discussion

The present study investigated the effects of three contrasting soils and their related water availabilities along the season on vine anatomy, ecophysiology, and productive characteristics of two cultivars in a fully developed vineyard.

The analysis started with the interpretation of the productive characteristics of the plots in terms of shoot growth, berry growth and grape ripening, where C soil presented the most interesting balance between quality and quantity. This soil induced mild water deficits, which maintained a high photosynthetic rate but limited shoot growth after veraison. During this phase, the partition of photoassimilates and secondary metabolites shifted towards reproductive tissues, therefore these conditions limited positively the competition for carbohydrates during fruit ripening. The result was berries with an optimal balance between sugar concentration and water content. In a long term study in the same vineyard the influence of the main *terroir* components on vine development and fruit quality has been previously addressed (van Leeuwen et al. 2004,2009). Key findings were the effects of vine water reserve on shoot growth dynamics, berry size and sugar accumulation. In this work, we aimed at identifying the role of the hydraulic architecture on the ecophysiological mechanisms involved in regulating stomatal conductance and plant resistance to summer drought. The above-mentioned observations were in agreement with the uncoupled growth from photosynthesis in drought conditions, shoot growth appearing more sensitive to water deficit than photosynthesis (Souza et al. 2005; Pellegrino et al. 2006; Muller et al. 2011) and could be interpreted through the analysis of the hydraulic architecture of the plants.

Shoot xylem architecture was a major factor in limiting water supply vs demand in grapevine plants (Lovisolo and Schubert 1998, Lovisolo et al. 2002a; Alsina et al. 2011). The observation made on the proportion between vessel number and size (Fig. 6) revealed the effect of both cultivar and soil components on anatomical acclimation to water shortage. Therefore, the intrinsic anatomical characteristics of the plant (cultivar effect, Fig.6.A) were modulated by the environmental conditions (Chouzouri and Schultz 2005). When water availability increased from G soil to C soil and from C soil to S soil, vessel size increased before vessel number (Fig.6.B). Knowing that particularly reduced or large vessels are more likely to embolize (Hölttä et al. 2005), we can hypothesize that, under mild drought condition, the investment in size is more efficient than the investment in number of xylem elements. This would also explain why the significantly highest "investment" in xylem tissues was present on C soil (Fig. 7.B).

The statistical analysis conducted on the main ecophysiological parameters (water potentials and gas exchanges) showed the predominance of the soil effect, while cultivar effect was subordinate. The endogenous biological control implied by the variety appeared less powerful than the exogenous hydraulic control imposed by the soil component (and the related water availability) in modulating the plant gas-exchange. The loss of significance of soil effect while moving from Ψ_{PD} to Ψ_{stem} to Ψ_{leaf} implied that the three water potentials, while consistent in pointing out differences in vine water status between plots, gave complementary information on a single plant (i.e., Ψ_{leaf} gives a more precise information on the cultivar and climate effect than Ψ_{stem}, while Ψ_{stem} and Ψ_{PD} better reflect the soil effect). Substomatal CO_2 concentration (c_i) seemed to be the only variable where most of the variation was due to a date effect (Schulz et al. 1996), while differences due to soil or cultivar effects were scarcely evident: this implied only a minor (if any) metabolic variability produced by the different water regimes on the three soils.

The different physiological behaviour of vines on the three contrasting soils emerged more clearly when correlating stomatal conductance (g_s) with predawn leaf water potential (Ψ_{PD}; Fig. 4). G soil limited g_s and Ψ_{PD} more than C and S soil On S soil, g_s was strongly variable in spite of high water availability. For Ψ_{PD} ranging between -0.15 MPa and -0.25 MPa, plant grown on C soil maintained a g_s higher than plants grown on G soil and a g_s more stable than plants grown on S soil. On G soil g_s remained constantly low, independently of the level of water stress. An interesting aspect concerned the range in Ψ_{PD} values. According to Ojeda et al. (2002) Escalona et al. (1999) and Schultz (2003), at $\Psi_{PD} > -0.2$ MPa the grapevines do not face any water stress. In a recent review, Schultz and Stoll (2010) observed that several studies on potted plants reported substantial physiological effects under very low water stress and questioned the reasons producing these apparently contradictory results (e.g. Lovisolo et al. 2002b; Pellegrino 2003; Pou et al. 2008). Although the present experiment was conducted on fully developed field plants, a high variability of g_s was observed in the absence of water deficit, particularly so on S soil. Moreover different responses of stomatal sensitivity to Ψ_{PD}, depending on soil type were observed. Another aspect, at least equally important, concerns the soil-related type of correlations. Beis and Patakas (2010) observed that the g_s over Ψ_{PD} depended on the grape variety. We observed a similar soil effect: this could imply that each soil promoted the development of different strategies in response to drought. Still due to the impact of water stress conditions on the distal part of the plant, R was particularly high on G soil all through the day, compared with C and S soil (Fig. 3.A). However, the resistance did not increase equally in the different plant compartments. On G soil with restricted water availability, the proximal component ($R_{\text{soil-stem}}$) appeared more prone to decrease in conductivity than the distal component (R stem-leaf) (Domec et al. 2009). Additional evidence was presented in Fig. 5, where the inverse of the above-mentioned R, which corresponded to the total conductance per leaf area unit (K_h), was correlated with g_s (Hubbard et al. 2001; Tyree 2003; Domec et al. 2009). The stomata active response to K_h was linear on S soil. On C soil, stomatal control was much less dependent on K_h. This suggested that on C soil part of the control of the stomatal conductance was not related to hydraulic conductance. Xylem vulnerability to cavitation can be interpreted in terms of its effect on stomatal sensitivity, by limiting further transpirational water loss(Jones and Sutherland 1991), therefore a correlation of the anatomical differences with transpiration and finally conductance was expected. K_h was also considered in dependence of the xylem area (Fig. 8). On the C soil, this correlation was weaker than on the other two soils. The influence of the soil on the xylem architecture added evidence to the hypothesis that this exogenous factor modified the ecophysiological behavior of the plant as a long term adaptation. The lower xylem area of vines on C soil, compared with vines on S soil, did not limit proportionally its conductance, which was a sign of the effectiveness of the “investment” on xylem tissues produced under moderate stress. The large size vessels induced a higher risk of drought-induce embolism on C soil than on S soil, due to the different water availability. This risk was likely to be compensated by the tighter stomatal control observed on the C soil (Fig. 4).

The explanation of these long-term differences, partially due to anatomical differences, may be found from the intrinsic characteristics of these two soils. When C soil dried out, soil matric potential decreased progressively (i.e. becomes more negative). Hydraulic conductance decreased also very progressively because of high microporosity and the capillaries in the soil were not disrupted. To meet evaporative demand during the season, the soil continued to supply water to the roots, which maintained high A. It should be mentioned that the behaviour of the clayey soil in this study was linked to its particular characteristics: clay content >50% and predominant clay minerals being smectites. Hence, results may not be valid for other clayey soils (clay content <50%, clay minerals being kaolinite). In G soil, soil matric potential decreased dramatically when water reserves had depleted. Soil hydraulic conductivity was high when the soil was wet (higher than in the clayey soil) but decreased dramatically when the soil dried out. Hence, the soil was unable to supply much water to the roots when the soil immediately adjacent to the roots was dry. As a consequence, A and g_s dropped dramatically. On the sandy soil, water uptake was clearly more influenced by the presence of the water table in the proximity of the roots than to the sandy texture of the soil. This water table ensured unlimited water supply to the roots, as shown by Ψ_{PD} values that never fell below -0.2MPa. A and g_s were high, but shoot growth continued and competed for carbohydrates during grape ripening.

We expected that on C soil an important role was played by root-shoot hormonal signaling, putatively ABA, with the effect of limiting transpiration and leaf area against canopy water losses (Stoll et al. 2000; Davies et al. 2002). The combination of the intrinsic characteristics of C soil on water availability concurred to improve grape quality, favoring solute concentration, while berry size remained small (Davies et al. 2002).

Our results suggested that the limited soil moisture induced an increase in endogenous ABA, which in turn triggered the increase in stomatal responsiveness to soil drying. The stomatal closure likely occurred in response to a decrease in leaf or stem hydraulic conductance, but other factors cannot be excluded. Feed-forward behavior of stomata with respect to regulation of Ψ_{leaf} has been attributed to the presence of chemical signals brought to the leaf in the transpiration stream (Davies et al. 1994). Thus a combination of hydraulic and hormonal signal in some species could be a mechanism allowing grapevine to maintain adequate leaf water status and stomatal control of water loss (Rogiers et al. 2011; Domec and Johnson 2012).

It is likely that on S soil the constant water availability did not promote root-to-shoot stress signaling to the stomata, therefore the high photosynthetic rate was not balanced by a sufficient stomatal control. Moreover, unlimited water supply resulted in excessive vigor and berry size. Grape quality was low on S soil. On G soil, the scarce water availability determined a tight stomatal control, probably through a high ABA signaling (Lovisolo et al. 2008), even in the absence of limiting conditions, inducing low A and, consequently, moderately low grape sugar despite small berries. The C soil induced mild water stress probably favored the release of non hydraulic signals (putatively ABA) without impairing water potential in the plants, but sufficient enough to favor fruit ripening at the expenses of vegetative growth.

This hypothesis would explain why under the mild water stress conditions of C soil the observed grapevines expressed a “more isohydric” behavior, without significant metabolic interactions at the sink level. As shown in Table 1, c_i did not present any clear correlation with soil or cultivar. This behavior, favorable to grape quality, was mimicked in vineyards managed with the partial root drying irrigation mode (Chaves et al. 2010), and provided the well-known optimal sink-source balance needed to reach the searched premium quality mentioned above.

Conclusions

The present study investigated the main factors and processes that enhance berry and wine quality through the hydraulic architecture of the plant. The research was conducted with an integrated approach, where several ecophysiological and morphometric measurements were considered simultaneously, in order to assess plants responses in field conditions.

The soil effect is shown to be predominant over genetic characteristics of the cultivar, so far as to influence the root-to-shoot hydraulic messages. This variability reflects on the productive potential of the plants, expressed in terms of yield and quality. This result strongly confirms the soil as a key factor for vine productivity and fruit quality.

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Figure 1: Cumulative shoot elongation at the end of the season (21 September 2011) (A.), measured on vine plants of Cabernet franc and Merlot on clayey (C, grey), gravelly (G, white) and sandy (S, black) soils. Average berry weight (B.) and grape sugar (C.) at ripeness, where each point is the average of four replicates. Values of bars topped by common letters are not significantly different, while different letters identify significantly different groups ($P<0.05$; Tukey Test).

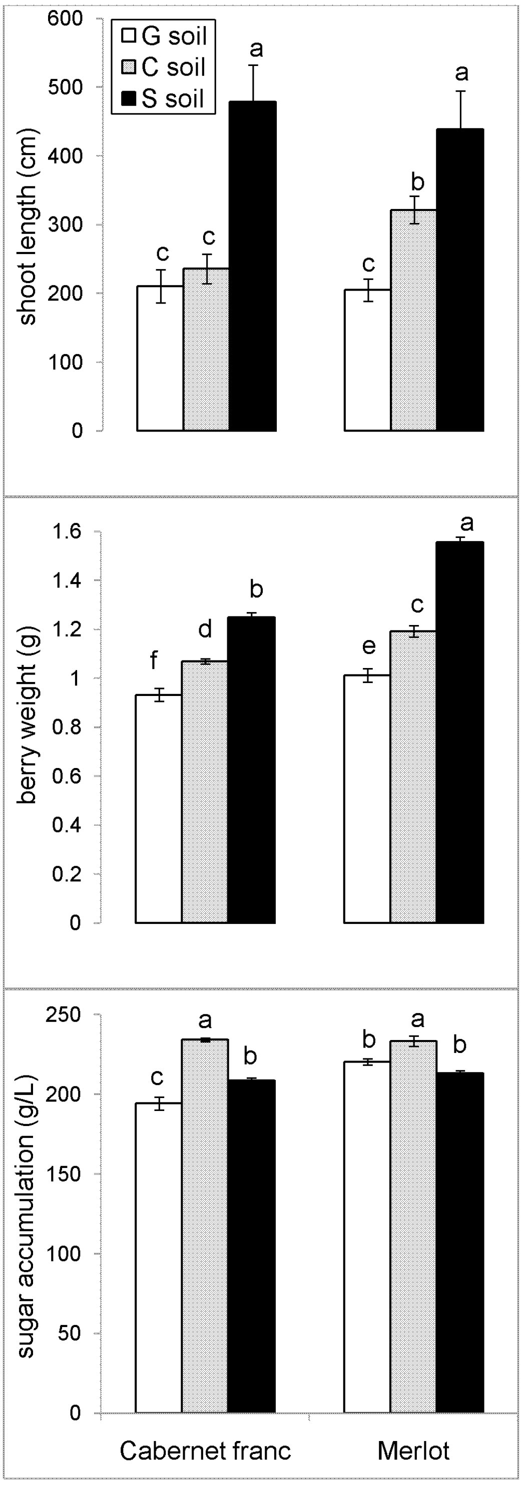

□ G soil
▨ C soil
■ S soil
shoot length (cm)
0
100
200
300
400
500
600
c
c
a
c
b
a
berry weight (g)
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
f
d
b
e
c
a
sugar accumulation (g/L)
0
50
100
150
200
250
c
a
b
b
a
b
Cabernet franc
Merlot

Figure 2: Seasonal dynamic of pre-dawn water potentials (Ψ_{PD}) (Fig.2 A. and B.) and stem water potentials (Ψ_{stem}) Fig.2 C. and D.) measured on vine plants of Cabernet franc (triangles) and Merlot (circles) on clayey (C, grey-filled symbols), gravelly (G, white-filled symbols) and sandy (S, black-filled symbols) soils from the 6 June to the 29 of August 2011. Each point is the average of 8 measurements. Errors smaller than the symbols are hidden.

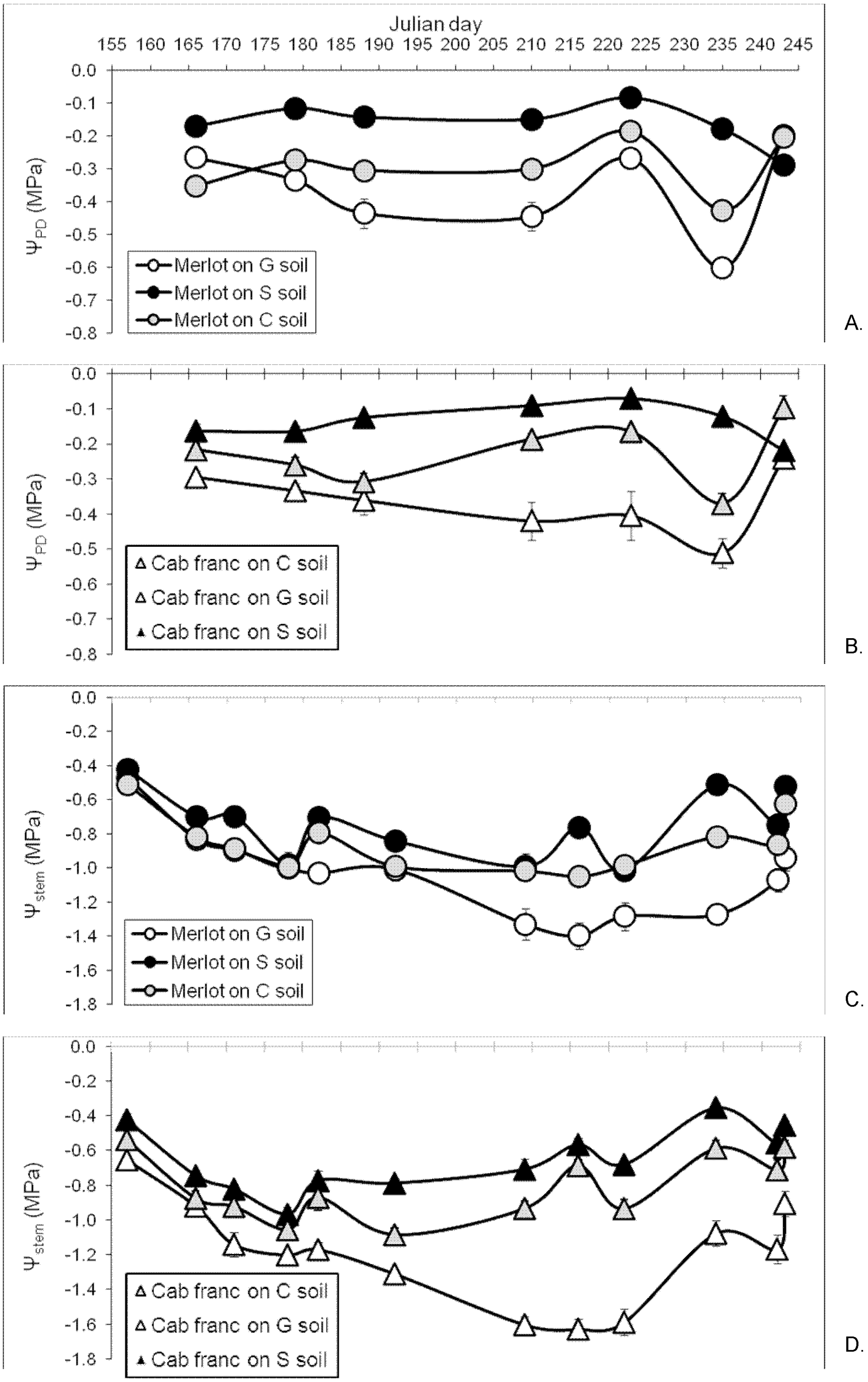

Julian day
155 160 165 170 175 180 185 190 195 200 205 210 215 220 225 230 235 240 245
Ψ_{PD} (MPa)
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
-0.7
-0.8
Merlot on G soil
Merlot on S soil
Merlot on C soil
A.
Ψ_{PD} (MPa)
Cab franc on C soil
Cab franc on G soil
Cab franc on S soil
B.
Ψ_{stem} (MPa)
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
-1.2
-1.4
-1.6
-1.8
Merlot on G soil
Merlot on S soil
Merlot on C soil
C.
Ψ_{stem} (MPa)
Cab franc on C soil
Cab franc on G soil
Cab franc on S soil
D.

Figure 3: A., average of daily dynamics of resistance (R, MPa s m^2 $mmol^{-1}$) on vine plants on gravelly (G, left), clayey (C, center), and sandy (S, right) soil types. Data from Cabernet franc and Merlot plants have been averaged together in order to observe the effect of the soil. The total R from soil to leaf (black-filled symbols) is presented together with its two components: R between soil and stem (grey-filled symbols), and R between stem and leaf (white-filled symbols). Each point is the average of measurements collected during four days (1 and 11 July, 9, 10 and 11 August, 2011). Errors lower than symbols are hidden. B., the partitioning of R in its two components is presented as proportion of the total R (%). Grey-filled columns are from ($R_{soil\text{-}stem}$ / $R_{soil\text{-}leaf}$)*100 and white-filled columns are from ($R_{stem\text{-}leaf}$ / $R_{soil\text{-}leaf}$)*100: the fact that the total amount doesn't reach exactly the 100% is because Rsoil-leaf has not been calculated as the sum of $R_{soil\text{-}stem}$ and $R_{stem\text{-}leaf}$ but, separately, as $R = \Delta\Psi / E$.

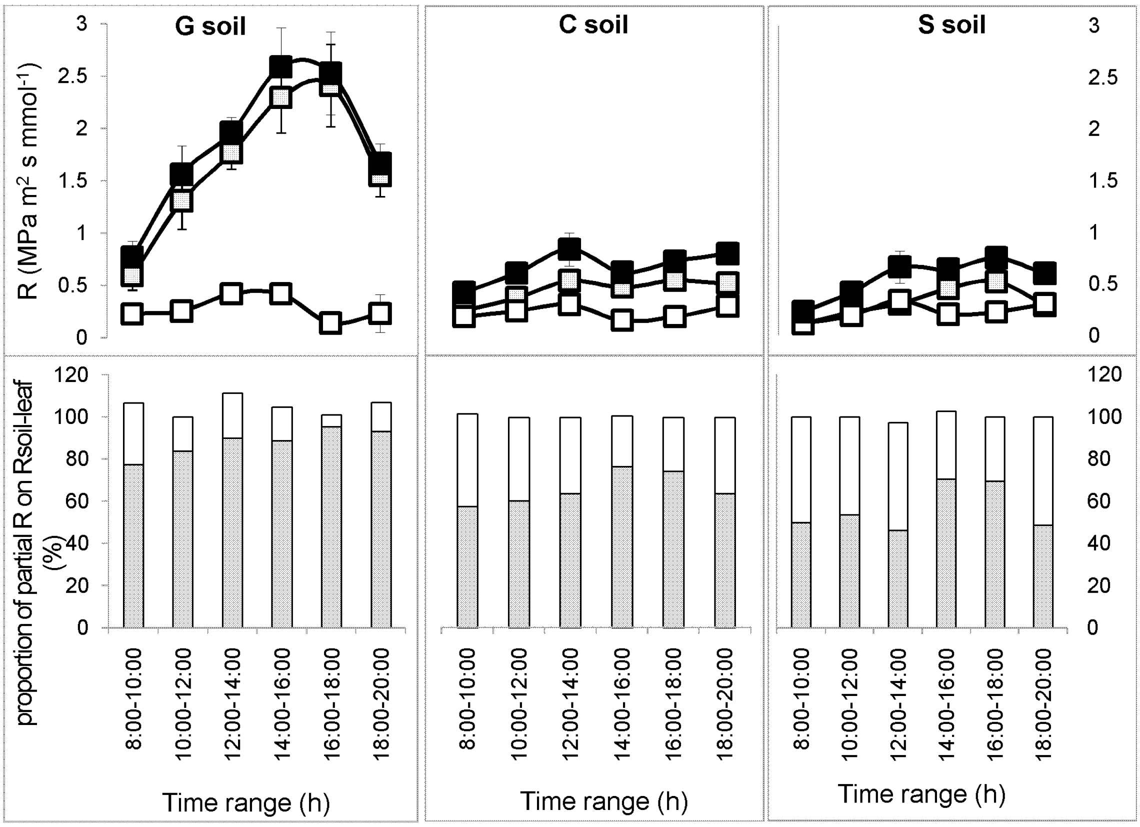
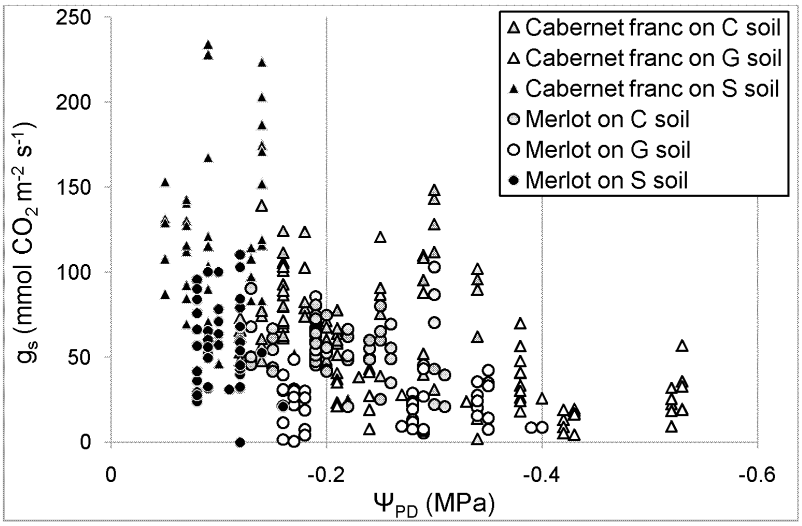
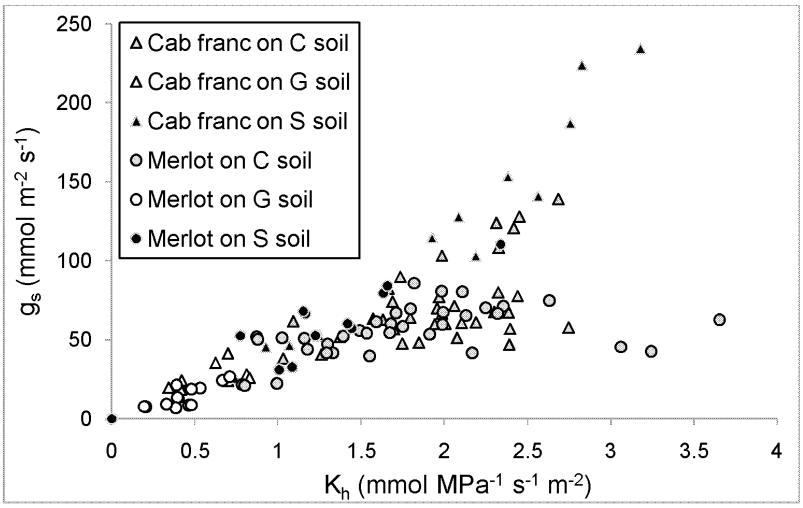

G soil
C soil
S soil
R (MPa m2 s mmol-1)
0
0.5
1
1.5
2
2.5
3
proportion of partial R on Rsoil-leaf (%)
0
20
40
60
80
100
120
8:00-10:00
10:00-12:00
12:00-14:00
14:00-16:00
16:00-18:00
18:00-20:00
Time range (h)

Figure 4: Relationship between stomatal conductance (g_s, mmol H_2O m^{-2} s^{-1}) and predawn leaf water potential (Ψ_{PD}, MPa) on vine plants of Cabernet franc (triangles) and Merlot (circles) on clayey (C, grey-filled symbols), gravelly (G, white-filled symbols) and sandy (S, black-filled symbols) soil at PAR between 300 and 2000 µmol m^{-2} s^{-1}. Vertical grindlines help to characterize the Ψ_{PD} ranges corresponding to null (0 MPa > Ψ_{PD} > -0.2 MPa), weak (-0.2 MPa > Ψ_{PD} > -0.4 MPa) and medium (-0.4 MPa > Ψ_{PD} > -0.6 MPa) water deficit according to Ojeda et al. (2002).



250
200
150
100
50
0
0
-0.2
-0.4
-0.6
g_s (mmol CO$_2$ m^{-2} s^{-1})
Ψ_{PD} (MPa)
Cabernet franc on C soil
Cabernet franc on G soil
Cabernet franc on S soil
Merlot on C soil
Merlot on G soil
Merlot on S soil

Figure 5: Relationship between total conductance (K_h, mmol MPa^{-1} s^{-1} m^{-2}) and stomatal conductance (g_s, mmol m^{-2} s^{-1}) on vine plants of Cabernet franc (triangles) and Merlot (circles) on clayey (C, grey-filled symbols), gravelly (G, white-filled symbols) and sandy (S, black-filled symbols). Each point represents measurements on an individual vine.



Cab franc on C soil
Cab franc on G soil
Cab franc on S soil
Merlot on C soil
Merlot on G soil
Merlot on S soil
g_s (mmol m^{-2} s^{-1})
K_h (mmol MPa^{-1} s^{-1} m^{-2})
250
200
150
100
50
0
0
0.5
1
1.5
2
2.5
3
3.5
4

Figure 6: Relationship between vessel size and number of vessels per wedge from observations of xylem tissues at the level of the fifth internode of primary shoots. A. Differences between Cabernet franc and Merlot. Each point is the average of 45 observations. Both values differ significantly ($P < 0.05$) between the two varieties. B. Differences among clayey soil (C soil), gravelly soil (G soil), and sandy soil (S soil). Each point is the average of 30 observations. The average number of vessels per wedge is significantly different ($P < 0.05$) for vine plants grown on S soil and the average vessel size is significantly different ($P < 0.05$) for vine plants on G soil.

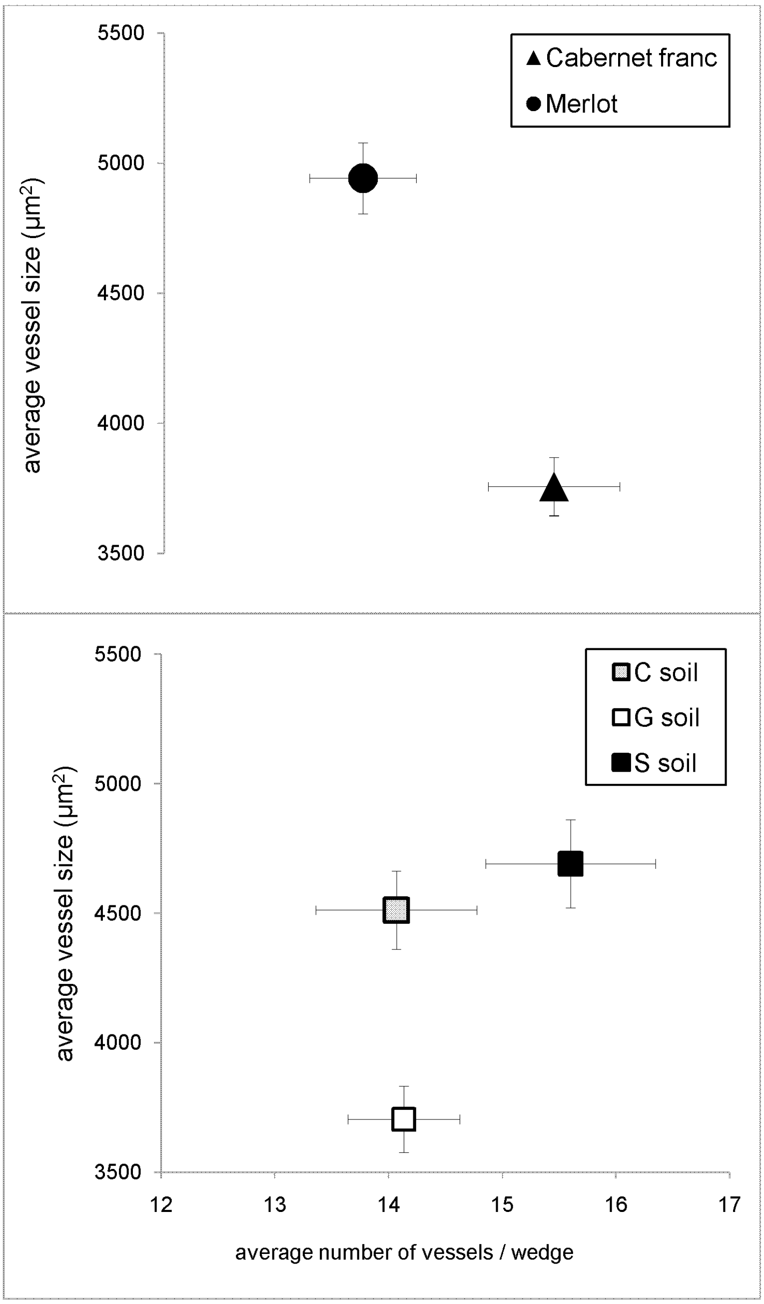

5500
5000
4500
4000
3500
average vessel size (μm^2)
▲ Cabernet franc
● Merlot
5500
5000
4500
4000
3500
average vessel size (μm^2)
▨ C soil
☐ G soil
■ S soil
12
13
14
15
16
17
average number of vessels / wedge

Figure 7: Average percentage of section area devoted to xylematic tissues on the total area of the section. Means ± standard error; within each group of histograms, values labelled by different letters differ significantly at $P < 0.05$, according to variance analysis and Tukey test.

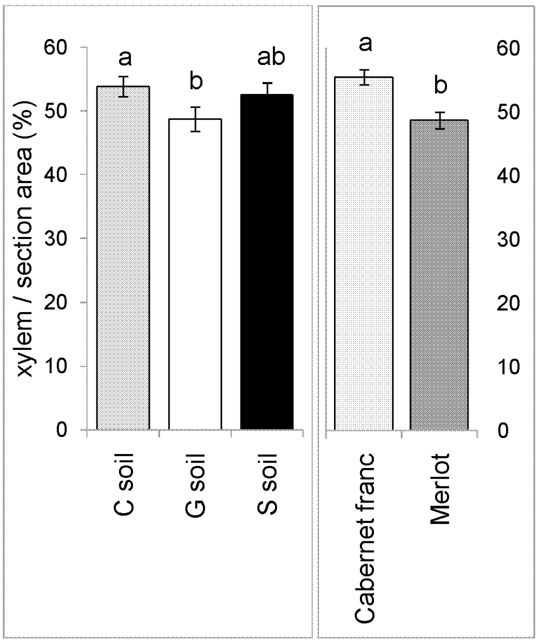
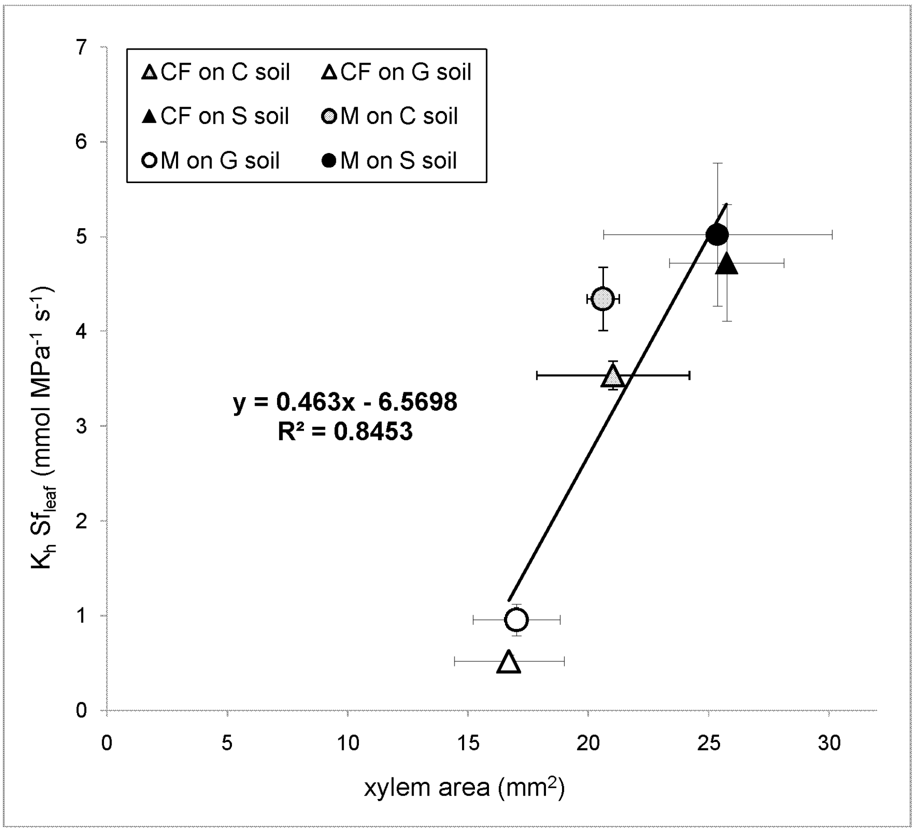

xylem / section area (%)
60
50
40
30
20
10
0
a
b
ab
C soil
G soil
S soil
a
b
Cabernet franc
Merlot
60
50
40
30
20
10
0

Figure 8: Relationship between xylem area of primary shoots sections taken at the fifth internode (mm^2) and hydraulic conductance of the whole vine plant, from soil to leaves and multiplied for the total canopy area (K_h Sf_{leaf}, mmol MPa^{-1} s^{-1}) on vine plants of Cabernet franc (triangles) and Merlot (circles) on clayey (C, grey-filled symbols), gravelly (G, white-filled symbols) and sandy (S, black-filled symbols) soil.. Each point is the average of five measurements for the xylem area and of all the measurements collected during the central hours of the day (between 12:30 and 16:30) and repeated for four days (1 and 11 July, 9, 10 and 11 August, 2011) for K_h. Errors smaller than symbols are hidden.



7
6
5
4
3
2
1
0
0
5
10
15
20
25
30
K$_h$ Sf$_{leaf}$ (mmol MPa^{-1} s^{-1})
xylem area (mm^2)
△CF on C soil
△CF on G soil
▲CF on S soil
◎M on C soil
○M on G soil
●M on S soil
y = 0.463x - 6.5698
R² = 0.8453

Table 1: Effects of the components of cultivar × soil model on water potentials and gas exchange. The model considers soil × cultivar × date pairwise interactions. Percentages of variance attributable to each of the following variables (predawn leaf water potential, Ψ_{PD}; midday stem water potential, Ψ_{stem}; leaf water potential, Ψ_{leaf}; assimilation rate, A; intercellular CO_2, c_i; transpiration rate, E; stomatal conductance, g_s) were calculated. The software used was SAS software (version 9.2, SAS 2009).

	cultivar × soil model						
	R-Square	% variance attributable					
		Soil	Cultivar	Date	Soil × Cultivar	Date × Cultivar	Date × Soil
Ψ_{PD}	0.580999	87.02***		12.98**			
Ψ_{stem}	0.611732	62.26***	4.68*	15.14**	17.92***		
Ψ_{leaf}	0.63225	8.26*	28.86***	33.82***	13.25**	15.81***	
A	0.787424	52.27***	14.54***	13.01***		20.18***	
c_i	0.652927	11.43**		47.27***	13.35**	9.31**	18.64**
E	0.81556	78.10***	12.37***	2.65*		6.87***	
g_s	0.849281	67.13***	13.72***	3.80**		15.34***	