



Wood hydrosystem of three cultivars of *Vitis vinifera* L. is modified in response to contrasting soils

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Abstract

Background and aims In *Vitis vinifera* L., the same genotype can express different phenotypic characteristics depending on the environmental conditions, e.g. soil deepness. Wood anatomy, specifically xylem vessel traits, provide information about the plant's eco-

physiological responses to the environment. Slight changes in vessel diameter and density may impact plant hydrosystem functionality, since large vessels are more efficient in the volume of transported water compared to narrower ones, although the latter are more effective in avoiding stress-induced embolism. The aim of this study was to analyze variations in the wood hydraulic structure of three grapevine cultivars, induced by soils with strong contrast in depth, texture and rock volume, providing evidence of their adaptative capacities.

Methods Anatomical and growth traits of each annual growth ring were measured in 8-year-old plants of Bonarda, Malbec and Tempranillo cultivars growing in contrasting depths of soils.

Results Bonarda exhibited no differences in wood productivity between soils with different depths, showing the ability to modulate the earlywood vessel lumen area. Malbec and Tempranillo did show differences in wood productivity between the two types of soils, with major changes in the trade-off between vessel density and lumen area in Tempranillo, while in Malbec there were few changes in the vessel traits.

Conclusions Xylem hydraulic characteristics of the grapevine stems varied in response to soil environment and cultivar. This knowledge may help to select management strategies in areas of soil heterogeneity.

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Introduction

Argentine viticulture dates back to the 16th century when several cultivars were initially introduced by the Spanish colonizers and later by French and Italian immigrants (Fanet 2008). During the last decades, viticulture in Argentina has undergone a significant geographical expansion, reaching areas of higher altitude, compared to those traditionally used. Mendoza is currently the territory with the largest area of vineyards, where Malbec is the iconic cultivar and with the largest surface planted. Other red grape cultivars, such as Bonarda and Tempranillo, have an important presence in Mendoza (INV 2019). These cultivars are distributed in soils geomorphologically associated to gently-sloping Quaternary alluvial soil deposits at 450–900 m of altitude, or to alluvial fans at the Andes foothills between 1000 and 1400 m altitude (Fanet 2008). Vineyards at higher altitudes, such as those considered in this study, are subject to high soil heterogeneity, ranging from deep sandy-loam textured soils to sand textured shallow soils (0.1–0.2 m depth) in a rock matrix. Each soil variety implies diverse physicochemical properties, especially in relation to water holding capacity, which plays an essential role in plant growth (De Andrés-De Prado et al. 2007).

In *Vitis vinifera*, vigor expression is mainly related to soil water capacity and the ability of plants to absorb this water (Leeuwen and Seguin 2006; Chavarria and dos Santos 2012). Although grapevines adapt to a wide range of environments (Leeuwen and Seguin 2006), small environmental changes may cause different growth responses (Santo et al. 2016), a phenomenon that is defined as phenotypic plasticity (Nicotra et al. 2010). This phenotypic plasticity plays an important role in plant response to climate change (Weiner 2004; Van Kleunen and Fischer 2005), which is relevant in adaptive processes to strong environmental modifications. Furthermore, responses to the environment may vary depending on the cultivar (Schultz 2003), i.e. some cultivars might be more suitable for a particular environment than others. Pertaining our study, researchers have found that Malbec and Tempranillo are cultivars that are sensitive to environmental changes (Berli et al. 2008; Tomás et al. 2012; Shellie and Bowen 2014; Alonso et al. 2016), whereas information about Bonarda is still scarce.

Within the different adaptation mechanisms to the environment, water use is a key aspect of plant adaptation. This, in turn, influences water management in

irrigated crops, intended to increase the efficiency of water use by plants under certain climatic and soil conditions. Consequently, it is essential to understand the design of the vascular system involved in the internal transport of water in plants (Hacke et al. 2001; Lovisolo 2002). In this sense, little is known in grapevines about how differences in soil type affect the hydraulic design of the xylem. Variations in xylem vessel diameter and density are relevant traits to evaluate environmental plant responses (Hacke et al. 2017). According to Hagen-Poiseuille's law, slight changes in vessel lumen diameter cause considerable modifications in the volume of xylem-sap flow (Chavarria and dos Santos 2012; Hacke et al. 2017; Islam et al. 2019). Thus, the efficiency in water transport to keep reproductive and photosynthetic organs hydration is crucial. This is directly related to the plasticity of the vascular cambium to create an apoplastic hydrosystem adapted to the environmental growth conditions in which wood is formed (Anderegg and Meinzer 2015; Hacke et al. 2017; De Melo et al. 2018; Islam et al. 2019). This in turn is reflected by changes in vessel size at inter and intra species level (Hacke et al. 2017) when plants are influenced by any growth limiting factor, such as water shortage, salinity, early and late frosts or soil structure and fertility (Schmitz et al. 2006; Robert et al. 2009; De Melo et al. 2018).

Water transport along the plant is ensured as the liquid stands subject to negative pressure through a continuous column, as a result of leaf transpiration, as explained by the cohesive-transpiratory theory (Brodersen et al. 2010; Chavarria and dos Santos 2012). In this context, failures in the hydraulic system may occur under different circumstances, e.g. freezing and drought events (Zimmermann and Milburn 1982; Tyree and Sperry 1989; Baas et al. 2004; Hacke et al. 2017), producing obstruction of the hydraulic conduction system, and eventually death of the plant due to embolism (Brodersen et al. 2010). This phenomenon could be related, among other things, to vessel diameter, as large vessels are less resistant than narrow ones (Davis et al. 1999). Therefore, vessel anatomical characteristics contain important information to understand the effects of the environmental conditions to which plants are exposed (Robert et al. 2009).

Grapevine is relatively vulnerable to drought stress, a fact that can be related to its xylem anatomy (Munitz et al. 2018). The wood anatomy of grapevines is characterized by a rather porous ring pattern, with very large

and mainly solitary vessels distributed in the earlywood, and a smaller growth ring area occupied by narrow vessels grouped in a pattern of radial multiples in the latewood (Fig. 2; Schweingruber 1990). Even though large vessels are considered more efficient in hydraulic conductivity, this trait can result in cavitation under extreme weather stress (Bush et al. 2008; Hacke et al. 2017). While the link between conduit diameter and vulnerability to cavitation is not so simple, narrow vessels are considered safer (Robert et al. 2009; Hacke et al. 2017), but detrimental for water transport flow according to the Poiseuille's equation (Chavarria and dos Santos 2012; Islam et al. 2019). Several intraspecific studies showed that changes in vessel dimension respond to gradients in humidity, temperature or soil salinity, indicating particular adaptations to the growth environment (Robert et al. 2009; Hacke et al. 2017; Islam et al. 2019). This suggests that plants tend to strike a balance between efficiency in water flow and safety of the transportation system (De Melo et al. 2018). Knowledge of the possible variations in the conductive system of the main stem of *Vitis vinifera* in relation to the characteristics of the soil is presently scarce. Most studies, however, have addressed the anatomical characteristics of grapevine wood based on one-year old shoots (Lovisolo and Schubert 1998; Galat-Giorgi et al. 2013; Tramontini et al. 2013; Santarosa et al. 2016), evidencing that xylem architecture and hydraulic properties of young shoots differ from those of the mature trunk, at least for 4-year-old plants (Munitz et al. 2018). Furthermore, the analysis of the hydraulic structure of the xylem in non-grafted mature stems of Bonarda, Malbec and Tempranillo cultivars does not exist.

The goal of the present study was to analyze the impact of soil depth (including texture and rock volume) on the design of the hydraulic system of the main stem of three cultivars of *Vitis vinifera* implanted on alluvial soils at the foothills of the Central Andes. Our hypothesis claims that soil heterogeneity modifies the soil water retention capacity, which in turns models the hydraulic anatomy within and amongst cultivars. Thus, plants growing in deep (shallow) soils, with larger (shorter) water retention capacity, develop a larger (reduced) hydraulic conduction capacity. This could provide ecophysiological information useful for viticulture management strategies in areas of strong soil heterogeneity.

Materials and methods

Experimental design, soil characterization and plant material

The study was carried out in a vineyard located in the geographical indication "Paraje Altamira" (33°46'20.29" S; 69°9'14.62" W; 1100 m altitude), placed on the alluvial fan of the Tunuyán River in the San Carlos region, Mendoza, Argentina (Figs. 1). Climate at the experimental area was classified as semi-arid and continental (Bwk, according to Köppen classification; Kottek et al. 2006).

In the genesis of this alluvial fan, river flows were the most important geomorphological processes responsible for modifying the fan surface, generating sectors of greater or lesser accumulation of fine-textured sediments as well as pebble accumulation. These processes are responsible for the presence of sectors with soils of contrasting depth (Fig. 2). In the sectors with the greatest accumulation of sandy-loam textured sediments, the soils have a depth of approximately two meters, from which granite boulder deposits of relative abundance appear (< 25 % of total volume). We define these sectors as deep soils (DS). Other sectors appear with a superficial layer of sandy textured sediments not exceeding 0.2–0.3 m in depth, from which the boulder deposit begins with boulders with diameters larger than 0.3 m and occupying 85 % of the total volume at this level. We define these soils as shallow soils (SS). In this study, the characterization of the depth of the soils was carried out using soil electromagnetic conductivity maps developed with measurements obtained with a EM38 MK2 ground conductivity meter (Geonics Ltd, Canada) at 0.75 m depth and corroborated through trench excavations in which the depth of the free pebble soil profile was measured.

For the experimental design, a stratified sampling by type of soil was chosen within which another stratum corresponding to the parcel was established. Since the deep and shallow soil sectors in each parcel were too large (approximately 1 ha), six experimental units were established in each soil typology, within which a random sampling was carried out. In this way, an attempt was made to avoid pseudoreplication, in accordance with the field sampling criteria of Hurlbert (1984) and the sampling techniques of Cochran (1977). For the random selection of the experimental units within each type of soil, a georeferenced and numbered grid was



Fig. 1 Upper boxes, indicate the location of the study area in Mendoza, Argentina. Grey rectangle indicates the geographical position of the Paraje Altamira GI. In the image at the right, broken lines demarcate the limits of the alluvial fan where the vineyard is

placed. Below, the vineyard where the experimental units considered in this study are located (as referenced in Fig. 2). On the left, the pile of rocks that have been extracted from the surface to facilitate mechanized work

generated with the help of a GIS program. Then, by random drawing, the experimental units were placed on the map. Each experimental unit consisted of an area of 184 m², each containing a total of 128 plants from which only one was randomly chosen to proceed with the wood sampling. Figure 3 shows the experimental unit distribution on the field for Malbec, Bonarda and Tempranillo plants (Fig. 3a, b, and c, respectively). Blue polygons in the figure correspond to shallow soils while red polygons to deep ones, indistinctly for each of the three cultivars.

Once the experimental units were located, soil texture (Bouyoucos 1951), cation exchange capacity (CEC) (Richards et al. 1954) and holding water capacity (including saturated water content [Ws], field capacity [Wc] and permanent wilting point [Wp]) were analyzed after trench excavations, one for each experimental unit. Ws, Wc and Wp calculation were performed from a generated model based on soil textural values (Mastrantonio and Perez, personal communication). The generation of this model was based on 154

georeferenced records of soil data (Vallone et al. 2008) that included sedimentation volume (Nijensohn and Maffei 1996), granulometry (Bouyoucos 1951) and water content in equilibrium with tensions of 10, 30 and 1500 kPa (matric potential), through the application of soil transfer functions. The consistency of the obtained data was verified by observing the maximum and minimum values, and comparing the data obtained with the normal values of water content according to the soil texture. The soil type was determined based on the USDA classification triangle (USDA-NRCS 2000).

The Paraje Altamira vineyard is made up of Bonarda, Malbec and Tempranillo cultivars, among others. These three cultivars were considered for this study. Non-grafted grapevines selected from a mass selection based on high yields were planted in 2009. The vineyard was managed in a vertical trellis system pruned as double Guyot (1.8 m trellis height), with rows oriented in N-S direction and protected with anti-hail nets (black polyethylene). In each row,

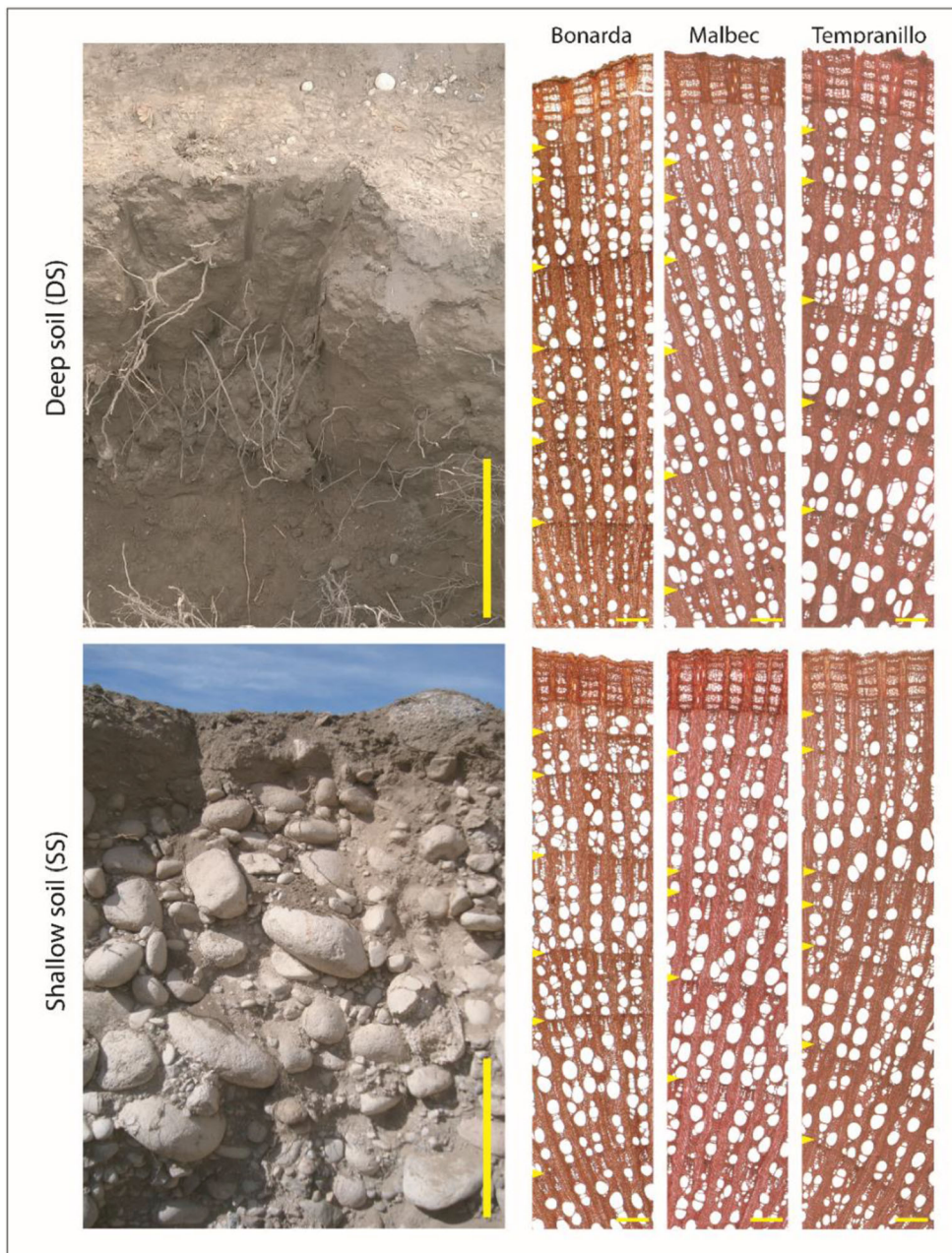


Fig. 2 Left, vertical profiles of soil structure and depth for DS and SS, respectively. In DS, no rocks were observed at the root exploration level. In SS, a profuse boulder deposit was evidenced below a reduced soil layer (~0.30 m depth). Right, examples of transversal sections of the stem xylem of the tree cultivars planted

on both DS and SS soils, respectively. Arrows indicate the annual growth ring boundary where vessel diameter and number were measured. Horizontal bars indicate a size of 500 μm , while vertical ones correspond to 0.5 m

the spacing between plants was 0.8 m and between rows 1.8 m, representing a density of 6944 plants ha^{-1} . The whole experiment, regardless the soil type and cultivar, was drip irrigated with the same volume of water and frequency.

Wood sampling and anatomical analysis

During the austral dormant season (July 2018), wood cores of one representative plant at each experimental unit (avoiding diseased or young replants) were taken

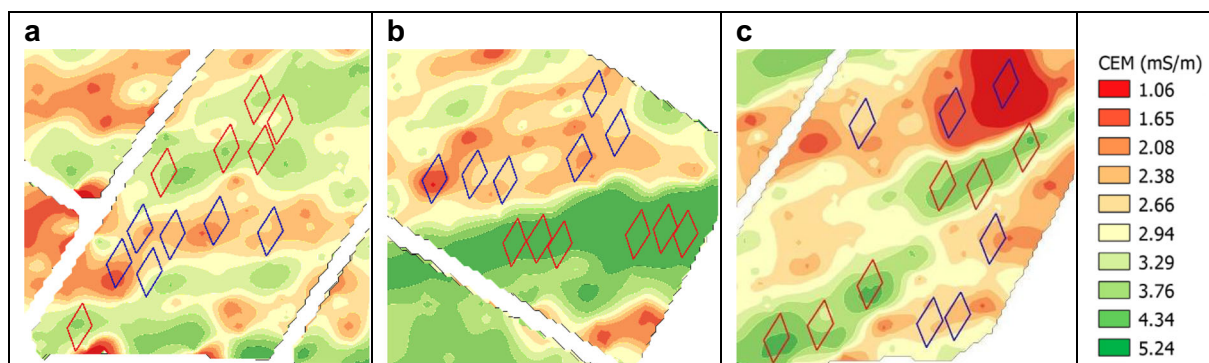


Fig. 3 The experimental blocks considered in this study for Bonarda (a), Malbec (b) and Tempranillo (c). The experimental units are indicated by red and blue parallelograms distributed both in SS and DS soils, respectively. The depth of the soil is indicated

by electromagnetic conductivity soil maps, where red areas are related to shallow soils while green areas to deep soils, as measured with a ground conductivity meter EM38 MK2 (Geonics Ltd, Canada) at 0.75 m deepness

from their main stem at 0.4 m above the ground and in a perpendicular orientation by using a 6" Pressler increment borer of 5.15 mm \varnothing (Haglöf, Sweden). Increment cores were extracted crosswise from bark to bark so including the two opposite radii, and ensuring that the pith was included in the core. For each cultivar, 6 samples were extracted from SS plants and 6 samples from DS plants. Since each wood core included two radii, each radius was analyzed separately as a replication of the same sample. Eight annual growth rings were analyzed for each sample, therefore, for this work a total of 576 annual growth rings were analyzed for the three cultivars and the two types of soil. Samples were preserved in a 50 % ethanol:water solution.

For wood anatomy analysis, samples were transversely sectioned with a sliding microtome (WSL Core Microtome, Switzerland) in slices of ca. 15 μ m thickness. Then, they were decolorized with chlorinated water (NaClO 1 %), washed with distilled water and subsequently dehydrated using an incremental concentration of ethanol from 40 to 100 %. After that, the slides were stained with safranin, mounted in glass with Canada balsam and observed with a light microscope (Zeiss Axio Imager M2m, Germany). Panoramic photographs were obtained with a digital camera (Zeiss AxioCam 503 color, Germany), with 25x magnification and a resolution of 1300 \times 1030 pixels. The diameter and number of the xylem vessels for each of the growth rings formed during the life span of the plants (8 years, 2011–2018), was recorded using the WinCell (Regent Instruments Inc) software facilities. Only the earlywood section was taken into account, since more than 80 % of the hydraulic area is concentrated in this portion of the wood. For

each growth ring, the ring width, number of vessels and vessel diameter were directly measured through the facilities of WinCell software. Vessel density was calculated dividing the number of vessels by the analyzed unit area. Mean individual vessel (lumen) area was calculated dividing the total vessel area by the number of vessels per ring. Total hydraulic area was calculated based on the sum of the total vessel area per ring width. In order to obtain a quantification of wood production, the ring width values were transformed into basal area increments (BAI). The BAI of any given year reflected a direct indication of the wood production of the plant in that year. The BAI calculation was based on the difference between the total growth of the ring up to year "x" and the total growth up to year "x-1" (Johnson and Abrams 2009). On the other hand, and based on both mean individual vessel area and vessel density values, the vessel lumen fraction (F) was calculated as well as an index of hydraulic conductivity (Zanne et al. 2010; Scholz et al. 2013). In addition, the vessel density values as a function of vessel area interval classes were calculated. This measure was performed by using the WinCell software, resulting in 10 vessel density intervals defined between the maximum and minimum extreme vessel areas.

Meteorological data

Air temperature and rainfall data at the study site were recorded between September and April (months corresponding to the austral spring-summer season, coinciding with the phenophases between budburst and leaf fall, respectively) through an automatic weather station

located in the same vineyard, installed at 1.5 m above ground and in operation since 2002 (OMIXOM, model OMXH, Argentina). Data were collected every 30 min and daily mean temperature and total precipitation were calculated.

Statistical analysis

Multifactorial ANOVA were done for soil type (SS y DS), grapevine cultivar (Malbec, Bonarda, and Tempranillo) and their soil traits interaction (Fisher's LSD $P \leq 0.05$). For the wood anatomical variables, generalized linear mixed models (GLMM) were performed using the seasons as fixed effects and soil type as random effects (Fisher's LSD $P \leq 0.05$). One-way ANOVA was used for the mean values. All the analyses were made using the InfoStat software (version 2018, Universidad Nacional de Córdoba, Argentina).

Results

Soil physicochemical properties

SS and DS soil categories were different for all the variables analyzed (Table 1). While SS showed a higher sand content, DS showed higher values in all other measured soil parameters, i.e. clay, silt, CEC, W_s , W_c and W_p . According to the USDA classification triangle, SS would correspond to sandy soil, while DS to sandy loam. Bonarda, Malbec and Tempranillo in DS were placed in the sandy loam category, while Tempranillo in DS was associated with the loamy sand category. On the other hand, Malbec and Bonarda in SS were classified as loamy sand, while Tempranillo in SS as sand (Table 1). No significant interactions were found between cultivar and soil.

Meteorological data

For the period analyzed (2011–2018), the spring-summer rainfall was markedly variable, ranging from 75 mm to 743 mm per year. 2017-18 was the driest and the 2015-16 the wettest seasons, respectively. Considering the whole period, the spring-summer mean precipitation was 261.9 mm per year. Annual mean temperature was 18.2 °C. 2011-12 was the warmest and the 2015-16 the coolest seasons, respectively (Fig. 1S).

Basal area increment (BAI)

Figure 4 shows that annual wood productivity (BAI) varied according to the season. In general, and regardless of the cultivar and the type of soil, there was a high production of wood during the first years of the plant's life (2011-12, but also 2012-13 and 2013-14). An important peak in productivity was observed in the 2015-16 season. The increase in the accumulated basal area was markedly different amongst cultivars (BAI acc, Fig. 4). Bonarda did not show differences between the two soil types, while Malbec and Tempranillo showed significant differences in the accumulative values in favor of DS plants.

Vessel size and hydraulic-related characteristics

The accumulated total hydraulic area (ATHA) and the mean vessel area showed distinctive behaviors between cultivars and soil types (Fig. 5). The time series corresponding to the Bonarda cultivar showed an increase in total hydraulic area for SS plants (Fig. 5a, left column). This difference in the hydraulic conductivity was progressively increasing from the third year of life to reach significant differences between the two soil types towards the last year of analysis (2017-18). Similarly, the mean values of the vessel area were higher in SS plants (Fig. 5a, right column). Malbec tended to a larger total hydraulic area in DS plants during the first years of the plant's life, reaching significant differences between soils in the 2016-17 season (Fig. 5b, left column). However, the mean vessel area did not vary in relation to the type of soil (Fig. 5b, right column). Similar to Malbec, Tempranillo showed a larger total hydraulic area in DS plants. This difference between the two types of soils was generated from the first years, showing significant differences from the fourth year of life (2013-14) onwards (Fig. 5c, left column). The mean vessel area was higher in DS plants (Fig. 5c, right column).

The vessel lumen fraction (F) for Bonarda showed variations in hydraulic conductivity year to year, but in all cases, there was a trend toward higher values in SS plants (Fig. 6a, left column). The mean F values indicated that Bonarda experienced greater hydraulic conduction in the SS plants (Fig. 6a, right column). The same situation occurred with the cultivar Malbec where the F values seemed to depend seasonally, but with a higher conductivity capacity in the SS plants (Fig. 6b, left and right column). On the other hand, Tempranillo

Table 1 Soil holding water capacity (as indicated by Ws, saturated water content; Wc, field capacity; Wp, permanent wilting point), soil texture (clay, silt and sand), soil cation exchange capacity (CEC), and USDA soil classification

Treatments	Ws (g%g)	Wc (g%g)	Wp (g%g)	Clay (%)	Silt (%)	Sand (%)	CEC (meq%g)	Soil classification (USDA)
Soil								
Deep	30.56 a	14.37 a	7.52 a	8.63 a	14.21 a	77.11 b	12.71 a	Sandy loam
Shallow	26.52 b	10.97 b	5.52 b	4.5 b	7.8 b	87.66 a	7.46 b	Sand
Cultivar								
Bonarda	29.29 a	13.23 a	6.84 a	6.89 a	11.52 a	81.55 b	10.5 a	Loamy sand
Malbec	29.74 a	13.63 a	7.09 a	8.01 a	13.26 a	78.69 b	11.93 a	Loamy sand
Tempranillo	26.59 b	11.14 b	5.64 b	4.79 b	8.24 b	86.93 a	7.84 b	Loamy sand
Cultivar*Soil								
Bonarda/Deep	30.62 ab	14.41 ab	7.54 ab	8.27 b	13.66 b	78.02 c	12.26 b	Sandy loam
Bonarda/Shallow	27.96 c	12.05 c	6.14 c	5.51 c	9.38 c	85.07 b	8.75 c	Loamy sand
Malbec/Deep	31.59 a	15.33 a	8.1 a	10.64 a	17.33 a	71.98 d	15.27 a	Sandy loam
Malbec/Shallow	27.89 c	11.94 c	6.07 c	5.38 c	9.18 c	85.4 b	8.58 c	Loamy sand
Tempranillo/Deep	29.47 bc	13.36 bc	6.92 bc	6.97 bc	11.65 bc	81.34 bc	10.61 bc	Loamy sand
Tempranillo/Shallow	23.70 d	8.92 d	4.36 d	2.61 d	4.83 d	92.52 a	5.06 d	Sand
ANOVA								
<i>p</i> (soil)	≤0.0001	≤0.0001	≤0.0001	≤0.0001	≤0.0001	≤0.0001	≤0.0001	
<i>p</i> (cultivar)	0.0001	0.0001	0.0002	0.0002	0.0002	0.0002	0.0002	
<i>p</i> (soil*cultivar)	0.0868	0.2192	0.2568	0.2383	0.2380	0.2381	0.2383	

Treatments: soil type (shallow and deep), grapevine cultivar (Malbec, Bonarda and Tempranillo), and their interaction. Values are means and different letters within each factor and column indicate a statistically significant difference ($p \leq 0.05$, LSD Fisher's test)

did not show a clear trend in F values for any portion of the time series, indicating that there were no differences in hydraulic conductivity between plants growing in different soil types (Fig. 6c, left and right column).

The density of the vessels in each area interval varied according to the cultivar and the type of soil (Fig. 7). Bonarda showed a trend towards a higher density of vessels with intermediate sections in SS plants, with significant differences between 28,007 and 35,005 μm^2 and a higher density of vessels with smaller sections (10 to 7009 μm^2) in DS plants (Fig. 7a, left column). Bonarda did not show differences in mean values (Fig. 7a right column). Malbec, similar to Bonarda, also showed a higher density of vessels of intermediate area category (between 28,007 and 42,004 μm^2) in SS plants (Fig. 7b, left column), not showing differences between mean values (Fig. 7b, right column). Tempranillo cultivar showed the most conservative behavior from the point of view of hydraulic safety, presenting a higher density of vessels with small sections (from 10 to 21,007 μm^2) in SS plants, while in DS a higher density of vessels corresponding to

sections of larger area was observed (35,006 to 70,000 μm^2 ; Fig. 7c, left column). The mean values presented differences in favor of DS plants (Fig. 7c, right column).

Discussion and conclusion

Our data suggest that the Malbec, Bonarda and Tempranillo vine cultivars showed differential trends in productivity and wood anatomy traits, depending on soil depth. The basal area increment (BAI) values indicated a strong dependence on soil depth in Malbec and Tempranillo, with marked differences throughout the time period analyzed (Fig. 4b and c, left column, respectively). On the contrary, the relative uniformity of the BAI in Bonarda would suggest a certain degree of independence of this cultivar from the depth of the soil in which it grows (Fig. 4a, left column). The accumulated growth of BAI for each cultivar also reflected these trends. However, the outstanding difference in BAI observed in Tempranillo suggests that the growth of this cultivar is particularly stimulated in deeper

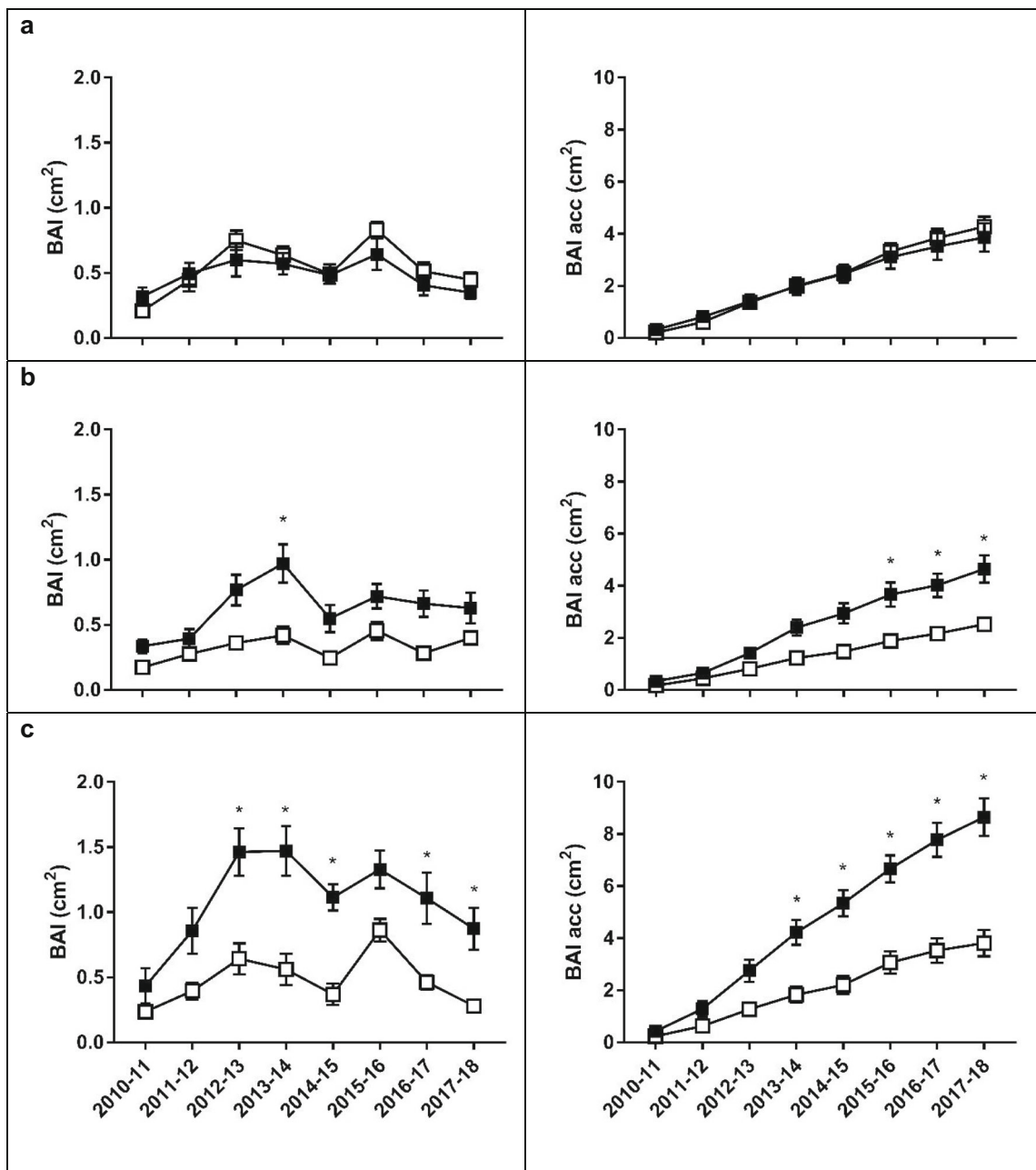


Fig. 4 Left column, basal area increment (BAI) temporal series for the period 2010–2018. DS (black squares) and SS (white squares) for Bonarda (a), Malbec (b), and Tempranillo (c), respectively. Right column, BAI accumulated temporal series. In both

cases, values are means \pm SEM ($n=6$) and significantly different years between the curves was indicated with an asterisk ($p \leq 0.05$, LSD Fisher's test)

soils (Fig. 4, right column). Malbec also showed this trend and preference for DS conditions, although not as demanding as Tempranillo. Since the soil depth was found directly related to the Wc value, as reflected in Table 1, lower Wc values in SS soils would help interpret the lower BAI values, as has also

been suggested for the Merlot cultivar (Munitz et al. 2018). In this sense, lower Wc values would have a higher effect on the growth of Malbec and Tempranillo, while the cultivar Bonarda would be less sensitive to variations of Wc, even in different soil depths.

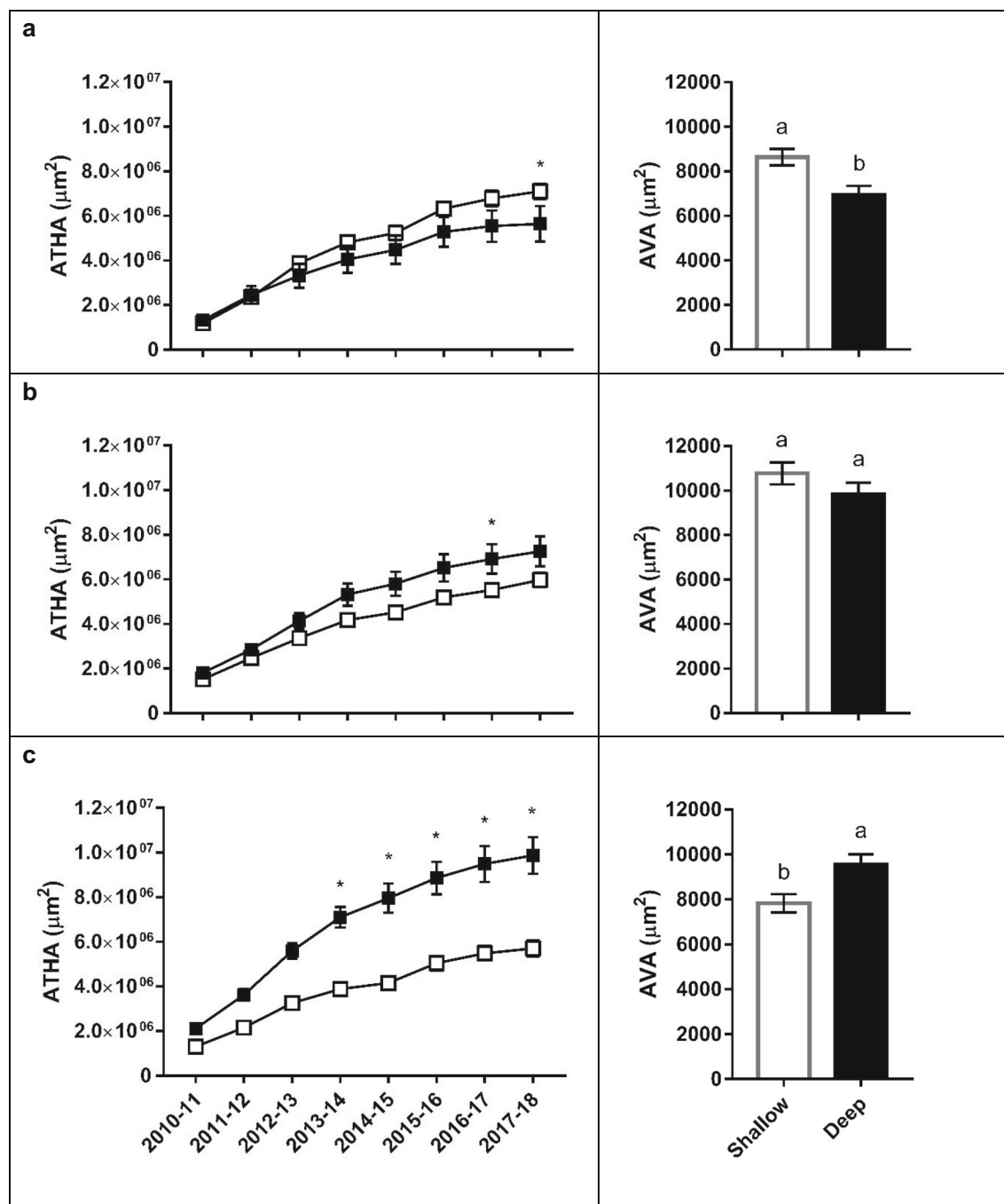


Fig. 5 Left column, accumulated total hydraulic area (ATHA) temporal series for the period 2010–2018. DS (black squares) and SS (white squares) for Bonarda (a), Malbec (b), and Tempranillo (c), respectively. Values are means \pm SEM and significant

differences between soils for each year are indicated with an asterisk ($p \leq 0.05$, LSD Fisher's test). Right column, the overall means \pm SEM ($n = 6$) of vessel area; different letters above the bars indicate significant differences

Evidence for the impact of soil depth on the growth of each analyzed cultivar was also detected in the xylem hydraulic conduction system. In this sense, Malbec and

Tempranillo produced a larger hydraulic area in plants growing in DS conditions (Fig. 5b, c, left column), while in Bonarda, the accumulated hydraulic area was

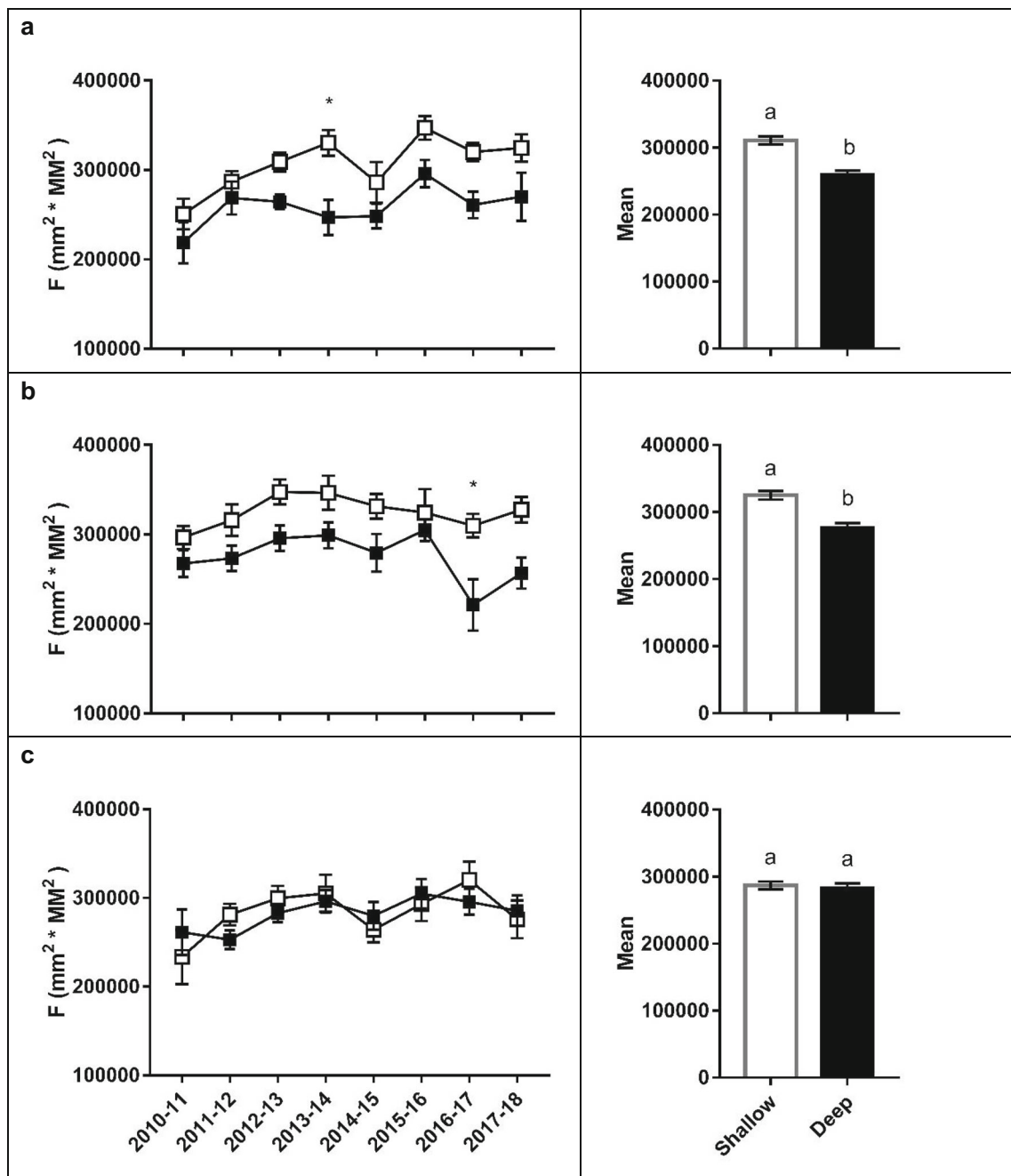


Fig. 6 Left column, vessel lumen fraction (F) calculated annually for the period 2010–2018 for Bonarda (a), Malbec (b) and Tempranillo (c) planted in DS (black) and SS (white), respectively. Values are means ± SEM and significant differences between soils

for each year are indicated with an asterisk ($p \leq 0.05$, LSD Fisher's test). Right column, the overall means ± SEM (n = 6) of F; different letters above the bars indicate significant differences

slightly higher for plants in SS (Fig. 5a, left column). This last result could indicate a particular adaptation of Bonarda to this type of soil. Broadly, Tempranillo presented the largest and significant ATHA differences

between plants growing in both types of soils. The vessel lumen fraction index (F; Fig. 6) also reflected the different behavior of cultivars associated with the soil depth. The F index indicated that both Bonarda and

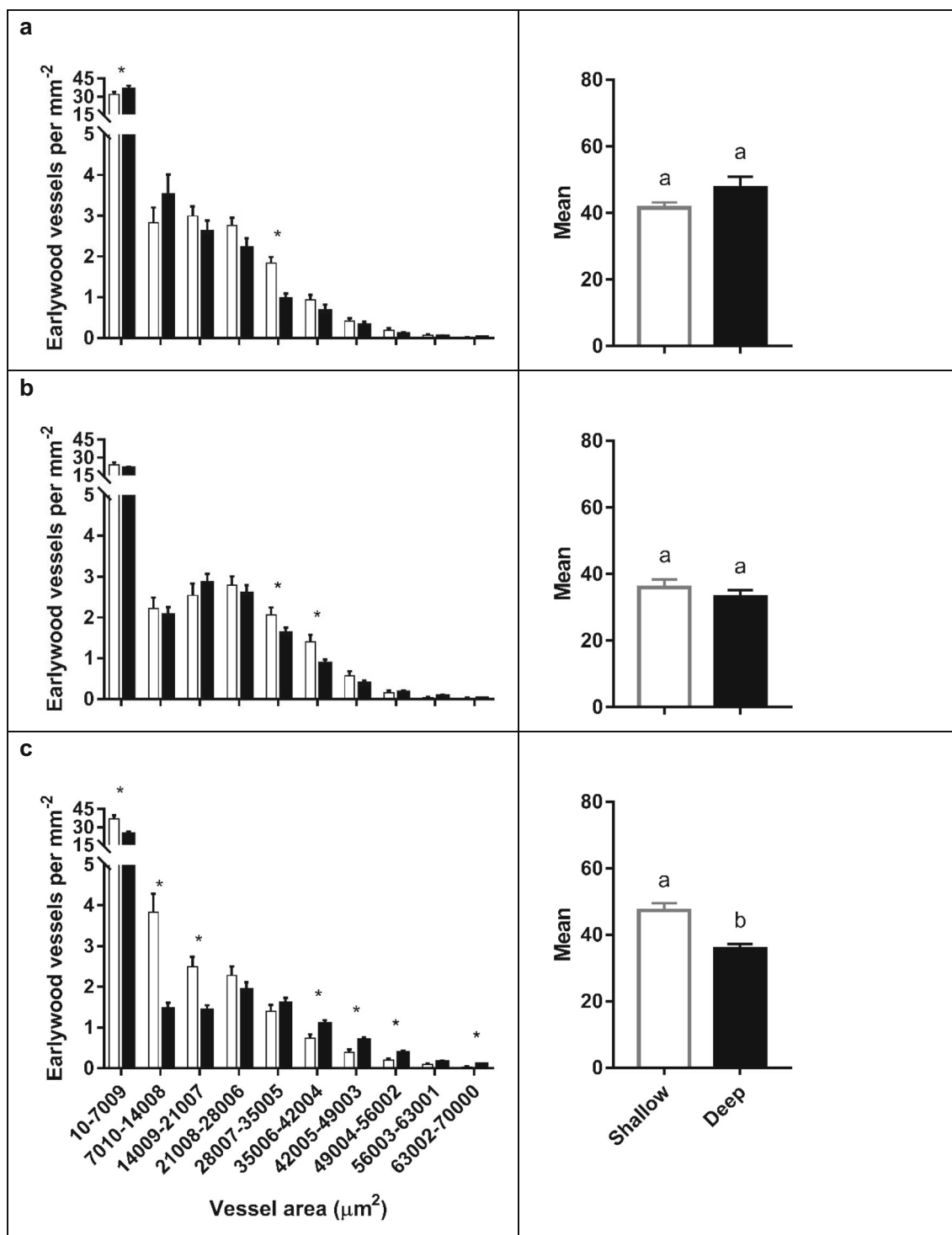


Fig. 7 Vessel density variation according to the type of soil and cultivar. Vessel density, expressed as a function of the lumen vessel size, shows a negative logarithmic trend as size categories increase. Left column, earlywood vessel density distribution per vessel area interval for Bonarda (a), Malbec (b) and Tempranillo (c) growing on DS (black bars) and SS (white bars), respectively.

Values are means ± SEM (n = 6) and significant differences between soils for each vessel area interval are indicated with an asterisk ($p \leq 0.05$, LSD Fisher's test). Right column, the overall means ± SEM for earlywood vessel density values; different letters above the bars indicate significant differences

Malbec developed a larger hydraulic conduction capacity under SS situations, while Tempranillo did not modify its conduction capacity based on the soil type. The fact that Tempranillo maintained its conduction capacity regardless of the type of soil could be explained by trade-offs between the density and the mean area of the vessels. In Malbec, larger F values found in SS contrasted with a larger total hydraulic area in DS conditions. This, which at first may seem contradictory, may be explained by the larger wood surface (BAI) produced by plants in DS (Fig. 4b).

As previously stated, for Bonarda no significant differences were observed in BAI between soil types, which would indicate a larger hydraulic conduction capacity in SS plants. This characteristic would be related to variations in the mean vessel area, as reflected by F values. Increased vessel area has a strong effect on the ability of wood to conduct water, since conductivity increases exponentially with this trait (Figure S2), while vessel density should have a relatively small effect on conductance (Preston et al. 2006). According to this, it could be concluded that Bonarda plants growing in SS presented a larger efficiency in water transport, as indicated by higher F values. This result is in agreement with the Hagen-Poiseuille law, since the area of the vessel lumen strongly affects the capacity of xylem to transport water (Preston et al. 2006; Chavarria and dos Santos 2012). Therefore, the similar values of BAI registered in both types of soil depth suggest that Bonarda cultivar would have a higher adaptive plasticity when compared to Malbec and Tempranillo (Nicotra et al. 2010).

Regarding the density of vessels, from which the F value is derived, the significantly higher mean vessel density observed in Tempranillo in lower interval categories (Fig. 7c, left column) for plants growing in SS conditions contrasted with plants growing in DS conditions (Fig. 2). This dual behavior could support the idea that, for both types of soils, a compensation mechanism would be established between the number of vessels and the area they occupy, achieving a comparable water conduction capacity. It also suggests a safety strategy when the plant is subject to conditions of water stress, since a higher density of vessels (including vessels of different diameter) could guarantee the active transport of water, even when a portion of this conduction system would be affected by cavitation (Baas et al. 1983; Schmitz et al. 2006; Islam et al. 2019). The Bonarda cultivar did not show significant differences in the

vessel density between DS and SS (Fig. 7a, right column), although a significantly larger vessel area was identified in SS compared to DS (Fig. 5a, right column). This combination of variables could sustain higher water conduction performance in SS conditions, a behavior that can be also assigned to the Malbec cultivar.

Unlike what was observed in Bonarda and Malbec, Tempranillo seems to be a highly conservative cultivar from the point of view of safety in water transport, since plants growing under SS conditions produce more vessels of smaller diameter (Fig. 7c, left column). This type of response makes sense in more water-stressing soils, since a fraction of smaller vessels would partially preserve the safety of the water conduction system (Robert et al. 2009), but at the cost of decreased hydraulic conduction capacity. On the other hand, Tempranillo showed a higher density of vessels with a larger diameter in DS. Because these soils could experience a buffering capacity in the regulation of water availability, this cultivar allows itself to produce vessels with larger areas that prioritize water conduction for the benefit of plant growth. There are reports in literature of this sensitivity in Tempranillo, indicating a poor adaptation of this cultivar to warm and dry stressful conditions (Medrano et al. 2003), in correspondence with a low water use efficiency during episodes of water stress (Tomás et al. 2012; Martorell et al. 2015). In this sense, Tempranillo seems to follow the general rule in which both variables, vessel density and area, are negatively associated to each other, since according to Preston et al. (2006) the presence of large vessels would be typical of soils with high moisture content. Bonarda seems, however, to challenge this trade-off between safety and efficiency in the water transport system by increasing the mean vessel area in soils under stressful water conditions, as can be seen in Fig. 2. Thus, an interesting question arises: How does Bonarda avoid systemic failure in water conduction under a water stress situation? Fig. 7 shows that, for both soil depths, this cultivar exhibits mean vessel density values similar to those of Tempranillo in SS, in the ranges from 10 to 21,007 μm^2 , but with a trend towards larger vessel density in SS plants with significantly greater differences in the range of vessel diameters between 28,007 and 35,005 μm^2 . This type of response, along with the ability to increase the mean area of their vessels in stressful situations, would allow SS plants to achieve high levels of security against cavitation and good water conduction performance due to the simultaneous

presence of small and large vessels. Bonarda, in terms of annual wood production, was more adapted to the contrasting soil conditions probably due to a marked response in variations in vessel density and area. Malbec and Tempranillo appear to be more sensitive to stressful soil conditions considering BAI values, concomitantly with fewer changes in the Malbec anatomy and large anatomical variations in Tempranillo, in response to SS situations.

In conclusion, the present results showed that phenotypic plasticity seems to depend on the cultivar and the variables evaluated, since grapevines of the same genotype –considered in a population genetic sense (Nicotra et al. 2010)- exhibited different phenotypic characteristics depending on the depth of the soil. Therefore, our results confirmed that the hydraulic anatomy of *Vitis vinifera* was modified in response to contrasting soil characteristics in three emblematic cultivars of the Argentine wine industry. This information, scarce at the moment, indicates that the grapevine experiences adaptation mechanisms to the edaphic environment through the development of xylem hydraulic system patterns adequate to overcome conditions of low water retention capacity in soils. According to our results, Bonarda could be a successful alternative for plantations in shallow soils with low water holding capacity. Therefore, this cultivar shows an interesting potential in the exploration of new places for grapevine cultivation, with the goal of differentiating wines, which conceptually is known as terroir (Fanet 2008).

This study suggests that the anatomical analysis of the *V. vinifera* annual growth rings is an appropriate tool to deeper understand the dynamics of growth and interaction between plant and soil. The recognition of these anatomical adaptations can help in planning an adequate selection of cultivars and in adopting management strategies in areas of strong soil heterogeneity, which can be implemented in regions where the analyzed cultivars are implanted.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11104-021-04907-y>.

Abbreviations CEC, Cation exchange capacity; DS, deep soil; ECs, electromagnetic soil conductivity; Wc, field water capacity; NDVI, normalized difference vegetation index; SS,

shallow soil; Ws, saturated water content; Wp, permanent wilting point

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Author contributions F. Roig-Puscama, F. Berli and P. Piccoli developed the original project and prepared the draft manuscript. F. Roig-Puscama and F. Berli conducted the experiment in the field and analyzed the data with P. Piccoli. F. Roig-Puscama and F. Roig carried out the anatomical analysis in collaboration with M. Tomazello-Filho. F. Roig-Puscama and L. Mastrantonio conducted the soil physicochemical analysis. All authors reviewed, edited and approved the final version of the manuscript.

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