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► **To cite this version:**

J. Pouzoulet, A. L. Pivovarov, M. E. de Guzman, P. E. Rolshausen, L. S. Santiago. Contrasting adaptation of xylem to dehydration in two *Vitis vinifera* L. sub-species. *Vitis*, 2020, 59 (2), pp.53-61. 10.5073/vitis.2020.59.53-61 . hal-03176146

HAL Id: hal-03176146

<https://hal.inrae.fr/hal-03176146>

Submitted on 22 Mar 2021

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Contrasting adaptation of xylem to dehydration in two *Vitis vinifera* L. sub-species

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Summary

Xylem hydraulic properties of agricultural crop species can be linked to their region of origin, but because crop systems are often irrigated to reach optimum quality and yield, key differences in drought resistance are not often considered. We investigated how hydraulic conductivity and xylem vulnerability to drought-induced cavitation of two grapevine cultivars correspond to their centers of domestication with 'Merlot' (*Vitis vinifera* subspecies *occidentalis*) having been domesticated in a temperate forest region, and 'Thompson Seedless' (*Vitis vinifera* subspecies *orientalis*) domesticated in a semi-arid region. We used anatomical measurements and xylem vulnerability curves to evaluate hydraulic traits and drought resistance. Our results showed that 'Thompson Seedless' was significantly more vulnerable to drought-induced cavitation than 'Merlot'. Bench dehydration produced significantly different estimations of xylem vulnerability to cavitation in each cultivar. This result was consistent with anatomical measurement, with 'Thompson Seedless' stems having greater maximum stem-specific hydraulic conductivity, more vessels, higher vessel density and a greater lumen fraction than 'Merlot'. The relatively large amount of xylem vessels and lumen area in 'Thompson Seedless' is consistent with domestication in a semi-arid habitat where a greater number and size diversity of xylem vessels would be needed to transport water and meet evaporative demand as opposed to cultivars that were domesticated in temperate forest regions like 'Merlot'. These differences appear to expose 'Thompson Seedless' to high xylem vulnerability to cavitation.

Key words: center of domestication; drought resistance; grapevine; hydraulic conductivity; *Vitis vinifera*; vulnerability curve; wine; xylem.

Introduction

Understanding how plants cope with water shortage in natural and agricultural systems is important in the context of climate change and in anticipation of longer, more frequent, or more intense drought (PACHAURI *et al.* 2014). The 2012–2014 drought in California was the worst in 1200 years (GRIFFIN and ANCHUKAITIS 2014) and illustrated the seriousness of water conservation and water-use efficiency in natural and agricultural systems (HOWITT *et al.* 2014, MANN and GLEICK 2015). Cultivated grapevine, *Vitis vinifera* L. *sativa*, is the most planted perennial crop in the world and is of great socio-economic interest. Grapevine is mostly grown in Mediterranean climate regions where seasonal drought and temperature exert large constraints on yield and quality (CHAVES *et al.* 2010, MOSEDALE *et al.* 2016). In the context of increasing demand for crop irrigation and declining water quantity or quality for agriculture, dramatic improvements in water-use efficiency and better understanding of how plants can sustain yields under water scarcity is of major concern (COSTA *et al.* 2016).

Grapevine was domesticated from its wild ancestor, *Vitis vinifera* L. *sylvestris*. Wild grape typically grows as a liana or a scrambling shrub in riparian forests around the Mediterranean basin, and can be found from the Atlantic shore of Western Europe to the Middle East around Turkmenistan (CATTONARO *et al.* 2014). Population genetic studies suggest that the phenotypic diversity observed across grapevine cultivars results from a long and complex domestication process, with several centers of domestication, geographic movement of plant material along historical trade routes, and local hybridization between domesticated cultivars and wild genetic pools (SEFC *et al.* 2003, ARROYO-GARCIA *et al.* 2006, THIS *et al.* 2006, DE MATTIA *et al.* 2008, MYLES *et al.* 2011, DE ANDRES *et al.* 2012, BACILIERI *et al.* 2013). Seven decades ago, NEGROUL (1946) identified three main ecological-geographical groups of cultivars (proles): 1) *Occidentalis*,

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comprising most of the Western Europe wine cultivars such as 'Merlot'; 2) *Pontica*, comprising the Eastern and Central Europe wine cultivars; and 3) *Orientalis*, represented mostly by table-grape cultivars (including 'Thompson Seedless') traditionally grown in Northern Africa and the Middle East (TROSHIN *et al.* 1990). This classification has since been supported by morphological and molecular studies (TROSHIN *et al.* 1990, BACILIERI *et al.* 2013). Early evidence of wine making, as well as molecular studies, provide clues about the first center of domestication of grapevine by ancient civilizations in the Transcaucasian area (CATTONARO *et al.* 2014). Viticulture and domesticated grapes may have spread to Central and Western Europe, where domestic populations were most likely crossed locally with endemic wild populations (MYLES *et al.* 2011). Yet, morphological particularities noted in cultivars of *Orientalis*, sub-prole *antasiatica*, led NEGROUL (1946) to postulate that these cultivars might have been domesticated from a different wild population than cultivars of other proles, and apart from the first center of domestication (TROSHIN *et al.* 1990). This hypothesis was recently confirmed by means of molecular approaches, with seedless table-grape cultivars such as prole *Orientalis* subprole *antasiatica* clustering with the wild population found in Uzbekistan, Tajikistan, Kyrgyzstan, Central Asia rather than Eastern and Western Europe cultivars (MARRANO *et al.* 2015).

Considering the vast geographic distribution of wild grape and its isolated location in certain regions, it is likely that endemic populations underwent physiological adaptation to local climatic conditions and resource availability. In addition, it can be hypothesized that traits such as drought tolerance were reinforced through human selection processes, especially in cultivars traditionally grown in semi-arid areas such as the Middle East. A good example of such cultivars can be found in the seedless table-grape cultivar 'Sultanina', introduced to California in 1872 by Sir W. N. Thompson, and now extensively cultivated in this area under the name 'Thompson Seedless' (BIOLETTI 1919).

Plants that evolve in dry environments usually develop a combination of physiological adaptations that limit leaf evapo-transpiration when water is not available and maximize water use for productivity during short but intense bursts of water availability (DE MICCO and ARONNE 2012, PIVOVAROFF *et al.* 2016, SANTIAGO *et al.* 2016). Deep roots are critical for maintaining water transport in dry environments, otherwise, allocation to features that prevent hydraulic failure, such as a cavitation resistant xylem, large hydraulic safety margin, or dry-season deciduousness are considered key features of plants in dry habitats (CHOAT *et al.* 2012, COCHARD *et al.* 2013, URLI *et al.* 2013, PIVOVAROFF *et al.* 2016). Our current understanding is that there is a trade-off between the 'efficiency' of xylem, characterized as the ability to transport water at high rates, and the 'safety' of xylem, characterized as the ability to avoid drought-induced xylem cavitation (POCKMAN and SPERRY 2000, MARTÍNEZ-VILALTA *et al.* 2002, GLEASON *et al.* 2016). The safety-efficiency trade-off in plants is based on hydraulic theory and data showing that plants with high xylem conductivity are more vulnerable to drought-induced cavitation than plants with low xylem conductivity (POCKMAN and SPERRY 2000, MARTÍNEZ-VILALTA *et al.* 2002,

WHEELER *et al.* 2005). Understanding this trade-off and how it is manifested across plant species is especially important when considered in combination with deep-rooting. Deep roots in dry habitats can effectively decouple plants from atmospheric drought, promoting allocation to high hydraulic conductivity and relatively little allocation to a safe xylem. Grapevine is known to have deep roots, ranging from 6 to > 25 m depth depending on soil type (DOLL 1954, SEGUIN 1972, SMART *et al.* 2006).

Predicting the ability of agricultural species to withstand drought is important, yet in the past century agricultural cultivars have been bred mostly for food quality or yield with high inputs of water and nutrients. Indeed, the starting material for domestication may be important and the climate of the center of domestication for different cultivars could be associated with variation in stress tolerance. We tested this in two contrasting varieties of grapevine. The first is 'Merlot', which comes from Western Europe and traditionally grows under a temperate climate. The second is 'Thompson Seedless', which comes from the Middle East and traditionally grows under a desert climate. Our questions were: 1) How do two cultivars of grapevine domesticated in contrasting climates vary in xylem cavitation resistance and hydraulic conductivity? 2) Are differences in cavitation resistance related to xylem structural features?

Material and Methods

Plant material: Certified *Vitis vinifera* L. cuttings provided by the Foundation Plant Service (FPS, University of California, Davis, USA) in 2014 were used for propagation of plant material. *V. vinifera* 'Merlot' (FPS selection #6) and *V. vinifera* 'Thompson Seedless' (FPS selection #02A) were propagated and grown in 4 l pots containing a mix of horticultural compost and sand (1:1) for a period of three months to allow the root system to develop. After this period, the main shoot of plants was pruned at the third internode and leaves and lateral shoots were removed to induce shoot regeneration from latent buds. After three weeks one vigorous shoot was selected per plant and trained vertically using a stake while other shoots were removed. Plants were organized in a complete random design. Plants were watered to saturation 2-3 times a week, one watering being performed with a 21:5:20 (N:P:K; 0.6 g·L⁻¹) fertilizer solution (Peters EXCEL; Scotts Inc.). Plants were grown for an additional 3 months until shoot harvest and analysis. Temperature in the glass-house ranged from 21-32 °C. Plants were inspected daily and sprayed for the control of diseases and pests as needed.

Bench dehydration vulnerability curve: Bench dehydration vulnerability curves were conducted over a 1-week period with subsets of plants of both cultivars randomly sampled and analyzed every day. A total of 13 plants and thus shoots were collected for 'Merlot' and 14 were collected for 'Thompson'. Shoots were lignified for most of their length and were approximately 2.5 meters long. The evening before collection, plants were watered to saturation to assure maximum stem hydration at the time of the sampling. Whole shoots were sampled in the morning

and excised under water. The basal wound was then heavily wrapped with parafilm and the whole shoot was placed in a sealed plastic bag. Shoot dehydration was induced by opening and ventilating bags periodically. Maximum dehydration time did not exceed 48 h. A 20 cm-long stem segment, distant from 50 cm or more above the basal wound was cut under water. Leaves were removed from the stem segment and wounds were immediately sealed with cyanoacrylate glue (The Gorilla Glue Company, Sharonville, Ohio, USA). About 5 cm long xylem fragments were collected above and below the conductivity sample, were divided into 4 pieces and were pooled to measure xylem water potential (Ψ_x) in a thermocouple psychrometer (C-30, Wescor, Inc., Logan, Utah, USA) connected to a water potential datalogger (PSYPRO, Wescor Inc.) and placed inside an insulated water bath at 24 °C. Values were logged every 0.5 h and Ψ_x was recorded when stable readings were achieved.

Stem hydraulic conductivity was determined by connecting the 20 cm long stem segment to tubing with filtered (0.2 μm), de-gassed 20 mM KCl solution flowing from an elevated source, through the stem, and into a reservoir on a balance (± 0.1 mg; Denver Instrument P-214; Sartorius, Göttingen, Germany) that was interfaced with a computer to record flow rate, allowing the calculation of conductivity (SPERRY *et al.* 1988). We corrected for stem passive water uptake by beginning and ending each conductivity measurement with a 'background' measurement (TORRES-RUIZ *et al.* 2012). Stem hydraulic conductivity (K_h ; $\text{kg}\cdot\text{m}^{-1}\cdot\text{s}^{-1}\text{MPa}^{-1}$) was calculated as:

$$K_h = F \times L/dP \text{ [Eqn 1]}$$

where F is the flow rate ($\text{kg}\text{ s}^{-1}$), L is the stem length (m), and dP is the driving force (MPa). The pressure was kept at or below 1.35 kPa. Stem hydraulic conductivity was divided by the trans-sectional xylem area (see microscopy and morphological analysis of xylem section below) to determine sapwood-specific hydraulic conductivity (K_s ; $\text{kg}\cdot\text{m}^{-1}\cdot\text{s}^{-1}\text{MPa}^{-1}$). For the determination of the maximum stem hydraulic conductivity ($K_{s,max}$), stems were flushed for a period of 10 min at 100 kPa with filtered, de-gassed 20 mM

KCl solution. While a slight decline in $K_{s,max}$ was noticed across the range of Ψ_x , no significant effect of Ψ_x on $K_{s,max}$ was found (*i.e.* $p > 0.05$, $x = 0$ within the 95 % confidence interval of the linear regression curve), using datasets from each cultivar independently or by pooling them (Fig. 1). The percent loss of conductivity (PLC) was determined as:

$$\text{PLC} = 100 \times (1 - (K_s/K_{s,max})) \text{ [Eqn 2]}.$$

A PLC' was also calculated after the method proposed by JACOBSEN and PRATT (2012), in which the $K_{s,max}$ used in the calculation of PLC' following the Eqn. 2 consisted of the averaged $K_{s,max}$ value from three different stems freshly collected and flushed.

Data analysis and modeling of vulnerability curves: Vulnerability curves were constructed by plotting water potential versus PLC using the Weibull model (Eqn 3; OGLE *et al.* 2009).

$$\text{PLC} = 100 \times (1 - \exp(-(\Psi/\alpha)^\beta)) \text{ [Eqn 3]}.$$

Optimization of model parameters was achieved by nonlinear least square optimization using the solver tool in Excel 2010 (Microsoft corporation, Redmond, Washington, USA). The model parameters Ψ_{50} and Ψ_{88} (Ψ corresponding to 50 % and 88 % PLC) were determined with a leave-one-out cross-validation (LOOCV). Note that for the ES model, $-\beta$ corresponds to Ψ at PLC = 50 % (Ψ_{50}), and α corresponds to the slope of the curve (sensitivity index; S_x at Ψ_{50} sensu OGLE *et al.* 2009). We carried out analysis of variance (ANOVA) on Ψ_{50} and Ψ_{88} values predicted using different Ψ measurement methods, models, and cultivars. Post-hoc analysis of predicted LOOCV residual Ψ_{50} was used to test the effect of the Ψ_x measurement methods in both 'Merlot' and 'Thompson Seedless'. Trait means between cultivars were compared with non-parametric t -tests.

Microscopy and morphological analysis of xylem: Following K_h determination during bench dehydration, we collected a 1-cm long stem segment from the 20 cm long sample stem using a razor blade. Samples were fixed in 80 % ethanol at 4 °C for 48 h, after which the ethanol solution was replaced and the samples were kept at 4 °C. Prior to sectioning, stem fragments were sequentially rehydrated with 1:1 and 1:3 ethanol:water and water only. Specimens were prepared using a razor blade to obtain 5 mm long fragments. Samples were then attached to an aluminum support with cyanoacrylate glue and 70 μm thick cross sections were made in water using a vibrating microtome (EMS, Hatfield, Pennsylvania, USA) equipped with a sapphire knife (DDK, Wilmington, Delaware, USA). Sections were stained with an aqueous solution of Toluidine O (0.05 %, pH = 4.3), rinsed briefly in water and observed using a light microscope (Leica DM4000, Leica microsystems CMS GmbH, Wetzlar, Germany) in bright field mode. Micrographs (100 \times magnification) were assembled using LAS v4.2 (Leica microsystems CMS GmbH, Wetzlar, Germany) to create high definition images (430 pixels per mm) covering the whole stem cross section. Pith, secondary xylem, fascicular portions and rays were delineated manually using GIMP v2.0 software so that the corresponding area could be easily detected by ImageJ v1.48 (<http://imagej.nih.gov>). Vessel lumens presenting shading that could compromise the accuracy of the analysis were analyzed using GIMP v2.0 software (<http://www.gimp.org/>). For each stem, number of vessels and vessel density

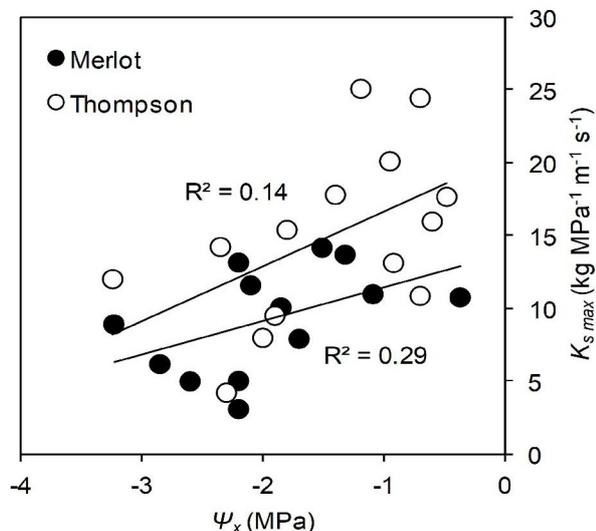


Fig. 1: Relationship between Ψ_x and $K_{s,max}$ observed for *Vitis vinifera* 'Merlot' and 'Thompson Seedless' in this study. No significant relationship was found between Ψ_x and $K_{s,max}$ ($p > 0.05$).

were determined in the secondary xylem on the whole section with ImageJ (SCHOLZ *et al.* 2013). Arithmetic vessel diameter was determined using the vessel area and vessel distribution per diameter class for each sample. Narrow vessels found in xylem next to the cambium corresponding to the end of the growing period and primary xylem were excluded from the analysis. Morphological parameters related to the spatial distribution of vessels including the vessel grouping index, the ratio of the total number of vessels to the total number of vessel groupings, the total intervessel wall thickness, measured as the double intervessel wall in the middle of adjacent vessels, and the intervessel contact fraction, the portion of the vessel wall in contact with other vessels, were determined manually using ImageJ in six consecutive fascicular portions in the dorsal and ventral areas of the stem. All morphological parameters displayed in this study were determined and calculated following the definitions of SCHOLZ *et al.* (2013).

Results

Xylem vulnerability curves: Comparison of cultivars showed that 'Merlot' was less vulnerable to dehydration induced xylem cavitation than 'Thompson Seedless' (Fig. 2, Tab. 1). For 'Merlot', *s*-shaped curves were found with both PLC and PLC' calculation methods (Fig. 2 A and B). However for 'Thompson Seedless', vulnerability curves show *r*-shaped curves with the PLC calculation and *s*-shaped curves with the PLC' calculation (Fig. 2 A and B). ANOVA found a significant interaction between PLC calculation method and cultivar ($\text{Pr(>F)} < 0.001$) and a significant effect of cultivar on Ψ_{50} ($\text{Pr(>F)} < 0.001$) (Tab. 2). There was non significant interaction between PLC calculation method and cultivar ($\text{Pr(>F)} = 0.47$), but a direct effect of cultivar ($\text{Pr(>F)} < 0.001$) and PLC calculation method ($\text{Pr(>F)} < 0.001$) on Ψ_{88} (Tab. 2). Posthoc tests showed that the two cultivars differed significantly in their Ψ_{50} and Ψ_{88} across different PLC calculation methods, with 'Merlot' ($\Psi_{50} = -2.45$ and -2.45 ; $\Psi_{88} = -3.39$ and -2.99 for PLC and PLC' methods, respectively) always less vulnerable than 'Thompson Seedless' ($\Psi_{50} = -1.29$ and -1.47 ; $\Psi_{88} = -2.62$ and -2.42 for PLC and

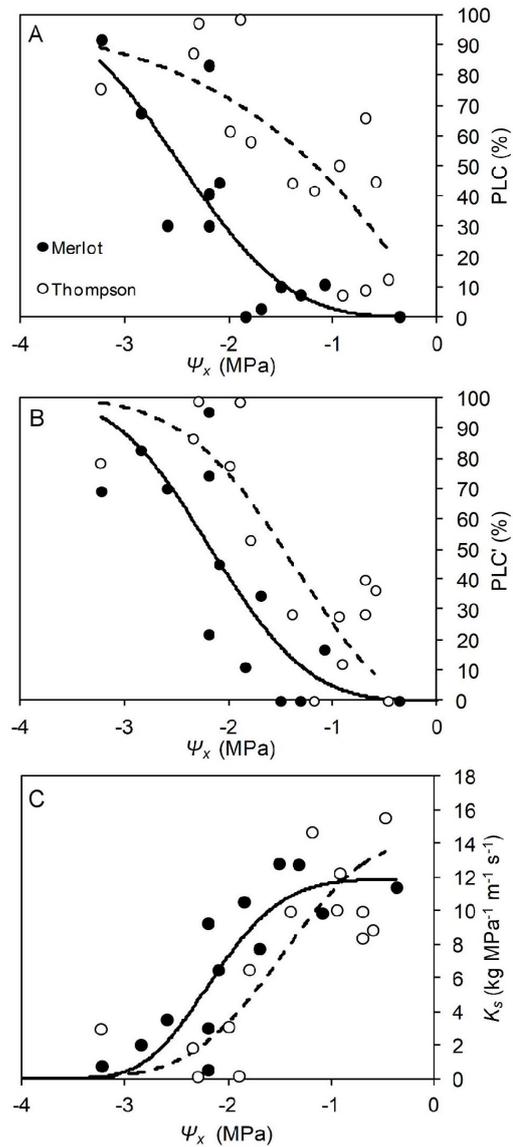


Fig. 2: Xylem vulnerability curves showing percent loss of hydraulic conductivity (PLC) or native hydraulic conductivity (K_s) as a function of xylem water potential (Ψ_x) generated with the bench dehydration method on *V. vinifera* 'Merlot' and 'Thompson Seedless'. See text for the calculation (A) PLC and (B) PLC'. All curves were fitted with Weibull models.

Table 1

Curve-fit parameters (α and β) and statistical results of xylem vulnerability curves with predicted values for the water potential at 50 % (Ψ_{50}) and 80 % (Ψ_{88}) loss of hydraulic conductivity for *V. vinifera* 'Merlot' and 'Thompson Seedless' cultivars, with two calculation methods for percent loss of hydraulic conductivity (PLC and PLC'), coefficient of the determination (R^2) for the observed versus predicted relationship, root mean square error (RMSE) for standard and leave-one-out cross-validation (LOOCV) analyses. MSE = mean squared error. Different letters for values of Ψ_{50} or Ψ_{88} indicate difference at the significance level of 0.05 using a Bonferroni-Holm test

Cultivar	Model	α (SE)	β (SE)	R^2 (n)	Ψ_{50}	Ψ_{88}	RMSE	LOOCV RMSE
Merlot	PLC	-2.12 (± 0.72)	2.45 (± 0.15)	0.68 (13)***	-2.45 ^a	-3.39 ^a	17.29	21.32
	PLC'	-3.47 (± 1.28)	2.40 (± 0.17)	0.66 (13)***	-2.17 ^b	-2.99 ^b	19.17	26.85
Thompson Seedless	PLC	-1.49 (± 0.48)	1.29 (± 0.18)	0.58 (14)**	-1.29 ^d	-2.62 ^b	18.85	22.2
	PLC'	-2.25 (± 0.67)	1.73 (± 0.17)	0.70 (14)***	-1.47 ^c	-2.42 ^c	18.92	23.39

Significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 2

ANOVA output of predicted Ψ_{50} and Ψ_{88} provided by PLC and PLC' calculation methods for the *Vitis vinifera* 'Merlot' and 'Thompson Seedless' using leave-one-out cross-validation (LOOCV)

Effect	Ψ_{50}			Ψ_{88}		
	df	F	P (Pr > F)	df	F	P (Pr > F)
PLCs calculation method	1	0.002	0.96	1	72	< 0.001***
Cultivar	1	3404	< 0.001***	1	67	< 0.001***
PLCs calculation method x cultivar	1	285	< 0.001***	1	0.50	0.47

Significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

PLC' methods, respectively) (Tab. 1). Applying the PLC' calculation shifted the vulnerability curve to make 'Merlot' more vulnerable and 'Thompson Seedless' less vulnerable relative to PLC (Tab. 1). The mean $K_{s,max}$ (i.e. from flushed stem, please see Fig. 1) of $15.18 \pm 5.59 \text{ kg MPa}^{-1} \cdot \text{m}^{-1} \cdot \text{s}^{-1}$ in 'Thompson Seedless' was 60 % higher and significantly greater than the mean $K_{s,max}$ of $9.33 \pm 3.76 \text{ kg MPa}^{-1} \cdot \text{m}^{-1} \cdot \text{s}^{-1}$ in 'Merlot' ($P = 0.002$). Vulnerability curve analysis showed that for a given water potential, 'Merlot' maintained a higher K_s than 'Thompson Seedless' as water potential declined (Fig. 1, Fig. 2C).

Comparison of hydraulic, anatomical and morphological traits: No significant differences in total xylem cross-sectional or pith surface area were found between 'Merlot' and 'Thompson Seedless' ($P > 0.05$; Tab. 3). However, there were differences in the general morphology of the vascular system (Fig. 3). 'Thompson Seedless' had equal or higher numbers of vessels than 'Merlot' in all vessel diameter classes (Fig. 3 C), and an overall higher vessel density than 'Merlot' ($P = 0.02$), although maximum

vessel diameter was statistically similar ($P = 0.79$; Tab. 3). Theoretical specific hydraulic conductivity calculated from vessel diameter data was 31% and significantly higher ($P = 0.04$) in 'Thompson' ($58 \pm 12.2 \text{ kg MPa}^{-1} \cdot \text{m}^{-1} \cdot \text{s}^{-1}$) than 'Merlot' ($44.1 \pm 4.84 \text{ kg MPa}^{-1} \cdot \text{m}^{-1} \cdot \text{s}^{-1}$), which was consistent with the observations from $K_{s,max}$ measurements (Tab. 3, Fig. 3D). Vessel lumen fraction was also significantly greater in 'Thompson Seedless' ($P = 0.001$), at 24.2 % of xylem area, compared to 20.4 % of the xylem area in 'Merlot' (Tab. 3). There was a strong significant difference in vessel grouping index ($P = 0.005$), with 'Thompson Seedless' harboring a greater ratio of total vessels to the total number of vessel groupings than 'Merlot'. In addition, 'Thompson Seedless' showed much greater inter-vessel contact length ($P < 0.001$) and inter-vessel contact fraction ($P < 0.001$) than 'Merlot' (Tab. 3). Finally, there were differences between cultivars in the organization of xylem parenchyma, with no significant differences for relative total ray surface parenchyma fraction ($P = 0.97$), and significantly greater total number of rays in 'Thompson Seedless' than in 'Merlot' ($P = 0.02$; Tab. 3).

Table 3

Mean (± 1 SE) and two-tailed non-parametric t -test results of xylem anatomical traits in *V. vinifera* 'Merlot' and 'Thompson Seedless' cultivars. ($n = 12$; $df = 10$)

Xylem morphological trait	Merlot	Thompson	P-value
Xylem surface (mm ²)	5.18 (± 0.45)	5.26 (± 0.53)	0.76
Pith surface (mm ²)	1.65 (± 0.22)	2.07 (± 0.79)	0.29
Number of rays per stem	32.33 (± 0.81)	36.16 (± 2.78)	0.02*
Ray surface fraction (%)	21.01 (± 1.36)	21.03 (± 0.89)	0.97
Hydraulic diameter (μm)	71.07 (± 5.04)	68.99 (± 5.47)	0.51
Maximum vessel diameter (μm)	122.05 (± 9.12)	123.89 (± 13.21)	0.79
Vessel density (nbr/mm ²)	68.58 (± 12.95)	88.94 (± 12.31)	0.02*
Vessel lumen fraction (%)	20.39 (± 0.88)	24.15 (± 1.62)	0.001**
K_s (kg.MPa ⁻¹ .s ⁻¹ .m ⁻¹)	44.1 (± 4.84)	58 (± 12.2)	0.04*
Vessel grouping index	1.76 (± 0.13)	2.78 (± 0.53)	0.005**
Intervessel wall length (μm per mm ²)	883.1 (± 251.7)	1976.2 (± 337.3)	< 0.001***
Intervessel contact fraction (%)	6.42 (± 1.5)	11.71 (± 1.37)	< 0.001***

Significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

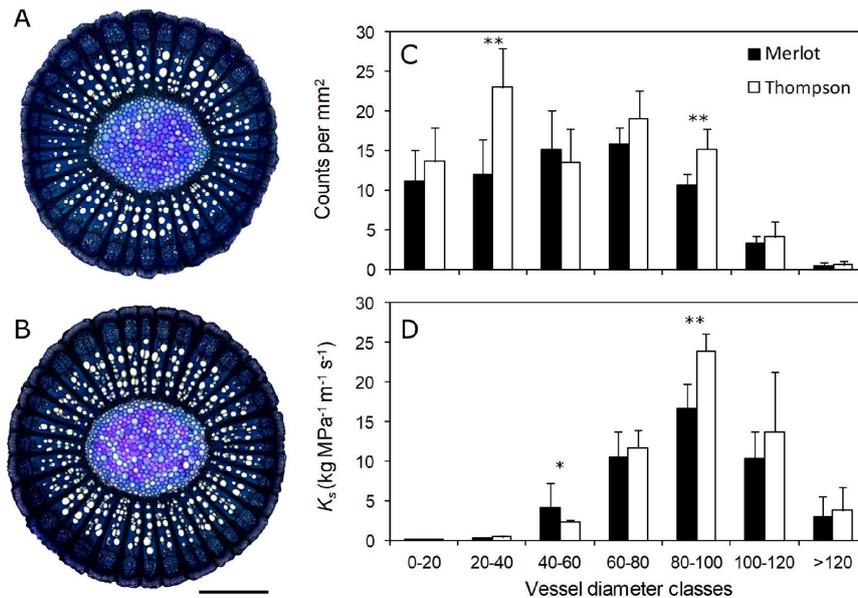


Fig. 3: Micrographs of stem cross-sectional xylem morphology of (A) *V. vinifera* 'Merlot' and (B) *V. vinifera* 'Thompson Seedless' plants. Note the overall difference in the number of vessels, as well as the difference in their spatial distribution. Scale bar = 1mm. See Tab. 3 for more detailed analysis. (C) Distribution of vessel diameter classes in the secondary xylem of *V. vinifera* 'Merlot' and *V. vinifera* 'Thompson Seedless' shoots ($n = 6$ per cultivar). (D) Calculation of the specific hydraulic conductivity provided by the different classes of vessel diameter for *V. vinifera* 'Merlot' and *V. vinifera* 'Thompson Seedless'. (*) and (**) indicates differences at the significance level of 0.05 and 0.01 respectively using a Student's test.

Discussion

Our results show that differences in xylem vulnerability to drought-induced cavitation occur between 'Merlot' and 'Thompson Seedless', two cultivars domesticated from different and isolated *Vitis vinifera* L. *sylvestris* populations. 'Thompson Seedless' showed greater hydraulic conductivity than 'Merlot', suggesting that grapevine in the semi-arid desert regions of the Middle East benefit from large xylem vessels and a high $K_{s,max}$ that can consistently supply water to distal shoots during very high evaporative demand. Resistance to xylem cavitation was greater in 'Merlot', however, indicating that the high hydraulic conductivity in 'Thompson Seedless' potentially comes at the expense of a more vulnerable xylem. Thus, in 'Thompson Seedless', drought survival is probably achieved with very deep roots that allow avoidance of perceived drought conditions, and provide a large water supply for meeting a sizeable evaporative demand. 'Merlot', on the other hand, is a cultivar originating from temperate climates in Western Europe with moderate water constraints during the summer, and can likely meet the evaporative demand of its temperate climate with a moderate hydraulic conductivity. Overall, it appears that native hydraulic strategies to cope with differences in seasonal drought have occurred across isolated populations of wild and domesticated grapevines throughout history.

Our finding that 'Thompson Seedless' was more vulnerable to drought-induced xylem cavitation than 'Merlot' is consistent with comparable studies of grape cultivars derived from the *occidentalis* proles, such as 'Cabernet Sauvignon' and 'Chardonnay' (ALSINA *et al.* 2007, CHOAT *et al.* 2010, BRODERSEN *et al.* 2013). Interestingly, our Ψ_{50} and Ψ_{88} values for 'Thompson Seedless' agree with those of ALSINA *et al.* (2007), who showed that 'Tempranillo',

'Alicante Bouschet' and 'Parellada', three cultivars derived from *orientalis* proles where 'Thompson Seedless' belongs, showed greater xylem vulnerability to cavitation than those derived from *occidentalis* proles (BACILIERI *et al.* 2013). Thus our results are consistent with greater vulnerability in cultivars derived from *orientalis* than *occidentalis* proles. This suggests that survival in semi-arid climates for deep-rooted plant species such as grapevine is favored by a high $K_{s,max}$ that can continue to conduct deep water sources to living shoots when there is a large pressure gradient across the soil-plant-atmosphere continuum, and the specialized xylem adaptations, including a high xylem vessel density and lumen area, appear to push the hydraulic safety versus efficiency trade-off towards maximizing efficiency rather than safety. Indeed tropical woody lianas show greater $K_{s,max}$ and more vulnerable Ψ_{50} than co-occurring trees in seasonally dry tropical forests (DE GUZMAN *et al.* 2016), consistent with the idea that $K_{s,max}$ can be more important than Ψ_{50} and Ψ_{88} in arid environments where deep water is available. It is also possible that domestication and cultivation in a semi-arid climate required irrigation, and that cultivation under high water availability led to the selection of phenotypes that maximize water transport, growth and yield over drought resistance.

Despite obvious differences observed between 'Merlot' and 'Thompson Seedless', Ψ_{50} in both cultivars suggests a sufficient safety margin such that a cycle of cavitation formation and repair would not occur on a daily basis under normal irrigation conditions. Indeed, field observations from California indicate that 'Thompson Seedless' leaves might not experience midday water potential below -0.8 MPa under moderate irrigation conditions (WILLIAMS *et al.* 2012). In addition, leaf water potential did not drop below -1.4 MPa in 'Thompson Seedless', even while enduring a prolonged

period of water scarcity under the Californian climate (WILLIAMS 2012, WILLIAMS *et al.* 2012). The xylem structure of 'Thompson Seedless' may also partially compensate for its vulnerability. Our anatomical results show high values of vessel density and absolute number in 'Thompson Seedless'. The histogram in Fig. 3 supports the idea that vessel redundancy could potentially buffer the hydraulic safety margin because it reduces the overall impact of cavitation in any one vessel (TYREE and ZIMMERMANN 2002, EWERS *et al.* 2007). Thus, as concluded by CHARRIER *et al.* (2018) on a large pool of cultivars from the *occidentalis* prole. 'Thompson Seedless', despite its apparent vulnerability, manages to maintain a sufficient safety margin to avoid major hydraulic failure under drought conditions.

Grapevine is often grown under irrigation restriction (*i.e.* France) or under deficit irrigation to improve water use and grape quality (CHAVES *et al.* 2010, PERMANHANI *et al.* 2016). Many studies provide evidence of acclimation processes to abiotic factors such as water availability in woody crops including grapevine (HOCHBERG *et al.* 2017, MARTORELL *et al.* 2015). Morphological traits of the vascular system such as the diameter of vessels are known to present a developmental plasticity that responds to environmental factors during plant growth (LOVISOLO and Schubert 1998, MUNITZ *et al.* 2018). These morphological adjustments likely allow the plant to scale its hydraulic needs with the available resources. This developmental plasticity could have a potential role in drought acclimation (CHOAT *et al.* 2018). Evidence of ontogenic effects on the level of resistance to drought induced cavitation also exist, whereby the highest stem resistance is reached at the end of the growing season (CHARRIER *et al.* 2018). In our experimental conditions, plants were grown with non-limiting water and nutrient supplies, thus favoring optimal growth. Measurements were also done on three-month-old canes, when resistance to drought induced cavitation was in theory not at its highest along the course of plant development. Comparison of vascular architecture of stem samples collected from 'Merlot' and 'Thompson' grapevines grown in a same area (*i.e.* FPS collection, Davis, California), supported that strong differences in structural traits related to hydraulics exist between these varieties under field conditions (POUZOLET *et al.* 2017). We demonstrate here that differences in hydraulic behavior between these varieties are also observed in experimental conditions. Thus, field work should now address the functional impact of these contrasted hydraulic strategies, along with their plasticity, in the context of drought adaptation.

One other aspect that should be considered with regards to xylem adaptation of grapevine genotypes domesticated under contrasting climates is the relationship between xylem anatomy and susceptibility to bacterial and fungal vascular pathogens. Grapevine xylem function is greatly affected by Petri and esca diseases caused by *Phaeomonniella chlamydospora* and *Pheoacremonium* spp. (MUGNAI *et al.* 1999) as well as Pierce's disease caused by the bacteria *Xylella fastidiosa* (PÉREZ-DONOSO *et al.* (2016). There is some evidence that the xylem structural elements that promote vulnerability to drought stress induced cavitation might also affect disease resistance (PÉREZ-DONOSO *et al.* 2016, POUZOLET *et al.* 2014, DEYETT *et al.* 2019). PÉREZ-DONOSO *et al.* (2016) reported

that embolism contributes to the loss of xylem function upon *X. fastidiosa* infection on grapevine. Interestingly, 'Thompson Seedless' has been reported to be among the most susceptible *Vitis vinifera* cultivars to both esca and Pierce's disease after experimental inoculation (FELICIANO *et al.* 2004, POUZOLET *et al.* 2017, RASHED *et al.* 2011). Thus, linkages between drought and pathogen resistance is important to consider, given that pathogens have been implicated as a mortality agent in plants that are weakened from drought (MCDOWELL *et al.* 2008, SALA *et al.* 2010).

Conclusions

Our data support that different strategies regarding water transport might have occurred across grapevine cultivars from different centers of domestication. Hence, 'Thompson Seedless' showed greater hydraulic conductivity supported by a greater abundance and interconnectivity of xylem vessels in comparison to 'Merlot'. We propose that 'Thompson Seedless' adheres to the relatively efficient side of the hydraulic safety versus efficiency trade-off, as xylem vulnerability to drought-induced xylem cavitation was consistently greater than 'Merlot'. Our results also indicate that although differences in the absolute values of Ψ_{50} depend on the vulnerability curve method, the relative differences between cultivars is maintained across different approaches. Overall, we emphasize that the center of historical domestication should be considered to better understand the strategies adopted in given crops to cope with stress. This approach could be key for breeding programs and selecting alternative cultivars under changing environments.

Acknowledgements

The authors thank the Department of Botany and Plant Sciences at the University of California, Riverside, and the USDA-ARS Salinity Laboratory, Riverside, California, U.S. for logistical support. This research was funded by the U.S. Department of Agriculture (USDA), National Institute of Food and Agriculture, Specialty Crop Research Initiative Grant #2012-51181-19954.

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Received February 26, 2019

Accepted December 2, 2019

