Differences in hydraulic traits of grapevine rootstocks are not conferred to a common *Vitis vinifera* scion

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Abstract. Cultivars of grapevine are commonly grafted onto rootstocks to improve resistance against biotic and abiotic stress, however, it is not clear whether known differences in hydraulic traits are conferred from rootstocks to a common scion. We recently found that *Vitis riparia* and *Vitis champinii* differed in drought-induced embolism susceptibility and repair, which was related to differences in root pressure generation after rewatering (Knipfer *et al.* 2015). In the present study, we tested whether these and other physiological responses to drought are conferred to a common *V. vinifera* scion (Cabernet Sauvignon) grafted on *V. riparia* and *V. champinii* rootstocks. We measured xylem embolism formation/repair using *in vivo* microCT imaging, which was accompanied with analysis of leaf gas exchange, osmotic adjustment and root pressure. Our data indicate that differences in scion physiological behaviour for both rootstock combinations were negligible, suggesting that the sensitivity of Cabernet Sauvignon scion to xylem embolism formation/repair, leaf gas exchange and osmotic adjustment is unaffected by either *V. riparia* or *V. champinii* rootstock in response to drought stress.

Additional keywords: drought, grafting, grapevines, osmotic adjustment, root pressure, rootstock–scion interactions, water relations, xylem.

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Introduction

Increasing drought resistance of cultivated species through breeding and management is a priority for adapting crop production to future climatic conditions. Several wild *Vitis* species have potential use as drought resistant rootstocks as they originate from arid regions of North America. *Vitis* spp. used for rootstock breeding could improve the root system's capacity to withstand extreme low soil moisture and promptly recover its water uptake capacity after re-watering (e.g. irrigation or a precipitation event). With decreasing soil moisture, water is held more tightly in soil micropores, and the higher driving force from the unmet shoot transpirational demand increases water tension in the soil–plant-atmosphere continuum (Blum 2011). Higher water tensions can induce root mechanical failure (e.g. lacunae formation; Cuneo *et al.* 2016), disrupt hydraulic conductivity via the formation of xylem embolism (Tyree and Sperry 1988; Steudle 2000). A decrease in the water transport capacity from roots to shoot by xylem embolism can affect leaf gas exchange, carbon (C) assimilation, and plant performance. Knipfer *et al.* (2015) showed that three distinct wild *Vitis* species differed in their ability to maintain and recover xylem transport

capacity, root pressure, and leaf transpiration rate at the onset of drought and after recovery. For instance, own-rooted *V. riparia* showed higher sensitivity to drought-induced embolism formation than *V. champinii*, but the former had higher capacity for vessel refilling and the latter exhibited negligible refilling. It is unclear if and how differences in hydraulic traits between rootstocks can be transferred to the scion of grafted plants.

Different studies on grapevine have shown mixed interactions between rootstocks and scions (Winkel and Rambal 1993; Düring 1994; Padgett-Johnson *et al.* 2000; Alsina *et al.* 2006; Koundouras *et al.* 2008). Soil water deficits result in the regulation of the transpirational flux via stomata control, but grapevines differ in the stomatal response to several environmental stimuli (e.g. solar radiation, vapour pressure deficit), which affect rates of water loss (Winkel and Rambal 1993; Chaves *et al.* 2003). Root-to-shoot communication through changes in xylem tension, signalling molecules (e.g. ABA) and sap osmotic potential regulate the scion response to drought (Shabala *et al.* 2016). Poor stomatal regulation can lead to faster embolism formation and decrease in cell turgor,

affecting metabolic processes and ultimately the leaf C assimilation capacity. One way that plants compensate for the decrease in water status is by the active accumulation of solutes, i.e. osmotic adjustment (OA), resulting in higher leaf relative water content and turgor than plants at the same water potential with no OA (Düring and Dry 1995; Patakas *et al.* 2002; Blum 2011). Osmotic adjustment has the capacity to stabilise plant performance (e.g. yield) under stress (Blum 2011), and the interplay of grapevine rootstocks with a common scion may affect the OA response with decreasing water potentials.

The aim of this study was to test if the observed difference in physiological behaviour among own-rooted *Vitis champinii* Planch. (1882) and *Vitis riparia* Michx., as reported by Knipfer *et al.* (2015), are transferred into a grafted common scion (here *Vitis vinifera* L. cv. Cabernet Sauvignon) following rootstock-scion grafting. Xylem embolism formation and repair was evaluated *in vivo* in stem xylem of the *V. vinifera* scion using microCT imaging, and root pressure responses following re-watering (i.e. potential traits contributing to embolism repair) were evaluated after the scion was excised above the graft union using pressure sensors. In addition, responses in leaf gas exchange and leaf osmotic adjustment of the scion were investigated in response to a controlled rootstock dry down. Contrary to common belief, only minor differences in common scion physiological behaviour were detected when Cabernet Sauvignon was grafted to a *V. champinii* or *V. riparia* rootstock. The possible implications of these findings are discussed.

Materials and methods

Plant material and experimental setup

A common *Vitis vinifera* L. cv. Cabernet Sauvignon scion was grafted onto rootstocks Ramsey (*Vitis champinii* Planch. (1882); Ram\CS) and Riparia Gloire (*Vitis riparia* Michx.; Rip\CS). Plant material was obtained from mother plants kept at UC Davis fields and propagated with standard methods (Fort *et al.* 2013). Bench-grafted hardwood cuttings were callused and rooted in a slightly moist mixture of peat, perlite and vermiculite (one part each) for 2 weeks at 27°C. After initial root growth, material was transferred to a growing substrate composed of 40% washed sand, 20% sphagnum peat moss, 20% redwood compost, and 20% pumice rock, and placed in a shaded mist bed with 27°C bottom heat. After 6 weeks, plants were actively growing roots and a shoot, and were transplanted into 0.7 L pots for *in vivo* imaging of stem xylem tissue using microCT (see below); a subset of plants was transplanted into bigger 4.0-L pots and used for a controlled dry down experiment (details below). After at least 4 weeks of plant establishment, all plants were pruned to a similar size and the new shoot trained on a bamboo stick with all lateral shoot growth restrained. All experiments used plants with uniform growth that were ~1.1-m tall. Watering was done twice a day with a 10% Hoagland solution to maintain plants under well-watered conditions before the dry down experiments (see below). All plant material was grown in greenhouse facilities at the University of California, Davis with the following conditions: day/night temperature between 28/20°C, RH between 40 and 80%, and average photosynthetically active radiation of ~1100 μmol m^{-2} s^{-1} at solar noon. The daylength was on average 14/10 h for day/night respectively.

Stem water potential (Ψ_{stem})

For measurement of Ψ_{stem}, a mature leaf from the base of the plant was bagged with a Mylar-wrapped plastic bag for at least 15 min, excised and Ψ_{stem} was determined with a Scholander-style pressure chamber (#3005; Soil Moisture Equipment Corp.) (Knipfer *et al.* 2015).

X-ray computed microtomography (microCT)

Plants grown in 0.7-L pots were subjected to three water treatments in the greenhouse: (1) 'well-watered' with Ψ_{stem} > −0.3 MPa; (2) 'drought-stressed' with Ψ_{stem} < −1.2 MPa; and (3) 're-watered' with Ψ_{stem} < −1.2 MPa during water stress and Ψ_{stem} > −0.3 MPa after rewatering. Plants were water stressed in the greenhouse by not watering for 3–5 days to reach the targeted water potential; the re-watering period was up to 5 days. Plants were scanned at the microCT facility (Beamline 8.3.2) at the Lawrence Berkeley National Laboratory Advanced Light Source (ALS) (for details see Brodersen *et al.* (2013), McElrone *et al.* (2013), Knipfer *et al.* (2015)). The day of scanning, plants were transported from the greenhouse to the ALS ~3 h before the start of analysis. Each plant was subjected to a single scan (i.e. avoid possible effects of X-ray exposure on embolism repair) within 24 h after being at the ALS, with one replicate of each treatment by species combination scanned within a 2–3 h time frame. The Ψ_{stem} was measured <15 min before each scan. For visualisation of plant tissue, the pot of an intact plant was placed in an aluminium cage and fixed on an air-bearing stage. A section of 1–5 mm of the Cabernet Sauvignon stem just above the grafting junction with the rootstock was scanned in the 15 to 19 keV synchrotron X-ray beam, while the plant was rotating continuously yielding 1025 two dimensional images with a 4.5 μm pixel resolution captured on a 4008 × 2672 pixel CCD camera (#PCO and PCO.edge, PCO AG). The acquired two-dimensional projection images were reconstructed into a stack of transverse images with a custom software plugin for Fiji imaging-processing software (www.fiji.sc, ImageJ; accessed 10 September 2018) that used Octopus 8.3 software (Institute for Nuclear Sciences, Ghent University, Belgium) in the background. The number of embolised vessels and vessel diameter were determined from representative transverse images taken out of the three-dimensional (3D) image stack using a semi-automated routine within Fiji (for details see Brodersen *et al.* (2013)). The total number of embolised and water-filled vessels was counted on the same transverse image manually using the 'point selection' tool in Fiji software.

Root pressure

A subset of plants grown in 0.7-L pots (similar to plants for microCT scan) was used to assess the ability of a water-stressed plant to generate root pressure following re-watering, and evaluate the apparent link of this process to embolism repair. Prior to conducting the root pressure measurements, plants were subjected to different watering treatments to induce water stress similar to that described above. These plants were taken to the laboratory in the morning, and a leaf was bagged with a Mylar-wrapped plastic bag for measuring Ψ_{stem} before excising the shoot for root pressure measurements. The stem was excised under water with a sharp pruning shears 2 cm

above the grafting junction. A 1-cm segment of the remaining stem was inserted into a semi-rigid 2-cm PVC tubing and secured with a zip-tie. A pressure transducer (PX26–005GV, Omega Engineering Inc.) and the connection to the stem were filled with 20 mM KCl and extra care was taken to remove any air bubbles. The pressure transducer and the stem connection were coupled through a polypropylene male–female luer fitting (Value Plastics). Plastic repair epoxy was used to seal all joints of the connection (Part #: 17394, Ace Hardware Corp.). Several pressure transducers were connected to a datalogger (model CR7, Campbell Scientific) for continuous data collection every 2 min for up to 48 h. The substrate was fully hydrated after the shoot was severed, and monitoring of the system for leaks was done continuously for the first 5 h (for details see Barrios-Masias *et al.* (2015), Knipfer *et al.* (2015)). A steady-state root pressure (P_{rs}) was reached between 16 and 20 h.

Leaf gas exchange and osmotic adjustment: controlled dry-down experiment

The purpose of this experiment was to control the reduction in Ψ_{stem} over time. Plants grown in 4-L pots, that had not seen drought stress before the beginning of the study, were subjected to an 8-day dry down. On day 1 (= well-watered plants), plants were watered, allowed to drain and the initial weight recorded as the 100% water holding capacity of the pot. Subsequently, the substrate moisture content was gradually lowered over the 8-day (= drought-stressed) period by adjustment of the water volume applied to the pot (the target moisture for each day was: 1: 100%, 2: 80%, 3: 60%, 4:60%, 5: 40%, 6: 20%, 7: 10% and 8: 0%). Moisture content (i.e. pot weight) was adjusted twice daily to the target moisture following weighing of pots before watering. During the dry down period (except day 4), leaf gas exchange, Ψ_{stem} and leaf osmotic potential (Ψ_{π}) were measured. Leaf gas exchange was measured on a mature, fully expanded leaf from the top of the plant with a field portable open flow infrared gas analyser (IRGA) (Model 6400, LI-COR Biosciences). Measurements were taken between 1030 and 1230 hours with a 6-cm^2 chamber, with the CO_2 reference set at 400 mmol m^{-2} s^{-1}, and with saturating light using a LED source (PAR in: 1500 mmol m^{-2} s^{-1}). Intrinsic water use efficiency (WUE$_i$) was calculated from the ratio of photosynthetic rate (P_n) and stomatal conductance (g_s). For Ψ_{π}, a mature leaf from the centre of the plant was used to core leaf-lamina disks of 1.1 cm^2. Two areas of the lamina were separately sampled: at the centre around the main vein and close to the lamina and petiole junction (four disks total per leaf), and at the edge of the leaf (i.e. most distant from the centre; six disks total per leaf). Leaf disks were placed in a 2.0-mL Eppendorf tube fitted with an in-house sieve made to retain disks above the bottom of tube for later sap extraction. Disks were kept on dry ice until transferred to a −20°C freezer. Within a week, leaf disks were thawed and centrifuged at 7500 rpm for 10 min, and osmotic potential determined from sap collected at the bottom of the tube. The osmotic pressure of the sap was measured using the VAPRO 5600 osmometer (Wescor Inc.). The osmotic potential was expressed in MPa, where 40.75 mOsmol kg^{-1} corresponds to 0.1 MPa.

Statistical analysis

Data analyses were conducted using the MIXED procedure of SAS, ver. 9.3 (SAS Institute). The X-ray microCT scan data was analysed as complete randomised design with 'rootstock' and 'watering treatment' as main factors. The X-ray microCT scan data had the following number of plants for each treatment: Rip\CS: well-watered $n = 9$, drought $n = 8$, rewatered $n = 5$; and Ram\CS: well-watered $n = 4$, drought $n = 4$, rewatered $n = 4$. The dry-down scion data analysis included a total of 8 plants measured during 7 out of the 8 total days of the dry-down. The dry-down experiment was analysed as a randomised complete block design with 'rootstock' and 'dry-down day' as main factors. 'Dry-down day' was specified as a classification variable with repeated structure. The Shapiro–Wilk W was used to test the data for normal distribution, and data were transformed as necessary. Tukey-Kramer HSD test was used to determine significant differences among treatments. For the root pressure data, 15 Rip\CS and 14 Ram\CS plants were used for a polynomial regression between the P_{rs} and the Ψ_{stem} performed with SigmaPlot (ver. 11.0, Systat Software Inc.). Smooth curves for gas-exchange data were fit using 'Proc transreg' in SAS.

Results

The number of embolised vessels in Cabernet Sauvignon grafted on *V. champinii* and *V. riparia* was similar within each of the moisture treatments (Figs 1, 2). The well-watered and the re-watered treatments had a similar mean number of embolised vessels (15 and 17) and Ψ_{stem} (–0.01 and –0.02 MPa), respectively (Fig. 2*a, b*). The number of embolised vessels more than doubled in the drought-stressed treatment, and the Ψ_{stem} was on average 10 times lower (–1.7 MPa) than the other two treatments. In the well-watered treatment, the stems of Cabernet Sauvignon embolised mostly towards the centre in the oldest xylem adjacent to the pith, regardless of rootstock (Fig. 1, left column). Recovery of the re-watered plants to similar levels of embolism showed similar capacity to repair embolism in both rootstock scion combinations (Fig. 1).

The P_{rs} measured at the base of the Cabernet Sauvignon stem (i.e. above the grafting junction) showed a similar response in both rootstocks to the changes in Ψ_{stem} (Fig. 3). The dry-down treatment resulted in a wide range of Ψ_{stem} in both rootstocks: –0.10 to –2.22 MPa. The P_{rs} was the highest when Ψ_{stem} was around –0.97 MPa and the lowest when drought stress was severe ($\Psi_{stem} < -1.75$ MPa). Under well-watered conditions P_{rs} was intermediate (0.20 MPa).

Leaf gas exchange of Cabernet Sauvignon grafted on *V. riparia* and *V. champinii* responded similarly as Ψ_{stem} decreased during the dry down (Fig. 4 and Fig. S1, available as Supplementary Material to this paper). The Ψ_{stem} were similar within each day of the dry down and with decreasing soil moisture (Fig. S1). When Ψ_{stem} was above –0.6 MPa leaf gas exchange was maintained and plants did not show signs of drought stress; at this Ψ_{stem} the average g_s and P_n were 400 mmol m^{-2} s^{-1} and 17.3 μmol m^{-2} s^{-1}, respectively. Leaf gas exchange showed a sharp decrease only after the Ψ_{stem} was below –0.6 MPa (Fig. 4 *a–c*), which only occurred after day 6 even though soil moisture decreased gradually
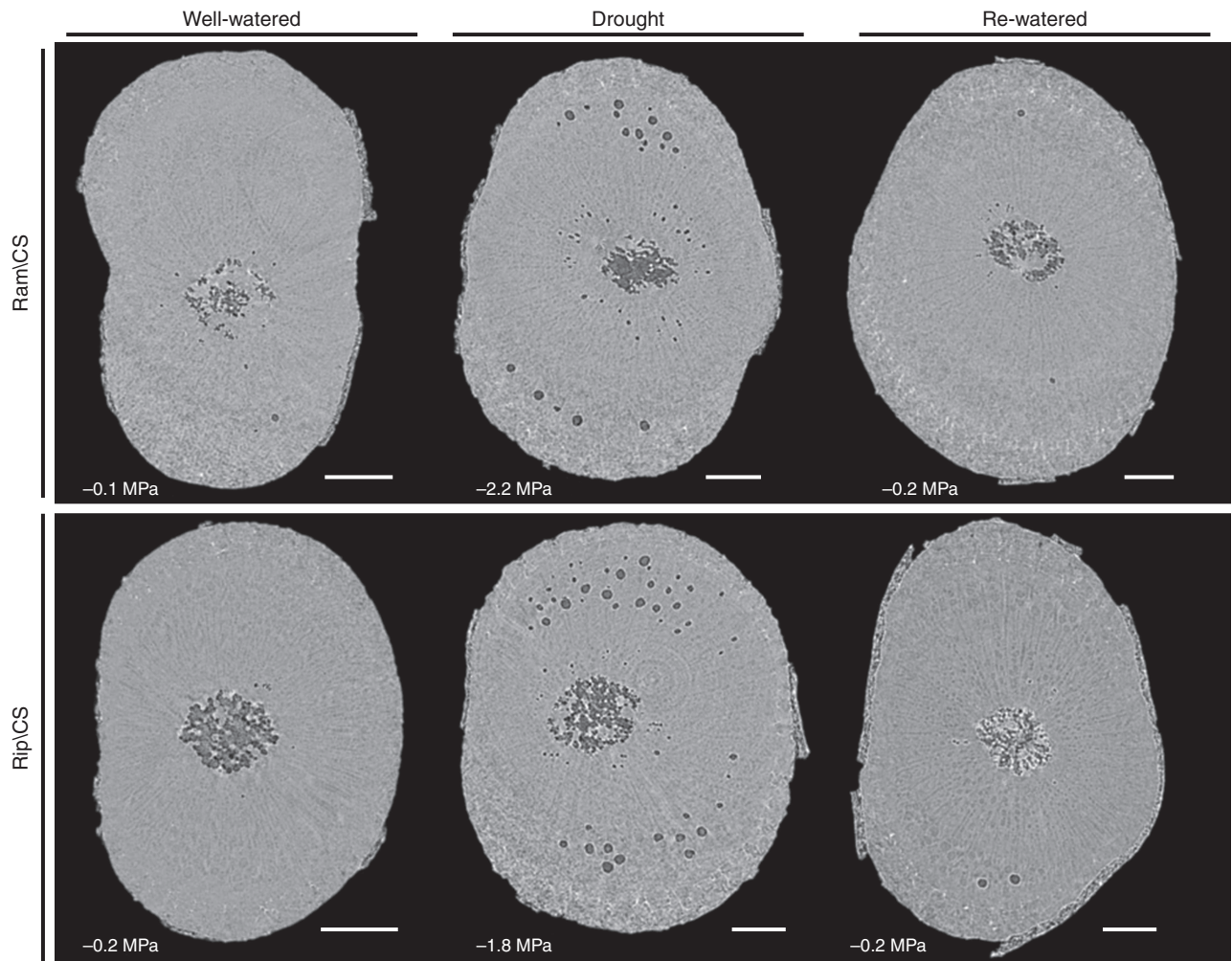
Fig. 1. Representative transverse microCT images through grapevine stems of Cabernet Sauvignon grafted on *Vitis champinii* (Ram\CS) and *Vitis riparia* (Rip\CS) showing embolism in well-watered, drought-stressed, and re-watered plants. Values in MPa is stem water potential. Embolised vessels appear dark grey and water-filled vessels as light grey. The pith is visible in the centre of each cross-section. Scale bar = 1 mm.

from 97 to 31% during the same period (Fig. S1). Over time, the Ψ_{stem} was slightly lower in Rip\CS than in Ram\CS when compared over the 8-day dry down period ($P < 0.02$). As Ψ_{stem} decreased, the g_s showed a sharp decline in all plants, whereas P_n was better maintained even when g_s decreased by 75% to around 100 mmol m^{-2} s^{-1} (Figs 4c, S2). At the end of the dry down, g_s and P_n were very low in all plants, showing severe signs of drought stress.

The Ψ_{π} of Cabernet Sauvignon was similar between the rootstocks although the Ψ_{π} of Rip\CS decreased >15% on days 7 and 8 (Ψ_{π}: –1.4 MPa) compared with days 1 and 2 (Ψ_{π}: –1.2 MPa) (Fig. 5). The Ψ_{π} of Ram\CS was similar over the course of the dry down (average Ψ_{π}: –1.2 MPa). For both rootstock\scion combinations, the Ψ_{π} was 12% higher in the outer than the inner part of the leaf lamina, but sampling location did not affect the patterns observed in Ψ_{π} of either rootstock\scion combination (data not shown).

Total leaf biomass of Cabernet Sauvignon tended to be 30% higher when grafted on *V. champinii*, but was not significantly different (Ram\CS: 50 g plant^{-1} and Rip\CS: 38 g plant^{-1};

$P < 0.10$). Leaf area was proportional to leaf biomass and specific leaf areas (SLA) was similar regardless of the rootstock (data not shown). Stem biomass was not different (Ram\CS: 75 g plant^{-1} and Rip\CS: 63 g plant^{-1}), and the leaf : stem ratios were similar (Ram\CS: 0.65 and Rip\CS: 0.61).

Discussion

Despite the documented differential responses of *V. champinii* and *V. riparia* to drought stress (e.g. Knipfer *et al.* 2015), these responses were not conferred to a common Cabernet Sauvignon scion grafted onto these rootstocks. The number of embolised vessels and P_r, both measured above the rootstock-scion graft union, and leaf gas exchange were affected by changes in Ψ_{stem} before, during, and after the dry down, but there were no significant differences in these parameters between the two rootstocks. The only difference observed was a slight increase in OA of *V. riparia* grafted plants under severe drought stress conditions. For both rootstock scion combinations, the increase in xylem tension resulted in a higher number of embolised
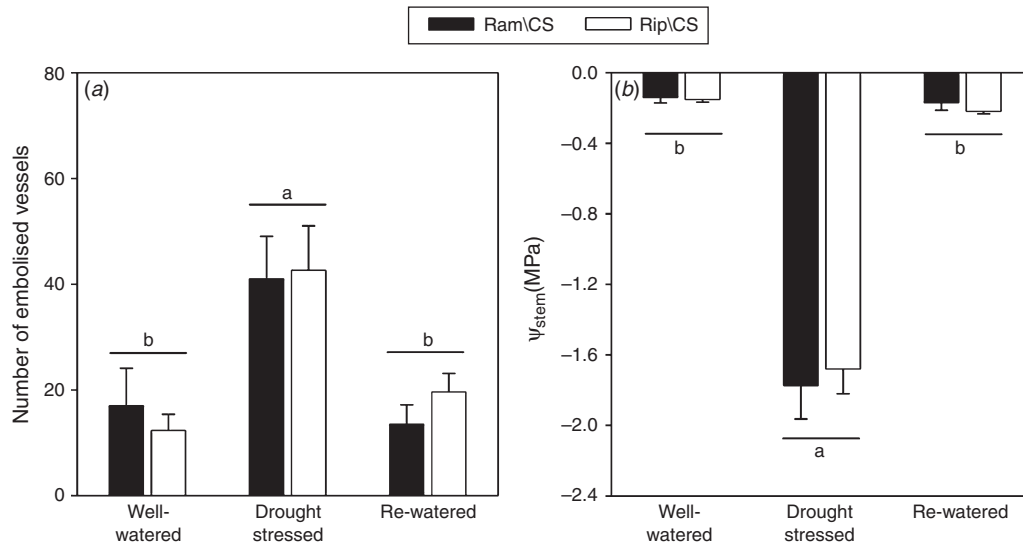
Fig. 2. Number of embolised vessels in stem xylem (*a*) and stem water potential (Ψ_{stem}; *b*) of Cabernet Sauvignon grafted on *Vitis champinii* (Ram\CS) and *Vitis riparia* (Rip\CS) rootstocks under well-watered, drought stressed and re-watered conditions. Total number of vessels was 1130 ± 83 for Ram\CS and 987 ± 229 for Rip\CS. Each bar represents the mean $\pm$ s.e. (Ram\CS $n = 3–4$, Rip\CS $n = 5–9$). Statistically significant differences ($P < 0.05$) among watering treatments are indicated by different letters. Rootstock\scion combinations were similar within each treatment.
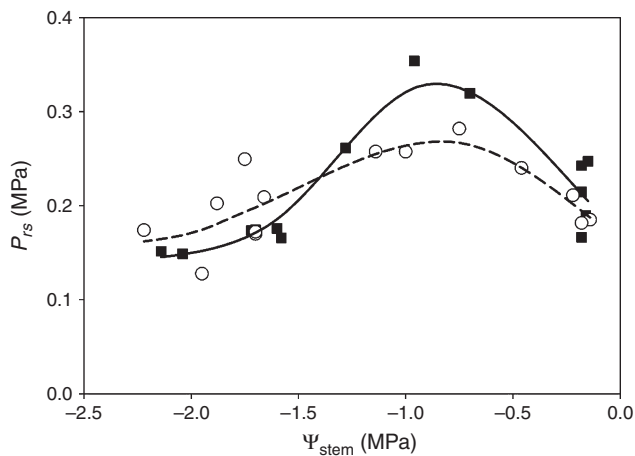

Fig. 3. Relationship of steady-state root pressure (P_{rs}) and stem water potential (Ψ_{stem}) as measured before re-watering for Cabernet Sauvignon grafted on rootstocks *Vitis champinii* (black squares and solid line) and *Vitis riparia* (white circles and dashed line). Each symbol represents an individual plant. Linear regression lines were not significant.

vessels and the regulation of stomatal conductance as soil and plant Ψ decreased. Root pressure showed a unique pattern of response to Ψ_{stem}, which did not resemble responses of the own-rooted rootstocks (Knipfer *et al*. 2015), and emphasises the importance that the interaction of rootstock and scion may play in viticulture.

Drought-induced embolism susceptibility in stems of Cabernet Sauvignon determined *in vivo* using microCT imaging was similar regardless of the rootstock, and suggests that grafting did not change the xylem structure or the function of this tissue in the scion. Similarly, Charrier *et al*. (2018) reported that Grenache and Syrah grafted onto three rootstocks

did not differ in stem susceptibility to embolism as determined on excised stem material using the *in situ* flow centrifuge technique and the bench dehydration method. Xylem vessel anatomy and connectivity plays an important role in the formation and propagation of embolism and affects stem hydraulic conductivity (e.g. Brodersen *et al*. 2013). In grafted grapevines, the hydraulic resistance to water flow in two rootstocks differed up to the grafting point, but the common scion showed similar trunk hydraulic conductivity (Alsina *et al*. 2006), suggesting no induced changes in xylem structure aboveground. Similar observations were reported for peach (Basile *et al*. 2003) and kiwifruit (Clearwater *et al*. 2004), but not for apple (Bauerle *et al*. 2011). Changes in xylem structure may eventually result from long-term interactions of the rootstocks and scions in mature vines (e.g. due to differential rooting depth and water accessibility), but it was not apparent in the current study system using young vines. In the present study, embolised vessels were determined on new shoots, but it may be important to consider that cane susceptibility may change as they mature due to ontogenic processes (e.g. stem lignification and xylem diameter) that reduce the possibility for air seeding (Lens *et al*. 2011; Charrier *et al*. 2018).

Embolism repair in stems after re-watering was also unaffected by the rootstock, which supports recent findings that embolism repair is a locally driven mechanism that does not rely on long-distance signalling or P_r generated in the root systems (Knipfer *et al*. 2016). Yet, P_r is considered to integrate root traits associated with drought resistance (e.g. development of suberised barriers and hydraulic conductivity) that could decrease the capacity of roots to rehydrate after re-watering (Barrios-Masias *et al*. 2015). In this study, P_r of grafted Cabernet Sauvignon responded differently to decreasing Ψ_{stem} and it was higher than that reported for own-rooted grapevine
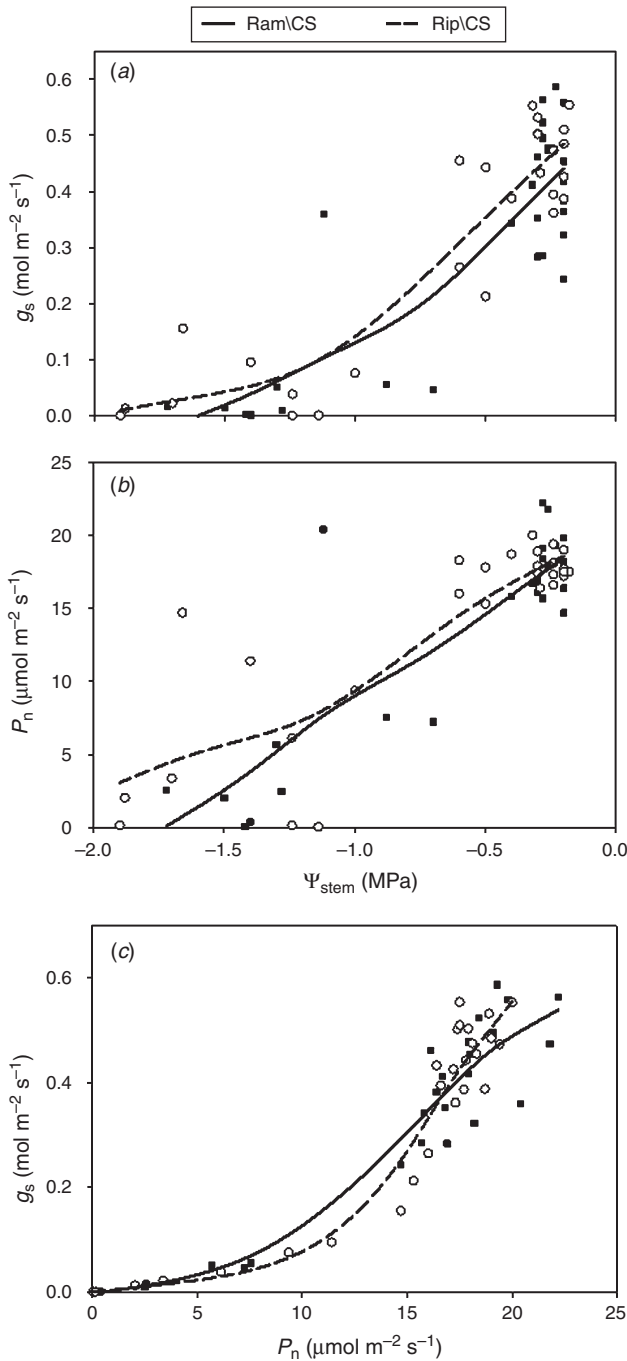
Fig. 4. Relationship between (*a*) stomatal conductance (g_s) and (*b*) photosynthetic rate (P_n) with stem water potential (Ψ_{stem}), and (*c*) g_s with P_n of Cabernet Sauvignon grafted on *Vitis champinii* (Ram\CS; black squares) and *Vitis riparia* (Rip\CS; white circles) during an eight-day dry down period. Symbols represent repeated gas-exchange spot measurements for seven days during the dry down ($n = 4$; 56 total data points).

Fig. 5. Leaf osmotic potential (Ψ_π) of Cabernet Sauvignon grafted on *Vitis champinii* (Ram\CS; black squares) and *Vitis riparia* (Rip\CS; white circles) during an 8-day dry down period. Within each rootstock\scion combination, statistically significant differences ($P < 0.05$) between days are shown with different letters (Ram\CS = a; Rip\CS = x to y).

slow recovery after drought due to reduced root hydraulic conductivity (Steudle 2000; Barrios-Masias *et al.* 2015) and lower stomatal conductance (Knipfer *et al.* 2015). In this study, P_r decreased with Ψ_{stem} of < –1.3 MPa, and it can be speculated that this is due to an increase in root leakiness likely due to structural damage in the roots and/or higher root turnover rates.

The leaf gas exchange of Cabernet Sauvignon was similar regardless of rootstock although the own-rooted rootstocks differed in g_s (Fig. S2; Knipfer *et al.* 2015). The differences in leaf gas exchange between the grafted Cabernet Sauvignon and the own-rooted rootstocks suggest that leaf gas exchange was determined by the scion and that the root hydraulic conductance of either rootstock was not limiting. Other studies have shown that rootstocks affect g_s (Padgett-Johnson *et al.* 2000) but not P_n (Koundouras *et al.* 2008), which may be related to rooting depth and increased access to water in field studies. In this study, as the Ψ_{stem} dropped to below –0.6 MPa, the g_s and P_n showed a slight decrease (25 and 10% respectively) as an early indicator of reduced soil water availability. The regulation of g_s may have prevented earlier embolism formation and maintained the plant water status. Although P_n can be maintained even at low Ψ_{stem} (Kriedemann and Smart 1971), shoot growth is affected and higher amounts of C assimilates accumulate in the leaves and potentially change the leaf osmotic potential. In this study, osmoregulation was observed in Cabernet Sauvignon grafted on *V. riparia*, but with no clear effect on embolism formation and repair or leaf gas exchange. Yet, this suggests that the signalling between rootstock and scion may have differed slightly during the dry down although no other evaluated variables were affected. We believe that an early root-to-shoot interplay in water relations, as new shoots and roots develop, result in plant acclimation to cycles of water availability between irrigations. For instance, changes in root hydraulic conductivity (Barrios-Masias *et al.* 2015), xylem vessel structure (Bauerle *et al.* 2011), and stomatal density (Murchie *et al.* 2009; Barrios-Masias *et al.*

rootstocks (Knipfer *et al.* 2015), suggesting that roots were responding to transient water stress with earlier suberisation in this study; earlier root suberisation is a strategy to reduce the risk of water leaking out to drying soils (Molz and Peterson 1976). The detrimental effects of this response may include
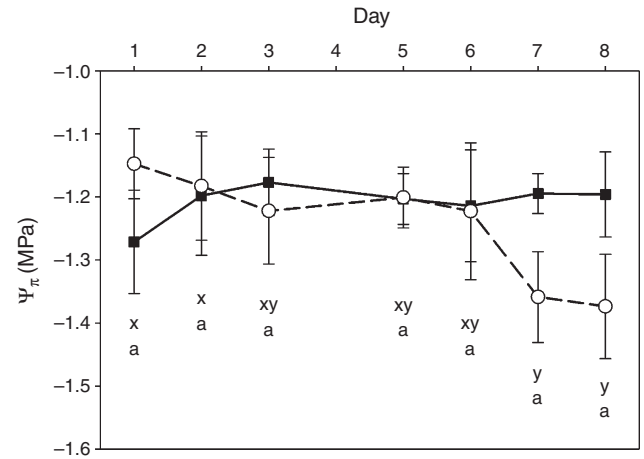
2014) may prevent or reduce extreme xylem tensions and embolism formation. This fine balance between the high Ψ gradients at the leaf-atmosphere interface and high resistance to radial water movement in the roots can define the root–leaf conductive system.

Lower precipitation and precise irrigation technologies will limit the water stored in the soil, and the root physiological capacity to maintain water uptake could become more important than rooting depth alone. High vigour grapevines with larger canopies could rely on a root system able to take up water either by a larger root surface area or higher root hydraulic conductance to maintain the plant water status (Gambetta *et al.* 2012). Yet, plant acclimation to drought may only require a consistent water deficit to obtain a synchronised response from the roots and shoot (Marguerit *et al.* 2012; Barrios-Masias *et al.* 2015). Our results suggest that the sensitivity of Cabernet Sauvignon to embolism formation and repair, and water relations were unaffected by two disparate rootstocks, but the rootstock physiological performance may have been altered by the scion.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgements

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