



VITICULTURE ORIGINAL RESEARCH ARTICLES

Differential wind impact on Malbec and Cabernet-Sauvignon xylem structure

Rodrigo Alonso^{1,*}, Federico Roig-Puscama², Fidel A. Roig³, Mario Tomazello-Filho⁴, Patricia Piccoli¹, Federico J. Berli^{1,†}

¹ Grupo de Bioquímica Vegetal, Instituto de Biología Agrícola de Mendoza (IBAM), CONICET- Facultad de Ciencias Agrarias, UNCuyo, Almirante Brown 500, Chacras de Coria, Mendoza, Argentina

² Biogéosciences, UMR 6282 CNRS, Université Bourgogne Franche-Comté, Dijon, France

³ Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), CONICET- UNCuyo

⁴ Escola Superior de Agricultura Luiz de Queiroz, Universidad de São Paulo (USP), Av. Pádua Dias 11, Piracicaba, SP CEP 13418-900, Brazil

[†] Deceased; dedicated to his memory

Article number: 9448



*correspondence:
ralonso@fca.uncu.edu.ar

Associate editor:
Stefanos Koundouras



Received:
3 June 2025

Accepted:
29 July 2025

Published:
10 October 2025



This article is published under
the **Creative Commons**
licence (CC BY 4.0).

Use of all or part of the content
of this article must mention
the authors, the year of
publication, the title,
the name of the journal,
the volume, the pages
and the DOI in compliance with
the information given above.

ABSTRACT

Argentine Patagonia, recognised as the southernmost wine-producing region in the world, frequently experiences moderate to strong winds. Wind is a key environmental factor that affects plant growth, development, and fruit yield. This study investigates how two contrasting wind conditions (exposed and sheltered) influence the xylem structure of *Vitis vinifera* L. cultivars Malbec (Mb) and Cabernet-Sauvignon (CS) throughout the lifespan of the vines (2011–2021). We hypothesised that wind exposure modulates xylem structure and hydraulic performance differently depending on the cultivar, based on differences in phenotypic plasticity. During the 2021 dormant season, wood cores were extracted from the main trunk of vines growing under wind exposure and sheltered sectors of the vineyard plot. The differential wind conditions were given by a poplar windbreak. The analysis focused on the response to wind intensity through different anatomical variables, including basal area increment (BAI), cumulative BAI, vessel lumen fraction (F), and vessel area relative to ring area. Climatic data were integrated to explore correlations with xylem modifications. Results showed that CS vines under wind sheltered conditions had significantly greater mean vessel area, indicating enhanced growth and potential hydraulic efficiency, whereas CS vines under wind exposure exhibited vessels with smaller diameter and higher vessel density, maintaining F values while reducing wood productivity. This pattern suggests a structural trade-off between anatomical traits such as vessel size and vessel density, which are typically associated with hydraulic efficiency and resistance to cavitation, rather than a direct assessment of hydraulic safety margin. Results also showed that Mb vines had no significant differences in radial growth but increased vessel size and F under wind conditions, reflecting a more stable and plastic hydraulic strategy. The correlations with seasonal climatic variables revealed a spatial dichotomy: while wind exposure directly shaped anatomy in wind-exposed vines (reducing vessel size, increasing density), temperature was the dominant driver influencing xylem traits in sheltered conditions. These findings provide new evidence of cultivar-specific xylem responses to wind and highlight the importance of considering the phenotypic plasticity in vineyard management. Tailored strategies may enhance vine performance and resilience in windy environments.

KEYWORDS: environmental factors, mechanically-induced stress, phenotypic plasticity, xylem anatomy, grapevine adaptation

INTRODUCTION

The study of woody plants' growth rings provides valuable information about environmental conditions and plant physiology over time. Dendrochronology and wood anatomy analysis offer a historical record of xylem development and its relationship with climatic variables (Schweingruber, 1996; Andregg & Meinzer, 2015). In woody species, several structural traits such as vessel dimensions or tracheid wall thickness have been shown to influence drought resilience (Camarero *et al.*, 2024). In contrast, in grapevines, these techniques have proven useful for understanding differential cultivars' phenotypic plasticity when the vines were grown in contrasting soil depth vineyard plots (Roig-Puscama *et al.*, 2021). Xylem anatomical traits, such as vessel diameter and density, are directly linked to water transport efficiency and resistance to cavitation under stress conditions (Hacke *et al.*, 2017; Islam *et al.*, 2019). Soil water availability influences xylem structure across different grapevine cultivars (Munitz *et al.*, 2018; Roig-Puscama *et al.*, 2021). Variations in vessel diameter can significantly affect sap flow and the plant's ability to maintain hydration in its photosynthetic and reproductive tissues (Chavarria & Dos Santos, 2012).

Basal Area Increment (BAI) is widely used to quantify wood production (Rubino & McCarthy, 2000). BAI typically follows a sigmoidal growth pattern, rising rapidly from youth to middle age, stabilising for a prolonged period, and declining as the plant ages (Johnson & Abrams, 2009), providing an integrated measure of tree growth (Biondi & Qeadan, 2008) and other plants like grapevines (Roig-Puscama *et al.*, 2021). Xylem structure largely determines water conduction capacity in woody plants, influencing physiological performance by regulating both the efficiency and safety of water transport under environmental stressors such as drought or freezing (Hacke *et al.*, 2001; Gleason *et al.*, 2016; Loeffe *et al.*, 2007). In this context, water transport safety refers to the xylem's ability to resist the formation and spread of embolisms under stress conditions (Hajek *et al.*, 2014; Gleason *et al.*, 2016). Two key traits are commonly used to evaluate this capacity: i) vessel area–cross-sectional lumen area of individual vessels–, and ii) vessel density–the number of vessels per unit area–(Preston *et al.*, 2006; Roig-Puscama *et al.*, 2021). Among anatomical indices, the vessel lumen fraction (F), which represents the proportion of the wood's cross-sectional area occupied by conducting vessels, is a clear indicator of the efficiency of water transport. Higher F values indicate greater water transport efficiency, although they may be linked to weaker hydraulic safety, since as the proportion of large vessels increases, plants will be more vulnerable to cavitation or embolism under thermal or water stress (Preston *et al.*, 2006; Zanne *et al.*, 2010).

Wind is a key environmental factor in many viticultural regions worldwide (e.g., Hawke's Bay in New Zealand, the Swan Valley in Australia, the Rhône Valley in France, the Western Cape in South Africa or the Salinas Valley in California), although its impact on wood anatomy has received less attention. Wind can cause mechanical damage and induce

different forms of stress, both mechanical and physiological, and act as both an acclimation factor and an environmental signal (Gardiner *et al.*, 2016). Wind increases transpirational demand and affects both xylem structure and hydraulic efficiency (Brodersen *et al.*, 2013; Hacke *et al.*, 2001). Wind acts at multiple organisational levels within the plant. At the foliar level, increased turbulence reduces the boundary layer around the leaves, thereby enhancing water vapour loss and increasing evaporative demand (Gardiner *et al.*, 2016). At the vascular level, the mechanical strain induced by wind has been shown to trigger anatomical responses such as increased vessel wall reinforcement or changes in vessel arrangement, contributing to tigmomorphogenetic responses aimed at improving structural stability (Gardiner *et al.*, 2016; Telewski, 2016). Such responses may influence the balance between hydraulic efficiency and safety, particularly in species or cultivars exposed to chronic wind stress.

Argentina is one of the world's leading wine-producing countries, ranking among the top ten globally (OIV, 2024). Malbec (Mb) is Argentina's emblematic cultivar and the most widely cultivated in the country, while Cabernet-Sauvignon (CS) ranks fourth in Argentina. These two cultivars exhibit distinct phenotypic plasticity: Mb tends to be more plastic, whereas CS maintains more stable phenotypes across diverse environments (Dal Santo *et al.*, 2018). Climate change is expected to push Argentine viticulture towards higher latitudes and altitudes in search of cooler thermal conditions, including regions such as Patagonia, where wind is a prominent environmental feature (Cabr   *et al.*, 2020). Our previous studies in this region revealed that wind exposure and deficit irrigation reduced vegetative growth while enhancing biomass partition to fruit yield and also increasing berry skin phenolic, key compounds for wine quality (Alonso *et al.*, 2024). In this context, analysing grapevine xylem anatomical responses to persistent and intense wind exposure is essential to understand adaptation mechanisms and develop vineyard management strategies for wind-prone regions. This study investigates how two contrasting wind conditions (exposed and sheltered) influence the xylem structure of *Vitis vinifera* L. cultivars Mb and CS throughout the lifespan of the vines.

MATERIALS AND METHODS

1. Plant material and experimental design

The study was conducted between 2021 and 2023, in an experimental vineyard in the windy region of Casa de Piedra (38° 09' 10"S, 67° 09' 20" W; 405 m above sea level), located in the south of La Pampa Province, Argentina, at the northern edge of Patagonia (Figure 1A). The region is characterised by a temperate, continental, arid climate, with average maximum temperatures of 22.2 °C, minimum averages of 6 °C, and an annual mean of 15 °C, based on data from the past fifty years. Annual precipitation averages around 200 mm, and effective heliophany during the vegetative cycle reaches 2014 hours (Villarreal *et al.*, 2007).

Since south-westerly winds are the most frequent and intense in this area (Alonso *et al.*, 2024), a 13-meter-high poplar windbreak was installed along the side of the vineyard plot perpendicular to the dominant wind direction. Two vineyard plots were established for the experiment: one planted with a selected clone of *Vitis vinifera* L. cv. Malbec (Mb) and the other with *Vitis vinifera* L. cv. Cabernet-Sauvignon (CS). Both cultivars, own-rooted and trained in a vertical trellis system of 1.8 m high, were planted in 2011 in north-south-oriented rows, at a distance of 2.20 m between rows and 1 m between vines. Following Alonso *et al.* (2024), vines located 15 to 21 m downwind from the windbreak were categorised as sheltered, while those positioned 37 to 43 m east of the sheltered zone were classified as exposed (Figure 1B). Three rows were selected within each treatment zone (sheltered/exposed) to represent spatial variability. In every row, two panels, each composed of seven consecutive vines between trellis posts, were identified. Each experimental unit comprised two plants selected based on homogeneity within each panel. Sampling was carried out using a structured approach, with locations distributed to ensure spatial coverage and replicate independence.

General vineyard management included drip irrigation applied twice per week during the vegetative cycle, with an estimated total annual water input of approximately 800 mm. Fertilisation was based on conventional nutrient doses equivalent to 26 kg/ha of nitrogen (N), 36 kg/ha of phosphorus (P), 13 kg/ha of

potassium (K), and 5 kg/ha of magnesium (Mg), complemented occasionally by applications of composted guano. Winter pruning was carried out following a bilateral cordon system. No bunch thinning was performed during the growing season.

2. Wood sampling and anatomical analysis

During the dormant season (July 2021), wood cores were extracted from one representative plant per experimental unit ($n = 6$), avoiding young or diseased replants. Samples were collected at 0.4 m above ground level, perpendicular to the trunk, using a 6-inch Pressler increment borer with a 5.15 mm diameter (Haglöf, Sweden). Each core included the pith and two opposing radii, which were analysed separately as technical replicates to characterise intra-core variability and improve measurement accuracy. The wood samples were preserved in a 50 % ethanol:water solution (v/v).

For anatomical analysis, transverse sections of approximately 15 μm thickness were obtained using a sliding microtome (Leica SM 2000 R, Leica Biosystems, Nussloch, Germany). These sections were bleached in 1 % NaClO, rinsed in distilled water, and then dehydrated through a graded ethanol series (from 40 % to 100 %). Subsequently, the samples were stained with safranin, mounted on microscope slides using Canada balsam, and examined under a light microscope (LEICA DM 2700M). Panoramic images were captured with a digital camera (Olympus Evolt E-330 SLR) at 25 \times magnification and a resolution of 1300 \times 1030 pixels.

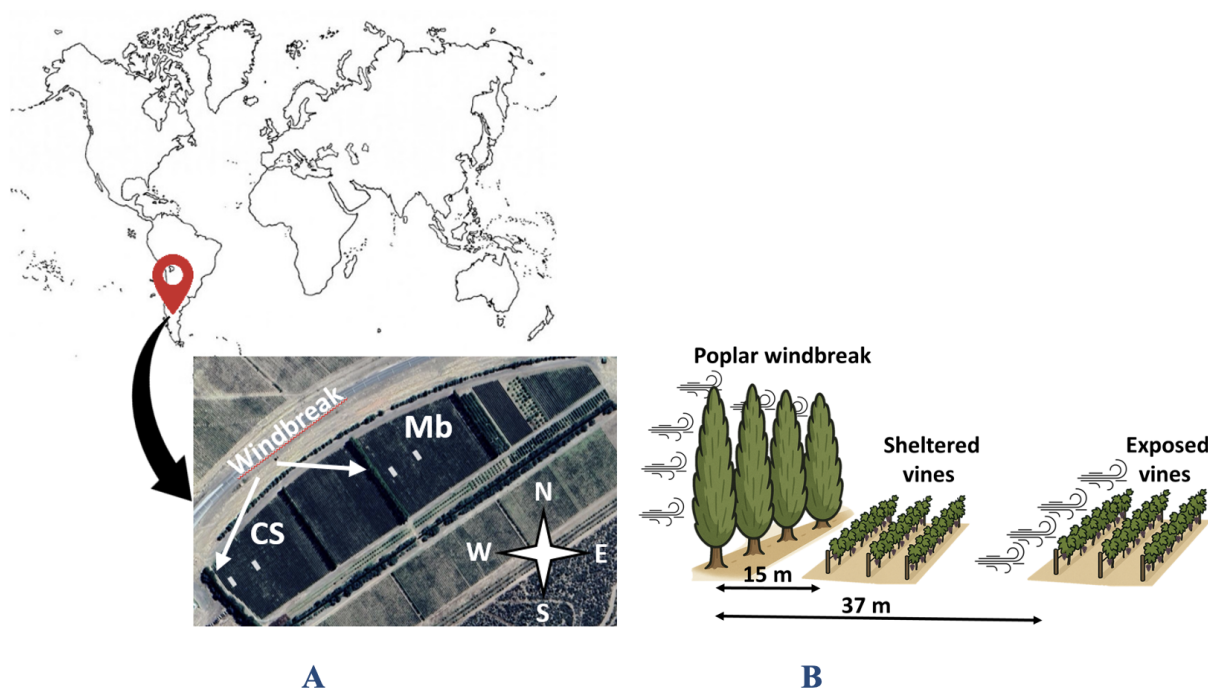


FIGURE 1. A) A world map indicating the location of the experimental site grapevines in Argentine Patagonia with a red marker. Below, a satellite image provides a detailed view of the study area, showing Malbec (Mb) and Cabernet-Sauvignon (CS) plots, with their respective windbreaks. A compass rose is included for orientation. B) Schematic representation of the experimental design. The diagram illustrates the spatial arrangement of vineyard rows in relation to the windbreak, highlighting the two wind exposure conditions (sheltered and exposed) applied to both Malbec and Cabernet-Sauvignon. Arrows indicate predominant wind direction, emphasising differences in microclimatic conditions between treatments.

Xylem analysis was carried out on the growth rings formed during the lifespan of the vines from 2011 to 2021, using the image analysis software WinCell (Regent Instruments Inc). For each ring, ring width (RW), number of vessels, and vessel diameter were measured directly with the software. Vessel density was calculated as the number of vessels per unit area, and mean lumen area was obtained by dividing the total vessel area by the number of vessels per ring. Total conductive area was estimated by multiplying the total vessel area by the RW. The first three years of the vine's growth (2011, 2012, and 2013) were excluded from the analysis to avoid the influence of the juvenile exponential growth phase characteristic of woody plants (Johnson & Abrams, 2009). To estimate annual wood production, RW values were converted into BAI (Johnson & Abrams, 2009). Additionally, the vessel lumen fraction (F), an anatomical proxy related to xylem conductivity capacity, was calculated using the mean vessel lumen area and vessel density, following the methodologies proposed by Zanne *et al.* (2010) and Scholz *et al.* (2013). This index describes the proportion of xylem area occupied by vessels and is computed as the product of mean vessel area (A) and the vessel density (N), expressed as $F = A \times N$.

3. Partitioning of shoot dry biomass and vegetative growth

Shoot dry biomass partitioning (leaves, laterals, cane, and bunches) and vegetative growth parameters (shoot length and leaf area) were measured at harvest during two seasons, 2022 and 2023, following the protocols described in Alonso *et al.* (2024).

4. Meteorological data

Air temperature (T), relative humidity (RH), and wind speed (WS) were continuously monitored from 2013 to 2021 (from September to January each year) using an automatic weather station (iMetos II, Pessl Instruments GmbH, Weiz, Austria) installed at 1.5 m height. This phenological window (budbreak to veraison) was specifically analysed because it encompasses the period of maximal xylem vessel formation and secondary growth in grapevines, when cambial activity and vascular development are most climate-sensitive (Jacobsen *et al.*, 2015). For each growing season, we calculated: average daily relative humidity (Avg RH), average daily mean temperature (Avg Mean T), average of daily maximum (Avg Max T) and minimum temperatures (Avg Min T), number of days with maximum temperature $\geq 35^\circ\text{C}$ ($T \geq 35^\circ\text{C}$), number of days with mean wind speed $> 2\text{ m/s}$ ($WS > 2\text{ m/s}$), and accumulated wind speed (Acc Wind) as the sum of daily mean values.

5. Statistical analysis

All analyses of variance (ANOVA) were performed using InfoStat software (version 2020, Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina). Comparisons were performed using Fisher's least significant difference (LSD) test, with significance set at $p \leq 0.05$. Wood anatomical traits were analysed using generalised linear mixed models

(GLMM), where treatment, season, and their interactions were considered fixed effects, while replicates were treated as random effects. Spearman's rank correlation coefficients among wood anatomical traits and climatic variables were calculated using R (version 4.4.2) in RStudio, employing the corplot package for visualisation.

RESULTS

Notable differences were observed in wood production and xylem anatomical traits in Mb and CS in response to wind exposure conditions across the considered seasons.

In CS, RW tended to be greater in vines sheltered from the wind, with statistically significant differences depending on the season, particularly in 2015, 2016, and 2018 (Figure 2B). This trend became more pronounced when considering cumulative RW, as sheltered vines consistently showed higher values of radial growth than exposed vines from 2016 onward (Figure 2D). Annual BAI further emphasised this pattern, with greater wood productivity observed in sheltered vines and significant differences in 2015 and 2016. These differences became even more apparent in cumulative BAI: from 2017 onward, sheltered plants exhibited significantly higher wood production, indicating more sustained growth under reduced wind stress (Figure 2H). In contrast, Mb showed no significant differences in RW or BAI between treatments (Figure 2A and 2E), and both cumulative RW and cumulative BAI evolved similarly under both exposed and sheltered conditions (Figure 2C and 2G).

Regarding xylem anatomy, relevant contrasts were observed between cultivars and treatments. In CS, vessel density was consistently higher in exposed vines, with significant differences between 2015 and 2020 (Figure 3B). Total vessel area showed variable differences across years, though without a clear pattern (Figure 3D), while mean vessel area was consistently higher in sheltered vines (Figure 3F). This compensation between vessel density and size across treatments resulted in no significant differences in F between contrasting wind conditions (Figure 3H), suggesting comparable hydraulic efficiency in both scenarios.

In Mb, anatomical differences were less marked and followed less defined patterns. Vessel density tended to be slightly higher in exposed vines during some seasons (Figure 3A), and a growing trend was observed in total vessel area, mean vessel area, and F values in exposed vines (Figure 3C, 3E and 3G). This suggests a possible gradual anatomical response to environmental conditions, with an increase in vessel size and, consequently, in hydraulic conductivity (F) under wind exposure. However, these differences were not statistically significant at the time of sampling.

While xylem anatomical traits (2014–2021) revealed wind-driven adaptations in hydraulic architecture (Figures 2 and 3), subsequent vegetative growth measurements (2022–2023) demonstrated parallel adjustments at the whole-plant scale. Under wind exposure, both cultivars shifted carbon allocation toward reproductive structures (8–19 % increase in bunch

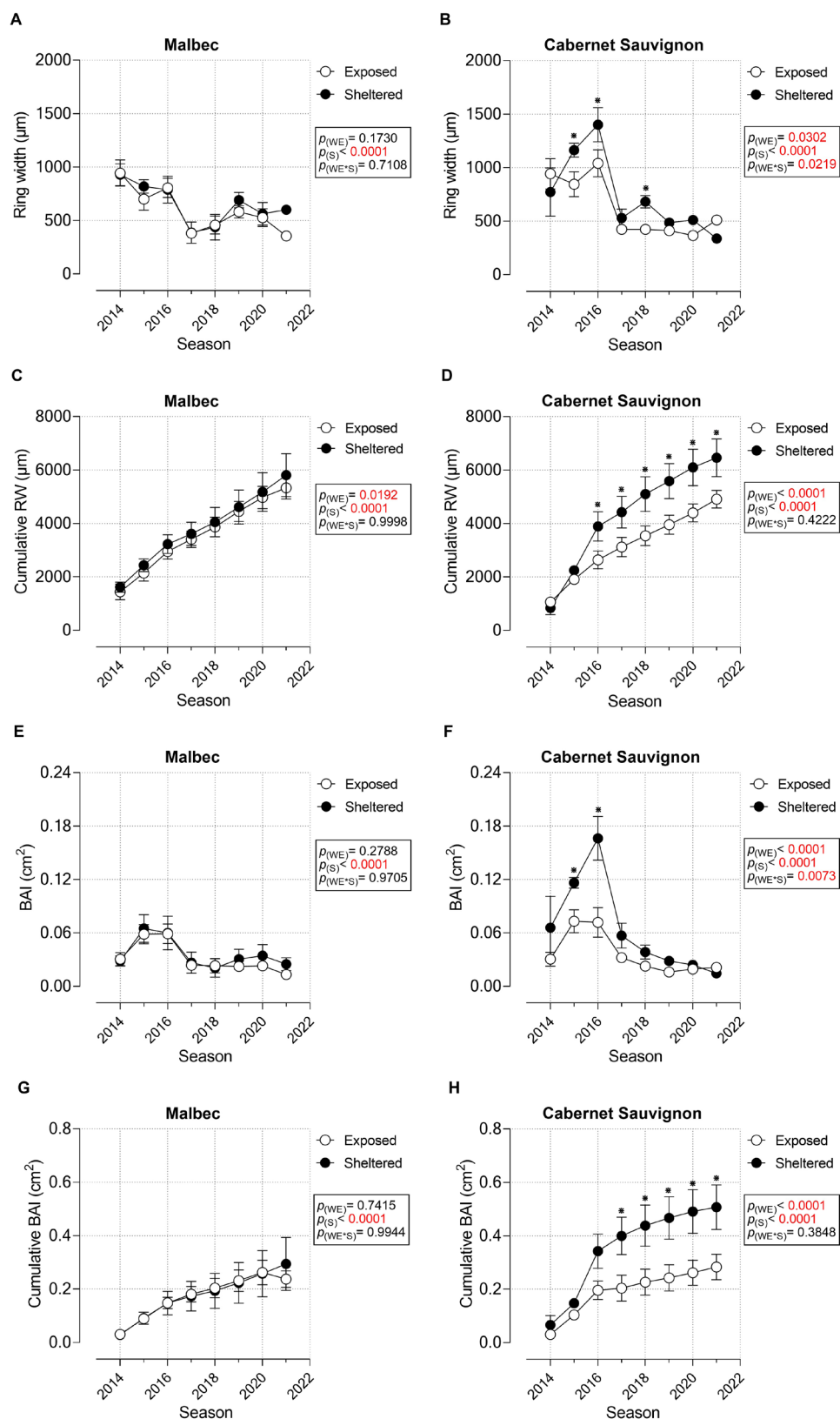


FIGURE 2. Ring width (RW), cumulative RW, basal area increments (BAI), and cumulative BAI, calculated annually for the seasons 2014–2021 for Malbec and Cabernet-Sauvignon vines subjected to wind exposure (WE) treatments. Data are presented as means \pm SEM ($n = 6$) and significant differences between treatments for each season are indicated by asterisks (Fisher's LSD test, $p \leq 0.05$).

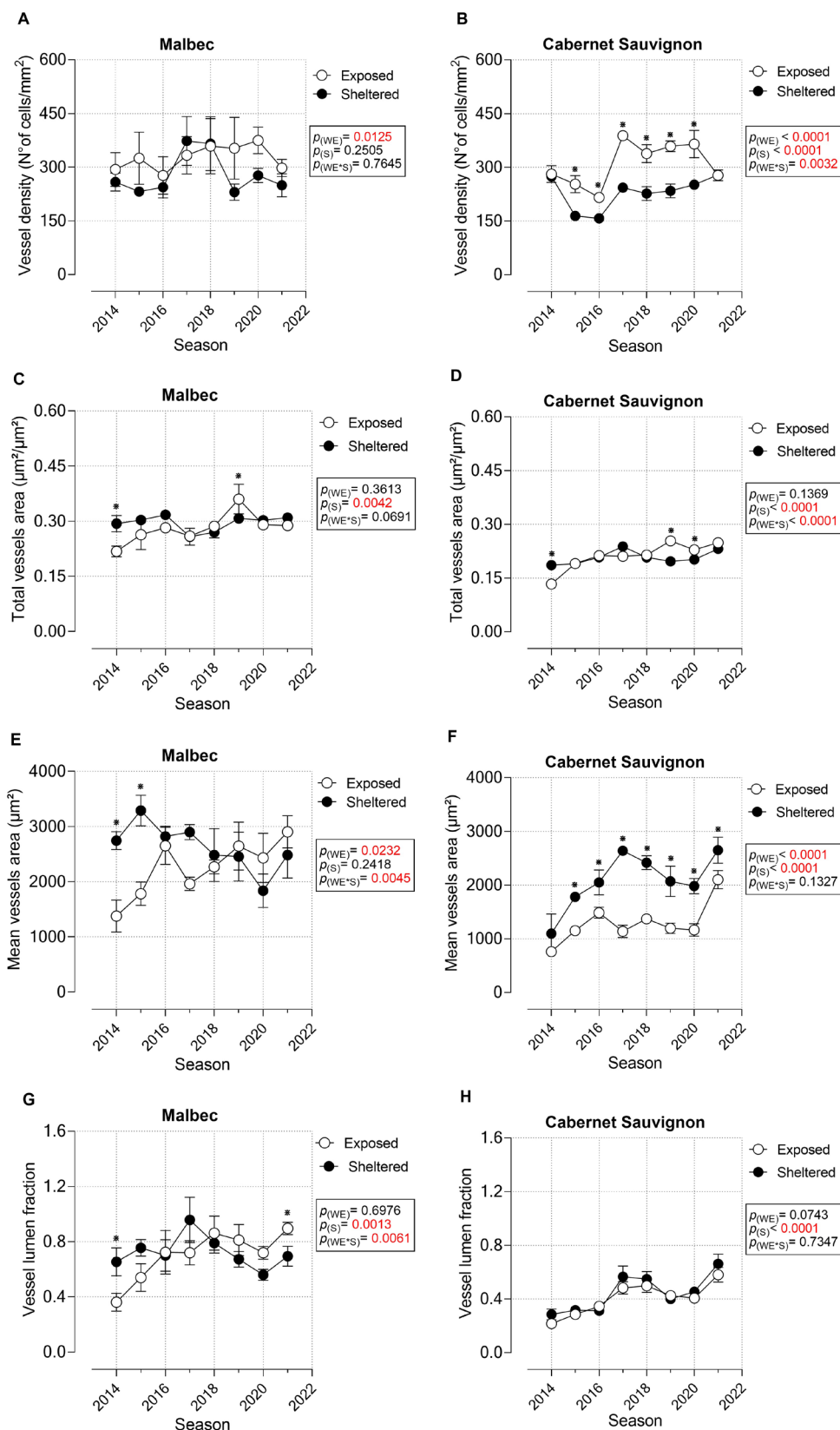


FIGURE 3. Vessel density, total vessel area, mean vessel area, and vessel lumen fraction (F) were calculated annually for the period 2014–2021 for Malbec and Cabernet-Sauvignon vines subjected to wind exposure (WE) treatments. Data are presented as means \pm SEM ($n = 6$) and significant differences between treatments for each season are indicated by asterisks (Fisher's LSD test, $p \leq 0.05$).

biomass; Tables S1–S2) at the expense of vegetative growth (reduced shoot length and leaf area). Notably, Mb’s anatomical resilience (e.g., higher vessel lumen fraction) aligned with its milder biomass reductions compared to CS.

Overall, climatic variables and wind exposure differentially influenced xylem anatomy across cultivars (Figure 4). In exposed vines, CS exhibited pronounced negative correlations between RW and both Avg Max T and $T \geq 35\text{ }^{\circ}\text{C}$, suggesting greater sensitivity to heat stress compared to Mb. Wind and considered related parameters, such as windy days ($WS > 2\text{ m/s}$) and accumulated wind (Acc Wind), showed positive associations with vessel traits (Mean VA, Total VA, and F) in Mb, suggesting anatomical adaptations to wind. Conversely, under sheltered conditions, both varieties shared trends observed in the broader dataset: RW and BAI correlated negatively with $T \geq 35\text{ }^{\circ}\text{C}$ but positively with Avg RH, while Mean VA and F were linked to higher temperatures (Avg Mean T, Avg Max T). However, CS’s stronger negative responses to wind exposure in exposed conditions underscored its heightened vulnerability relative to Mb’s resilience.

DISCUSSION

From an anatomical perspective, the response observed in CS under windy conditions reflects a well-documented compensatory strategy in woody species exposed to mechanical stress: a decrease in vessel size, which tends to reduce embolism risk, is offset by an increase in vessel density (Badel *et al.*, 2015; Telewski, 2016). This anatomical reorganisation allows the preservation of the lumen fraction (F), theoretically maintaining a constant conductive capacity despite the more demanding environment. However, this apparent hydraulic efficiency does not translate into increased

productivity: even with similar F values, wind-exposed plants continue to exhibit lower radial growth and wood accumulation. This result suggests that although the xylem structure adapts hydraulically to stress, the maintenance of this anatomical functionality under increased mechanical and evaporative load ultimately impacts wood productivity and radial growth. This interpretation is consistent with the principles proposed by Hacke *et al.* (2001) and Hacke *et al.* (2017), who emphasise the importance of structural trade-offs between efficiency and resistance in the context of potential cavitation.

This apparent contradiction can be explained by considering that the F index, while quantifying the proportion of conductive tissue in the xylem (derived from the mean vessel area multiplied by density), does not directly account for the effect of diameter on actual flow efficiency. According to Poiseuille’s law, the hydraulic conductivity of a vessel is proportional to the fourth power of its radius ($K \propto r^4$), implying that small variations in diameter produce large differences in conductive capacity (Giordano *et al.*, 1978; Hajek *et al.*, 2014). In this sense, systems dominated by smaller vessels, as observed in wind-exposed Cabernet-Sauvignon, may exhibit a higher F due to high vessel density, but also greater internal friction, thereby restricting water flow through the xylem. This increased flow resistance means that the plant must generate higher tensions to sustain water transport, with a greater energy cost and possible impacts on cell turgor, tissue expansion, photosynthesis, and ultimately radial growth and wood productivity (BAI). As Brodersen (2016) noted, aggregated hydraulic indices such as F, based on vascular geometry, may overestimate system efficiency when frictional effects and structural vulnerability under environmental stress are not considered. In other words, even if the F index indicates preserved conductive capacity,

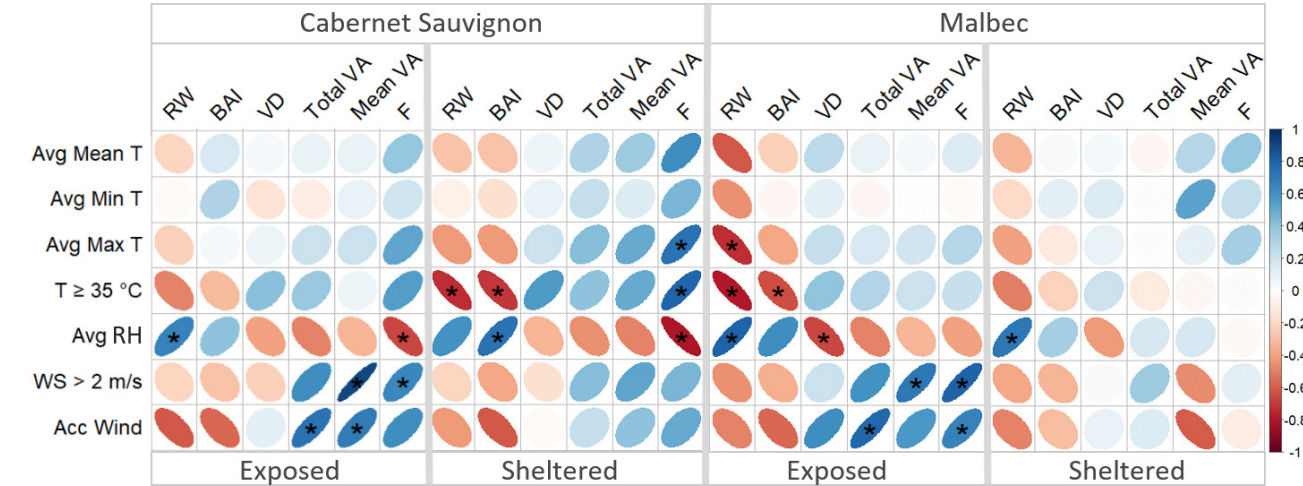


FIGURE 4. Spearman’s rank correlation coefficients among wood anatomical traits of Malbec and Cabernet-Sauvignon vines subjected to wind exposure treatments and climatic data from Casa de Piedra weather station during the budbreak-veraison period (September-January) for 2014–2021. Red denotes negative and blue positive correlation coefficients. *, significant at $p \leq 0.05$. Avg Mean T, Avg Min T, Avg Max T, average mean, minimum and maximum temperature, respectively; $T \geq 35\text{ }^{\circ}\text{C}$, number of days with maximum temperature $\geq 35\text{ }^{\circ}\text{C}$; $WS > 2\text{ m/s}$, number of days with mean wind speed $> 2\text{ m/s}$; Acc Wind, accumulated wind speed; RW, ring width; BAI, basal area increment; VD, vessel density; Total VA, total vessel area; Mean VA, mean vessel area; F, vessel lumen fraction.

its value may mask significant hydraulic limitations when achieved through a xylem architecture oriented toward safety but less efficient in transport speed. This observation has also been reported in woody species such as *Handroanthus vellosi*, where combinations of smaller vessels and thicker cell walls, while providing mechanical resistance, result in lower net hydraulic conductivity (Longui *et al.*, 2017). Therefore, actual hydraulic efficiency should not be inferred solely from global structural indices but interpreted in relation to the interaction between vessel diameter, density, and the physical properties of flow in the vascular system.

In contrast, the cultivar Mb did not exhibit significant differences in radial growth or wood productivity between treatments, which may indicate lower wind sensitivity or greater phenotypic plasticity. Nevertheless, trends were observed in anatomical variables, such as a progressive increase in mean vessel area and the vessel lumen fraction (F) under wind exposure throughout the series. Although these differences were not statistically significant compared to the protected treatment, they may reflect a gradual, genotype-dependent response to environmental stress. As Jasińska *et al.* (2015) argue, even in the absence of marked differences, the direction of anatomical changes may reveal functional adaptations. This subtle yet functional response pattern is consistent with observations by Roig-Puscama *et al.* (2021), who described relatively stable vascular anatomy in Malbec across soils of varying depth, with slight differences in F but no significant alterations in mean vessel size. In both cases, anatomical plasticity appears to act as a buffering mechanism against different types of environmental stress, allowing the preservation of hydraulic efficiency without compromising radial growth. Beyond these trends, and unlike CS, Mb did not show significant changes in vessel density or mean diameter between treatments, although it consistently exhibited higher total vessel area under both conditions, suggesting a stable and elevated water conduction capacity at the vascular level, regardless of wind exposure. In other words, Mb maintains considerable vessel area and a high F index in both conditions, enabling high hydraulic efficiency without being compromised by wind exposure. Logically, this could lead to the assumption that, by not modifying its vascular anatomy, Mb would adopt compensatory strategies to mitigate the stressful effects of wind, such as reduced shoot elongation or a decrease in leaf area. Interestingly, however, despite this anatomical stability, Mb exhibited greater shoot length and leaf area than CS, even under wind exposure (Table S1). This apparent paradox suggests that Mb may not rely exclusively on xylem structural plasticity to cope with wind-induced stress, but instead may employ alternative mechanisms such as more efficient stomatal regulation or lower stomatal density. The ability to sustain larger vegetative organs without major adjustments in xylem anatomy may indicate a decoupling between vegetative vigour and vascular plasticity, pointing to a conservative yet resilient hydraulic strategy. In grapevines, both stomatal size and density have been shown to vary in response to environmental conditions, particularly water availability, directly influencing stomatal conductance and consequently transpiration and photosynthesis (Boso *et al.*, 2016; Güler *et al.*, 2024). While

this aspect was not addressed in the present study, it would be relevant for future research to explore whether Mb employs adjustments in stomatal density, as well as other physiological parameters related to plant water status, such as water potential, transpiration, or turgor loss point, as a compensatory strategy under wind-induced stress. These contrasts between Mb and CS reflect differences in adaptive capacity between genotypes, with important implications for varietal management in contexts of higher wind exposure.

In Mb, the positive correlation between the number of windy days ($WS > 2$ m/s) and xylem anatomical traits may reflect a functional strategy that allows the maintenance of high hydraulic conductance capacity even under mechanical and evaporative stress, possibly reflecting an adaptive plasticity strategy, allowing hydraulic function to be maintained without major anatomical changes, a pattern aligning with its milder vegetative growth reductions in 2022–2023 (Tables S1–S2). In contrast, in Cabernet-Sauvignon, wind exposure triggered anatomical reorganisation aimed at reducing embolism risk (smaller vessel size and increased density), maintaining a theoretically constant F index, but at the expense of lower wood productivity and radial growth. This trade-off mirrors its sharper declines in shoot length and leaf area under wind, underscoring a genotype-dependent cost of stress tolerance. Conversely, under protected conditions, xylem anatomy appears to respond more directly to temperature, particularly the number of warm days. Both varieties exhibited similar physiological trade-offs: RW and BAI correlated negatively with extreme heat ($T \geq 35$ °C) but positively with Avg RH, suggesting that even in protected environments, excessive temperatures limit radial growth, while humidity supports it. In CS, F linked positively to warmer temperatures, indicating that sheltered vines prioritise larger vessels and hydraulic efficiency under moderate heat. Without mechanical and evaporative stress induced by wind, grapevines may prioritise hydraulic efficiency by forming larger vessels capable of transporting more water per unit time. This strategy aligns with increased evapotranspirative demand under elevated temperatures, where a more efficient vascular system supports leaf cooling and photosynthesis by maintaining a continuous water flow from the soil to the leaves. This flow is essential to compensate for high transpiration rates and depends on xylem hydraulic efficiency as well as its ability to resist failure under extreme negative pressures (Brodersen, 2016; Hacke *et al.*, 2001; Hajek *et al.*, 2014; Venturas *et al.*, 2017). Such structural adjustment has already been documented in *Vitis vinifera* as an adaptive mechanism under edaphic constraints, where small variations in vessel lumen area and density allow the maintenance of conductive efficiency (Roig-Puscama *et al.*, 2021). Moreover, it has been shown that the F index varies globally in response to environmental conditions and is associated with potential conductive capacity without necessarily compromising wood density (Preston *et al.*, 2006; Zanne *et al.*, 2010). Together, these results reveal a hierarchy of environmental modulation: wind dominates as a selective pressure in exposed conditions, driving varietal-specific anatomical and growth adjustments, while temperature governs hydraulic architecture in sheltered vines. Malbec's

coordinated responses (from xylem plasticity to stable biomass allocation) suggest a systemic adaptation to abiotic stress, whereas Cabernet-Sauvignon's sacrifices in growth and radial increment highlight its vulnerability.

This study reveals patterns consistent with woody species literature while providing novel evidence for grapevine cultivars, a species for which anatomical responses to wind in the xylem remain scarcely documented. Our findings demonstrate that CS shows stronger, more structured responses characterised by xylem reorganisation to preserve hydraulic functionality under stress, albeit at high physiological costs reflected in reduced wood production and radial growth. In contrast, Mb exhibits milder responses, suggesting alternative functional strategies. These cultivar-specific patterns constitute one of the first integrated assessments of wind's impact on secondary growth and xylem structure in cultivated grapevines. They support considering differential phenotypic plasticity as an agronomic criterion in vineyard planning for windy regions. Practically, the results allow us to propose cultivar-specific recommendations: Malbec, due to its structural and functional resilience, can be grown in either exposed or protected conditions without compromising its hydraulic efficiency or productivity. Furthermore, as we showed in Alonso *et al.* (2024), wind exposure may even enhance grape quality by increasing anthocyanin content in the skin. Cabernet-Sauvignon should preferably be cultivated in more sheltered environments, implementing wind mitigation strategies (e.g., forest windbreaks or artificial barriers). Where barriers are not feasible, specific practices like adjusting exposed leaf area per hectare (Deloire *et al.*, 2022) or modifying the leaf-to-fruit ratio (Kliewer & Dokoozlian, 2005) can optimise ripening under stress. These management decisions, based on anatomical and functional knowledge of xylem, open new avenues for designing viticultural systems more adapted to their environment, contributing to physiologically and qualitatively efficient sustainable production.

ACKNOWLEDGEMENTS

This research was funded by the Agencia Nacional de Promoción de la Investigación, el Desarrollo Tecnológico y la Innovación (PICT-2020-SERIEA-01946) and the Ente Provincial del Río Colorado (EPRC). The authors express their gratitude to Roberto Bigorito and Enzo Mugnani from EPRC for their invaluable support in this project.

REFERENCES

- Alonso, R., Muñoz, F., Bottini, R., Piccoli, P., & Berli, F. J. (2024). Effects of wind exposure and deficit irrigation on vegetative growth, yield components and berry composition of Malbec and Cabernet-Sauvignon. *Plants*, 13(10), 1292. <https://doi.org/10.3390/plants13101292>
- Anderegg, W. R. L., & Meinzer, F. C. (2015). Wood anatomy and plant hydraulics in a changing climate. In U. Hacke (Ed.), *Functional and Ecological Xylem Anatomy* (pp. 235–253). Springer International Publishing. https://doi.org/10.1007/978-3-319-15783-2_9
- Badel, E., Ewers, F. W., Cochard, H., & Telewski, F. W. (2015). Acclimation of mechanical and hydraulic functions in trees: Impact of the thigmomorphogenetic process. *Frontiers in Plant Science*, 6. <https://doi.org/10.3389/fpls.2015.00266>
- Biondi, F., & Qeadan, F. (2008). A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. *Tree-Ring Research*, 64(2), 81–96. <https://doi.org/10.3959/2008-6.1>
- Boso, S., Gago, P., Alonso-Villaverde, V., Santiago, J. L., & Martínez Rodríguez, M. C. (2016). Density and size of stomata in the leaves of different hybrids (*Vitis* sp.) and *Vitis vinifera* varieties. *Vitis*, 55, 902 KB. <https://doi.org/10.5073/VITIS.2016.55.17-22>
- Brodersen, C. R. (2016). Finding support for theoretical tradeoffs in xylem structure and function. *New Phytologist*, 209(1), 8–10. <https://doi.org/10.1111/nph.13763>
- Brodersen, C. R., Choat, B., Chatelet, D. S., Shackel, K. A., Matthews, M. A., & McElrone, A. J. (2013). Xylem vessel relays contribute to radial connectivity in grapevine stems (*Vitis vinifera* and *V. arizonica*; Vitaceae). *American Journal of Botany*, 100(2), 314–321. <https://doi.org/10.3732/ajb.1100606>
- Cabré, F.; Nuñez, M. (2020). Impacts of climate change on viticulture in Argentina. *Regional Environmental Change*. Volume 20, article number 12. <https://doi.org/10.1007/s10113-020-01607-8>
- Camarero, J. J., Pizarro, M., Gernandt, D. S., Gazol, A. (2024). Smaller conifers are more resilient to drought. *Agricultural and Forest Meteorology* 350: 109993. <https://doi.org/10.1016/j.agrformet.2024.109993>
- Chavarria, G., & Dos Santos, H. P. (2012). Plant water relations: absorption, transport and control mechanisms. In G. Montanaro (Ed.), *Advances in Selected Plant Physiology Aspects*. InTech. <https://doi.org/10.5772/33478>
- Dal Santo, S., Zenoni, S., Sandri, M., De Lorenzis, G., Magris, G., De Paoli, E., Di Gaspero, G., Del Fabbro, C., Morgante, M., Brancadoro, L. (2018). Grapevine field experiments reveal the contribution of genotype, the influence of environment and the effect of their interaction (G × E) on the berry transcriptome. *The Plant Journal*, 93, 1143–1159. <https://doi.org/10.1111/tpj.13834>
- Deloire, A., Rogiers, S., & Baeza Trujillo, P. (2022). What could be the architectural forms of future vines adapted to climate change: A new challenge! Let's discuss the Gobelet (Bush Vine). *IVES Technical Reviews, vine and wine*. <https://doi.org/10.20870/IVES-TR.2022.5384>
- Gardiner, B., Berry, P., & Moulia, B. (2016). Review: Wind impacts on plant growth, mechanics and damage. *Plant Science*, 245, 94–118. <https://doi.org/10.1016/j.plantsci.2016.01.006>
- Giordano, R., Salleo, A., Salleo, S., & Wanderlingh, F. (1978). Flow in xylem vessels and Poiseuille's law. *Canadian Journal of Botany*, 56(3), 333–338. <https://doi.org/10.1139/b78-039>
- Gleason, S. M., Westoby, M., Jansen, S., Choat, B., Hacke, U. G., Pratt, R. B., Bhaskar, R., Brodribb, T. J., Bucci, S. J., Cao, K. F., Cochard, H., Delzon, S., Domec, J. C., Fan, Z. X., Feild, T. S., Jacobsen, A. L., Johnson, D. M., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., McCulloh, K. A., Mencuccini, M., Niinemets, Ü., Pittermann, J., Reich, P. B., Santiago, L. S., Scholz, F. G., Skelton, R. P., Wheeler, J. K., & Zanne, A. E. (2016). Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. *New Phytologist*, 209(1), 123–136. <https://doi.org/10.1111/nph.13646>
- Güler, S., Kunter, B., & Şehit, A. (2024). Stomatal density, type and their relationships with leaf morphological traits in *Vitis vinifera* L. varieties. *International Journal of Agriculture Environment and Food Sciences*, 8(1), 78–87. <https://doi.org/10.31015/jaefs.2024.1.9>

- Hacke, U. G., Sperry, J. S., Pockman, W. T., Davis, S. D., & McCulloh, K. A. (2001). Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia*, 126(4), 457–461. <https://doi.org/10.1007/s004420100628>
- Hacke, U. G., Spicer, R., Schreiber, S. G., & Plavcová, L. (2017). An ecophysiological and developmental perspective on variation in vessel diameter. *Plant, Cell & Environment*, 40(6), 831–845. <https://doi.org/10.1111/pce.12777>
- Hajek, P., Leuschner, C., Hertel, D., Delzon, S., & Schuldt, B. (2014). Trade-offs between xylem hydraulic properties, wood anatomy and yield in *Populus*. *Tree Physiology*, 34(7), 744–756. <https://doi.org/10.1093/treephys/tpu048>
- Islam, M., Rahman, M., & Bräuning, A. (2019). Impact of extreme drought on tree-ring width and vessel anatomical features of *Chukrasia tabularis*. *Dendrochronologia*, 53, 63–72. <https://doi.org/10.1016/j.dendro.2018.11.007>
- OIV. (2024). State of the world vine and wine sector 2024, *International Organization of Vine and Wine*. https://www.oiv.int/sites/default/files/2025-04/OIV-State_of_the_World_Vine-and-Wine-Sector-in-2024.pdf
- Jacobsen, AL., Rodriguez-Zaccaro, FD., Lee, TF., Valdovinos, J., Toschi, HS., Martinez, JA., Pratt, RB. (2015). Grapevine xylem development, architecture, and function. In: Functional and ecological xylem anatomy. pp 133-162. https://doi.org/10.1007/978-3-319-15783-2_5
- Jasińska, A. K., Alber, M., Tullus, A., Rahi, M., & Sellin, A. (2015). Impact of elevated atmospheric humidity on anatomical and hydraulic traits of xylem in hybrid aspen. *Functional Plant Biology*, 42(6), 565. <https://doi.org/10.1071/FP14224>
- Johnson, S. E., & Abrams, M. D. (2009). Basal area increment trends across age classes for two long-lived tree species in the eastern US. *Trace*, 7: 127-134.
- Kliwer, W. M., & Dokoozlian, N. K. (2005). Leaf area/crop weight ratios of grapevines: influence on fruit composition and wine quality. *American Journal of Enology and Viticulture*, 56(2), 170–181. <https://doi.org/10.5344/ajev.2005.56.2.170>
- Loepfe, L., Martinez-Vilalta, J., Piñol, J., & Mencuccini, M. (2007). The relevance of xylem network structure for plant hydraulic efficiency and safety. *Journal of Theoretical Biology*, 247(4), 788–803. <https://doi.org/10.1016/j.jtbi.2007.04.032>
- Longui, E. L., Oliveira, I. R. D., Graebner, R. C., Freitas, M. L. M., Florsheim, S. M. B., & Garcia, J. N. (2017). Relationships among wood anatomy, hydraulic conductivity, density and shear parallel to the grain in the wood of 24-year-old *Handroanthus vellosi* (Bignoniaceae). *Rodriguésia*, 68(4), 1217–1224. <https://doi.org/10.1590/2175-7860201768406>
- Munitz, S., Netzer, Y., Shtein, I., & Schwartz, A. (2018). Water availability dynamics have long-term effects on mature stem structure in *Vitis vinifera*. *American Journal of Botany*, 105(9), 1443–1452. <https://doi.org/10.1002/ajb2.1148>
- Preston, K. A., Cornwell, W. K., & DeNoyer, J. L. (2006). Wood density and vessel traits as distinct correlates of ecological strategy in 51 California coast range angiosperms. *New Phytologist*, 170(4), 807–818. <https://doi.org/10.1111/j.1469-8137.2006.01712.x>
- Roig-Puscama, F., Berli, F., Roig, F. A., Tomazello-Filho, M., Mastrantonio, L., & Piccoli, P. (2021). Wood hydrosystem of three cultivars of *Vitis vinifera* L. is modified in response to contrasting soils. *Plant and Soil*, 463(1–2), 573–588. <https://doi.org/10.1007/s11104-021-04907-y>
- Rubino, D. L., & McCarthy, B. C. (2000). Dendroclimatological analysis of white oak (*Quercus alba* L., Fagaceae) from an old-growth forest of southeastern Ohio, USA. *Journal of the Torrey Botanical Society*, 240–250. <https://doi.org/10.2307/3088761>
- Scholz, A., Klepsch, M., Karimi, Z., & Jansen, S. (2013). How to quantify conduits in wood? *Frontiers in Plant Science*, 4. <https://doi.org/10.3389/fpls.2013.00056>
- Schweingruber, F. H. (1996). *Tree rings and environment: dendroecology*. Switzerland: Paul Haupt AG Bern.
- Telewski, F. W. (2016). Flexure wood: mechanical stress induced secondary xylem formation. In *Secondary xylem biology* (pp. 73–91). Academic Press. <https://doi.org/10.1016/B978-0-12-802185-9.00005-X>
- Venturas, M. D., Sperry, J. S., & Hacke, U. G. (2017). Plant xylem hydraulics: What we understand, current research, and future challenges. *Journal of Integrative Plant Biology*, 59(6), 356–389. <https://doi.org/10.1111/jipb.12534>
- Villarreal, P., Romagnoli, S., & Llorente, A. (2007). *Pautas tecnológicas: vid para vinificar*. Ediciones INTA
- Zanne, A. E., Westoby, M., Falster, D. S., Ackerly, D. D., Loarie, S. R., Arnold, S. E. J., & Coomes, D. A. (2010). Angiosperm wood structure: Global patterns in vessel anatomy and their relation to wood density and potential conductivity. *American Journal of Botany*, 97(2), 207–215. <https://doi.org/10.3732/ajb.0900178>