Quantifying the grapevine xylem embolism resistance spectrum to identify varieties at risk in a future dry climate

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Keywords: hydraulic failure, *Vitis vinifera*, drought, hybrid cultivars, climate change

Abstract

Maintaining wine production under climate warming partly relies on optimizing choice of plant materials for a given viticultural landscape and developing drought-resistant cultivars. However, progress in these directions is slowed down by the lack of mechanistic understanding of drought resistance variations among *Vitis* genotypes. We quantified xylem embolism resistance in 30 grape varieties originating from different locations and climates worldwide, and assessed the global risk of hydraulic failure under drought in 329 wine growing regions. Significant variability in xylem embolism vulnerability arose across varieties. Ugni blanc and Chardonnay featured among the most vulnerable varieties, while Pinot noir, Merlot and Cabernet Sauvignon ranked among the most resistant. Regions bearing a significant proportion of vulnerable varieties were found at greater risk of large-scale hydraulic failure under severe drought. More interestingly, those regions, such as Poitou-Charentes (France) and Marlborough (New Zealand), are not necessarily from arid and semi-arid zones. We demonstrate that grapevine varieties may not respond equally to drier conditions, and highlight that physiological studies assessing trait variation in space and time are crucial in understanding viticulture suitability under climate change.

Introduction

Understanding how grapevine responds to extreme weather such as increasingly severe and sustained droughts is crucial to advise the wine industry about which varieties and viticultural practices would be best adapted to increased drought risk. Adaptation of viticulture to climate change has first been approached from a phenological perspective. Specific grapevine varieties have historically been chosen for specific regions so that their phenological cycles match local climate (Gladstones et al, 2011). As phenological diversity within *Vitis vinifera* is high (Wolkovich et al, 2017), it has even been suggested that increasing diversity of varieties with different phenology may mitigate losses of agricultural areas and negative impacts of climate change (Morales-Castilla et al, 2020). However, plant productivity relies on water transport efficiency and photosynthetic capacities and therefore, phenology alone cannot explain drought tolerance in grapevine.
Regarding drought tolerance, grapevine stands out from other major crops because of two peculiar features. First, it is a perennial crop that is expected to produce for many decades. Thus, it must tolerate drought periods over both short- and long terms, i.e. be able to produce annually while avoiding drought-induced mortality thresholds over the years (Gambetta, 2016). Second, water deficit can improve berry and wine quality, especially for red wines, through increases in sugar, anthocyanin, and tannin concentration (Gambetta et al, 2020). As a result, producers in regions where irrigation is allowed tend to restrict water to maximize production of high-quality grapes while minimizing yield reductions. For these reasons, a large body of literature has focused on water use efficiency attempting to elucidate the underlying mechanisms of grapevine stomatal regulation and photosynthesis limitation (Charrier et al, 2018).
Water-carbon linkages in plants also rely on efficient hydraulic functioning that move water passively from the soil up to the sites of photosynthesis. During prolonged drought, this system can be disrupted by air entry

in water conducting xylem cells (c.f. xylem embolism), which become non-functional. Failure to maintain permanent hydraulic conductivity constrains the photosynthetic yield and productivity of plants (Cardoso et al, 2018), and ultimately limits survival under severe drought (Choat et al, 2012). Yet, hydraulics in grapevine has been described in just a handful of common *Vitis vinifera* L. varieties (Bortolami et al, 2021; Charrier et al, 2016, 2018; Dayer et al, 2020; Hochberg et al, 2017; Sorek et al, 2021). The magnitude of variation in vulnerability to xylem embolism among varieties is currently unknown. This limits our ability to provide growers and wine makers with robust recommendations for promoting specific varieties better adapted to warmer and drier regions.
In this study, we evaluated the global spectrum of vulnerability to xylem embolism in grapevine, with measurements conducted among varieties originating from different locations and climates worldwide. A total of 30 grapevine varieties were screened, including (i) red and white *Vitis vinifera* varieties that collectively account for ~1,902,000 hectares cultivated around the world, (ii) hybrid varieties recently developed by INRAE and characterized by a polygenic resistance for powdery and downy mildews (Merdinoglu et al, 2018), and (iii) commonly used rootstocks. These analyses allowed us to assess global wine regions with respect to their varietal diversity and resulting risk of hydraulic failure.

Materials and methods

Vulnerability to xylem embolism

The variability in stem vulnerability to xylem embolism among grapevine species and varieties was characterized by measuring 176 one-year-old plants in September and early October after shoot hardening. Measurements were carried out at the high-throughput phenotyping platform for hydraulic traits (Caviplace, Phenobois platform, University of Bordeaux, Pessac, France), using the Cavitron technique equipped with 100-cm diameter rotor (Burlett et al, 2022). The vulnerability curves obtained, corresponding to the percentage loss of hydraulic conductivity (PLC, %) as a function of stem water potential were fitted based on the following equation (Pammenter & Van der Willigen, 1998): $PLC = 100/(1+\exp(S/25.(\Psi-\Psi_{50})))$, where Ψ_{50} (MPa) is the xylem pressure inducing 50% loss of hydraulic conductivity and S (% MPa^{-1}) is the slope of the vulnerability curve at the inflexion point. Xylem pressures inducing 12% (Ψ_{12}) and 88% (Ψ_{88}) loss of hydraulic conductivity were calculated as follows: $\Psi_{12} = 50/S+\Psi_{50}$ and $\Psi_{88} = -50/S+\Psi_{50}$. The Pammenter model was fitted on each vulnerability curve to obtain a Ψ_{50} and slope values per individual, and subsequently an average value per variety and season.

Regional risk index of hydraulic failure

A risk index of embolism vulnerability was calculated per wine producing region or country by coupling winegrape varietal coverage data with stem Ψ_{50} values of *Vitis vinifera* varieties. First, information on *Vitis vinifera* varietal coverage were retrieved from the online database of regional and national winegrape bearing areas by variety (Anderson & Nelgen, 2020). The dataset we compiled provided varietal coverage for a total of 653 wine regions across 48 countries. Second, this dataset was used to calculate, for each wine region, the bearing area of four clusters of vulnerability to xylem embolism (low, low-to-medium, medium-to-high, high) that were identified from a hierarchical clustering analysis. Third, each cluster was assigned a specific 'weight' on a 0-1 scale of vulnerability to xylem embolism: (i) low vulnerability: range 0-0.25 (median = 0.125); (ii) low-to-medium vulnerability: range 0.25-0.50 (median = 0.375); (iii) medium-to-high vulnerability: range 0.50-0.75 (median = 0.625); (iv) high vulnerability: range 0.75-1 (median = 0.875). The risk index (RI), taking into account both the bearing area and the vulnerability to xylem embolism of each cluster, was then calculated as follows: RI = 0.125.bearing area[low] + 0.375.bearing area[low-to-medium] + 0.625.bearing area[medium-to-high] + 0.875.bearing area[high], where each bearing area is represented as a percent of the regional area. The RI was mapped for 329 regions for which our varietal coverage dataset represented at least 40% of the regional or national winegrape bearing area. Thus, we provided an index for 52% of the global wine producing regions.

Statistical analyses

Overall differences in stem vulnerability to xylem embolism among grapevine varieties were examined with one-way analyses of variance and Student-Newman-Keuls post hoc tests (ANOVA procedure in SAS 9.4). Differences in stem vulnerability to xylem embolism among types of varieties (*Vitis vinifera* vs hybrids vs rootstocks), as well as among *Vitis vinifera* subspecies (occidentalis vs orientalis vs pontica), geographical origins (Balkans vs Eastern Mediterranean vs Iberian Peninsula vs Western & Central Europe) and between berry skin colors (black vs white) were studied with generalized linear models (GLM procedure in SAS 9.4), where type of varieties/geographical origin/berry skin color was treated as a fixed factor and variety nested within type of varieties/geographical origin/berry skin color as a random factor.

Results and discussion

Vulnerability to xylem embolism

Stem vulnerability to xylem embolism varied significantly among the 30 grapevine varieties screened. Water potentials inducing 12%, 50% and 88% embolism ranged from -0.4 to -2.7 MPa, -1.8 to -3.4 MPa, and -2.9 to -5.0 MPa, respectively (Figure 1). Hybrid varieties showed the highest mean vulnerability to xylem embolism as Floreal, Vidoc and Voltis ranked among the four most vulnerable varieties. In contrast, the onset of embolism (c.f. Ψ_{12}) in rootstocks and *Vitis vinifera* varieties was reached at a xylem pressure being almost twice more negative. Significant variability in embolism vulnerability also arose within *Vitis vinifera*, with varieties distributed along a range of Ψ_{12} of 2 MPa and a range of 1.3 MPa for both Ψ_{50} and Ψ_{88} (Figure 1). Vulnerable varieties with both less negative Ψ_{12} and Ψ_{50} included Sultanine, Cabernet franc and Chardonnay, whereas Cabernet Sauvignon, Merlot, Pinot noir and Syrah displayed high resistance to xylem embolism by constantly showing significantly lower Ψ_{12} and Ψ_{50}. Finally, differences in vulnerability to xylem embolism within *Vitis vinifera* were also observed with respect to subspecies and geographic origin. *Vitis vinifera* subsp. orientalis significantly exhibited less negative Ψ_{12} and Ψ_{50}, while *Vitis vinifera* subsp. occidentalis showed the lowest Ψ_{88}. Regarding the geographical origins of varieties, there was no difference in Ψ_{12} among the four geographical groups. Yet, varieties from the Iberian Peninsula and from Western & Central Europe significantly exhibited Ψ_{50} and Ψ_{88} values that were 0.4-0.5 MPa lower compared to varieties from Balkans. The Ψ_{88} of varieties from the Iberian Peninsula was also significantly lower than that of varieties from the Eastern Mediterranean region.

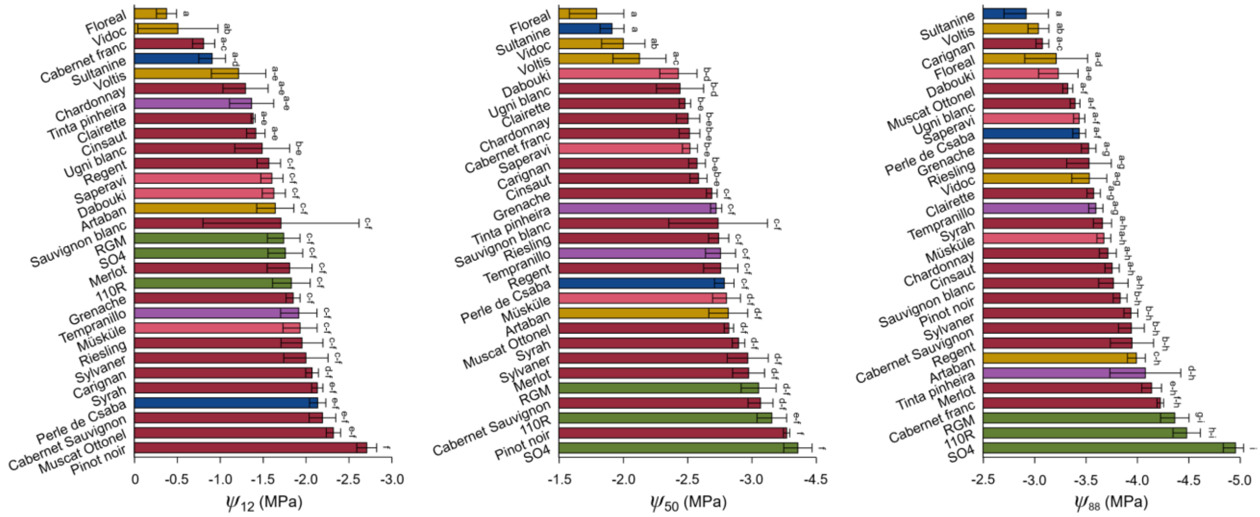

Figure 1. Variability in stem vulnerability to xylem embolism among grapevine varieties. Thresholds of 12%, 50% and 88% embolism (c.f. Ψ_{12}, Ψ_{50} and Ψ_{88}) for the 30 varieties screened. Bars and errors represent means ± standard errors. Letters refer to the results of post-hoc tests. Different letters indicate significant differences among varieties. The color code is as follows: hybrid cultivars in yellow, rootstocks in green, and *Vitis vinifera* varieties originating from Balkans, Eastern Mediterranean, Iberian Peninsula, and Western & Central Europe in blue, pink, purple, and red, respectively.

These findings first highlighted that grapevine can sustain significant levels of water deficit before embolism occurs. This is in accordance with recent imaging technique-based studies (Dayer et al, 2020; Charrier et al, 2016; Hochberg et al, 2017) reporting that grapevine is more resistant to xylem embolism than initially suggested. Second, *Vitis vinifera* exhibited high intraspecific variability in embolism vulnerability compared to what has generally been reported in other species, which is particularly striking considering the history of grapevine domestication and the combined action of migration, selection and admixture in shaping *Vitis vinifera* genetic structure (Arroyo-Garcia et al, 2006). Considering that in grapevine, like in plants in general, stomata close before the onset of embolism to operate within a positive hydraulic safety margin (Dayer et al, 2020; Sorek et al, 2021), this result questions stomatal regulation and photosynthetic capacities, and therefore productivity, in the most vulnerable varieties. However, the scarcity of physiological functioning data and multi-year Ψ_{min} records under field conditions for the majority of varieties makes it difficult to draw conclusions about the possible significant difference in safety margin among *Vitis vinifera* varieties. Finally, interspecific hybrid varieties that are resistant to mildew were highly vulnerable to xylem embolism, suggesting that they would be prone to substantial hydraulic failure on a regular basis throughout summer. While additional investigations regarding their physiological functioning are required, this result provides evidence that breeding approaches dedicated to the resistance to pathogens and/or yield maintenance under abiotic stress must actively account for hydraulic traits associated with resistance to hydraulic failure under drought conditions.

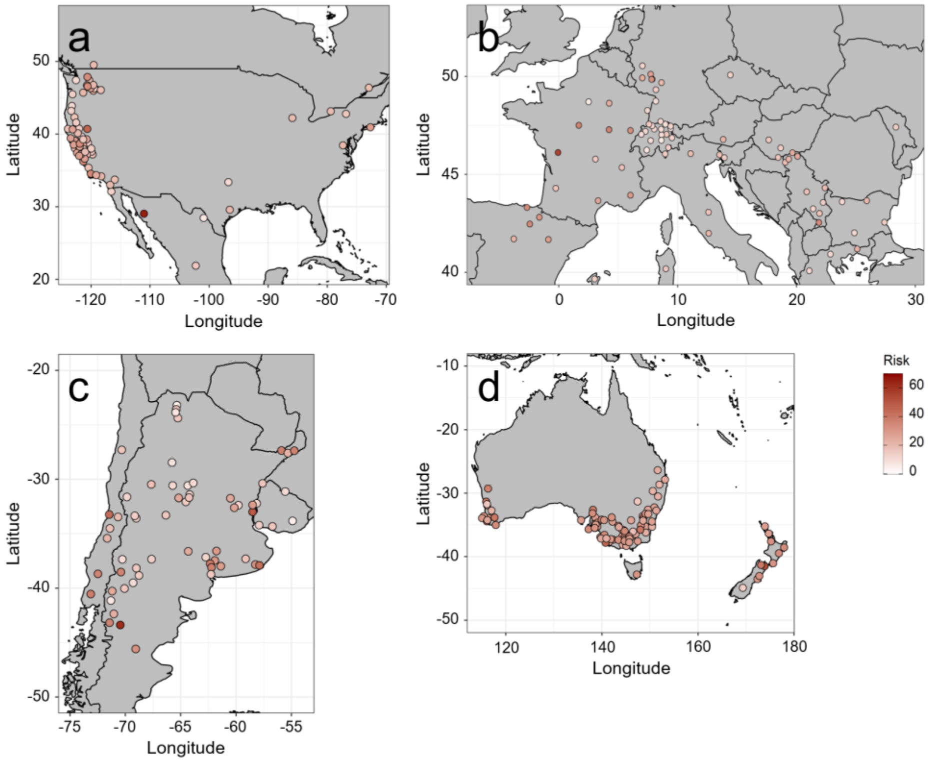

Figure 2. Regional risk of hydraulic failure.The index was calculated for 329 wine growing regions worldwide, by coupling winegrape varietal coverage data (Anderson & Nelgen, 2020) with stem Ψ_{50} values of *Vitis vinifera* varieties. It was restricted to regions where *Vitis vinifera* varieties included in this study cumulatively cover ≥ 40% of the regional winegrape bearing area. The index is presented here for wine growing regions in (a) North America, (b) Europe, (c) South America, and (d) Oceania.

Regional risk index of hydraulic failure

The risk index varied between 5 and 65, ranging between 20 and 40 for 56% of the regions analyzed (Figure 2). Regions with the lowest risk index, such as Lavalleja (Uruguay), Humahuaca (Argentina), Ile de France (France), and Uri (Switzerland), corresponded to areas that were almost exclusively covered by the most embolism resistant varieties such as Cabernet Sauvignon and Merlot. On the contrary, Marlborough (New Zealand) and Poitou-Charentes (France) displayed higher risk of large-scale hydraulic failure as they mostly grow varieties with the greatest vulnerability to embolism such as Sauvignon blanc and Ugni blanc. Overall, the risk of hydraulic failure at the regional scale varies independently from the number of grapevine varieties produced. This illustrates that from a physiological point of view, embolism vulnerability of specific varieties matters more than the diversity of varieties grown regionally. This result softens conclusions of studies advocating for the use of phenological diversity to mitigate the negative effects of climate change on wine production (Morales-Castilla et al. 2020, Wolkovich et al. 2017). Moreover, the risk of hydraulic failure varies independently from climate and shows a spatial heterogeneity around the world. Regions that are at greater risk of large-scale hydraulic failure are not necessarily those from arid and semi-arid zones. This indicates that no traditional wine growing region is immune to impacts of climate change regarding the risk of xylem embolism during prolonged drought.

Conclusion

Grapevine varieties display significant variability in the risk of xylem embolism. Consequently, wine producing regions bearing few varieties with high embolism vulnerability are particularly at risk to undergo large-scale events of hydraulic failure in vineyards under sustained drought periods. Our comparative approach further outlines that studies accounting for hydraulic trait variation in space and time holds great potential for improving understanding of viticulture suitability under climate change.

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