

RESEARCH PAPER

Temperature and evaporative demand drive variation in stomatal and hydraulic traits across grape cultivars

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Abstract

Selection for crop cultivars has largely focused on reproductive traits, while the impacts of global change on crop productivity are expected to depend strongly on the vegetative physiology traits that drive plant resource use and stress tolerance. We evaluated relationships between physiology traits and growing season climate across wine grape cultivars to characterize trait variation across European growing regions. We compiled values from the literature for seven water use and drought tolerance traits and growing season climate. Cultivars with a lower maximum stomatal conductance were associated with regions with a higher mean temperature and mean and maximum vapor pressure deficit ($r^2=0.39-0.65$, $P<0.05$, $n=14-29$). Cultivars with greater stem embolism resistance and more anisohydric stomatal behavior (i.e. a more negative water potential threshold for 50% stomatal closure) were associated with cooler regions ($r^2=0.48-0.72$, $P<0.03$, $n=10-29$). Overall, cultivars grown in warmer, drier regions exhibited traits that would reduce transpiration and conserve soil water longer into the growing season, but potentially increase stomatal and temperature limitations on photosynthesis under future, hotter conditions.

Keywords: Climate, drought tolerance, embolism resistance, grape, hydraulic, stomatal closure, stomatal conductance, turgor loss point, viticulture.

Introduction

Crop species have largely been selected for reproductive traits, while domestication has generally had less impact on the vegetative physiology traits that determine plant stress tolerance and resource demand (Cao *et al.*, 2014; Lin *et al.*, 2014). However, these traits are expected to strongly affect crop responses to the warmer, drier climatic conditions projected for many agricultural areas under global change (Rosenzweig *et al.*, 2014; Grossiord *et al.*, 2020). Here we evaluated whether growing

region climate is related to physiological diversity across wine grape (*Vitis vinifera*) cultivars, which could have important implications for cultivar and regional differences in grapevine productivity and water use under future conditions.

The sensitivity of grapevines to climate is a central tenet in winemaking. Most grape cultivars only produce high-quality wine within narrow climatic ranges, but the optimal climate varies widely across cultivars, driving a close association between

Abbreviations: ϵ , leaf cell wall modulus of elasticity; π_o , leaf osmotic potential at full hydration; π_{ld} , leaf turgor loss point; g_{max} , maximum stomatal conductance; g_s , Ψ_{50} , leaf water potential threshold for a 50% stomatal closure; $K_{leaf} \Psi_{50}$, leaf water potential threshold for a 50% decline in hydraulic conductance; $K_{stem} \Psi_{50}$, stem water potential threshold for a 50% decline in hydraulic conductance; T_{mean} and T_{max} , mean and maximum growing season temperature; VPD_{mean} and VPD_{max} , mean and maximum vapor pressure deficit.

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cultivars and growing regions (Jones *et al.*, 2005; Gladstones, 2015). Many wine regions are expected to become too warm to produce high-quality wine from their traditional cultivars over the next several decades, but predictions for the impacts of global change on viticulture rarely account for phenotypic diversity (Hannah *et al.*, 2013; Vivin *et al.*, 2017). Evaluating the relationships between physiology traits and climate would assess trait diversity as a potential driver of regional differences in grapevine responses to global change and provide insight into grapevine adaptations to warm and dry conditions. We compiled trait and climate data from the literature for 34 cultivars from wine regions with a wide range of climatic conditions to conduct the first test of these relationships.

We collected values for seven traits that characterize plant water use and drought tolerance, namely the maximum stomatal conductance (g_{\max}), the leaf water potential threshold for 50% stomatal closure ($g_s \Psi_{50}$), the leaf and stem water potentials inducing a 50% decline in leaf and stem hydraulic conductance ($K_{\text{leaf}} \Psi_{50}$ and $K_{\text{stem}} \Psi_{50}$), and the leaf turgor loss point (π_{tlp}), osmotic potential at full hydration (π_o), and cell wall modulus of elasticity (ϵ) (Cheung *et al.*, 1975; Maherali *et al.*, 2004; Klein, 2014). A higher g_{\max} supports a greater maximum rate for transpiration and photosynthesis, and a more negative $g_s \Psi_{50}$ indicates a more anisohydric stomatal strategy, where the stomata remain open under more negative water potentials (Santiago *et al.*, 2004; Klein, 2014). Species with a more negative $K_{\text{leaf}} \Psi_{50}$ and $K_{\text{stem}} \Psi_{50}$ maintain water transport under more severe water stress, and species with a more negative π_{tlp} lose turgor in the leaf cells and wilt under more negative water potentials (Cheung *et al.*, 1975; Maherali *et al.*, 2004; Martorell *et al.*, 2015b). Plants achieve a more negative π_{tlp} through a higher cell solute concentration (i.e. a more negative osmotic potential, π_o) (Bartlett *et al.*, 2012). These traits are correlated with climate for wild species, and thus are potentially important to geographic associations in grapevines (Bartlett *et al.*, 2016; Murray *et al.*, 2019). A higher ϵ , which indicates a stiffer cell wall, was not related to climate, but protects leaf structure under water stress by resisting changes in cell volume as water potentials decline (Bartlett *et al.*, 2012).

Heat and water stress potentially favor the opposite stomatal trait values (Chaves *et al.*, 2016). Water stress generally favors a lower g_{\max} to reduce the maximum rate of water loss from the canopy (i.e. the maximum transpiration rate), which prevents strong declines in plant water potential and saves water in the soil to use over the growing season (Sinclair *et al.*, 2005; Chaves *et al.*, 2016). However, a lower stomatal conductance (g_s) also reduces photosynthesis by limiting both CO_2 uptake and the evaporative cooling effect of transpiration, which allows leaf temperatures to increase beyond the optimal range for the photosynthetic reactions (Greer and Weedon, 2012). Thus, dry environments also typically favor a more negative $g_s \Psi_{50}$ to maintain greater gas exchange as plant water potentials decline (Bartlett *et al.*, 2016). This combination of stomatal traits

would reduce g_s early in the growing season, when soil water is abundant and plant water potentials are high, while preventing strong declines in g_s later in the growing season, when the soil, atmosphere, and plants are drier. Grapevines receive relatively little precipitation during the growing season and have historically been grown without irrigation, suggesting that cultivars in drier regions would benefit from these traits (Chaves *et al.*, 2010, 2016). High temperatures could produce the same, or opposite, traits. Heat exacerbates water stress by increasing the evaporative demand of the atmosphere, or the vapor pressure deficit (VPD). Transpiration is determined by VPD and g_s , allowing plants to compensate for a high VPD through stomatal traits that reduce g_s . However, grapevines have been found to increase g_s during heat waves, suggesting that warmer regions could instead favor a higher g_{\max} to increase the capacity for evaporative cooling (Soar *et al.*, 2009; Sadras *et al.*, 2012). We evaluated these opposing pressures by testing relationships between the stomatal traits and growing season temperature, precipitation, and VPD.

Alternatively, diversity in stomatal traits could reflect the impacts of climate on ripening. The cultivars that produce high-quality wine in each region generally reach maturity in the beginning of autumn, when temperatures are favorable for the production of pigment, flavor, and aroma compounds (Gladstones, 2015). However, warmer regions reach the temperature thresholds for budbreak earlier in the spring, lengthening the growing season (Moncur *et al.*, 1989). Warmer regions could favor stomatal traits that reduce g_s , photosynthesis, and thus the carbon supply for growth and ripening (Medrano *et al.*, 2003; Dai *et al.*, 2009). Limiting carbon uptake to reduce the rate of berry sugar accumulation could increase the time required for ripening (Dai *et al.*, 2009), compensating for the earlier budbreak and allowing secondary metabolites to develop under favorable conditions in early autumn.

We expected the stomatal traits to drive the relationships between the hydraulic and water relations traits and climate. Dry environments generally favor more negative values for $K_{\text{leaf}} \Psi_{50}$, $K_{\text{stem}} \Psi_{50}$, π_o , and π_{tlp} to support a more anisohydric stomatal strategy (Bartlett *et al.*, 2012, 2016; Martorell *et al.*, 2015b). Conversely, warm regions would favor a greater capacity for water transport if grapevines use a higher g_{\max} to increase evaporative cooling (Santiago *et al.*, 2004). However, anatomical constraints produce trade-offs between water transport capacity and drought tolerance. The xylem anatomical traits that facilitate water movement also increase embolism spread, preventing plants from exhibiting both a highly negative $K_{\text{stem}} \Psi_{50}$ and high maximum stem conductance (Gleason *et al.*, 2016). Further, a more negative π_o increases the osmotic pressure in the leaf epidermal cells, which opposes the expansion of the guard cells and constrains stomatal opening, creating a trade-off between a high g_{\max} and a highly negative π_o and π_{tlp} (Franks, 2003). These relationships drive a trade-off between a high g_{\max} and an anisohydric $g_s \Psi_{50}$ (Henry *et al.*,

2019). In this case, warmer wine regions would be associated with less negative values for $K_{\text{leaf}} \Psi_{50}$, $K_{\text{stem}} \Psi_{50}$, π_o , and π_{dp} .

Finally, historical, cultural, and enological factors could be more important drivers for geographic associations in wine grapes than plant performance (Van Leeuwen and Seguin, 2006). Management practices, including rootstock selection and canopy management, may have allowed viticulturists to grow cultivars with physiology traits that are not adaptive to local conditions, decoupling these traits from growing season climate (Fraga *et al.*, 2012). We tested correlations between traits and between traits and climate to evaluate these hypotheses and provide new insight into the potential impacts of global change on diverse cultivars and regions.

Materials and methods

Compiling the trait dataset

We compiled values for the seven physiology traits from the literature. We identified studies to include in the dataset by searching the Web of Science database for terms related to the traits, including ‘stomatal closure’, ‘stomatal responses to water stress’, ‘embolism resistance’, ‘pressure–volume curve’, ‘turgor loss point’, and ‘osmotic adjustment’, and the study system, including ‘wine grape’ and ‘*Vitis vinifera*’. We also examined the references cited in recent meta-analyses on grapevine stomatal behavior (Lavoie-Lamoureux *et al.*, 2017; Hochberg *et al.*, 2018). We included studies that met the following criteria. (i) For studies reporting stomatal responses to water potential, g_s was measured at a saturating light level (i.e. $>1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) to reduce variation due to light exposure. (ii) The methods specified whether g_s was measured with a porometer or an infra-red gas analyzer (IRGA), since a previous meta-analysis for grapevine showed that porometers reported significantly higher g_s values (Lavoie-Lamoureux *et al.*, 2017). (iii) g_s and water potential (Ψ) were measured for each plant within a 3 h time frame, and this time frame was the same on every sampling date, to limit the effects of diurnal environmental variation on this relationship. (iv) For studies reporting stem embolism resistance ($K_{\text{stem}} \Psi_{50}$) values, this trait was measured with the bench dehydration method, to limit variation due to methodological differences (Choat *et al.*, 2010).

These criteria produced a dataset of 34 cultivars from 57 European wine regions and 23 studies (Table 1; Figs 1–3; Dataset 1 at Dryad Digital Repository <https://doi.org/10.25338/B8M61H>). This dataset mostly contained field-grown vines (82%), but also vines grown in pots in field (4%) or greenhouse (14%) conditions, subjected to deficit irrigation or no irrigation over the growing season or experimental period. Trait values were compiled from only one study for 23 of the 34 cultivars (68%), a few (i.e. 2–4) studies for eight cultivars (24%), and many (i.e. 7–12) studies for only three cultivars (8%; Cabernet Sauvignon, Grenache, and Syrah).

g_{max} and $g_s \Psi_{50}$ were not reported by most studies, so we calculated these traits by fitting the relationships between g_s and Ψ values. We used the WebPlotDigitizer tool to collect points from plots of g_s and Ψ (Rohatgi, 2019). Since the functional form of these relationships can vary

among plants, we fitted these points with sigmoidal ($g_s = \frac{a}{1 + e^{-\left(\frac{\Psi - c}{b}\right)}}$), exponential ($g_s = ae^{-b\Psi}$), logistic ($g_s = \frac{a}{1 + \left(\frac{\Psi}{c}\right)^b}$), and linear ($g_s = a + b\Psi$) relationships with the ‘anneal’ function in R (v. 3.6.2) (Murphy, 2015). We used the Aikake information criterion corrected for small sample sizes (AICc) to identify the best-fit model for each relationship. We defined the model with the minimum AICc value as the best-fit model, except in the case where the AICc values were within 2 units for all models, and

thus none of the non-linear models was more strongly supported than the more parsimonious linear model (Burnham and Anderson, 2010). We then used the best-fit model to calculate g_{max} as the g_s at $\Psi=0$ MPa, and $g_s \Psi_{50}$ as the water potential at $g_s = g_{\text{max}}/2$. We excluded values from poorly correlated best-fit relationships ($r^2 < 0.2$).

We compiled g_{max} values calculated from relationships between g_s and water potential, measured either concurrently with gas exchange or at pre-dawn, for stems or leaves. However, we only included $g_s \Psi_{50}$ values calculated for leaf water potentials measured concurrently with gas exchange (Ψ_L). Water potentials in transpiring plants are less negative in the stems than in the leaves, and thus we expected thresholds for 50% stomatal closure to be less negative (Williams and Araujo, 2002). We also repeated the analyses for all g_{max} values pooled and for the subset of g_{max} values estimated from relationships with Ψ_L ($g_{\text{max,L}}$). We focused on g_{max} and $g_s \Psi_{50}$ values extrapolated from Ψ_L because most values were available in the literature for these measurements.

Some studies measured the leaf water relations traits (π_o , ϵ , and π_{dp}) repeatedly for different environmental conditions, since grapevines adjust π_o and ϵ in response to water stress to produce a more negative π_{dp} or greater cell hydration at π_{dp} (i.e. RWC_{dp}) (Patakas *et al.*, 2002; Martorell *et al.*, 2015b). We categorized trait values measured under fully irrigated conditions, or under deficit irrigation but early in the growing season (i.e. early June), when soil water availability is typically still high, as well watered. We categorized values from greenhouse drought treatments or deficit-irrigated vines measured late in the growing season (i.e. mid-September) as water stressed. We analyzed correlations separately for well-watered and water-stressed trait values. RWC_{dp} was not reported for enough cultivars to include in these analyses.

Defining optimal climate

We used a global dataset for wine grape production to define growing season climate for each cultivar. Anderson and Nelgen (2020) compiled the land surface area producing grapes for winemaking (i.e. wine grape-bearing area) from governmental or wine industry databases for 629 wine-growing regions worldwide. The growing regions were defined by the source databases, based on geographic, historical, and cultural differences in winemaking within each country. The authors defined geographic coordinates for each region from a representative town. We compiled the most recent bearing area data, from 2016, for each cultivar in the trait dataset, and calculated weighted mean climate variables from the relative bearing area in each European wine region. We defined relative bearing areas as the percentage of each cultivar’s total European bearing area occurring in each European wine region (relative bearing areas summed to 100% for each cultivar.) We restricted this study to European regions, where irrigation is either not permitted or is strictly limited, to focus on the regions where local climate most strongly impacts vine performance. We also focused on the most representative growing regions for each cultivar by excluding regions with a relative bearing area $\leq 5\%$. These criteria produced a dataset of 57 wine regions (Fig. 1; Dataset 2 at Dryad). Each cultivar was associated with 1–6 regions that accounted for 41–99% (mean=82%) of the total European bearing area (Dataset 3 at Dryad).

We used the coordinates from the global dataset and the ‘speciesmap’ package in R to extract monthly mean temperature, precipitation, and VPD values for each region from the WorldClim database (Anderson and Nelgen, 2020; Duursma and Duursma, 2020). We used the values from April to October to calculate the mean and maximum growing season temperature (T_{mean} and T_{max}) and VPD (VPD_{mean} and VPD_{max}), and mean and minimum precipitation (P_{mean} and P_{min}) for each region (Jones *et al.*, 2005). We then recalculated the relative bearing areas from the total area of the most representative regions and used the new relative bearing areas to calculate weighted mean climate variables for each cultivar (Fig. 2).

Table 1. Trait and climate variable values compiled from the literature for 34 cultivars from 23 studies

Cultivar	Loc.	Inst.	T _{mean}	VPD _{mean}	g _{max}	Type	g _s Ψ ₅₀	K _{stem} Ψ ₅₀	WW π _o	WS π _{tip}	Reference
Aglianico	F	P	16.3	1.31	459	L	-1.42		-0.64	-2.11	Levin et al. (2020)
Alicante Bousc.	F		18.7	1.29					-1.06	-2.31	Alsina et al. (2007)
Cabernet Sauvignon	F	I	17.4	1.37	449	S		-2			Alsina et al. (2007)
Cabernet Sauvignon	G		17.4	1.37			-1.73				Bota et al. (2016)
Cabernet Sauvignon	F	P	17.4	1.37	444	L	-1.48				Charrier et al. (2016)
Cabernet Sauvignon	F	P	17.4	1.37	382	L	-1.17				Levin et al. (2020)
Cabernet Sauvignon	F	P	17.4	1.37	474	L	-1.03				Speirs et al. (2013)
Cabernet Sauvignon	G	P	17.4	1.37	61	S					Speirs et al. (2013)
Cabernet Sauvignon	F	I	18.7	1.51	324	L	-1.2	-2.09	-1.8	-1.8	Tramontini et al. (2014)
Carmenère	F	I	18.7	1.51			-1.09		-1.67	-1.67	Villalobos-González et al. (2019)
Castelão	F	P	19.1	1.42	348	PD					Villalobos-González et al. (2019)
Castelão	F	P	19.1	1.42	255	PD					Villalobos-González et al. (2019)
Chardonnay	F	P	15.8	1.32	415	S		-2.52	-0.98	-2.33	Rodrigues et al. (2008)
Chardonnay	F	I	15.8	1.32				-2.97			Rodrigues et al. (2008)
Chardonnay	F	I	15.8	1.32							Alsina et al. (2007)
Chardonnay	G	I	15.8	1.32	323	L	-1.36		-1.53	-2.22	Bota et al. (2016)
Chasselas	F	I	13.9	1.14	393	PD					Choat et al. (2010)
Cinsault	F	P	18.6	1.46	402	L	-1.47				Park (2001)
Ekgaina	F	I	16.7	1.39	626	PD					Zufferey and Smart (2012)
Freisa	F	P	17.8	1.47	438	L	-1.52				Levin et al. (2020)
Grenache	F	I	18.7	1.37				-1.47	-1.12	-2.21	Alsina et al. (2007)
Grenache	F	I	18.7	1.37	366	S		-2.95			Bota et al. (2016)
Grenache	G		18.7	1.37							Charrier et al. (2018)
Grenache	FP	P	18.7	1.37	85	PD				-1.38	Dayar et al. (2020)
Grenache	G	I	18.7	1.37	274	S					Gezron et al. (2015)
Grenache	F	P	18.7	1.37	398	L	-1.47				Levin et al. (2020)
Grenache	F	I	18.7	1.37	442	L	-0.96		-0.93	-1.23	Martorell et al. (2015a)
Grenache	F	I	18.7	1.37	418	PD					Prieto et al. (2010)
Grenache	F	I	18.7	1.37	341	L	-0.92		-1.5	-1.35	Schultz (2003)
Malbec	F	P	16.8	1.38	477	L	-1.48				Levin et al. (2020)
Marselan	F	I	18.4	1.47	687	PD					Prieto et al. (2010)
Mavrodafni	O	I	19.8	1.53	380	PD					Beis and Patakas (2010)
Merlot	F	I	17.0	1.41	608	S					Bota et al. (2016)
Merlot	G	I	17.0	1.41	408	S			-1.02	-1.31	Hochberg et al. (2016)
Montepulciano	F	P	19.1	1.55	426	L	-1.59				Levin et al. (2020)
Montepulciano	FP	I	19.1	1.55	256	L	-0.86			-1.36	Tombesi et al. (2014)
Moscato	F	P	20.3	1.54	394	PD					Rodrigues et al. (2008)
Moscato	F	P	20.3	1.54	281	PD					Rodrigues et al. (2008)
Mourvedre	F	I	20.3	1.44	316	PD					Prieto et al. (2010)
Parellada	F		18.7	1.51				-0.99	-1.21	-2.57	Alsina et al. (2007)
Petit Verdot	F	P	18.8	1.28	424	L	-1.5				Levin et al. (2020)
Refosco	F	P	17.6	1.42	489	L	-1.4				Levin et al. (2020)
Riesling	G	I	15.1	1.25	272	L	-1.25		-1.75	-1.9	Park (2001)

Table 1. Continued

Cultivar	Loc.	Inst.	T _{mean}	VPD _{mean}	g _{max}	Type	g _s Ψ ₅₀	K _{stem} Ψ ₅₀	WW π _o	WS π _{rip}	Reference
Sangiovese	FP	I	18.7	1.48	275	L	-0.96			-1.67	Tombesi et al. (2014)
Sauvignon Blanc	F	I	16.6	1.34	419	L	-1.61	-3	-1.01	-2.26	Alsina et al. (2007)
Sauvignon Blanc	F	I	16.6	1.34	388	PD					Naor et al. (1994)
Savatiano	FP	I	21.4	1.50	112	PD					Beis and Patakas (2010)
Semillon	FP	P	16.6	1.40	465	L	-1.51			-1.92	Dayar et al. (2020)
Sousao	F	P	16.6	1.21	480	S					Levin et al. (2020)
Syrah	F	I	18.6	1.42	90	PD		-2.74			Bota et al. (2016)
Syrah	G	P	18.6	1.42	342	S					Charrier et al. (2018)
Syrah	FP	P	18.6	1.42	590	L	-1.34				Dayar et al. (2020)
Syrah	G	I	18.6	1.42	715	PD					Gerzon et al. (2015)
Syrah	F	P	18.6	1.42	252	S					Levin et al. (2020)
Syrah	F	I	18.6	1.42	300	L	-1.05				Prieto et al. (2010)
Syrah	F	I	18.6	1.42	80	S					Romero et al. (2017)
Syrah	F	I	18.6	1.42	348	L	-1.23				Schultz (2003)
Syrah	G	P	18.6	1.42	304	L	-1.05				Tramontini et al. (2014)
Syrah	F	I	18.6	1.42	475	S					Villabos-González et al. (2019)
Syrah	F	I	18.6	1.42	480	L	-1.53				Villabos-González et al. (2019)
Tannat	F	P	16.8	1.38	480	L					Zufferey and Smart (2012)
Tempranillo	F	I	18.1	1.20	495	S					Levin et al. (2020)
Tempranillo	F	I	18.1	1.20	466	L	-1.54				Alsina et al. (2007)
Tempranillo	F	P	18.1	1.20	439	L	-1.2				Bota et al. (2016)
Tempranillo	F	I	18.1	1.20	468	L	-1.38				Levin et al. (2020)
Tinta Madeira	F	P	20.2	1.53	483	L	-1.27				Martorell et al. (2015a)
Touri Nacional	F	P	17.5	1.24	483	L	-1.55				Levin et al. (2020)
Trincadeira	F	P	18.2	1.28	483	L					Levin et al. (2020)
White Grenache	F	I	18.6	1.49							Alsina et al. (2007)

'Loc.' indicates location (F=field, G=greenhouse, FP=potted plants grown in field conditions). 'Inst.' indicates the instrument used for the stomatal trait measurements (P=porometer, I=infra-red gas analyzer). Trait variables are the maximum stomatal conductance (g_{max}), the leaf water potential inducing 50% stomatal closure (g_s Ψ₅₀), the stem water potential inducing a 50% decline in stem hydraulic conductance (K_{stem} Ψ₅₀), and the leaf osmotic potential at full hydration (π_o) and turgor loss point (π_{rip}) under well-watered (WW) and water-stressed (WS) conditions, respectively. 'Type' indicates the water potential variable used to extrapolate g_{max} (L=midday leaf water potentials, S=midday stem water potentials, PD=pre-dawn leaf water potentials). Climate variables are the mean growing season temperature (T_{mean}) and vapor pressure deficit (VPD_{mean}).

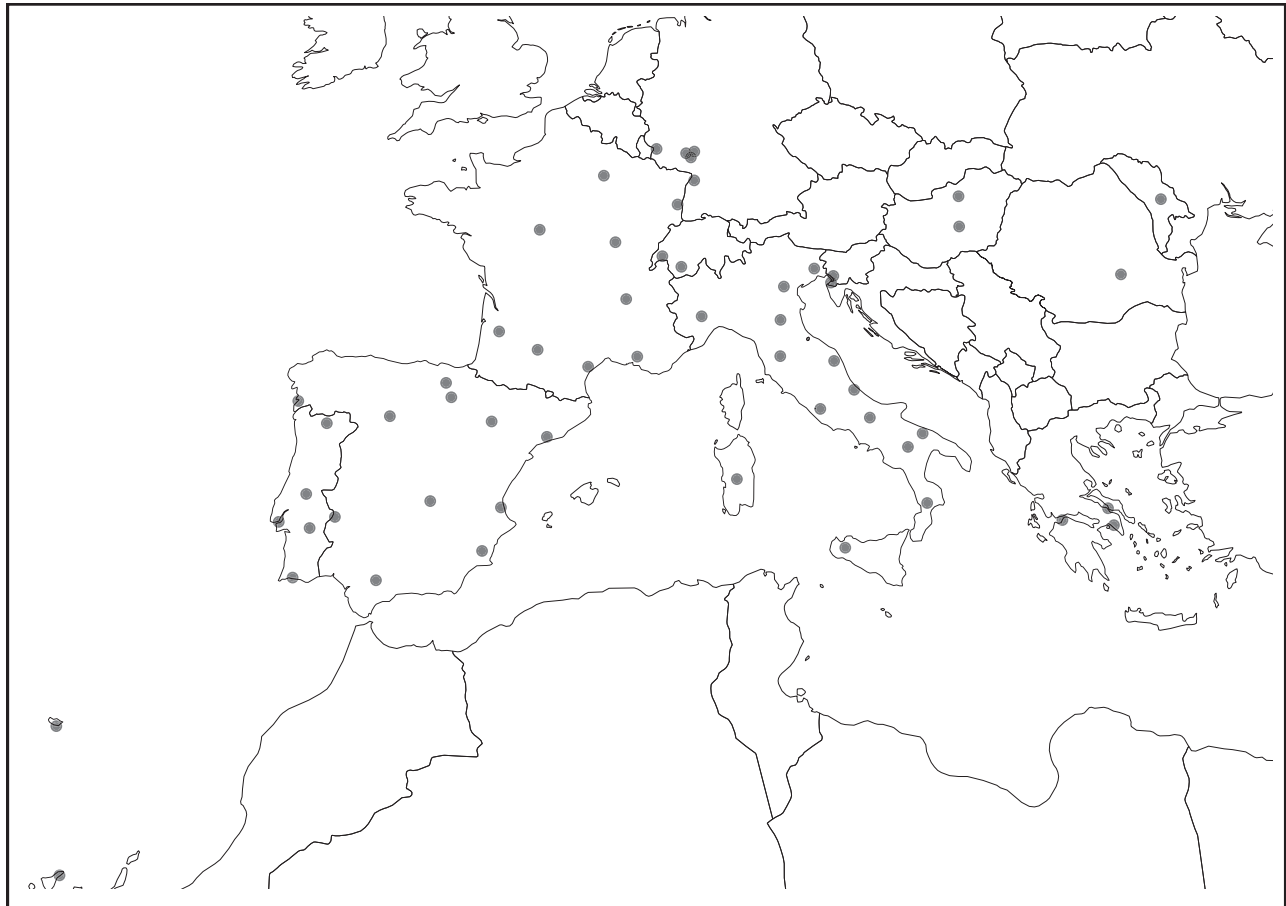


Fig. 1. Map of the 57 European wine regions used to define growing season climate for the 34 wine grape cultivars with physiology trait values reported in the literature. Each region contains >5% of the total European bearing area of at least one cultivar. Regional categories and coordinates follow Anderson and Nelgen (2020). The coordinates and climate variables for each region are provided in Supplementary Table S1 and the regions associated with each cultivar are given in Supplementary Table S2.

Analyses

We tested the correlations between traits and between traits and climate for all combinations with values from ≥ 5 cultivars. The trait and climate relationships were tested for field-grown vines, to capture trait variation in realistic growing conditions.

We used mixed-effects models to account for the statistical dependence between trait values collected for the same cultivar from different studies (Fig. 3). We included a single climate or trait predictor variable as a fixed effect and cultivar as a random effect. Models predicting stomatal traits also included the gas exchange instrumentation and an interaction term between the instrument and the trait or climate predictor as fixed effects, to allow the slope and intercept of these relationships to vary with instrumentation. We ensured relationships were robust to highly influential points by removing values with a Cook's distance $> 4/(N-k-1)$, where N is the number of observations and k is the number of fitted parameters. This criterion removed 0–2 data points from each relationship (shown in red in Fig. 4). We tested the significance of the fixed effects by using F -tests to compare models with all fixed effects, each subset of the fixed effects, and only random effects. We defined the best-fit model for each relationship as the most parsimonious model that significantly improved fit compared with those with fewer predictors. We assessed goodness-of-fit for the fixed effects in the best-fit model by using conditional and marginal r^2 to compare the proportion of variance explained by the full model and the fixed effects alone (Nakagawa and Schielzeth, 2013).

We used ordinary least-squares regression (OLS) to test the relationships with a single trait value for each cultivar, or trait values for $n < 7$ cultivars, since mixed-effects models did not converge for these small sample sizes (Table 4). We also used OLS to test correlations within the two studies with ≥ 5 cultivars, to evaluate whether these relationships were robust across cultivars growing in the same environmental conditions (Alsina *et al.*, 2007; Levin *et al.*, 2020). Each cultivar was measured only once in these studies.

Results

Stomatal and hydraulic traits are correlated with optimal growing season climate

The stomatal traits and stem embolism resistance were significantly correlated with growing season climate. The g_{\max} values determined from relationships with Ψ_L ($g_{\max, L}$) were correlated with VPD_{mean} and VPD_{max} (marginal $r^2 = 0.63$ and 0.65 , $P < 0.03$, $n = 29$) (Tables 2, 3; Fig. 4A, B). $g_{\max, L}$ was significantly lower in the cultivars in wine regions with a higher VPD. Porometer measurements produced significantly higher

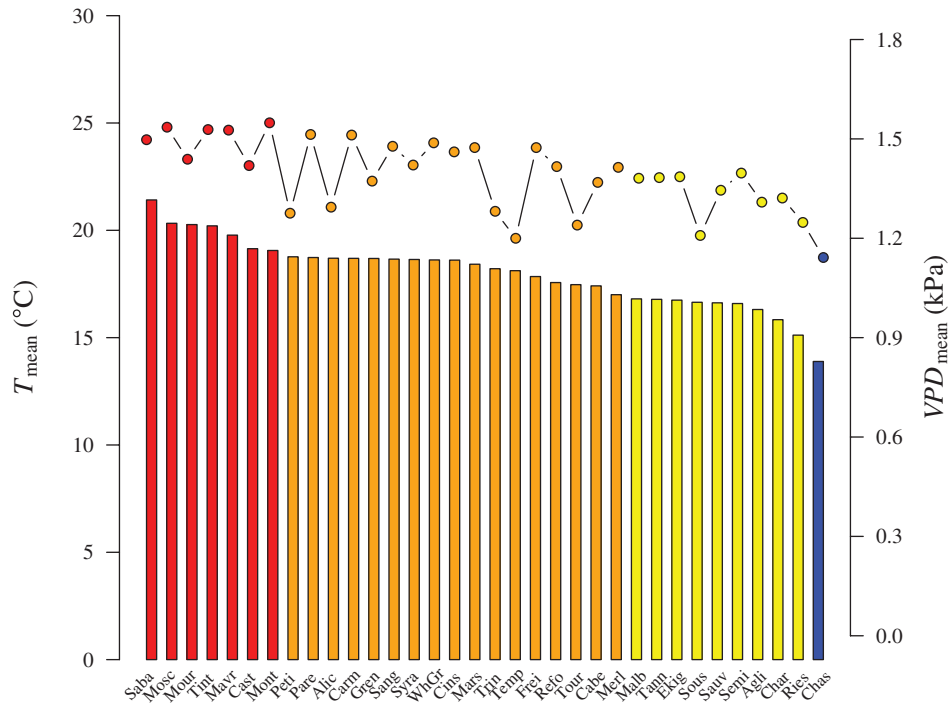


Fig. 2. Mean growing season (April–October) temperature (T_{mean} , bars) and vapor pressure deficit (VPD_{mean} , points) for each of the 34 cultivars included in the physiology trait dataset. Colors indicate the climate and maturity groupings from Jones (2005), with red=hot-climate varieties ($T_{\text{mean}} > 19^\circ\text{C}$), orange=warm-climate varieties ($17^\circ\text{C} < T_{\text{mean}} \leq 19^\circ\text{C}$), yellow=intermediate varieties ($15^\circ\text{C} < T_{\text{mean}} \leq 17^\circ\text{C}$), and blue=cool-climate varieties ($T_{\text{mean}} < 15^\circ\text{C}$). Labels are the first four letters of the cultivar names in Table 1.

$g_{\text{max,L}}$ values, but instrumentation did not affect the slope of the $g_{\text{max,L}}$ and VPD relationships (Table 3). However, the climate variables were not correlated with the g_{max} values pooled from relationships with different water potential variables ($g_{\text{max,to}}$) (Table 2). Correlations across cultivars from a common garden study partly supported the relationships across studies (Levin *et al.*, 2020). Cultivars with a lower $g_{\text{max,L}}$ were significantly associated with regions with a higher maximum growing season temperature (T_{max}) (OLS $r^2=0.39$, $P < 0.01$, $n=14$). However, $g_{\text{max,L}}$ was not significantly correlated with VPD_{mean} or VPD_{max} for these varieties (OLS $r^2=0.03$, $P=0.2$ and $r^2=0.15$, $P=0.08$, respectively).

$g_s \Psi_{50}$ was significantly correlated with mean growing season temperature (T_{mean}) (marginal $r^2=0.72$, $P < 0.001$, $n=29$) (Tables 2, 3; Fig. 4C). Cultivars with a more negative $g_s \Psi_{50}$ (i.e. more anisohydric cultivars) were associated with cooler growing regions. This relationship depended strongly on instrumentation. $g_s \Psi_{50}$ was less negative in the cultivars measured with a porometer, and the slope of this relationship was significantly higher in the cultivars measured with an IRGA (Table 3; Fig. 4C). However, $g_s \Psi_{50}$ was not significantly correlated with climate across the cultivars from the common garden study (Levin *et al.*, 2020) (OLS $r^2 < 0.02$, $P > 0.5$, $n=14$).

$K_{\text{stem}} \Psi_{50}$ was also significantly correlated with T_{mean} , with more embolism-resistant cultivars associated with cooler regions (marginal $r^2=0.48$, $P=0.03$, $n=10$) (Tables 2, 3; Fig. 4D).

This relationship was also significant across cultivars from a common garden study (Alsina *et al.*, 2007) (OLS $r^2=0.49$, $P=0.04$, $n=6$) (Fig. 4D).

$K_{\text{leaf}} \Psi_{50}$ and the leaf water relations traits (π_o , ε , and π_{tp}) were not significantly related to climate. Further, none of the traits was correlated with mean or minimum growing season precipitation.

The stomatal traits are related to leaf osmotic potential and turgor loss point

The stomatal and leaf pressure–volume curve traits were strongly related. $g_{\text{max,L}}$ was significantly correlated with π_o under well-watered conditions (OLS $r^2=0.96$, $P < 0.001$, $n=6$) (Table 4; Fig. 5A). π_o was less negative in cultivars with a higher g_{max} . Conversely, $g_s \Psi_{50}$ was significantly correlated with π_{tp} under water-stressed conditions, which was more negative in more anisohydric cultivars (marginal $r^2=0.67$, $P=0.03$, $n=12$) (Table 4; Fig. 5B). However, the well-watered and water-stressed values for π_{tp} and π_o were not significantly correlated, even within a common garden study (marginal $r^2 < 0.05$, $P > 0.3$, $n=15$ across studies and OLS $r^2 < 0.01$, $P > 0.7$, and $n=7$ across the cultivars from Alsina *et al.*, 2007) (Table 4; Fig. 5C). This allowed $g_{\text{max,L}}$ and $g_s \Psi_{50}$ to vary independently. Including $g_s \Psi_{50}$ did not significantly improve predictions for $g_{\text{max,L}}$ beyond instrumentation alone (F -test, $P=0.5$, $n=31$) (Fig. 5D). The

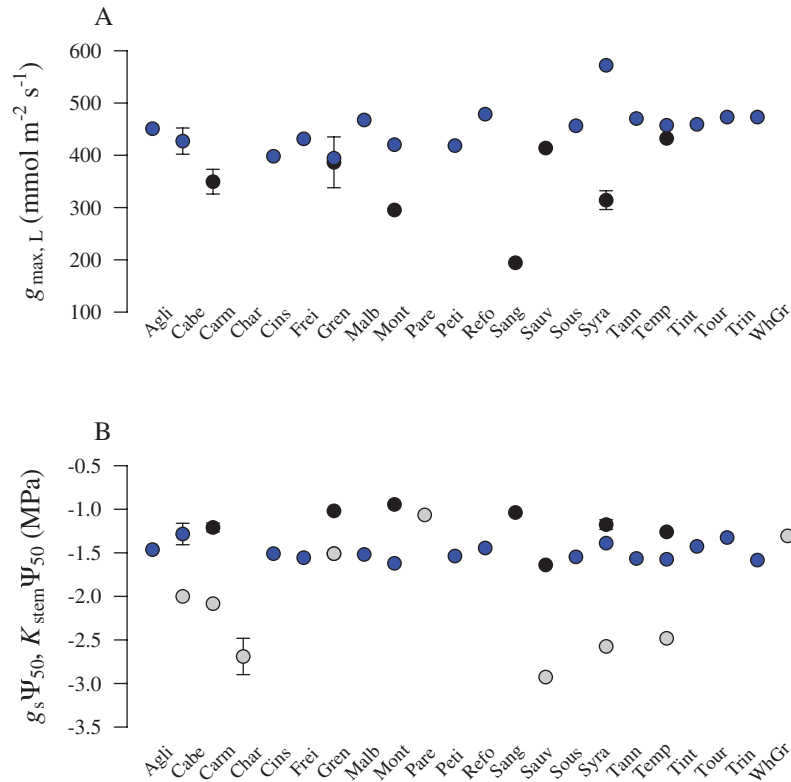


Fig. 3. Cultivar means for the traits that were significantly correlated with climate (Table 2), including the maximum stomatal conductance, extrapolated from relationships with leaf water potential ($g_{\max,L}$, A), the leaf water potential threshold for 50% stomatal closure ($g_s \Psi_{50}$, B), and the stem water potential inducing a 50% decline in stem hydraulic conductance ($K_{\text{stem}} \Psi_{50}$, B). Blue points show porometer and black points show IRGA measurements. Gray points show $K_{\text{stem}} \Psi_{50}$. Error bars are SEs. Labels are the first four letters of the cultivar names in Table 1.

pooled g_{\max} values ($g_{\max,\text{tot}}$) were not significantly correlated with the other traits (Table 4).

Osmotic potential at full hydration was significantly correlated with ϵ and π_{tp} under well-watered conditions (marginal $r^2 > 0.5$, $P < 0.03$, $n = 15$) (Table 4). π_o and π_{tp} were correlated under water stress (marginal $r^2 = 0.83$, $P < 0.001$, $n = 24$), while ϵ values in both conditions were strongly related (marginal $r^2 = 0.58$, $P = 0.02$, $n = 15$), indicating that π_{tp} under water stress was mainly determined by osmotic adjustment.

$K_{\text{stem}} \Psi_{50}$ was not significantly correlated with the pressure–volume curve traits, while there were insufficient data to test relationships with the stomatal traits (Table 4). $K_{\text{leaf}} \Psi_{50}$ values were also not available for enough cultivars to test trait correlations.

Discussion

Grapevine stomatal and hydraulic traits were significantly related to growing season climate, despite the importance of historical and cultural factors in the associations between cultivars and wine regions, and the considerably stronger focus of artificial selection on fruit chemistry than on vegetative physiology traits. Cultivars associated with warm regions with a

high evaporative demand exhibited stomatal traits that would reduce transpiration and conserve soil water longer into the growing season (Fig. 4A–C). Embolism resistance was more strongly associated with cool temperatures than water stress, while π_{tp} and π_o were not correlated with climate, but were tightly coordinated with the stomatal traits (Figs 4D, 5A, B). Altogether, these findings suggest that the impacts of global change on grapevine water use and carbon gain will vary strongly across cultivars and wine regions, with cultivars from warmer, drier regions at greater risk for embolism and canopy temperature stress under future conditions. These findings also point to π_{tp} and π_o as promising traits for breeders to use to select for stomatal behavior that improves grapevine resilience to global change.

The lower $g_{\max,L}$ and less negative $g_s \Psi_{50}$ values in warm-climate cultivars would partly compensate for the effects of a greater evaporative demand on transpiration, maintaining a high soil water availability longer over the growing season but reducing maximum rates for photosynthesis and evaporative cooling. The relationships between $g_{\max,L}$ and climate were robust to differences in instrumentation, while only IRGA measurements for $g_s \Psi_{50}$ were strongly responsive to climate (Table 4; Fig. 4A–C). However, this may reflect a stronger impact of environmental plasticity on $g_s \Psi_{50}$, since the IRGA

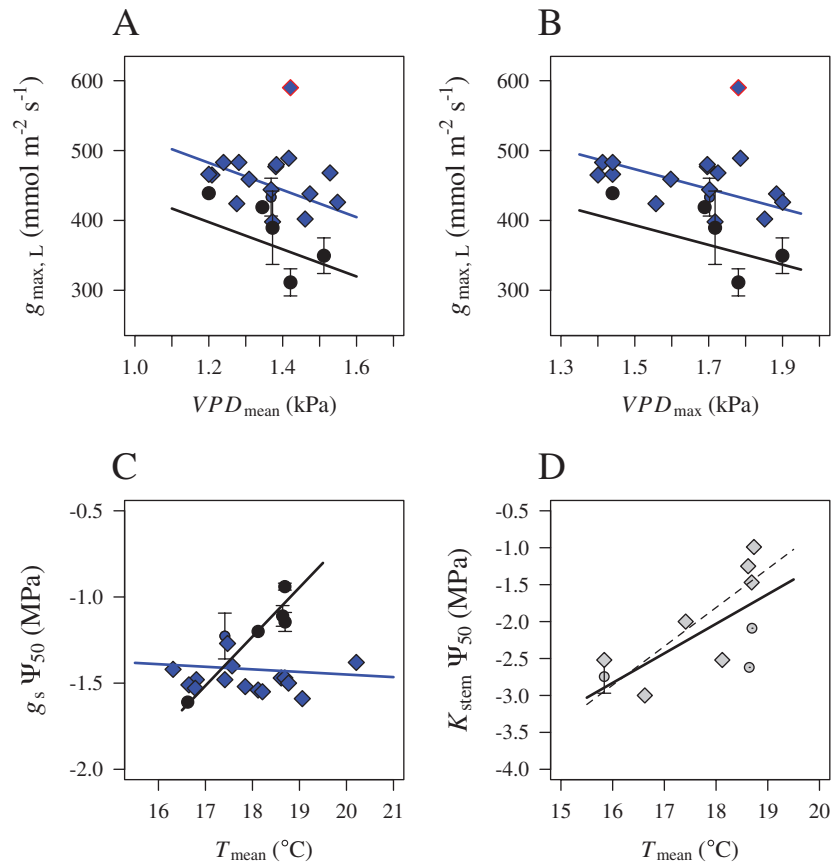


Fig. 4. Correlations between traits and climate across wine grape cultivars. The stomatal traits $g_{\max,L}$ (A, B) and $g_s \Psi_{50}$ (C) and stem embolism resistance $K_{\text{stem}} \Psi_{50}$ (D) were significantly correlated with mean and maximum growing season vapor pressure deficit (VPD_{mean} and VPD_{max}) and mean temperature (T_{mean}). Cultivars with a higher $g_{\max,L}$ were associated with wine regions with a lower VPD_{mean} and VPD_{max} (marginal $r^2=0.63$ and 0.65 , $P<0.03$, $n=29$) (A, B). Cultivars with a more negative $g_s \Psi_{50}$ were associated with significantly cooler wine regions, and this relationship depended strongly on gas exchange instrumentation (marginal $r^2=0.72$, $P<0.001$, $n=29$) (C). More embolism-resistant cultivars were also associated with cooler wine regions, both across and within studies (marginal $r^2=0.48$, $P=0.03$, $n=10$ and OLS $r^2=0.49$, $P=0.04$, $n=6$, respectively) (D). Blue points show porometer and black points show infra-red gas analyzer measurements (A–C) and gray points show $K_{\text{stem}} \Psi_{50}$ values (D). Points with error bars indicate means and SEs for cultivars with trait values compiled from multiple studies. The means and SEs are calculated for values measured with the same gas exchange instruments. The points with a red outline in (A) and (B) were identified as influential outliers by Cook’s distance metrics and removed from the model fits. Diamond-shaped points indicate values from common garden experiments (Levin *et al.* 2020 in A–C and Alsina *et al.*, 2007 in D). Solid lines indicate the best-fit relationships across studies (Tables 2, 3). Dashed lines are significant correlations within common garden studies (D). Line colors correspond to gas exchange instrument.

values were largely compiled from across studies, while most of the porometer values were from a common garden (Levin *et al.*, 2020) (Fig. 4C). Indeed, $g_s \Psi_{50}$ has been shown to exhibit significant plasticity over the growing season in grapevines, shifting to more negative values in leaves that developed later in the season (Sorek *et al.*, 2020). Further, $g_{\max,L}$ was correlated with VPD across studies and temperature within the common garden comparison, but both relationships showed a lower $g_{\max,L}$ in regions with greater evaporative demand. Thus, we consider these findings to strongly support an association between greater atmospheric dryness and lower transpiration early in the growing season, when plant water potentials are high. Further common garden and cross-site comparisons are needed to conclusively resolve the relationships between

climate and stomatal closure, with these findings suggesting that a less negative $g_s \Psi_{50}$ also limits transpiration later in the season, when vines are typically more water stressed.

Previous work supports crop species benefitting from a lower g_{\max} under hot, dry conditions. Hydraulic models predict that reducing the maximum transpiration rate would maintain greater soil water availability over the growing season, reducing the risk of severe water stress in grapevines (Gambetta *et al.*, 2020) and improving yield under high VPD in soybeans (Zaman-Allah *et al.*, 2011). Reducing the maximum transpiration has also been experimentally shown to increase yields under non-irrigated conditions in soybeans, peanut, chickpeas, and sorghum (Sinclair *et al.*, 2008, 2010; Zaman-Allah *et al.*, 2011; Vadez *et al.*, 2014). Further, the highest yielding chickpea

Table 2. Correlations between the physiology traits and climate variables

	T_{mean}	T_{max}	VPD_{mean}	VPD_{max}	P_{mean}	P_{min}	n (obs.)	n (cult.)
$g_{\text{max, L}}$	-0.7	-0.7	-0.8**	-0.8**	0.3	0.1	27	18
$g_{\text{max, tot}}$	-0.3	-0.2	-0.2	-0.2	0.1	0.1	50	29
$g_s \Psi_{50}$	0.8**	0.7	0.7	0.7	0.2	0.2	29	19
$K_{\text{stem}} \Psi_{50}$	0.7*	0.6	0.6	0.6	-0.1	-0.1	10	9
WW π_o	-0.3	-0.2	-0.3	-0.3	0.1	0.1	12	9
WW ϵ	0.1	0.1	0.1	0.1	-0.2	-0.1	12	9
WW π_{tip}	-0.1	0	-0.1	-0.1	0	0	12	9
WS π_o	0.4	0.3	0.1	0.1	0	0	21	13
WS ϵ	0.2	0.3	0	0.1	-0.1	-0.2	17	12
WS π_{tip}	0.4	0.3	0.2	0.1	0	0	21	13

Relationships are fitted with mixed-effects models, including the climate variable as a fixed effect and cultivar as a random effect. Values are r values calculated from the marginal r^2 , which indicates the proportion of variance explained by the fixed effects. Asterisks indicate significant correlations ($*P < 0.05$, $**P < 0.01$). n is the number of observations and cultivars. Trait variables are the maximum stomatal conductance, extrapolated from relationships with leaf water potential ($g_{\text{max, L}}$) or both stem and leaf water potentials ($g_{\text{max, tot}}$), the leaf water potential inducing 50% stomatal closure ($g_s \Psi_{50}$), the stem water potential inducing a 50% decline in stem hydraulic conductance ($K_{\text{stem}} \Psi_{50}$), and the leaf osmotic potential at full hydration (π_o), cell wall modulus of elasticity (ϵ), and turgor loss point (π_{tip}) under well-watered (WW) and water-stressed (WS) conditions. There were insufficient data to test correlations with $K_{\text{leaf}} \Psi_{50}$. Climate variables are the mean and maximum growing season temperature (T_{mean} and T_{max}) and vapor pressure deficit (VPD_{mean} and VPD_{max}), and mean and minimum growing season precipitation (P_{mean} and P_{min}) across the major European wine regions for each cultivar.

Table 3. Significant relationships between trait and climate variables (i.e. the relationships indicated with asterisks in Table 2)

Model	a	b	c	d	Mar. r^2	Cond. r^2	P	n (obs.)	n (cult.)
$g_{\text{max, L}} = a + b \times VPD_{\text{mean}} + c \times \text{Instrument}$	631	-195	85		0.62	0.63	<0.001	27	18
$g_{\text{max, L}} = a + b \times VPD_{\text{max}} + c \times \text{Instrument}$	605	-141	80		0.65	0.66	<0.001	27	18
$g_s \Psi_{50} = a + b \times T_{\text{mean}} + c \times \text{Instrument} + d \times \text{Instrument} \times T_{\text{mean}}$	-6.4	0.3	5.2	-0.3	0.72	0.75	<0.001	29	19
$K_{\text{stem}} \Psi_{50} = a + b \times T_{\text{mean}}$	-9.2	0.4			0.48	0.50	0.03	10	9

Predictors shown in the model equations were modeled as fixed effects, and cultivar was modeled as a random effect. The best-fit models were defined as the most parsimonious models that significantly improved fit, compared with models with only random effects. Letters indicate the fitted slope and intercept parameters. Marginal and conditional r^2 values show the proportion of variance explained by the fixed effects alone and the fixed and random effects, respectively. P -values are from the F -tests comparing the best-fit model with the model with only random effects. n is the number of observations and cultivars. Cultivars with a lower $g_{\text{max, L}}$ were associated with growing regions with a higher mean and maximum VPD, and cultivars with more negative $g_s \Psi_{50}$ and $K_{\text{stem}} \Psi_{50}$ were associated with cooler regions. Porometer measurements increased $g_{\text{max, L}}$ and $g_s \Psi_{50}$ values (Instrument=1 for porometer and 0 for IRGA measurements). Gas exchange instrumentation significantly impacted the slope and intercept of the relationship between $g_s \Psi_{50}$ and T_{mean} .

genotypes used a lower transpiration rate to save water early in the season, although these genotypes also exhibited greater gas exchange later in the season to support fruit set (Zaman-Allah *et al.*, 2011), contrary to our findings for $g_s \Psi_{50}$. Common garden experiments have not conclusively demonstrated a benefit for these traits in grapevines. g_s was not significantly correlated with biomass growth across wine grape cultivars or North American *Vitis* species in common garden comparisons in high-VPD wine regions (Padgett-Johnson *et al.*, 2003; Rogiers *et al.*, 2009). However, variation in other traits could have reduced the effects of the stomatal traits, especially since these vines were own-rooted, and thus could have had access to different soil water resources (Smart *et al.*, 2006). Experimental studies and modeling approaches that account for a wider range of physiology traits are needed to quantify the impacts of the stomatal traits on performance under different climatic

conditions, including the future, hotter conditions projected for most wine regions (Hannah *et al.*, 2013).

These stomatal traits could also compensate for the longer growing season in warm regions, by down-regulating photosynthesis to extend the time to ripening into autumn (Gladstones, 2015). Conversely, cultivars in cooler regions could require greater gas exchange to gain sufficient carbon for ripening, since growing seasons are shorter and photosynthesis is potentially limited by cooler temperatures (i.e. leaf temperatures < 30 °C) (Hendrickson *et al.*, 2004; Greer and Weedon, 2012). Indeed, Tempranillo vines with higher photosynthetic rates accumulated sugar more rapidly in the berries (Salazar-Parra *et al.*, 2018). Further, the cooler-climate cultivar Sauvignon Blanc exhibited a higher $g_{\text{max, L}}$ than warmer-climate Syrah in this dataset (IRGA $g_{\text{max, L}} = 419$ and mean IRGA $g_{\text{max, L}} = 315$ $\text{mmol m}^{-2} \text{s}^{-1}$, respectively) (Fig. 3A) (Naor

Table 4. Correlations between the physiology traits

	Predictor	Marginal <i>r</i>	OLS <i>r</i>	<i>n</i> (obs.)	<i>n</i> (cult.)
$g_{\max, L}$	$g_s \Psi_{50}$, Instr.	-0.54		31	21
$g_{\max, L}$	WW π_o		0.98**	6	5
$g_{\max, L}$	WW ε		-0.80	6	5
$g_{\max, L}$	WW π_{tip}		0.84	6	5
$g_{\max, L}$	WS π_o	0.60		12	8
$g_{\max, L}$	WS ε		0.17	8	7
$g_{\max, L}$	WS π_{tip}	0.33		12	8
$g_s \Psi_{50}$	WW π_o		0.50	6	5
$g_s \Psi_{50}$	WW ε		0.57	6	5
$g_s \Psi_{50}$	WW π_{tip}		-0.58	6	5
$g_s \Psi_{50}$	WS π_o	0.60		12	8
$g_s \Psi_{50}$	WS ε		-0.11	8	7
$g_s \Psi_{50}$	WS π_{tip}	0.82*		12	8
$K_{stem} \Psi_{50}$	WW π_o		-0.31	7	7
$K_{stem} \Psi_{50}$	WW ε		-0.33	7	7
$K_{stem} \Psi_{50}$	WW π_{tip}		0.14	7	7
$K_{stem} \Psi_{50}$	WS π_o		-0.18	9	9
$K_{stem} \Psi_{50}$	WS ε		0.57	7	7
$K_{stem} \Psi_{50}$	WS π_{tip}		-0.10	9	9
WW π_o	WW ε	-0.71*		15	11
WW π_o	WW π_{tip}	0.71*		15	11
WW π_o	WS π_o	0.23		15	11
WW π_o	WS ε	-0.64		15	11
WW π_o	WS π_{tip}	0.03		15	11
WW ε	WW π_{tip}	-0.65		15	11
WW ε	WS π_o	0.20		15	11
WW ε	WS ε	0.76*		15	11
WW ε	WS π_{tip}	0.28		15	11
WW π_{tip}	WS π_o	0.17		15	11
WW π_{tip}	WS ε	-0.64		15	11
WW π_{tip}	WS π_{tip}	-0.09		15	11
WS π_o	WS ε	0.22		20	14
WS π_o	WS π_{tip}	0.91***		24	15
WS ε	WS π_{tip}	0.31		20	14

Relationships with trait values for $n \geq 7$ cultivars and multiple values for at least one cultivar were fitted with mixed-effects models, including the variables from the Predictor column as fixed effects and cultivar as a random effect. Marginal *r* indicates the *r* values for the fixed effects. Asterisks indicate significant correlations with the trait predictor (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Only the correlation between $g_{\max, L}$ and $g_s \Psi_{50}$ included porometer and IRGA measurements, while the stomatal traits were only measured with an IRGA in the other correlations. Relationships with a single observation per cultivar or $n < 7$ cultivars were fitted with ordinary least-squares (OLS) regression. A larger $g_{\max, L}$ was significantly associated with a less negative π_o under well-watered conditions, and a more negative $g_s \Psi_{50}$ was significantly correlated with a more negative π_{tip} under water stress. All of the pressure–volume curve traits were correlated in well-watered conditions, while only π_{tip} and π_o were correlated under water stress. $K_{stem} \Psi_{50}$ was not correlated with the other traits.

et al., 1994; Schultz, 2000; Villalobos-González *et al.*, 2019), and reached flowering and veraison and accumulated sugar in the berries more quickly under common garden conditions (Greer and Weston, 2016). However, photosynthesis is determined by both stomatal and biochemical traits, and a greater biochemical efficiency could compensate for the impact of a lower $g_{\max, L}$ in the warmer-climate cultivars (Prieto *et al.*, 2010). Stomatal and biochemical traits were not reported for enough cultivars to test these relationships in this study. Thus, more work incorporating both stomatal and biochemical limitations is

needed to quantify the relative importance of these traits for cultivar differences in photosynthesis.

Contrary to our expectations, drier regions were not associated with greater embolism resistance. Instead, $K_{stem} \Psi_{50}$ was significantly more negative in cooler regions, suggesting that cold, rather than drought tolerance, has been the main selective pressure for embolism resistance in wine grapes (Table 2; Fig. 4D). In spring, water transport through the previous year's xylem rehydrates the dormant buds and stimulates budbreak (Sperry *et al.*, 1987). Freezing embolizes the xylem,

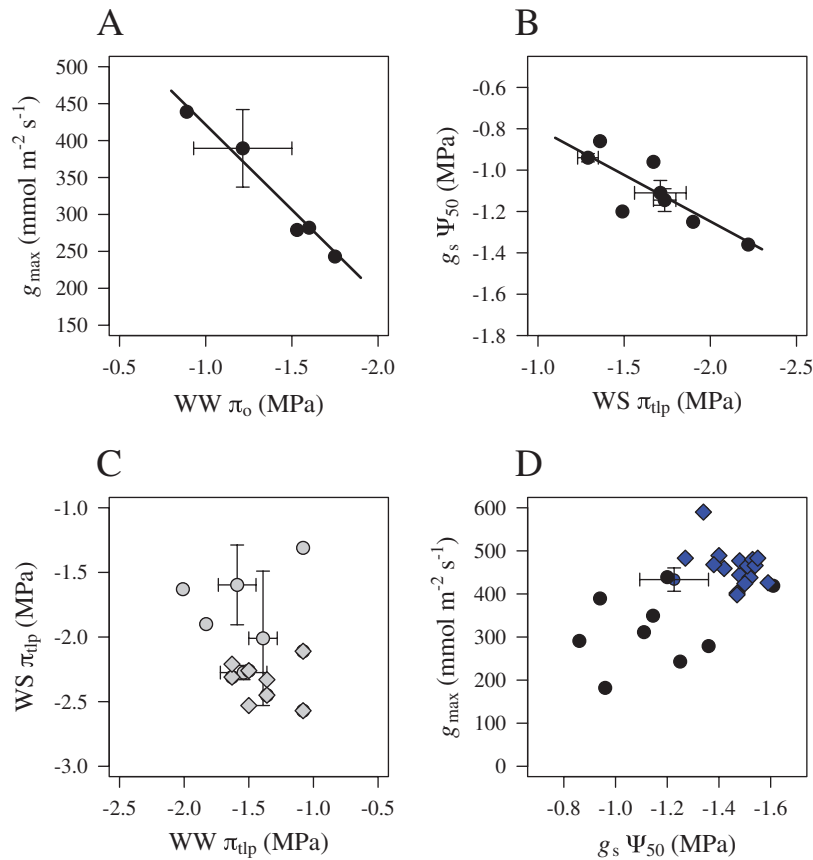


Fig. 5. Correlations between physiology traits. Symbols follow Fig. 4. A higher $g_{max,L}$ was significantly associated with a less negative π_o under well-watered conditions (WW π_o) (OLS $r^2=0.96$, $P<0.001$, $n=6$) (A). A more negative turgor loss point under water-stressed conditions (WS π_{tlp}) was significantly associated with a more negative $g_s \Psi_{50}$ (marginal $r^2=0.67$, $P=0.03$, $n=12$) (B). However, well-watered and water-stressed π_{tlp} values were not correlated (marginal $r^2=0.01$, $P=0.6$, $n=15$), even across cultivars from a common garden study (Alsina *et al.*, 2007) (C). $g_s \Psi_{50}$ and g_{max} also did not exhibit a trade-off across cultivars (D).

which limits water transport and induces structural damage that increases xylem vulnerability even after the conduits are refilled (Christensen-Dalsgaard and Tyree, 2014). The xylem anatomical traits that confer embolism resistance during drought also reduce freezing damage (Yin *et al.*, 2018), potentially driving the relationship between $K_{stem} \Psi_{50}$ and climate. Indeed, grapevines may experience more xylem damage from cold than from water stress. Grapevines exhibit multiple mechanisms, including conservative stomatal behavior, leaf abscission, and vulnerability segmentation between the leaves and stems, that generally prevent strong declines in stem water potential and conductivity (Hochberg *et al.*, 2017; Charrier *et al.*, 2018). Instead, performance under water stress may be more strongly limited by leaf than by stem vulnerability. Conversely, the relationship between $g_s \Psi_{50}$ and temperature suggests that anisohydric stomatal behavior could have favored embolism resistance in cool regions, though there were insufficient data to test the correlations between the stomatal traits and $K_{stem} \Psi_{50}$. However, further work is needed to determine whether the relationship between $g_s \Psi_{50}$ and climate

is robust to environmental differences between studies (Sorek *et al.*, 2020).

The leaf water relations traits were not correlated with climate, but the leaf osmotic potential and turgor loss point were strongly related to the stomatal traits. Grapevines used a more negative π_{tlp} under water stress to support a more anisohydric $g_s \Psi_{50}$, while the maximum stomatal opening appeared to be limited by a more negative π_o under well-watered conditions (Franks, 2003). However, grapevines used extensive osmotic adjustment to avoid the trade-off between g_{max} and $g_s \Psi_{50}$ observed in other species (Alsina *et al.*, 2007; Henry *et al.*, 2019). The π_o and π_{tlp} values under water stress were not constrained by the values from well-watered conditions (Fig. 5C), pointing to osmotic adjustment as a crucial adaptation to relax trade-offs between stomatal responses to environmental conditions earlier and later in the growing season.

The stomatal and hydraulic traits were important to cultivar associations with climate, despite the wide range of management practices available to regulate vine water use. Growers can reduce transpiration through canopy management practices

that decrease the light-exposed surface area (Williams and Ayars, 2005). Irrigation is restricted in many European wine regions, but growers can increase the water available to the vine through deeper rooting rootstocks and soil amendments that increase water-holding capacity (Medrano *et al.*, 2015; Dodson Peterson *et al.*, 2019; Gambetta *et al.*, 2020). Rootstocks also impact vine hydraulics and carbon allocation (Zhang *et al.*, 2016; Peccoux *et al.*, 2018), but there was insufficient replication to test for an effect of rootstocks on trait and climate relationships in this dataset, which included 12 different varieties (Dataset 1 at Dryad). However, previous work has shown that the scion traits analyzed here, including stomatal responses to water potential, turgor loss point, and stem embolism resistance, are not altered by the rootstock (Barrios-Masias *et al.*, 2019). Our findings suggest that, despite the potential for management practices to reduce transpiration and water stress, a water-saving stomatal strategy is still important to grapevine performance in high-VPD regions. Future work should incorporate trait data and climate projections to develop new management recommendations for specific regions and cultivars.

Overall, this work provides a basis for future studies to incorporate physiological diversity into predictions for the impacts of global change on viticulture. These findings suggest that the effects of climate change on grapevine water use and carbon gain will vary across cultivars and regions. The lower embolism resistance and greater reliance on a water-saving stomatal strategy suggest that cultivars in warm regions, with a high evaporative demand, will be more vulnerable to temperature and CO₂ limitations on photosynthesis under future conditions (Soar *et al.*, 2009; Chaves *et al.*, 2016). Osmotic adjustment also emerged as a critical trait for grape breeders to leverage to produce the stomatal behavior that is most adaptive under future conditions. These findings for wine grapes, where cultivation has been strongly influenced by factors beyond plant performance, suggest that physiology traits are important to cultivar associations with climate broadly across crop species. Thus, analyzing trait and climate relationships has the strong potential to inform predictions for cultivar and regional responses to climate change in many economically important fruit and nut species.

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Author contributions

GS compiled the trait dataset and contributed to manuscript preparation. MKB designed and conducted the analyses and led manuscript preparation.

Data availability

All data supporting the findings of this study are included in the supplementary datasets, which are available in the Dryad Digital Repository (<https://doi:10.25338/B8M61H>; Bartlett and Sinclair, 2021).

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