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Grape cultivars adapted to hotter, drier growing regions exhibit greater photosynthesis under hot conditions despite less drought-resistant leaves

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Grape Cultivars Adapted to Hotter, Drier Growing Regions Exhibit Greater Photosynthesis Under Hot Conditions Despite Less Drought-Resistant Leaves

By

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Contents

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Abstract

Many agricultural areas are expected to face hotter, drier conditions from climate change. Understanding the mechanisms crops use to mitigate these stresses can guide breeding for more tolerant plant material. We tested relationships between traits, physiological function under hot conditions, and historical climate associations to evaluate these mechanisms for winegrapes. We hypothesized a more negative leaf osmotic potential at full hydration (π_o), which reduces leaf turgor loss during drought, and either a metabolically cheaper or more osmoprotectant leaf chemical composition, to allow cultivars associated with hot, dry regions to maintain greater gas exchange under hot growing conditions. We measured π_o, gas exchange, and leaf chemistry for 7 commercially important winegrape cultivars that vary widely in historical climate associations (i.e., originate or predominantly grown in different global regions that experience a wide range of different environmental conditions). Vines were grown under common garden field conditions in a hot wine-growing region (Davis, California) and measured over the hottest period of the growing season (July – September). Our results show π_o varied significantly between cultivars, and all cultivars significantly reduced π_o (osmotically adjusted) over the study period, though osmotic adjustment did not vary across cultivars. π_o was correlated with gas exchange and climate associations, but in the opposite directions than expected. Photosynthesis and π_o were higher in the cultivars associated with hotter, less humid regions. Leaf chemical composition varied between cultivars, but was not related to climate of origin associations. These findings suggest that leaf turgor maintenance is not a primary limitation on grapevine adaptation to hot or atmospherically dry growing conditions. Thus, selecting for a more negative π_o or greater osmotic adjustment is not a promising strategy to develop more climate-resilient grape varieties,

contrary to findings for other crops. Future work is needed to identify the mechanisms increasing photosynthesis in the cultivars associated with hot, dry regions.

Introduction

Climate change is projected to exacerbate heat and drought stress in many agricultural regions worldwide, with detrimental impacts on crop yield and quality (Hasegawa et al. 2022, DaMatta et al. 2009, Lobell et al. 2006). Breeding or genetic engineering of more stress tolerant cultivars is a promising strategy to mitigate impacts from climate change, but these efforts have been limited by uncertainty around the traits that confer stress tolerance (Paleari et al. 2022, Vivin et al. 2017). Evaluating trait and climate associations across existing cultivars that are adapted to a diverse range of climatic conditions can identify the traits that have been important for adaptation to hot and dry conditions (Cortés and López-Hernández 2021).

Two leaf water relations traits - osmotic potential at full hydration (π_o) and osmotic adjustment ($\Delta\pi_o$) – are considered strong predictors of drought performance across cultivars of other crops and wild plant species (Baltzer et al., 2008, Bartlett et al., 2012, 2014, 2016, Blum 2016), but have not been tested as predictors for stress tolerance in grape cultivars. π_o and $\Delta\pi_o$ impact drought tolerance by affecting leaf vulnerability to damage from dehydration. Adaptations to reduce dehydration damage are crucial to maintain gas exchange and carbon assimilation under hot and dry conditions. Much of this damage is caused by the cells losing turgor – the pressure exerted by water pushing out against the cell walls – as they dehydrate. Turgor supports the cell walls and drives cell expansion (Hsiao et al. 1984; Morgan 1984). Losing turgor impairs growth and causes the cell walls to collapse and deform, which impedes water and CO_2 transport and causes leaves to wilt (Turner and Jones 1980; Scoffoni et al. 2018). The ability to maintain turgor during dehydration is strongly determined by the osmotic potential at full hydration (π_o), which measures the potential energy for water influx generated by the cell

solutes (Hsiao et al. 1984). Cells with a higher solute concentration exert a stronger driving force for water influx, reducing dehydration and turgor loss. Thus, species or cultivars with higher leaf cell solute concentrations, measured as more negative leaf osmotic potentials at full hydration, typically undergo disruptions in leaf water transport, stomatal closure, and wilting under more severe water stress (Bartlett et al. 2016, Baltzer et al. 2008, Scoffoni et al. 2018). Water-stressed plants, including grapevines, can also make leaf osmotic potentials more negative (i.e., osmotically adjust) by accumulating solutes in the leaf cells, which helps maintain turgor and reduce leaf vulnerability to wilting, hydraulic dysfunction, and stomatal closure (Sorek et al. 2021, Rodriguez-Dominguez et al. 2016, Martorell et al. 2015). Leaf osmotic potentials are typically more negative in plant species adapted to hotter, drier environments, and crop cultivars with greater osmotic adjustment (i.e., larger declines in π_o under water stress) typically maintain higher yields under drought (Bartlett et al. 2012, Blum 2016).

Despite the importance of osmotic potential to drought tolerance in other plants, it is largely unknown how osmotic potential and adjustment vary across grape cultivars or impact grapevine performance under dry conditions. Most studies have focused on one or two cultivars and have shown that grapevines osmotically adjust over the growing season or during drought, and that vines that have undergone adjustment are less vulnerable to (i.e., have more negative leaf water potential thresholds for) leaf hydraulic dysfunction and stomatal closure (Sorek et al. 2021, Rodriguez-Dominguez et al. 2016, Martorell et al. 2015). However, the only study comparing π_o across more cultivars found that osmotic potential was unrelated to stem drought tolerance traits, raising uncertainty about the importance of this trait to whole-plant drought tolerance (Alsina et al. 2008). Furthermore, other work has found that cultivars typically grown in hotter, drier regions exhibit more water-saving stomatal behavior, including a lower maximum

stomatal conductance (Bartlett and Sinclair 2021). These findings suggest that the opposite trait values (a less negative osmotic potential and lower osmotic adjustment) would be most adaptive to hotter, drier conditions, if grapevines benefit more from conserving water than maintaining high gas exchange rates. Evaluating how these traits contribute to cultivar differences in stress tolerance would provide insight into whether these traits are worthwhile targets for cultivar improvement efforts for grapevine, and the direction these traits should be changed.

Previous work has also suggested that the chemical composition of the solutes could impact stress tolerance. Leaf cells can accumulate a wide range of solutes during osmotic adjustment, including inorganic ions, sugars, amino acids, and proteins, and solute composition varies widely across species (Zivcak et al. 2016). Synthesizing organic solutes, such as sugars or amino acids, is more resource intensive and energetically expensive than increasing inorganic ion uptake from the soil. Additionally, some organic solutes (e.g., proline) also serve as osmoprotectants, which enhances drought tolerance by stabilizing protein and membrane structures to reduce damage from dehydration (Zivcak et al. 2016, Gagneul et al. 2007). Leaf solute composition has only been measured for a few grape cultivars, and it is unknown whether solute composition contributes to cultivar differences in drought or heat tolerance (Patakas et al. 2002, Degu et al. 2019). If so, this would indicate that identifying specific solutes and their role in osmotic adjustment could lead to cultivar improvement efforts could target genotypes that produce specific solutes to achieve optimal values for osmotic potential and osmotic adjustment.

In this study, we tested whether osmotic potential, osmotic adjustment, and solute composition vary across *Vitis vinifera* wine grape cultivars historically adapted to different climatic conditions and are associated with cultivar differences in vine physiological performance (i.e., gas exchange and water potentials) under hot conditions. Specifically, we

tested whether 1: there are significant differences in osmotic potential, osmotic adjustment, and solute composition between cultivars, 2: these differences correspond to cultivar differences in climate associations (i.e., the typical climatic conditions where each cultivar is grown), and 3: these traits are correlated with vine water potentials and gas exchange. We compared these variables across seven cultivars growing under common garden conditions in a hot wine region. We hypothesized that cultivars that are typically grown in hotter, drier regions would exhibit greater osmotic adjustment and maintain more negative osmotic potentials. We also hypothesized that these traits would enable these cultivars to undergo greater leaf water stress and maintain greater stomatal conductance and photosynthesis over the hottest, most water-stressed period of the growing season. We also expected solute composition to vary across cultivars and correspond to differences in climate associations, though it was unknown from previous work whether adapting to heat and drought stress would favor ion accumulation, as a metabolically 'cheap' strategy to lower osmotic potentials, or the production of organic osmoprotectants to protect the biochemical machinery from dehydration. We evaluated relationships between these traits, plant physiological performance, and historical climate associations in winegrapes, which are an excellent study system for climate adaptation, since cultivars have diverse and well-characterized climatic niches (Anderson and Nelgen 2020). Furthermore, winegrapes are an economically important crop (valued at $70 billion worldwide) under considerable threat from climate change (Alston and Sambucci 2019, Jones et al. 2004). Addressing these hypotheses should provide crucial insight into the physiological mechanisms adapting winegrapes to stressful growing conditions.

Materials and Methods

Plant Material and Growth Conditions

We measured leaf water relations and chemistry on mature vines of 7 *Vitis vinifera* cultivars typically grown in different climatic regions (i.e., Riesling and Pinot Noir from cool regions, Chardonnay, Merlot and Syrah from warm regions, and Zinfandel and Sangiovese from hot regions) (N = 3 - 4 vines/cultivar).

The vines are established in an experimental vineyard on the University of California, Davis campus (lat: 38.53, lon: -121.75). Half of the vines of each cultivar were divided between two adjacent blocks. The blocks are established with a north-south row orientation and are all trained using a California vertical shoot-positioned (VSP) trellis system. All vines are grafted onto the same rootstock (420A). Soil types at the site range from a Reiff to a Yolo loam (USGS Web Soil Survey). During the experimental period, all plants received the same irrigation and no precipitation. The vineyard is drip irrigated approximately once per week to replace 80% of water loss. The replacement amount is based on reference evapotranspiration values generated by the Davis California Irrigation Management Information System (CIMIS) and the seasonal crop coefficient (K_c) values, which are calculated based on equations from Williams et al. (2014).

We conducted measurements from the onset of berry ripening (veraison) to harvest (July to September) in 2020, to capture osmotic adjustment during the hottest period of the growing season. The experimental vineyard is located in a hot (Winkler V) growing region. Daily mean and maximum temperatures ranged from 21 to 31℃ and 26 to 40℃ over the study period, respectively, based on climate data collected by the Davis CIMIS station

(https://cimis.water.ca.gov/). The site experienced a severe heat wave in mid-August (14 to 18 August 2020) that considerably increased atmospheric evaporative demand (Fig. 1).

Climate associations

We defined cultivar climate associations in two ways. First, we represented climate as a set of continuous variables, using the methods from Bartlett and Sinclair (2021). To summarize, we used the 2016 global winegrape dataset from Anderson and Nelgen (2020) to identify the Old-World growing regions where each cultivar in our study is well represented. For each cultivar, we defined the well-represented regions as those containing at least 5% of the cultivar's total Old-World bearing area. We then used this subset to calculate the bearing area fraction in each well-represented region, so that the sum of bearing area fractions across well-represented region equals 100% for each cultivar. We used the coordinates from Anderson and Nelgen (2020) to extract maximum monthly temperature (T_{max}) and vapor pressure deficit (VPD_{max}) for each growing region from the WorldClim dataset, since these variables were the most strongly correlated with gas exchange in a previous meta-analysis (Bartlett and Sinclair 2021). We then used the bearing area fractions for each region to calculate a weighted average T_{max} and VPD_{max} for each cultivar.

Second, to test a common simplified approach, we classified cultivars according to the climate categories from Anderson and Nelgen (2020). This dataset records the global bearing area of each cultivar located in cool, warm, or hot growing regions. Mean growing season temperature is < 15ºC for cool regions, 17 - 19ºC for warm regions, and >19ºC for hot regions. The climate category for each cultivar is defined as the category containing most of its bearing area. Our cultivars were divided among three groups: Cool: Riesling and Pinot, Warm: Chardonnay, Merlot and Syrah, and Hot: Zinfandel and Sangiovese. Similar methods have been used to define regional suitability for cultivars and predict cultivar responses to future climate

conditions (Lamarque et al. 2023, Bartlett and Sinclair 2021, Fraga et al. 2016). We used both approaches in our study to test whether these methods identify the same relationships between physiology and climate.

Plant water status and gas exchange

We measured leaf water potential (Ψ) and gas exchange at midday (between 1100hr and 1300hr) once per week from July 16 to September 3, 2020. We selected healthy, newly expanded mature leaves 8-12 nodes below the shoot tip consistently on the east side of the canopy. We measured stomatal conductance and photosynthesis on two leaves per vine with a portable gas exchange system (Li-Cor 6800, Nebraska USA), using a fan speed of 10,000 rpm, CO_2 concentration of 400 µmol mol^{-1} and light intensity of 1900 µmol m^{-2} s^{-1}. We allowed humidity and air temperature in the sample chamber to match ambient conditions. We selected two adjacent leaves per vine and measured midday water potential with a pressure chamber (PMS Instrument; model 1505D) (N = 6 - 8 leaves per cultivar). Leaves were excised at the base of the petiole, sealed in humidified Whirl-pak bags, and either measured immediately or stored in the refrigerator for up to one week before measuring. We also measured one leaf per vine for predawn leaf water potential between 0400 hr to 0600 hr at the beginning, middle, and end of the experimental period (23 July, 5 August, and 3 September 2020).

Osmotic potential at full turgor

We measured leaf osmotic potential at full turgor (π_o) on three sampling dates (15 July, 18 August, and 16 September 2020). We excised one shoot per vine, placed the end of the shoot in deionized water, and covered the shoots in a dark, humidified plastic bag to rehydrate overnight. We double-bagged two leaves per shoot in humidified Whirl-pak bags at the same time the following morning to standardize the leaf rehydration time. We then measured leaf osmotic potential following the rapid osmometer method from Bartlett et al. 2012. Briefly, we punctured

and froze leaf discs in liquid nitrogen, then sealed the discs in a vapor pressure osmometer (Wescor, Vapro 5600, Logan, Utah, USA) to determine the osmotic potential at full turgor.

Sampling for leaf chemistry

To measure leaf solute composition, we collected two leaves per plant from the same shoots used to measure osmotic potential on two of the sampling dates (July 15 and September 16, 2020), then flash-froze the leaves in liquid nitrogen. Leaves were cryogenically pulverized to a fine powder using a tissue lyser (Retsch, Newton, PA, USA) with steel jars containing 2 cm diameter steel balls. Samples were stored at -80C until analysis.

Inorganic Ions

K, Ca, Mg, and Na ion concentrations were measured by the UC Davis Analytical Lab (Davis, CA), following standard analytical methods (Sah and Miller 1992, Meyer Keliher 1992). Briefly, ions were extracted from 0.4 g of dry leaf biomass using nitric acid-hydrogen peroxide microwave digestion and quantified with Inductively Coupled Plasma Atomic Emission Spectrometry (ICP-AES). Each sample was digested with 2 mL ultra-pure DI water, 2 mL hydrogen peroxide, and 1 mL trace metal grade nitric acid, using a microwave digestion system (Mars Xpress, Matthews, NC, USA). Each sample was brought up to a final volume of 15mL with DI water (dilution factor 30x), then diluted 4x again and analyzed with a Thermo ICP 6500 (Thermo Scientific, Waltham, Massachusetts, USA). Detection limits for this method range from 0.5 ppm to 100 ppm.

Amino Acids

Amino acids were extracted from 100 mg of fresh leaf tissue using an EZ:FAAST GC-FID kit (Phenomenex, Torrance, CA) following methods from Wallis et al. (2012). Briefly, 100 mg of fresh weight leaf tissue was extracted in a 500ul in a phosphate buffered saline (PBS) solution adjusted to a pH of 6.8. Samples were vortexed and shaken overnight at 4℃. The following day,

the samples were centrifuged for 1.5 min at 10,000g. The supernatant was removed and the pellet was washed with 500ul of fresh PBS, centrifuged and left overnight at 4℃ once again. The supernatants were then combined to total 1000uL. 100 uL of the supernatant collected the following day and was used for amino acid quantification, following the user instructions in the EZ: FAAST GC-FID kit. The column, eluting medium, reagents, and standards used to identify amino acids were all supplied by the kit. Samples were prepared and measured the same day with a Shimmadzu GC-2010 Gas Chromatography (GC) system using a flame ionization detector (FID).

Statistical Analyses

We used a Type III ANOVA to test the model $\pi_o \sim$ Date + Variety + Date × Variety, to determine whether π_o varied significantly over the study period (Date) and across cultivars (Variety), and whether adjustment in π_o varied significantly across varieties (Date × Variety). We repeated this analysis for each of the gas exchange, water potential, and solute concentration variables. We were unable to fit a Type III ANOVA for g_s and A because of multicollinearity between the main effects and interaction term, so we tested for main effects of Date and Variety with a Type II ANOVA, which has more power for models without interaction terms. For consistency, we used a Type II ANOVA to also test the main effects for the other dependent variables with insignificant interaction terms, and this did not impact the significance of the main effects for any of these variables. We used post-hoc Tukey's HSD tests to compare differences between varieties. We used the same approach to test differences between climate groups (i.e., $\pi_o \sim$ Date + Climate Group + Date × Climate Group).

We used linear regression to test correlations between π_o, gas exchange, and pre-dawn and midday water potentials. We tested correlations between values measured in the same week,

to avoid confounding effects from measuring these variables under highly different environmental conditions. We also tested correlations between osmotic adjustment ($\Delta\pi_{o)}$ and changes in gas exchange and water potential, and between osmotic adjustment at the water potential at the beginning of each adjustment period, to test if the more water-stressed cultivars exhibited greater adjustment. Finally, we used linear regression to test correlations between the weighted average climate variables and π_o, osmotic adjustment, gas exchange, and water potentials. All analyses were conducted with Rstudio (version 4.2.2).

Results:

Osmotic Potential and Osmotic Adjustment

All cultivars significantly reduced osmotic potential at full hydration (π_o) over time, and mean osmotic potential was significantly different across cultivars (ANOVA, $p < 0.05$) (Table 1, Fig. 2). However, the interaction between date and variety was not significant, indicating that osmotic adjustment was not different across varieties. Cultivar mean π_o values ranged from -1.05 ± 0.06 to -1.48 ± 0.08 (mean + standard error (SE)) at veraison (July) and from -1.68 ± 0.05 to -2.23 ± 0.04 at harvest (September). The mean adjustment in π_o across cultivars was larger from July to August ($\Delta\pi_o$ = -0.44 MPa) than from August to September ($\Delta\pi_o$ = -0.22 MPa) (Table 1).

Notably, the ranking in osmotic potential across cultivars was largely consistent over the season (Fig. 2). Mean π_o was consistently the most negative in Merlot, followed by Riesling, intermediate in Pinot Noir and Chardonnay, and consistently higher in Sangiovese, Syrah, and Zinfandel.

Plant Water Status and Gas Exchange

Stomatal conductance (g_s), photosynthesis (A), and midday leaf water potentials (Ψ_{md}) were significantly different between sampling dates and cultivars (ANOVA, $p < 0.05$, Table 2).

Cultivar mean g_s values from July to September ranged from 0.212 ± 0.010 mmol m^{-2} s^{-1} (mean ± SE) for cool-climate Riesling to 0.341 ± 0.011 mmol m^{-2} s^{-1} for warm-climate Syrah. Mean *A* values ranged from 16.26 ± 0.35 µmol m^{-2} s^{-1} for cool-climate Pinot Noir to 18.36 ± 0.38 µmol m^{-2} s^{-1} for Syrah (Table 2, Fig. 3). Post-hoc tests indicated that g_s was higher in Syrah than the other cultivars, while *A* was higher in Syrah than Riesling and Pinot Noir (Tukey HSD, $p < 0.05$, Table 2). Midday leaf water potentials ranged from -1.06 ± 0.05 MPa for Pinot Noir to -1.35 ± 0.05 MPa for Chardonnay and were lower for Chardonnay and Riesling than for Zinfandel and Pinot Noir (Tukey HSD, $p < 0.05$) (Table 2, Fig. 3). All cultivars experienced the most negative midday leaf water potentials in late August. In response, there was a wide range in midday leaf water potential from -1.44 MPa (Sangiovese) to -1.83 MPa (Merlot) (Fig. 3). In contrast, predawn leaf water potentials were not significantly different between cultivars or sampling dates.

Relationships Between Osmotic Potential, Gas Exchange, and Midday Water Potential

We tested correlations between π_o, gas exchange, and Ψ_{md} for each of the three sampling periods when these variables were measured in the same week. π_o was significantly correlated with photosynthesis in September ($R^2 = 0.51$, $p < 0.05$, $N = 8$) (Table 3, Fig. 4). Stomatal conductance was not significantly correlated with π_o during the study period. Ψ_{md} was significantly correlated with π_o early in the season during the month of July ($R^2 = 0.63$, $p < 0.05$, $N=8$) (Table 3).

In contrast, osmotic adjustment was not significantly correlated with changes in gas exchange or midday water potential at the beginning of the adjustment period, but the midday water potential at the end of the adjustment period was significantly correlated with osmotic adjustment ($R^2 = 0.055$, $P < 0.05$, $N = 6$-8) (Table 4, Fig. 5).

Leaf Chemical Composition

All inorganic ion concentrations, except for Na, significantly changed over time, and mean Ca, Mg, and K concentrations were significantly different across cultivars (Table 5, Fig. 5). However, the interaction between Date and Variety, indicating that cultivars showed different patterns in accumulation, was only significant for Mg (Table 5, Fig. 5). Mean Mg and Ca concentrations increased from July to September, while K concentrations decreased. The absolute change in concentration was largest for Ca.

Total amino acid (TAAs) content significantly decreased over the season, but mean concentrations were not significantly different across cultivars (Fig. 6, Table 6). Proline concentrations were also not significantly different across cultivars and did not significantly change over time (Fig. 6, Table 6).

Climate of Origin and Climate Groups

Photosynthesis and π_o were significantly correlated with cultivars' climate associations, and significantly different between categorical climate groups. Photosynthesis was significantly correlated with the weighted maximum growing season temperature (T_{max}, $R^2 = 0.85$, p =<0.05, $N = 8$) and vapor pressure deficit (VPD_{max}, $r^2 = 0.73$, p = <0.05), and π_o was significantly correlated with VPD_{max} ($R^2 = 0.69$, p =<0.05) (Fig. 7). Photosynthesis and π_o were both higher in the cultivars associated with hot, less humid growing regions. These traits were also significantly higher in the hot-climate cultivars (i.e., Zinfandel and Sangiovese) than the other climate groups (Table 2). Conversely, osmotic adjustment, water potentials, and inorganic and organic solute concentrations were not significantly different across the climate groups.

Discussion

We found that mean osmotic potential varied significantly between winegrape cultivars, and that all cultivars significantly reduced osmotic potential (i.e., osmotically adjusted) over the ripening period, but that adjustment was largely uniform, preserving cultivar rankings in osmotic potential (Table 1, Fig. 2). Mean osmotic potentials were correlated with cultivar climate associations, but in the opposite direction than expected, with cultivars typically grown in hotter, less humid wine regions exhibiting less negative osmotic potentials (Table 1, Fig. 7). Depending on the sampling date, osmotic potential and osmotic adjustment were either uncorrelated with gas exchange and leaf water stress, or correlated in the opposite direction than expected, with a less negative osmotic potential associated with greater gas exchange (Tables 1, 4, Figs. 4, 5). Photosynthesis, but not stomatal conductance, was higher in the cultivars typically grown in hotter, less humid regions (Table 2, Fig. 3). Leaf chemical composition varied between cultivars and over the study period, but this variation was not related to climate associations (Table 5, Fig. 5). Altogether, these findings suggest that reducing leaf osmotic potentials has not been a primary mechanism for winegrapes to adapt to hotter, drier regions, contrary to other plant species (Bartlett et al. 2012). Instead, other mechanisms, such as increasing photosynthetic rates under hot conditions, could be more promising targets for developing climate-resilient grape cultivars.

More negative osmotic potentials increase leaf drought tolerance by improving turgor maintenance, which reduces leaf vulnerability to wilting, hydraulic dysfunction, and stomatal closure during drought (Herrera et al. 2021, Scoffoni et al. 2018, Martorell 2015 et al., Patakas et al. 1999). Thus, we expected cultivars adapted to hotter, drier regions to exhibit more negative mean osmotic potentials and greater osmotic adjustment. However, we found the opposite patterns. Osmotic potentials were significantly less negative for the hot-climate cultivars than the other climate groups, and less negative osmotic potentials were significantly associated with a

higher maximum growing season vapor pressure deficit (VPD_{max}) and a higher growing season temperature maximum (T_{max}) (Fig. 7). These findings could indicate that less drought-resistant leaves are adaptive for winegrapes under hot, dry conditions. Hot-climate cultivars could use earlier turgor loss to initiate transpiration declines or leaf shedding under less severe water stress, using vulnerability segmentation to protect the stems from dehydration and embolism spread (Tyree and Ewers 1991, Hochberg et al. 2016; Charrier et al., 2018). Notably, stem embolism resistance was significantly lower in hot-climate cultivars in a meta-analysis (Bartlett and Sinclair 2021), suggesting these cultivars could require more vulnerable leaves for vulnerability segmentation. However, osmotic potential was not correlated with stem embolism resistance in the only common garden study to test this relationship for grape (Alsina et al., 2008). Alternatively, our findings could indicate that osmotic potential is determined by adaptations beyond drought tolerance. For example, cool-climate cultivars could accumulate more solutes in the leaves during ripening to translocate to the woody tissues before dormancy, to provide greater protection from freezing. Many species use solute accumulation in woody tissues to prevent freezing damage, by reducing tissue freezing points and avoiding cellular dehydration (Yuanyuan et al. 2009). Cool-climate cultivars also typically finish ripening and stop translocating sugars and nutrients to the berries earlier in the growing season, which could contribute to greater solute accumulation in the leaves.

All cultivars significantly osmotically adjusted over the ripening period, which is consistent with findings from other field studies for grape (Herrera et al. 2021, Alsina et al. 2007). Most work in other crops has assumed that increasing osmotic adjustment improves drought tolerance (Blum et al. 2016, Zivcak et al. 2016), but we found that osmotic adjustment was not significantly different between climate groups or correlated with climate variables.

These findings suggest that osmotic adjustment is not a key trait driving diversification across climates for winegrapes.

We expected that more negative osmotic potentials would allow for greater gas exchange during our study period, where the vines experienced a record-breaking heatwave at an already hot-climate site. However, osmotic potential was mostly uncorrelated with gas exchange, or correlated in the opposite direction than expected. Osmotic potential was only correlated with gas exchange in July and September (Table 3), and a less negative osmotic potential was associated with greater photosynthesis (Table 3). Osmotic adjustment was also not correlated with changes in gas exchange (Table 4). These findings contrast with previous work showing that grapevine stomatal and hydraulic conductance became less sensitive to leaf water potential over the growing season as osmotic potentials declined (Martorell et al. 2015, Sorek et al. 2021, Herrera et al. 2022). Thus, while osmotic adjustment may affect gas exchange for individual plants, our findings suggest that limitations on gas exchange from turgor maintenance is not an important mechanism driving variation in gas exchange across cultivars.

Photosynthesis was significantly correlated with the weighted climate variables, and higher in cultivars typically grown in regions with a higher maximum temperature and VPD (Fig. 7). However, the climate variables were not correlated with stomatal conductance, suggesting this relationship was not driven by stomatal behavior and that, instead, the heat-adapted cultivars have a more heat tolerant photosynthetic biochemistry. High temperatures (> 35°C) can limit photosynthesis by reducing maximum rates of carboxylation (V_{cmax}) and the electron transport chain reactions (J_{max}) (Gallo et al. 2020). V_{cmax}, J_{max}, and their temperature dependence vary between cultivars. For example, V_{cmax} and J_{max} were more strongly downregulated as temperatures increased above 35°C in Grenache than Syrah (Gallo et al. 2020)

and in Chardonnay than Merlot (Greer et al. 2017). The heat-adapted cultivars could have a greater capacity to protect or repair the photosynthetic biochemical machinery from heat stress, allowing these cultivars to maintain a higher J_{max}, V_{cmax}, and overall photosynthetic rate at our hot study site.

Leaf chemistry varied between cultivars and changed over the ripening period, but accumulation was only significantly different between cultivars for Mg. Mean Ca, K, and Mg concentrations varied significantly between cultivars (Fig. 5). For all cultivars, Ca was the most concentrated mineral at each timepoint and most accumulated mineral over time, as observed previously for individual cultivars (e.g., Merlot) (Degu et al. 2019). Ca is immobile in the phloem, which limits translocation to the berries and facilitates accumulation in the leaves as berry hydraulics become phloem-dominated at veraison (Hocking et al. 2016). Mg concentrations increased and K concentrations decreased over the season for all cultivars, contrary to previous findings for K accumulating in response to water stress (Patakas et al. 2002; Degu et al 2019) (Fig. 5). Post-veraison competition between the leaf and berry could have driven the decreases in K, since berry osmotic regulation and demand for K increases near harvest (Monder et al. 2021). K also mediates drought responses by assisting with stomatal regulation (Monder et al. 2021) and, notably, Syrah exhibited the highest K concentrations and gas exchange rates. Mg and K also compete for plant uptake, and the relatively low soil K/Mg ratio at our site (< 0.1) could have contributed to the greater accumulation of Mg. Altogether, our findings show that cultivars growing at the same site and grafted to the same rootstock can vary significantly in nutrient content. The mechanisms driving these differences are poorly understood, and these differences were not explained by climate associations (Table 10). Finally, total amino acid and proline content were not significantly different between cultivars or climate

groups, contrary to our hypothesis that heat-adapted cultivars would generate osmoprotectant compounds to protect the photochemical machinery from stress.

In sum, contrary to findings for other crops and wild plant species, we did not find that winegrape cultivars have adapted to hotter, drier conditions by increasing osmotic adjustment or reducing osmotic potentials (Blum 2016 et al., Bartlett et al. 2012, Bartlett et al. 2014). Instead, osmotic potentials were either unrelated or positively correlated with gas exchange, and heat-adapted cultivars exhibited both higher photosynthetic rates and less negative osmotic potentials (Fig.4, Tables 1 & 2). These findings suggest that cultivar differences in gas exchange are primarily driven by traits besides the capacity for turgor maintenance, and that osmotic potentials in grape are more closely related to other processes than leaf water relations. Increasing photosynthesis under hot conditions emerged as a more promising target for cultivar improvement than reducing osmotic potentials, if breeding programs build on existing adaptations, but more work is needed to evaluate whether this strategy is beneficial under the new conditions expected from climate change.

Conclusions

We tested whether leaf osmotic potential and osmotic adjustment, classical water relations traits that have been highly predictive of drought tolerance in other crops and naturally occurring plant species, have been important drivers of environmental diversification for winegrapes. We hypothesized that grape cultivars have adapted to hotter, drier growing regions by using greater osmotic adjustment and more negative osmotic potentials to improve turgor maintenance and reduce vulnerability to wilting, hydraulic dysfunction, and stomatal closure. Our seven geographically diverse focal cultivars varied significantly in mean osmotic potentials and significantly osmotically adjusted from the onset of ripening (veraison to harvest), but the cultivars associated with the hottest, driest regions exhibited the least negative osmotic

potentials, contrary to our hypotheses. Osmotic potentials were either uncorrelated or positively correlated with gas exchange, indicating that grapevines have not improved gas exchange under hot conditions by increasing the capacity for turgor maintenance. Instead, grapevine osmotic potentials could be more closely related to nutrient storage or sugar translocation. Photosynthesis, but not stomatal conductance, was significantly higher in the heat-adapted cultivars at our hot study site, suggesting that a more heat-tolerant photochemical machinery has been a key adaptation to hot growing regions. Leaf chemistry was not related to climate, indicating that heat-adapted cultivars did not maintain greater photosynthesis through increased production of osmoprotectants. Overall, these findings suggest that leaf turgor maintenance is not a primary limitation on grapevine adaptation to hot, dry atmospheric growing conditions, and other traits, including photochemical heat tolerance, would be a more promising focus for cultivar improvement efforts.

Figures

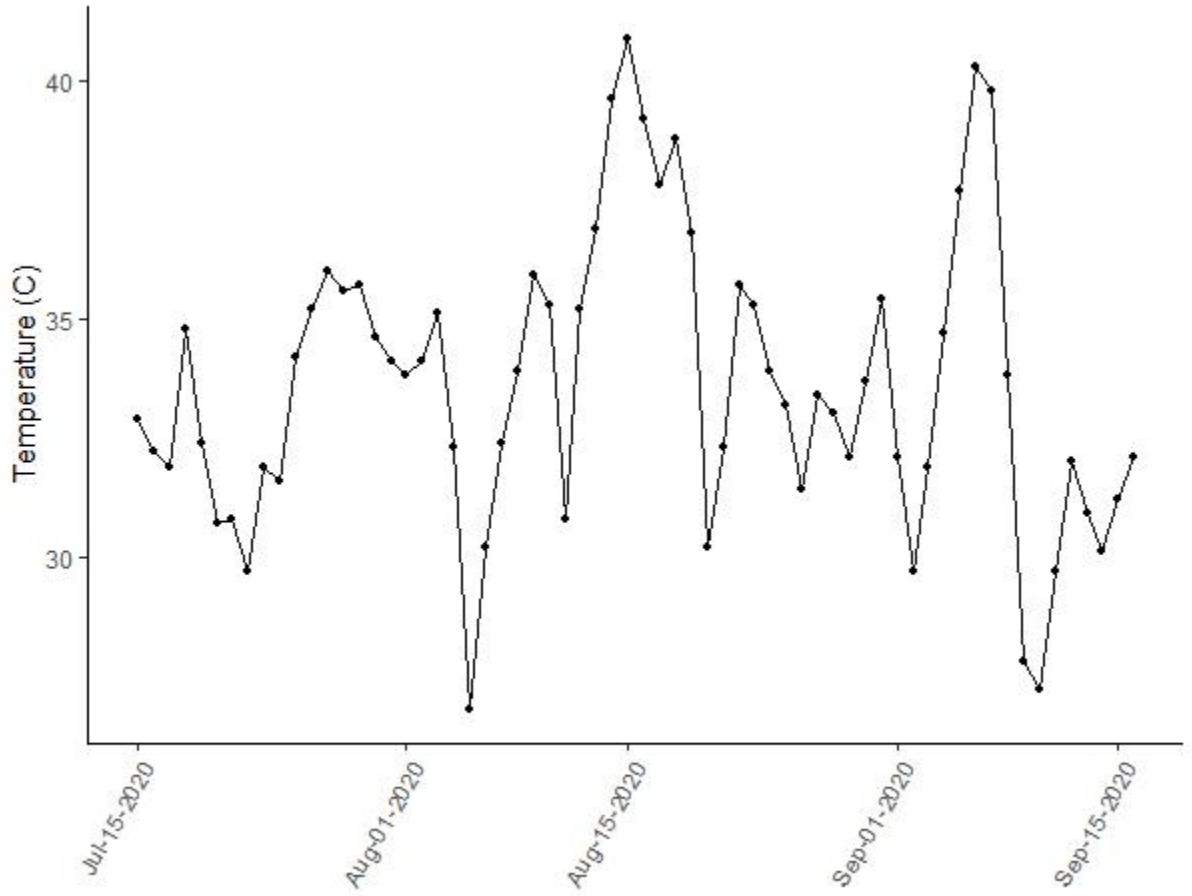

Figure 1. Mean daily temperatures at the study site over the summer 2020 study period compiled from the University of California, Davis CIMIS station (station #6) (https://cimis.water.ca.gov/).

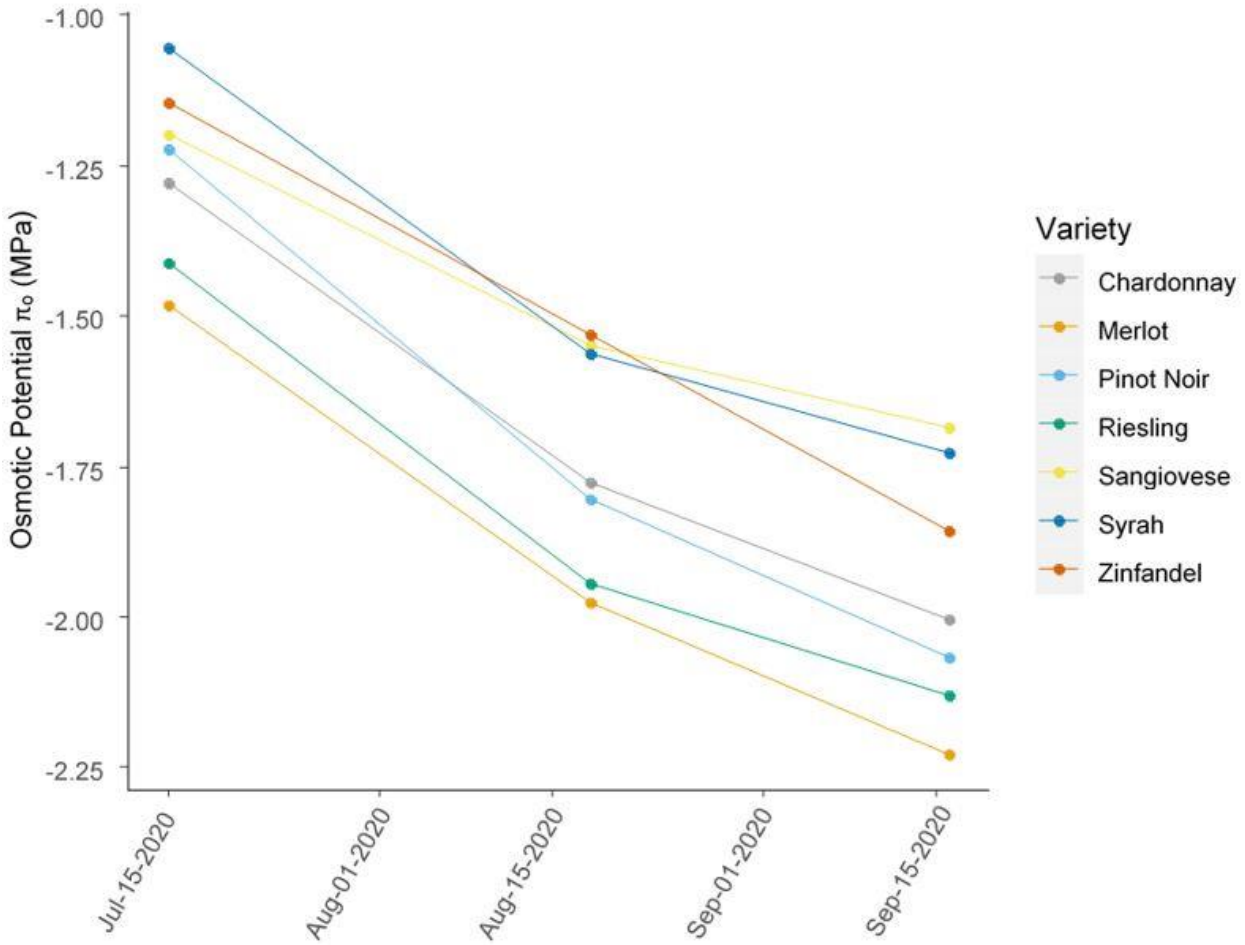

Figure 2. Leaf osmotic potential at full hydration (π_o) measurements from July, August, and September. Data points represent mean osmotic π_o for each cultivar and sampling date (N = 6-8). π_o varied significantly between Date, Variety, and Climate group ($p < 0.05$) (Tables 1, 2). However, there was no significant interaction between Date and Variety or Variety and Climate group, indicating there were no significant differences in osmotic adjustment ($\Delta\pi_o$) (Tables 1, 2).

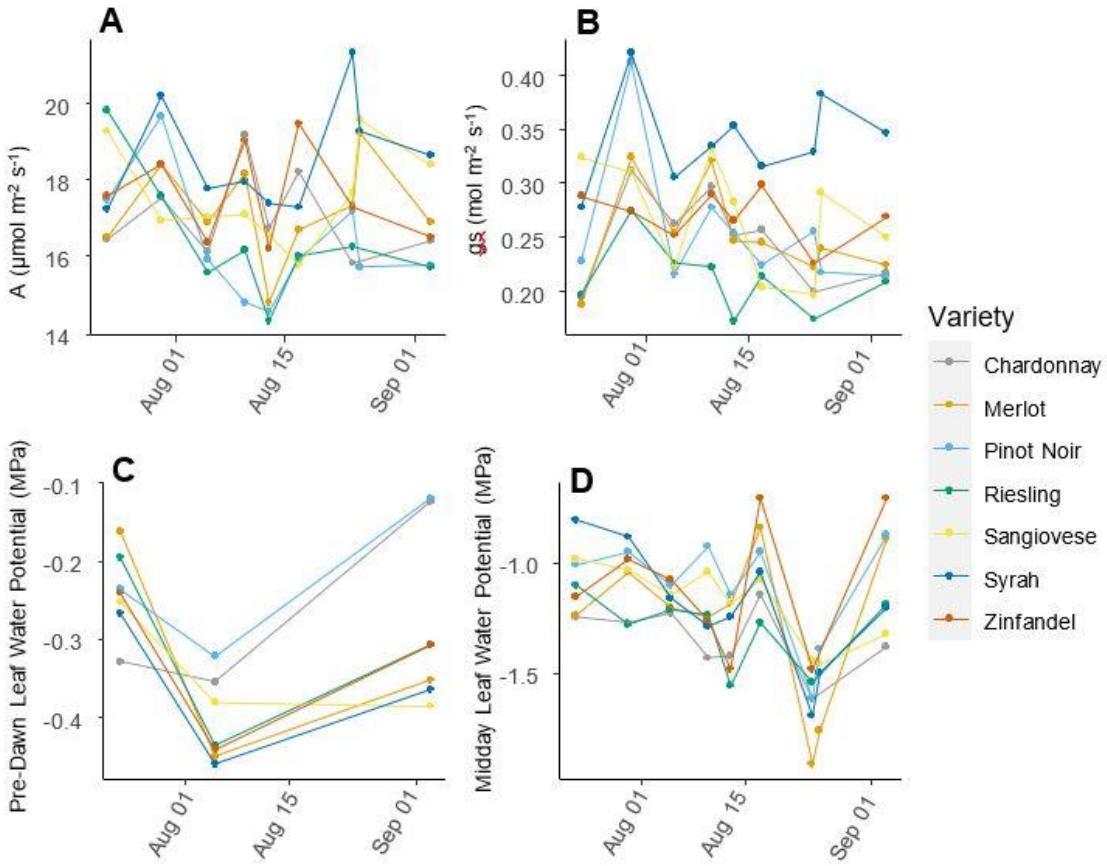

Figure 3. Photosynthesis (*A*) (**a**), stomatal conductance (g_s) (**b**), pre-dawn leaf water potential (Ψ_{pd}) (**c**), and midday leaf water potential (Ψ_{md}) (**d**) measurements over the study period. Points are cultivar means (N = 6-8). *A* and g_s varied significantly between Date, Variety, and Climate group, but there was no significant interaction between Date and Variety or Variety and Climate group (Table 2) (**a, b**). Midday water potentials also varied significantly between Date and Variety, though not Climate groups, while there was no significant variation in pre-dawn leaf water potential (Table 2) (**c, d**).

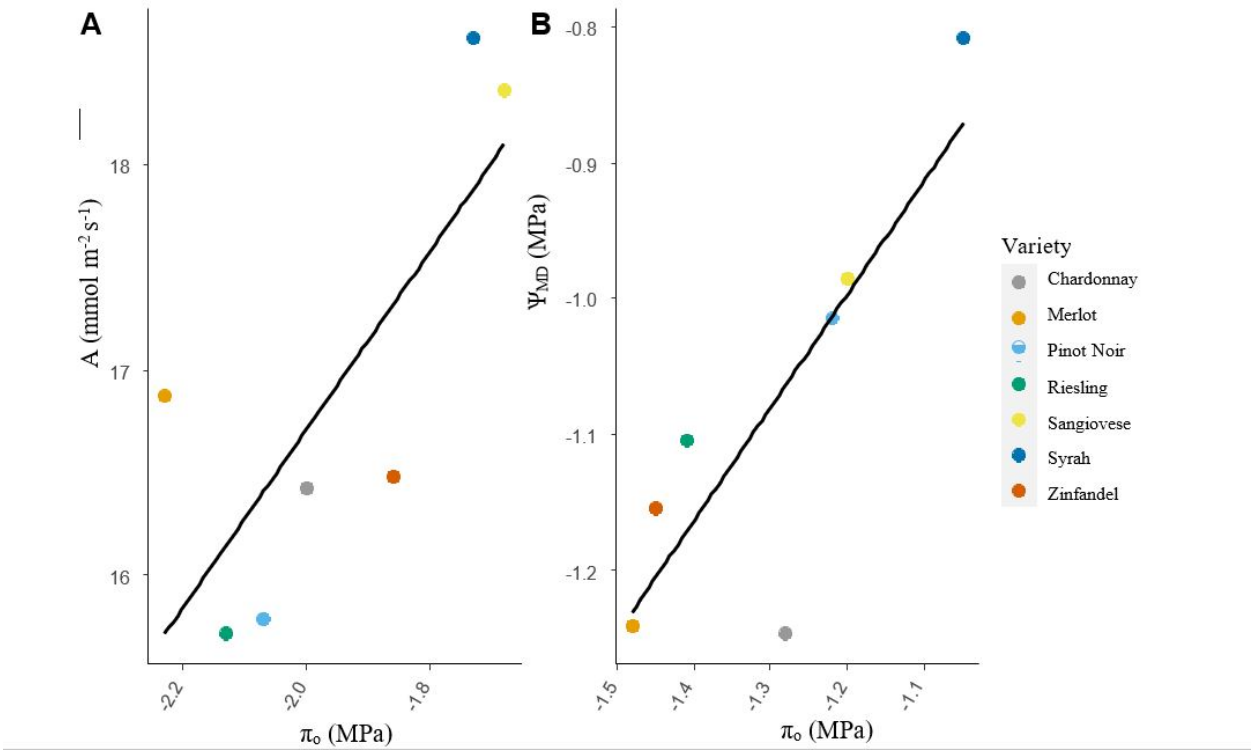

Figure 4. Correlations between osmotic potential (π_o) and significant gas exchange variable (*A*) in the month of September and midday leaf water potential (Ψ_{md}) in July. *A* was significantly correlated with π_o across cultivars, but only in the month of September ($R^2 = 0.51$, $p < 0.05$, $N = 8$) (**a**). Ψ_{md} was significantly correlated with π_o, but only in the month of July ($R^2 = 0.63$, $p < 0.05$) (**b**). *A* rates were highest in the cultivars with the least negative π_o values, and π_o was not significantly correlated to stomatal conductance contrary to expectation.

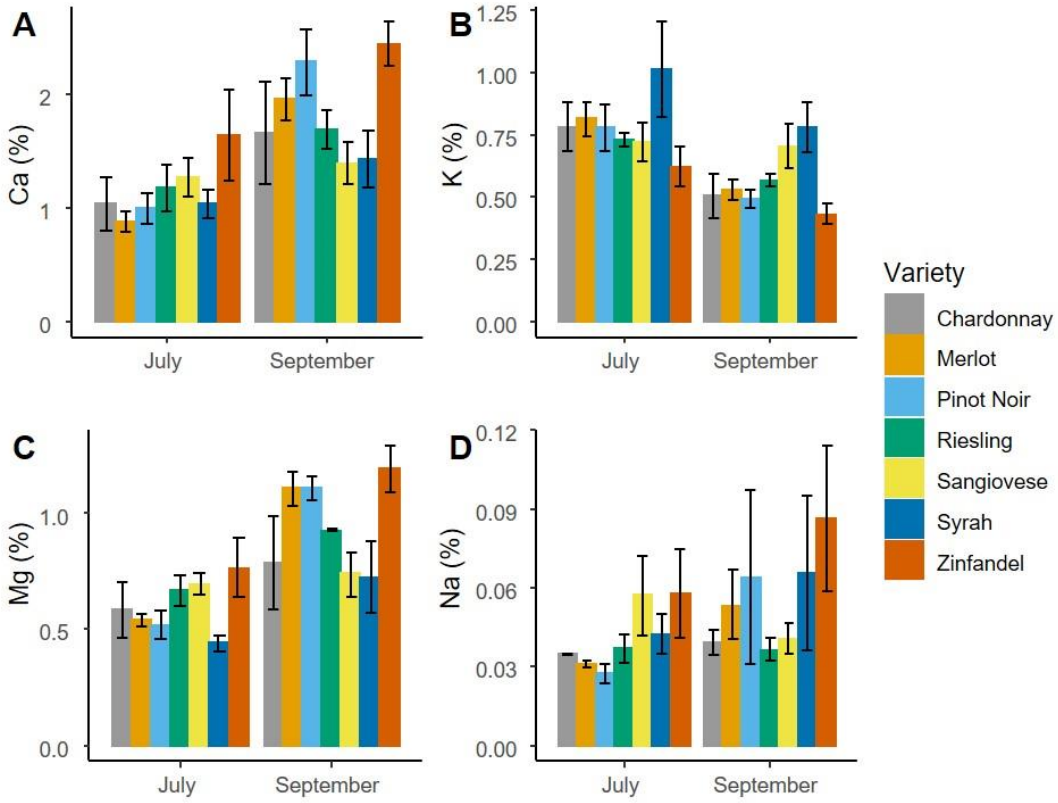

Figure 5. Mean Ca (**a**), K (**b**), Mg (**c**), and Na (**d**) concentrations, expressed as % dry leaf sample, at the beginning and end of the sampling period. Bars are means for cultivars and sampling dates (July and September) (n=6-8). Error bars represent standard error. Ca, K, and Mg varied significantly with Date, Variety, and Climate group. Only Mg displayed a significant interaction between Date and Variety. Na concentration levels were insignificant across all main effects.

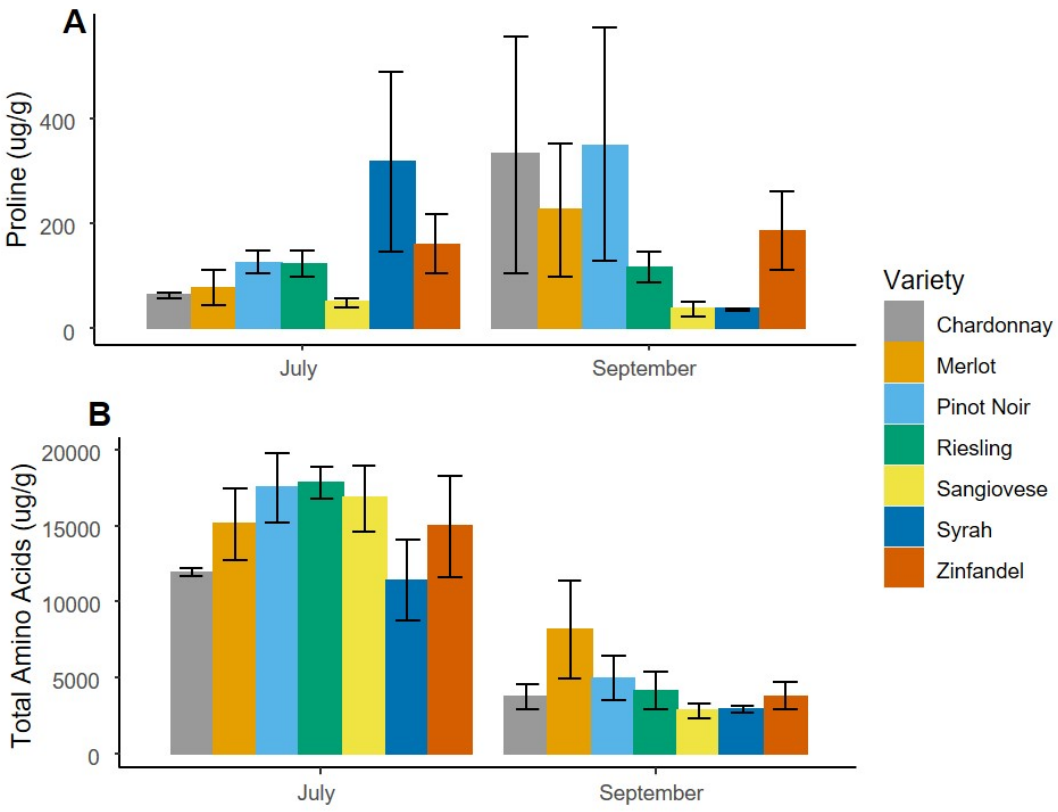

Figure 6. Mean proline (**a**) and total amino acids (TAAs) (**b**) concentrations at the beginning and end of the experimental period (July and September). Error bars are standard errors. Proline did not significantly vary between Date, Variety, or Climate group, while TAAs only varied significantly with Date.

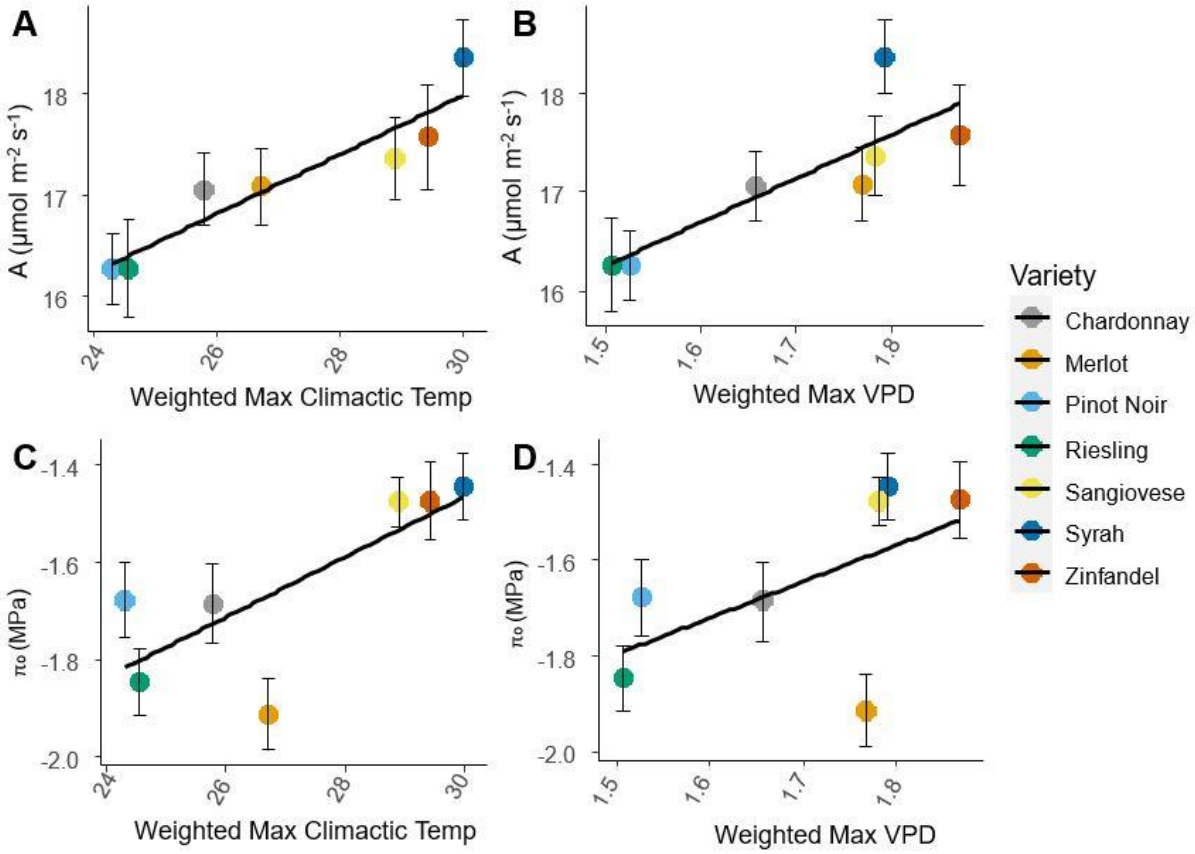

Figure 7. Correlations between π_o and gas exchange and cultivar climate associations. Climate associations capture growing season climate conditions in the regions where each cultivar is typically grown. Maximum growing season temperature (T_{max}) and vapor pressure deficit (VPD_{max}), were significantly correlated with mean photosynthesis (r^2 = 0.85 and 0.73, respectively, $p < 0.05$, $N = 8$) and π_o (r^2 = 0.51 and 0.69, $p < 0.05$) over the study period. Cultivars associated with hotter, drier climates had higher photosynthetic rates in our hot common-garden study, but less negative π_o values, contrary to our predictions.

Tables

Table 1: Monthly osmotic potential (π_o) measurements. Values are cultivar means +/- standard errors. Letters show post-hoc Tukey HSD test results.

Variety	July π_o	August π_o	September π_o
Chardonnay	-1.28 ± 0.09^{abc}	-1.77 ± 0.04^{b}	-2.0 ± 0.06^{bc}
Merlot	-1.48 ± 0.08^{c}	-1.98 ± 0.06^{b}	-2.23 ± 0.04^{c}
Pinot Noir	-1.22 ± 0.06^{abc}	-1.8 ± 0.03^{b}	-2.07 ± 0.05^{c}
Riesling	-1.41 ± 0.04^{bc}	-1.94 ± 0.04^{b}	-2.13 ± 0.04^{c}
Sangiovese	-1.2 ± 0.04^{abc}	-1.55 ± 0.05^{a}	-1.68 ± 0.05^{a}
Syrah	-1.05 ± 0.06^{a}	-1.56 ± 0.04^{a}	-1.73 ± 0.07^{a}
Zinfandel	-1.45 ± 0.09^{ab}	-1.53 ± 0.04^{a}	-1.86 ± 0.07^{ab}

Table 2: Cultivar mean gas exchange and water potential values over the study period. Gas exchange is measured as stomatal conductance (g_s) and photosynthesis (A) and water potentials are measured as pre-dawn (Ψ_{PD}) and midday water potentials (Ψ_{MD}). Values are means +/- standard errors. Letters show Tukey HSD test results.

Variety	g_s (mmol m^{-2} s^{-1})	A (µmol m^{-2} s^{-1})	Ψ_{PD} (MPa)	Ψ_{MD} (MPa)
Riesling	0.212 ± 0.01^{c}	16.27 ± 0.048^{b}	-0.31 ± 0.06^{a}	-1.3 ± 0.04^{b}
Pinot Noir	0.26 ± 0.012^{b}	16.26 ± 0.35^{b}	-0.22 ± 0.04^{a}	-1.06 ± 0.05^{a}
Chardonnay	0.25 ± 0.012^{bc}	17.06 ± 0.36^{ab}	-0.27 ± 0.06^{a}	-1.35 ± 0.05^{b}
Merlot	0.257 ± 0.011^{b}	17.08 ± 0.38^{ab}	-0.32 ± 0.05^{a}	-1.18 ± 0.06^{ab}
Syrah	0.341 ± 0.011^{a}	18.36 ± 0.38^{a}	-0.36 ± 0.06^{a}	-1.17 ± 0.05^{ab}
Sangiovese	0.269 ± 0.012^{b}	17.37 ± 0.4^{ab}	-0.34 ± 0.05^{a}	-1.16 ± 0.04^{ab}
Zinfandel	0.27 ± 0.011^{b}	17.58 ± 0.52^{ab}	-0.33 ± 0.05^{a}	-1.12 ± 0.05^{a}

Table 3: Linear regressions between osmotic potential and stomatal conductance (g_s), photosynthesis (A), and midday water potentials (Ψ_{MD}) for each sampling date for osmotic potential. Bold values show significant correlations (p-value < 0.05).

Predictor	p-value	r^2
July g_s	0.30	0.05
July A	0.99	-0.19
July Ψ_{MD}	**0.02**	**0.63**
Aug g_s	0.29	0.07
Aug A	0.36	0.0004
Aug Ψ_{MD}	0.57	-0.12
Sep g_s	0.07	0.41
Sep A	**0.04**	**0.51**
Sep Ψ_{MD}	0.48	-0.07

Table 4: Linear correlations with gas exchange and (Δ πo) and midday leaf water potential and (Δ πo) across all individuals. Boldened text signifies significant values.

Linear Regression Models:	p-value	R^2
Δ gs~ Δ πo	0.8964	-0.012
Δ A~ Δ πo	0.3912	-0.0031
Δ MD LWP~ Δ πo	**0.014**	**0.055**

Table 5: Leaf ion concentrations at the beginning and end of the study period. Values are percentages per dry biomass sample +/- standard errors. Letters show Tukey HSD test comparisons.

Variety	Date	Ca (%)	Mg (%)	K (%)	Na (%)
Chardonnay	July	1.03 ± 0.23[a]	0.59 ± .012[a]	0.78 ± 0.1[a]	0.03 ± 0.0[a]
Merlot	July	0.87 ± 0.09[a]	0.54 ± 0.02[a]	0.81 ± 0.06[a]	0.03 ± 0.0[a]
Pinot Noir	July	0.99 ± 0.13[a]	0.52 ± 0.06[a]	0.78 ± 0.09[a]	0.03 ± 0.0[a]
Riesling	July	1.17 ± 0.21[a]	0.67 ± 0.07[a]	0.73 ± 0.03[a]	0.04 ± 0.01[a]
Sangiovese	July	1.26 ± 0.17[a]	0.69 ± 0.05[a]	0.72 ± 0.08[a]	0.06 ± 0.02[a]
Syrah	July	1.03 ± 0.13[a]	0.44 ± 0.03[a]	1.01 ± 0.19[a]	0.04 ± 0.01[a]
Zinfandel	July	1.63 ± 0.4[a]	0.76 ± 0.13[a]	0.62 ± 0.08[a]	0.06 ± 0.02[a]
Chardonnay	September	1.65 ± 0.46[a]	0.79 ± 0.2[a]	0.5 ± 0.09[ab]	0.04 ± 0.0[a]
Merlot	September	1.95 ± 0.19[a]	1.11 ± 0.07[a]	0.53 ± 0.04[ab]	0.05 ± 0.01[a]
Pinot Noir	September	2.27 ± 0.29[a]	1.11 ± 0.05[a]	0.49 ± 0.03[ab]	0.06 ± 0.03[a]
Riesling	September	1.68 ± 0.16[a]	0.93 ± 0.0[a]	0.57 ± 0.03[ab]	0.04 ± 0.0[a]
Sangiovese	September	1.39 ± 0.19[a]	0.74 ± 0.1[a]	0.7 ± 0.09[ab]	0.04 ± 0.01[a]
Syrah	September	1.42 ± 0.26[a]	0.73 ± 0.15[a]	0.78 ± 0.1[a]	0.07 ± 0.03[a]
Zinfandel	September	2.43 ± 0.2[a]	1.2 ± 0.1[a]	0.43 ± 0.04[b]	0.09 ± 0.03[a]

Table 6. Proline and total amino acid (TAA) concentrations at the beginning and end of the study period.

Variety	Date	Proline (µg/g)	TAA (µg/g)
Chardonnay	July	63.4 ± 6.4[a]	11931.48 ± 407.18[a]
Merlot	July	77.87 ± 38.78[a]	15121.09 ± 2711.53[a]
Pinot Noir	July	126.6 ± 22.03[a]	17547.43 ± 2274.82[a]
Riesling	July	123.58 ± 26.12[a]	17750.59 ± 1056.66[a]
Sangiovese	July	50.53 ± 8.98[a]	16839.51 ± 2485.52[a]
Syrah	July	317.38 ± 171.07[a]	11366.88 ± 2623.6[a]
Zinfandel	July	160.58 ± 56.81[a]	14953.77 ± 3342.76[a]
Chardonnay	September	330.3 ± 259.11[a]	3737.68 ± 961[a]
Merlot	September	226.58 ± 126.39[a]	8139.59 ± 3195.13[a]
Pinot Noir	September	349.53 ± 221.47[a]	4944.17 ± 1433.79[a]
Riesling	September	116.43 ± 28.93[a]	4113.03 ± 1196.83[a]
Sangiovese	September	37.75 ± 12.79[a]	2751.01 ± 446.7[a]
Syrah	September	37.1 ± 1.65[a]	2900.52 ± 217.4[a]
Zinfandel	September	186.4 ± 86.86[a]	3746.1 ± 988.61[a]

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