Introduction

Though commonly grafted to rootstocks with different genetic backgrounds, most cultivated grapevines belong to the species Vitis vinifera L., which was domesticated from Vitis sylvestris L. in the Caucasus region and southwestern Asia (Dong et al. 2023). Climates across this region range from cool to hot and, matching its climatic diversity, the region is home to diverse wild and cultivated grape genotypes (Sargolzaei et al. 2021, Sivan et al. 2021). Therefore, at least some cultivars should be tolerant of heat and drought. Though unaware of the evolutionary history and genetic makeup of V. vinifera, the Roman author Lucius Columella (c. 4 to 70 AD) had a keen sense of the value of exploiting its intraspecific variability and the importance of climate for grape production. In Columella’s reference text on agriculture, De Re Rustica, he recommended matching cultivars to the prevailing climate and soil, and planting high-yielding cultivars in warm climates. Writing nearly 2000 years before the downy and powdery mildew pathogens and phylloxera arrived in Europe, Columella emphasized that while vineyards do not thrive in cold or overly hot climates, they prefer warm weather over cold weather, and dry soils over soils drenched by excessive rainfall.

Grapes grown in warm, dry climates are the focus of this article. Following the definition by Jones et al. (2010), warm climates for grape production have an average seven-month growing season temperature between 17 and 19°C; hot climates fall between 19 and 21°C. The seasonal growing degree day (GDD > 10°C) equivalent is roughly 1500 to 2000 for warm climates and 2000 to 2400 for hot climates. However, average temperatures do not tell the whole story. Warm climates are often characterized by experiencing hot days during the growing season. Hot days are defined as those whose daily maximum temperature (T_{max}) exceeds 35°C;

1Department of Viticulture and Enology, Washington State University, Irrigated Agriculture Research and Extension Center, Prosser, WA.

*Corresponding author (mkeller@wsu.edu)

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many physiological processes decline above this threshold (Keller 2020). While the number of hot days is projected to increase under future climate scenarios (White et al. 2006), the western United States experienced as many days with $T_{\text{max}} > 35^\circ\text{C}$ in 2021 and 2022 as the number predicted for the end of this century.

Warmer temperatures also raise the atmosphere’s evaporative demand, estimated as vapor pressure deficit, and accelerate transpiration from plant leaves (Katul et al. 2012). But while the rising temperature is increasing the plant water demand, the irrigation water supply is declining. In many regions, including the western U.S., the water supply during the summer depends on the water stored in mountain snowpacks in spring (Elsner et al. 2010, Wagner et al. 2021). As dwindling snowpacks and earlier snowmelt are shifting peak river flows from early summer to early spring, the irrigation water availability decreases and the drought risk during the summer increases. On a worldwide scale, mountain glaciers are predicted to lose 26 to 41% of their mass by the end of this century (relative to 2015), causing most low- and mid-latitude glaciers to disappear (Rounce et al. 2023). In addition, groundwater levels are declining in many regions (Wang et al. 2022, Xanke and Liesch 2022). At the same time, the increasing frequency, severity, and duration of both extremely wet and extremely dry conditions is challenging adaptation and mitigation practices (Stevenson et al. 2022).

This Insight explores some responses of grapevines to aspects of climate change, focusing on temperature and water availability. Vineyard management practices, including the use of different rootstocks, aimed at mitigating the impact of climate change have been recently reviewed elsewhere (van Leeuwen et al. 2019, Gutiérrez-Gamboa et al. 2021, Marin et al. 2021, Naulleau et al. 2021, Romero et al. 2022, Theron and Hunter 2022). Therefore, mitigation practices are mentioned here only in passing, with the main goal of encouraging further research.

### Yield: Drought and Heat May Leave Your Glass Empty

Even as the drought risk is intensifying, Charrier et al. (2018) asserted that grapevine water status, measured as predawn or midday leaf water potential ($\Psi_l$), never falls below a threshold that would trigger vine mortality because vines sacrifice their leaves under drought. That work was conducted in Bordeaux (annual precipitation [AP] ≈ 800 mm), France, and the Napa Valley (AP ≈ 700 mm) of California; recent research in Israel (AP ≈ 600 mm) reinforced that conclusion (Sorek et al. 2021). *V. vinifera* is indeed quite drought tolerant and, except in vineyards on very sandy soils (or in many pot experiments), $\Psi_l$ declines over periods of weeks when water supply is interrupted (Romero et al. 2017, Sorek et al. 2021). Nevertheless, in dry regions such as southeastern Washington (AP ≈ 200 mm), canopy dieback does occur when irrigation is discontinued over extended periods and may result in vine mortality over successive years (Figure 1). New models predict that by the end of this century, current *V. vinifera* cultivars will not survive without irrigation in climates that are currently considered warm and dry (Dayer et al. 2022).

Dry soil in spring due to low winter precipitation may leave vines unable to generate sufficient root pressure to restore the functionality of their vascular system, resulting in erratic budbreak, slow shoot growth, and yield loss (Galat Giorgi et al. 2020, Keller 2020, Bonada et al. 2021; Figure 2). Once canopy transpiration begins to drive water up the vine’s xylem conduits, water deficit leads to a decline in $\Psi_l$. To protect themselves from drought stress, vines close their stomata at a higher $\Psi_l$ than that which triggers leaf wilting and abscission due to xylem cavitation (Charrier et al. 2018, Sorek et al. 2021). But the stomatal closure reduces photosynthesis, limiting the amount of carbon that is available for export from the leaves. In vines on sandy soils, photosynthesis can decline within days after an irrigation event (Tarara et al. 2011).

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**Figure 1** Vineyard in the Yakima Valley of southeastern Washington, a region with ~200 mm annual precipitation, in late July 2021, after two years without irrigation.
Unlike mild water deficit (midday $\Psi_l > -1 $ MPa), moderate water deficit may reduce yield, depending on a vine’s growth stage. Water stress before bloom may induce inflorescence abortion, during bloom it reduces fruit set, and before veraison it reduces berry size and bud fruitfulness (Hardie and Considine 1976, Matthews and Anderson 1989, Vasconcelos et al. 2009, Gambetta et al. 2020, Levin et al. 2020). As berries begin to ripen, they become such strong sinks that even severe water deficit ($\Psi_l \leq -1.5 $ MPa) will not stop berry growth, sugar accumulation, and color change (Keller et al. 2015b). Nevertheless, severe stress slows sugar accumulation and permits berry shrinkage. In dry regions, therefore, growers can manipulate berry size via preveraison irrigation water supply, while postveraison irrigation can mitigate, but not reverse, berry shrinkage (Keller et al. 2006, 2023).

Like water deficit, heat stress also compromises yield. The optimum $T_{\text{max}}$ for fruit set and subsequent berry growth may lie between 30 and 35°C (Keller 2020, Keller et al. 2022). Temperatures below 15°C and above 40°C compromise pollen viability and curtail fruit set, seed and berry growth, and bud fruitfulness (Vasconcelos et al. 2009, Gouot et al. 2019a), while sun-exposed berries heated to above ~45°C may shrivel due to sunburn injury (Gambetta et al. 2021, Muller et al. 2023). However, how water and heat stress interact quantitatively and temporally to influence yield formation in the current and subsequent cropping year remains to be determined.

**Fruit Composition:**

**Temperature Trumps Water Status**

Some water deficit is advantageous for grape quality (Medrano et al. 2015), but just how vine water status alters quality traits remains unresolved. Perhaps surprisingly, changes in fruit composition seem unlikely to be mediated by abscisic acid (Castellarin et al. 2007b), and changes in gene expression in the berries cannot be taken as evidence for a direct effect of water deficit. Moreover, upregulation of genes responsible for anthocyanin and terpenoid biosynthesis in water-stressed grapevines persists long after the stress is relieved (Castellarin et al. 2007b, Palai et al. 2022a, 2023). While severe water stress induces leaf abscission, even mild to moderate stress limits shoot growth and, unless it occurs too late (e.g., postveraison), will result in smaller, more open canopies, which in turn increases the cluster sun exposure. The solar radiation that brings more light to sun-exposed berries also heats those berries, sometimes by >15°C above the ambient temperature (Spayd et al. 2002; Figure 3). Consequently, many berries on water-stressed vines are not only smaller but also warmer than berries on non-stressed vines, which has implications for fruit composition (Keller et al. 2016, Scholasch and Rienth 2019).

The lower acidity that is often observed in grapes from water-stressed vines has been attributed to greater sun exposure of the fruit (Intrigliolo and Castel 2010). Malate metabolism during ripening may be unresponsive to water deficit per se but is accelerated by higher temperatures (Sweetman et al. 2009, Hewitt et al. 2023). Measuring skin flavonoids in sun-exposed and shaded berries, or in east- and west-exposed berries, also revealed a strong exposure effect but no consistent water effect in irrigation experiments (Rocchi 2015, Zarrouk et al. 2016). The ultraviolet portion of the solar spectrum enhances flavonol accumulation, while the higher temperature in combination with visible light may favor production of flavan-3-ols, which can polymerize into tannins (Price et al. 1995, Kolb et al. 2003, Koyama and Goto-Yamamoto 2008, Gouot et al. 2019b, Torres et al. 2020). Anthocyanin accumulation requires only ~100 μmol/m² of visible light but like flavonol accumulation, responds strongly to temperature, declining at berry temperatures above 35°C (Bergqvist et al. 2001, Spayd et al. 2002, Pastore et al. 2017). While anthocyanin biosynthesis at the onset of ripening is closely tied to sugar accumulation, temperature variation may lead to increasing variability in anthocyanins...
as the berries ripen (Keller et al. 2005, Zarrour et al. 2016, Gouot et al. 2019b, Hernández-Montes et al. 2021, Kurtural and Gambetta 2021). Sadras and Moran (2012), by contrast, concluded that heat delays the onset but not the rate of anthocyanin accumulation relative to sugar accumulation. Yet across their experiments there was a threshold of ~10 Brix at which anthocyanin accumulation started, consistent with other studies (Castellarin et al. 2007a, 2007b, Hernández-Montes et al. 2021). Thus, while water deficit may sometimes advance the onset and rate of sugar and anthocyanin accumulation (Castellarin et al. 2007a), excessive berry temperatures might delay ripening in general, which can result in visible differences in berry size and color on opposite sides of a canopy or of sun-exposed clusters (Figure 4).

The influence of water deficit, and its interaction with light and temperature, on aroma volatiles or their bound precursors in grapes, are not well understood (Scholasch and Rienth 2019, Rienth et al. 2021). For example, though the optimum temperature for monoterpene accumulation might be <20°C, severe preveraison water stress leading to basal leaf abscission, but not postveraison water stress, may increase monoterpenes (Savoi et al. 2016, Palai et al. 2022b, 2023). In vines that had most basal leaves removed, however, monoterpenes remained largely unaltered by pre- or postveraison water deficit (Kovalenko et al. 2021). Consequently, while there is compelling evidence for an indirect effect of water deficit via its influence on canopy microclimate, a direct effect on fruit composition has yet to be conclusively demonstrated.

**Growth and Physiology—But Not Phenology: Water Status Trumps Temperature**

Provided chilling has been sufficient to break dormancy, the time of budbreak is driven by bud temperature (Camargo-Alvarez et al. 2020) but is rather insensitive to soil moisture; only extremely dry soil will delay budbreak (Figure 2). Though threshold temperatures remain a matter of debate, higher temperatures induce earlier budbreak, which can increase the risk for spring frost damage, especially in winter-hardy genotypes that tend to lose hardiness faster in spring, and thus grow out earlier than less hardy genotypes (Keller and Tarara 2010, Ferguson et al. 2014, Martínez-Lüscher et al. 2016, Poni et al. 2022). Higher temperatures during budswell and budbreak also increase the xylem’s transport capacity in the emerging shoots, “priming” them for greater seasonal vigor and yield (Keller and Tarara 2010, Keller et al. 2010, Galat Giorgi et al. 2020). Water deficit suppresses this temperature effect, thus limiting vigor irrespective of temperature. During the growing season, shoot growth, $\Psi_l$, and leaf photosynthesis remain much more limited by water deficit than by high temperature, even at $T_{max} \geq 40°C$ (Galat Giorgi et al. 2019, Arrizabalaga-Arriazu et al. 2021, Lehr et al. 2022). But unless leaves have already been abscised, $\Psi_l$ generally recovers within days upon water supply, while photosynthesis may take somewhat longer to recover to prestress levels (Romero et al. 2017, Galat Giorgi et al. 2019).

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**Figure 3** Infrared image superimposed on visible image of a Riesling canopy in the Yakima Valley of Washington in 2020. Rows are oriented north-south, and fruit-zone leaves were removed after fruit set on the east side only. The image was taken with a FLIR ONE Pro for Android camera (Teledyne FLIR). Temperatures are shown for (from top) sun-exposed leaf, shaded leaf, and sun-exposed cluster. The purple band at the bottom is the shaded vineyard floor; the white “hotspot” is the sun-exposed vineyard floor. The ambient air temperature, recorded at 1.5 m by an on-site weather station, was 24°C. For details, see Fritzke (2022). Photo courtesy of Evan Fritzke.

**Figure 4** Cabernet Sauvignon clusters in a vineyard in the Yakima Valley of Washington in 2022. Rows are oriented north-south, and clusters are exposed on (A) west side of the canopy and (B) east side of the same canopy, with (C) sun-exposed side and (D) shaded side of the same cluster on the west side. All pictures were taken on the same day.
Unlike its dominant influence on growth and leaf physiology, the effect of water availability on phenology tends to be inconsistent, whereas rising temperatures accelerate the progression of phenological stages (however, see Figure 4). Temperature variation leads to high variability in phenology among and within regions and between years (Parker et al. 2013, de Rességuier et al. 2020). Even among eight generally warm years (2015 to 2022), the date of veraison varied by two to five weeks for 31 own-rooted grape cultivars grown in the same vineyard in southeastern Washington (Figure 5). A similar variation in veraison date (for 2012 to 2018) was observed for 50 cultivars grafted to SO4 rootstock in the somewhat cooler and considerably wetter climate of Bordeaux (van Leeuwen et al. 2019). Moreover, the cultivar rankings for veraison in Washington and Bordeaux are comparable (Spearman rank \( r_s = 0.85, p < 0.001, n = 17 \) common cultivars), with Chardonnay among the earliest cultivars and Petit Verdot the latest cultivar at both sites. The Washington cultivar ranking also correlates with that based on GDD developed by Parker et al. (2013) for multiple sites \( (r_s = 0.77, p < 0.001, n = 24 \) common cultivars, various rootstocks). This natural variation may be used to adjust the cultivar makeup within regions (Morales-Castilla et al. 2020); cultivars with a late veraison date may be planted in warm sites. Moreover, even if the wine industry is not ready to embrace modern molecular approaches, breeding programs could exploit the genetic variability present among existing cultivars (Duchêne et al. 2010, Parker et al. 2013) and among extant V. sylvestris or other Vitis genotypes.

Nevertheless, comparing Figure 5 with Figure 7 in van Leeuwen et al. (2019) shows that some cultivars might shift in the veraison rank order between locations. A global phenology network could help to confirm whether, or to what extent, cultivars differ in their phenological response to diverse climates, and identify the genetic basis for such variability. Additionally, the correlation between the veraison ranking in Figure 5 and that for average growing season temperature by cultivar across the world (Puga et al. 2022) is relatively weak \( (r_s = 0.58, p = 0.02, n = 17 \) common cultivars). Thus, while cultivars with a later veraison date tend to be grown in warmer climates, some cultivars might perform well in diverse climates. For example, a blind tasting of 30 Chardonnay wines from nine countries on five continents revealed that 12 Chardonnay experts could not reliably identify the country of origin (Vaterlaus 2013). Neither the correlation between perceived origin and actual origin \( (r = 0.16, p = 0.4) \), nor that between bottle price (>10-fold range) and tasting score \( (r = 0.06, p = 0.76) \), was significant. This outcome echoes the results from another blind tasting, where 11 expert judges could not distinguish Chardonnay wines from Burgundy (France) and California (Taber 2005). Apparently, phenotypically plastic cultivars such as Chardonnay, despite its propensity to ripen early, can produce similar wine styles across diverse climates (and soils). The date of veraison by itself is thus not a useful marker for cultivar suitability in different climates.

### Crop Load: Implications for Ripening and Water-use Efficiency (WUE)

As climate change is progressing, grapes are being harvested earlier and the wine alcohol content is increasing (Petrie and Sadras 2008, Cook and Wolkovich 2016, Edwards et al. 2017). A seemingly obvious strategy to counter this trend would be to increase crop loads to delay ripening. Raising yields would also be an effective way to improve the WUE of grape production. For example, despite requiring more irrigation water, juice grapes cropped at 43 t/ha in southeastern Washington had a 2.5-fold higher irrigation WUE (6.9 t/ML) and lower total water footprint (200 m³/t) than winegrapes cropped at 8 t/ha (2.7 t/ML and 530 m³/t; Keller et al. 2016, 2023). Nevertheless, the wine industry and its regulators remain fixated on low yields as a presumed prerequisite for high quality. Reviewing viticultural practices that may improve WUE, Medrano et al. (2015) excluded yield increases, asserting that these would reduce fruit quality. In their meta-analysis of practices
designed to delay grape ripening in the face of rising temperatures, Previtali et al. (2022) considered reducing leaf area (i.e., limiting source size) but not increasing yield (i.e., increasing sink size).

However, increasing yield by lowering the pruning severity resulted in Cabernet Sauvignon wines with more fruity and less vegetal aromas (Chapman et al. 2004). Similar to the water deficit effect discussed above, the pruning effect might be mediated by shoot vigor and, perhaps, berry size, as both berry and rachis methoxypyr-azine concentrations correlate with vigor (Scheiner et al. 2012, Sanders et al. 2022). Because vigor and berry size tend to decrease as the shoot number or crop load increases, machine pruning could be applied to increase yield (Keller et al. 2008, 2015a, Poni et al. 2016). In unusually cool growing seasons, mechanical harvesters could be used to thin the crop (Kurtural and Fidelibus 2021). In a case study in southeastern Washington, machine-pruned, deficit-irrigated Syrah vines had 40% more but 17% lighter clusters, and hence higher yield (5-year average 15.6 t/ha), than hand-pruned vines (13.4 t/ha). Thinning the machine-pruned vines using a mechanical harvester between pea size and bunch closure effectively reduced yield (12.7 t/ha) by decreasing the cluster size further without altering the cluster number (Figure 6A). Therefore, unlike manual cluster thinning, mechanical berry thinning has the added benefit of decreasing the cluster compactness (Tardaguila et al. 2008; Figure 6B).

Figure 6 Machine-pruning and machine-thinning effects in a Syrah vineyard in the Columbia Valley of Washington. (A) Relationship between number of clusters per vine and average cluster weight of manually-pruned or machine-pruned vines with and without machine-thinning. Data for 2014 through 2018 were pooled. (B) Berries, cluster fragments, and leaves on the vineyard floor after machine-thinning. Own-rooted vines were planted in 2000 in a vineyard owned and operated by Ste. Michelle Wine Estates near Paterson, WA. Rows were oriented north/northwest to south/southeast and spaced at 2.74 m. Vines spaced at 1.83 m were trained to unilateral cordon at 1 m and converted from spur pruning to box pruning (10 to 12 cm on either side and above the cordon) in 2013; some rows were converted back to spur pruning in 2014 (24 to 30 buds per vine). Crop thinning was done with a machine harvester (Vinestar 990/500, ground speed 2.5 km/hr, bow-rod frequency 425 rpm) between pea size and lag phase. Treatments were applied to four replicated three-row blocks with four data vines in each middle row.

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Conclusion

V. vinifera is a resilient species whose cultivars are adapted to diverse climates. Nevertheless, climate change poses challenges for grape production, especially in warm and dry regions, where rising temperatures are increasing the plant water demand, while decreasing the irrigation water supply. Both heat stress and water stress limit crop yield, and excessive water stress may threaten plant survival. Even moderate water stress limits canopy gas exchange and growth, which results in more sun-exposed and warmer clusters with smaller berries and altered fruit composition. Future experiments should disentangle the relative importance of direct versus indirect effects of water stress for fruit composition. Higher temperatures accelerate vine growth and development and may advance or delay fruit ripening. However, temperature responses of grapevine phenology, growth, productivity, and fruit composition should be quantified to determine optimum and threshold temperatures. A global network of vineyard sites across diverse climates and with diverse cultivars would facilitate this effort. In addition to improving our knowledge of the genetic and phenotypic diversity among existing V. vinifera cultivars, it might be possible to identify and preserve distinct genotypes of V. sylvestris (and other wild species) with desirable traits that could be exploited to choose or develop adapted cultivars. Research into viticultural practices aimed at mitigating the effects of climate change should include the interaction between crop load and ripening rate under different climate scenarios. Finally, investigating mechanization as a tool to manipulate crop yields could help to improve vineyard WUE and counter the trend to earlier harvests and higher wine alcohol contents.

References


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