Review Article

The Effects of Elevated Atmospheric Carbon Dioxide on the Vineyard System of *Vitis vinifera*: A Review

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Abstract: Global atmospheric carbon dioxide concentrations will continue increasing throughout the next century, with profound impacts on agriculture. The literature concerning the effects of climate change on viticulture has largely focused on the isolated impacts of variables such as temperature and soil water deficit. Likewise, the research on the effects of elevated atmospheric CO2 on grapevines is stunted at the categorical level, chiefly because of the difficulty of experimentally controlling the gaseous environment in situ for the years necessary to replicate the vineyard system in a future climate condition. Despite numerous studies on the short-term influence of environmental and cultural factors on grapevine development at elevated carbon dioxide, the long-term impacts remain poorly understood.

The lack of field based elevated CO2 experiments in the United States is an added challenge to predicting viticultural changes, particularly in California. This review focuses on the systemic impact of atmospheric CO2 on *Vitis vinifera*, synthesizing physiological, phenological, and plant-pest interactions.
Major findings from this synthesis inform of a predicted increase in pest pressure, advanced phenological timing, transient increase in water use efficiency for grapevine, and changes in grape berry chemistry. While water use efficiency is highly desirable, the prediction for current winegrape growing regions is a transient increase in water use efficiency subsequently limited by a lack of available soil water. Grapevine is influenced by the negative synergistic effects of heat, drought, and elevated CO$_2$, which will alter cultural practices including harvest and pest/disease control, with downstream effects on winemaking. Several options for adaptation are discussed including leaf removal, planting alternative varieties and selective breeding of new varieties.

**Key words:** carbon storage, climate change, elevated CO$_2$, phenology, physiology, viticultural impact, water use, yield

**Introduction**

Rising atmospheric carbon dioxide levels are well documented by the International Panels on climate change, and carbon dioxide is expected to reach levels between 530 and 720 mg/L by the year 2100 according to intermediate scenarios (IPCC 2014). The last time Earth experienced levels of carbon dioxide consistently above 400 mg/L was the early Miocene era, approximately 23 million years ago (Pearson and Palmer 2000). The earliest agriculture was cultivated between 23,000 and 12,000 years ago (Weiss et al. 2004), with the earliest grape domestication estimated between 6,000 and 9,000 years ago (Terral et al. 2009). Grapevine has historically been sensitive to changes in climate, including the “Little Ice Age” in Europe (Mariani et al. 2018) and the more recent heat waves of the 21st century (Galat Giorgi et al. 2019, Venios et al. 2020, Bertamini et al. 2021).
While grapevine is typically cultivated in regions with wet winters and dry summers, increasing events of severe water stress will impede growth and reduce quality and yield in grapevine under climate change (Chaves et al. 2010, Mosedale et al. 2016, Scholasch and Rienth 2019, Morales-Castilla et al. 2020). Mean climate projections underestimate the impact of climate change on grapevine, in particular the impact of extreme temperature spikes/drops in areas growing premier winegrapes, currently characterized by few days with extreme heat or cold (White et al. 2006, Parker et al. 2020). While vines in Mediterranean areas will have to adapt to a more variable climate, elevated CO₂ will compound the effects of heat and drought stress at a global scale, impacting the quality and quantity of grapevine yield (Jones et al. 2005, Schultz 2010, Mosedale et al. 2016, Van Leeuwen and Darriet 2016, Bertamini et al. 2021). Carbon dioxide levels present a relatively novel challenge as they have been increasing at an unprecedented rate since the start of the Industrial Revolution (IPCC 2014).

Winegrapes are one of the most culturally and economically important crops worldwide, with an annual production of 60 million tons of fruit annually, the highest monetary value of fruit crops, and wine being part of the UNESCO intangible cultural heritage of humanity (Vivier and Pretorius 2002, Owens 2008, Ponti et al. 2018, Delrot et al. 2020, Santos et al. 2020). While wild grapevines can be very resilient to abiotic stress, domesticated winegrapes are far more sensitive; a result of the meticulous conservation of berry phenotype with emphasis on flavor over stress tolerance since 400 BC (Terral et al. 2009, Mariani et al. 2018). While this careful preservation of grape berry phenotype benefits the culture and industry of winegrape growing, as an ecological system the vineyard is vulnerable to a changing climate and elevated atmospheric CO₂ levels (Jones 2005).

Heat, elevated carbon dioxide, and limited water availability are necessary for cultivating quality grapes, however, studies on their interactive effects indicate these will have a negative synergistic
impact on grapevine (Lobell et al. 2006, Edwards et al. 2017, Galat Giorgi et al. 2019). The variety-specific responses to these environmental conditions introduces further variability to any study of grapevine response to future climate (Wohlfahrt et al. 2017), while variability in viticultural production is often viewed as undesirable. The varying physiology of cultivars and the long-term perennial nature of grapevine creates a challenging subject for adaptation studies; we expect that any adaptation will be much slower than that of annual crops (Lobell et al. 2006, Venios et al. 2020).

This review synthesizes recent literature published on the direct effects of elevated carbon dioxide on grapevine physiology, as well as the indirect effects on phenology and ecological responses of grapevines, including studies of the interactive effects of climate variables. This synthesis focused on literature specific to grapevine, and in addition, included studies on Arabidopsis to explore relevant hypotheses illustrating mechanisms of carbon dynamics in C3 plants. Results were compared from the four predominant experimental approaches; growth chambers, greenhouses, open top chambers, and Free Air CO2 Enrichment (FACE), all evaluated for predictive value. Finally, this review concludes by discussing potential research necessary for understanding the future of growing grapevine with elevated CO2 and adaptive viticultural management.

Impacts on the Vine and Berry Composition

Physiology

The physiological advantage of increased atmospheric carbon available for crops such as grapevine must be weighed against other factors likely to cooccur in the context of climate change, including water scarcity and temperature increases (Gray et al. 2016, Faralli et al. 2017). The literature asserts that the RUBISCO of C3 plants, including grapevines, are currently limited by ambient CO2
substrate (Long and Drake 1992, Ainsworth and Rogers 2007) and any increases should stimulate carbon
assimilation rates and increase vegetative growth (Bowes 1993), in the absence of other stressors.  
However, grapevine specific studies provide evidence for down regulation of net photosynthesis as vines 
acclimate to higher carbon environments (Salazar-Parra et al. 2014, Rangel da Silva et al. 2017). Salazar-
Parra et al. (2012) observed a transient increase in maximum photosynthesis in grapevine at elevated CO2,
but this effect dissipated over time. A short-term study in a temperature gradient greenhouse at 700 mg/L
CO2 showed grapevine photosynthesis increased around the time of veraison (Arrizabalaga-Arriazu et al.
2020), however studies of this duration are more reflective of a high dose of carbon enrichment rather 
than simulating future climate scenarios. 

One possible explanation for photosynthetic down regulation, i.e. acclimation, is lowered capacity 
of the photochemical machinery due to reductions in nitrogen concentrations in the leaf (Luo et al. 1994,
Moutinho-Pereira et al. 2009), limiting the activity of the enzyme RUBISCO. Species that are not nitrogen 
fixing such as grapevine are more likely to experience acclimation in elevated CO2 environments because 
of limited RUBISCO content (Ainsworth et al. 2002). The nitrogen dilution effect is well documented in 
other crop species, therefore in grapevine, nitrogen use efficiency could increase in elevated CO2 
environments because RUBISCO acclimation allows for nitrogen to be redistributed for other growth in 
the vine, however, FACE experiments documented nitrogen gains lower than predicted (Leaky et al.
2009).

The long-term impact of elevated CO2 on rates of grapevine photosynthesis has been shown to be 
dependent on other climate factors such as temperature and water availability (Wohlfahrt et al. 2018). 
Water scarcity, a concomitant climate change variable with elevated CO2, can impact the carbon storage 
in trunks of vines, as demonstrated in fruit tree orchards, and in turn, drought stress can be partially
relieved in elevated CO2 scenarios (Paudel et al. 2018). Three general physiological responses will benefit grapevine in an elevated CO2 climate with limited water availability; starting with partial stomatal closure limiting water loss, a subsequent increase in soil water content as transpiration decreases, and an increase of starch storage to provide for drought recovery (Salazar-Parra et al. 2015, Paudel et al. 2018). Acclimation to elevated CO2 will decrease rates of assimilation, while starch reserves increase, as the carbon sink may be driving rates of photosynthesis rather than carbon availability driving metabolism (Li et al. 2020). Therefore, the widespread observed reduction in stomatal conductance and density (Rangel da Silva et al. 2017, Kizildeniz et al. 2018) may have a greater impact on grapevine water use efficiency (WUE) from decreasing transpiration rather than increasing carbon assimilation.

In the past ten years, grapevine physiology research under elevated CO2 has focused on the impacts on WUE defined as carbon assimilated per unit of water transpired. Grapevine relies on stomatal aperture to facilitate cooling and CO2 uptake, releasing latent heat as the plant reaches physiological temperature thresholds; however, closure is essential to avoid detrimental water loss, heat damage, and reduced photosynthate production (Martínez-Lüscher et al. 2016b). With higher levels of carbon dioxide in the atmosphere, stomata can facilitate a lower water per CO2 molecular exchange, increasing the leaf level WUE (Figure 1). An early study of grapevine under elevated CO2 treatment for one season found no significant effect on stomatal conductance (gs) and transpiration (Moutinho-Pereira et al. 2009). Subsequently, a study using 650 mg/L in a similar open top chamber treatment found gs and transpiration decreased at elevated CO2 (Edwards et al.2017). In contrast, at only at 500 mg/L, higher gs and transpiration rates were observed in grapevines in a consistently elevated CO2 environment for three consecutive seasons (Wohlfahrt et al. 2018). On a morphological level, multiple studies have documented the reduction in stomatal density in several varieties of grapevine (Moutinho-Pereira et al. 2009, Rogiers
et al. 2011, Rangel da Silva et al. 2017). Scaling intrinsic water use efficiency to the whole plant level will require documenting changes in microclimate as well as morphology, such as stomatal density and leaf area (Medrano et al. 2015).

Further complicating predictions of WUE, combination studies of either elevated temperature and/or reduced soil water availability with elevated CO$_2$ reveals synergistic effects. In an open top chamber (OTC) study, combining temperature and CO$_2$ did not result in $g_s$ being significantly reduced, contrary to results of elevated CO$_2$ alone (Edwards et al. 2017). When latent heat is trapped, overheating subsequently decreases the activity of RUBISCO activase, for most plants at temperatures higher than 37°C (Crafts-Brandner and Salvucci 2000), and in grapevine between 35-40°C, varying by species (Luo et al. 2011, Salazar-Parra et al. 2012). The elevated CO$_2$ and temperature treatments showed an increase in transpiration (Edwards et al. 2016), and the effects of drought were only temporarily delayed (Rangel da Silva et al. 2017). Temperature and elevated CO$_2$ had an additive effect on plant leaf area for multiple grapevine clones (Arrizabalaga-Arriazu et al. 2020), highlighting that overall higher leaf area without increased WUE could be detrimental for heat stressed vines. Measurements of predawn water potential were more negative in vines at elevated CO$_2$, indicating the demand for soil water availability of vines with increased productivity (Wohlfahrt et al. 2018). Notedly, the production of fine roots was positively impacted by an elevated CO$_2$ treatment, which would theoretically increase water absorption of water available (Reddy et al. 2018).

There remain inconsistent predictions of the effects of elevated CO$_2$ on grapevine whole plant water use efficiency, which seem to be contingent upon other factors such as soil water availability, temperature, and variety of grapevine. With the evidence from these studies of elevated CO$_2$ and combination studies of soil water availability and temperature, grapevines most likely will not benefit
from a long-term increase in photosynthesis under elevated CO$_2$. The lack of soil water available and biological temperature thresholds for RUBISCO will limit the gains in photosynthesis, and more likely the vines will struggle to release latent heat as temperatures rise.

**Phenology**

Grapevine phenology is categorized into four life cycle stages of periodic development: budburst, flowering, veraison, and maturation. The grapevine phenological cycle is a two-year process; bud formation occurs in the first year which develop into shoots in the second year. Therefore, clusters are significantly impacted by the previous year’s climate (Vasconcelos et al. 2009). For grapevine grown at elevated CO$_2$, advances in phenology compound significantly over seasons (Edwards et al. 2017). This is likely the result of stored carbon photosynthate from the productive previous year. As a result, it can take several years to observe the effects of elevated CO$_2$ on grapevine phenology (Edwards et al. 2017), which leads to the question of: “To what extent does elevated CO$_2$ impact the timing of phenological stages over the long-term?”

Studies of Arabidopsis, another C3 flowering plant, provide insight to the mechanisms of phenological changes observed in grapevine. Excess carbohydrates may act similarly to phytohormones to delay the upregulation of genes involved in flowering time, as well as cell wall invertases in the meristem that downregulate photosynthesis under treatments of elevated CO$_2$, which leads to earlier flowering (Springer and Ward 2007). For grapevine, it is possible that excess photosynthate could trigger early flowering through the transfer of carbohydrates from leaves. One of the most robust findings to support this hypothesis is that growth under elevated CO$_2$ results in increased carbohydrate reserves in plants (Kizildeniz et al. 2021).
The sugars produced by photosynthesis contribute only a fraction of the source of carbon needed for rapid growth and development from budbreak to flowering and sugar accumulation in berries at veraison, the remaining needed for these growth spurts is mobilized from long-term storage of total nonstructural carbohydrates (TNC) in trunks and roots (Zufferey et al. 2012). Over several growing seasons, storage of carbohydrates in the trunk will be impacted by elevated CO2 (Lebon et al. 2008) and could therefore contribute to shifts in phenology. In a greenhouse study of fruiting cuttings where sugar accumulation in berries was measured, elevated CO2 increased the rate of ripening correlated with the photosynthetic rate (and was only slightly mediated by UV-B treatments) (Martínez-Lüscher et al. 2015). The effect of elevated CO2 on phenology was greater than the treatment of temperature elevated by 4°C (Martínez-Lüscher et al. 2016b). Therefore, an increase in total nonstructural carbohydrates could be a driver of advances in phenology long term, on its own, as well as with concomitant increases in growing season temperatures.

Carbohydrate reserves regulate the growth and differentiation of flowers, which only occurs after the grapevine shoot is resource independent from the rest of the vine (Lebon et al. 2008, Vasconcelos et al. 2009). These findings suggest that with an increase in carbon reserves stored as starch in roots, trunks and canes, second season shoots may grow faster and achieve independence earlier in the growing season. This could contribute to early flowering as a result of lifted competition for resources between vegetative and reproductive growth. In contrast, long-term studies in grapevine decreasing the leaf to fruit ratios (measured as light-exposed leaf area to fruit) decreased essential reserves of the TNC in the roots (Zufferey et al. 2012). The well-known viticultural technique of strategic leaf removal has been shown to delay maturation, highlighting the importance of carbon availability for phenological development (Poni et al. 2006, Parker 2012, Parker et al. 2014).
While the mechanism for phenological shifts in grapevine grown under elevated CO\textsubscript{2} is understudied, these shifts have been quantified using FACE experiments. The combination of elevated CO\textsubscript{2} and temperature in open top field chambers caused an advance in flowering time by three days and veraison by two weeks (Edwards et al. 2016). The impact of elevated CO\textsubscript{2} on phenological timing is greatest during the period between fruit set to veraison and this impact increases when combined with a temperature treatment (Martínez-Lüscher et al. 2016a, Arrizabalaga-Arriazu et al. 2020). During fruit set, elevated CO\textsubscript{2} treatments with and without temperature treatments increased total soluble solids (hastening maturation), as well as decreased anthocyanins and malic acid concentration, which would contribute to an earlier veraison and harvest (Salazar-Parra et al. 2010). However, the impact of high temperature may have a greater impact on this phenological period (Arrizabalaga-Arriazu et al. 2020).

The quality of fruit harvested is the utmost concern when considering advanced phenology. Grapevines vulnerable to frost damage will suffer from early budburst, with subsequent losses in yield (Fraga et al. 2016). One consequence of increased shoot vigor at elevated CO\textsubscript{2} is the expected increase in bud fertility, which will likely increase the number of flowers per vine (Figure 1) (Delrot et al. 2020, Bindi et al. 2001). Changes in cluster density and phenological timing impact the carefully articulated annual harvest. Unbalanced sugar/acid ratios resulting from early harvest decrease the quality of grapes and wine produced, discussed further in the “Berry and Wine Chemistry” section below (Jones et al. 2005, Jones 2013). Shifting the lifecycle of grapevine will have a global impact on winegrape production.
Berry and wine chemistry

Fruit composition is a major area of concern for growers and winemakers alike, especially aromatic compounds. The changes in pest interactions, physiology, and timing of veraison in response to elevated CO₂ will collectively impact the resulting grape and wine quality (Ollat et al. 2017). For successful wines, in the grape berry there is a balance of acid and sugar at harvest. Increasing atmospheric carbon available impacts the balance as ripening advances and sugar accumulation is accelerated (Martínez de Toda et al. 2014). Flavonoids and anthocyanins are important for the flavor, color, and mouthfeel of wine. The molecular analysis from the original Italian FACE experiments showed increases in total flavonoids, total anthocyanins, and total non-anthocyanin flavonoids in the wine produced with carbon enriched grapes grown at 700 mg/L (Bindi et al. 2001), which typically would affect the color and mouthfeel of wine.

Interestingly, a subsequent experiment using 500 mg/L CO₂ open top chambers determined there were significant increases in ethyl 2-methylbutyrate (apple), isoamyl acetate (burnt), ethyl hexanoate (apple, pineapple), ethyl octanoate (fruit/fat), butyric acid (rancid), and isovaleric acid (rancid) concentrations and a significant decrease in ethyl acetate (fruity) concentration in wines produced from enriched CO₂ grapes after one year (Gonçalves et al. 2008), which contribute to the balance of floral and fruity characteristics in wines (Francis 2012). In the second year they found lower methionol (raw potato), 1-octanol (alcohol), and 4-ethylguaiacol (smoke), and they found higher ethyl lactate (butter) and linalool (floral) concentrations, although these changes in berry chemistry did not appear significantly in the quality of wine produced (Gonçalves et al. 2008). Despite the chemical changes in berries at harvest, Gonçalves et al. (2008) determined there was not a significant impact on the quality of wine even with the changes in molecular components of the juices, similar to the early studies led by Bindi et al. (2001) (Table 1).
Although the changes observed in compounds contributing to flavor have been noted as so far insignificant for quality, a major concern for winemakers is the increase in alcohol content resulting from an increase in sugar concentrations in berries, as a result of higher CO₂ concentrations (Van Leeuwen and Darriet 2016, Teslić et al. 2018, Delrot et al. 2020, Ubeda et al. 2020). In the past, winemakers have added sugar to the fermentation to increase the final alcohol percentage (chaptalization where legal), depending on legal regulations for winemaking. However, in recent years winemakers have begun removing sugar through processes like reverse osmosis in order to prevent alcohol levels from rising (Christmann et al. 2017, Delrot et al. 2020). Overall, elevated CO₂ is altering the balance of sugar accumulation, the levels tartaric and malic acids in berries and wine, and the impact on wine quality continues to be investigated (Table 1) (Gonçalves et al. 2008, Pons et al. 2017).

The most recent FACE studies on grapes continue to evaluate the berry chemistry and quality developing over years of exposure to elevated CO₂. The GrapeFACE in Germany analyzed must from grapes after pressing and did not find a significant increase in sugar content from conditions of carbon enrichment (Wohlfahrt et al. 2018). The Gonçalves (2008) study also concluded that changes in water availability and heat stress could change their predictions in wine quality. We should expect that with the shifts in phenology and physiological changes to berries, early harvest will impact the quality of grapes in terms of reaching maturation too quickly (Martínez-Lüscher et al. 2016a). Viticulturists could also anticipate altered physiological demands to have long-term impacts on berry quality (Pons et al. 2017).

**Pest and disease pressure**

In contrast to the ecological pressures discussed above, the rates of some fungal infections may be reduced in elevated CO₂ scenarios. With higher carbon allocation to roots, grapevine mycorrhizal colonization may be promoted by elevated CO₂ (Torres et al. 2018), which has been shown to protect
grapevine against the nematode *Xiphinema index* by stimulating defense gene response (Hao et al. 2012). A study of elevated CO$_2$ on several varieties of grapevine seedlings showed a reduced severity of the infection of *Xanthomonas campestris pv viticola*, a vector of bacterial canker in immature grapevine (Table 1) (Conceição et al. 2017). This may be the result of lower stomatal conductance ($g_s$); with stomatal aperture reduced, there is less opportunity for bacteria to invade the leaf pores (Conceição et al. 2017, Kizildeniz et al. 2018). Also, researchers recorded a reduced instance and severity of powdery mildew infection in cv Barbera, at elevated CO$_2$ (Table 1) (Pugliese et al. 2010). The Geisenheim GrapeFACE site recorded changes in the bunch architecture but did not see an increase in the frequency of *B. cinera*, botrytis bunch rot, a necrotrophic fungus, occurrence (Wohlfahrt et al. 2018).

Changes in leaf chemistry phenotype, specifically carbon content, (e.g. higher soluble carbohydrates due to higher carbon dioxide levels), will increase the pressure of grapevine pests in future climates. Increasing available carbon dioxide, without a concomitant increase in nutrient levels in the soil, leads to an increase in C:N ratios in leaves (Figure 1) (Hunter 2001, Ainsworth and Long 2004, Moutinho-Pereira et al. 2009, Arrizabalaga-Arriazu et al. 2020, Kizildeniz et al. 2021). Insects consume at higher rates when nitrogen has been diluted to meet their nitrogen intake needs and chewing insect pests will generally eat more leaf tissue in elevated carbon dioxide scenarios (Hunter 2001). Elevated CO$_2$ increased individual survival rates and increased the fecundity of female mealybugs, which eat phloem of grapevine damaging the temporal and perennial plant tissue (Bordeu et al. 2012, Schulze-Sylvester and Reineke 2019, Schulze-Sylvester, Corronca and Paris 2021). The European grapevine moth, *Lobesia botrana*, is a major problem for European vineyards, affecting both the berries and flowers of grapevines; and has already invaded North and South American vineyards (Reineke and Selim 2019). *L. botrana* is also responsible for spreading Ochratoxin A-producing *Aspergillus* fungi,
which typically spikes in occurrence during hotter and drier years (Mondani et al. 2020). At higher temperatures simulating future climate conditions, *L. botrana* female growth rate and pupal mass increased (Iltis et al. 2018), while researchers found a down regulation of expression of ethylene-responsive factors, which suggests grapevines can become more vulnerable to herbivory or abiotic stress under future climate change as these are the major stress and defense response factors (Reineke and Selim 2019).

A comprehensive study of soil and elevated CO\(_2\) showed the decomposition pathway is altered by the carbon-, nitrogen-, and phosphorus-acquiring enzymes in the soil with a significant increase in nematode density (Thakur et al. 2019). More than 4,000 plant-parasitic nematodes exist, posing a well-known global issue for grapevine, reducing total crop production by 8.8-14.6%, and one of the worst threats from the nematode *Xiphinema index* is GLRV (Grapevine Leaf Roll Virus) (Andret-Link et al. 2017). Under elevated CO\(_2\) conditions, if ethylene is suppressed and salicylic acid is increased, it is likely that grapevine will struggle with an increase in pest and disease vectors such as nematodes and fungi (Reineke and Selim 2019). Grapevines largely rely on human intervention for defense against pests and diseases (Pertot et al. 2017), and this reliance could increase in future climates. Consider the grapevine “immune system” as weakened in terms of chemical defense, but some altered carbon dynamics under elevated CO\(_2\) may be beneficial for reducing severity of pest pressure.

**Discussion**

An anticipated management solution to phenological shifts is planting later ripening and stress tolerant alternative varieties. Government response to climate change will determine the actions European growers are allowed to take to adapt to climate change, considering the current trials of alternative varieties.
planted in small diversity blocks in France as a positive example (Morales-Castilla et al. 2020). Ancient varieties being tested in temperature gradient greenhouses in Spain for response to combination stresses of drought, heat, and elevated CO₂ showed greater resiliency to stress and did not shift phenological timing, although this was a short-term experiment (Antolín et al. 2021, Goicoechea et al. 2021). In some cases, alternative varieties may be hybrid crosses between existing cultivars and later ripening varieties. However, hypothetical crosses between very late ripening varieties were modelled and still struggle to be late-ripening enough to endure the predicted 23-day shift and potential increase of 7°C expected by the end of this century for major wine grape growing areas (Duchêne et al. 2010). Alternative varieties can be identified by oenological and ecological principals that make them suitable candidates for replacing existing cultivars, such as flavor profile and ability to survive long term through stressful climate change conditions (Antolín et al. 2021, Goicoechea et al. 2021). The challenge of adapting new varieties is highlighted by current popular varieties struggling with increases in growing season temperatures (Jones 2021), however a combination of diversity block trials and greenhouse experiments will guide predictions of the best alternatives (Wolkovich et al. 2018).

Our present knowledge of grapevine climate niches is limited relative to the vast diversity of cultivars (Duchêne et al. 2010). With California as an example, there are many potential late ripening varieties suitable as alternatives to early ripening Chardonnay that have yet to be tested in diversity blocks (Wolkovich et al. 2018). Even clones can have a varied response to climate change variables (Arrizabalaga-Arriazu et al. 2020). Varieties with heat and drought tolerance traits are a starting point for elevated CO₂ studies, as we expand from understanding the mechanisms of change into exploring mitigation strategies. Exploring the vast diversity of grapevine using diversity plots is a straightforward
ecological approach, which could be enhanced by evaluating the success of plants under several biotic and abiotic stresses predicted for the future.

Many studies on the impacts of leaf removal suggest that manipulating canopy cover is an effective way to mitigate phenological shifts caused by climate change (Martínez de Toda et al. 2014, Parker 2012). Leaf removal at pre-bloom positively influences cell division in inflorescence, by reducing sugar transport and decreasing flower fertility, which mitigates cluster compactness (Lebon et al. 2004, VanderWeide et al. 2020). Not only can leaf removal aid in delaying phenology, but other positive impacts also include increasing acid to sugar ratio at harvest, increasing production of anthocyanins and flavonoids, and decreasing incidence of bunch rot disease (Kliewer and Smart 1989, Martínez de Toda et al. 2014, VanderWeide et al. 2020).

Ecologists generally study a system’s responses and interactions, and viticulturists need this system perspective for the challenges presented by climate change. Our understanding of the effects of elevated CO₂ on the vineyard system is profoundly complicated by the interactive effects of other biotic and abiotic stressors. From an ecological perspective, long-term FACE studies are the most realistic predictors of response to elevated CO₂. Advocating for long-term agroecological studies is necessary to evaluate the top-down and bottom-up impacts of higher carbon availability on pest/disease interactions, grapevine growth and phenology dynamics, and the resulting quality of wine produced.

Grapevine physiology will be impacted by elevated carbon dioxide, increasing temperatures, and extreme heat events during the growing season (De Cortázar-Atauri et al. 2017, Ugaglia et al. 2019). FACE experiments highlight the necessity of water availability for grapevines to take advantage of increased carbon dioxide for productivity. Soil water availability impacts the opening of stomata, and in the case of GrapeFACE, the vines had increased gs with more CO₂ available (Wohlfahrt et al. 2018).
Grapevines may need more water under future climate conditions of elevated CO₂ and temperature, while precipitation is expected to decrease in most of the wine growing regions of the world. Desiccation threatens vines through water loss from latent cooling under elevated temperature, resulting in higher cumulative water loss even when operating at higher water use efficiency. The modulating response of stomata documented across literature is dependent on the soil water availability and temperature regimes (Arrizabalaga-Arriazu et al. 2020). In this synthesis, the varying levels of CO₂, ambient temperatures, and duration of these experiments could have contributed to these contrasting results of stomatal behavior, as well as the conditions of the chambers and greenhouses, versus FACE infrastructure.

Physiological response to abiotic stresses in future climate change conditions is likely to weaken grapevine, creating a vulnerability for biotic stresses such as pests. Overall, chewing pest pressure is anticipated to increase as carbon dioxide and temperature increase (Reineke and Selim 2019). It is unknown whether pest pressure can be compensated by the predicted increase in foliar growth and the effect of lower nutrient density on the populations of pests. The growing season for grapes may require drastic changes in viticultural practices to manage pests, alleviate heat and drought stress, and predict harvest dates. Fungal infections are responsible for the lion’s share of crop damage, with most of the elevated CO₂ studies focusing on yield, it is critical to gain more insight into the response of specific fungal pressures will decrease in the future.

One of the biggest challenges for grape growers will be the shifts in phenological timing, with the potential for frost at early budbreak, alterations in cluster formation and density, and compromising harvest with early maturation. Many of the short-term experiments described here did not find significant effects on phenology and yield, while long term studies account for acclimation and
compounding effects of seasonal exposure to elevated carbon dioxide. Predictions of overall vineyard response to climate change are more accurate when experiments are field based, multi-seasonal, and combine the variables of water availability and temperature.

**Conclusion**

A combination of the impacts of pest pressure, phenology, and physiology predict a much different future environment for growing grapes. Elevated carbon dioxide is a pervasive threat to the vineyard system because it fuels undesirable growth. Grapevine will sustain the impacts of elevated carbon dioxide for generations, as a perennial crop with a rich memory and sensitive expression of climate. We can strengthen the vineyard system by introducing more diverse cultivars, with an ideal candidate fitting the profile of heat and drought tolerant, late ripening, with strong pest resistance.

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Table 1  Studies of carbon enrichment with grapevine, using temperature growth chambers (GC), greenhouse (GH), temperature gradient greenhouses (TGG), open top chambers (OTC) and Free Air Carbon Enrichment (FACE) with significant findings are summarized here. The contrast in results for photosynthetic response is likely due to the duration of the studies and the material used (fruiting cuttings for the Salazar-Parra et al. 2015 study versus field grown vines for Wohlfahrt et al. 2017, 2018). Photosynthesis (A_{net}) increased in response to elevated CO₂ in all of these studies. However, the downstream impact on phenology has unclear results, as the Edwards FACE studies (2016, 2017) showed a significant impact on the timing of veraison, while the more recent temperature gradient greenhouse study by Arrizabalaga-Arriazu et al. 2020 did not. Few studies document long-term impacts on phenology, and there have been no studies in the United States using FACE.

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<td>No significant impact on wine quality (20 year old vines)(^a)</td>
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<td>Gonçalves et al. 2008</td>
<td>500</td>
<td>OTC</td>
<td>No significant impact on wine quality</td>
<td>Portugal</td>
</tr>
<tr>
<td>Moutinho-Pereira et al. 2009</td>
<td>500</td>
<td>OTC</td>
<td>↑ Net photosynthetic rate (A)</td>
<td>Portugal</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Intrinsic water use efficiency (A/gs)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↑ Leaf thickness</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↑ Mg concentration</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↑ C/N, K/N and Mg/N ratios</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↓ Stomatal density and N concentration</td>
<td></td>
</tr>
<tr>
<td>Pugliese et al. 2010</td>
<td>800</td>
<td>GC</td>
<td>↓ Chlorophyll content</td>
<td>Italy</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↑ Instance and severity of powdery mildew increased for cv. Moscato</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↑ Instance and severity of powdery mildew increased for cv. Barbera</td>
<td></td>
</tr>
<tr>
<td>Salazar-Parra et al. 2012</td>
<td>700</td>
<td>GH</td>
<td>↓ Reactive Oxygen Species</td>
<td>Spain</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>No significant change in photosynthetic pigments</td>
<td></td>
</tr>
<tr>
<td>Salazar-Parra et al. 2015</td>
<td>700</td>
<td>TGG</td>
<td>No effect on photosynthetic rates</td>
<td>Spain</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↓ Stomatal conductance and transpiration at 20 days</td>
<td></td>
</tr>
<tr>
<td>Martínez-Lüscher et al. 2015</td>
<td>700</td>
<td>GH</td>
<td>↑ Photosynthesis (as A_{net})</td>
<td>Spain</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↑ Dark respiration</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↓ Photorespiration</td>
<td></td>
</tr>
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<td></td>
<td></td>
<td></td>
<td>↑ Chlorophyll a and b content</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↑ Ripening rates</td>
<td></td>
</tr>
<tr>
<td>Study</td>
<td>Year</td>
<td>Experiment</td>
<td>Effect</td>
<td>Location</td>
</tr>
<tr>
<td>--------------------------------------</td>
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<tr>
<td>Martinez-Lüscher et al. 2016a</td>
<td>700</td>
<td>TGG</td>
<td>Advanced phenology with and without combination of elevated temperature, with cultivar specific response</td>
<td>Spain</td>
</tr>
<tr>
<td>Edwards et al. 2016, 2017</td>
<td>650</td>
<td>OTC</td>
<td>Anthesis and veraison advanced in the third season, Photosynthesis (as $A_{sat}$)</td>
<td>Australia</td>
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<tr>
<td>Rangel da Silva et al. 2017</td>
<td>800</td>
<td>GC</td>
<td>18% reduction in leaf nitrogen content, 25% reduction in stomatal density, Generally increased drought tolerance</td>
<td>USA</td>
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<tr>
<td>Conceição et al. 2017</td>
<td>770</td>
<td>GC</td>
<td>Decreased infection of bacterial disease of <em>Xanthomonas campestris pv viticola</em></td>
<td>Brazil</td>
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<tr>
<td>Wohlfahrt et al. 2017, 2018</td>
<td>480 - 500 (+20% ambient)</td>
<td>FACE</td>
<td>net assimilation rates, intrinsic water use efficiency (WUEi), pre-dawn leaf water potential, bunch compactness, weight, and length, Ethylene signals and ethylene responsive factors</td>
<td>Germany</td>
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<tr>
<td>Kizildeniz et al. 2018</td>
<td>700</td>
<td>TGG</td>
<td>$g_s$, with additive effect of temperature and drought, Stimulated more vegetative than reproductive growth, WUE increases did not compensate for water stress</td>
<td>Spain</td>
</tr>
<tr>
<td>Reineke and Selim 2019</td>
<td>500</td>
<td>FACE</td>
<td>Ethylene signalling hormones, defensive compounds, including salicylic acid, vulnerability to moth <em>L. botrana</em></td>
<td>Germany</td>
</tr>
<tr>
<td>Arrizabalaga-Arriazu et al. 2020</td>
<td>700</td>
<td>TGG</td>
<td>Phenology and cluster traits not significantly impacted, Increased leaf area at maturity, Photosynthesis ($A_{net}$), Stomatal conductance</td>
<td>Spain</td>
</tr>
</tbody>
</table>

- ↑ indicates increase
- ↓ indicates decrease
- ± indicates no change
Figure 1  At a biophysiological level, elevated CO₂ affects the production and storage of sugars (total non-structural carbohydrates) and the balance of growth. Indirect effects of rising CO₂ levels catalyze top-down effects of increased C:N ratios with subsequent increases in herbivory. Grapevine phenology is a sensitive two-year cycle of growth spurts and acid degradation before harvest, with profound impacts on grape berry quality when the timing is shifted. Intrinsic water use efficiency at the leaf level increases as stomatal conductance decreases and more carbon is available per water molecule lost. However, water use efficiency at the whole plant level depends on soil water available, which will vary depending on microclimate and future climate conditions.