

1 **Review Article**

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

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17
18 **Abstract:** Global atmospheric carbon dioxide concentrations will continue increasing throughout the
19 next century, with profound impacts on agriculture. The literature concerning the effects of climate
20 change on viticulture has largely focused on the isolated impacts of variables such as temperature and
21 soil water deficit. Likewise, the research on the effects of elevated atmospheric CO₂ on grapevines is
22 stunted at the categorical level, chiefly because of the difficulty of experimentally controlling the
23 gaseous environment in situ for the years necessary to replicate the vineyard system in a future climate
24 condition. Despite numerous studies on the short-term influence of environmental and cultural factors on
25 grapevine development at elevated carbon dioxide, the long-term impacts remain poorly understood.
26 The lack of field based elevated CO₂ experiments in the United States is an added challenge to
27 predicting viticultural changes, particularly in California. This review focuses on the systemic impact of
28 atmospheric CO₂ on *Vitis vinifera*, synthesizing physiological, phenological, and plant-pest interactions.

29 Major findings from this synthesis inform of a predicted increase in pest pressure, advanced
30 phenological timing, transient increase in water use efficiency for grapevine, and changes in grape berry
31 chemistry. While water use efficiency is highly desirable, the prediction for current winegrape growing
32 regions is a transient increase in water use efficiency subsequently limited by a lack of available soil
33 water. Grapevine is influenced by the negative synergistic effects of heat, drought, and elevated CO₂,
34 which will alter cultural practices including harvest and pest/disease control, with downstream effects on
35 winemaking. Several options for adaptation are discussed including leaf removal, planting alternative
36 varieties and selective breeding of new varieties.

37 **Key words:** carbon storage, climate change, elevated CO₂, phenology, physiology, viticultural impact,
38 water use, yield

39 Introduction

40 Rising atmospheric carbon dioxide levels are well documented by the International Panels on
41 climate change, and carbon dioxide is expected to reach levels between 530 and 720 mg/L by the year
42 2100 according to intermediate scenarios (IPCC 2014). The last time Earth experienced levels of carbon
43 dioxide consistently above 400 mg/L was the early Miocene era, approximately 23 million years ago
44 (Pearson and Palmer 2000). The earliest agriculture was cultivated between 23,000 and 12,000 years ago
45 (Weiss et al. 2004), with the earliest grape domestication estimated between 6,000 and 9,000 years ago
46 (Terral et al. 2009). Grapevine has historically been sensitive to changes in climate, including the “Little
47 Ice Age” in Europe (Mariani et al. 2018) and the more recent heat waves of the 21st century (Galat
48 Giorgi et al. 2019, Venios et al. 2020, Bertamini et al. 2021).

49 While grapevine is typically cultivated in regions with wet winters and dry summers, increasing
50 events of severe water stress will impede growth and reduce quality and yield in grapevine under climate
51 change (Chaves et al. 2010, Mosedale et al. 2016, Scholasch and Rienth 2019, Morales-Castilla et al.
52 2020). Mean climate projections underestimate the impact of climate change on grapevine, in particular
53 the impact of extreme temperature spikes/drops in areas growing premier winegrapes, currently
54 characterized by few days with extreme heat or cold (White et al. 2006, Parker et al. 2020). While vines
55 in Mediterranean areas will have to adapt to a more variable climate, elevated CO₂ will compound the
56 effects of heat and drought stress at a global scale, impacting the quality and quantity of grapevine yield
57 (Jones et al. 2005, Schultz 2010, Mosedale et al. 2016, Van Leeuwen and Darriet 2016, Bertamini et al.
58 2021). Carbon dioxide levels present a relatively novel challenge as they have been increasing at an
59 unprecedented rate since the start of the Industrial Revolution (IPCC 2014).

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

69 Heat, elevated carbon dioxide, and limited water availability are necessary for cultivating quality
70 grapes, however, studies on their interactive effects indicate these will have a negative synergistic

71 impact on grapevine (Lobell et al. 2006, Edwards et al. 2017, Galat Giorgi et al. 2019). The variety-
72 specific responses to these environmental conditions introduces further variability to any study of
73 grapevine response to future climate (Wohlfahrt et al. 2017), while variability in viticultural production
74 is often viewed as undesirable. The varying physiology of cultivars and the long-term perennial nature
75 of grapevine creates a challenging subject for adaptation studies; we expect that any adaptation will be
76 much slower than that of annual crops (Lobell et al. 2006, Venios et al. 2020).

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

86 **Impacts on the Vine and Berry Composition**

87 *Physiology*

88 The physiological advantage of increased atmospheric carbon available for crops such as
89 grapevine must be weighed against other factors likely to cooccur in the context of climate change,
90 including water scarcity and temperature increases (Gray et al. 2016, Faralli et al. 2017). The literature
91 asserts that the RUBISCO of C3 plants, including grapevines, are currently limited by ambient CO₂

92 substrate (Long and Drake 1992, Ainsworth and Rogers 2007) and any increases should stimulate carbon
93 assimilation rates and increase vegetative growth (Bowes 1993), in the absence of other stressors.
94 However, grapevine specific studies provide evidence for down regulation of net photosynthesis as vines
95 acclimate to higher carbon environments (Salazar-Parra et al. 2014, Rangel da Silva et al. 2017). Salazar-
96 Parra et al. (2012) observed a transient increase in maximum photosynthesis in grapevine at elevated CO₂,
97 but this effect dissipated over time. A short-term study in a temperature gradient greenhouse at 700 mg/L
98 CO₂ showed grapevine photosynthesis increased around the time of veraison (Arrizabalaga-Arriazu et al.
99 2020), however studies of this duration are more reflective of a high dose of carbon enrichment rather
100 than simulating future climate scenarios.

101 One possible explanation for photosynthetic down regulation, i.e. acclimation, is lowered capacity
102 of the photochemical machinery due to reductions in nitrogen concentrations in the leaf (Luo et al. 1994,
103 Moutinho-Pereira et al. 2009), limiting the activity of the enzyme RUBISCO. Species that are not nitrogen
104 fixing such as grapevine are more likely to experience acclimation in elevated CO₂ environments because
105 of limited RUBISCO content (Ainsworth et al. 2002). The nitrogen dilution effect is well documented in
106 other crop species, therefore in grapevine, nitrogen use efficiency could increase in elevated CO₂
107 environments because RUBISCO acclimation allows for nitrogen to be redistributed for other growth in
108 the vine, however, FACE experiments documented nitrogen gains lower than predicted (Leaky et al.
109 2009).

110 The long-term impact of elevated CO₂ on rates of grapevine photosynthesis has been shown to be
111 dependent on other climate factors such as temperature and water availability (Wohlfahrt et al. 2018).
112 Water scarcity, a concomitant climate change variable with elevated CO₂, can impact the carbon storage
113 in trunks of vines, as demonstrated in fruit tree orchards, and in turn, drought stress can be partially

114 relieved in elevated CO₂ scenarios (Paudel et al. 2018). Three general physiological responses will benefit
115 grapevine in an elevated CO₂ climate with limited water availability; starting with partial stomatal closure
116 limiting water loss, a subsequent increase in soil water content as transpiration decreases, and an increase
117 of starch storage to provide for drought recovery (Salazar-Parra et al. 2015, Paudel et al. 2018).
118 Acclimation to elevated CO₂ will decrease rates of assimilation, while starch reserves increase, as the
119 carbon sink may be driving rates of photosynthesis rather than carbon availability driving metabolism (Li
120 et al. 2020). Therefore, the widespread observed reduction in stomatal conductance and density (Rangel
121 da Silva et al. 2017, Kizildeniz et al. 2018) may have a greater impact on grapevine water use efficiency
122 (WUE) from decreasing transpiration rather than increasing carbon assimilation.

123 In the past ten years, grapevine physiology research under elevated CO₂ has focused on the impacts
124 on WUE defined as carbon assimilated per unit of water transpired. Grapevine relies on stomatal aperture
125 to facilitate cooling and CO₂ uptake, releasing latent heat as the plant reaches physiological temperature
126 thresholds; however, closure is essential to avoid detrimental water loss, heat damage, and reduced
127 photosynthate production (Martínez-Lüscher et al. 2016b). With higher levels of carbon dioxide in the
128 atmosphere, stomata can facilitate a lower water per CO₂ molecular exchange, increasing the leaf level
129 WUE (Figure 1). An early study of grapevine under elevated CO₂ treatment for one season found no
130 significant effect on stomatal conductance (g_s) and transpiration (Moutinho-Pereira et al. 2009).
131 Subsequently, a study using 650 mg/L in a similar open top chamber treatment found g_s and transpiration
132 decreased at elevated CO₂ (Edwards et al. 2017). In contrast, at only at 500 mg/L, higher g_s and
133 transpiration rates were observed in grapevines in a consistently elevated CO₂ environment for three
134 consecutive seasons (Wohlfahrt et al. 2018). On a morphological level, multiple studies have documented
135 the reduction in stomatal density in several varieties of grapevine (Moutinho-Pereira et al. 2009, Rogiers

136 et al. 2011, Rangel da Silva et al. 2017). Scaling intrinsic water use efficiency to the whole plant level will
137 require documenting changes in microclimate as well as morphology, such as stomatal density and leaf
138 area (Medrano et al. 2015).

139 Further complicating predictions of WUE, combination studies of either elevated temperature
140 and/or reduced soil water availability with elevated CO₂ reveals synergistic effects. In an open top
141 chamber (OTC) study, combining temperature and CO₂ did not result in g_s being significantly reduced,
142 contrary to results of elevated CO₂ alone (Edwards et al. 2017). When latent heat is trapped, overheating
143 subsequently decreases the activity of RUBISCO activase, for most plants at temperatures higher than
144 37°C (Crafts-Brandner and Salvucci 2000), and in grapevine between 35-40°C, varying by species (Luo
145 et al. 2011, Salazar-Parra et al. 2012). The elevated CO₂ and temperature treatments showed an increase
146 in transpiration (Edwards et al. 2016), and the effects of drought were only temporarily delayed (Rangel
147 da Silva et al. 2017). Temperature and elevated CO₂ had an additive effect on plant leaf area for multiple
148 grapevine clones (Arrizabalaga-Arriazu et al. 2020), highlighting that overall higher leaf area without
149 increased WUE could be detrimental for heat stressed vines. Measurements of predawn water potential
150 were more negative in vines at elevated CO₂, indicating the demand for soil water availability of vines
151 with increased productivity (Wohlfahrt et al. 2018). Notedly, the production of fine roots was positively
152 impacted by an elevated CO₂ treatment, which would theoretically increase water absorption of water
153 available (Reddy et al. 2018).

154 There remain inconsistent predictions of the effects of elevated CO₂ on grapevine whole plant
155 water use efficiency, which seem to be contingent upon other factors such as soil water availability,
156 temperature, and variety of grapevine. With the evidence from these studies of elevated CO₂ and
157 combination studies of soil water availability and temperature, grapevines most likely will not benefit

158 from a long-term increase in photosynthesis under elevated CO₂. The lack of soil water available and
159 biological temperature thresholds for RUBISCO will limit the gains in photosynthesis, and more likely
160 the vines will struggle to release latent heat as temperatures rise.

161 *Phenology*

162 Grapevine phenology is categorized into four life cycle stages of periodic development:
163 budburst, flowering, veraison, and maturation. The grapevine phenological cycle is a two-year process;
164 bud formation occurs in the first year which develop into shoots in the second year. Therefore, clusters
165 are significantly impacted by the previous year's climate (Vasconcelos et al. 2009). For grapevine grown
166 at elevated CO₂, advances in phenology compound significantly over seasons (Edwards et al. 2017).
167 This is likely the result of stored carbon photosynthate from the productive previous year. As a result,
168 it can take several years to observe the effects of elevated CO₂ on grapevine phenology (Edwards et al.
169 2017), which leads to the question of: "To what extent does elevated CO₂ impact the timing of
170 phenological stages over the long-term?"

171 Studies of Arabidopsis, another C₃ flowering plant, provide insight to the mechanisms of
172 phenological changes observed in grapevine. Excess carbohydrates may act similarly to phytohormones
173 to delay the upregulation of genes involved in flowering time, as well as cell wall invertases in the
174 meristem that downregulate photosynthesis under treatments of elevated CO₂, which leads to earlier
175 flowering (Springer and Ward 2007). For grapevine, it is possible that excess photosynthate could
176 trigger early flowering through the transfer of carbohydrates from leaves. One of the most robust
177 findings to support this hypothesis is that growth under elevated CO₂ results in increased carbohydrate
178 reserves in plants (Kizildeniz et al. 2021).

179 The sugars produced by photosynthesis contribute only a fraction of the source of carbon needed
180 for rapid growth and development from budbreak to flowering and sugar accumulation in berries at
181 veraison, the remaining needed for these growth spurts is mobilized from long-term storage of total
182 nonstructural carbohydrates (TNC) in trunks and roots (Zufferey et al. 2012). Over several growing
183 seasons, storage of carbohydrates in the trunk will be impacted by elevated CO₂ (Lebon et al. 2008) and
184 could therefore contribute to shifts in phenology. In a greenhouse study of fruiting cuttings where sugar
185 accumulation in berries was measured, elevated CO₂ increased the rate of ripening correlated with the
186 photosynthetic rate (and was only slightly mediated by UV-B treatments) (Martínez-Lüscher et al.
187 2015). The effect of elevated CO₂ on phenology was greater than the treatment of temperature elevated
188 by 4°C (Martínez-Lüscher et al. 2016b). Therefore, an increase in total nonstructural carbohydrates
189 could be a driver of advances in phenology long term, on its own, as well as with concomitant increases
190 in growing season temperatures.

191 Carbohydrate reserves regulate the growth and differentiation of flowers, which only occurs after
192 the grapevine shoot is resource independent from the rest of the vine (Lebon et al. 2008, Vasconcelos et
193 al. 2009). These findings suggest that with an increase in carbon reserves stored as starch in roots, trunks
194 and canes, second season shoots may grow faster and achieve independence earlier in the growing
195 season. This could contribute to early flowering as a result of lifted competition for resources between
196 vegetative and reproductive growth. In contrast, long-term studies in grapevine decreasing the leaf to
197 fruit ratios (measured as light-exposed leaf area to fruit) decreased essential reserves of the TNC in the
198 roots (Zufferey et al. 2012). The well-known viticultural technique of strategic leaf removal has been
199 shown to delay maturation, highlighting the importance of carbon availability for phenological
200 development (Poni et al. 2006, Parker 2012, Parker et al. 2014).

201 While the mechanism for phenological shifts in grapevine grown under elevated CO₂ is under-
202 studied, these shifts have been quantified using FACE experiments. The combination of elevated CO₂
203 and temperature in open top field chambers caused an advance in flowering time by three days and
204 veraison by two weeks (Edwards et al. 2016). The impact of elevated CO₂ on phenological timing is
205 greatest during the period between fruit set to veraison and this impact increases when combined with a
206 temperature treatment (Martínez-Lüscher et al. 2016a, Arrizabalaga-Arriazu et al. 2020). During fruit
207 set, elevated CO₂ treatments with and without temperature treatments increased total soluble solids
208 (hastening maturation), as well as decreased anthocyanins and malic acid concentration, which would
209 contribute to an earlier veraison and harvest (Salazar-Parra et al. 2010). However, the impact of high
210 temperature may have a greater impact on this phenological period (Arrizabalaga-Arriazu et al. 2020).

211 The quality of fruit harvested is the utmost concern when considering advanced phenology.
212 Grapevines vulnerable to frost damage will suffer from early budburst, with subsequent losses in yield
213 (Fraga et al. 2016). One consequence of increased shoot vigor at elevated CO₂ is the expected increase
214 in bud fertility, which will likely increase the number of flowers per vine (Figure 1) (Delrot et al. 2020,
215 Bindi et al. 2001). Changes in cluster density and phenological timing impact the carefully articulated
216 annual harvest. Unbalanced sugar/acid ratios resulting from early harvest decrease the quality of grapes
217 and wine produced, discussed further in the “Berry and Wine Chemistry” section below (Jones et al.
218 2005, Jones 2013). Shifting the lifecycle of grapevine will have a global impact on winegrape
219 production.

220

221 *Berry and wine chemistry*

222 Fruit composition is a major area of concern for growers and winemakers alike, especially aromatic
223 compounds. The changes in pest interactions, physiology, and timing of veraison in response to elevated
224 CO₂ will collectively impact the resulting grape and wine quality (Ollat et al. 2017). For successful wines,
225 in the grape berry there is a balance of acid and sugar at harvest. Increasing atmospheric carbon available
226 impacts the balance as ripening advances and sugar accumulation is accelerated (Martínez de Toda et al.
227 2014). Flavonoids and anthocyanins are important for the flavor, color, and mouthfeel of wine. The
228 molecular analysis from the original Italian FACE experiments showed increases in total flavonoids, total
229 anthocyanins, and total non-anthocyanin flavonoids in the wine produced with carbon enriched grapes
230 grown at 700 mg/L (Bindi et al. 2001), which typically would affect the color and mouthfeel of wine.
231 Interestingly, a subsequent experiment using 500 mg/L CO₂ open top chambers determined there were
232 significant increases in ethyl 2-methylbutyrate (apple), isoamyl acetate (burnt), ethyl hexanoate (apple,
233 pineapple), ethyl octanoate (fruit/fat), butyric acid (rancid), and isovaleric acid (rancid)
234 concentrations and a significant decrease in ethyl acetate (fruity) concentration in wines produced from
235 enriched CO₂ grapes after one year (Gonçalves et al. 2008), which contribute to the balance of floral and
236 fruity characteristics in wines (Francis 2012). In the second year they found lower methionol (raw potato),
237 1-octanol (alcohol), and 4-ethylguaiacol (smoke), and they found higher ethyl lactate (butter) and linalool
238 (floral) concentrations, although these changes in berry chemistry did not appear significantly in the
239 quality of wine produced (Gonçalves et al. 2008). Despite the chemical changes in berries at harvest,
240 Gonçalves et al. (2008) determined there was not a significant impact on the quality of wine even with the
241 changes in molecular components of the juices, similar to the early studies led by Bindi et al. (2001) (Table
242 1).

243 Although the changes observed in compounds contributing to flavor have been noted as so far
244 insignificant for quality, a major concern for winemakers is the increase in alcohol content resulting from
245 an increase in sugar concentrations in berries, as a result of higher CO₂ concentrations (Van Leeuwen and
246 Darriet 2016, Teslić et al. 2018, Delrot et al. 2020, Ubeda et al. 2020). In the past, winemakers have added
247 sugar to the fermentation to increase the final alcohol percentage (chaptalization where legal), depending
248 on legal regulations for winemaking. However, in recent years winemakers have begun removing sugar
249 through processes like reverse osmosis in order to prevent alcohol levels from rising (Christmann et al.
250 2017, Delrot et al. 2020). Overall, elevated CO₂ is altering the balance of sugar accumulation, the levels
251 tartaric and malic acids in berries and wine, and the impact on wine quality continues to be investigated
252 (Table 1) (Gonçalves et al. 2008, Pons et al. 2017).

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

261 *Pest and disease pressure*

262 In contrast to the ecological pressures discussed above, the rates of some fungal infections may
263 be reduced in elevated CO₂ scenarios. With higher carbon allocation to roots, grapevine mycorrhizal
264 colonization may be promoted by elevated CO₂ (Torres et al. 2018), which has been shown to protect

265 grapevine against the nematode *Xiphinema index* by stimulating defense gene response (Hao et al.
266 2012). A study of elevated CO₂ on several varieties of grapevine seedlings showed a reduced severity of
267 the infection of *Xanthomonas campestris* pv *viticola*, a vector of bacterial canker in immature grapevine
268 (Table 1) (Conceição et al. 2017). This may be the result of lower stomatal conductance (gs); with
269 stomatal aperture reduced, there is less opportunity for bacteria to invade the leaf pores (Conceição et al.
270 2017, Kizildeniz et al. 2018). Also, researchers recorded a reduced instance and severity of powdery
271 mildew infection in cv Barbera, at elevated CO₂ (Table 1) (Pugliese et al. 2010). The Geisenheim
272 GrapeFACE site recorded changes in the bunch architecture but did not see an increase in the frequency
273 of *B. cinera*, botrytis bunch rot, a necrotrophic fungus, occurrence (Wohlfahrt et al. 2018).

274 Changes in leaf chemistry phenotype, specifically carbon content, (e.g. higher soluble
275 carbohydrates due to higher carbon dioxide levels), will increase the pressure of grapevine pests in
276 future climates. Increasing available carbon dioxide, without a concomitant increase in nutrient levels in
277 the soil, leads to an increase in C:N ratios in leaves (Figure 1) (Hunter 2001, Ainsworth and Long 2004,
278 Moutinho-Pereira et al. 2009, Arrizabalaga-Arriazu et al. 2020, Kizildeniz et al. 2021). Insects consume
279 at higher rates when nitrogen has been diluted to meet their nitrogen intake needs and chewing insect
280 pests will generally eat more leaf tissue in elevated carbon dioxide scenarios (Hunter 2001). Elevated
281 CO₂ increased individual survival rates and increased the fecundity of female mealybugs, which eat
282 phloem of grapevine damaging the temporal and perennial plant tissue (Bordeu et al. 2012, Schulze-
283 Sylvester and Reineke 2019, Schulze-Sylvester, Corronca and Paris 2021). The European grapevine
284 moth, *Lobesia botrana*, is a major problem for European vineyards, affecting both the berries and
285 flowers of grapevines; and has already invaded North and South American vineyards (Reineke and
286 Selim 2019). *L. botrana* is also responsible for spreading Ochratoxin A-producing *Aspergillus* fungi,

287 which typically spikes in occurrence during hotter and drier years (Mondani et al. 2020). At higher
288 temperatures simulating future climate conditions, *L. botrana* female growth rate and pupal mass
289 increased (Iltis et al. 2018), while researchers found a down regulation of expression of ethylene-
290 responsive factors, which suggests grapevines can become more vulnerable to herbivory or abiotic stress
291 under future climate change as these are the major stress and defense response factors (Reineke and
292 Selim 2019).

293 A comprehensive study of soil and elevated CO₂ showed the decomposition pathway is altered
294 by the carbon-, nitrogen-, and phosphorus-acquiring enzymes in the soil with a significant increase in
295 nematode density (Thakur et al. 2019). More than 4,000 plant-parasitic nematodes exist, posing a well-
296 known global issue for grapevine, reducing total crop production by 8.8-14.6%, and one of the worst
297 threats from the nematode *Xiphinema index* is GLRV (Grapevine Leaf Roll Virus) (Andret-Link et al.
298 2017). Under elevated CO₂ conditions, if ethylene is suppressed and salicylic acid is increased, it is
299 likely that grapevine will struggle with an increase in pest and disease vectors such as nematodes and
300 fungi (Reineke and Selim 2019). Grapevines largely rely on human intervention for defense against
301 pests and diseases (Pertot et al. 2017), and this reliance could increase in future climates. Consider the
302 grapevine “immune system” as weakened in terms of chemical defense, but some altered carbon
303 dynamics under elevated CO₂ may be beneficial for reducing severity of pest pressure.

304 Discussion

305 An anticipated management solution to phenological shifts is planting later ripening and stress
306 tolerant alternative varieties. Government response to climate change will determine the actions European
307 growers are allowed to take to adapt to climate change, considering the current trials of alternative varieties

308 planted in small diversity blocks in France as a positive example (Morales-Castilla et al. 2020). Ancient
309 varieties being tested in temperature gradient greenhouses in Spain for response to combination stresses
310 of drought, heat, and elevated CO₂ showed greater resiliency to stress and did not shift phenological
311 timing, although this was a short-term experiment (Antolín et al. 2021, Goicoechea et al. 2021). In some
312 cases, alternative varieties may be hybrid crosses between existing cultivars and later ripening varieties.
313 However, hypothetical crosses between very late ripening varieties were modelled and still struggle to be
314 late-ripening enough to endure the predicted 23-day shift and potential increase of 7°C expected by the
315 end of this century for major wine grape growing areas (Duchêne et al. 2010). Alternative varieties can be
316 identified by oenological and ecological principals that make them suitable candidates for replacing
317 existing cultivars, such as flavor profile and ability to survive long term through stressful climate change
318 conditions (Antolín et al. 2021, Goicoechea et al. 2021). The challenge of adapting new varieties is
319 highlighted by current popular varieties struggling with increases in growing season temperatures (Jones
320 2021), however a combination of diversity block trials and greenhouse experiments will guide predictions
321 of the best alternatives (Wolkovich et al. 2018).

322 Our present knowledge of grapevine climate niches is limited relative to the vast diversity of
323 cultivars (Duchêne et al. 2010). With California as an example, there are many potential late ripening
324 varieties suitable as alternatives to early ripening Chardonnay that have yet to be tested in diversity blocks
325 (Wolkovich et al. 2018). Even clones can have a varied response to climate change variables
326 (Arrizabalaga-Arriazu et al. 2020). Varieties with heat and drought tolerance traits are a starting point for
327 elevated CO₂ studies, as we expand from understanding the mechanisms of change into exploring
328 mitigation strategies. Exploring the vast diversity of grapevine using diversity plots is a straightforward

329 ecological approach, which could be enhanced by evaluating the success of plants under several biotic
330 and abiotic stresses predicted for the future.

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

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

346 Grapevine physiology will be impacted by elevated carbon dioxide, increasing temperatures, and
347 extreme heat events during the growing season (De Cortázar-Atauri et al. 2017, Ugaglia et al. 2019).
348 FACE experiments highlight the necessity of water availability for grapevines to take advantage of
349 increased carbon dioxide for productivity. Soil water availability impacts the opening of stomata, and in
350 the case of GrapeFACE, the vines had increased g_s with more CO₂ available (Wohlfahrt et al. 2018).

351 Grapevines may need more water under future climate conditions of elevated CO₂ and temperature,
352 while precipitation is expected to decrease in most of the wine growing regions of the world.
353 Desiccation threatens vines through water loss from latent cooling under elevated temperature, resulting
354 in higher cumulative water loss even when operating at higher water use efficiency. The modulating
355 response of stomata documented across literature is dependent on the soil water availability and
356 temperature regimes (Arrizabalaga-Arriazu et al. 2020). In this synthesis, the varying levels of CO₂,
357 ambient temperatures, and duration of these experiments could have contributed to these contrasting
358 results of stomatal behavior, as well as the conditions of the chambers and greenhouses, versus FACE
359 infrastructure.

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

369 One of the biggest challenges for grape growers will be the shifts in phenological timing, with the
370 potential for frost at early budbreak, alterations in cluster formation and density, and compromising
371 harvest with early maturation. Many of the short-term experiments described here did not find
372 significant effects on phenology and yield, while long term studies account for acclimation and

373 compounding effects of seasonal exposure to elevated carbon dioxide. Predictions of overall vineyard
374 response to climate change are more accurate when experiments are field based, multi-seasonal, and
375 combine the variables of water availability and temperature.

376 **Conclusion**

377 A combination of the impacts of pest pressure, phenology, and physiology predict a much different
378 future environment for growing grapes. Elevated carbon dioxide is a pervasive threat to the vineyard
379 system because it fuels undesirable growth. Grapevine will sustain the impacts of elevated carbon dioxide
380 for generations, as a perennial crop with a rich memory and sensitive expression of climate. We can
381 strengthen the vineyard system by introducing more diverse cultivars, with an ideal candidate fitting the
382 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 CO_2 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.

Citation	eCO ₂ levels (mg/L)	Method	Notable Results	Location
Bindi et al. 2001	550 and 700	FACE	<ul style="list-style-type: none"> ↑ vegetative growth — No significant impact on wine quality (20 year old vines)^a 	Italy
Gonçalves et al. 2008	500	OTC	<ul style="list-style-type: none"> — No significant impact on wine quality 	Portugal
Moutinho-Pereira et al. 2009	500	OTC	<ul style="list-style-type: none"> ↑ Net photosynthetic rate (A) ↑ Intrinsic water use efficiency (A/gs) ↑ Leaf thickness ↑ Mg concentration ↑ C/N, K/N and Mg/N ratios ↓ Stomatal density and N concentration 	Portugal
Pugliese et al. 2010	800	GC	<ul style="list-style-type: none"> ↓ Chlorophyll content ↑ Instance and severity of powdery mildew increased for cv. Moscato ↓ Instance and severity of powdery mildew increased for cv. Barbera 	Italy
Salazar-Parra et al. 2012	700	GH	<ul style="list-style-type: none"> ↓ Reactive Oxygen Species — No significant change in photosynthetic pigments 	Spain
Salazar-Parra et al. 2015	700	TGG	<ul style="list-style-type: none"> — No effect on photosynthetic rates ↓ Stomatal conductance and transpiration at 20 days 	Spain
Martínez-Lüscher et al. 2015	700	GH	<ul style="list-style-type: none"> ↑ Photosynthesis (as A_{net}) ↑ Dark respiration ↓ Photorespiration ↑ Chlorophyll a and b content ↑ Ripening rates 	Spain

Martínez-Lüscher et al. 2016a	700	TGG	<ul style="list-style-type: none"> ↑ Advanced phenology with and without combination of elevated temperature, with cultivar specific response 	Spain
Edwards et al. 2016, 2017	650	OTC	<ul style="list-style-type: none"> ↑ Anthesis and veraison advanced in the third season ↑ Photosynthesis (as A_{sat}) 	Australia
Rangel da Silva et al. 2017	800	GC	<ul style="list-style-type: none"> ↓ 18% reduction in leaf nitrogen content ↓ 25% reduction in stomatal density ↑ Generally increased drought tolerance 	USA
Conceição et al. 2017	770	GC	<ul style="list-style-type: none"> ↓ Decreased infection of bacterial disease of <i>Xanthomonas campestris</i> pv <i>viticola</i> 	Brazil
Wohlfahrt et al. 2017, 2018	480 - 500 (+20% ambient)	FACE	<ul style="list-style-type: none"> ↑ net assimilation rates ↑ intrinsic water use efficiency (WUEi) ↑ pre-dawn leaf water potential ↑ bunch compactness, weight, and length ↓ Ethylene signals and ethylene responsive factors 	Germany
Kizildeniz et al. 2018	700	TGG	<ul style="list-style-type: none"> ↓ g_s, with additive effect of temperature and drought ↑ Stimulated more vegetative than reproductive growth — WUE increases did not compensate for water stress 	Spain
Reineke and Selim 2019	500	FACE	<ul style="list-style-type: none"> ↓ ethylene signalling hormones ↑ defensive compounds, including salicylic acid ↑ vulnerability to moth <i>L. botrana</i> 	Germany
Arrizabalaga-Arriazu et al. 2020	700	TGG	<ul style="list-style-type: none"> — Phenology and cluster traits not significantly impacted ↑ Increased leaf area at maturity ↑ Photosynthesis (A_{net}) ↓ Stomatal conductance 	Spain
			<ul style="list-style-type: none"> ↑ indicates increase ↓ indicates decrease — indicated 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.

