



Sensitivity of Grapevine Phenology to Water Availability, Temperature and CO₂ Concentration

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In recent decades, mean global temperatures have increased in parallel with a sharp rise in atmospheric carbon dioxide (CO₂) levels, with apparent implications for precipitation patterns. The aim of the present work is to assess the sensitivity of different phenological stages of grapevine to temperature and to study the influence of other factors related to climate change (water availability and CO₂ concentration) on this relationship. Grapevine phenological records from 9 plantings between 42.75°N and 46.03°N consisting of dates for budburst, flowering and fruit maturity were used. In addition, we used phenological data collected from 2 years of experiments with grapevine fruit-bearing cuttings with two grapevine varieties under two levels of water availability, two temperature regimes and two levels of CO₂. Dormancy breaking and flowering were strongly dependent on spring temperature, while neither variation in temperature during the chilling period nor precipitation significantly affected budburst date. The time needed to reach fruit maturity diminished with increasing temperature and decreasing precipitation. Experiments under semi-controlled conditions revealed great sensitivity of berry development to both temperature and CO₂. Water availability had significant interactions with both temperature and CO₂; however, in general, water deficit delayed maturity when combined with other factors. Sensitivities to temperature and CO₂ varied widely, but higher sensitivities appeared in the coolest year, particularly for the late ripening variety, 'White Tempranillo'. The knowledge gained in whole plant physiology and multi stress approaches is crucial to predict the effects of climate change and to design mitigation and adaptation strategies allowing viticulture to cope with climate change.

Keywords: climate change, viticulture, fruit development, ripening, chilling, dormancy, partial least squares regression

INTRODUCTION

Evolution of Environmental Factors Linked to Climate Change

Analyses of historic climatic changes indicate an increase in mean land surface temperature by 1.06°C over a period of more than 100 years, with the lion's share of this amount—0.85°C—occurring over the past two decades (IPCC, 2014b). Climate projections for the end of the 21st century forecast increases in temperature within a rather wide range, from stabilization at 1.5°C higher than the current reference period to a more than 4°C increase in average global temperature, depending on the mitigation measures adopted (IPCC, 2014a). The main driver of the temperature increase has been human emission of greenhouse gases. Among these, CO₂ is the most relevant in volume and global effect (IPCC, 2014a), with its concentrations increasing from a preindustrial level of 280 μL L⁻¹ to currently more than 400 μL L⁻¹ in 2016, with predictions for the end of the century ranging from 421 to a 936 μL L⁻¹ (Meinshausen et al., 2011). Rainfall in many major wine growing regions of the world has decreased and is expected to decrease further in the future (IPCC, 2014b).

Dependence of Grapevine on Temperature

Important effects of temperature on grapevine (*Vitis vinifera* L.) have long been recognized as influencing plant physiology, berry composition and ultimately wine characteristics (Jones et al., 2005; Bonada and Sadras, 2015). Thermal time integrals are even used as one of the main criteria to assess the suitability of a given cultivar to a given location (Gladstones, 1992). Premium commercial vineyards have been traditionally distributed across a relatively wide range of latitudes, ranging from the subtropics to temperate climates like the south of England (at 53°N). Across this range, temperature during dormancy and growing season varies widely (Jones, 2006, 2007). However, the distribution of grape growing regions is not necessarily aligned with the acclimation or adaptation thresholds of the species, and in the case of quality wine production, the upper temperature limits are hard to assess even at the variety level (van Leeuwen et al., 2013). Evidence of the plasticity of this species and the apparent lack of thermal restrictions for growing grapes is the recent increase in production of both table and wine grapes in subtropical and tropical areas (Demir, 2014).

Temperature Thresholds for Wine Typicity

Although basic climatic conditions for grape growing are easily satisfied, rising temperatures may make it difficult to consistently fulfill specific criteria required for grape quality in many places without adjusting variety, clone or accession within a given variety, or changing management practices. This is especially relevant for wine grapes, as most wine appellations in the world aim to deliver a very specific product, resulting from the wine-making, grapevine genetic material (cultivar and clone), cultural practices, edaphic factors and climatic conditions (van Leeuwen et al., 2004). Final grape composition results from numerous processes leading to accumulation and/or decay of metabolites, which are affected to a considerable degree by

climatic conditions (Kuhn et al., 2014). Consequently, aromas, aroma precursors, phenolic compounds, organic acids, and sugars have very different accumulation patterns throughout grape development and, what is most relevant, their responses to increasing temperatures may differ in magnitude. The best example is that temperature increases can enhance both sugar accumulation and organic acid decay, but acidity is more affected than sugar levels. This results in lower acidity for the same sugar level in grapes grown under warmer conditions (Lakso and Kliewer, 1975; Sweetman et al., 2009; Etienne et al., 2013). This decoupling has been reported for other relevant metabolites, such as anthocyanins (decreasing the anthocyanin/sugar ratio) (Sadras and Moran, 2012; Martínez-Lüscher et al., 2016), proanthocyanidins (Cohen et al., 2012) and aromas (Bonada et al., 2015). In contrast, a decoupling of anthocyanins and sugars was reported with increasing water stress, in favor of anthocyanins in Cabernet Sauvignon (Sadras et al., 2007). During the ripening period, in summer, elevated temperature and drought occur simultaneously, and therefore, the effects on the decoupling of anthocyanins and sugars can be moderate due to the contrasting responses elicited by these two factors. In this sense, Sadras and Moran (2012) reported that restricted water supply during berry development can contribute to partially restore anthocyanin/sugar ratios disrupted by high temperature.

Relationship between Wine Composition and Altered Phenology

Despite the scarcity of data, some attempts have been undertaken to relate grape composition to records of environmental conditions (Bonada and Sadras, 2015). Grapevine phenology records, however, are relatively abundant and can be a good proxy for altered grape composition in response to environmental factors (Sadras and Moran, 2013; Bonada and Sadras, 2015). The duration of the phenophases can affect metabolite dynamics (Kuhn et al., 2014; Martínez-Lüscher et al., 2016), but it is also likely that advancing phenology shifts the ripening period toward the warmest part of the year (Webb et al., 2007; Duchene et al., 2010), which is not compatible with the production of high quality table wines (van Leeuwen and Seguin, 2006). Other factors, such as water deficit and elevated CO₂, did not affect significantly grape development speed of 'Red Tempranillo' fruit-bearing cuttings when applied individually (Salazar Parra, 2011). Only, a significant hastening in grape ripening was observed when these two factors were applied simultaneously from veraison to maturity.

Annual Cycle of Grapevine Development

Most temperate fruit crops need a period of cool temperatures before they can produce flowers (Campoy et al., 2011; Considine and Considine, 2016). Satisfaction of the chilling requirement influences the timing of budburst, flowering and subsequent phenological stages (Luedeling, 2012). However, grapevine flowering and veraison can be modeled quite successfully using spring temperatures as the only predictor variable (Parker et al., 2011), suggesting a weak effect of temperatures during bud dormancy (García de Cortazar-Atauri et al., 2009). While the period from the breaking of dormancy to flowering is

strongly determined by temperature, flowering to veraison is often influenced by other abiotic factors such as water deficit (Davies et al., 1994; Antolin et al., 2003; Martínez-Lüscher et al., 2015a), and the correlation is usually weaker (Duchene et al., 2010). This becomes even more evident for the period from flowering or veraison to fruit maturity, which is influenced by an even larger number of factors (Petrie and Sadras, 2008; Webb et al., 2012). Even though ripeness is defined by subjective criteria, and therefore is not a phenological event strictly, it can be reliably measured in relation to metabolite concentrations, such as sugars, anthocyanins and organic acids (Bonada and Sadras, 2015). For instance, regarding the implications of sugar content for the potential alcohol content of resulting wine, the concentration of total soluble solids (TSS) is a straightforward and reliable marker for the progress of ripening (Bonada and Sadras, 2015).

Aim of the Study

In recent years, phenology responses of perennial crops to projected future climates have been assessed. These projections have often focused on response to temperature, with a few cases including water availability, but they have not convincingly considered CO₂. The present study aims to give an overview of the effect of climate change-related phenomena (water deficit, increasing temperature and elevated CO₂) on the phenology of grapevine, a temperate perennial woody crop. For this purpose, we evaluated historical data of phenological records and conducted some experiments under controlled conditions. The combination of these two data sources—historical records and fruit-bearing cuttings under controlled conditions—allows immediate extrapolation to the field when analyzing historical data, but it also allows studying the direct effects of these environmental factors at reasonable cost, when performing experiments under semi-controlled conditions.

MATERIALS AND METHODS

Field Phenology Records

Grapevine phenological records of Croatia were obtained from the pan European phenology project (PEP725 Pan European Phenology Data; dataset accessed on 2015-09-23 at <http://www.pep725.eu>). Croatia has a long tradition in phenological observations carried out by the Meteorological and Hydrological Service from 1951, which was extended to vineyards in 1958. In this study, the records were used to calculate the time elapsed between March 1st and the beginning of budburst (BBCH 7), budburst to beginning of flowering (BBCH 60) and from flowering to fruit maturity (BBCH 87), to test the influence of temperature on grapevine development (Lorenz et al., 1995). The database consisted of 307 seasonal records collected between 1961 and 2013 from nine commercial vineyards in five phenological stations in Croatia (Mandicevac, Daruvar, KriZevCi, Cepic and Trsteno). These sites, which are distributed between latitudes 42.75°N and 46.03°N and between longitudes 14.13°E and 19.23°E, are representative of the average latitude for the distribution of northern hemisphere vineyards. The nine plots had different climate and soil conditions but none were

irrigated. Most of them were in south-orientated hills. In the continental part (Mandicevac, Daruvar and KriZevCi) and the northern Adriatic Coast (Cepic), vines were trained with trellis, distance between rows varied from 1.6 to 2.2 m, and distance within plants in a row ranged from 0.7 to 1.2 m. In the southern Adriatic Coast (Trsteno), there was no training, and separation between plants was 1 × 1 m. The white varieties observed in the vineyards were ‘Chasselas Dore,’ present in Mandicevac, KriZevCi and Trsteno; ‘Riesling Italico,’ present in Mandicevac, KriZevCi and Daruvar; and ‘Istrian Malmsey,’ present in Cepic. ‘Plavac Mali,’ an autochthonous red variety present in Trsteno, was also observed.

Temperature and Rainfall Records

Field temperature and rainfall records were extracted from the E-OBS European gridded data set (Haylock et al., 2008). As this database contains daily minimum and maximum temperatures, hourly records were constructed with procedures contained in the chillR package (Luedeling, 2016), for R programming language (R Development Core Team, 2016). These procedures follow the recommendations of Linvill (1990). Sunrise, sunset and day length data for this method were modeled using each site latitude (Spencer, 1971; Almorox et al., 2005).

Identification of Chilling and Warming Periods

Partial Least Squares (PLS) regression was used at one of the locations (Mandicevac) to correlate variation in daily chill and heat accumulation to grapevine budburst dates. Daily chill accumulation (in Chill Portions) was calculated according to the so-called Dynamic Model (Fishman et al., 1987), which is regarded as the most accurate under a wide range of circumstances (Campoy et al., 2011). Daily heat accumulation (in Growing Degree Hours) was calculated according to Anderson et al. (1986), with a curvilinear model using a base temperature of 4°C and an optimum temperature of 26°C, which are representative of grapevine response to temperature (Parker et al., 2011). Formulas for each model are given in Luedeling and Brown (2011) and Luedeling et al. (2009), respectively. Eleven-day running means were constructed to facilitate interpretation of the results (Luedeling and Gassner, 2012). Forty-one datasets were created, consisting of 694 independent variables—daily heat and chill accumulation from June 1st (of the year preceding the year of recorded budburst) to May 14th, which was the latest budburst date recorded at the site (data for May 14th were omitted in leap years)—and one bud break date each. PLS regression outputs—variable importance in the projection (VIP) and model coefficients—were used to delineate the periods where an increase in daily chill accumulation indicated a bloom-advancing effect (negative correlation between chill accumulation and budburst date; this was interpreted as the chilling phase) and where an increase in daily heat accumulation implied a bloom-advancing effect (negative correlation; warming phase). The VIP threshold for importance was set to 0.8, which is commonly adopted by other studies (Wold et al., 2001). Further details of the procedures are described in Luedeling et al. (2013). Once these periods were identified, three-dimensional

interpolation (Kriging) was used to illustrate the differential effects of temperature during the chilling and warming periods on budburst dates. This aims to facilitate the interpretation of the effect of two predictor variables that are highly correlated. The angle of the contour lines that are generated indicates, which one of the two factors is dominant in determining budburst dates (Guo et al., 2015).

Plant Material and Growth Conditions

Dormant cuttings of *Vitis vinifera* L. cvs 'Red Tempranillo' (accession T43, Clone RJ-43) and 'White Tempranillo' (accession CI-101 in the "La Grajera" germplasm bank, Government of Rioja, Spain) were collected in January of 2014 and 2015 from an experimental vineyard of the Institute of Sciences of Vine and Wine (ICVV) in Logroño (La Rioja, Spain).

Three node cuttings of *V. vinifera* L. cv. 'Red Tempranillo' and 'White Tempranillo' were selected to produce fruit-bearing cuttings according to Mullins (1966), as described in Kizildenz et al. (2015). Rooting was induced using indole butyric acid (300 mg L⁻¹) in a heated moist-bed (25–27°C) kept in a cool chamber (5°C). After 1 month, the rooted cuttings were planted in 0.8 L plastic pots containing a mixture of sand, perlite and vermiculite (1:1:1, v/v) and transferred to the greenhouse. At fruit set, plants were planted in 13 L plastic pots containing a mixture of peat and perlite (2:1, v/v). Only a single flowering stem was allowed to develop on each plant, resulting in only one grape bunch per plant. Pruning was used to control vegetative growth until fruit set, thus allowing only 4 leaves per plant to grow. Growth conditions in the greenhouse were 26/15°C and 60/80% relative humidity (RH) (day/night), with a photoperiod of 15 h with natural daylight supplemented with high-pressure metal halide lamps (OSRAM®, Augsburg, Germany). The supplemental system was triggered when photosynthetically active radiation (PAR) dropped below a photosynthetic flux density (PPFD) of 900 μmol m⁻² s⁻¹, providing a PPFD of 500 μmol m⁻² s⁻¹ at inflorescence level. Plants were irrigated with the nutrient solution described by Ollat et al. (1998): NH₄NO₃ (64.5 mg L⁻¹), (NH₄)₂HPO₄ (75 mg L⁻¹), KNO₃ (129 mg L⁻¹), MgSO₄·7H₂O (125 mg L⁻¹), Ca(NO₃)₂·4H₂O (248 mg L⁻¹), (NH₄)₂SO₄ (66 mg L⁻¹), Fe (EDDHA) (280 mg L⁻¹), H₃BO₃ (2.86 mg L⁻¹), MnCl₂·4H₂O (1.81 mg L⁻¹), ZnSO₄·7H₂O (0.22 mg L⁻¹), CuSO₄·5H₂O (0.08 mg L⁻¹) and (NH₄)₆Mo₇O₂₄·4H₂O (0.016 mg L⁻¹). Plants grew under these conditions until fruit set (from March to May, both in 2014 and 2015).

Temperature Gradient Greenhouse Experiment Design and Analyses

Treatments were applied in the temperature gradient greenhouses (TGGs), located at the University of Navarra (42.80°N, 1.67°W) in Pamplona (Navarra, Spain), from June to August (i.e., from fruit set to maturity) in 2014 and 2015. TGGs are designed as temperature gradient tunnels (Rawson, 1995), which allows investigating the effects on plants of environmental changes, such as elevated temperature, elevated CO₂ and drought, acting separately or in combination. They

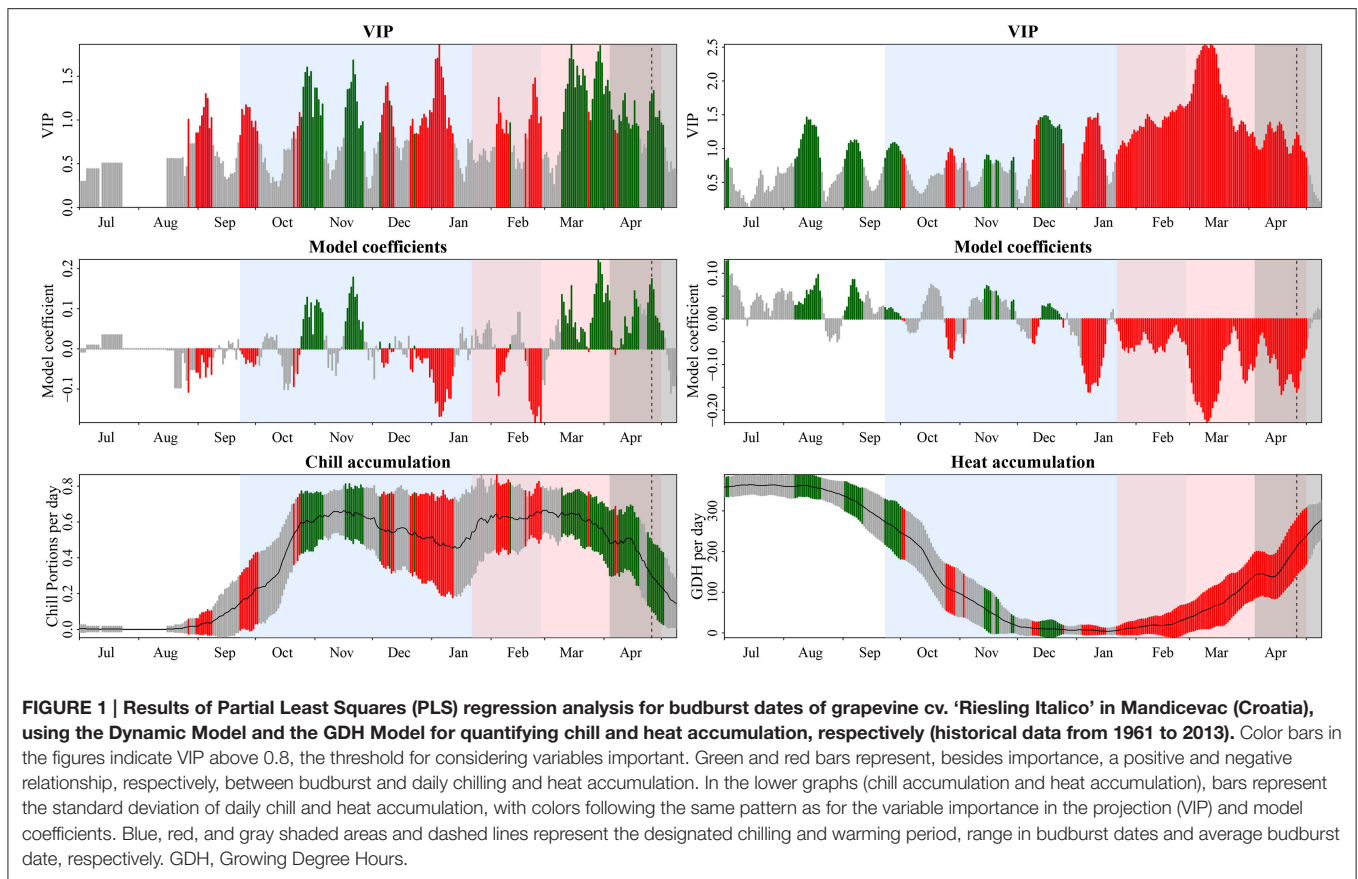
were constructed with a modular design with three temperature modules, which creates a temperature gradient ranging from near-ambient temperature in module 1 to ambient temperature +4°C in module 3. CO₂ can be injected into the greenhouse to increase the air CO₂ concentration as desired (more details in Morales et al., 2014). When fruit set was complete for all plants, fruit-bearing cuttings of 'Red Tempranillo' and 'White Tempranillo' cultivars were subjected to a combination of two temperature regimes (ambient and ambient +4°C, no experimental plants were set in module 2 with intermediate temperature) and two CO₂ concentrations (current ca. 400 μL L⁻¹ and elevated ca. 700 μL L⁻¹) until maturity (defined as TSS = 21–23°Brix). Each treatment consisted of 10 plants, which were selected on the basis of similar grape bunch sizes. Plants were maintained with free vegetative growth. CO₂ concentration, temperature, relative humidity and radiation were measured and/or controlled by an automated monitoring system. Data were analyzed with XLStat (Addinsoft, Paris, France) by a factorial ANOVA (2 × 2 × 2 × 2 × 2). Only main factors and two-level interaction *P*-values were presented.

RESULTS

Effect of Temperature on Grapevine Dormancy Breaking Under Field Conditions

PLS regression results for budburst dates (Figure 1) showed several periods with significant variable importance in the projection (VIP) scores (>0.8) and negative coefficients between September 23rd and February 27th, suggesting that during this period, increases in chilling were correlated to advanced budburst. Although there was a period of negative correlations before this period—between August 31st and September 8th—and a large period of significant scores and positive coefficients from October 25th to November 26th, it seemed reasonable to interpret the period between September 23rd and February 27th as the chilling phase, in agreement with studies showing the effectiveness of chilling in October (Dokoozlian, 1999; Li and Dami, 2016). Days with significant VIP scores coupled with negative correlation coefficients for daily heat accumulation were also discontinuous, but they were concentrated in two major periods: January 4th to January 16th and January 22nd to May 1st, with only a brief interruption, during which model coefficients did not remain negative every day. In addition, mean heat accumulation during the first period—January 4th to January 16th—was very low and most likely did not have a strong effect in most years. It must be noted that this species may fulfill its critical chilling requirement much earlier than most perennial crops, and therefore, important and negative scores for heat accumulation could be expected at any time of the chilling period when adequate temperature levels are reached. We delineated the warming phase as the period between January 22nd and May 1st.

The delineation of chilling and warming phases allowed calculation of mean temperature during these phases. Results showed a weak effect of changes in temperature during the



chilling phase on budburst date (Figure 2). Taking into account the angle and the separation of the contour lines in Figure 2, the sensitivity of budburst date to changes in temperature during the chilling period was small ($0.03 \text{ d } ^\circ\text{C}^{-1}$), compared to $-4.38 \text{ d } ^\circ\text{C}^{-1}$ for temperatures during the warming phase. The almost horizontal contour lines of the interpolation surface suggest that temperature during the warming period strongly affected budburst date compared to the effect of temperatures during the chilling period. In addition, variation in mean temperature during the delineated chilling phase is much lower than during the warming phase (ranges of -4.2 to 3.9°C and 3.0 to 9.2°C , respectively).

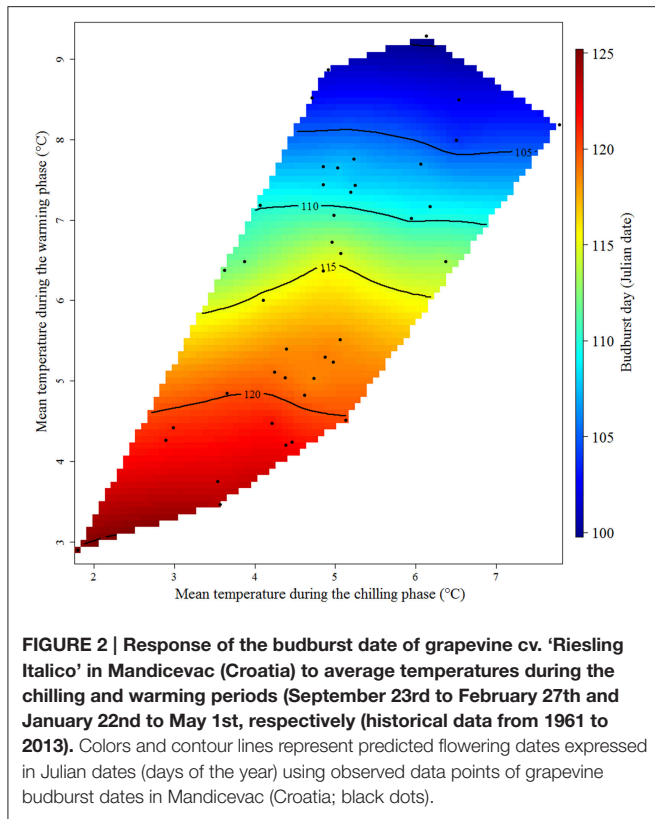
Decoupling of the Effects of Water Availability and Temperature on Grapevine Phenophases under Field Conditions

The linear regression trend determined for all sites (Figure 3) shows that the sensitivity is -4.49 days change in budburst date for each degree of temperature increase ($\text{d } ^\circ\text{C}^{-1}$) from March 1st to budburst. This sensitivity is higher than for any other phenophase displayed, as the stage from budbreak to flowering had a sensitivity of $-3.29 \text{ d } ^\circ\text{C}^{-1}$ and the stage from flowering to harvest had a sensitivity of $-2.57 \text{ d } ^\circ\text{C}^{-1}$. When the effect of temperature on field phenological data was decoupled from rainfall (Figure 4), precipitation showed a differential effect on phenological periods. The interpolation

surface of the period from March 1st to budburst (Figure 4A) shows some delaying effects in rainy years and advancing effects in dry years, but this was not a general trend and it resulted in a high degree of patchiness. Contrarily, the period from budburst to flowering and flowering to ripe fruit resulted in smoother interpolation surfaces (Figures 4B,C, respectively). In the case of budburst to flowering (Figure 4B), only temperature and not rainfall showed an advancing effect. This is suggested by decreasing values of contour lines and interpolation surface with increasing temperature, but not with rainfall. However, in the case of the period from flowering to ripe fruit (Figure 4C), this effect was shared by increases in temperatures and decreases in precipitation.

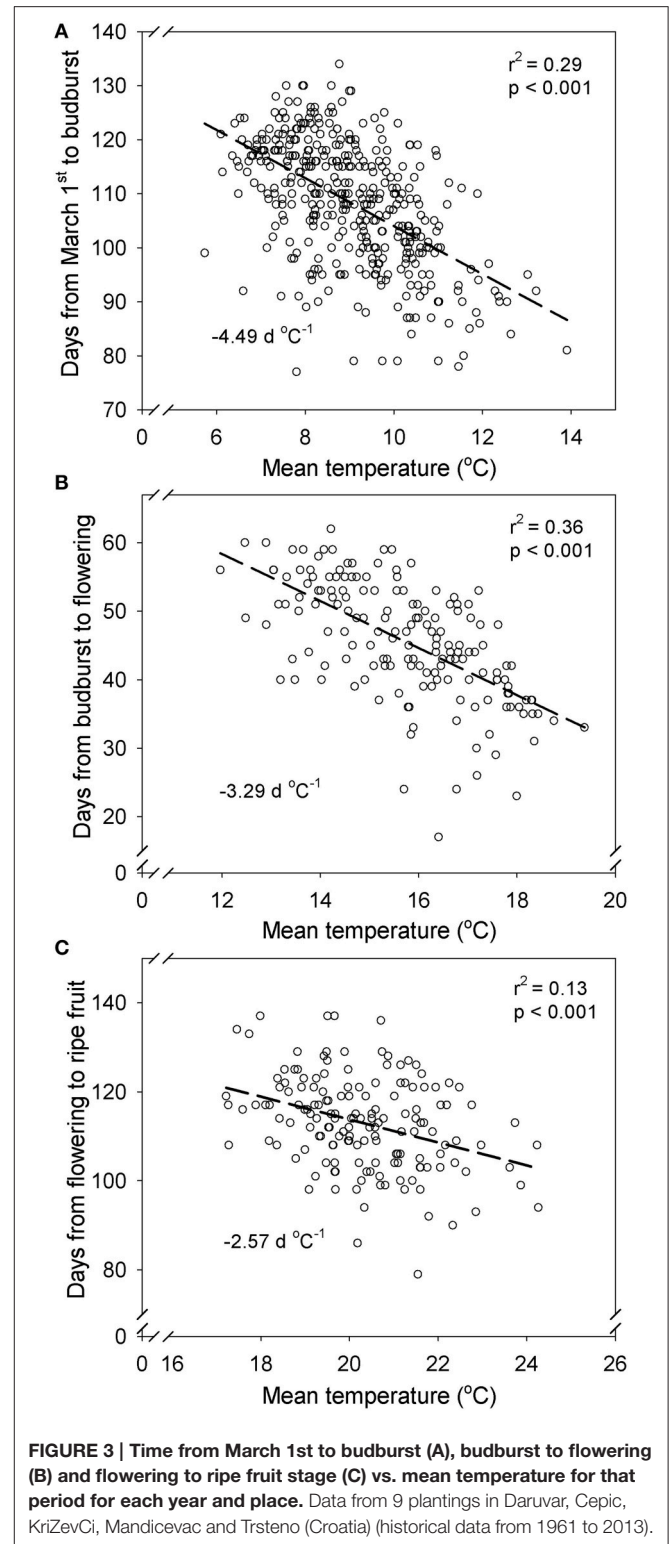
Effects of Water Availability, Temperature, CO₂ Concentration and their Interactions under Semi-Controlled Conditions

The two varieties ('Red Tempranillo' and 'White Tempranillo') showed different sensitivities to increasing temperatures (Figure 5). The figures obtained were $-1.52 \text{ d } ^\circ\text{C}^{-1}$ in 2014 and $0.15 \text{ d } ^\circ\text{C}^{-1}$ in 2015 for 'Red Tempranillo' and $-2.03 \text{ d } ^\circ\text{C}^{-1}$ in 2014 and $-0.90 \text{ d } ^\circ\text{C}^{-1}$ in 2015 for 'White Tempranillo'. The lower sensitivity to temperature observed in 2015 for both varieties was most likely associated with higher temperatures recorded in that year and a higher number of days with temperatures above 35°C (Table 1). Atmospheric

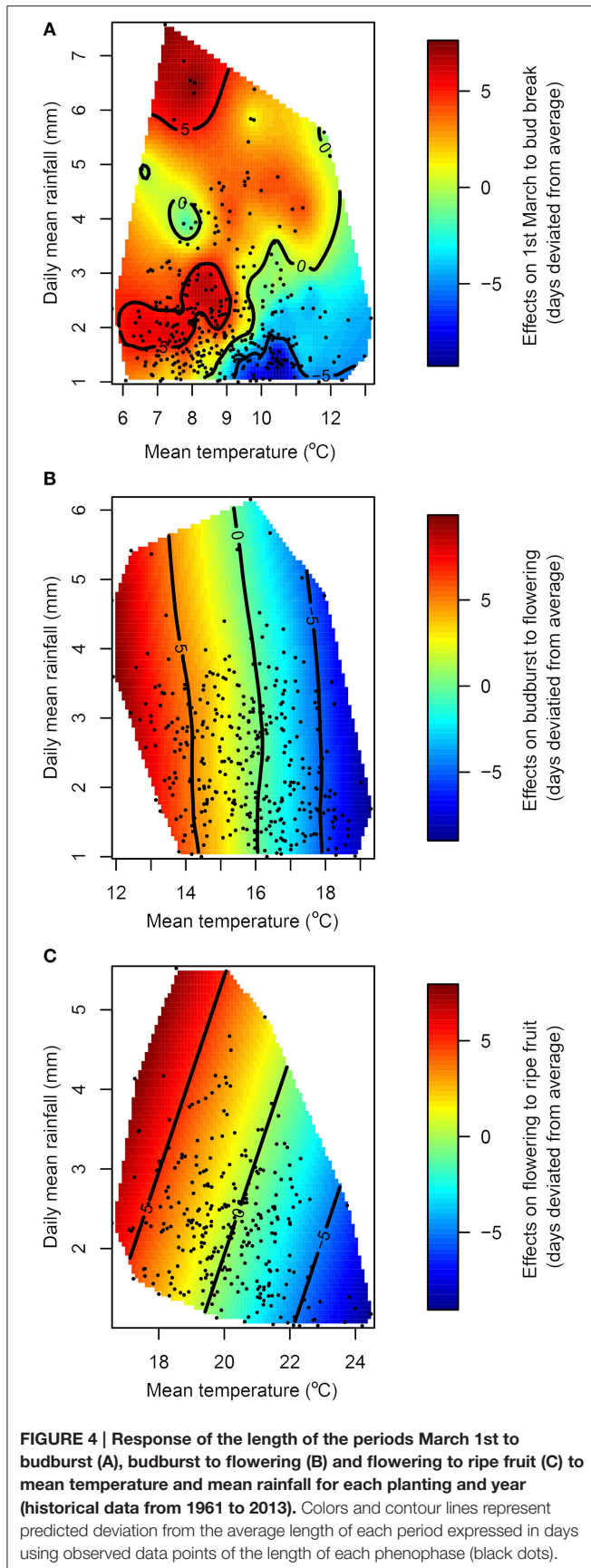


CO₂ did not change the sensitivity to temperature in any case, and this is supported by the lack of interactions in the two-way ANOVA analysis. The overall effect of CO₂ and temperature was highly significant [$p(\text{CO}_2) < 0.001$ and $p(\text{Temp}) = 0.001$], with elevated CO₂ having an advancing effect of 4.37 d and 3.54 d in T and T+4°C treatments, respectively. However, looking at the varieties separately, the effect was not significant for the 'Red Tempranillo' variety [$p(\text{CO}_2)$ and $p(\text{Temp}) > 0.05$], whereas the effect for 'White Tempranillo' was strong [$p(\text{CO}_2) < 0.001$ and $p(\text{Temp}) = 0.005$]. Considering all years and varieties, high CO₂ advanced phenology by 6.75 d and 4.06 d in the T and T+4°C treatments, respectively.

It must be noted that several two-level interactions were significant for time from fruit set to veraison, veraison to harvest and fruit set to harvest (Table 2). Therefore, the significance of the main effects must be interpreted with caution. For instance, 5 out of 11 interactions involved the Year main effect, which reflects the inconsistency of some factor effects from year to year. Other important interactions were found between the Cultivar and CO₂ for time from veraison to maturity and fruit set to maturity. These findings point out the higher susceptibility of the white cultivar under all the combinations of conditions. Still, it must be noted that for most combinations of treatments, elevated CO₂ plants completed fruit development and ripening earlier than their ambient CO₂ homolog. Interactions between environmental factors were also found, including between water deficit and temperature and between water deficit and CO₂. In the main effect comparisons, water deficit extended the ripening



period by an average of 3 days. However, looking at the effect of water deficit combined with other factors, cyclic drought (CD) had an advancing effect (i.e., 'Red Tempranillo' under T-E CO₂ in 2015 and 'White Tempranillo' under T-E CO₂ in 2014 and



2015), which explains the significant interactions between water availability and temperature and CO₂.

DISCUSSION

Effect of Temperature

Many studies have reported the accelerating effects of rising temperatures on phenology based on events typically occurring in spring (i.e., budburst, leaf unfolding, and flowering). While most species show a clear advance in phenology, an exception to this general trend may be those species that are starting to experience difficulties in meeting their chilling requirements (Guo et al., 2015). In this respect, grapevine (*Vitis vinifera* L.) is presented in the literature as a species with a low chill requirement, despite its tendency to burst and flower rather late (Mullins et al., 1992). Although they are believed to need a very small exposure to chilling temperatures to resume growth and flower normally, incremental exposure to chilling temperatures reduces the time to respond to high temperatures and increases the percentage of budburst, which suggests some sensitivity to chilling (Dokoozlian, 1999). In the present study, grapevines do not show a major change in budburst date in response to changes in temperature during the chilling period. Instead, temperature during the warming period was the overriding factor influencing this phenophase (Figure 2). The high variable importance in the projection (VIP) values and negative coefficients for heat accumulation observed at the beginning of March highlight the importance of taking into account this period for the prediction of budburst and flowering. These results support previous studies that find best model performance for models using the March 1st as a start date for the accumulation of thermal time, instead of the classical approach of taking into account temperatures from January 1st (García de Cortazar-Atauri et al., 2009; Duchene et al., 2010; Parker et al., 2011).

For later phenological events, such as onset of ripening, thermal time models have proven to be valuable tools. However, as the growing season goes on, the level of complexity increases and factors such as yield, cultural practices and water availability may also influence the timing of phenophases (Petrie and Sadras, 2008; Sadras and Petrie, 2011; Martínez de Toda et al., 2013). Simply, the ripening of non-climacteric fruits relies to a great extent on photoassimilation in the leaves, translocation and storage of photoassimilates, which are reactions greatly enhanced by temperature (Greer and Weedon, 2013). Historical data also support the relationship between temperature and commercial ripeness in grapes (Chuine et al., 2004; Daux et al., 2012). In the historical data used in this study, the effect of temperature on the time between flowering and harvest was visible, but—as expected—the correlation was weaker than for the completion of previous stages, such as budburst or flowering. This advancement of the ripening period, shifting dates from September to August in the northern hemisphere, has the additional effect of shifting this period to what is usually the warmest part of the year (Webb et al., 2007; Duchene et al., 2010). In this study, this effect resulted in an increase of the temperature during the ripening period by 1.27°C for each °C increase in the average temperature (Figure S1).

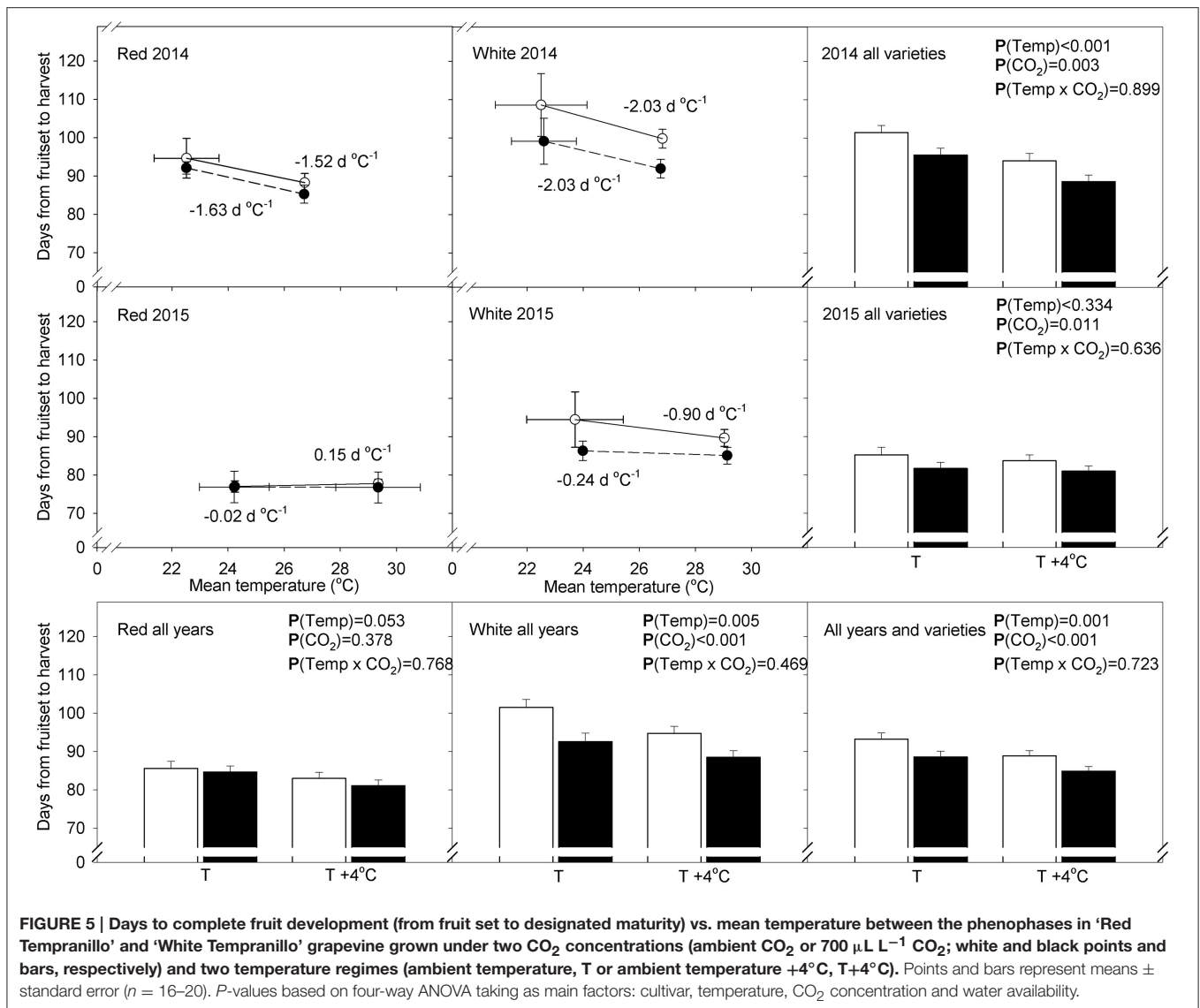


TABLE 1 | Temperature recorded in the temperature gradient greenhouse experiments with 'Red Tempranillo' and 'White Tempranillo' grapevine.

Year	2014		2015	
	T	T+4°C	T	T+4°C
Mean daily minimum (°C)	14.8	18.8	15.4	19.65
Daily mean (°C)	22.1	26.5	22.9	27.1
Mean daily maximum (°C)	28.7	33.5	29.7	35.11
Days above 30°C	46	85	44	77
Days above 35°C	8	42	19	50

T, ambient temperature and T+4°C, ambient temperature +4°C.

Effect of Water Availability in Relation to Temperature

Our studies show differences in the effects of rainfall depending on the phenological period. Whereas events occurring before

berry development do not show a clear dependence on rainfall, berry development shows a higher dependence both on temperature and water availability (Figure 4). Mild water deficit has proven to enhance ripening through several processes, such as altering plant abscisic acid (ABA) signaling, reduction in berry size or concentrating berry contents (i.e., anthocyanins and sugars) (Deluc et al., 2009; van Leeuwen et al., 2009; Chaves et al., 2010). In fact, environmental cues such as water deficit, as well as solar radiation, and even heat within the suboptimal range of temperature of a variety, may promote signaling mechanisms, such as ABA biosynthesis, and enhance ripening (Kuhn et al., 2014). ABA signaling during grape ripening interacts with plant responses to exogenous stresses, by regulating the process of plant adaptation (Ferrandino and Lovisolo, 2014). Many key genes involved in flavonoid biosynthesis are up-regulated during ripening, therefore ABA accumulation induced by stress conditions may induce the activation of these key

TABLE 2 | Days to complete phenological periods: fruit set to veraison, veraison to designated maturity and fruit set to designated maturity in 'Red Tempranillo' and 'White Tempranillo' grapevine grown under two water availability levels (FI, full irrigation or CD, cyclic drought), two temperature regimes (ambient temperature, T or ambient temperature +4°C, T+4°C) and two CO₂ concentrations (A CO₂, ambient CO₂, or E CO₂, 700 μL L⁻¹ CO₂).

Cultivar	Water availability	Temperature	CO ₂ level	Years	Fruit set to veraison	Veraison to maturity	Fruit set to maturity
Red	FI	T	A CO ₂	2014	64.1 ± 1.5	29.8 ± 3.4	93.9 ± 3.0
				2015	53.0 ± 1.1	25.6 ± 2.3	78.6 ± 2.5
			E CO ₂	2014	57.9 ± 1.3	31.5 ± 1.9	89.4 ± 2.5
				2015	51.6 ± 1.1	27.0 ± 1.8	79.1 ± 1.8
		T+4	A CO ₂	2014	56.2 ± 1.1	25.3 ± 1.3	81.5 ± 1.8
				2015	54.2 ± 1.5	20.8 ± 2.3	75.0 ± 1.1
			E CO ₂	2014	54.9 ± 1.5	27.1 ± 2.2	82.0 ± 3.6
				2015	51.1 ± 1.0	24.5 ± 1.4	75.6 ± 1.7
	CD	T	A CO ₂	2014	68.7 ± 2.3	27.8 ± 2.2	95.4 ± 2.0
				2015	48.7 ± 1.5	26.7 ± 1.3	75.4 ± 1.6
			E CO ₂	2014	57.5 ± 1.7	37.3 ± 2.3	94.8 ± 1.7
				2015	51.4 ± 0.9	23.0 ± 1.4	74.3 ± 1.1
		T+4	A CO ₂	2014	66.5 ± 2.2	28.5 ± 1.8	95.0 ± 3.3
				2015	54.8 ± 1.7	25.7 ± 2.1	80.5 ± 1.5
			E CO ₂	2014	57.0 ± 1.4	31.5 ± 2.4	88.5 ± 2.8
				2015	50.2 ± 1.4	27.8 ± 1.7	78.0 ± 0.9
White	FI	T	A CO ₂	2014	66.5 ± 2.4	40.1 ± 2.0	106.6 ± 3.0
				2015	50.4 ± 0.7	39.4 ± 3.5	90.0 ± 3.7
			E CO ₂	2014	56.9 ± 0.6	47.5 ± 3.0	104.4 ± 3.4
				2015	49.5 ± 0.9	41.2 ± 3.6	90.7 ± 3.7
		T+4	A CO ₂	2014	58.9 ± 1.3	31.8 ± 1.6	90.7 ± 0.9
				2015	51.5 ± 1.6	40.7 ± 4.3	92.2 ± 3.3
			E CO ₂	2014	55.0 ± 0.5	30.3 ± 1.0	85.3 ± 1.1
				2015	51.5 ± 1.4	33.1 ± 2.1	84.6 ± 2.8
	CD	T	A CO ₂	2014	62.9 ± 2.1	50.4 ± 3.2	111.1 ± 3.3
				2015	49.6 ± 0.8	49.2 ± 2.6	98.9 ± 2.6
			E CO ₂	2014	59.6 ± 1.1	37.0 ± 4.2	93.3 ± 5.1
				2015	48.3 ± 0.5	33.6 ± 3.0	81.9 ± 2.9
		T+4	A CO ₂	2014	60.9 ± 0.9	48.1 ± 2.5	109.0 ± 2.5
				2015	48.8 ± 0.6	38.3 ± 3.2	87.1 ± 2.8
			E CO ₂	2014	58.3 ± 1.2	40.4 ± 3.4	98.7 ± 3.6
				2015	48.1 ± 0.5	37.4 ± 3.7	85.5 ± 3.5
Means of main factors				'Red Tempranillo'	56.1 ± 0.6	27.5 ± 0.6	83.6 ± 0.8
				'White Tempranillo'	54.8 ± 0.5	39.9 ± 0.9	94.4 ± 1.0
				Full irrigation	55.2 ± 0.5	32.2 ± 0.8	87.5 ± 0.9
				Water deficit	55.7 ± 0.6	35.2 ± 0.9	90.5 ± 1.1
				Ambient temperature	56.0 ± 0.6	35.4 ± 0.9	91.1 ± 1.1
				Elevated temperature	54.9 ± 0.5	32.0 ± 0.8	86.8 ± 0.9
				Ambient CO ₂	57.2 ± 0.6	34.3 ± 0.9	91.3 ± 1.1
				Elevated CO ₂	53.7 ± 0.4	33.1 ± 0.8	86.6 ± 0.9
				2014	60.1 ± 0.5	35.3 ± 0.8	95.0 ± 1.0
				2015	50.8 ± 0.3	32.1 ± 0.9	83.0 ± 0.8
ANOVA P of main factors				P (Cult)	<0.001	<0.001	<0.001
				P (WA)	n.s.	0.005	0.01

(Continued)

TABLE 2 | Continued

Cultivar	Water availability	Temperature	CO ₂ level	Years	Fruit set to veraison	Veraison to maturity	Fruit set to maturity
			P(Temp)		0.014	<0.001	<0.001
			P(CO ₂)		<0.001	n.s.	<0.001
			P(Year)		<0.001	0.001	<0.001
ANOVA 2 level interactions			P(Cult) × P(WA)		n.s.	n.s.	n.s.
			P(Cult) × P(Temp)		n.s.	n.s.	n.s.
			P(Cult) × P(CO ₂)		n.s.	<0.001	0.004
			P(Cult) × P(Year)		n.s.	n.s.	n.s.
			P(WA) × P(Temp)		n.s.	0.007	<0.001
			P(WA) × P(CO ₂)		n.s.	0.028	0.014
			P(WA) × P(Year)		<0.001	n.s.	<0.001
			P(Temp) × P(CO ₂)		n.s.	n.s.	n.s.
			P(Temp) × P(Year)		<0.001	n.s.	0.002
			P(CO ₂) × P(Year)		<0.001	n.s.	n.s.

Values are elapsed time (days) mean ± SE, n = 8–10. Cult, Cultivar; Temp, Temperature; WA, water availability and n.s., not significant.

genes (Nicolas et al., 2014), thus improving berry quality (Ferrandino and Lovisolo, 2014). For example, despite hastening fruit ripening, mild water deficit normally has a desirable effect, increasing the concentration of some phenolic compounds in the grapes (Chaves et al., 2010). However, as climate change continues, places experiencing a risk of severe water deficit may encounter contrasting effects. Severe water deficit can induce stomatal closure, greatly reduce carbon fixation, and subsequently, impair berry ripening (Martínez-Lüscher et al., 2015a). This may explain the results obtained with fruit-bearing cuttings, where a water deficit appeared to generally delay maturity. In addition, water availability had significant interactions with both temperature and CO₂ concentration. For conditions such as ambient temperature and elevated CO₂, where plants were presumably less stressed, the general tendency of cyclic drought to delay ripening was reverted. Contrasting effects of water deficit have also been reported by Cook and Wolkovich (2016) in large scale field data analyses, where precipitation correlates positively with harvest date anomalies in France, while they correlate negatively in the drier vineyards of Spain. Cook and Wolkovich (2016) highlight that the relationship between water deficit and early harvest has weakened in recent decades in central Europe due to the decoupling of the incidence of high temperatures and drought.

The influence of temperature and water availability on grape ripening may depend on other factors, such as soil type, variety and rootstock, among others. Soil is a key factor for vine productivity and fruit quality, and the response of *V. vinifera* to water deficit may depend on the soil water retention capacity (Oliveira et al., 2003). In addition, the increase in phenolic concentrations observed in higher clay soils were greater in wet and intermediate years than in dry years when abundant ABA biosynthesis controls plant responses to drought, independently from soil properties (references in Lovisolo et al., 2016). Soils with moderate water retention capacity induced mild water stress, thus favoring fruit ripening, compared with soils with either very low or unlimited water availability (Tramontini et al., 2013). Also,

they stated that water availability in the soil overrides differences due to cultivar in determining the vineyard productive potential. van Leeuwen et al. (2004), who studied the effect of weather, soil and cultivar simultaneously, found that soil had little effect on phenology (1 day change in flowering-harvest) compared with weather and cultivar (up to 14 and 9 day difference in the flowering-harvest period, respectively). For fruit quality, however, impacts of weather and soil were greater than that of cultivar, with effects being mediated through their influence on vine water status. Concerning rootstocks, a small and possibly insignificant 3-day difference for the time between flowering and harvest in a comparison among three different rootstocks was reported by Dias Tofaneli et al. (2011). In contrast, Corso et al. (2016), using a selection of the most representative rootstocks and scions of mid-latitude vineyards, showed a rather strong effect of rootstocks on ripening rates. Varieties can also differ in their response to increased temperatures and water deficit. Based on the results under controlled conditions, late ripening varieties may be more sensitive than early ones. Probably, early ripening varieties may be more predetermined to ripen during the warmest part of the year, reaching a threshold of precocity where further advances are not possible, whereas late ripening varieties may be advanced to a greater extent, and therefore, the increase in ambient temperature during their ripening period may be greater.

Effect of CO₂ Concentration in Relation to Temperature

Grapevine fruit-bearing cuttings grown under semi-controlled conditions showed similar sensitivities to increasing temperatures compared to field grown vines, although sensitivities were lower in the warmer year, 2015, and for the early cultivar, 'Red Tempranillo.' The change induced by elevated CO₂ followed similar variation, but this effect was greater than the effect of the 4°C increase. In recent studies with grapevine fruit-bearing cuttings, a correlation between

carbon fixation rates and grape development rates has been reported (Martínez-Lüscher et al., 2015b). This behavior has been described under field conditions as well, where leaf removal treatments, which presumably reduce overall grapevine carbon fixation, resulted in a delay in grape maturity (Martínez de Toda et al., 2013; Parker et al., 2014, 2015). Plants exposed to elevated CO₂ often show photosynthetic acclimation, which is characterized by an initial increase in carbon fixation rates and reduction to initial levels or even lower after a mid-term exposure (Leakey et al., 2009). However, this is not a generalized response and, even if this were the case, it would not mean that plant performance and fruit yield would be strongly affected (Idso and Kimball, 1991; Leakey et al., 2009). One of the greatest efforts to study the effect of elevated CO₂ on fruiting woody perennials is a 17-year experiment on sour orange trees (*Citrus aurantium* L.) with open-top-chambers, which showed a constant increase in yield despite photosynthetic acclimation (Kimball et al., 2007). To the best of our knowledge, a paper by Bindi et al. (2001) is the only FACE experiment study in the literature, where an increase in sugar accumulation in the grapes was reported. Although this effect was diluted in the latest stages of ripening, this is evidence for accelerated ripening in grapes grown under elevated CO₂. In previous reports, Salazar Parra et al. (2010) and Martínez-Lüscher et al. (2016) showed how grapes grown under both elevated CO₂ and increased temperature met the sugar criteria for harvest much earlier, and this led to a decrease in anthocyanin concentration. In contrast, Kizildeniz et al. (2015), who studied the interaction between elevated CO₂ and increasing temperature, reported that elevated CO₂ showed mitigating effects, generally increasing anthocyanin concentration and increasing either grape organic acid concentration or decreasing grape pH, probably related to the precocity of these treatments. Thus, due to its complexity, the relationship between different environmental factors and grape composition should be assessed with caution, as phenology-mediated effects are likely.

Martínez de Toda and Balda Manzanos (2013) and Martínez de Toda et al. (2013) showed that cultural practices, such as canopy density reduction, can have an opposite effect to that resulting from high temperature, reducing TSS concentration for a fixed date. However, in that case, this contributed to restore grape pH, but reduced anthocyanin concentration. Interestingly, Martínez de Toda et al. (2014), in a similar experiment but harvesting grapes at a designated TSS concentration, found that delayed phenological development contributed to increasing anthocyanin concentration. These findings suggest that carbon translocation into the grapes can be controlled, thus altering the timing of phenological stages, which can contribute to mitigating the effects of climate change.

CONCLUSIONS

The results of the present study suggest that temperature, water deficit and CO₂ levels representative of the conditions

expected for the end of the 21st century may strongly advance budburst, flowering, and berry designated maturity. Some uncertainties still exist, such as whether the delaying effect of severe water deficit or the decreasing sensitivity under extreme temperature, which have been observed both in fruit-bearing cuttings in the present study and in other field studies, will be generally observable in vineyards in the future. Future efforts should be directed to investigating how grapevine whole-plant physiology may be altered in response to climate change-related factors, and to uncoupling the effects of environmental factors such as temperature, water deficit and CO₂, from their potential effects on berry phenology. These are crucial topics to establish successful mitigation and adaptive strategies for viticulture in a changing environment.

AUTHOR CONTRIBUTIONS

JM performed the analysis and elaborated the draft of the manuscript. ZD and EL designed the analysis of the field data. IP, JI, and FM designed the TGG experiments, TK performed the TGG experiments. VV provided the field data and reviewed the manuscript. JM, TK, ZD, EL, CV, EG, IP, JI, FM, and SD contributed to the interpretation of the results and elaboration of the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <http://journal.frontiersin.org/article/10.3389/fenvs.2016.00048>

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