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Drivers of grape berry sugar accumulation in field conditions at local scale

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ABSTRACT

The final sugar concentration in grapes is an important parameter for winegrowers as it determines the alcohol content by volume of the final wine, allowing the timing of harvest to be optimised. In this research, a comprehensive dataset spanning seven years and 18 sites located in Saint-Émilion, Pomerol and satellite appellations (Bordeaux, France) was used to assess how growth and developmental factors (berry weight and mid-veraison date, respectively) and environmental factors (vine water status, nitrogen status, and mean air temperature) influence the dynamics of sugar accumulation.

The results of this study highlight the strong influence of mean temperature on the timing of maximum sugar accumulation, the duration of sugar accumulation and maximum sugar concentration in grape berries. Berry weight and the rate of sugar accumulation also appeared to be significant drivers of final sugar concentration. Fast ripening and increased berry weight were associated with lower sugar concentrations. Sites were clustered according to parameters driving sugar accumulation dynamics and mapped at the scale of the study area, in order to link these findings to terroir expression. In this study, vine nitrogen status did not emerge as a significant explanatory variable in any of the models developed to analyse sugar accumulation dynamics and berry weight. A small but significant effect of vine water status on the precocity of the plateau and on berry weight was found.

These results provide a better understanding of the factors that affect the dynamics of sugar accumulation in grape berries, which can help vine growers adapt to climate change. For example, by promoting practices that delay the onset of ripening to shift to a cooler period of ripening through choice of plant material and management practices. Alternatively, this can be done through an increase in berry weight, which lowers grape sugar and therefore wine alcohol concentration, taking care not to excessively alter the skin-pulp ratio to avoid reducing secondary metabolites.

KEYWORDS: Terroir 2024, grapevine, grape ripening, temperature, berry development, *Vitis vinifera* L. cv. Merlot, climate change, water status

INTRODUCTION

Understanding the factors that influence grape sugar concentration is crucial for winegrowers, not only to determine the optimal timing for harvest, but also to anticipate future adaptations to climate change. Recent temperature trends have affected the wine producing sector, leading to increased sugar concentrations at harvest, reduced ripening duration and a shift in ripening period to earlier in the season, when temperatures are higher (Jones & Davis, 2000; van Leeuwen *et al.*, 2024). As global surface temperatures are projected to continue to rise during the 21st century (IPCC, 2021), a comprehensive understanding of the effects of environmental factors on grape berry ripening dynamics is necessary to better anticipate adaptation strategies (Rogiers *et al.*, 2022).

Grape sugar accumulation can be influenced by changes in the timing of the ripening phase and in the kinetics of sugar accumulation. The onset of sugar accumulation (veraison) is influenced by both cultivar and air temperature prior to veraison (Parker *et al.*, 2011; Suter *et al.*, 2021). It can be modulated by other factors, such as carbohydrate dynamics, as is shown by the ability of reduced the leaf area/fruit weight (LA:FW) ratio to delay veraison (Parker *et al.*, 2014; Petrie *et al.*, 2000).

In a berry population, sugar accumulation follows a sigmoid curve due to the heterogeneity of veraison. It starts at veraison (berry softening) and is followed by rapid sugar accumulation, leading to a plateau sugar concentration (Suter *et al.*, 2021). However, at the berry level, sugar accumulation starts abruptly (Ollat *et al.*, 2002). This curve can extend beyond the sigmoidal plateau concentration in cases where berry dehydration occurs (Keller *et al.*, 2015; Deloire *et al.*, 2021).

The kinetics of sugar accumulation is also affected by similar factors to that of the onset of ripening (veraison): cultivar, temperature (Moukarzel *et al.*, 2023) and their interaction (Parker *et al.*, 2020). In terms of climate factors, vapour pressure deficit impacts sugar accumulation, as lower evaporative demand leads to a lower transpiration rate resulting in lower sugar accumulation (Rebucci *et al.*, 1997; Sadras & Petrie, 2011), while higher photosynthetically active radiation leads to faster sugar accumulation (Jones & Davis, 2000; Suter *et al.*, 2021). Furthermore, water deficit can have differing responses depending on severity, with moderate water deficit increasing ripening rates (Suter *et al.*, 2021).

Management practices that alter the LA:FW ratio, such as source limitation via reduced leaf area, can lead to slower sugar accumulation rates, with a sugar concentration plateau sometimes not being achieved within a season (Parker *et al.*, 2015); meanwhile, crop removal, which increases the LA:FW ratio, can in some cases accelerate ripening rates (Parker *et al.*, 2014; Parker *et al.*, 2015). A ratio of 0.8 to 1.2 m^2/kg fruit is required for maximum total soluble solids accumulation, berry weight and coloration at harvest for single-canopy trellis systems (Kliewer & Dokoozlian, 2005).

Nitrogen has also been demonstrated to play a role in the timing of sugar accumulation, with high nitrogen availability delaying fruit ripening (Keller *et al.*, 1998). This can be interrelated with sink size, given that berry weight increases when vine nitrogen status is high (Trégoat *et al.*, 2002; Triolo *et al.,* 2018).

Various models have been developed, ranging from complex mechanistic models based on sugar import, sugar metabolism and water budget at berry level (Dai *et al.*, 2009), to simpler models based on berry populations that can be used by winemakers to predict the timing of harvest (Sadras & Petrie, 2011) or specific sugar concentrations (Parker *et al.*, 2020), and help understand the drivers of sugar accumulation. The growing degree day model of Parker *et al.* (2020) is based on mean temperature only. Sadras & Petrie (2012) found the onset of ripening in various wine-growing regions of Australia to be influenced by temperature. However, regarding the rate of sugar accumulation, in most cases these authors did not find a model based on a thermal rate ([Sugar]/degree.days (°Cd)) to be superior to a model based on a chronological rate ([Sugar]/week).

While many climate and management practices have been identified or modelled in order to determine sugar accumulation dynamics in grapevines, few studies have taken into account the interaction or relative importance of different factors. One example of a study in which interactions were considered was carried out by Martínez-Lüscher *et al.* (2016): they found that water availability significantly interacted with temperature and CO_2, delaying maturity when there was a water deficit. This confirms the increasing importance of understanding different drivers of sugar accumulation in the context of climate change, in which growers may need to implement multiple management adaptation strategies to counter effects of a warming climate.

Therefore, our aim was to evaluate the influence and relative importance of several abiotic factors that influence sugar accumulation: mean temperature, vine water and nitrogen status. These were considered in conjunction with the influence that development factors, such as berry weight and timing of mid-veraison, have on the dynamics of sugar accumulation. Seven years-worth of data from 18 plots in commercial vineyards located in Saint-Émilion, Pomerol and their satellite appellations (Bordeaux, France) were used. We specifically aimed to investigate i) the factors determining timing and maximum concentrations of sugar accumulation at different locations (sites), ii) why some plots accumulate grape sugar faster than others, and the factors involved (abiotic and development factors), and iii) whether geographical locations or terroirs with homogeneous ripening dynamics could be determined in this study area.

MATERIALS AND METHODS

1. Experimental set-up and data collected

Data used for this project were collected from 2012 through 2019 in 18 plots of 20 vines of *Vitis vinifera* L. cv. Merlot located in the area of Saint-Émilion, Pomerol and their satellite appellations (Figure S1). The 2017 vintage was eliminated from this study because of major spring frost damage.

Plots were selected for contrasting temperature conditions and, as a result, differences in the timing of subsequent phenological stages. The plots were located on different soil types (Table S1). All vines were Guyot-pruned and vertical shoot-positioned (VSP trellis), but planting density and soil management practices differed (Table S1).

Daily minimum (Tn) and maximum (Tx) temperature data were recorded by temperature data loggers (Tinytag Talk2, Gemini Data Loggers, UK) located within the different plots at a height of 1.2 m close to the vegetation (de Rességuier *et al.*, 2020). Mean temperature (Tm) was calculated as (Tn+Tx)/2.

In order to determine mid-veraison (DOY Ver) [*i.e.*, the day on which 50 % of berries reached the BBCH 85 stage (Meier, 2001)], the progression of veraison was monitored visually (colour change) twice a week in each plot of 20 vines.

For maturity, samples of 100 berries were collected from the four rows surrounding the temperature sensor each week, starting immediately after mid-veraison up to a date close to harvest. Berries were collected from different parts of the grape bunches on both sides of the canopy, to take into account, as much as possible, asynchronous ripening among berries (Coombe, 1980). Berry weight of 100 berries was determined for each plot on each sampling date, as was sugar concentration measured by Fournier Transform Infrared Spectroscopy (FT-IR) [FOSS Analytical, France].

The environmental variables potentially affecting sugar accumulation (*i.e.*, vine water and nitrogen status) were assessed in grape juice using the δ^{13}C method (Gaudillère *et al.*, 2002), and yeast available nitrogen (YAN) was measured using the enzymatic method from 2013 to 2019 and formol titration in 2012 (van Leeuwen *et al.*, 2000). These two analyses were carried out on the same day for all the locations, just prior to the harvest of the earliest plot.

The number of year/site combinations are summarised in Table S2. Two parcels were pulled out during the project and the data loggers and sampling sites were relocated to nearby plots with a similar soil type. Specifically, Site 4 was transferred to Site 20, and Site 11 was transferred to Site 91 (Table S2). When processing the results of all the analyses, these four respective plots were considered independently, except when producing the heatmap for which these plots were averaged by site and year to equalise the populations.

2. Modelled data and explanatory variables of sugar accumulation

A sigmoid curve was fitted for each plot and year in order to model sugar concentration by using a 3-parameter logistic function (Triboï *et al.*, 2003; Sadras *et* al., 2008; Suter *et al.*, 2021):

$$\mathrm{S(t)} = \frac{\mathrm{S}max}{1 + 0.05.\mathrm{e}^{\left(-4.\mathrm{r}.\left(\frac{\mathrm{t}-\mathrm{t95}}{\mathrm{Smax}}\right)\right)}}$$

where Smax is the estimated maximum sugar concentration (g/L), t is day of the year (DOY), t95 is DOY when 95 % of the maximum had accumulated, and r is the estimated maximum rate of accumulation (g/L per day). To avoid overshooting the asymptotic stage, a constraint was applied on the t95 parameter, which could not be estimated at more than 3 % of the last value of sugar concentration measured.

The following variables were interpolated from each curve fit and used to characterise the sugar accumulation dynamics in this study: day of year when sugar concentration reached 95 % of the maximum (DOY 95% Sug), sugar concentration (g/L) at t95 (Plateau 95% Sug), and number of days between modelled t95 and observed mid-veraison (Dur 95% Sug-Ver).

The following variables were chosen as potential predictors of sugar accumulation dynamics: the mean temperature from observed mid-veraison to the day of the year when sugar concentration reached 95 % of the maximum (Tm Ver_95% Sug, in °C), δ^{13}C (in ‰), YAN (in mg/L), and the closest measured berry weight to DOY 95% Sug (Berry weight 95% Sug, in g). The timing of mid-veraison was added for the analyses of DOY 95% Sug and Plateau 95% Sug, and the Dur 95% Sug-Ver as a proxy for ripening speed for Plateau 95% Sug analysis.

3. Statistical analysis

The fit of the sigmoid model to berry sugar accumulation for each site and year was evaluated by calculating the coefficient of determination (R^2) and the root mean squared error (RMSE). R^2 represents the proportion of variance of the response variable predicted by a model, and RMSE is a measure of the error of prediction and corresponds to the square root of the average squared differences between the model prediction and the observed values.

Descriptive analyses were performed for all response and predictive variables (δ^{13}C, YAN, Tm Ver_95% Sug, Berry weight 95% Sug, and DOY Ver, DOY 95% Sug, Plateau 95% Sug, Dur 95% Sug-Ver) by using boxplot representation with the *ggplot2* package (Wickham, 2016). After conducting a Kruskal-Wallis test, Dunn nonparametric pairwise comparison was performed to evaluate significant differences between years. A Bonferroni correction was applied to adjust for multiple comparisons by using *FSA* (Ogle *et al.*, 2023) and *rcompanion* R packages (Mangiafico, 2024).

The effects of Tm Ver_95% Sug, Dur 95% Sug-Ver, Year, δ^{13}C, YAN, Site, Berry weight 95% Sug and DOY Ver on sugar accumulation dynamics were investigated by linear mixed-effects models (Pinheiro & Bates, 2000). "Site" and "year" were considered as random effects on the intercept to account for intra-year and intra-plot correlation. These linear mixed-effects models were fitted using the function *lmer* from the *lmerTest R* package (Kuznetsova *et al.*, 2017). Total variance explained by the models was partitioned with the function *r.squaredGLMM* from the *MuMIn* package (Burnham & Anderson, 2002), in order to estimate the fraction of variance explained by the fixed and random effects. The presence of collinearity between predictors was tested by calculating the variance inflation factor (VIF) with the function *check collinearity* from the package *performance*. Partial effects (with only one predictor varying) were plotted using the *predictor Effect* function from the package *effects* (Fox & Weisberg, 2018).

TABLE 1. Sigmoidal model variance evaluated by root mean squared error (RMSE) and R^2 per year. Means are followed by standard deviations.

Year	RMSE (g/L)	RMSE min (g/L)	RMSE max (g/L)	R^2
2012	3.1 ± 1.2	1.7	6.2	0.99 ± 0.01
2013	2.7 ± 1.4	0.4	5.2	0.98 ± 0.01
2014	2.6 ± 1.0	0.6	5.4	0.99 ± 0.01
2015	1.6 ± 0.8	0.2	3.0	0.99 ± 0.01
2016	2.5 ± 0.7	1.2	4.0	0.99 ± 0.00
2018	2.0 ± 1.0	0.5	5.1	0.98 ± 0.01
2019	5.8 ± 1.7	3.2	8.8	0.95 ± 0.03

To perform unsupervised hierarchical clustering of the variables describing maturity dynamics by site and year, heatmaps were generated using the *pheatmap* package. For the site-specific heatmaps, values for different years were averaged per site, and for the year-specific heatmaps, values for all sites were averaged per year. Due to the different units and scales of the variables, the data were standardised prior to heatmap visualisation.

All analyses were conducted on Rstudio version 4.3.1.

RESULTS

1. Modelling of sugar accumulation dynamics

The sigmoid curve fit well according to the obtained R^2 and RMSE (Table 1, examples in Figure 1; full dataset of curve fits shown in Figure S1). RMSE varied across sites, with a minimum error of 0.2 g/L and a maximum error of 8.8 g/L. Accuracy of the model fitting varied according to year, from 1.6 g/L of error in 2015 to 5.8 g/L in 2019, and a site effect was also observed (Table S3).

The timing of the plateau (DOY 95% Sug), sugar accumulation rate measured as the number of days between DOY Ver and DOY 95% Sug (Dur 95% Sug-Ver), and sugar concentration at 95 % of plateau (Plateau 95% Sug) differed depending on site and year (Figure 1 and Figure 2).

There was important site variation in the timing of the plateau, with high intra-annual variation of 45 days between sites in 2013. To a lesser extent, there was also inter-annual variation of up to 15 days between years (the latest observed in 2019 and the earliest in 2015) [Figure 2A].

The duration of sugar accumulation also varied from year to year and site to site, with a particularly long period of sugar accumulation of 37 days in 2013 and 2019 (Figure 2C). In 2013, Site 1 ripened faster (21 days) [Figure 1B1] than Site 84 (52 days) [Figure 1B3], and ripening in Site 1 was faster in 2013 (21 days) [Figure 1B1] than in 2012 (43 days) [Figure 1A1].

For Plateau 95% Sug, site-to-site variability remained relatively consistent across the years. However, a significant year effect was observed, with an average accumulation of only 196 g/L in 2013 compared to 242 g/L in 2019 (Figure 2B).

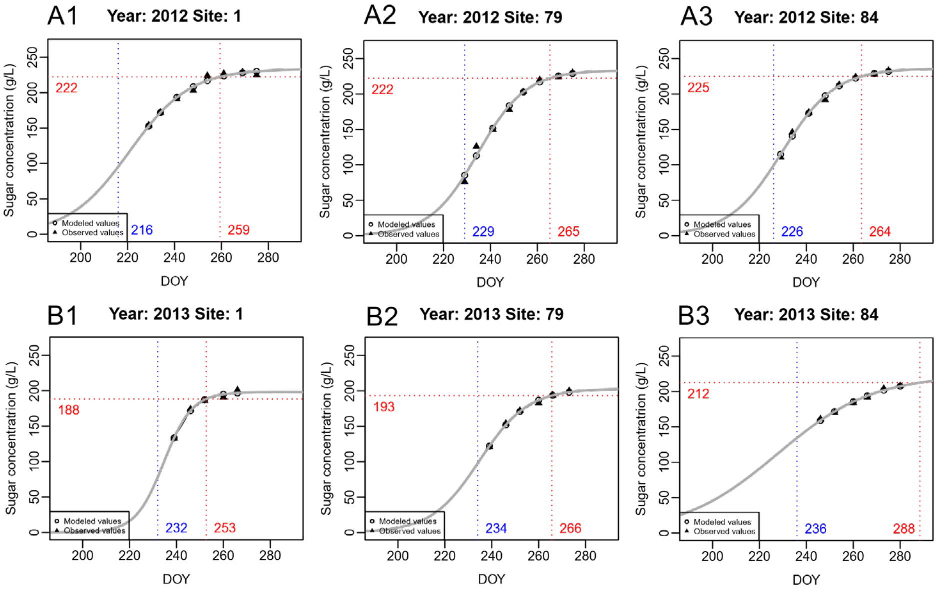


FIGURE 1. Examples of sugar concentration accumulation data and fitted curves for sites 1, 79 and 84 in A) 2012 and B) 2013. The vertical dashed blue line indicates observed mid-veraison (DOY Ver), and the vertical dashed red line indicates the modelled day of 95 % of sugar concentration (DOY 95% Sug). The horizontal dashed red line marks the modelled sugar concentration (Plateau 95% Sug).

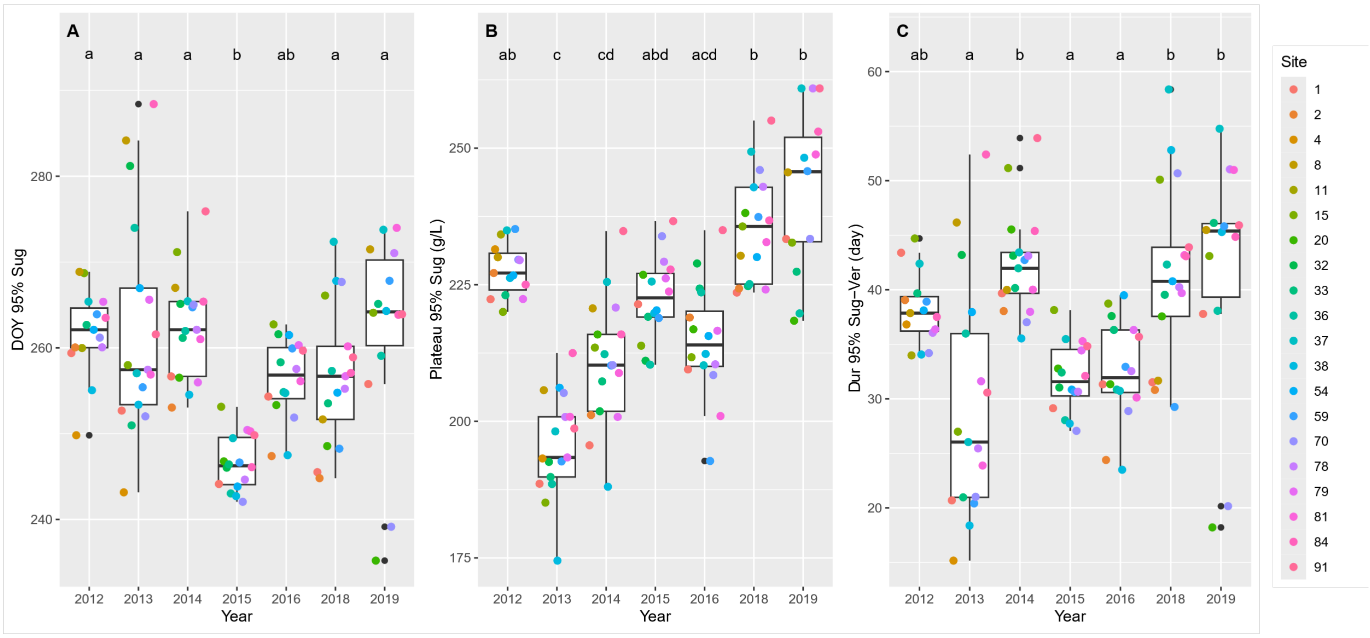


FIGURE 2. Boxplots of variables for the sites per year: A) day of year when 95 % of maximum concentration had accumulated (DOY 95% Sug), B) sugar concentration (g/L) at t95 (Plateau 95% Sug), and C) rate of sugar accumulation as number of days between DOY 95% Sug and DOY Ver (Dur 95% Sug-Ver). Different coloured dots indicate different sites. Letters indicate years that differ statistically according to Dunn's nonparametric pairwise multiple-comparison procedure with 5 % type I error threshold and a Boneferroni correction.

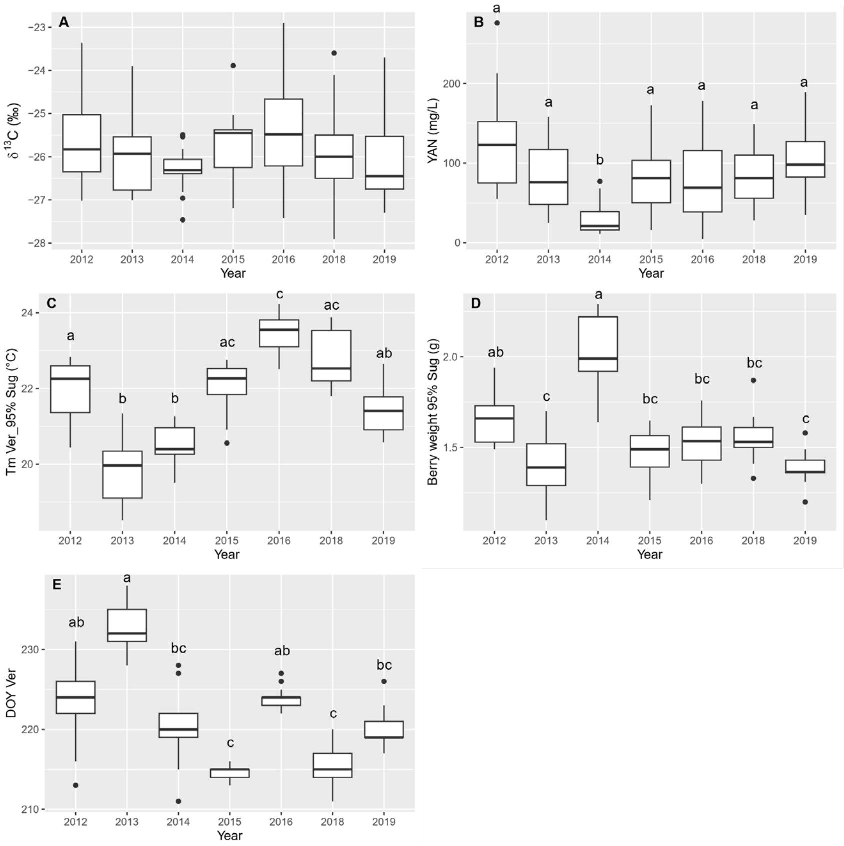


FIGURE 3. Boxplots of variables across sites and years: A) variation of δ^{13}C, B) yeast available nitrogen (YAN), C) mean temperature between mid-veraison and day of sugar concentration at 95 % (Tm Ver_95% Sug), D) berry weight at 95 % of sugar concentration (Berry weight 95% Sug), and E) day of observed mid-veraison (DOY Ver). Letters indicate years that differ statistically according to Dunn's nonparametric pairwise multiple-comparison procedure, with 5 % type I error threshold and a Boneferroni correction. Absence of letters indicate that no statistically significant difference was found.

TABLE 2. Linear mixed-effects models used to explain: berry weight at 95 % of sugar concentration (Berry weight 95% Sug); timing of 95 % maximum sugar concentration (DOY 95% Sug); sugar concentration at 95% of maximum sugar accumulation (Plateau 95% Sug); number of days from mid-veraison to 95% of sugar concentration (Dur 95% Sug-Ver). Factors in bold are statistically significant at different p-values.

Explained variable	Fixed effect	Estimated	Std. error	t value	p-value	Random effect	Variance	Std. Dev	% variance explained by the model	% variance explained by fixed effects
Berry weight 95% Sug (g)	Intercept	0.72	0.74	0.97	ns	Site	0.01	0.07	84.4%	7.7%
	Tm Ver_95% Sug (°C)	-0.03	0.02	-1.23	ns	Year	0.05	0.22		
	$\delta^{13}C$ (‰)	**-0.06**	**0.02**	**-3.32**	**	Residual	0.01	0.10		
	YAN (mg/L)	0.00	0.00	0.61	ns					
DOY 95% Sug	**Intercept**	**142.61**	**67.69**	**2.11**	*	Site	3.72	1.93	78.5%	53.0%
	Tm Ver_95% Sug (°C)	**-4.08**	**1.08**	**-3.78**	***	Year	37.32	6.11		
	$\delta^{13}C$ (‰)	**-1.95**	**0.85**	**-2.30**	*	Residual	34.70	5.89		
	YAN (mg/L)	0.03	0.02	1.85	ns					
	Berry weight 95% Sug (g)	7.56	4.79	1.58	ns					
	DOY Ver	**0.63**	**0.23**	**2.69**	**					
Plateau 95% Sug (g/L)	Intercept	143.99	87.70	1.64	ns	Site	13.90	3.73	83.0%	48.5%
	Tm Ver_95% Sug (°C)	**4.95**	**1.51**	**3.28**	**	Year	74.83	8.65		
	$\delta^{13}C$ (‰)	-1.35	1.08	-1.25	ns	Residual	43.68	6.61		
	YAN (mg/L)	-0.03	0.02	-1.30	ns					
	Berry weight 95% Sug (g)	**-23.35**	**5.94**	**-3.93**	***					
	DOY Ver	-0.28	0.29	-0.96	ns					
	Dur 95% Sug-Ver	**0.99**	**0.11**	**8.67**	***					
Dur 95% Sug-Ver (day)	Intercept	57.09	34.67	1.65	ns	Site	4.28	2.07	72.0%	29.9%
	Tm Ver_95% Sug (°C)	**-3.59**	**1.00**	**-3.59**	***	Year	47.45	6.89		
	$\delta^{13}C$ (‰)	-1.57	0.84	-1.87	ns	Residual	34.42	5.87		
	YAN (mg/L)	0.03	0.02	1.89	ns					
	Berry weight 95% Sug (g)	9.15	4.75	1.93	ns					

YAN = yeast available nitrogen, DOY Ver = day on which 50 % of the berries reached veraison, Std.Dev = standard deviation, t value = Student t-test, p-value = 'ns' not significant, '***' significant at $p < 0.001$; '**' significant at $p < 0.01$; '*' significant at $p < 0.05$.

2. Analysis of explanatory variables of sugar ripening dynamics

The variation in explanatory variables across sites and years (vine water and nitrogen status, berry weight, mean temperature during grape ripening and day of mid-veraison) was analysed (Figure 3). While $\delta^{13}C$ was not affected by the year (Figure 3A), significant variation in water deficit existed between sites, ranging from 'no water deficit' to 'severe water deficit', according to published thresholds for the interpretation of $\delta^{13}C$ values (van Leeuwen *et al.*, 2023a). Conversely, Tm Ver_95% Sug and DOY Ver were strongly influenced by the year (Figures 3C and 3E). High inter-annual variation was observed for the timing of mid-veraison (18 days difference between the later 2013 vintage and the earlier 2015 and 2018 vintages), as well as high intra-annual variation (5 days in 2016 compared to 18 days in 2012) [Figure 3E]. For yeast available nitrogen, intra-annual variation was similar in the different years, but 2014 was significantly different from the others, with less YAN in the grape must. Regarding berry weight, little variation was observed among the vintages, except in 2014 when berry weight was particularly high, and in 2013 and 2019 when berry weight was lower than in the other years (Figure 3D).

A linear mixed-effects model was used to explore factors impacting berry weight, which also accounted for unquantified site and year effects. Berry weight was fitted as a function of average mean temperature from mid-veraison to the sugar accumulation plateau, $\delta^{13}C$ and YAN. Although a significant effect of $\delta^{13}C$ on berry weight was observed, the total fixed effects only explained 7.7 % of the variance out of a total of 84.4 % explained by the model, including both fixed and random effects (Table 2). While water deficit conditions tended to result in lower berry weight, this effect was low compared to the impact of year and site. The model-effect plot between $\delta^{13}C$ and berry weight showed that, in the conditions of this study, small berries were produced even without water deficits, while severe water deficits consistently led to small berries (Figure 4A).

3. Factors involved in the timing of the plateau of 95 % maximum sugar accumulation (DOY 95% Sug)

The main factor influencing the DOY 95% Sug was the Tm Ver_95% Sug: a temperature increase of 1° C during grape ripening advanced the DOY 95% Sug by 4.1 days (Table 2 and Figure 4B1). To a lesser extent, a positive effect of the timing of mid-veraison (DOY Ver) on the timing of maximum sugar accumulation (DOY 95% Sug) was observed (Table 2 and Figure 4B2). An effect of δ^{13} was also shown (*i.e.*, the timing of mid-veraison advanced with water deficit), although this effect was weak (Table 2 and Figure 4B3). The model explained 78.5 % of the variance, with fixed effects contributing to 53.0 %. The year was responsible for more residual variance than the site.

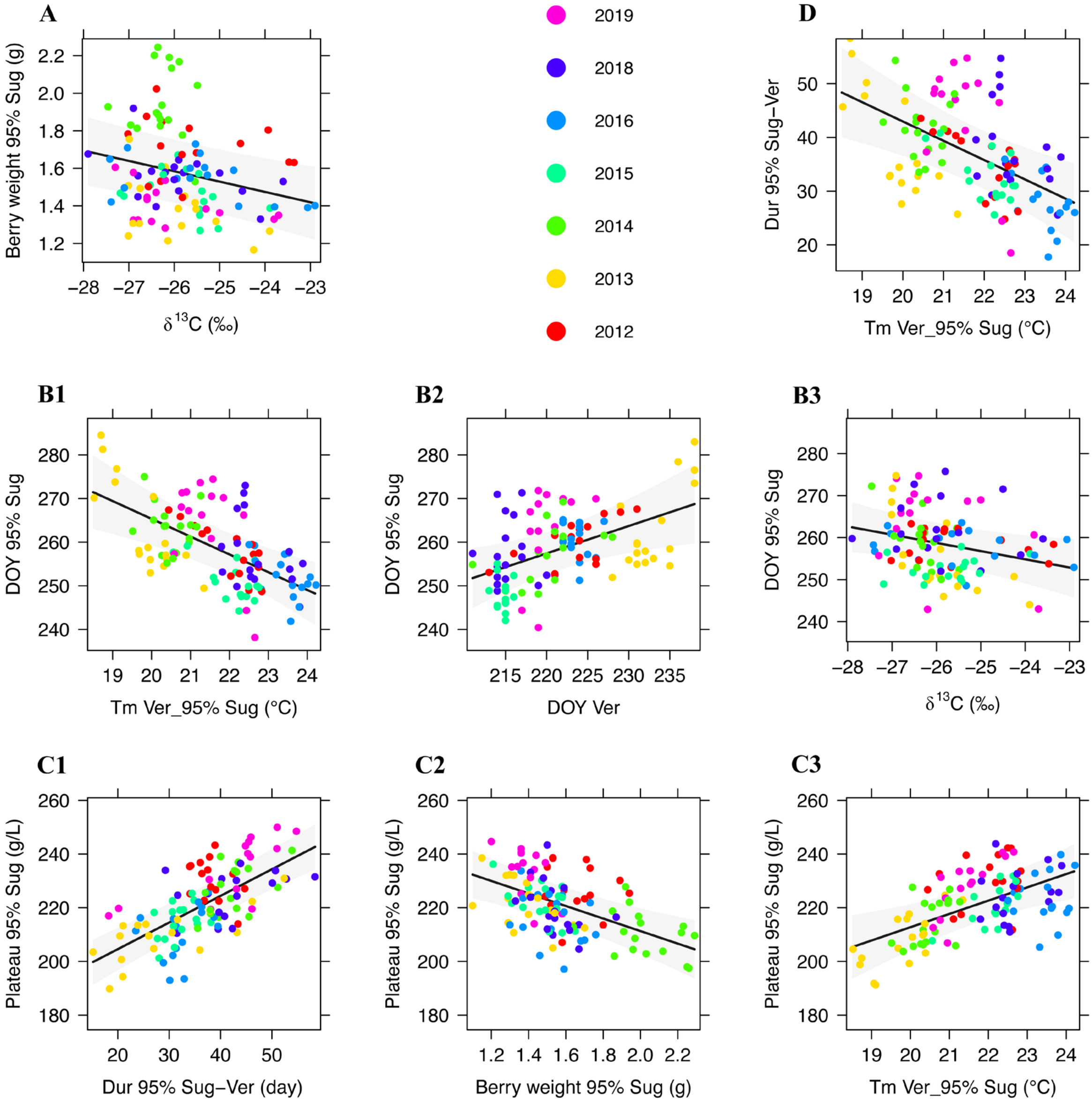


FIGURE 4. Effects of significant predictors on the response variables of each mixed-effects models used in the study: A) berry weight at DOY 95% of maximum sugar accumulation (Berry weight 95 % in g), B) timing of 95 % of maximum sugar accumulation (DOY 95% Sug), C) 95 % of maximum sugar accumulation (Plateau 95% Sug in g/L), and D) number of days between mid-veraison and day of 95 % of maximum sugar accumulation (DOY 95% Sug in day). Dots with different colours indicate different years.

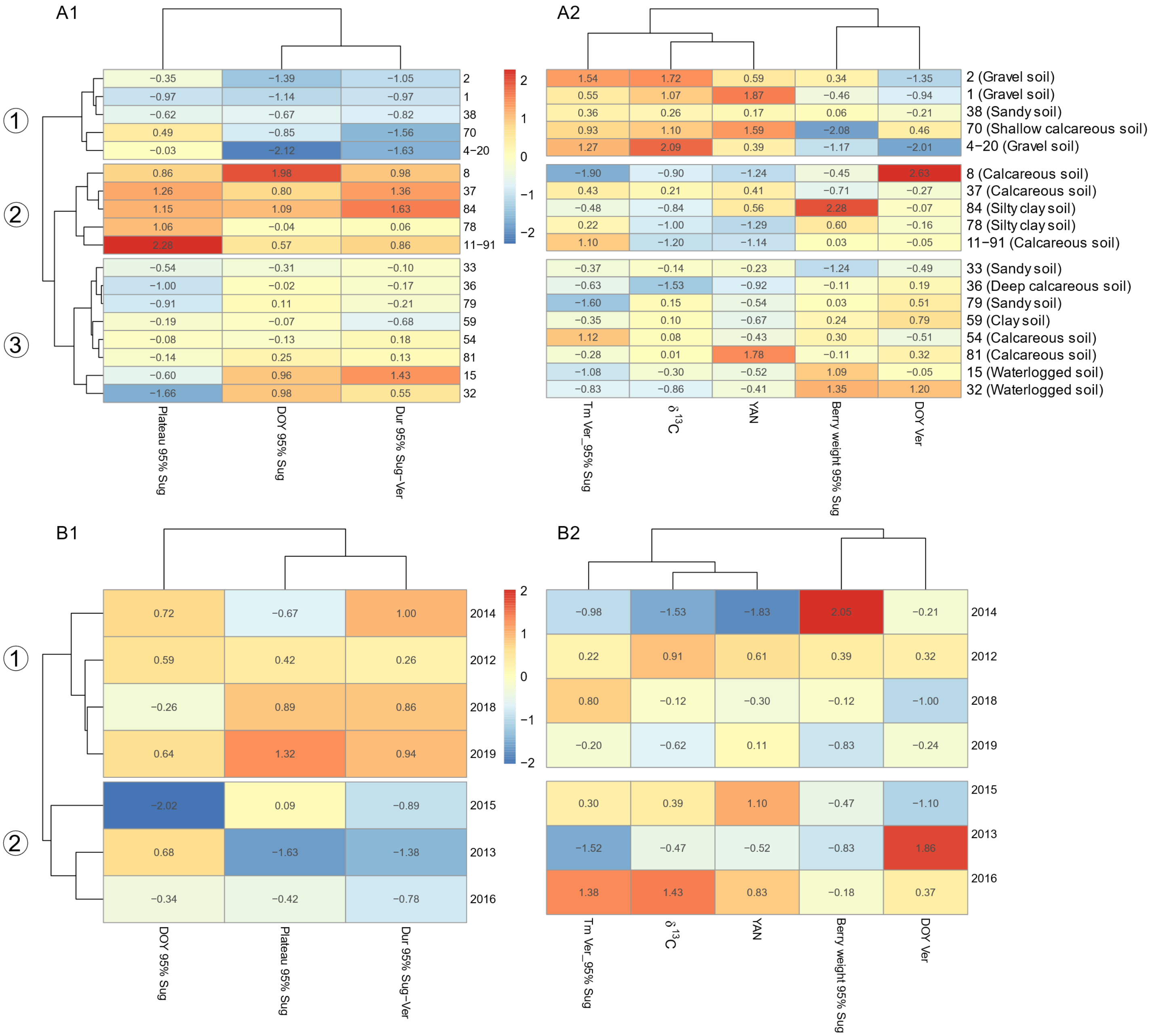
4. Factors influencing the sugar concentration at the plateau (Plateau 95% Sug)

To study the factors influencing plateau sugar concentration (Plateau 95% Sug), the following factors were considered: length of sugar accumulation period (Dur 95% Sug-Ver), temperature during this period (Tm Ver_95% Sug), vine water status ($\delta^{13}C$), vine nitrogen status (YAN), DOY Ver, and berry weight at the plateau of sugar concentration (Berry weight 95% Sug).

The sugar concentration obtained at 95 % of plateau was impacted by (in order of impact size): Dur 95% Sug-Ver (*i.e.*, the shorter the duration, the lower the sugar concentration at 95 %), Berry weight 95% Sug (*i.e.*, the heavier the berry, the less sugar accumulated), and Tm Ver_95% Sug (*i.e.*, the higher the temperature, the higher the sugar concentration at 95 % in grape berries) (Table 2 and Figure 4C). The combination of these fixed effects explained 48.5 % of the variance, and the model as a whole explained 83.0 % of the variance. The year showed higher residual variance (standard deviation of 8.65 g/L) than the site (standard deviation of 3.73 g/L).

5. Factors influencing the rate of sugar accumulation (Dur 95% Sug-Ver)

Tm Ver_95% Sug, DOY 95% Sug, $\delta^{13}C$, YAN and Berry weight 95% Sug were examined as factors that could influence rate of sugar accumulation. These fixed effects explained only 29.9 % of the rate, with increased temperatures reducing the ripening period duration (Table 2 and Figure 4D): an increase of 1° C in mean temperature during the ripening period reduced its duration by 3.6 days.



A1

	Plateau 95% Sug	DOY 95% Sug	Dur 95% Sug−Ver
2	−0.35	−1.39	−1.05
1	−0.97	−1.14	−0.97
38	−0.62	−0.67	−0.82
70	0.49	−0.85	−1.56
4−20	−0.03	−2.12	−1.63
8	0.86	1.98	0.98
37	1.26	0.80	1.36
84	1.15	1.09	1.63
78	1.06	−0.04	0.06
11−91	2.28	0.57	0.86
33	−0.54	−0.31	−0.10
36	−1.00	−0.02	−0.17
79	−0.91	0.11	−0.21
59	−0.19	−0.07	−0.68
54	−0.08	−0.13	0.18
81	−0.14	0.25	0.13
15	−0.60	0.96	1.43
32	−1.66	0.98	0.55

A2

	Tm Ver_95% Sug	$\delta^{13}C$	YAN	Berry weight 95% Sug	DOY Ver
2 (Gravel soil)	1.54	1.72	0.59	0.34	−1.35
1 (Gravel soil)	0.55	1.07	1.87	−0.46	−0.94
38 (Sandy soil)	0.36	0.26	0.17	0.06	−0.21
70 (Shallow calcareous soil)	0.93	1.10	1.59	−2.08	0.46
4−20 (Gravel soil)	1.27	2.09	0.39	−1.17	−2.01
8 (Calcareous soil)	−1.90	−0.90	−1.24	−0.45	2.63
37 (Calcareous soil)	0.43	0.21	0.41	−0.71	−0.27
84 (Silty clay soil)	−0.48	−0.84	0.56	2.28	−0.07
78 (Silty clay soil)	0.22	−1.00	−1.29	0.60	−0.16
11−91 (Calcareous soil)	1.10	−1.20	−1.14	0.03	−0.05
33 (Sandy soil)	−0.37	−0.14	−0.23	−1.24	−0.49
36 (Deep calcareous soil)	−0.63	−1.53	−0.92	−0.11	0.19
79 (Sandy soil)	−1.60	0.15	−0.54	0.03	0.51
59 (Clay soil)	−0.35	0.10	−0.67	0.24	0.79
54 (Calcareous soil)	1.12	0.08	−0.43	0.30	−0.51
81 (Calcareous soil)	−0.28	0.01	1.78	−0.11	0.32
15 (Waterlogged soil)	−1.08	−0.30	−0.52	1.09	−0.05
32 (Waterlogged soil)	−0.83	−0.86	−0.41	1.35	1.20

B1

	DOY 95% Sug	Plateau 95% Sug	Dur 95% Sug−Ver
2014	0.72	−0.67	1.00
2012	0.59	0.42	0.26
2018	−0.26	0.89	0.86
2019	0.64	1.32	0.94
2015	−2.02	0.09	−0.89
2013	0.68	−1.63	−1.38
2016	−0.34	−0.42	−0.78

B2

	Tm Ver_95% Sug	$\delta^{13}C$	YAN	Berry weight 95% Sug	DOY Ver
2014	−0.98	−1.53	−1.83	2.05	−0.21
2012	0.22	0.91	0.61	0.39	0.32
2018	0.80	−0.12	−0.30	−0.12	−1.00
2019	−0.20	−0.62	0.11	−0.83	−0.24
2015	0.30	0.39	1.10	−0.47	−1.10
2013	−1.52	−0.47	−0.52	−0.83	1.86
2016	1.38	1.43	0.83	−0.18	0.37

FIGURE 5. hierarchical clustering of sites (A1) and years (B1) by the three maturity variables (DOY 95% Sug, Plateau 95% Sug, Dur 95% Sug-Ver). A second heatmap was added to sites (A2) and years (B2) with the variables of interest, using the rows clustering order of the first heatmap and by clustering on columns.

6. Clustering and mapping of sugar accumulation dynamics across the winegrowing area

Heatmaps were generated for the three maturity variables per site (Figure 5A) and per year (Figure 5B). The unsupervised hierarchical cluster analysis revealed three notable clusters for site analysis (Figure 5A). Cluster 1 is characterised by parcels with rapid sugar accumulation, an early plateau and moderate sugar concentration at the plateau. It corresponds to sites with water deficit, low berry weight, high yeast available nitrogen (YAN) concentrations and early mid-veraison (Figure 5A); these sites were located in the western region of the area, with gravel and superficial calcareous soils characterised by a water deficit higher than the mean (Figure S2 and Figure S3).

Cluster 2 contains sites characterised by slow ripening, late plateau time and high final sugar concentration (Figure 5A1). Regarding the other variables (Figure 5A2), $\delta^{13}C$ was below the mean (less water deficit) and a high inter-site variation was observed within the cluster. Cluster 2 aggregated soils with similar texture and depth: deep calcareous or non-calcareous silty clay soils (Figure 5A2).

Cluster 3 was characterised by low final sugar concentration, and average plateau time and ripening rate. Tm Ver_95% Sug was lower than the inter-site average, as was YAN (except for one site per variable). Greater geographical dispersion and soil diversity was observed in this cluster, although a subcluster of waterlogged soils with heavy berries and no water deficit was also differentiated within the cluster (Figure 5A2). This cluster also contains the plots located at the bottom of the valleys (Figure S2).

When the heatmaps are considered by year, two groups of vintages emerge (Figure 5B1): one with slow ripening (2012, 2014, 2018 and 2019) and high sugar concentration at 95 % of the plateau (2012, 2018 and 2019), and the other with fast ripening (2013, 2015 and 2016) but low sugar concentration at 95 % of the plateau (2013 and 2016) and small berries (Figure 5B2).

DISCUSSION

1. Analysis of drivers of grape sugar accumulation kinetics

The originality of this study lies in the use of a grape sugar accumulation model to quantify specific parameters (Suter *et al.*, 2021), in order to analyse the sugar accumulation dynamics of Merlot within an area characterised by high local temperature and phenological variability (de Rességuier *et al.*, 2020). The study confirmed the strong impact of mean temperature during ripening on the timing of the plateau of sugar accumulation, which is consistent with many published phenology models based on mean temperature only (Duchêne *et al.*, 2010; Parker *et al.*, 2011; Costa *et al.*, 2019). A predominant negative influence of the ripening speed on the sugar concentration at 95 % of plateau was shown (*i.e.*, the shorter the duration of the ripening, the lower the final sugar concentration). Moreover, the influence of berry weight was negative and the effect of temperature was positive, albeit limited. Temperature summation from mid-veraison to 95 % sugar accumulation was also considered as a potential driver of ripening speed, but turned out to be auto-correlated with the duration of ripening (data not shown), meaning that quick ripening (short duration) resulted in lower temperature summations. Hence, it was left out of the statistical analysis. The analysis of the factors impacting the duration of ripening highlighted the positive role of temperature during the sugar accumulation period (the higher the temperature, the shorter the duration). However, the percentage of variance explained by the fixed effects on the duration of the ripening period (Dur 95% Sug-Ver) was only 29.9 %, compared to 72.0 % of variance with random effects, with higher residual variance accounted for by "year"; therefore, other factors involved in the year effect that were not considered in this study may play an important role. According to Greer & Weedon (2014), the maximum ripening rates of Merlot increased exponentially in response to temperature (up to a maximum of 40 °C considered in their study), while Chardonnay and Semillon showed maximum ripening rates at 25 °C and 35 °C, respectively. In addition to the cultivar effect, also shown by Sadras *et al.* (2008), the evaporative demand can also affect the rate of sugar accumulation (Rebucci *et al.*, 1997; Sadras & Petrie, 2011). Suter *et al.* (2021) found that Merlot sugar concentration at 95 % of the plateau was significantly impacted by rainfall between flowering and veraison (used as a metric for characterising pre-veraison vine water status), average photosynthetic active radiation between flowering and veraison, and vine water status measured by $\delta^{13}C$ on a sample collected prior to harvest.

From a physiological point of view, it would be of interest to understand why sugar accumulation (expressed as a concentration) stops earlier when ripening is fast. This is a relevant question, because sugar concentration in berries is an increasingly important issue in the context of climate change, as it leads to higher alcohol wines and disrupts wine balance (Mira de Orduña, 2010; van Leeuwen & Darriet, 2016). Understanding these mechanisms could help guide potential adaptations to climate change and identify levers to limit the final concentration of sugars. When the different drivers of sugar accumulation are shown in a heat map (Figure 5A), the plots in Cluster 1 can be seen to be characterized by a short Dur 95% Sug-Ver, high Tm Ver_95% Sug and high-water deficit as assessed by $\delta^{13}C$ (note that soils in this cluster have low soil water-holding capacity, because they are either coarse textured or shallow). It can be hypothised that early veraison and short Dur 95% Sug-Ver in this cluster are explained by high Tm Ver_95% Sug, but that Plateau 95% Sug is limited by a restriction in photosynthesis induced by water deficit at the end of the ripening period. This hypothesis cannot be verified by a statistical analysis of our data, because $\delta^{13}C$ represents water deficit in the four weeks around veraison and does not specifically assess water deficit at the end of the ripening period. Stanfield *et al.* (2024) also showed that phloem area in the pedicel was related more to sugar accumulation rate in grape berries than to water deficit. We did not have the anatomical data in our experiment to verify this assumption, but it is a possible avenue for future investigations.

The important role of temperature in pre-plateau sugar accumulation as confirmed in this study was also demonstrated in a study conducted on potted vines, with total soluble solids being significantly increased at 30 °C compared to 22 °C (Moukarzel *et al.*, 2023). Conversely, our results contradict those of Sadras & Petrie (2012), who did not find thermal rates to be superior to chronological rates when predicting ripening, except in one region. However, it should be noted that their study was conducted on a different cultivar at a different scale in different environmental conditions, and which was managed using different viticultural techniques.

A simple model, based only on mean daily temperature summation and calibrated by cultivar, was developed to predict sugar concentration in grapes . However, this model showed lower accuracy than similar temperature-based phenological models for predicting flowering and veraison (Parker *et al.*, 2013), suggesting that factors other than temperature alone are involved in sugar accumulation. Given the influence of berry weight on the concentration at the plateau shown in the present study, taking into account berry weight in models could improve predictions of the timing of specific sugar concentrations in grape berries. However, it is worth noting that this approach may be less applicable/

practical for growers, as they do not systematically measure this parameter.

It should be noted that this study was based on the field sampling of grape berries. In such conditions, berry ripening is asynchronous; *i.e.*, the samples contain berries with different levels of maturity. Other studies have considered berry ripening at the individual berry level (Rienth *et al.*, 2016; Torregrosa *et al.*, 2017; Shahood *et al.*, 2020). While this individual berry approach helps increase knowledge of the physiological mechanisms of berry ripening, including the effects of gene expression, it is not easily transferable to a production setting. However, the two levels of approach are complementary, with studies at the berry level contributing to the understanding of physiological mechanisms, and those at plot level to operational applications.

2. Influence of vine water status on berry weight and the timing of the sugar accumulation at plateau

Surprisingly, the effect of vine water status on the precocity of the plateau (Plateau 95% Sug) and on berry weight was small, albeit significant. When grown in water deficit conditions, berries tended to have lower berry weight, but compared to the effects of year and site, this effect was small. While the $\delta^{13}C$ method assesses post-veraison water deficits, it has been shown that pre-veraison water deficits have a prevalent effect on berry weight (Ojeda *et al.*, 2001). Hence, the relationship between vine water status and berry weight could have been stronger if an indicator of pre-veraison water status had been used. This analysis did not allow us to identify the variables involved in the effect of year on berry weight. The weather conditions around flowering may have had an impact, as it has been shown that berry seed number positively influences berry mass (Walker *et al.*, 2005; Triolo *et al.*, 2018), and that the lower the number of seeds per berry, the earlier the onset of ripening (Staudt *et al.*, 1986; Keller, 2015). For example, 2013 and 2019 were characterised by rather low berry weight, although these years were not characterised by high water deficits (Figure 3). The sub-optimal weather conditions during flowering in 2013 and heavy rainfall at the end of the flowering period in 2019 may have affected pollination, leading to decreased seed number.

3. No effect of nitrogen status

Vine nitrogen status was not an explanatory variable in any of the models developed to analyse sugar accumulation dynamics and berry weight in this study. Vine nitrogen status was assessed by yeast available nitrogen, which is measured only at the end of the ripening period. In order to investigate whether differences in vine nitrogen status earlier in the season have an influence on berry ripening dynamics, another indicator was also tested: the so-called “N-tester”. This device measures leaf blade colour intensity at veraison, which is the result of pre-veraison nitrogen absorption and re-distribution throughout the vegetative parts (van Leeuwen *et al.*, 2000). Similar to YAN, no significant effect of N-tester readings was found on sugar accumulation and berry weight parameters (data not shown).

4. Factors not considered in this study

As this study was conducted in field conditions, it was not possible to control all the factors possibly influencing sugar accumulation, like plant material and management practices. Rootstock and clone effects were not explored in this study, since these data were not available for all of the plots. However, these effects have been highlighted in previous studies (van Leeuwen *et al.*, 2013; Theocharis *et al.*, 2024) and comprise the site effect, because plant material and practices were constant over the whole study period.

Another important factor in sugar accumulation in grape berries is the leaf-to-fruit ratio. The ratio required to fully mature grape ranges from 0.8 to 1.2 m^2 of leaves/kg of fruit in single-canopy trellis systems (Kliewer & Dokoozlian, 2005). In this study, yields were not consistently measured. However, for 55 % of the sites, the yield was provided by wineries, allowing us to calculate the leaf area to fruit weight ratio. All the computed leaf-to-fruit-weight ratios were above 1.1 m^2 of leaf area per kg of fruit, meaning that the source sink balance was unlikely to have influenced the kinetics of sugar accumulation or berry weight in this study.

With planting dates ranging from 1948 to 2004 (Table S1), the age of the vineyard can lead to differences in reserve levels and sugar transport from the woody tissues to the clusters. Planting dates were not taken into account in this study, because these were not available for all sites (Table S1). Moreover, in the older vineyards the missing vines had been replaced over time, thus parcel vine age was not homogeneous. Rigorous experimental set-ups in which the exact age of vines are recorded would be necessary in order to specifically study the effect of vine age on physiology and grape ripening (Bou Nader *et al.*, 2019).

Lastly, in this study, no tests were carried out to detect the presence of grapevine viruses in the experimental plots; viruses can affect berry composition and berry weight (Martínez-Lüscher *et al.*, 2016).

5. Spatial analysis of maturity clusters identified by heatmaps per plot and year

Heatmaps were used to group the plots according to the maturity parameters studied in order to cluster terroirs with similar ripening behaviour at the local scale of this wine-growing area. Three clusters were identified as having different maturity dynamics (high Plateau 95% Sug and long Dur 95% Sug-Ver; moderate Plateau 95% Sug and short Dur 95% Sug-Ver; low Plateau 95% Sug and moderate Dur 95% Sug-Ver), which were mapped and linked to terroir parameters and berry weight. The heatmap generated by year provided little information in this study, probably because the number of years considered was limited (7 years). However, the approach could be useful for grouping vintages with similar ripening dynamics and for visualising the terroir characteristics associated with each vintage when longer time series are available.

Heatmaps have already been used in terroir studies, particularly in Argentina, for the hierarchical clustering of geographical indications of the phenolic composition of wines (Urvieta *et al.*, 2021). This clustering method (preceded by the modelling of maturity dynamics) is a useful tool that could be applied in large areas of contrasting terroirs by cooperative wineries or producers, who process grapes from many blocks and contrasting environmental conditions, in order to characterise ripening kinetics and group parcels with similar behaviour. Grouping parcels in this way could help optimise sampling strategies, fix harvest dates and possibly create “cuvées” with specific sensory attributes. Another application could be to quickly identify plots with atypical parameters; for example, the very high YAN concentration in Parcel 81 of Cluster 3, or the very high berry weight in Parcel 84, is relevant information that could be used by winegrowers to adjust their vineyard management practices (Figure 5A2).

6. Adaptations to climate change

The results of this study provide an understanding of the factors that affect the dynamics of sugar accumulation in grape berries, which can help wine growers to adapt to climate change. Wine growers increasingly face the challenge of high sugar concentrations in grapes at harvest, leading to undesirable high alcohol by volume concentration in wines. Delaying the onset of the ripening phase till a cooler period of ripening through choice of plant material or management practices, or implementing practices to increase berry weight, could reduce final sugar concentrations in grapes. However, some caveats need to be considered, particularly for red wines, as larger berries are associated with a lower skin-to-pulp ratio, which can reduce anthocyanin and polyphenol content (Triolo *et al.*, 2019). Knowing that higher temperature leads to a reduction in polyphenol and anthocyanin synthesis and accumulation (Gouot *et al.*, 2019), the interplay between these important factors for berry sugars needs to be evaluated across secondary metabolites in the future in order to understand the effects on grape quality potential in wine making.

This study also identified geographical terroir zones with different behaviours in terms of grape ripening dynamics, which could enable differentiated adaptation practices. For example, Cluster 1, located in the western part of the area (Figure S2), was characterised by gravel soils with limited water supply. Implementing practices to conserve soil water reserves, such as increasing organic matter and limiting soil evapotranspiration by mulching, or using drought resistant rootstocks could result in heavier berries resulting in lower final sugar concentrations (Santos *et al.*, 2020; Mirás-Avalos & Araujo, 2021).

Adaptation to climate change also affects other metabolites in grapes, such as organic acids and phenolic and aromatic compounds (Mira de Orduña, 2010; van Leeuwen *et al.*, 2022), which were not considered in this study, but need to be taken into account for a more precise assessment of the adaptation strategies.

A recently developed model for characterising grape ripening dynamics based on the sugar-to-total acidity ratio could also be applied to characterise grape ripening dynamics (van Leeuwen *et al.*, 2023b). This model, coupled with clustering as used in this study, would enable the analysis of spatial terroir variability, simultaneously taking into account sugar accumulation and total acidity.

CONCLUSION

This study investigated the drivers of grape berry sugar accumulation in Merlot under field conditions in a wine-growing area. The effect of ripening rate, berry weight and mean temperature during the ripening period on final sugar concentration was demonstrated. Furthermore, ripening dynamics were clustered and spatialised at a local scale and related to terroir parameters. These findings provide a better understanding of the factors involved in the dynamics of sugar accumulation and can be used as guidelines for adaptation to climate change; for example, it could be beneficial to promote practices that increase berry weight (being careful not to impact secondary metabolites) or delay the onset of ripening to shift the sugar accumulation period to a part of the season when temperatures are cooler. Further research into the mechanism of sugar unloading in grape berries in field conditions is necessary in order to unravel the complex mechanisms leading to the concentration and timing of maximum sugar accumulation, and potentially confirm the hypothesis of water deficit having an effect.

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