frontiers in Plant Science

ORIGINAL RESEARCH
published: 05 February 2021
doi: 10.3389/fpls.2021.624867

Adapting Wine Grape Ripening to Global Change Requires a Multi-Trait Approach

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In winegrowing regions around the world increasing temperature associated with climate change is responsible for earlier harvests and is implicated in undesirably high sugar concentrations at harvest. Determining the suitability of grapevine varieties in existing or new winegrowing areas has often been based on temperature, without considering other factors. The purpose of this study was to quantify key berry sugar accumulation traits and characterize their plasticity in response to several climate variables. Data was collected from 36 different cultivars over 7 years (2012–2018) from an experimental vineyard in Bordeaux, France. Sugar amounts were obtained through weekly berry sampling starting at mid-veraison and continuing until after technological maturity. The variation in sugar accumulation traits for all cultivars, when considered together, were well explained by cultivar, year, and their interaction, highlighting the relative roles of genetic variation and phenotypic plasticity. Sugar accumulation traits were affected by antecedent and concurrent climate factors such as photosynthetically active radiation, temperature, and vine water status, whether before, or after mid-veraison. In addition, other traits such as berry weight at mid-veraison and date of mid-veraison had an important influence on sugar accumulation traits. More notably, the relative importance of these factors varied significantly by cultivar. The specific physiological mechanisms driving the plasticity of these traits remain to be identified. Adaptation to climate change cannot be based on temperature alone and crop responses cannot be generalized across genotypes, even within species.

Keywords: grapevine cultivars, berry sugar accumulation traits, phenotypic plasticity, climate change, genotype-environment interaction, modeling

OPEN ACCESS

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Specialty section:
This article was submitted to Crop and Product Physiology, a section of the journal Frontiers in Plant Science

Received: *11 November 2020*
Accepted: *07 January 2021*
Published: *05 February 2021*

Citation:
Suter B, Destrac Irvine A, Gowdy M, Dai Z and van Leeuwen C (2021) Adapting Wine Grape Ripening to Global Change Requires a Multi-Trait Approach. Front. Plant Sci. 12:624867. doi: 10.3389/fpls.2021.624867

INTRODUCTION

Wine grape (*Vitis vinifera* L.) vineyards covered more than 7.4 million hectares worldwide (OIV, 2018). As of 2015, the estimated net worth of the wine industry was more than 258 billion euros (Lecat et al., 2019). Winegrowers have classically selected different cultivars of wine grapes for the phenotypic traits that best match their (micro-)climates (Wolkovich et al., 2018) and soils. They

maintain those cultivars that produce consistent yields and reach appropriate balance of sugar, acid, and other compounds under local climatic conditions (van Leeuwen and Seguin, 2006).

A major concern is that crop yields and quality may be significantly affected by climate change (Fraga et al., 2012). It is expected that temperatures will increase and drought will intensify in many regions across the globe (Intergovernmental Panel on Climate Change [IPCC], 2014). Climatic conditions during grape ripening have already been affected, resulting in altered grape composition at harvest (Fraga et al., 2012). Grapes are being harvested at increasingly higher sugar levels, resulting in wines with increased alcohol levels (Duchène and Schneider, 2005; Godden et al., 2015).

Sugar is one of the most important metabolites in grape berries used for wine production. Not only is the sugar concentration a major driver of the alcohol level of the finished wine, its levels during berry ripening are also involved in regulating development of the phenolic compounds that give color, flavor, and tannin structure to the wine (Conde et al., 2007). Duration of sugar loading may also be of interest to growers concerned with achieving adequate phenolic maturity of the grapes (Deloire et al., 2005).

Moving viticultural production to areas with more suitable climates may lead to conflicts in land use and freshwater ecosystems (Hannah et al., 2013). In addition, the land previously cultivated with grapevines may be unsuitable for other types of agriculture. A more sustainable adaptation, which can readily be implemented by winegrowers, would be to change to cultivars that are better suited to their objectives as the climate warms. To assess their adaptability, however, it is necessary to identify key ripening traits and their plasticity under different environmental conditions for a wide range of those cultivars.

Sugar accumulation during ripening is the net sum of sugar loading into, and sugar metabolism within the berry, with changes in the berry water balance affecting concentration. This ripening process starts at veraison, concurrent with berry softening and color change and can be subsequently affected by environmental conditions and vineyard management practices (Dai et al., 2009). The timing of veraison is a trait that can indirectly affect sugar accumulation. It drives the start of ripening and may be a factor in determining both the length of time available for ripening and the climatic conditions that the vine and berries will experience during ripening. The veraison date is influenced by both cultivar genetics and environmental conditions prior to veraison, and can be considered as a proxy for those conditions (Parker et al., 2011). For growers, both the earliness of the cultivar and its sugar accumulation traits are important considerations in assessing whether a given cultivar is adapted to their local climatic conditions.

The trajectory of sugar accumulation in grape berries follows a sigmoidal pattern with slow accumulation at the onset of veraison, rapid accumulation just after veraison and several weeks later reaching a plateau phase (Coombe and McCarthy, 2000). At the end of the ripening period, sugar content per berry no longer increases, but sugar concentration may continue to increase due to berry dehydration (Keller et al., 2016) or decrease due to dilution. Several researchers have already captured the dynamics of sugar accumulation through modeling approaches that estimate the rate of sugar accumulation, the amount of sugar at maturity and the timing of the plateau phase (Parker et al., 2020). This information is available, however, for only a few grape cultivars. Also, direct comparison of results from different studies may be difficult due to differences in experimental conditions, such as soils and climate.

Sugar accumulation traits have been found to be influenced by climatic variables, such as average temperature, photosynthetically active radiation (PAR), and water availability, with the effect depending on whether it was experienced during berry development pre-veraison, or post-veraison (Jones and Davis, 2000). Temperature was found to have an important effect on the rate and the total content of sugar accumulated (Greer and Weedon, 2014), but a relatively small effect on final sugar concentrations (Coombe, 1987) and corresponding rates of concentration increase (Sadras and Petrie, 2011). High levels of insolation together with temperatures greater than 30°C during the sugar accumulation period were found to promote berry growth (Jones and Davis, 2000), while limited sunlight during veraison delayed grape ripening (Keller et al., 1998). Results from Bergqvist et al. (2001) suggested that the effects of light on fruit composition are heavily dependent upon the extent to which berry temperature is elevated as a result of increased PAR.

Vine water status can also have an important effect on sugar accumulation rates due to its effect on photosynthesis (Zufferey et al., 2000), shoot growth (Pellegrino et al., 2005), berry weight (Ojeda et al., 2001), berry water budget (Greenspan et al., 1994), and carbohydrate partitioning (Dry and Loveys, 1998). Water deficits can also increase berry sugar concentrations when moderate, but decrease berry sugar concentrations when severe (Peyrot des Gachons et al., 2005; van Leeuwen et al., 2009). Individual cultivars manage their water status differently in response to changes in climatic conditions (Schultz, 2003; Domec and Johnson, 2012). The effects of these and other climatic variables on sugar accumulation traits have been studied, but not extensively quantified for a wide variety of grape genotypes under comparable conditions.

Sugar accumulation traits can also be affected indirectly by other factors, such as phenology and berry weight, and their responses to changes in climate. There is significant genotypic variation in the phenology of different cultivars and in their phenotypic plasticity in response to antecedent temperatures conditions (Parker et al., 2011, 2013). In turn, within a given year, such differences in phenology will have an important effect on the climate conditions (temperature, PAR, soil water deficits) experienced by each cultivar during different stages of its development (van Leeuwen and Darriet, 2016).

It is difficult with this type of research to find data from multiple cultivars grown in the same climate in a sound experimental layout, such as with a randomized block design. The cultivar repositories that exist to date often have not been planted with replicates, making it impossible to study genotype × environment interactions (Destrac Irvine and van Leeuwen, 2016). And generally, such genotypic and phenotypic data is available for only a limited set of widely grown varieties (Wolkovich et al., 2018). The VitAdapt experimental vineyard

is unique in that it allows for collection of data with replicates, allowing for statistically robust analysis across a wide range of varieties (Destrac Irvine and van Leeuwen, 2016).

The purpose of this study is to describe key sugar accumulation traits and characterize their plasticity in response to seasonal variation in climatic and other variables for 36 different grapevine cultivars using data collected over 7 years (2012–2018) from an experimental vineyard in Bordeaux France. More specifically, the four objectives of this study are to: (i) fit a sigmoidal model to collected data and quantify key sugar accumulation traits; (ii) characterize and classify the 36 cultivars based on these sugar accumulation traits; (iii) determine the relative effect of genetic versus various environmental controls on these sugar accumulation traits; and (iv) evaluate how much of the variability in the plasticity of these sugar accumulation traits are affected by different independent variables.

MATERIALS AND METHODS

Experimental Setting

Data for this study was collected in the VitAdapt experimental vineyard at Domaine de la Grande Ferrade of the INRAE (Institut national de recherche pour l'agriculture, l'alimentation et l'environnement) research center in Bordeaux, France (44°47′23.8″N, 0°34′39.3″W) (Destrac Irvine and van Leeuwen, 2016). The VitAdapt vineyard was planted with 48 *V. Vinifera* (L.) and four hybrid cultivars in 2009, with the purpose of studying the response of these varieties to climate change in Bordeaux. The cultivars have been phenotyped each year starting in 2012 for many traits, including phenology (mid-budbreak, mid-flowering, and mid-veraison), grape composition during ripening, carbon isotope discrimination in berry juice sugars, and others. The cultivar names, origins, clones, and years of plantation are listed in **Supplementary Table 1**. The vineyard is located on a relatively homogeneous gravel soil in the Pessac-Léognan appellation. Soil physical and chemical properties are presented in **Supplementary Table 2**.

The 0.6 ha vineyard has 46 rows with five buffer vines at each end of each row that are not included in the study. The vineyard was laid out using a randomized block design with four blocks for each cultivar and each block consisting of two parallel rows of five grapevines each. All grapevine clones were grafted on Sélection Oppenheim 4 (SO4) rootstock. Irrigation was necessary at plantation in 2009 and in July of the same year. Once the rooting system was established, however, the vines have been dry-farmed. The vines are Guyot pruned and trained with a vertical shoot positioned trellis. The vines were estimated to have 2.0–2.4 m^2 of canopy leaf area per meter of row. The vineyard was managed according to good agricultural practices.

Phenology Observations

Phenological stages of all cultivars were tracked following the Biologische Bundesanstalt, Bundessortenamt und CHemische Industrie (BBCH) scale for monocots and dicots as described by Hack et al. (1992). Dates of mid-flowering (BBCH 65) mid-veraison (BBCH 85) were recorded for each cultivar through field observations. These are denoted as:

t_{flo} = time (DOY) of mid-flowering.
t_{ver} = time (DOY) of mid-veraison.

During each phenological stage, observations were carried out on Mondays, Wednesdays, and Fridays for each cultivar and replicated until the mid-point of that stage was identified. For missing data (7.7% of total), replacement values were obtained by averaging values from the other blocks for the same cultivar in the same year.

Climate and Water Stress Indicators

Climatic data were recorded by a weather station situated approximately 100 m from the experimental vineyard. The station is part of the CIMEL automated DEMETER network, and the data is obtained from the INRAE (Institut national de recherche pour l'agriculture, l'alimentation et l'environnement) Climatik meteorological database for the Villenave d'Ornon (la Grande-Ferrade) location.

To account for the differences in phenology between the cultivars, the observed dates of mid-flowering and mid-veraison are used for each replicate (cultivar × year × block) to calculate the various climate statistics used in this analysis. The following climate variables were used as input to the analysis of variance (ANOVA):

T_{f-v} = average air temperature (°C) between mid-flowering (t_{flo}) and mid-veraison (t_{ver}).
T_{v-95} = average air temperature (°C) between t_{ver} and time (DOY) of 95% maximum sugar content/concentration (t_{95}).
PAR_{f-v} = average photosynthetic active radiation (J cm^{-2}) between t_{flo} and t_{ver}.
PAR_{v-95} = average photosynthetic active radiation (J cm^{-2}) between t_{ver} and t_{95}.
RR_{f-v} = total rainfall (mm) between t_{flo} and t_{ver}.

In the absence of any direct measurements of soil water deficit or vine water status prior to mid-veraison, total rainfall between mid-flowering and mid-veraison is considered a good surrogate. After veraison, carbon isotope discrimination in berry juice sugar is well correlated to plant water status during the period of sugar accumulation (Gaudillère et al., 2002). Although intrinsically $\delta^{13}C$ is a measure of water use efficiency (WUE), is also a very good proxy for vine water status (van Leeuwen et al., 2009; Santesteban et al., 2015) $\delta^{13}C$ measurements were performed each year prior to harvest for every cultivar and every block. For missing $\delta^{13}C$ data (about 3%), to allow balanced statistical analysis, replacement values were obtained by averaging values from the other blocks for the same cultivar in the same year.

Berry Components

The berry sugar concentration and content per berry and their respective rates of accumulation over the course of the season are the key traits being evaluated in this study across the different cultivars. The size of berries (as measured by weight)

are also important factors influencing this development. Berries were analyzed during the 2012–2018 seasons starting at or a few days after mid-veraison. Approximately five healthy and representative berries per vine were harvested, adding to a total of 50 berries per plot. Berries were selected from different positions on the bunch. Berries were picked by hand and collected in bags containing a vertical filter (BagFilter® 400 ml, Interscience, Saint-Nom-la-Bretèche, France). Each plot was sampled weekly in the morning between 08:00 and 10:30 a.m. Berries were counted and weighted collectively.

The juice of the berries was extracted using a crusher (BagMixer® 400 W, Interscience, Saint-Nom-la-Bretèche, France) and collected in 50 ml tubes. The tubes were centrifuged at 20,089 × *g* for 10 min (Sigma 6K15, SIGMA Laborzentrifugen GmbH, Osterode am Harz, Germany). The juice was then analyzed by using a WineScan™ Auto based on Fourier Transform Infrared Spectroscopy (FTIR; FOSS Analytical, Hillerød, Denmark) (Destrac Irvine et al., 2015). Values of reducing sugars produced by the WineScan™ Auto were validated with a digital refractometer and were found to be similar ($P < 0.05$). Sugar content was calculated from berry weight and sugar concentration.

Statistical Analysis

Sugar Accumulation Curve Fitting

Values for reducing sugar were fitted with a non-linear model. Both sugar content and concentration in berries versus time follow a sigmoid curve and were well fitted by a 3-parameter logistic function (Eq. 1; Triboï et al., 2003) as given by:

$$S(t) = \frac{S_{max}}{1 + 0.05 \cdot e^{\left(-4 \cdot r \cdot \left(\frac{t - t_{95}}{S_{max}}\right)\right)}} \quad (1)$$

where, S_{max} = the estimated maximum content or concentration of reduced sugars, t = day of year (DOY), t_{95} = DOY when 95% of maximum was accumulated, and r represents the estimated maximum rate of accumulation defined as the derivative at the point of inflection. With this model the amount of sugar (as either content, or concentration) at mid-veraison (S_{ver}) and at 95% sugar accumulation (S_{95}) can be iteratively calculated. Each block for a cultivar was modeled separately in order that ANOVA could be performed. The modeling was implemented with the data expressed both in concentration (g L^{-1}) and content (mg $berry^{-1}$). The following traits were extracted from the model:

$t_{95-conc}$ = day of year (DOY) when sugar concentration reached 95% of maximum.
$t_{95-cont}$ = day of year (DOY) when sugar content reached 95% of maximum.
$S_{ver-conc}$ = sugar concentration (g L^{-1}) at t_{ver}.
$S_{ver-cont}$ = sugar content (mg $berry^{-1}$) at t_{ver}.
$S_{95-conc}$ = sugar concentration (g L^{-1}) at $t_{95-conc}$.
$S_{95-cont}$ = sugar content (mg $berry^{-1}$) at $t_{95-cont}$.
r_{conc} = maximum rate of sugar accumulation concentration (g L^{-1} day^{-1}).
r_{cont} = maximum rate of sugar accumulation as content (mg $berry^{-1}$ day^{-1}).
Dur_{conc} = number of days between t_{ver} and $t_{95-conc}$.
Dur_{cont} = number of days between t_{ver} and $t_{95-cont}$.
BW_v = berry weight (g) at t_{ver}.

Data were statistically analyzed using the open source software R (R Core Team, 2017) within the integrated development environment RStudio. The nonlinear model was fitted using the R function *nls*. The performance of the model for each cultivar was evaluated by calculating the coefficient of determination (r^2) and the root-mean-square error (RMSE). Assumptions of normality and equal variance were respectively checked by quantile plots and plotting standardized model residuals against fitted values, respectively. The standardized residual plots of the models were found to be homoscedastic. Graphs and tables were produced with RStudio and Microsoft Office Excel 2010.

Hierarchical Cluster Analysis

A clustering was performed to find structures within the gene pool (represented by the cultivars) based on key sugar accumulation traits. The clustering in **Figure 4** was made using the Euclidean distance measure. The six identified clusters closely resembled that of k-means clustering through minimization of within-cluster sum of squares. The clustering was based on t_{ver}, $S_{95-conc}$, and Dur_{cont}, which are key traits from both winemaking and physiological perspectives.

Correlation, ANOVA, and Multiple Regression Analysis

Correlation and ANOVA

Bravais-Pearson correlation coefficients (r) were calculated between traits of all cultivars together. ANOVA was used to determine the effect of year, cultivar, and their interaction on the modeled sugar accumulation traits. The sum-of-squares was used to determine their contribution to the explained variance in the traits. Type III ANOVA was used to quantify more specific genetic and environmental controls on the traits. Second-order interactions, albeit sometimes significant, were excluded from the analysis since they accounted for no more than 2.8% (no more than 16.1% together) of the total variance for each sugar accumulation trait. Multicollinearity was tested through calculation of variance inflation factors (VIF), which all remained less than six and were deemed acceptable given the large dataset. The *relaimpo* package in R (Grömping, 2006) was used to determine the contribution of regressors in explaining the variance of the traits. Tukey's HSD test was used for *post hoc* pairwise comparisons across cultivar means for the traits (**Supplementary Table 3**).

Multiple linear regression analysis

Multiple linear regression analysis was performed for each cultivar between the dependent traits in Dur_{cont}, $S_{95\text{-}cont}$, and $S_{95\text{-}conc}$ against various independent genetic and environmental variables. The optimum set of variables in each model was determined through an "all-possible combinations" regression method. The model selected for each individual cultivar had the highest possible adjusted r^2, while model

coefficients were significant ($P < 0.05$) and showed low multicollinearity (VIF < 2).

RESULTS

Climatic Conditions Experienced by Grape Cultivars

Bordeaux is classified as Cfb (warm temperate, fully humid, warm summers) according to the Köppen and Geiger climate classification (Beck et al., 2018). Cool and wet winters and springs, followed by warm and dry summers are responsible for some of the best wine vintages in Bordeaux (Baciocco, 2014). The average daily air temperature and PAR from DOY 130 to 290 for years 2012 to 2018 are plotted in **Figure 1**. PAR is closely related to temperature, but with slightly different trends over the progression of the different seasons. The peak in temperatures always occurs after the peak in PAR (**Figure 1**).

Since sugar accumulation in grape berries mainly occurs from veraison to maturity (Coombe and McCarthy, 2000), we further analyzed the climate variables for the periods prior and post to mid-veraison. The average temperature from mid-flowering to mid-veraison (T_{f-v}) was higher than that from mid-veraison to maturity in four out of the 7 years studied (**Table 1**). The average PAR from mid-flowering to mid-veraison (PAR_{f-v}) was higher in all 7 years compared to those from mid-veraison to maturity. In addition to temperature, the moderate to severe soil water deficits experienced in Bordeaux during berry ripening are also associated with high quality vintages (van Leeuwen et al., 2009). The total rainfall from flowering to veraison was higher than those from veraison to maturity in 6 out the 7 years.

There is considerable variability in the observed phenology across the 36 cultivars (Destrac Irvine and van Leeuwen, 2016). This phenological variability may affect the climatic conditions experienced by each cultivar within a given year. An ANOVA was conducted to assess the relative contributions of cultivar and year on the exact climatic conditions experienced by each cultivar over different development stages (**Table 2**). As expected, year explained a large amount of the variability (20.4–94.4%) in the climate conditions experienced by each cultivar. Interestingly, the T_{f-v}, T_{v-95}, and PAR_{v-95} were also

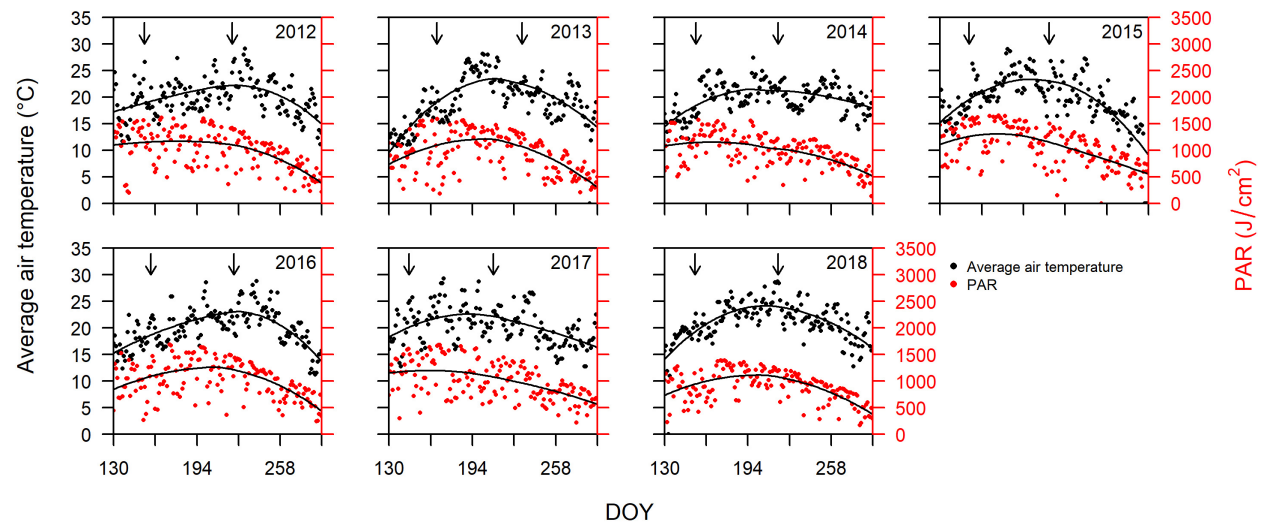


FIGURE 1 | Average daily air temperature (°C) on primary vertical axis, and photosynthetically active radiation (PAR; J cm^{-2}) on the secondary vertical axis, plotted versus day of year (DOY) between DOY 130 and 290 for years 2012 through 2018. Arrows indicate dates of mid-flowering and mid-veraison averaged over all cultivars for each year. The solid lines represent LOESS (locally estimated scatterplot smoothing) fitted to the data for temperature and PAR.

TABLE 1 | Average air temperatures, average PAR, and total rainfall over the flowering to veraison and the veraison to maturity periods (dates averaged across all cultivars) for 2012 to 2018.

	Average air temperature (°C)		Average PAR (J cm^{-2})		Total rainfall (mm)	
Year	Mid-flowering – veraison	Veraison – maturity	Flowering – veraison	Veraison – maturity	Flowering – veraison	Veraison – maturity
2012	20.3	22.0	1133.1	954.7	120	48
2013	22.0	19.4	1155.6	827.9	214	48
2014	21.4	20.7	1153.6	943.8	140	86
2015	22.5	21.3	1285.9	1013.3	46	111
2016	20.9	22.3	1192.2	1051.1	90	64
2017	22.1	21.2	1162.5	977.9	168	50
2018	22.9	23.1	1065.4	985.5	106	76

TABLE 2 | ANOVA analysis illustrating the effect of cultivar, year, and their interaction on pre- and post-veraison climatic variables, berry size, and $\delta^{13}C$.

		Contribution of variance components (%)						
Source	**Degrees of freedom**	**RR_{f-v}**	**PAR_{f-v}**	**T_{f-v}**	**PAR_{v-95}**	**T_{v-95}**	**BW_v**	**$\delta^{13}C$**
Cultivar	35	2.1	1.1	14.7	25.3	13.1	57.8	7.9
Year	6	87.4	94.4	85.2	35.1	54.0	20.4	63.5
Cultivar × year	210	8.7	4.5	0.1	20.3	15.1	9.1	6.1*
Residuals	756	1.8	0.0	0.0	19.3	17.8	12.7	22.4
Total variance explained		98.2	100.0	100.0	80.7	82.2	87.3	77.6

ns, not significant.

largely influenced (13.1–25.3%) by cultivar-specific phenology (**Table 2**). In addition, the BW_v and $\delta^{13}C$, two proxies of climatic conditions (see section "Materials and methods"), were also analyzed. The year effect was responsible for 63.5% of the variability in $\delta^{13}C$, while BW_V was mainly influenced by cultivar (57.8%). These results highlight the necessity to distinguish between antecedent and concurrent factors when analyzing the potential linkages between independent variables and sugar accumulation traits.

Modeling Sugar Accumulation

The sigmoidal model was applied as described in the section "Materials and Methods" to each single replicate (year × cultivar × block) providing a statistically strong fit. **Figure 2** presents the curve fits for four cultivars showing the sugar accumulation traits expressed both as concentration and content. The cultivars Touriga Franca and Saperavi consistently attain the lowest and highest berry sugar concentrations in this dataset, respectively. Whereas the cultivars Petit Verdot and Assyrtiko accumulate the lowest and highest berry sugar contents, respectively. The r^2 for each cultivar (averaged over blocks) was between 0.96–0.99 and 0.92–0.98 when expressed in concentration and content, respectively (**Supplementary Table 4**). RMSE for the curve fits for concentrations and content across all cultivars were between 3.30 and 5.56 g L^{-1} and between 9.73 and 29.49 mg $berry^{-1}$, respectively. The model performed well over a large range of cultivars with different sugar accumulation dynamics under different environmental conditions. **Figure 3** illustrates the variation in sugar accumulation curves for each cultivar (the same curves in mg $berry^{-1}$ can be found in **Supplementary Figure 1**).

Characterizing Cultivars by Accumulation Traits

Cluster Analysis

Figure 4 presents the clustering analysis of the 36 cultivars based on t_{ver}, $S_{95-conc}$, Dur_{cont}, showing the resulting six clusters, along with all the other sugar accumulation traits for reference (except for $S_{ver-conc}$ and $S_{ver-cont}$ which can be found in **Supplementary Table 3**). The timing of mid-veraison was selected for the clustering analysis as it can indirectly affect sugar accumulation. It drives the start of ripening and may be a factor in determining both the length of time available for ripening and the climatic conditions that the vine and berries will experience during ripening (**Table 2**). Sugar concentration at 95% of maximum was selected as it determines the potential alcohol content of the wine and is of great interest to winemakers. The duration of the sugar accumulation period is of interest to growers, together with t_{ver}, as it will determine in which part of the season the grapes will ripen. It may also be a concern with regard to achieving concurrent phenolic maturity of the grapes (Deloire et al., 2005). Expressed as content, this is the duration of active sugar loading to the berries and excludes the separate mechanism of sugar concentration caused by dehydration after loading has ceased. The main characteristics of the six clusters are described below.

Cluster I is characterized by cultivars that go through mid-veraison relatively early ($t_{ver} < 217.0$), ripen fast ($Dur_{cont} < 38.5$ days, with the exception of Sauvignon Blanc with 46.7 days) and show rather high concentrations of sugar at ripeness ($214.7 < S_{95-conc} < 241.6$ g L^{-1}).

Cluster II is a mix of cultivars that go through mid-veraison on average more than 5 days later than those in Cluster I. $S_{95-conc}$ are generally slightly lower and Dur_{cont} is notably lower for Touriga Nacional, Cot, and Merlot.

Cluster III cultivars go through mid-veraison later ($t_{ver} > 224.4$), but with short sugar accumulation periods ($Dur_{cont} < 38.0$ days). In this cluster, Petit Verdot is notably the latest grape cultivar to go through mid-veraison, but not the latest to reach a plateau in sugar concentration ($t_{95-conc}$) due to quick ripening.

Cluster IV cultivars have similar ripening dynamics to Cluster II. The major difference between Clusters II and IV is that the latter display only lower levels of sugar concentration and need more time to load sugars.

Cluster V represents cultivars that go through mid-veraison early ($t_{ver} < 218.2$) and end up with low concentrations of sugars ($S_{95-conc} < 204.2$ g L^{-1}) at ripeness. Touriga Franca is very typical for this behavior.

Cluster VI cultivars were not the latest to go through mid-veraison, but ripened the slowest and therefore have the longest ripening period ($Dur_{cont} > 50.7$ days).

In general, the coefficients of variation were slightly higher for the sugar accumulation traits expressed in content compared to those expressed in concentration. Although the coefficients of variation for Dur_{cont} and Dur_{conc} were higher than those for $S_{95-conc}$ and $S_{95-cont}$, both indicate the presence of some plasticity (**Figure 4**).

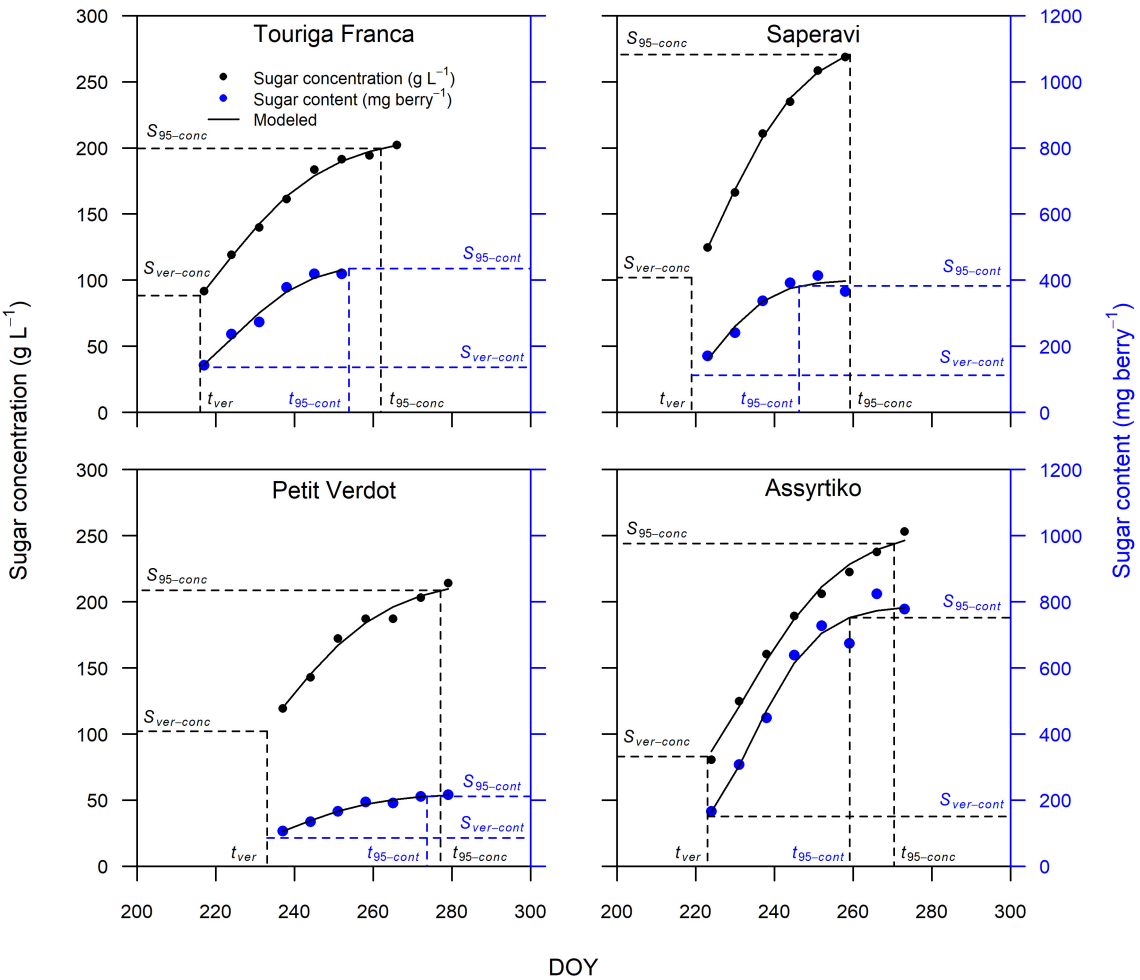


FIGURE 2 | Sugar accumulation data and fitted curves for Touriga Franca, Saperavi, Petit Verdot, and Assyrtiko expressed in both concentration (in black) and content (in blue) for 2016 (block 1). Vertical dashed lines identify t_{ver} and t_{95} concentration, or content. Horizontal dashed lines identify the corresponding sugar concentration (on primary vertical axis), or content (on secondary vertical axis).

Correlation Analysis

Correlations among the different sugar accumulation traits of the different cultivars were also evaluated to identify inter-relationships. **Table 3** presents the Bravais-Pearson correlation coefficients (r) between all sugar accumulation traits, time of mid-veraison, and berry weight at mid-veraison for all replicates (cultivar × year × block) considered together. Correlations shown in bold had $r > 0.71$, which corresponds to the $r^2 > 0.5$, meaning more than 50% of the variation in one variable explains the variation in the other variable.

In general, the rate of maximum increase in sugar concentration (r_{conc}) was negatively correlated to both the time of 95% maximum sugar concentration ($t_{95-conc}$) and the duration to that point starting at mid-veraison (Dur_{conc}), with the latter two also being positively correlated. Likewise, the maximum berry sugar loading rate (r_{cont}) was negatively correlated to both time of 95% maximum sugar content ($t_{95-cont}$) and the duration to that point starting at mid-veraison (Dur_{cont}), with the latter two also being positively correlated. Berry weight at mid-veraison (BW_v) is strongly and positively correlated to sugar content at 95% of maximum ($S_{95-cont}$).

Because all cultivars are considered together, the relationships between traits described in the above analysis are only general, with potentially much different, or possibly no such relationships existing for individual cultivars. Correlation analysis between these traits across years was also done separately for each cultivar (not shown) and found individual cultivars followed similar trends as the larger group, suggesting a consistency in these behaviors across individual cultivars, albeit with different slopes and intercepts.

Climate Versus Genetic Effects on Accumulation Traits

To understand the relative effect of cultivar genetics versus climate, **Table 4** presents an ANOVA showing the relative contribution of variance in sugar accumulation traits and t_{ver} associated with cultivar, year, cultivar × year interaction, and

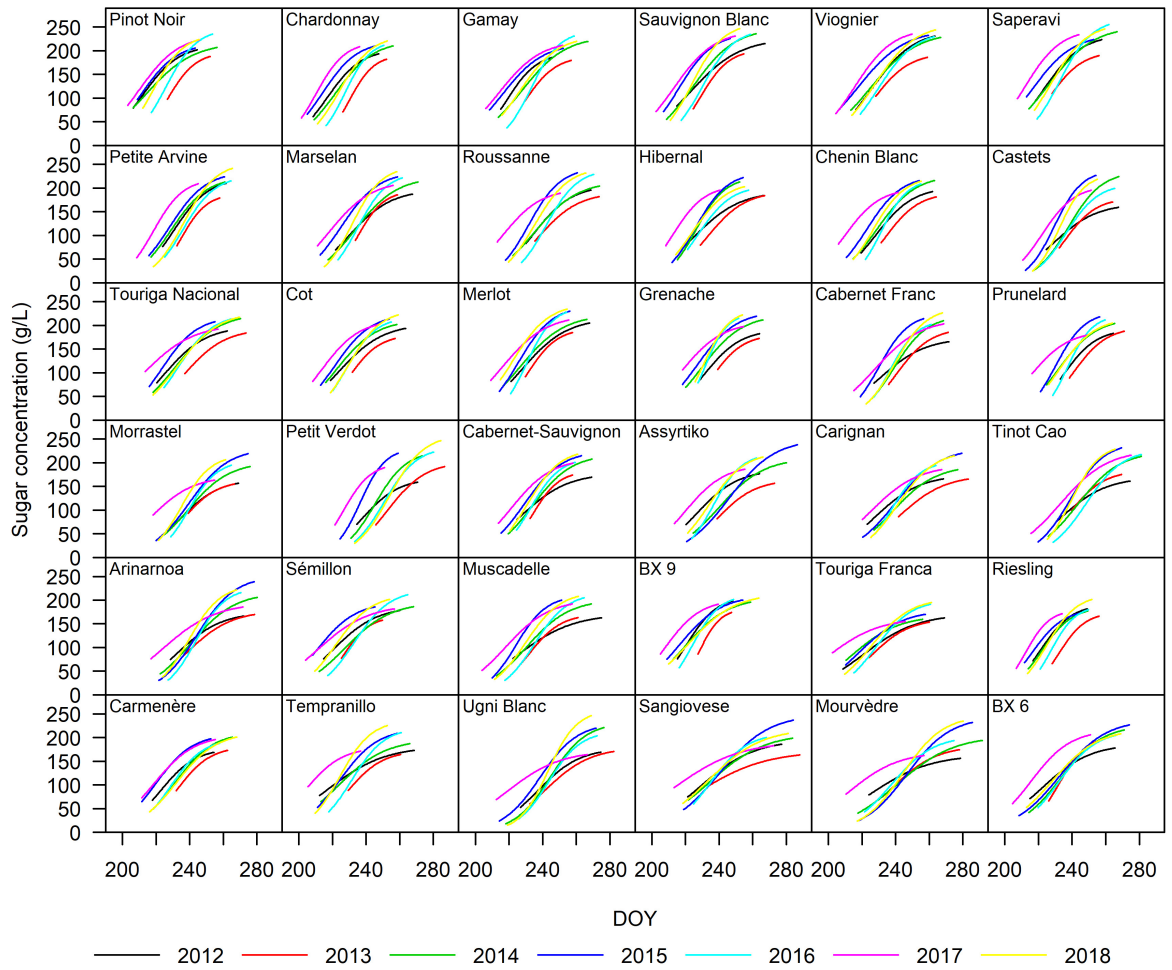


FIGURE 3 | Sugar accumulation dynamics of the 36 grape cultivars included in this study from 2012 to 2018. The curves represent a single year and were drawn from traits averaged over the four blocks.

residuals, together with the total variance explained. Year, cultivar, and their interaction were highly significant ($P < 0.001$) and explained much of the variance of most of the traits. For the key traits t_{ver} and $S_{95-conc}$, year explained around half of the variance, the latter showing a greater cultivar × year interaction effect. Dur_{cont} had relatively more variance explained by the cultivar and with larger cultivar × year interaction and residuals, although the overall variance explained by the model was less than the others at 59%. Much of the variation in $S_{95-cont}$ is explained by cultivar, this indicates that differences in berry weight are strongly genotype-dependent. The remaining traits generally had more variance explained by the cultivar, with the rest explained relatively evenly across the other factors. The relative contribution of the block effect to the total variance of the various traits was low at between 0.1 and 0.8%.

Plasticity of Accumulation Traits

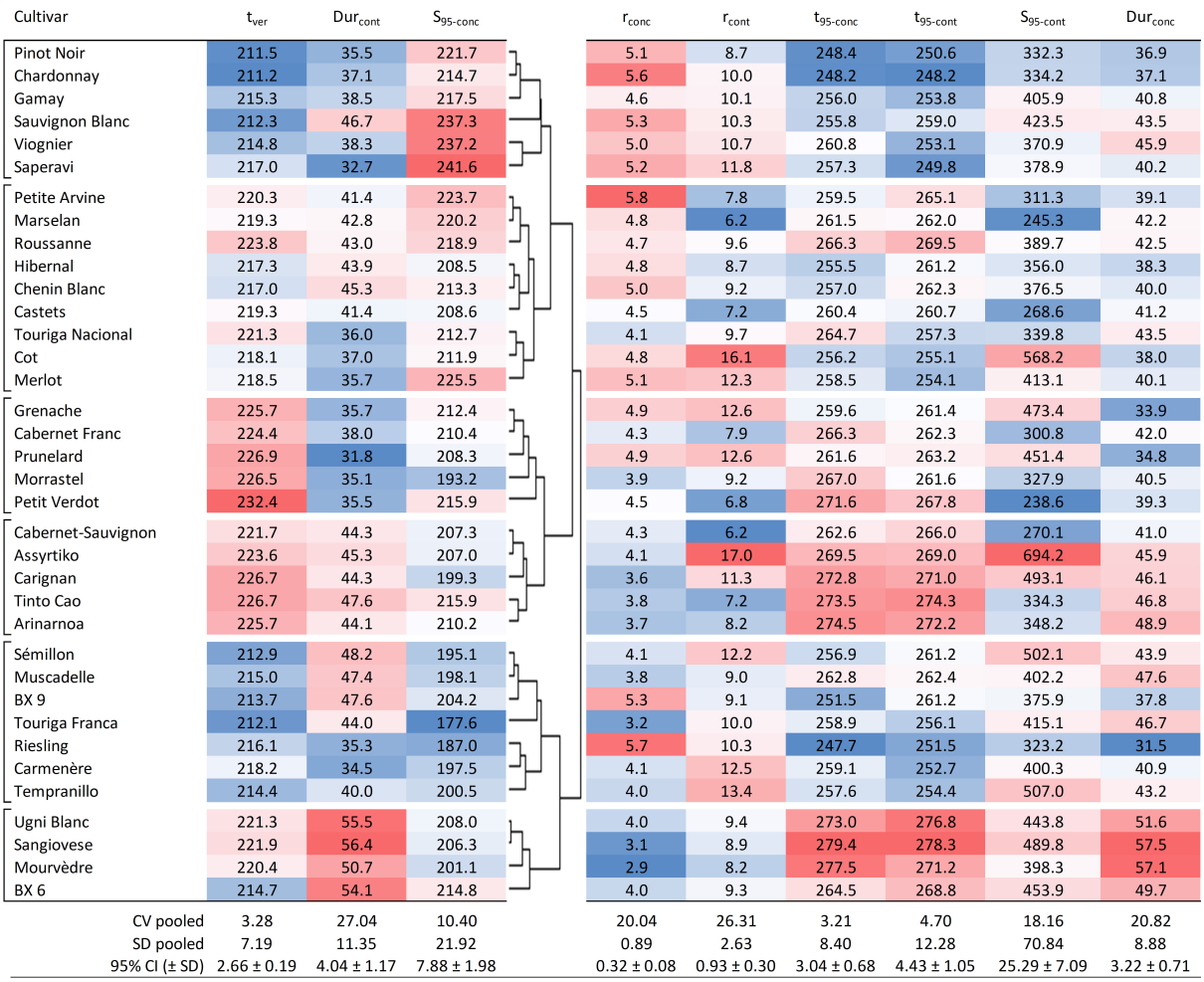
General Effects

Type III ANOVA was performed to test the main effects of climate related variables, t_{ver} and BW_v on the different sugar accumulation traits (**Table 5**). Overall, the total variation of the content-based sugar accumulation traits was better explained (48–77%) than the total variation for the concentration-based traits (28–44%). Rainfall prior to mid-veraison explains 44.1% of the variance in sugar concentration at maturity ($S_{95-conc}$). Average post mid-veraison PAR explained more of the variance than post mid-veraison temperature for four of the eight sugar accumulation traits and it explained a large part of the variation in three of the four content-based sugar accumulation traits. Sugar content per berry is strongly affected by berry weight at mid-veraison.

With all cultivar data considered together, this type of analysis identifies larger general trends, but can be blurred by the differential behavior of the 36 individual cultivars. Performing this analysis on a per cultivar basis will improve understanding of the dynamics.

Cultivar-Specific Effects

The effects of the same climatic factors, t_{ver} and BW_v included in **Table 5** are evaluated to quantify their contribution to the



	Cultivar	t_{ver}	Dur_{cont}	$S_{95\text{-}conc}$	r_{conc}	r_{cont}	$t_{95\text{-}conc}$	$t_{95\text{-}cont}$	$S_{95\text{-}cont}$	Dur_{conc}
I	Pinot Noir	211.5	35.5	221.7	5.1	8.7	248.4	250.6	332.3	36.9
	Chardonnay	211.2	37.1	214.7	5.6	10.0	248.2	248.2	334.2	37.1
	Gamay	215.3	38.5	217.5	4.6	10.1	256.0	253.8	405.9	40.8
	Sauvignon Blanc	212.3	46.7	237.3	5.3	10.3	255.8	259.0	423.5	43.5
	Viognier	214.8	38.3	237.2	5.0	10.7	260.8	253.1	370.9	45.9
	Saperavi	217.0	32.7	241.6	5.2	11.8	257.3	249.8	378.9	40.2
II	Petite Arvine	220.3	41.4	223.7	5.8	7.8	259.5	265.1	311.3	39.1
	Marselan	219.3	42.8	220.2	4.8	6.2	261.5	262.0	245.3	42.2
	Roussanne	223.8	43.0	218.9	4.7	9.6	266.3	269.5	389.7	42.5
	Hibernal	217.3	43.9	208.5	4.8	8.7	255.5	261.2	356.0	38.3
	Chenin Blanc	217.0	45.3	213.3	5.0	9.2	257.0	262.3	376.5	40.0
	Castets	219.3	41.4	208.6	4.5	7.2	260.4	260.7	268.6	41.2
	Touriga Nacional	221.3	36.0	212.7	4.1	9.7	264.7	257.3	339.8	43.5
	Cot	218.1	37.0	211.9	4.8	16.1	256.2	255.1	568.2	38.0
	Merlot	218.5	35.7	225.5	5.1	12.3	258.5	254.1	413.1	40.1
III	Grenache	225.7	35.7	212.4	4.9	12.6	259.6	261.4	473.4	33.9
	Cabernet Franc	224.4	38.0	210.4	4.3	7.9	266.3	262.3	300.8	42.0
	Prunelard	226.9	31.8	208.3	4.9	12.6	261.6	263.2	451.4	34.8
	Morrastel	226.5	35.1	193.2	3.9	9.2	267.0	261.6	327.9	40.5
	Petit Verdot	232.4	35.5	215.9	4.5	6.8	271.6	267.8	238.6	39.3
IV	Cabernet-Sauvignon	221.7	44.3	207.3	4.3	6.2	262.6	266.0	270.1	41.0
	Assyrtiko	223.6	45.3	207.0	4.1	17.0	269.5	269.0	694.2	45.9
	Carignan	226.7	44.3	199.3	3.6	11.3	272.8	271.0	493.1	46.1
	Tinto Cao	226.7	47.6	215.9	3.8	7.2	273.5	274.3	334.3	46.8
	Arinarnoa	225.7	44.1	210.2	3.7	8.2	274.5	272.2	348.2	48.9
V	Sémillon	212.9	48.2	195.1	4.1	12.2	256.9	261.2	502.1	43.9
	Muscadelle	215.0	47.4	198.1	3.8	9.0	262.8	262.4	402.2	47.6
	BX 9	213.7	47.6	204.2	5.3	9.1	251.5	261.2	375.9	37.8
	Touriga Franca	212.1	44.0	177.6	3.2	10.0	258.9	256.1	415.1	46.7
	Riesling	216.1	35.3	187.0	5.7	10.3	247.7	251.5	323.2	31.5
	Carmenère	218.2	34.5	197.5	4.1	12.5	259.1	252.7	400.3	40.9
	Tempranillo	214.4	40.0	200.5	4.0	13.4	257.6	254.4	507.0	43.2
VI	Ugni Blanc	221.3	55.5	208.0	4.0	9.4	273.0	276.8	443.8	51.6
	Sangiovese	221.9	56.4	206.3	3.1	8.9	279.4	278.3	489.8	57.5
	Mourvèdre	220.4	50.7	201.1	2.9	8.2	277.5	271.2	398.3	57.1
	BX 6	214.7	54.1	214.8	4.0	9.3	264.5	268.8	453.9	49.7
	CV pooled	3.28	27.04	10.40	20.04	26.31	3.21	4.70	18.16	20.82
	SD pooled	7.19	11.35	21.92	0.89	2.63	8.40	12.28	70.84	8.88
	95% CI (± SD)	2.66 ± 0.19	4.04 ± 1.17	7.88 ± 1.98	0.32 ± 0.08	0.93 ± 0.30	3.04 ± 0.68	4.43 ± 1.05	25.29 ± 7.09	3.22 ± 0.71

FIGURE 4 | Hierarchical cluster analysis based on t_{ver}, Dur_{cont}, and $S_{95-conc}$, showing six groups for the 36 cultivars together with other sugar accumulation traits for reference. Values shown are averages of each trait for each cultivar (over 7 years and four blocks, $n = 28$). Blue cells are increasingly lower values and red cells are increasingly higher values within the range observed for each of the traits. DOY, day of the year; CV pooled, pooled coefficient of variation; SD pooled, pooled standard deviation; 95% CI, average 95% confidence interval with standard deviation.

observed variation in the key sugar accumulation traits of Dur_{cont}, $S_{95-cont}$, and $S_{95-conc}$ for all the cultivars individually. Dur_{cont} is of interest to growers, together with t_{ver}, as it will determine in which part of the season the grapes will ripen. It may also be of interest with regards to achieving concurrent phenolic maturity of the grapes. Expressed as content, this is the duration of active sugar loading to the berries and excludes the separate mechanism of sugar concentration caused by dehydration after loading has ceased. $S_{95-cont}$ is of physiologic interest as it is the ultimate amount of sugar loaded into the berry, and $S_{95-conc}$ is of interest to winemakers as it drives the potential alcohol content, which is important in the final sensory attributes of the wine.

Multiple linear regression analysis was performed for each cultivar on the above dependent traits against the same set of independent variables in **Table 5**. On average the resulting models explained 69, 70, and 69% of the total variation in Dur_{cont}, $S_{95-conc}$, and $S_{95-cont}$, respectively and are described in more detail below.

Duration in content (Dur_{cont})

PAR_{v-95}, RR_{f-v}, BW_v, t_{ver}, and T_{f-v} were shown to significantly influence Dur_{cont} for 30, 25, 21, 19, and 14 out of the 36 cultivars, respectively, although the relative contribution of each was very different across the cultivars (**Figure 5** and **Supplementary Table 5**). An increase in PAR_{v-95}, RR_{f-v}, T_{f-v}, or t_{ver} reduced Dur_{cont}, while an increase in BW_v increased Dur_{cont}. Whereas PAR_{v-95} was important for most cultivars, it was replaced by T_{v-95} for the cultivars Arinarnoa, Ugni Blanc, Petit Verdot, Roussanne, and Carignan. During the mid-flowering to mid-veraison period, the effect of PAR_{f-v} was relatively small across all cultivars. During the mid-veraison to maturity period the effect of vines water status assessed with $\delta^{13}C$ was also relatively small.

95% maximum sugar content ($S_{95-cont}$)

BW_v, water deficit [$\delta^{13}C$ or $(\delta^{13}C)^2$], Dur_{cont}, and RR_{f-v} were shown to significantly influence $S_{95-cont}$ for 28, 25, 18, and 14 out of the 36 cultivars, respectively, while the effects

TABLE 3 | Bravais-Pearson coefficients (*r*) for correlation analysis performed between all sugar accumulation traits, t_{ver} and BW_v for all replicates (cultivar × year × block) considered together.

	t_{ver}	r_{conc}	r_{cont}	$S_{95-conc}$	$S_{95-cont}$	$t_{95-conc}$	$t_{95-cont}$	Dur_{conc}	Dur_{cont}	BW_v
t_{ver}	–	ns	−0.11	−0.31	−0.21	0.50	0.47	−0.29	−0.16	−0.11
r_{conc}	–	–	0.27	0.24	−0.16	−0.62	−0.33	**−0.73**	−0.40	−0.29
r_{cont}	–	–	–	0.17	0.58	−0.22	−0.48	−0.16	−0.47	0.57
$S_{95-conc}$	–	–	–	–	0.16	0.06	−0.21	0.33	ns	−0.19
$S_{95-cont}$	–	–	–	–	–	0.10	0.17	0.29	0.33	**0.92**
$t_{95-conc}$	–	–	–	–	–	–	0.59	0.68	0.32	0.11
$t_{95-cont}$	–	–	–	–	–	–	–	0.26	**0.80**	0.16
Dur_{conc}	–	–	–	–	–	–	–	–	0.49	0.21
Dur_{cont}	–	–	–	–	–	–	–	–	–	0.26
BW_v	–	–	–	–	–	–	–	–	–	–

The correlations shown in bold had $r > 0.71$, or $r^2 > 0.50$.

TABLE 4 | Analysis of variance showing relative contribution of variance in observed sugar accumulation-related traits associated with cultivar, year, cultivar × year interaction, block, and residuals, together with total variance explained.

		Contribution of variance components (%)								
Source	**Degrees of freedom**	t_{ver}	Dur_{cont}	$S_{95-conc}$	r_{conc}	r_{cont}	$t_{95-conc}$	$t_{95-cont}$	$S_{95-cont}$	Dur_{conc}
Cultivar	35	35.5	24.4	27.0	40.2	47.0	48.2	29.3	64.0	29.4
Year	6	57.6	9.8	45.2	17.4	5.7	14.9	17.0	13.9	26.7
Cultivar × year	210	4.0	24.2	18.6	25.3	20.8	21.0	21.0	9.6	23.7
Block	3	0.2	0.5	0.2	0.1	0.8	0.2	0.2	0.7	0.3
Residuals	753	2.8	41.2	9.1	16.9	25.8	15.7	32.5	11.8	19.9
Total variance explained		97.2	58.8	90.9	83.1	74.2	84.3	67.5	88.2	80.1

of T_{f-v} and T_{v-95} were generally small for most cultivars (**Figure 6** and **Supplementary Table 6**). An increase in BW_v or Dur_{cont} increased $S_{95-cont}$, while increased water deficit after veraison ($\delta^{13}C$) and RR_{f-v} reduced $S_{95-cont}$. Water deficit after veraison was included either as a linear or as a nonlinear function $(\delta^{13}C)^2$ in the multiple regression. The effect of $(\delta^{13}C)^2$ was quadratic, meaning that $S_{95-cont}$ increased with water deficit until a maximum and then decreased, if water deficit continued to increase.

95% maximum sugar concentration ($S_{95-conc}$)

RR_{f-v}, PAR_{f-v}, and $(\delta^{13}C)^2$ were shown to significantly influence $S_{95-conc}$ for 34, 20, and 18 out of the 36 cultivars, respectively (**Figure 7** and **Supplementary Table 7**). The effects of BW_v and t_{ver} were generally small and RR_{f-v} and PAR_{f-v} reduced $S_{95-conc}$. The influence of $(\delta^{13}C)^2$ was quadratic, meaning that $S_{95-conc}$ reached an optimum at a certain level of water deficit.

DISCUSSION

Berry sugar accumulation data from 36 grapevine cultivars were collected between veraison and maturity over 7 years from a vineyard in Bordeaux. Sigmoid curves provided a strong statistical fit to the data and were used to obtain key sugar accumulation traits. The diversity of these traits were then described and the dynamics of the sugar accumulation rate, duration, and concentration/content at maturity traits across cultivars were studied. Other grapevine traits that can influence sugar accumulation traits, such as phenology, berry weight, and water deficit response, were also considered.

Characterizing Cultivars

Clustering analysis was performed to assess similarities (or not) among cultivars across the 7 years of the study based on the date of mid-veraison (t_{ver}), sugar concentration at 95% of maximum ($S_{95-conc}$), and the duration between mid-veraison and the date of 95% sugar content (Dur_{cont}). Although the physiological mechanisms driving them differ, these traits are of agronomic interest and the clustering (as presented in **Figure 4**) provides a useful categorization of cultivars for easy reference.

Correlation analysis between the different sugar accumulation traits of all cultivars considered together found important general relationships between the maximum rate of accumulation, the duration, and the date of maturity. Faster maximum accumulation rates were generally associated with both earlier maturity dates and shorter durations between mid-veraison and maturity. Individual cultivars followed similar trends as the larger group, suggesting some consistency in these behaviors across cultivars, albeit with different slopes and intercepts.

Climate Versus Genetics

For each individual ripening trait, the results of this study give insight into how much their variation is driven by climate, cultivar, and climate × cultivar interaction.

TABLE 5 | Analysis of variance as performed by type III ANOVA showing the amount of variance in the eight sugar accumulation traits explained by different environmental variables for all cultivars considered together.

	Relative contribution of variance components (%)							
Source	Dur_{cont}	$S_{95-conc}$	r_{conc}	r_{cont}	$t_{95-conc}$	$t_{95-cont}$	$S_{95-cont}$	Dur_{conc}
t_{ver}	22.7	ns	12.4	7.6	43.5	ns	ns	27.2
BW_v	6.0	6.6	21.7	31.4	3.0	3.1	88.7	7.6
T_{f-v}	7.7	11.9	ns	7.5	ns	8.1	1.6	ns
PAR_{f-v}	ns	7.2	2.7	1.0	7.4	ns	0.9	8.3
RR_{f-v}	8.4	44.1	7.3	0.7	12.3	3.6	5.8	32.4
T_{v-95}	13.0	ns	31.2	ns	30.7	20.9	ns	22.8
PAR_{v-95}	40.3	13.6	22.8	51.9	ns	59.4	ns	ns
$\delta^{13}C$	1.9	16.5	2.0	ns	3.0	4.8	2.9	1.8
r^2 model	71.8	36.8	28.0	47.5	44.3	77.4	70.3	32.2

ANOVA run with n = 1008 individual observations.
ns, not significant.

Analysis of variance analysis of the variation in sugar accumulation traits, for all cultivars considered together, were well explained by cultivar, year, and their interaction, with total variance explained ranging between 59 and 97% across the different traits.

For the key traits of t_{ver} and $S_{95-conc}$, year explained around half of their respective variances, while cultivar explained roughly one third. This suggests that climate was a strong driver of those traits, with genetic variation also being important. About 19% of variance in $S_{95-conc}$ was explained by cultivar × year interaction, suggesting an additional contribution from phenotypic plasticity.

Compared to all other sugar accumulation traits, the ANOVA analysis found Dur_{cont} had the lowest amount of total variance explained (58.8%), suggesting other variables not included in the model had an effect. Of the total variance for this trait, little was explained by year, with both cultivar and cultivar × year interaction each explaining about 24%. The remaining traits generally had more variance explained by cultivar with the rest explained relatively evenly by other factors.

Phenotypic Plasticity

Analysis of variance analysis of sugar accumulation traits, with all cultivars considered together, found that the total variation of the content-based sugar accumulation traits were better explained by the selected environmental variables (48–77%) than the total variation for the concentration-based traits (28–44%). This could be due to the additional effect of berry dehydration on the latter that may occur after sugar loading is otherwise complete.

The following subsections provide a detailed look at the relationships between specific variables and the sugar accumulation traits of individual cultivars.

Pre -and Post-veraison Effects of PAR and Temperature

For duration as content (Dur_{cont}), PAR_{v-95} had a significant influence in 30 out of 36 cultivars and T_{v-95} had a significant influence on 5 of 36 cultivars, although to varying degrees in both cases. PAR_{v-95} and T_{v-95} were not found together in the same model of Dur_{cont} for a given cultivar for reasons of collinearity ($r = 0.73$, $P < 0.05$). This, however, does not imply that there were no effects of temperature on cultivars when T_{v-95} was not included in the regression. All cultivars ripened between DOY 190 and 290 in any given year. During this period, days are already getting shorter, thereby reducing the amount of received PAR, while temperature is at its peak and relatively stable for approximately 20 days after t_{ver} before starting to decrease more steeply in September. In this study, the variation in PAR for a given temperature is therefore higher at high temperatures. In a year with early phenology, the sugar accumulation period may coincide with both higher temperature and PAR. This may be important as it has been shown that increased light and temperature levels may increase the photosynthetic rate of plants (McIntyre et al., 1982). A reduction in Dur_{cont} is possible if more sugar was partitioned to the berries through an increased rate of photosynthesis. Conversely, with a late phenology, a cultivar may ripen under lower temperature and light conditions. This in turn reduces the rate of photosynthesis and theoretically increases the duration of the sugar accumulation period. The effects of PAR_{f-v} and T_{f-v} on $S_{95-conc}$ were found to be consistently small. For Dur_{cont}, the variables PAR_{f-v} and T_{f-v} were not found together in the same model for reasons of collinearity. Higher levels of PAR prior to mid-veraison, when days were longer, might have resulted in higher amounts of sugars accumulated. The 95% maximum sugar content trait ($S_{95-cont}$) showed only sporadic relationships between either temperature, or PAR, whether before, or after mid-veraison.

Effects of the Timing of Mid-Veraison

The trait t_{ver} may have an indirect effect on sugar accumulation. It drives the start of ripening and may be a factor in determining both the length of time available for ripening and the temperatures that the vine and berries will experience during ripening. The veraison date is influenced by both cultivar genetics and environmental conditions prior to veraison, in particular temperature (Parker et al., 2011). This makes t_{ver} somewhat of a proxy for those conditions driving the plasticity of sugar accumulation traits.

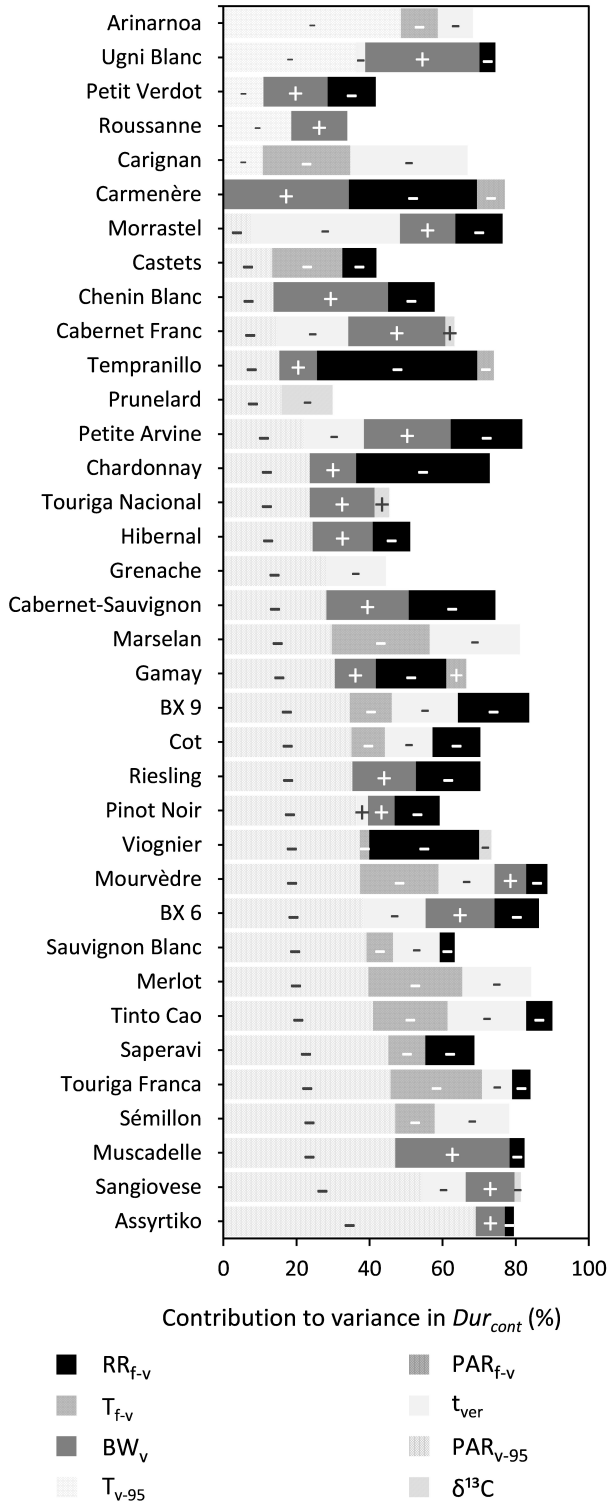


FIGURE 5 | Stacked bar plots of the variance components determined by multiple linear regression for trait Dur_{cont}. The cultivars are ordered based on the percentage explained by PAR_{f-v}. The independent variables included were RR_{f-v}, PAR_{f-v}, T_{f-v}, PAR_{v-95}, T_{v-95}, t_{ver}, BW_v, and $\delta^{13}C$. The – and + represent the directions in which coefficients of variables moved. **Supplementary Table 6** provides a numeric form of this figure.

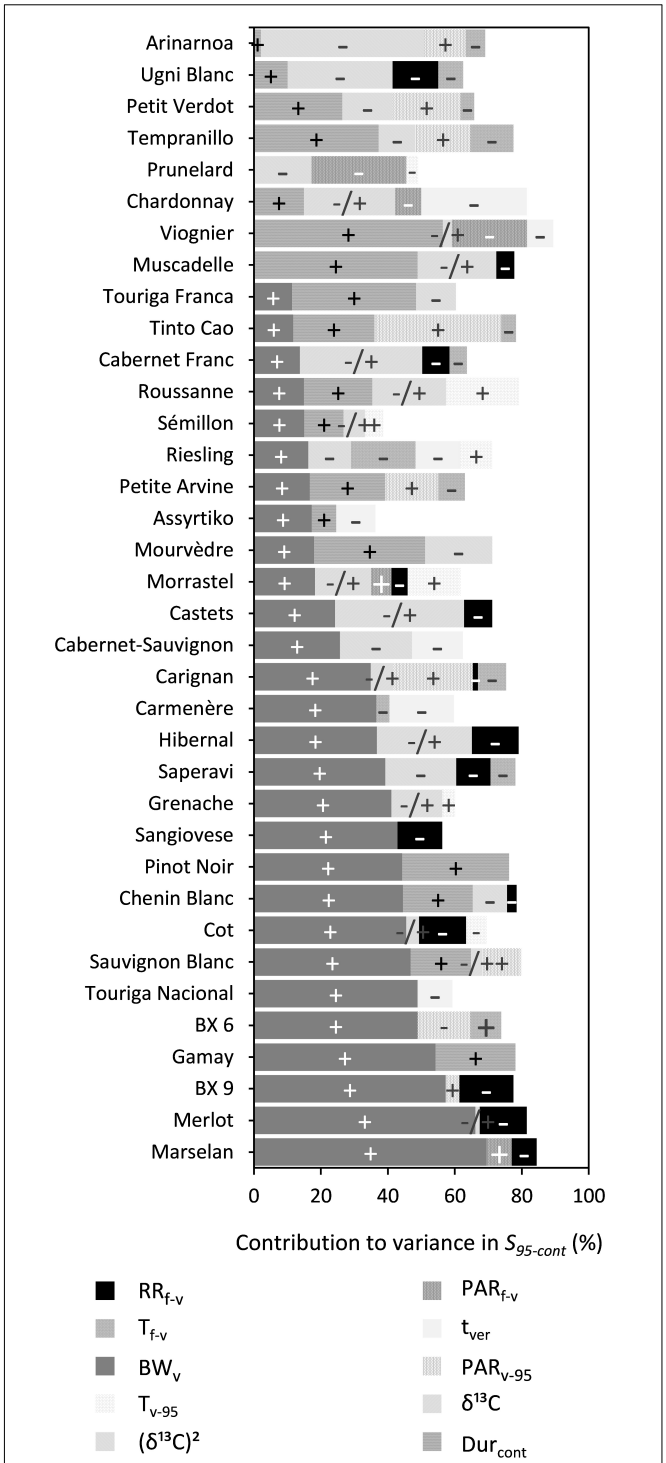


FIGURE 6 | Stacked bar plots of the variance components as determined by multiple linear regression for the trait $S_{95-cont}$. The cultivars are ordered based on the percentage explained by BW_v. The independent variables included were RR_{f-v}, PAR_{f-v}, T_{f-v}, PAR_{v-95}, T_{v-95}, t_{ver}, BW_v, and the trait Dur_{cont}. $\delta^{13}C$ was included as a linear term, whereas $(\delta^{13}C)^2$ was included using a power term into the regression. The –, + and –/+ represent the directions in which coefficients of variables moved. Where –/+ was only designated to the variable $(\delta^{13}C)^2$ because of its inherent quadratic character. **Supplementary Table 7** provides a numeric form of this figure.

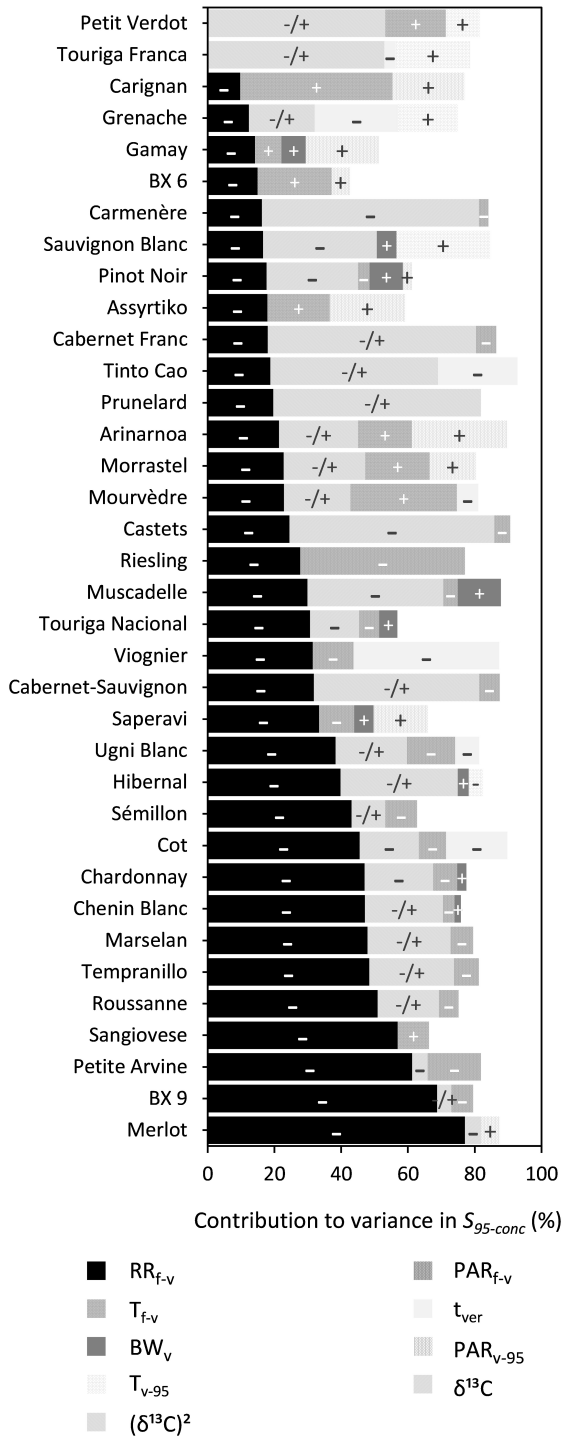


FIGURE 7 | Stacked bar plots of the variance components as determined by multiple linear regression for the trait $S_{95-conc}$. The cultivars are ordered based on the percentage explained by RR_{f-v}. The independent variables included were: RR_{f-v}, PAR_{f-v}, T_{f-v}, PAR_{v-95}, T_{v-95}, t_{ver}, and BW_v. $\delta^{13}C$ was included as a linear term, whereas $(\delta^{13}C)^2$ was included using a power term into the regression. The –, + and –/+ represent the directions in which coefficients of variables moved. Where –/+ was only designated to the variable $(\delta^{13}C)^2$ because of its inherent quadratic character. **Supplementary Table 8** provides a numeric form of this figure.

In this study, the duration of the sugar accumulation as content (Dur_{cont}) decreased with delayed t_{ver} in 19 out of 36 cultivars, although to varying degrees. Cultivars with delayed t_{ver} ripened in less favorable conditions, and may be eventually halted, resulting in lower sugar contents and shorter Dur_{cont}. In the 2013 growing season, not only were sugar accumulation rates lower, but final sugar contents were also lower for all cultivars (**Figure 3**). Date of mid-veraison (t_{ver}) only showed sporadic relationships with 95% maximum sugar content ($S_{95-cont}$) and sugar concentration ($S_{95-conc}$).

Pre-veraison Effects of Rainfall

Rainfall (RR_{f-v}) prior to mid-veraison had significant relationships with Dur_{cont}, $S_{95-cont}$, and $S_{95-conc}$ across 25, 14, and 34 of 36 cultivars, respectively. Any physiological response to rainfall prior to mid-veraison is most probably driven by its effect on soil water status. In the absence of any available soil water, or water potential measurements prior to veraison, rainfall provides a good surrogate. The variability associated with evapotranspiration (the other parameter besides rainfall important in determining soil water status) is accounted for by average temperature and PAR from mid-flowering to mid-veraison as already included in the model when significant.

Rainfall prior to veraison was found to decrease berry sugar concentrations. An increase in soil water content might have resulted in an increased water supply to the berries and caused a subsequent dilution of $S_{95-conc}$. In line with the previous statement, rainfall between budburst and veraison was found to be strongly correlated with berry weight at veraison ($r = 0.77$, $P < 0.05$). Another concurrent dilution effect may have been caused by partial failure of fruit-set and expansion (referred to as *millerandage* and *coulure* in French, or *hens and chickens* in English) caused by rainfall prior to mid-veraison. These two conditions can bring about a reduction in the number of berries per bunch, while increasing the size of the remaining berries.

Regarding its effect on reducing Dur_{cont}, the affect of rainfall prior to mid-veraison is more difficult to explain. Such rainfall may increase vine vigor and thereby the rate of sugar accumulation, which is generally related to Dur_{cont} across all cultivars (**Table 3**).

Effects of Berry Weight at Veraison

Berry weight at mid-veraison appeared to be an important driver of final sugar content ($S_{95-cont}$) for almost all cultivars in this study. Houel et al. (2013) obtained the same results for a wide range of cultivars and reasoned that cell division and cell expansion after anthesis were the main drivers of berry size. Any water deficit during the period could restrict berry cell division and thereby its potential final size (Shellie, 2014). On the other hand, cultivars such as Petit Verdot and Viognier vary little in berry weight. These cultivars are known for their relatively small and stable berry size to begin with and for these cultivars, the length of the sugar accumulation period explains most of the variation in $S_{95-cont}$. However, for 21 out of the 36 cultivars, increased berry weight also increased Dur_{cont}. A plausible explanation would be that bigger berries hold more sugar, and it takes more time to fill them.

Effects of the Duration of the Sugar Accumulation Period

Dur_{cont} was included as a variable in the multiple regression analysis to evaluate the effect of the length of the sugar accumulation period on $S_{95-cont}$ (**Figure 6**) and no significant relationships were found. For some cultivars $S_{95-cont}$ was quite variable for a given Dur_{cont} (e.g., Merlot and Mourvèdre). For these cultivars it was the level of water deficit and berry weight at mid-veraison that were also major determinants of $S_{95-cont}$.

Effects of Water Deficit ($\delta^{13}C$)

For the trait of 95% maximum sugar content ($S_{95-cont}$) and 95% maximum sugar concentration ($S_{95-conc}$) water status post-veraison as measured by $\delta^{13}C$ had an important effect for 25 and 18 cultivars of 36, respectively. $\delta^{13}C$ was only sporadically related to Dur_{cont} and to a small degree. For some cultivars, the effect of water deficits was found to be linear. This was generally the case for cultivars that either did not experience weak or severe water deficits in the seven seasons in this study. Otherwise, this relationship with $\delta^{13}C$ was best characterized by a power function, with higher sugar content or concentration when water deficit was moderate, and lower sugar content or concentration when water deficit was either weak or strong. This finding is consistent with van Leeuwen et al. (2009). Comparison of $\delta^{13}C$ is useful within but not across cultivars, because high sugar contents may be reached at different levels of water deficits. When water deficit is moderate, shoot growth is more reduced compared to photosynthesis (Pellegrino et al., 2005). Hence, more sugar is available for berry ripening. This effect, combined with smaller berries under water deficit (Ojeda et al., 2001), results in higher sugar concentrations. Also, water deficit after veraison can lead to berry shrinkage by dehydration when the sum of xylem efflux and berry transpiration exceed phloem influx (Keller, 2006). Severe water deficits decrease photosynthetic activity and thereby limit sugar accumulation in berries (Zufferey et al., 2000). A dilution effect may occur at low water deficits as berry growth may be faster than sugar accumulation (Santesteban and Royo, 2006). Also, at low water deficits the rate of sugar accumulation appears to decrease relative to moderate water deficit stress. This might be due to more partitioning of sugar to vegetative growth over berry ripening (Dry and Loveys, 1998). Additionally, the response of berry growth to water deficit can also depend on the crop load (Trégoat et al., 2002).

Effect of Leaf Area to Yield Ratios on Traits

The effect of yield (and its components) on sugar accumulation traits has been well-reported (Sadras and McCarthy, 2007; Dai et al., 2011; van Leeuwen and Darriet, 2016). Yield data was not recorded for the first 6 years of measurements and therefore was not included in the analyses. The grapevine canopy leaf area was estimated to be between 2.0 and 2.4 m^2 per meter of row. According to Kliewer and Dokoozlian (2005) maximum levels of total soluble solids and berry weight are attained when leaf to fruit ratios are higher than 0.8–1.2 $m^2\ kg^{-1}$. In such case, the canopies would be able to support 1.7–3.0 kg of fruit per meter of row. Although not consistently measured, occasional bunch counts and bunch weight assessments indicate that crop loads were lower than these levels in the vast majority of years. To the extent that actual leaf area to fruit load ratios may have limited sugar accumulation, this could explain some of the variance (residuals) not explained by the models.

Significance of Findings From the Perspective of Climate Change

A major concern in agriculture, and in particular in grape growing for wine production, is that crop yields and quality may be significantly affected by climate change (Fraga et al., 2012), speaking to the need for adaptational strategies. Crop genetic diversity is a valuable resource to exploit as an adaptation to a changing climate (Morales-Castilla et al., 2020) and planting cultivars that are better suited to a region's changing climate would allow grape growers to maintain cultivation in their current location.

Although the great genetic variation within the *V. vinifera* species is a valuable resource for adaptation (Wolkovich et al., 2018), phenotyping of relevant traits across the wide range of cultivars has been limited. Most existing data have been collected in cultivar repositories, which have not been planted with replicates, making it impossible to separate environmental from genotypic variability (Destrac Irvine and van Leeuwen, 2016). This study allowed for the evaluation of key traits relevant to winemakers and researchers regarding sugar accumulation in the context of climate change. Using multiple regression analysis, the variation in key sugar accumulation traits can be largely explained by climate variables such as PAR, temperature, and water status (both before and after mid-veraison), and by physiological variables such as berry weight and date of mid-veraison. The extent to which these different variables affected sugar accumulation traits, however, varied across grape cultivars. More research is needed to unravel the exact mechanisms underlying the differential genotypic responses of traits to environmental variables. Adaptation to climate change cannot be based on temperature alone and crop responses cannot be generalized across genotypes, even within species.

Climate change induces excessively high sugar levels in grapes, resulting in wines with increased alcohol content (Duchène and Schneider, 2005). It also results in earlier ripening, moving the ripening period to a part of the season when high temperatures are not optimum for producing high quality wines (van Leeuwen et al., 2019). Phenotyping specific sugar-related ripening traits across a wide range of cultivars provides useful information to growers, when adaptation to climate change drives them to change cultivars.

In this study we focussed only on sugar accumulation traits. Sugar, however, is only one of many determinants for grape cultivar suitability in wine regions. Other important traits include, but are not limited to, WUE, photosynthetic capacity, yield, and berry composition (e.g. organic acids, aroma precursors, tannins, color, etc.). Future research should focus on characterizing these key traits and their interaction with the environment to ultimately select for grape cultivars under future climate regimes. Also, the results observed in this study

are likely to depend on climate, soil, clone, and rootstock. So to complement the results from this study it would be very useful if experimental vineyards like VitAdapt were set up in other winegrowing regions with different soils, clones, and rootstocks and under different climatic conditions. Such initiatives are already underway, such as the GreffAdapt project in Bordeaux where 55 different rootstocks are tested (Marguerit et al., 2018), and the BritAdapt project in the United Kingdom with a similar experimental set up as that in VitAdapt. The common garden design of the VitAdapt experimental vineyard provides a prototype for such experimental designs and is worth being reproduced in other winegrowing areas around the world.

CONCLUSION

A sigmoidal model was successfully fit to weekly berry sugar accumulation data and key sugar accumulation traits were quantified. Cultivars were then clustered and characterized according to these traits. The variations in sugar accumulation traits for all cultivars, when considered together, were explained well by cultivar, year, and their interaction, highlighting the relative roles of genetic variation, climate factors, and phenotypic plasticity. As seen extensively in the literature and in practice, this study confirmed that increasing temperature has a significant effect on grapevine phenology, leading to advanced harvest dates. The results of this study, however, also showed that sugar accumulation traits were affected by other factors both antecedent and concurrent to veraison. Although the specific physiological mechanisms by which these traits respond to environmental variables remain to be identified, results of this study provide useful information to inform grower selection and management of cultivars in vineyards affected by climate change. Determining suitability of grapevine cultivars for existing or new winegrowing areas cannot be based on a single factor, as is currently done in most studies. Moreover, the major factors driving grape ripening dynamics cannot be generalized across cultivars.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

CL and ADI contributed to the conception and design of the study. ADI was in charge of data collection. BS organized the database. BS and ZD performed the statistical analysis. MG and BS wrote the first draft of the manuscript. CL and ZD wrote sections of the manuscript. All authors contributed to manuscript revision, read and approved the submitted version.

FUNDING

The VitAdapt Project was supported by the Conseil Interprofessionnel des Vins de Bordeaux (CIVB), the Conseil Régional d'Aquitaine and the Institut national de recherche pour l'agriculture, l'alimentation et l'environnement (INRAE). This study had been carried out with financial support from the French National Research Agency (ANR) in the frame of the Investments for the future Program, within the Cluster of Excellence COTE (ANR-10-LABX-45). It was also conducted as part of the International Associated Laboratory (LIA) Innogrape.

ACKNOWLEDGMENTS

We are grateful for support from the Experimental Viticultural Unit of Bordeaux (1442, INRAE, F-33883 Villenave d'Ornon) in managing the VitAdapt experiment. We are also grateful to Guillaume Pacreau for technical help; Marta Avramova, Astrid Jordana, Louise Durand, Amelie De Pizzol, Marie-Aglae Fougere, Adeline Gardier, Elena Morin, Lea Meslet, Lise Cahuzac, Diego Vergara, Alexandra Chabrerie, Claire Castany, Baptiste Etchamendy, Michel Datte, Quentin Druesne, Marie Thoelke, Guillaume Arrivé, Margaux Ravat, Martina Haines, Aurelien Zulli, Julien Fort, Sophie Louise, Bastien Arnaud, Tina Bakosi, Wenxin Li, Nicolas Lebe, Margot Larose, Solen Le Pivain, Stephan Lamy, Francesco Rinaudi, Song Yan, Charlene Pertuiset, and Cecile Caumette for help with field work.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2021.624867/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.