SELECTING VARIETIES BEST ADAPTED TO CURRENT AND FUTURE CLIMATE CONDITIONS BASED ON RIPENING TRAITS

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Abstract

Aim: The aim of this study was to quantify key berry sugar accumulation traits and characterize their plasticity in response to climate variation from data collected from different cultivars over seven years from an experimental vineyard.

Methods and Results: Berry samples were collected weekly from different *Vitis Vinifera* (L.) cultivars at four replicate locations within a common-garden randomized complete block design from 2012-2018 in Bordeaux, France. A logistic model was parameterized to the sugar accumulation data and ripening traits were extracted. The variation in sugar accumulation traits were well explained by cultivar, year, and their interaction, highlighting the relative roles of genetic variation and phenotypic plasticity. Sugar accumulation traits themselves were affected by antecedent and concurrent climate factors such as temperature, photosynthetically active radiation, and vine water status, whether before, or after mid-véraison. In addition, other traits such as berry weight at mid-véraison, and date of mid-véraison had an important influence on sugar accumulation traits. Further, the relative importance of these factors varied significantly by cultivar. More research is needed to unravel the exact mechanisms underlying the differential genotypic responses of traits to these factors.

Conclusions: The variations in sugar accumulation traits were well explained by cultivar, year, and their interaction, highlighting the relative roles of genetic variation, climate factors, and phenotypic plasticity. Sugar accumulation traits were found to be affected by antecedent and concurrent climate factors both before and after mid-véraison. The relative importance of these factors varied significantly by cultivar. In this study we focused only on sugar accumulation traits. Sugar is, however, only one of many determinants for grape cultivar suitability in wine regions. Other traits include, but are not limited to, water use efficiency, photosynthetic capacity, yield, and berry composition.

Significance and Impact of the Study: Climate change induces excessively high sugar levels in grapes, resulting in wines with increased alcohol content. It also results in earlier ripening, moving the ripening period to a part of the season where climatic conditions are not optimum for producing high quality wines. Variability among cultivars is a precious resource to adapt viticulture when environments change. This study highlighted the relative roles of genetic variation and phenotypic plasticity to environmental conditions in the variation of sugar accumulation traits. Moreover, it shows that a multi-trait approach is required to study wine grape ripening to select varieties in a context of global change.

Keywords: Grapevine cultivar, berry sugar accumulation, climate change, phenotypic plasticity, modelling

Introduction

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 (IPCC, 2014). Climatic conditions during grape ripening are already affected, resulting in altered grape composition at harvest *(*Fraga *et al.,* 2012). Grapes are harvested at increasingly higher sugar levels, resulting in wines with increased alcohol levels (Duchène and Schneider, 2005; Godden *et al.,* 2015). 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).

Moving viticultural production to areas with more suitable climates may lead to conflicts in land use and freshwater ecosystems (Hannah *et al.,* 2013). A more sustainable adaptation would be to exploit crop diversity (Morales-Castilla *et al.,* 2020). Planting cultivars that are better suited to a region's new climate would allow grape growers to maintain cultivation in their current location. 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. Although the great genetic variation within the *Vitis 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 and van Leeuwen, 2016).

The trajectory of sugar accumulation in grape berries follows a sigmoidal pattern with slow accumulation at the onset of véraison, rapid accumulation just after véraison 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 shrinkage (Keller *et al.,* 2016) or decrease due to dilution. Several researchers have already captured the dynamics of sugar accumulation through modelling approaches that estimate the rate of sugar accumulation, the amount of sugar at maturity and the timing of the plateau phase (Parker *et al.,* 2013, 2011). 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 is considered during berry development pre-véraison, or post-véraison (Jones and Davis, 2000). Individual cultivars manage their water status differently in response to changes in climatic conditions (Domec and Johnson, 2012; Schultz, 2003). 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.

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 seven years (2012-2018) from an experimental vineyard in Bordeaux, France.

Materials and Methods

Data for this study was collected (from 2012-2018) 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 centre in Bordeaux, France (Destrac and van Leeuwen, 2016). 36 cultivars were phenotyped for many traits, including phenology (mid-budbreak, mid-flowering and mid-véraison), grape composition during ripening, carbon isotope discrimination in berry juice sugars, and others.

The phenological stages mid-flowering and mid-véraison were recorded for each cultivar and were denoted as:

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

Climatic data were recorded by a weather station situated approximately 100 meters from the experimental vineyard. To account for the differences in phenology between the cultivars, the observed dates of mid-flowering and mid-véraison are used for each replicate (cultivar x year x block) to calculate the various climate statistics used in this analysis.

There is considerable variability in the observed phenology across the 36 cultivars (Destrac and van Leeuwen, 2016). This phenological variability may affect the climatic conditions experienced by each cultivar within a given year. This highlights the necessity to distinguish between antecedent and concurrent factors when analysing the potential linkages between independent variables and sugar accumulation traits. The following climate variables were used as input to the ANOVA:

$T_{f\text{-}v}$ = average air temperature (°C) between mid-flowering (t_{flo}) and mid-véraison (t_{ver})
$T_{v\text{-}95}$ = average air temperature (°C) between t_{ver} and time (DOY) of 95% maximum sugar concentration (t_{95})
$PAR_{f\text{-}v}$ = average photosynthetic active radiation (J cm^{-2}) between t_{flo} and t_{ver}
$PAR_{v\text{-}95}$ = average photosynthetic active radiation (J cm^{-2}) between t_{ver} and t_{95}
$RR_{f\text{-}v}$ = 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-véraison, total rainfall between mid-flowering and mid-véraison is considered a good surrogate. After véraison, the level of carbon isotope discrimination in berry juice sugar is considered a good measure of plant water stress during the period of sugar accumulation (Gaudillère *et al.,* 2002). Grape berry juice was analysed by using a WineScan^{tm} Auto based on Fourier Transform Infrared Spectroscopy (FTIR; FOSS Analytical, Hillerød, Denmark). The FTIR WineScan was calibrated each year with independent data.

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 [Equation 1] (Triboï *et al.,* 2003) as given by:

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

where, S_{max} = the estimated maximum concentration of reduced sugars, t = day of year (DOY), t_{95} = DOY when 95% of maximum was reached, and r represents the estimated maximum rate of accumulation defined as the derivative at the point of inflection. Each replicate for a cultivar was modelled separately in order that analysis of variance (ANOVA) could be performed. The modelling was implemented with the data expressed in concentration (g L^{-1}). Sugar content (mg berry^{-1}) was also calculated but the data is not presented in this paper. The following traits were extracted from the model:

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

Data were statistically analysed using the open source software R (R Core Team, 2017) within the integrated development environment RStudio.

Results and Discussion

The sigmoidal model was applied as described in the materials and methods section to each single replicate (year × cultivar × block) providing a statistically strong fit (Figure 1). The cultivars Touriga franca and Saperavi consistently attain the lowest and highest berry sugar concentrations in this dataset, respectively. The cultivars Petit Verdot and Assyrtiko accumulate the lowest and highest berry sugar contents, respectively. The r^2 for each cultivar was between 0.96-0.99 and 0.92-0.98 when expressed in concentration and content, respectively. RMSE for the curve fits for concentrations and content across all cultivars were between 3.30-5.56 g L^{-1} and between

9.73-29.49 mg berry^{-1}, respectively. The model performed well over a large range of cultivars with different sugar accumulation dynamics under different environmental conditions.

Correlations among the different sugar accumulation traits of the different cultivars were also evaluated to identify inter-relationships. In general, when considering all replicates (cultivar x year x block) together, the rate of maximum increase in sugar concentration (r_{conc}) was negatively correlated to both the time of 95% maximum sugar concentration ($t_{95\text{-}conc}$) and the duration to that point starting at mid-véraison (Dur_{conc}) (r = -0.62, r = -0.40, respectively), with the latter two also being correlated (r = 0.68). Likewise, the maximum berry sugar loading rate (r_{cont}) was correlated to both time of 95% maximum sugar content ($t_{95\text{-}cont}$) and the duration to that point starting at mid-véraison (Dur_{cont}) (r = -0.48, r = -0.47, respectively), with the latter two also being correlated (r = 0.80). Berry weight at mid-véraison (BW_v) is strongly and positively correlated (r = 0.92) to sugar content at 95% of maximum ($S_{95\text{-}cont}$). 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 behaviours across individual cultivars, albeit with different slopes and intercepts.

To understand the relative effect of cultivar genetics versus climate, Table 1 presents an ANOVA showing the relative contribution of variance in sugar accumulation traits and t_{ver} associated with cultivar, year, cultivar x year interaction, and residuals, together with the total variance explained for Dur_{cont}, t_{ver}, and $S_{95\text{-}conc}$. 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. $S_{95\text{-}conc}$ is of interest to winemakers as it drives the potential alcohol content, which is important in the final sensory attributes of the wine.

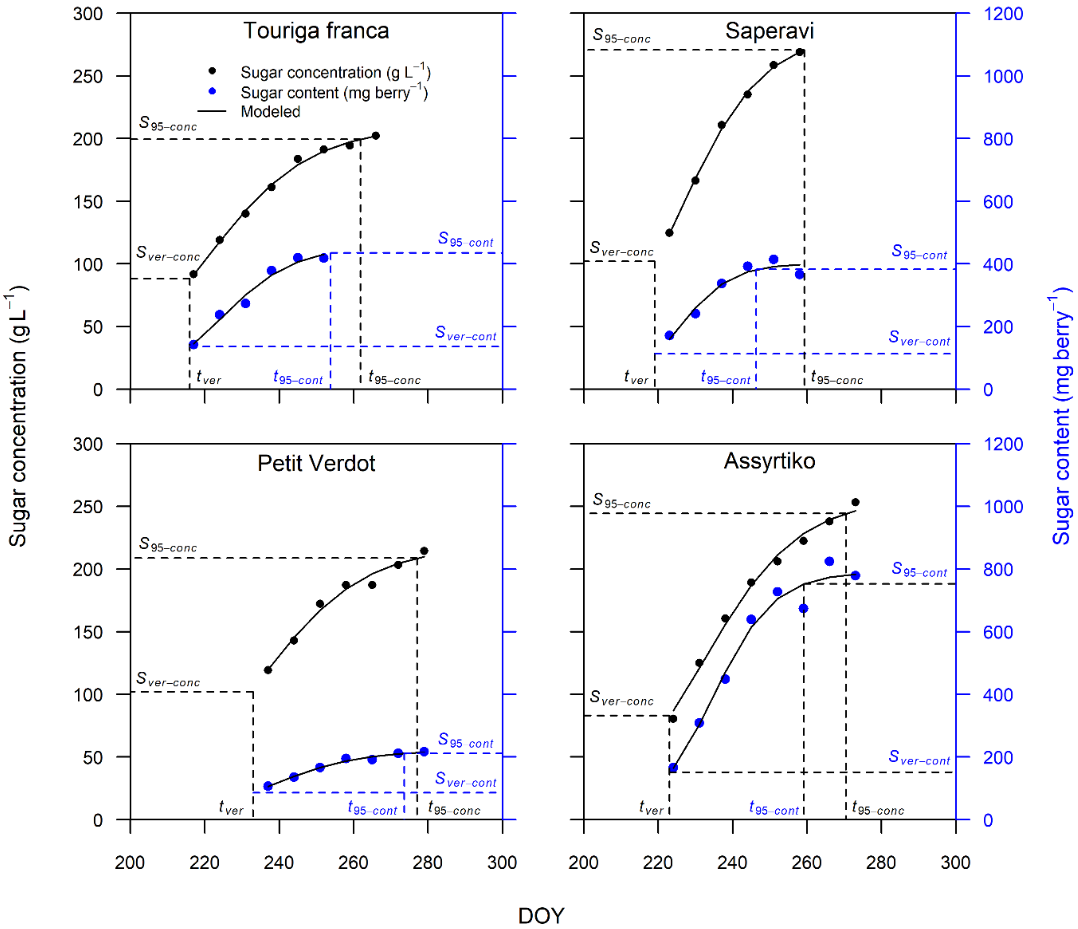

Figure 1: Sugar accumulation data and fitted curves for Touriga franca, Saperavi, Petit Verdot and Assyrtiko expressed in both concentration (in black) and content (in blue) for 2016 (block 1). Vertical dashed lines identify t_{ver} and t_{95} concentration, or content. Horizontal dashed lines identify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

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 $S_{95\text{-}conc}$, year explained around half of the variance, the latter showing a greater cultivar x year interaction effect. Dur_{cont} had relatively more variance explained by the cultivar and with larger cultivar x year interaction and residuals, although the overall variance explained by the model was less than the others at 59%. This suggests that climate was a strong driver of those traits, with genetic variation also being important. There was about 19% of variance in $S_{95\text{-}conc}$ explained by cultivar x year interaction, suggesting an additional contribution from phenotypic plasticity to the response of that trait.

Table 1. Analysis of variance showing relative contribution of variance in observed sugar accumulation-related traits associated with cultivar, year, cultivar x year interaction, block, and residuals, together with total variance explained.

	Contribution of variance components (%)			
Source	Degrees of freedom	t_{ver}	Dur_{cont}	$S_{95\text{-}conc}$
Cultivar	35	35.5	24.4	27.0
Year	6	57.6	9.8	45.2
Cultivar × Year	210	4.0	24.2	18.6
Block	3	0.2	0.5	0.2
Residuals	753	2.8	41.2	9.1
Total variance explained		97.2	58.8	90.9

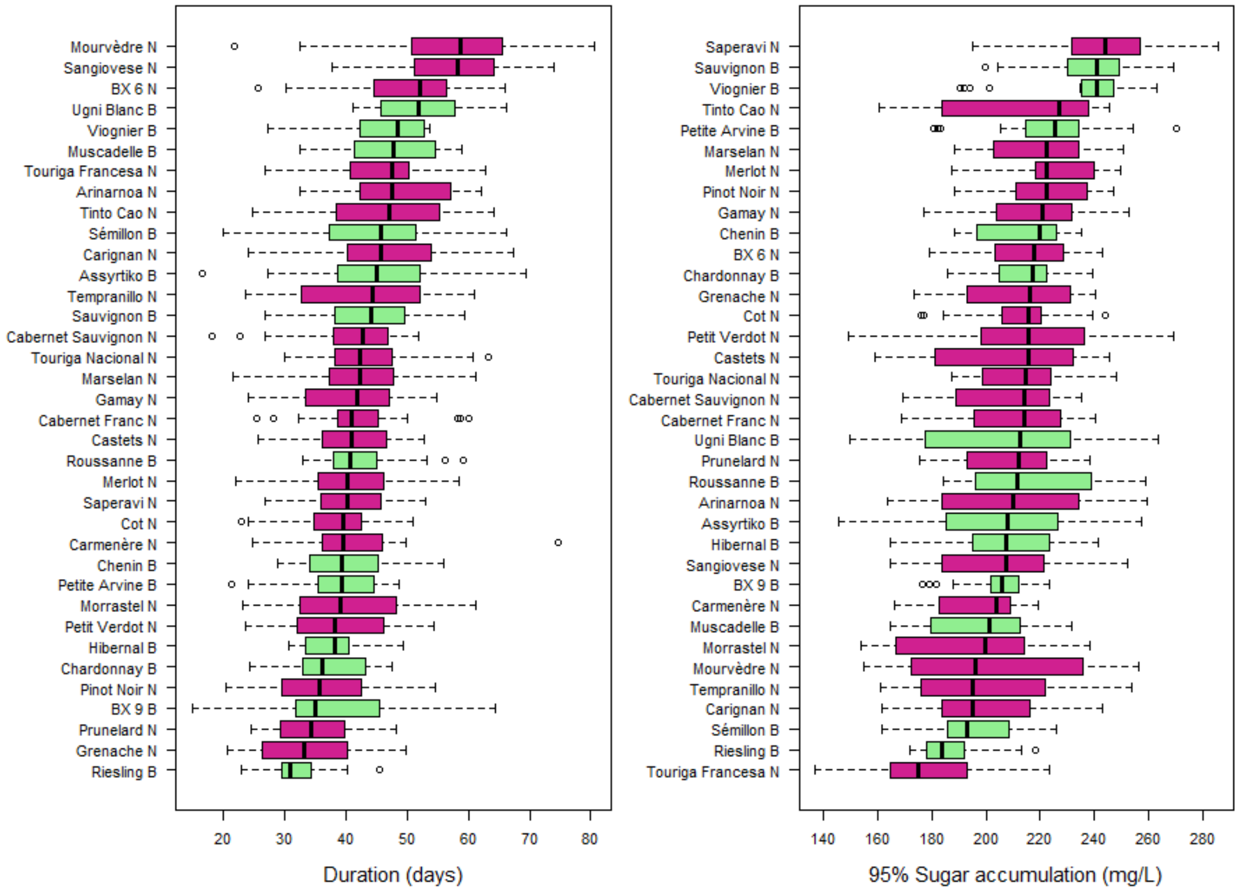

Figure 2: Boxplot of observed duration between mid-véraison and the day of Dur_{cont} (A) of varieties planted in the VitAdapt experiment and (B) 95% sugar accumulation ($S_{95\text{-}conc}$).

Table 2. 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. ANOVA run with n = 1,008 individual observations.

	Relative contribution of variance components (%)	
Source	Dur_{cont}	$S_{95\text{-}conc}$
t_{ver}	22.7	ns
BW_v	6.0	6.6
$T_{f\text{-}v}$	7.7	11.9
$PAR_{f\text{-}v}$	ns	7.2
$RR_{f\text{-}v}$	8.4	44.1
$T_{v\text{-}95}$	13.0	ns
$PAR_{v\text{-}95}$	40.3	13.6
$\delta^{13}C$	1.9	16.5
r^2 model	71.8	36.8

ns = not significant

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 2). Rainfall prior to mid-véraison explains 44.1% of the variance in sugar concentration at maturity ($S_{95\text{-}conc}$). It was found to decrease berry sugar concentrations. Average post mid-véraison PAR explained more of the variance than post mid-véraison 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-véraison (data not shown). With all cultivar data considered together, this type of analysis identifies larger general trends, but can be blurred by the differential behaviour of each of the 36 individual cultivars. Performing this analysis on a per cultivar basis would improve understanding of the dynamics.

Conclusions

This study allowed for the evaluation of key traits relevant to winemakers and researchers regarding sugar accumulation in the context of climate change. Genetic variation, climate factors, and phenotypic plasticity explained well the variation in sugar accumulation traits for all cultivars considered together. 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 before and after mid-véraison and other variables such as berry weight and the date of mid-véraison, although the extent to which these different variables affected sugar accumulation traits 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.

Phenotyping specific sugar-related ripening traits across a wide range of cultivars provides precious information to growers, when adaptation to climate change drives them to change cultivars. The common garden design of the VitAdapt experimental vineyard provides a powerful means for this type of study and might be useful to reproduce in other winegrowing areas around the world.

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