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An operational model for capturing grape ripening dynamics to support harvest decisions

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ABSTRACT

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Grape ripening is a critical phenological phase during which many metabolites that impact wine quality accumulate in the berries. Major changes in berry composition include a rapid increase in sugar and a decrease in malic acid content and concentration. Its duration is highly variable depending on grapevine variety, climatic parameters, soil type and management practices. Together with the timing of mid-veraison, this duration determines when grapes can be harvested.

Viticulturists and winemakers monitor the sugar-to-total acidity ratio (S/TA) during grape ripening and start harvesting grapes when this ratio reaches the optimum value for the desired wine style. The S/TA ratio evolves linearly as a function of thermal summation during the first four weeks following the onset of ripening. The linearity of the evolution of the S/TA ratio as a function of thermal time during the first four weeks following mid-veraison is applied in this study on two large data sets encompassing (1) 53 varieties studied during 10 years with two to four replicates for each combination of year and cultivar and (2) two varieties, cultivated on three soil types over 13 years. Grape ripening speed is highly variable. The effects of the year impact ripening speed more than the effects of the soil or the variety, although all three effects are highly significant. Grape ripening speed decreases with berry weight and also varies with vine water status. By using this approach, viticulturists and winemakers can assess four weeks after mid-veraison, for each individual vineyard parcel, at what speed grape ripening progresses. Combined with precise mid-veraison scoring, expertise from previous vintages and complementary approaches like sensory assessment of berries, it allows harvest date estimates to be fine-tuned. The results of this study can also be used to identify slow ripening varies, which are better performing in warm climates and, thus, better adapted to climate change.

KEYWORDS: grape ripening, sugar, total acidity, vine, climate change, harvest date

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INTRODUCTION

Grape ripening starts at veraison when berries become soft. Sugar starts to accumulate rapidly while organic acids are metabolized, in particular malic acid. Unlike budbreak, flowering and veraison, which are well-defined phenological stages (Destrac-Irvine et al., 2019), ripeness cannot be determined with great precision. Viticulturists define several types of ripeness, including technological ripeness (based on grape sugar and total acidity), phenolic ripeness and aromatic ripeness (van Leeuwen et al., 2022). Harvest date is often used as a proxy for ripeness, but this involves the human perception of the optimal grape composition in relation to the intended wine style. Harvest dates are highly variable, spanning over more than 30 days for a given wine-producing region depending on the climate of the vintage, the microclimate associated with the parcel, the cultivar and the soil type (Drappier et al., 2019; de Rességuier et al., 2020). Harvest date also depends on the timing of veraison and the length of the ripening period. While mid-veraison can either be scored in the vineyard with great precision (Destrac-Irvine et al., 2019), or modelled with good accuracy from air temperatures (Duchêne et al., 2010; Parker et al., 2011; Parker et al., 2013), predicting the length of the ripening period is more challenging. The reason is that grape ripening is not only driven by air temperature but also depends on other factors like vine water status or leaf area to fruit weight ratio (LA/FW). Hence, modelling grape sugar ripeness with air temperatures (e.g., Parker et al., 2020) is less accurate than modelling previous phenological stages with air temperature.

Considerable progress has been accomplished in unravelling the physiological mechanisms involved in grape ripening, but predicting the length of the ripening period remains challenging for viticulturists and winemakers. Moreover, in the context of increasing temperatures, as a result of climate change (IPCC, 2021), grape harvest takes place increasingly early in the season (Duchêne and Schneider, 2005; van Leeuwen and Darriet, 2016), which may negatively impact wine quality (van Leeuwen and Seguin, 2006). Planting slow-ripening varieties, which reach full ripeness later in the season when temperatures are cooler, is an effective adaptation strategy to maintain the production of high-quality wines under a changing climate (van Leeuwen *et al.*, 2019).

1. Physiology of grape ripening

1.1. Sugar accumulation

Sugar accumulation starts at berry softening and follows a sigmoid curve (Suter *et al.*, 2021). Changes in sugar concentration in grape berries during ripening depend on (1) sugar import, (2) sugar metabolism and (3) dilution in a growing berry (Coombe, 1992; Dai *et al.*, 2009). Sugar concentration is impacted by the leaf area/fruit weight (LA/FW) ratio. When LA/FW is limited (below 1 m² of leaf area per kg of fruit), sugar import is reduced more than sugar metabolism and berry water import, resulting in lower sugar concentration in berries (Kliewer and Dokoozlian, 2005; Dai *et al.*, 2009). The effect of water deficit on berry sugar concentration depends on its relative impact on sugar import (generally decreased through a limitation of photosynthesis), sugar metabolism and limitation of water import to the berry. When the water deficit is moderate, the decrease in respiration and water import to the berry is greater than the reduction in sugar import, increasing sugar concentration in berries (van Leeuwen and Seguin, 1994; Dai et al., 2009). When the water deficit is severe, the reduction in sugar loading may be greater than the reduction in water import in the berry, leading to reduced sugar concentration in grapes at harvest (Peyrot des Gachons et al., 2005). When sugar content in berries reaches a plateau, sugar concentration can still increase due to the back-flow of water through the xylem (Keller et al., 2015) or dehydration through the berry skin (Deloire et al., 2021). Sugar content and concentration at ripeness vary considerably with the genotype (Sadras et al., 2008; Suter et al., 2021). Berry ripening is highly asynchronous. Differences in the onset of ripening among berries on the same cluster can be up to 23 days (May, 2000; Bigard et al., 2019). Hence, a berry-per-berry approach allows for deeper insight into the physiological mechanisms involved in grape ripening (Shahood et al., 2020). These authors show that differences (expressed in number of days) in the onset of ripening of berries from the same cluster are approximately in the same order of magnitude as the duration of the ripening of each individual berry, i.e., three weeks. Hence, the perceived duration of grape ripening in field conditions of 45-50 days, is the combined result of asynchronous ripening of berries and the duration of ripening of each berry. For the ripening of each berry, sugar starts accumulating in berries without noticeable expansive growth for 6 days, followed by 20 days of berry growth and sugar loading, resulting in a 26-day ripening period for one individual berry (Shahood et al., 2020). Sugar loading in berries occurs at a constant rate, which implies that when berries increase in volume, the sugar concentration gain slows down.

1.2. Changes in total acidity

Total acidity (or more precisely, titratable acidity) depends mainly on tartrate, malate and potassium content in berries (Bigard et al., 2020). The tartaric acid content in berries is relatively stable after veraison, which means that a decrease in concentration is essentially resulting from a dilution caused by water import in the berry (Ruffner, 1982a; Duchêne et al., 2014). Malic acid reaches a maximum in grape berries at veraison and its breakdown starts as soon as sugars start to accumulate (Rienth et al., 2016). Malate degradation is accelerated under high temperatures, resulting in a lower malate-to-tartrate ratio (Lakso and Kliewer, 1978; Ruffner, 1982a; Sweetman et al., 2014; Rienth et al., 2016). Decreasing malate concentration in berries is driven both by decreases in malate content and dilution by imported water, while decreases in tartrate concentration are driven only by dilution. Hence, the decrease in total acidity in a ripening berry is mainly attributable to changes in malate (Duchêne et al., 2014). Total acidity is also impacted by potassium concentration in the berry, which depends on soil type, climatic conditions and the grapevine variety (Bigard *et al.*, 2020).

1.3. Sugar to total acidity ratio

The use of sugar to total acidity ratio for making harvest decisions goes back to the pioneering era of modern oenology (Amerine and Winkler, 1941). The sugar-to-total acidity ratio was used to characterize 98 different grapevine cultivars (Liu et al., 2006). In physiological studies of grape ripening, sugar to total acidity ratio (S/TA) is of limited use, because grape sugars and organic acids have separate pathways and dynamics during grape ripening (Rienth et al., 2016). It is, however, of major practical interest, because both sugar and total acidity are easy to measure in a production setting. Growers, viticulturists and winemakers monitor sugar to total acidity ratio (S/TA) during grape ripening and start harvesting grapes when this ratio reaches the optimum value for the desired wine style intended. Duteau (1990) suggested that this ratio, when expressed as a function of thermal summation (i.e., degree days), evolves in a strictly linear way during the first four weeks after mid-veraison. Hence, it can be expressed as:

 $y = \alpha x + \beta$

where y = S/TA ratio and x = thermal summation.

Duteau (1990) used August 1st for initializing the thermal summation. In this equation, the slope of the curve (α) represents the ripening speed. At mid-veraison, S/TA is close to zero. Moreover, $-\beta/\alpha$ can be used as a proxy for the timing of mid-veraison.

2. Impact of climate change on grape ripening dynamics and harvest decisions

2.1. Evidence of the impact of climate change on grape sugar concentrations and total acidity

Grape sugar content at harvest has steadily increased over the past decades (Duchêne and Schneider, 2005), while total acidity has decreased (van Leeuwen et al., 2019). Although these changes have several putative causes, including changes in plant material and management practices, the increase in temperatures during grape ripening is likely to be one of the drivers of the increased sugar-to-total acid ratio at harvest. Because the onset of grape ripening (i.e., veraison) occurs earlier in a warmer climate, temperature during grape ripening increases rapidly because of the combined effects of higher temperatures due to climate change and the shift of the ripening period to a warmer part of the season (Molitor and Junk, 2019). The increase in alcohol content in wines across many winegrowing regions worldwide is well documented in Alston et al. (2015), although these authors provide statistical evidence that the contribution of temperature to this phenomenon is limited. Coombe (2007) also considers the influence of air temperature on sugar concentration to be relatively small. However, after the arrest of sugar loading in the berry, grape sugar concentrations often continue to increase through water losses across the berry cuticle (Deloire et al., 2021). Under higher temperatures, these water losses are expected to be greater. Water deficits tend to be more frequent as a result of climate change, in particular in dry-farmed vineyards. Water deficit acts to increase berry sugar concentration, because the reduction in berry size (due to a modified berry water budget) is greater than the reduction in sugar import in the berry (Dai et al., 2009; van Leeuwen et al., 2009), except in situations of severe water deficit when sugar concentration at ripeness can be negatively impacted. There is much less debate about the impact of climate change on total acidity. The positive effect of high temperature on the breakdown of malate is well documented (among many references on the topic see Lakso and Kliewer, 1978; Ruffner, 1982b; Rienth et al., 2016). Because total acidity in grape berries is well correlated to the amount of malate (van Leeuwen and Seguin, 1994), total acidity will be reduced as a result of higher temperatures. Moreover, the water deficit also limits malic acid concentration in grape berries (van Leeuwen and Seguin, 1994).

2.2. Impact of S/TA ratio on wine quality

Increased berry sugar concentration and associated wine alcohol levels, together with reduced acidity in grapes, pose several challenges. Although alcohol has a positive effect on mouthfeel in red wines (Demiglio and Pickering, 2008), consumers tend to prefer wines with lower alcohol levels (Saliba *et al.*, 2013). Lower total acidity and higher pH reduce the microbiological stability of musts and wines (Zamora, 2009; Mira de Orduña, 2010). High pH negatively affects colour intensity in red wine (Morata *et al.*, 2006). These results show that there is a clear need for producers to manage the S/TA ratio to reasonable levels.

2.3. Adaptation through variety choices

Grapevine varieties show a great diversity in the timing of veraison (Duchêne *et al.*, 2010; Parker *et al.*, 2013), in grape sugar accumulation rate (Suter *et al.*, 2021), maximum sugar concentration at the arrest of sugar loading (Suter *et al.*, 2021), total acidity (Duchêne *et al.*, 2020), sugar to total acidity ratio (Liu *et al.*, 2006) and potassium accumulation (Bigard *et al.*, 2020). To contain sugar to total acidity ratios, choosing varieties which reach veraison late in the season and/or with slower ripening dynamics is an interesting option to adapt to in a changing climate. These varieties will ripen later in the season when temperatures are cooler. While the timing of veraison is well documented for a wide range of varieties (Parker *et al.*, 2013), comparative studies of the ripening speed of *Vitis vinifera* varieties based on easily measurable metrics are still rare.

2.4. The challenge of harvest decisions

The timing of harvest has a major impact on wine quality and style, as shown in studies based on sequential harvest dates (Casassa *et al.*, 2013; Bindon *et al.*, 2014; Antalick *et al.*, 2021). As the accumulation of quality-related compounds in grapes is asynchronous, the harvest date is a compromise between optimal technological, phenolic and aromatic maturity. Under warmer temperatures, the decoupling of sugar and anthocyanin accumulation in grape berries is more and more frequent (Sadras and Moran, 2012; Arrizabalaga *et al.*, 2018). As a

result, growers harvest at an increasing number of days after mid-veraison to pick grapes at supposed phenolic maturity (van Leeuwen and Darriet, 2016). Although not necessarily desired, these grapes have high S/TA ratios. Additionally, early determination of predicted harvest dates is important for wine growers to set up logistics, in particular in remote areas where labour is rare (Webb *et al.*, 2007). To date, no easily measurable metrics exist to better assess phenolic and aromatic maturity. Sensory assessment of grape berries allows to fine-tune the harvest date, but this approach poses specific challenges in terms of staff training and the number of samples that can be tested (Le Moigne *et al.*, 2008a; Le Moigne *et al.*, 2008b). Hence, harvest decisions remain mainly based on the S/TA ratio in production conditions.

3. Study objectives

The objectives of this study are (1) to provide an operational model to support harvest decisions, (2) to determine major drivers of ripening speed among climate, soil type and cultivar, and to test additional factors like water deficit, berry weight, or leaf area to fruit weight ratio, (3) to classify Vitis vinifera varieties according to their ripening speed, with the underlying idea that slow ripening varieties are better adapted to a warmer climate, and (4) to test whether $-\beta/\alpha$ can be used to estimate mid-veraison dates. The modified Duteau (1990) model allows the determination of the ripening speed for primary metabolites, assessed through the slope of the sugar to total acidity (S/TA) ratio as a function of thermal summation. This study was performed on two large databases. The first database (DB1) encompasses 10 years across 53 grapevine varieties; the second database (DB2) encompasses 13 years across two grapevine varieties and three different soil types. From these data, the hierarchical effect of climate and grapevine variety (DB1) and the effect of climate, grapevine variety and soil type (DB2) were established. Additionally, the impacts of vine water status as measured by δ^{13} C (Gaudillère *et al.*, 2002), pre-dawn leaf water potential (PDWP), berry weight at mid-veraison and harvest, and other parameters on grape ripening dynamics were investigated for the DB2 database. Using both datasets, it is also assessed whether an estimate for mid-veraison dates can be calculated from the model. The use of the model to select varieties best performing in warm climates (i.e., varieties adapted to climate change) and to fine-tune harvest decisions is discussed.

MATERIALS AND METHODS

1. Description of the databases

1.1. Database 1

Database 1 (DB1) was collected in the VitAdapt common garden vineyard (Destrac-Irvine and van Leeuwen, 2017), which is located at the ISVV campus in F-33882 Villenave d'Ornon, Protected Denomination of Origin (PDO) Pessac-Léognan, Bordeaux, France. 53 varieties (21 white, 32 red) are planted with five replicates in a randomized block design. The parcel was planted in 2009 and data were collected from 2012 through 2022. Data acquired in 2012 were discarded from this analysis because the young vines suffered from excessive water deficits due to their shallow root system (as suggested by water balance analysis, data not shown). Budbreak, flowering and veraison were scored with a frequency of three observations each week and vegetative expression was estimated by measuring pruning weight. Berry sampling started immediately after mid-veraison and lasted until full maturity with one sampling each week. Berry weight, grape sugar and total acidity were measured weekly on each replicate. Vine water status was assessed by measuring δ^{13} C on grape juice at full ripeness (Gaudillère *et al.*, 2002).

1.2. Database 2

Database 2 (DB2) was collected in a dry-farmed commercial winery in Saint-Emilion (van Leeuwen et al., 2004). Three soil types were investigated: gravel soil, heavy clay soil and sandy soil with a water table within access of the roots. The gravel soil is an Arenic Eutridept, containing over 50 % of coarse elements in every layer explored by the root system. Soil water holding capacity is low on this soil, hence vines meet frequently moderate to severe water deficits. The clay soil (Albuquic Hapludalf) contains more than 60 % of clay (particles $< 2 \mu m$) below 0.3 m depth. Rooting depth is restricted to 1.3 m because of soil compaction in deep layers. It has a medium water holding capacity and water deficit is moderate in most vintages. The sandy soil (Sandy Typic Psammaquent) is characterized by a water table varying in depth from 0.6 (winter) to 1.6 m (summer). Roots extend to 1.35 m, so they likely remain in contact with the capillary zone above the water table all through the growing season. Hence, vine water deficit is weak or non-existent on this soil, even in dry years. For each soil type, four rows of Merlot (clone 181) and Cabernet franc (clone 326) were grafted in 1994 on vines with an established root system of the rootstock 3309C. Data were collected from 2004 through 2016. Budbreak, flowering and veraison were scored bi-weekly and vigour was estimated by measuring pruning weight. Leaf area was estimated after establishing the relationship between shoot length and leaf area, separately for primary and secondary shoots, according to Mabrouk and Carbonneau (1996) and fruit weight was measured at full ripeness. Grapes were sampled weekly, starting at mid-veraison until maturity. Berry weight, grape sugar and total acidity were measured on each sampling date (see van Leeuwen et al., 2004 for the methodology used). Vine water status was assessed by measuring δ^{13} C on grape juice at full ripeness (Gaudillère et al., 2002) and by determining PDWP every two weeks between four weeks after anthesis and harvest.

2. Statistical analyses

Grape ripening dynamics were calculated using the function $y = \alpha x + \beta$, where y = S/TA ratio and x = thermal summation, according to Duteau (1990). The S/TA ratio was calculated from the data as the ratio of reducing sugar (g/L) divided by the total acidity as tartaric acid (g/L), then multiplied by 100 for each of the first four weekly berry sampling points after mid-veraison. The multiplication by 100 was carried out to obtain values for $\alpha > 1$, which are easier to interpret.

It was considered to take into account five weekly sampling points instead of four. Results were very similar, on DB2 average difference in R^2 across 78 combinations of soil, year and cultivar was +0.002 (data not shown). The decision to maintain the suggested four data points from the original Duteau model was based on the benefit to growers of being able to establish the slopes with only four versus five data points.

The thermal summation for each of the data points is the sum of average daily temperatures (°C) between July 1st (DOY 182) and the day before the corresponding sampling date. In the original formulation of the model, Duteau used August 1st as a start date. Choosing July 1st instead allows avoiding negative "x" values when mid-veraison takes place earlier (January 1st on the southern hemisphere). A base temperature of 0 °C was chosen according to Parker *et al.*, 2011. In this equation, α represents the ripening speed and was calculated from a linear regression of S/TA ratios and corresponding thermal summations for each year, variety and/or soil combination being considered. No sampling points were taken before mid-veraison. Hence, the start date of the temperature summation does not affect the slope of the equation.

The ratio $-\beta/\alpha$ becomes theoretically a proxy for the timing of mid-veraison. The effect of the year and grapevine variety were investigated for DB1 and DB2 and also the effect of soil type for DB2 using ANOVA. The effects of δ^{13} C, PDWP berry weight, mid-veraison date, yield, and leaf area/fruit weight ratio on α were also investigated by stepwise multiple linear regression for DB2.

RESULTS

1. Climatic conditions

1.1. Climatic conditions in Villenave d'Ornon 2013 - 2022

For the years included in DB1 (2013–2022), temperatures from April through September were plotted against rainfall in July and August for Villenave d'Ornon (Figure 1A). The weather station is located less than 100 m from the experimental parcel. The horizontal line represents the average rainfall from July to August for Villenave d'Ornon, and the vertical line is the average temperatures from April to September (1991–2020). In this way, years can be easily visualized as "cool and wet" (upper left panel), warm and wet (upper right panel), cool and dry (lower left panel) or warm and dry (lower right panel). Note that 2022 stands out as an exceptionally warm and dry vintage.

1.2. Climatic conditions in Saint-Emilion 2004 - 2016

In the same way, the climatic data from years included in DB2 (2004–2016) were plotted with data from a weather station in Saint-Emilion, located less than 500 m from the experimental parcels (Figure 1B). As 30-year averages were not available for this weather station, the horizontal and vertical lines represent the 1991–2020 Villenave d'Ornon

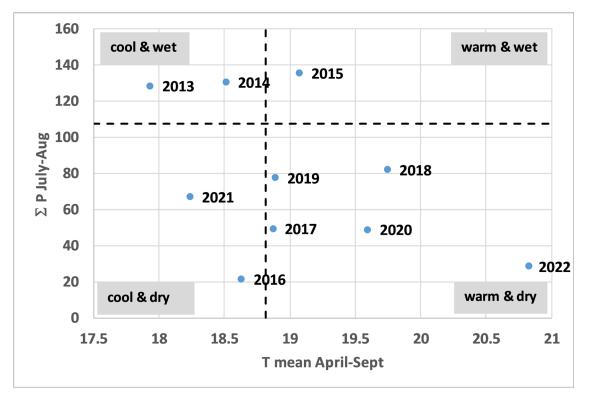


FIGURE 1A. Mean temperature from April to September versus the sum of July to August rainfall in Villenave d'Ornon for the years 2013–2022. The horizontal line represents the mean sum of rainfall from July to August and the vertical line is the mean temperature from April to September in Villenave d'Ornon for 1991–2020.

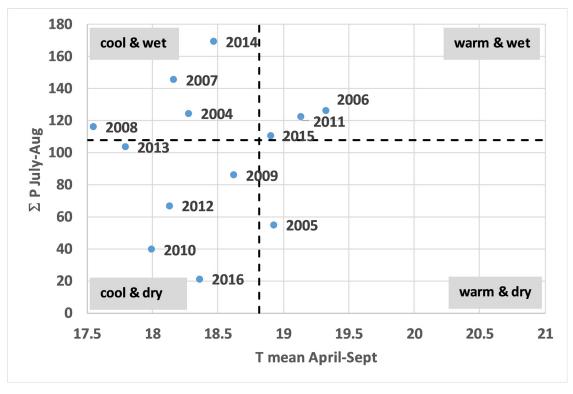


FIGURE 1B. Mean temperature from April to September temperatures versus the sum of July to August rainfall in Saint-Emilion for the years 2004–2016. The horizontal line represents the mean sum of rainfall from July to August and the vertical line is the mean temperature from April to September in Villenave d'Ornon, 1991–2020.

averages for July through August rainfall and mean April through September temperatures, respectively. Climatic conditions are very similar at both sites. For the period where data were available for the two stations (2000–2019), the Saint-Emilion station was marginally cooler (-0.1 °C) and dryer (-4.3 mm).

2. Grape ripening speed is driven by climate, soil and cultivar

2.1. S/TA evolves linearly during the first four weeks after mid-veraison

The sugar-to-acid ratio increases linearly as a function of thermal summation during the first four weeks after mid-veraison. The slope (α) is considered as the ripening speed for technological maturity. Examples are provided in Figure 2A, where the ripening speed is compared for Merlot, planted on three soil types in Saint-Emilion in 2005 (data extracted from DB2) and Figure 2B, where the ripening speed is compared for Carignan, Touriga National and Grenache in 2016 (data extracted from DB1). The linear approximation of the evolution of S/TA over the time range considered here yields excellent agreement with the data (R² ranges from 0.98 to 1.00). Grape ripening speed is much faster on the clay soil compared to the gravel soil and the sandy soil with the water table (α is 29 % smaller on sand compared to clay; Figure 2A). This means that despite similar mid-veraison dates (30 July 2005 on the three soils), the S/TA ratio for Merlot achieved on the sandy soil with the water table after four weeks is reached sooner by Merlot on the clay soil only after three weeks. Grapes from Grenache ripen much faster than those of Carignan, while the ripening of Touriga National is marginally faster compared to Carignan, with an earlier onset of ripening (Figure 2B).

Subsequently, α and β were calculated for each replicate of variety*year on DB1 and each combination variety*soil*year on DB2.

2.2. Grape ripening speed is driven by climate, soil and cultivar

The effects of climate, soil and cultivar on grape ripening dynamics were significant as assessed by ANOVA analysis. As the S/TA ratio was plotted against temperature summation to obtain ripening speed (α) and not the day of the year (DOY), the year effect did not account for temperature differences. For both datasets, the year had the greatest effect on ripening speed. For DB1, the year accounted for 41.2 % of the total variance in ripening speed, while the variety accounted for 25.5 %, with the remainder being residuals. In DB2 the year accounted for 45.0 % of the total variance in ripening speed, the soil accounted for 14.5 %, and the variety for 5.5 %, with the remainder being results are consistent with van Leeuwen *et al.*, 2004 who also found that climate (year effect) was predominant in terroir expression compared to soil and variety.

Based on the DB1 dataset, ripening speed (α) was calculated and compared using a box plot for the 10 years studied (Figure 3A). Differences between the years were substantial: in 2015, the ripening speed was almost two-fold compared to 2021. Considerable differences in ripening speed were

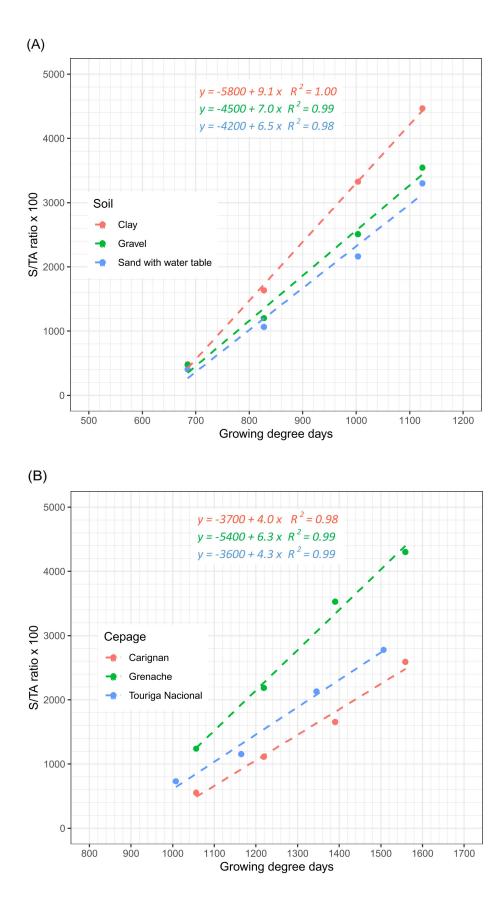


FIGURE 2. (A) Ripening speed for Merlot, on three soil types in Saint Emilion, 2005 (Gravel, Clay and Sand with a water table) and (B) for Carignan, Touriga National and Grenache in 2016. Ripening speed is expressed as Sugar (g/L) to Total Acidity (g tartrate/L) ratio (S/TA*100) as a function of thermal summation. Growing degree days is the sum of the average daily temperature starting from 1 July until the day before sampling.

also observed across the 53 varieties (Figure 3B). Because ripening speed is calculated from sugar accumulation and total acidity decline, the classification is somewhat different from the classification presented by Suter *et al.* (2021) where only sugar accumulation was taken into account. Grenache, Merlot and Sauvignon blanc are considered fast-ripening varieties in both classifications. Semillon stands out as a relatively fast-ripening variety here but not in Suter *et al.* (2021). A rapid decrease in total acidity in Semillon berries can explain these differences. Colombard, Sangiovese, Carignan and Mourvèdre are among the slowest ripening varieties (Figure 3B), not only because they slowly accumulate sugar in their berries (as expressed in concentration, Suter *et al.*, 2021), but also because their total acidity decreases relatively slowly during grape ripening.

Based on the DB2 dataset, ripening speed (α) was calculated and compared in a box plot for the 13 years studied (Figure 4A). Many statistically significant differences between years were observed. To obtain a deeper insight into the drivers of climate on ripening speed, a stepwise regression was then attempted on the DB2 dataset with the independent variables 50 % veraison date (DOY), δ^{13} C, berry weight, leaf area to fruit weight ratio and yield. In the best-fit model based on all variety and soil type data grouped together, berry weight explained 11.6 % of the total variance in ripening speed, with greater berry weight associated with slower ripening. When the two varieties were considered separately, the effect of berry weight on ripening speed is more pronounced for Merlot (R² = 0.323) when compared to Cabernet franc (R² = 0.095; Figure 4B). Whether, for all data together or grouped by variety, none of the other variables considered in the stepwise regression explained a significant portion of the variance in ripening speed.

2.3 The effect of water deficit on grape ripening speed

Professionals (viticulturists and winemakers) know that moderate water deficit can speed up ripening, while severe water deficit can slow it down or even totally block the ripening process. Some articles in the scientific literature tend to confirm this observation (see van Leeuwen *et al.*, 2009 for increased ripening speed under moderate water deficits, Peyrot des Gachons *et al*, 2005 for reduced ripening

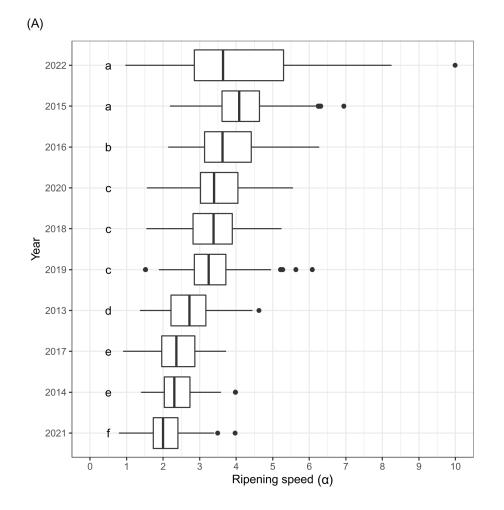


FIGURE 3A. Box plot of ripening speed by year with averages and Tukey significance classifications. Data from DB1 (VitAdapt experiment, Villenave d'Ornon) spanning over 10 years (2013–2022) and 53 grapevine varieties.

(D)	-	
(B)		

Variety

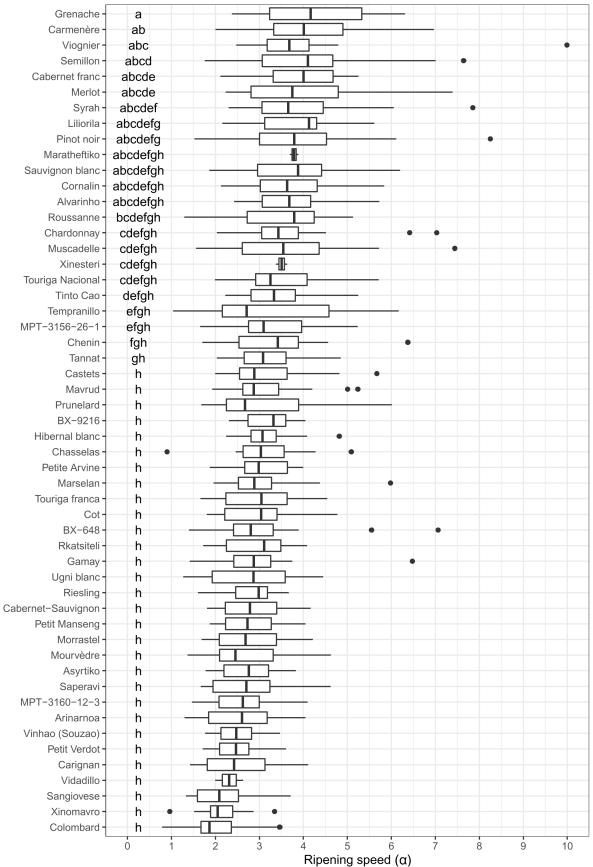


FIGURE 3B. Box plot of ripening speed by grapevine variety and Tukey significance classifications. Data from DB1 (VitAdapt experiment, Villenave d'Ornon) spanning over 10 years (2013-2022) and 53 grapevine varieties. Note that limited data were available for Vidadillo, Xinesteri and Maratheftiko, which explains their limited range in ripening speed.

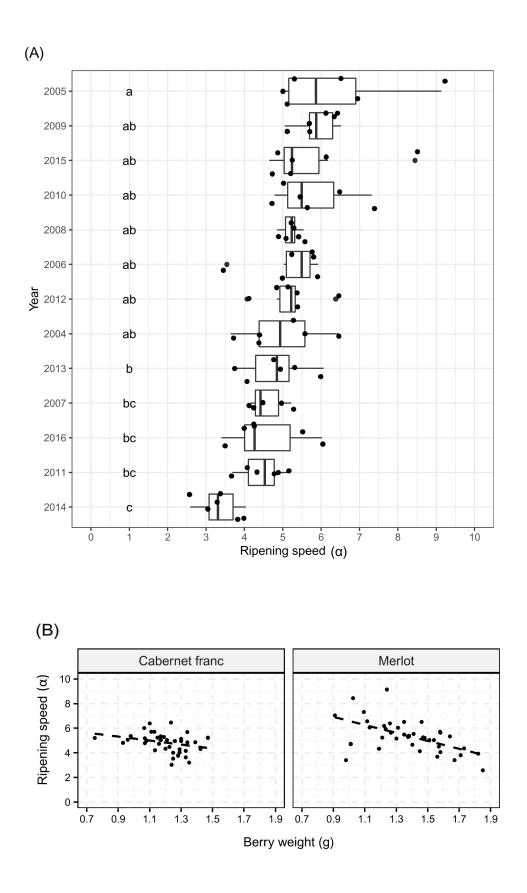


FIGURE 4. Box plot of ripening speed by year with averages and Tukey significance classifications (A) and (B) plot of berry ripening speed as a function of berry weight for Cabernet franc (R2 = 0.095) and Merlot (R2 = 0.323). Data from DB2, Saint-Emilion, covering 13 vintages (2004–2016), two varieties (Merlot and Cabernet franc) and three different soil types.

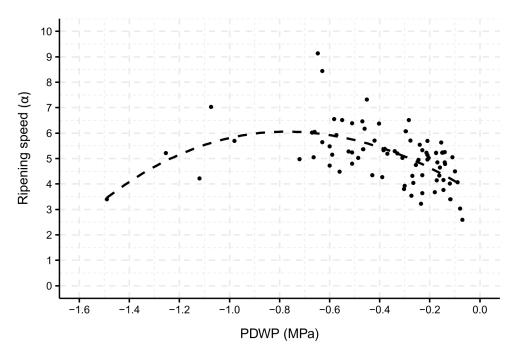


FIGURE 5. Ripening speed as a function of the lowest pre-dawn leaf water potential (PDWP) recorded over the season for Merlot and Cabernet franc planted in three soils over 13 years (2004–2016). A LOESS moving regression line is presented for reference.

speed under severe water deficits and Dai et al., 2009 for an explanation based on modelling). A precise water deficit threshold at which the effect changes from accelerating to limiting grape ripening is, however, lacking. In the stepwise regression implemented on DB2 (section 2.2), vine water status, measured by δ^{13} C, did not stand out as a driver of ripening speed. This was probably due to the colinearity with berry weight and also the fact that $\delta^{13}C$ may not be precise enough to show such an effect. On DB2, pre-dawn leaf water potential (PDWP) was measured bi-weekly from four weeks after anthesis until harvest. The most negative value of PDWP was extracted from DB2 for each combination year*soil*variety. Ripening speed is plotted as a function of minimum PDWP and a LOESS moving regression line is presented for reference (Figure 5). Ripening speed increases with increasing water deficits down to PDWPs of around -0.8 MPa and then decreases for more severe water deficits. Due to the experimental setting in field conditions with no control over the level of water deficit stress, the number of data points for severe water stress was limited and only two varieties were considered (Merlot and Cabernet franc). Hence, more research is needed to verify the exact level of the water deficit threshold limiting ripening speed for different varieties and environmental conditions.

2.4. Extrapolation of mid-veraison dates from the modified Duteau model

S/TA is very low at mid-veraison. Hence, when S/TA is set to zero, $-\beta/\alpha$ should represent a thermal summation close to the actual mid-veraison date. This thermal summation

was transformed into the closest day of the year (DOY) and subsequently compared to observed mid-veraison dates, for the DB1 (VitAdapt, Villenave d'Ornon, Figure 6A) and DB2 (Saint-Emilion, Figure 6B). The correlation between measured mid-veraison dates and mid-veraison estimated from $-\beta/\alpha$ is very good (0.85 and 0.95) and RMSE is 9.44 and 2.77 for DB1 and DB2, respectively (p < 0.001 in both cases). Figure 6A was redrawn with specific adjustments for each year (Supplementary Figure S1). Slopes and intercepts varied across years but were not related to average temperature during the first four weeks after mid-veraison (data not shown). Mid-veraison scoring in the field is very time-consuming and these results show that reasonable mid-veraison date estimations can be obtained from the modified Duteau grape ripening model.

2.5. Comparing the ripening speed with the real duration of the ripening period and S/TA ratios at harvest

DB2 was collected in a production setting, allowing the comparison of calculated ripening speed against the real length of the period from mid-veraison to harvest. There was a significant correlation between these two metrics, meaning that increased ripening speed resulted in a shorter duration from mid-veraison to harvest (Figure 7A). While significant, the correlation however, was not very strong. Interestingly, the correlation between the S/TA ratio at harvest and ripening speed was much better (Figure 7B). This means that professionals may push parcels with quick ripening berries to greater technological ripeness, rather than harvesting them more quickly after mid-veraison.

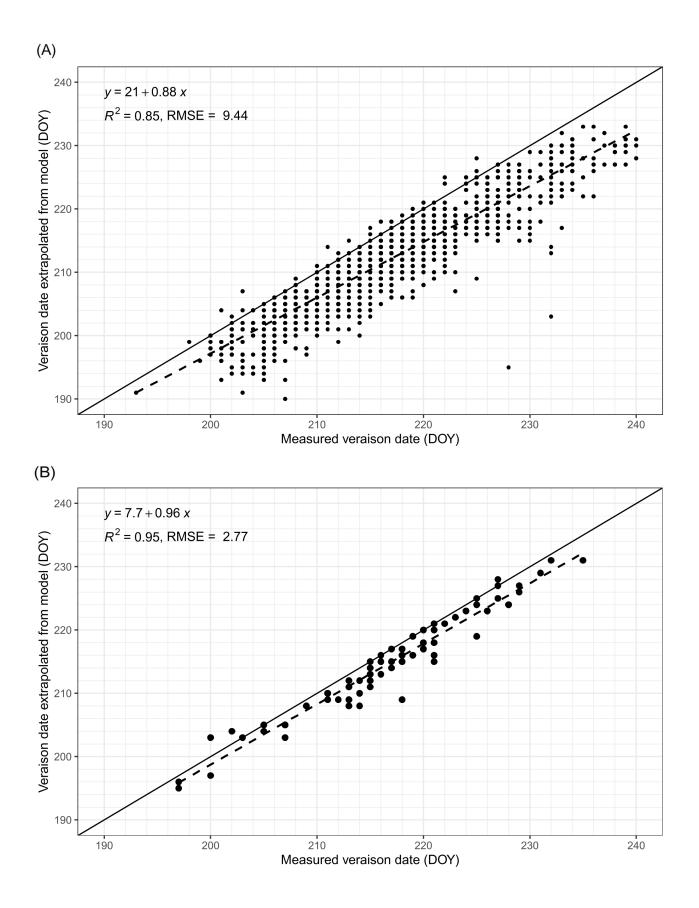


FIGURE 6. Estimated mid-version dates by converting the thermal summation $-\beta/\alpha$ into the closest day of the year (DOY) for (A) DB1 – VitAdapt and (B) DB2 – Saint-Emilion, regressed against measured mid-version dates.

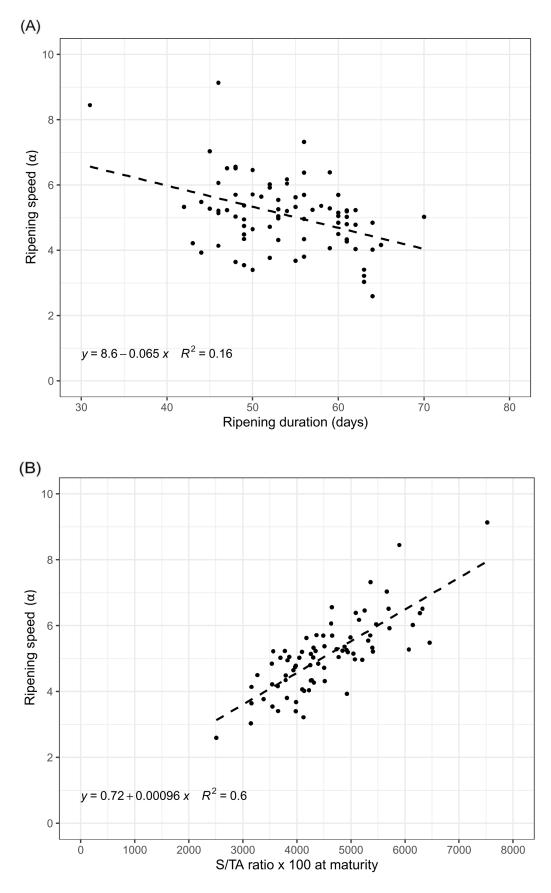


FIGURE 7. Ripening speed plotted versus length of the ripening period from mid-version to harvest (A) and ripening speed versus S/TA ratio*100 at harvest (B) both from DB2.

DISCUSSION

1. Complementary approaches for studying grape ripening dynamics

Several authors have shown that berry ripening is asynchronous, meaning that different berries from the same cluster start ripening at different time points, spanning over up to three weeks (May, 2000; Garcia de Cortázar-Atauri et al., 2009; Bigard et al., 2019). Hence, a deeper insight into the physiological and transcriptomic mechanisms involved in grape ripening requires (1) studying each metabolite accumulated or metabolized during ripening separately and (2) using a single-berry approach or sorting berries according to their density. Modelling, either at the organ or plant level (Dai et al., 2009; Garcia de Cortázar-Atauri et al., 2009) or at the crop level (Leolini et al., 2019; Suter et al., 2021) is another promising tool to deepen our mechanistic understanding of grape ripening. These methodologies, however, are not applicable in a production setting, because the sampling protocols are too time-consuming and the models developed too complex. Viticulturists and winemakers need a straightforward approach to assess grape maturity, based on easily accessible metrics. S/TA ratio is commonly used in commercial wineries to monitor grape ripening and has the advantage to integrate two grape attributes related to wine quality and balance: sugar concentration, which determines wine alcohol content and total acidity, associated with the sensory perception of "freshness" and wine stability.

Previously, Sadras and Petrie (2012) used a simple model based on a fixed increase in berry sugar content per week to predict the timing of harvest. These authors show that the model can be improved by taking into account variety-specific adjustments: Cabernet-Sauvignon accumulates sugar more slowly than Syrah, while Chardonnay accumulates sugar more quickly. Their model is also improved by regional parameterization, but not by replacing days with temperature summations. Varieties with a high rate of change in soluble solids reached ripeness earlier in the season (Sadras *et al.*, 2008).

published Another operational model was by Sadras and Petrie (2011). It is somewhat similar in concept to the one published herein, the major difference being that these authors only considered sugar accumulation and not S/TA ratios. Sadras and Petrie define a maximum increase in the rate of sugar concentration for a range of varieties and regions in Australia. Following, they consider several factors resulting in a slower accumulation rate defined as the gap between the maximum and actual sugar accumulation rate. Among the climatic parameters tested, high vapour pressure deficit (VPD) stands out as one having the most consistently slowing effect on sugar accumulation, although the effect of rainfall during the ripening period is also significant in some cases. The approach presented by Sadras and Petrie is useful for the Australian wine industry but would need significant parameterization with large datasets before it could be applied to other grapevine varieties and wine-growing regions.

Besides sugar, total acidity is also a parameter used by growers in making harvest decisions. In our model, S/TA has the advantage of being based on both sugar and TA to assess grape ripening dynamics. Most modelling approaches try to predict a calendar date or thermal summation when a given level of sugar is accumulated (Parker *et al.*, 2020). With such approaches, other factors impacting grape ripening, like water deficit or LA/FW ratio, can confound those predictions. With the modified Duteau model, the output is *ripening speed* instead of *sugar threshold date*. In this way, all factors accelerating or slowing down grape ripening are taken into account, although not automatically identified, as discussed in the following section.

Here, the model was tested and demonstrated to be valid over a wide range of temperature conditions, with average temperatures during 28-days post-veraison in Villenave d'Ornon (DB1) ranging from 19.8 °C (2013) to 25.0 °C (2022). Because the model is linear and not capped for high temperatures, it remains to be seen up to which temperature threshold the model will remain valid.

While Duteau (1990) initialised temperature summation on August 1st, in the modified formulation a start date of July 1st (January 1st in the Southern Hemisphere) is proposed to avoid negative « x » values when mid-veraison takes place in July (January on the SH).

2. The effect of berry weight and water deficit on grape ripening dynamics

The stepwise regression of the effects of 50 % veraison date (DOY), δ^{13} C, berry weight, leaf area to fruit weight ratio and yield on DB2 (Saint-Emilion) only showed a significant effect of berry weight. Larger berries ripen slower than small berries, which may be due to the dilution of a constant phloem sugar unloading rate in a bigger volume, and the fact that larger berries have a higher metabolic cost (Dai et al., 2009). Surprisingly, vine water status, assessed by the measurement of $\delta^{13}C$ on grape juice at harvest (Gaudillère et al., 2002), did not turn out to be a significant driver of ripening speed. Wine professionals often refer to "stuck ripening" in water stress conditions and in the literature, the effect of vine water status is shown, either as an accelerating factor on ripening speed when the water deficit is moderate (van Leeuwen and Seguin, 1994; van Leeuwen et al., 2009), or a slowing factor on ripening speed when severe (Peyrot des Gachons et al., 2005). Hence, it was considered that the effect of water deficit on grape ripening speed could either be masked because of co-linearity with berry weight (which is much impacted by water deficit, Ojeda et al., 2001; Triolo *et al.*, 2018), or that δ^{13} C is not reliable enough as an indicator of vine water status to show this putative effect. When PDWP was regressed against ripening speed, the water deficit turned out to increase ripening speed down to a PDWP of approximately -0.8 MPa and reduced when the water deficit was more severe water (Figure 5). The number of data points with severe stress, however, was limited and it needs to be investigated if a similar threshold holds across other varieties and environmental conditions. A PDWP of -0.8 MPa falls in the class of "moderate to severe" water deficit (van Leeuwen *et al.*, 2009), meaning that slow ripening as a result of water deficits may happen less frequently than professionals tend to claim.

3. The use of grape ripening speed as a tool for harvest decisions

On a given vineyard block, the timing of full ripeness depends on the date of mid-veraison and the length of the ripening period. The date of mid-veraison can either be observed with great precision in field conditions or estimated using the GFV model (Parker et al., 2011; Parker et al., 2013). Here we present an operational model to calculate the ripening speed of primary metabolites as early as four weeks after mid-veraison. The input data for this model are limited to mean daily temperatures, grape sugar and grape total acidity sampled at weekly intervals. This data can easily be acquired in a production setting. Hence, the timing of harvest can be estimated several weeks in advance. Beyond the S/TA ratio, grape harvest date also depends on phenolic ripeness, aromatic ripeness and sanitary status of the grapes, which taken together most likely account for the noise seen in the relationship between ripening speed and the actual harvest date (Figure 7A). Such complementary information needs to be gathered in the last two or three weeks before harvest to fine-tune the exact date of harvest.

The differences in ripening speed measured in this study are considerable, depending on the year (Figures 3A and 4A) or the variety (Figure 2B and 3B). Soil type also turns out to have a considerable effect on the ripening speed (Figure 2A). A two-fold higher ripening speed does not mean, however, that the ripening period will be two times shorter. Varieties with quicker ripening berries in the first four weeks after mid-veraison tend to be harvested at higher S/TA ratios. The same is true for years and soil types, with grapes harvested at higher technological ripeness in years and on soils where ripening is faster.

4. Using the ripening speed of individual varieties as a tool for adaptation to climate change

As a result of warming temperatures under climate change, grape ripening occurs increasingly early in the season, exposing grapes to high temperatures during the ripening period (Duchêne et al., 2005; van Leeuwen et al., 2019). For the production of high-quality wines expressing the place of origin (so-called terroir wines), ripening under relatively temperate conditions is mandatory (van Leeuwen and Seguin, 2006), because it guarantees a balance between sufficient but not excessive grape sugar (and hence wine alcohol) and the right amount of organic acids to provide a sensation of freshness in the mouth-feel while avoiding excessive acidity. Moderately cool ripening conditions are also important for aromatic complexity because hot temperatures during grape ripening induce undesirable cooked fruit aromas in wine (Allamy et al., 2018; van Leeuwen et al., 2022). The variability of the timing of ripeness among Vitis vinifera varieties is huge and spans more than two months when planted in the same environment (Robinson et al., 2013). The use of late ripening varieties is an important lever to delay the ripening period later in the season, when temperatures are lower compared to the warmest summer months (July and August in the Northern Hemisphere; January and February in the Southern Hemisphere). The timing of ripeness depends (1) on the date of veraison and (2) on the duration of the ripening period. Among other factors, addressed in the present study, ripening speed is also partly a function of the variety. In the context of climate change, it makes sense to choose varieties that reach veraison later and/or ripen their grapes more slowly. The classification presented in Figure 3B allows a comparison of 53 varieties based on their ripening speed. This classification is based on the dynamics of the S/TA ratio during grape ripening. Hence, a slow ripening variety is a variety that either more slowly accumulates sugar (see Suter et al., 2021 for a classification based on sugar accumulation rate alone), or slowly metabolizes organic acids (mainly malate), or both. It is striking that the slowest ripening variety in this classification (Colombard) has a ripening speed (α) two times lower than the quickest ripening variety (Grenache). Hence, Colombard needs twice the thermal time after veraison to reach similar S/TA ratios as Grenache.

5. The use of $-\beta/\alpha$ to estimate mid-veraison dates

Mid-veraison scoring in the vineyard is very time-consuming and, for this reason, not systematically implemented in commercial wineries. Here we show that the modified Duteau model can provide good estimates for mid-veraison dates. The estimation is very good when a limited number of varieties is considered (RMSE is 2.77 for DB2, encompassing two varieties). When 53 varieties are considered together (DB1) the estimation is less precise (RMSE=9.44) but remains reasonably good, given the fact that observed mid-veraison dates span over 48 days. Estimated mid-veraison dates show, on average, an early bias of three to seven days in DB1 (for early and late varieties, respectively) and of two to three days in DB2 (for early and late varieties, respectively). This bias likely results from the fact that the S/TA ratio at mid-veraison is low, but not zero. Hence, errors of bias-corrected estimates of mid-veraison dates from the modified Duteau model rarely exceed a few days. This precision is acceptable in a commercial winery setting. It should be noted that the model-based estimates can replace precise mid-veraison scoring, but some level of field observation of the progress of veraison is still needed for ripening speed modelling, as the first S/TA sampling point needs to be scheduled within the first seven days after mid-veraison.

CONCLUSION

Great progress has been made recently in the understanding of the physiological mechanisms involved in grape ripening. The models published in the scientific literature and the associated sampling protocols are, however, too complex to be deployed in a production setting. With the data presented here, we validate a simple modified Duteau model to estimate grape ripening speed, based on the evolution of the S/TA ratio as a function of thermal summation during the first four weeks after mid-veraison. The robustness of the model was validated on two large data sets covering multiple years, varieties and soil types and provides a classification of 53 varieties based on ripening speed. This ripening speed was found to be highly dependent on year, soil type and variety and tends to be faster when berries are smaller. The water deficit increases ripening speed until a certain level and decreases when the water deficit is more intense. Mid-veraison dates can be accurately estimated from the model. These results can be used by winemakers, viticulturists and consultants to fine-tune harvest decisions and allow the identification of slow-ripening varieties better adapted to warm climates.

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