ASYNCHRONOUS DYNAMICS OF GRAPEVINE (*VITIS VINIFERA*) MATURATION: EXPERIMENTAL STUDY FOR A MODELLING APPROACH

I. GARCIA DE CORTAZAR-ATAURI[1]*, N. BRISSON[1], N. OLLAT[2], O. JACQUET[3] and J.-Ch. PAYAN[4]

1: Unité Agroclim, INRA, Site Agroparc, Domaine Saint-Paul, 84914 Avignon cedex 9, France
2: UMR Ecophysiologie et Génomique Fonctionnelle de la Vigne, ISVV, Université Bordeaux 2 - INRA, BP 81, 33883 Villenave d'Ornon cedex, France
3: Chambre d'Agriculture Vaucluse, 2260, route de Grès, 84100 Orange France
4: ITV-France – Unité de Nîmes, Domaine Donadille, 30230 Rodilhan, France

Abstract

Aims: An analysis of the asynchrony and dynamics of dry matter accumulation and water content in the grape berries growth period (*Vitis vinifera* L.) was carried out on a macroscopic scale (berry population). Experimental studies suggest a framework to evaluate the asynchronous nature of grapevine maturation and to propose a simple model to simulate dry matter and water dynamics.

Methods and results: A methodology based on the measurement of the density of the berries was used, providing information on the dry matter, water content and distribution of the berry populations during the veraison - harvest period. The main experiment was carried out in Rhone valley vineyards on the « Grenache N » and « Syrah » varieties. Additional information was gathered in Burgundy vineyards on « Pinot noir » and « Chardonnay » varieties. A relationship between the sugar content (°Brix) and water content of a berry was observed, which was robust and identical for all varieties. The asynchronous nature of berry growth was confirmed and densimetry allows quantifying the homogeneity of harvest. A model was proposed to modelling dry matter growth, based on thermal time and final potential dry weight. A single relationship was obtained for the two varieties studied which seemed to be independent of field conditions (soil and year). To model water content dynamics (or °Brix, using the relationship obtained between them), two components were defined, one of which is related to the berry phenological stage and the other depends on the water status of the plant.

Conclusion: The results provide a conceptual framework to better understand and represent the dynamics of dry matter accumulation and water content of a population of grape berries, and to evaluate the asynchronous nature of grapevine maturity.

Significance and impact of the study: The models and relationships proposed could be used as a tool to better identify and understand key factors and processes occurring in the field until the detailed processes of berry growth are better understood and can be incorporated into the model. This model could be incorporated into a crop model of vine growth.

Key words: berry, modelling, dry mass, asynchrony, water content

Résumé

Objectif de l'étude : Une analyse de l'asynchronie et des dynamiques de la matière sèche et de la teneur en eau durant la maturation du raisin a été réalisée à une échelle macroscopique. L'étude expérimentale a permis de proposer un cadre pour évaluer le caractère asynchone de la maturation, ainsi que de présenter un modèle simple pour simuler les différentes dynamiques.

Méthodes et résultats : La méthodologie basée sur la mesure de la densité des raisins, la densimétrie, a permis d'obtenir des informations sur la matière sèche, la teneur en eau et la distribution des populations de raisins durant la période véraison - récolte. La principale expérimentation a été réalisée dans le vignoble de Côtes du Rhône pour les cépages Syrah et Grenache. D'autres informations ont été recueillies dans le vignoble de Bourgogne pour les cépages Pinot noir et Chardonnay. Une relation stable et identique pour tous les cépages a été observée entre la teneur en sucre (°Brix) et la teneur en eau de la baie. Le caractère asynchrone de la maturation a été confirmé par la méthode de densimétrie qui a permis par ailleurs d'évaluer l'homogénéité de la récolte. Un modèle pour simuler la croissance de la matière sèche de la baie a été proposé, basé sur le temps thermique et le poids final potentiel de la baie. Une seule relation a été obtenue pour les deux variétés étudiées, laquelle semble indépendante des conditions environnementales (sol et année). Pour modéliser la teneur en eau de la baie (ou le °Brix, en utilisant la relation obtenue entre eux), deux composantes ont été définies : une composante qui représente le développement de cette teneur en eau et une autre qui dépend de l'état hydrique de la plante.

Conclusion : Les résultats de cette étude fournissent un cadre conceptuel pour mieux comprendre et représenter les dynamiques de l'accumulation de la matière sèche et de la teneur en eau d'une population de baies en prenant en compte le caractère asynchrone de la maturation.

Significativité et impact de cette étude : Les modèles et relations proposés peuvent être utilisés comme outils pour mieux identifier et comprendre les facteurs et les processus qui ont lieu sur le terrain, et dans lesquels les nouvelles connaissances acquises sur la croissance et le développement des baies de raisin peuvent être intégrées. Ces modèles peuvent être incorporés dans un modèle de culture adapté à la vigne.

Mots-clés : baie, modélisation, matière sèche, asynchronie, teneur en eau

manuscript received the 21th of July 2008 - revised manuscript received the 2nd of June 2009

*Corresponding author: igarcia@avignon.inra.fr

J. Int. Sci. Vigne Vin, 2009, **43**, n°2, 83-97
©Vigne et Vin Publications Internationales (Bordeaux, France)

4-inaki 24/06/09 19:56 Page 84

INTRODUCTION

In viticulture, the notion of maturity is rather vague (Riou, 1994) since the final product sought is not the same for all vineyards. In fact, maturity and quality cannot be separated. Quality depends on a balance, specific to the vineyard, between sugars, acids, aromatic constituents and phenolic compounds present in the berries (Holt *et al.*, 2008a, b). However, up to now and in most vineyards, the sugar content is considered to be the most widely used indicator of maturity and quality (Champagnol, 1984; Riou, 1994). The maturity stage has been characterized in phenological scales only according to sugar concentration, such as the « stage 38 » on the modified scale of Eichhorn and Lorenz (Coombe, 1995) or « stage M » on the scale of Baggiolini (1952), when juice from berries reaches 20°Brix (Dry and Coombe, 1988).

Grape maturity is characterized by considerable asynchrony between berries within a bunch or a given plant. Coombe (1992) and May (2000) found differences in maturity of up to 23 days between two bunches from the same plant. These differences could be attributed to the spread of fruit setting, which affects the onset of ripening. Moreover many cultural and environmental parameters (such as irrigation, water balance, exposure, wind, pruning) could affect maturation (Freeman *et al.*, 1980; McCarthy, 1997, 1999, 2000; Ollat and Gaudillere, 1998; Pool, 2004; Ojeda *et al.*, 2002;2005; Pieri and Fermaud, 2005; Tarara *et al.*, 2005; Santesteban and Royo, 2006; Holt *et al.*, 2008a, b).

The developmental change in fresh and dry weight of the grape berries follows a double sigmoid curve. It has been divided into three phases (Coombe and McCarthy, 2000; Ojeda *et al.*, 2002; Ollat *et al.*, 2002; Matthews and Shackel, 2005) : phase I is a phase of cell multiplication and enlargement; phase II is an intermediate phase where growth slows down prior the onset of ripening; and phase III is a phase of cell enlargement only. These phases occur during the period from flowering to maturity, and veraison (a French term for the point at which berries begin to turn colour and become soft) plays an important role as an indicator in the dynamics of the growth of the berry. Some authors have proposed two growth phases only (Staudt *et al.*, 1986; Ollat and Gaudillère, 1998), phase II being the final part of phase I. Phases I and II are characterized by a significant accumulation of organic acids (especially malic and tartaric). The water status of the plant and the trophic competition between the leaves and the fruit during these periods have a major effect on the weight of the berries at veraison and maturity (Coombe and McCarthy, 2000; Ollat *et al.*, 2002; Ojeda *et al.*, 2001;2002), which is not related to the number of cells formed in the pericarp of the berry (Ojeda *et al.*, 2001). The duration of phase II is dependent on the variety, the soil and the weather conditions (Matthews and Shackel, 2005). Ojeda *et al.*, (2001) showed that severe water shortage can shorten or eliminate this phase.

Phase III berry growth extends from veraison to harvest. At veraison, sugar accumulation and berry softening occur before colour changes. This phase is characterised by cell enlargement and a great accumulation of sugars (hexoses, glucose and fructose) concomitant with a fall in the concentration of organic acids and a softening of the tissues. The effect of post-veraison water stress on the final fresh weight of the berries is unclear (Roby and Matthews, 2004): McCarthy (1997, 1999, 2000) reports no effect, while Ojeda *et al.* (2002;2001) explain that it affects cell elongation. On the other hand Coombe and McCarthy (2000) show that a loss of volume may occur at the end of maturation (from 18-20 °Brix) by a blockage of the xylem flow combined with a rapid loss of water by transpiration, thereby increasing the sugar concentration (°Brix).

Mechanistic crop models developed in the last thirty years offer a conceptual framework to study the dynamic interactions between the plant, the soil, the climate and the farming practices on a field scale (Sinclair and Seligman, 2000; Brisson *et al.*, 2009). Although fruit growth modelling is very important for yield prediction, this topic is not well documented. Lescourret and Genard (2005) presented the main studies on fleshy fruit modelling: photosynthesis-driven models for different species (grapes, apples, kiwifruit, olives, peaches and tomatoes); water accumulation modelling in fruit driven by transpiration and mechanistic models. For the grapevine, Fanizza and Colonna (1996) and Ollat and Gaudillere (1998) proposed different mathematical expressions to simulate the double sigmoid curve describing the growth of berries developing under various conditions. In addition, Ollat and Gaudillère (1998) consider that this approach, as well as being a convenient descriptive process, can have a biological significance (Pavel and Dejong, 1993).

In plant modelling, the use of proper time scales is of the utmost importance. The notion of thermal time is widespread in crop models (Bonhomme, 2000). This concept represents the effect of temperature on growth and allows a better expression of the length of the different phases of development as compared with calendar dates. For fleshy fruit models, thermal time has been used as a scale for dry matter growth (Lechaudel *et al.*, 2005; Lescourret and Genard, 2005) and cell extension (Lechaudel *et al.*, 2007). For the grapevine, several studies show that the thermal time between flowering and veraison is relatively constant between sites for the variety Syrah (*Vitis vinifera* L. cultivar « Syrah ») (McCarthy, 1999;

©Vigne et Vin Publications Internationales (Bordeaux, France)

Ojeda *et al.*, 2001; García de Cortázar-Atauri, 2006), but in fact in most studies, this period is expressed in number of days (Staudt *et al.*, 1986; Ollat *et al.*, 2002; Ojeda *et al.*, 2002 ; Coombe and McCarthy, 2000; Matthews and Shackel, 2005), leading to difficulties in making a comparative analysis. Coombe (1980) and McCarthy (1999, 2000) discuss the value of using only the degree-day concept between veraison and maturity. They consider that degree-days has proved useful to predict phenological stages in some regions, but in warm to hot regions, berry development has to be combined with plant water status (McCarthy, 2000).

Finally, as for all fleshy fruits, understanding the dynamics of water in the berry is very important, since on the one hand the water will be used to transport berry components (e.g. sugar, which represents a big fraction of dry weight) and secondly it will determine fresh weight at harvest. However, the modelling of water dynamics during fruit development is not very well documented. Moreover, water accumulation is regulated in eco-physiological models by complex processes such as fruit resistance (Bussières, 1994) or by the balance between xylem and phloem fluxes and transpiration (Lescourret and Génard, 2005). For grapevine, Ollat and Gaudillère's (1998) model simulates fresh weight accumulation over time.

In this study, we present results obtained using an experimental approach to study the asynchrony and dynamics of dry matter accumulation and water content in the grape berry growth period on a macroscopic scale (a population of berries). This experiment will try to observe whether there are relationships between different berry components and their dynamics by using simple measurements, without working at the organ scale. The results obtained will be used to propose a simple modelling approach to simulate berry population growth as a function of temperature and plant water status. Densimetry is proposed in order to take account of asynchrony in maturity. The experiment is based mainly on the monitoring of *Vitis vinifera* L. cultivars « Grenache N », « Syrah » berry growth period from the vineyards of the Rhone valley. Data from a Burgundy vineyard were used (varieties « Pinot noir » and « Chardonnay ») to confirm some of the results obtained.

MATERIALS AND METHODS

1. Experimental design

The experiment was carried out between 2003 and 2005 on grapevine plots situated in the vineyards of the Rhone valley and Burgundy (table 1). In every case, the viticultural practices conformed with the usual techniques

Table 1 - Description of the different experiments.

	Plot	Location	Rows Orientation	Density (plant m^{-2})	Pruning	Varieties	Rootstock	Year	Irrigation	Code Plot
Rhone valley	Serres	44°04' N-5°03' E	North - East	0,36	Cordon Royat	Grenache N	R 110	2003	232 mm *	SI03
								2003	No	SS03
								2004	No	SGr04
								2005	No	SGr05
						Syrah	RU 140	2004	No	SSy04
								2005	No	SSy05
	Piolenc	44°10' N - 4°08' E	North	0,44	Cordon Royat	Grenache N	Fercal	2004	No	PGr04
								2005	No	PGr05
						Syrah	161 - 49C	2004	No	PSy04
								2005	No	PSy05
	Bolchet	43°47' N - 4°24' E	North – East	0,39	Cordon Royat	Grenache N	RU 140	2004	No	BGr04
						Syrah	RU 140	2005	No	BSy04
Burgundy	Marsannay	47°16 N - 4°59' E	East	1	Double Guyot	Pinot Noir	SO4	2005	No	MPiN05
						Chardonnay	SO4	2005	No	MChy05
	Mont Battois	47°02' N - 4°49' W	East	1	Double Guyot	Pinot Noir	SO4	2005	No	MbPiN05

	Measurements realized in the experimental plots			
Code Plot	Phenology	Densimetry, dry and fresh matter weight (times)	Harvest (°BRIX)	Other measurements
SI03	50% Flowering and 50% Veraison	7	24	-
SS03		8	24	-
SGr04		7	24	-
SGr05		6	24	Yes **
SSy04		7	24	-
SSy05		6	24	Yes **
PGr04		8	23	-
PGr05		7	24	Yes **
PSy04		8	24	-
PSy05		7	24	Yes **
BGr04		4	24	-
BSy04		4	24	-
MPiN05		4	20	-
MChy05		4	20	-
MbPiN05		4	20	-

* Between flowering and harvest; ** Extra samples of 200 berries between flowering and veraison

©Vigne et Vin Publications Internationales (Bordeaux, France)

4-inaki 24/06/09 17:18 Page 86

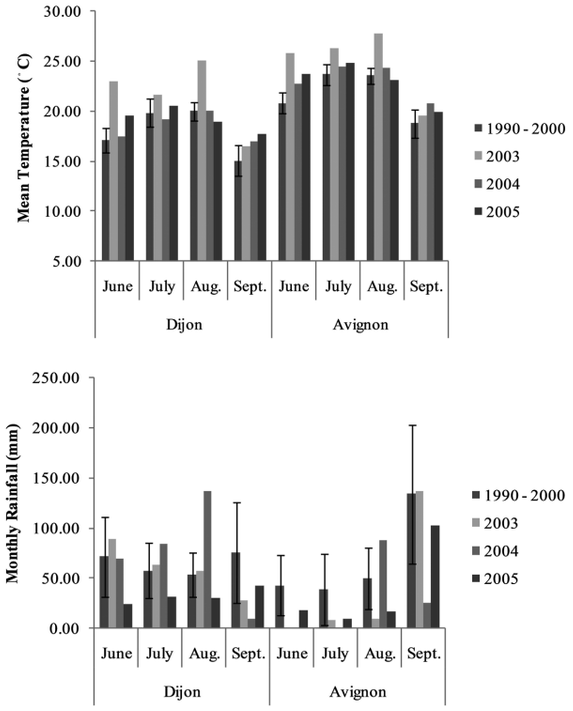


Figure 1 - Mean temperature (Tmean) and rainfall in the Rhone Valley and Burgundy areas during the growing seasons (April – October) of the three studied years (2003, 2004, 2005) compared to their means for 1990-2002.

practised in these regions. The weather data come from an automated weather station (WMO standards) located on the plots. The temperature and rainfall patterns of the flowering-harvest period (June – September) of the three years were compared with the mean for 1990-2002 (figure1). Years 2004 and 2005 were hot and dry, while 2003 was very hot in France (Chuine *et al.*, 2004).

Each plot was comprised of 120 plants growing on a homogeneous soil. Grapevine plants were sampled randomly without ever sampling twice on the same plant.

2. Phenological stages and harvest date

Two stages were recorded according to the modified scale of Eichhorn and Lorenz (Coombe, 1995): flowering (stage 23) and veraison (stage 35). The flowering and veraison stages were observed when 50% of the flowers of berries had reached that stage (Williams *et al.*, 1985; Carbonneau *et al.*, 1992; Riou, 1994).

The harvest day was defined as corresponding to a concentration of 24 °Brix. This choice was based on the observation that at this stage, the relationship between berry dry matter mass and °Brix becomes erratic (figure 2). This stage was determined in all the plots, except in Burgundy since it was not possible to reach this °Brix level because of the climatic conditions (figure 2). In Burgundy, fruit was harvested according to the decision of the wine grower. The phenological stages observed in each plot are represented in table 1.

3. Densimetry measurements between veraison and maturity

To characterise their maturity status, berries were separated according to their density, using a technique proposed by Singleton (1966). Berries of equivalent density are separated by immersing them in saline solutions of increasing concentration, affected by the flotation of the berries which is characteristic of their maturity stage. A preliminary study (data not shown) had determined the appropriate salinity scale to the range of sugar concentrations in the grapes according to 10 classes, interpreted as « Maturity classes » (table 2). For this, 12 bunches per plot were sampled randomly once a week (in the morning) between veraison and maturity on 12 different plants at each sampling. The berries were de-stalked by cutting the base of the pedicel so as to limit the effects of osmosis between the berry and the saline medium. Once classified, the berries were counted, weighed. The °Brix level was measured with a refractometer (Fabre RCT 30, Magenta, France) on a sub-sample of 10 berries taken at random in each class. The remaining berries were dried for 120 hours in an oven at 70 °C before being weighed again.

4. Other measurements of dry and fresh weight

In order to assess the flowering – veraison growth period, four extra samples of 200 berries each were collected once a week after flowering in 2005 to determine fresh and dry mass. Berries were dried using the method presented above. In this case, the densimetry measurements were not made because all the berries belonged to the same « Maturity class ».

5. Calculation of weather variables

The thermal time was calculated in growing degree days (G_{DD}) from flowering to maturity using the formula:

$$\text{if} \quad T_m(n) - T_b < 0 , \quad g_c(n) = 0$$
$$\text{if } T_m(n) - T_b \geq 0 , \quad g_c(n) = T_m(n) - T_b$$
$$G_{DD} = \sum_{n=F}^{H} g_c(n) \qquad (1)$$

where $T_m(n)$ is the mean air temperature on day n; T_b is the base temperature for development, in this case 10 °C (Winkler *et al.*, 1962; Carbonneau *et al.*, 1992); $g_c(n)$ is the growing degree days calculated on day n; F is the flowering date and H is the number of days at harvest date at maturity.

©Vigne et Vin Publications Internationales (Bordeaux, France)

Table 2 - Characteristics of the different « Maturity classes »: salt concentration of the different saline solutions; °Brix per class; Mean water content (%).

Data of °Brix and water content were obtained using all the data of different experiments.

Maturity class	Salt concentration (g/L)	Mean and standard deviation ° BRIX	Mean and standard deviation Water Content (%)
MC 1	< 60	7.7 ± 1.0	88.7 ± 1.6
MC 2	60	9.6 ± 0.9	86.6 ± 1.0
MC 3	75	12.2 ± 0.8	84.2 ± 0.7
MC 4	90	15.0 ± 0.5	82.1 ± 0.7
MC 5	105	17.4 ± 0.6	80.3 ± 0.7
MC 6	120	19.6 ± 0.7	78.3 ± 0.6
MC 7	135	21.7 ± 0.9	76.3 ± 0.7
MC 8	150	24.2 ± 0.5	74.1 ± 0.6
MC 9	165	26.0 ± 0.4	72.4 ± 1.2
MC 10	180	28.7 ± 0.2	72.1 ± 2.9

Table 3 - Values of thermal time (G_{DD}) obtained for the different phenological periods between flowering and harvest. The value of « fruit set » (stage 27) was made using a mathematical approach, as the stage was not observed.

An F test was done to compare the phenological stages of the two varieties.

Thermal time -G_{DD} (above 10°C)		Grenache N	Syrah
Flowering - Fruit set*	Mean	**133.4 a**	**131.8 b**
	Standard deviation	12,4	9
	Variation coefficient	0,09	0,07
Fruit Set* - Veraison	Mean	**760.9 a**	**616.6 b**
	Standard deviation	49,6	30
	Variation coefficient	0,07	0,05
Flowering - Veraison	Mean	**898.5 a**	**756.6 b**
	Standard deviation	49,6	30
	Variation coefficient	0,06	0,04
Veraison - Harvest	Mean	**548.3 a**	**581.8 b**
	Standard deviation	73,7	98,1
	Variation coefficient	0,13	0,17
Flowering - Harvest	Mean	**1446.9 a**	**1338.4 b**
	Standard deviation	106,7	121,3
	Variation coefficient	0,07	0,09

Means with different letters within rows differ at $p < 0.05$ using F test.
* Obtained from a non-linear extrapolation of the relationship between berry weight and temperature sum, the fruit setting stage being defined as the abscissa at zero weight (figure 5B).

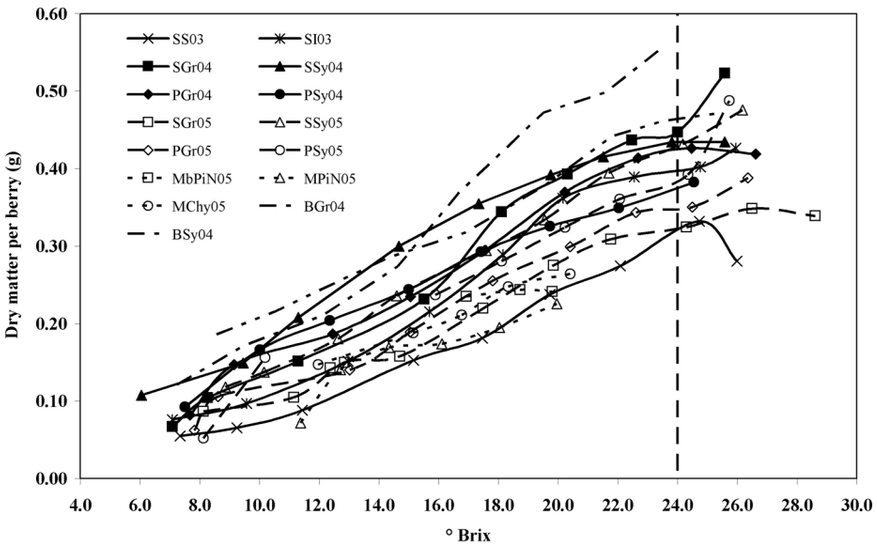


Figure 2 - Relation between dry matter mass per fruit (g) and °Brix by Maturity classes over the veraison-harvest period.

©Vigne et Vin Publications Internationales (Bordeaux, France)

4-inaki 24/06/09 17:18 Page 88

6. Crop temperature

Grapevine water status was estimated using crop temperature computed on a daily scale using the crop model STICS 6.0 (Brisson *et al.*, 2003; Brisson *et al.*, 2009) that it was run in prescribing the measured LAI dynamics (Ripoche *et al.*, 2001). This dynamics is calculated from the punctual LAI measurements interpolated using a statistical relationship representing the time course of the LAI (Brisson *et al.*, 2009). By prescribing the LAI, water (transpiration and evaporation) and nitrogen requirement levels suitable to cope with stress are also imposed. Soil and plant parameters and technical practices were carefully measured or deduced and introduced into the model to simulate grapevine development and growth (García de Cortázar-Atauri, 2006). The crop temperature is a synthesis of the water status of the plant, the crop soil cover and the weather (Brisson *et al.*, 2003). The energy balance allows the calculation of the crop temperature from the measured weather variables (temperature, rainfall, global radiation, wind and humidity), the calculated evapotranspiration and the structure of the described vegetation, taking into account micro-climatic interactions between soil and crop. For grapevine, STICS uses the Shuttleworth and Wallace model (resistive model) (Brisson *et al.*, 1998; Ortega-Farias *et al.*, 2008; Brisson *et al.*, 2009) to calculate water requirements of the plant.

7. Statistical analysis

A Fischer's test was performed (Microsoft Excel - Microsoft Corporation, USA) to determine if there are significant differences between the phenological phases (table 3). The graphical interface of the same software was also used to calculate the linear and non-linear regressions of the water and dry matter dynamics. Pearson's test was used to calculate the correlation coefficient between observed and simulated data. The statistic used to evaluate model performance was the root mean square error (RMSE), calculated as (Janssen and Heuberger, 1995):

$$RMSE = \sqrt{\frac{1}{N}\sum_{i=1}^{N}(p_i - o_i)^2}$$

where p_i is the predicted value, o_i is the observed value and N is the number of observations. Models with the lowest RMSE are considered best.

RESULTS

1. Variation in age of the berries and persistence of a dominant maturity class

Berry samples collected from the Rhone Valley and Burgundy plots were analysed in terms of dynamics of maturation (veraison – harvest period). Representative results from plot SI03 in 2003 are presented in figure 3. At any date, berries from several « Maturity classes » could be found, confirming that the berry population matured asynchronously. For any date, most of the berries were in four « Maturity classes » (figure 4). However, one dominant « Maturity class »(containing the largest number of berries) was observed, which evolves during the veraison-harvest period, from the first to the last class (figure 3). Sometimes, it was difficult to observe this dominant class, because it was between two measured classes (i.e. 6th August 2003 in figure 3). If this number of « Maturity classes » was expressed as variation of °Brix

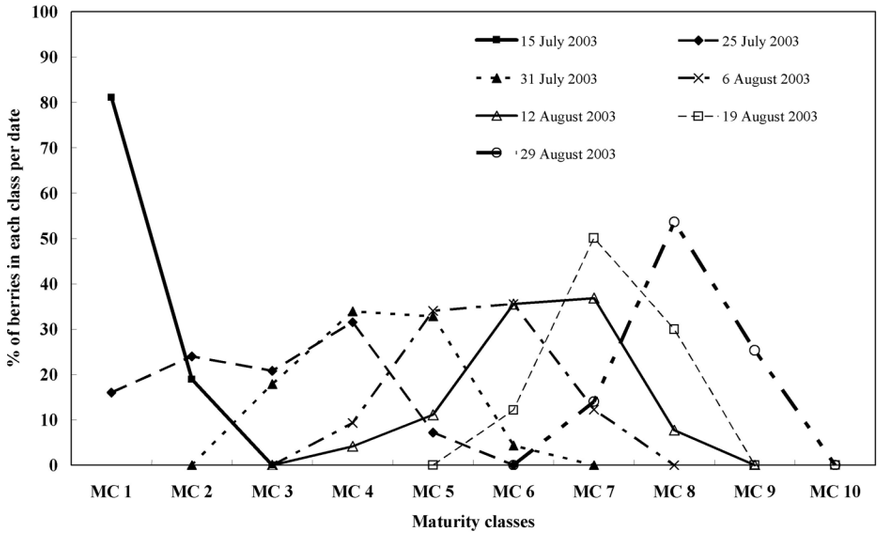


Figure 3 - Example of the development of berry populations by « Maturity classes » in plot SI03. We obtained the same developmental curves for all the experimental plots.

©Vigne et Vin Publications Internationales (Bordeaux, France)

4-inaki 24/06/09 17:18 Page 89

within a berry population and for a given day, a fairly wide average range of 8.2 ± 0.5 °Brix was obtained.

2. Regression between °Brix and water content of the berries

For each « Maturity class », mean sugar concentration (°Brix) and mean water content ((fresh weight–dry weight)/fresh weight) were determined using all the samples collected over the three years (table 2). During the whole maturation period, berry sugar concentration and water content were highly significantly correlated (figure 5). The equation of the linear regression was:

$$W_c = -0.82\ C_s + 94.40 \quad (R^2 = 0.95) \qquad (3)$$

W_c represents the water content of a berry (%) and C_s the °Brix of the berry. The relationship was independent of the variety and year ($p < 0.001$).

3. Growth dynamics of a mean berry of the dominant « Maturity class »

The following results were obtained from the varieties Syrah and Grenache N from the two plots Serres and Piolenc in Rhone Valley.

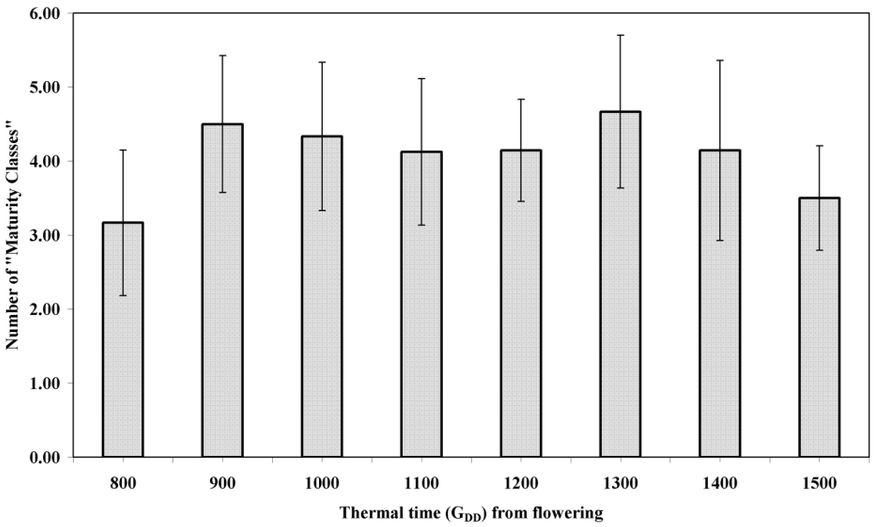


Figure 4 - Distribution of the number of « Maturity classes » for all the varieties as a function of thermal time (G_{DD}) from flowering. Number of « Maturity classes » is represented by mean value and the standard deviation.

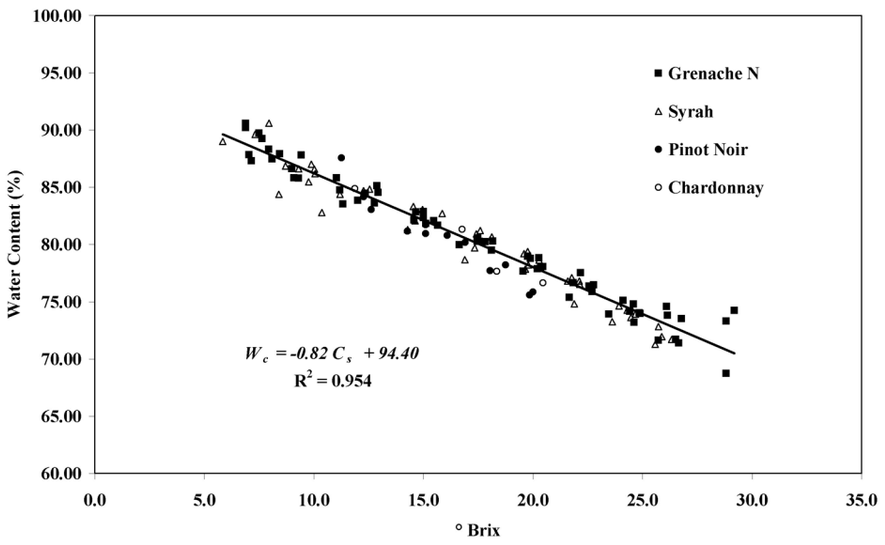


Figure 5 - Relation between °Brix and water content (% water) in a grape berry in each « Maturity classes ». The regression coefficient is calculated for all the cultivars and all the experiments. Regression coefficient $R^2 = 0.95$, $p < 0.001$.

©Vigne et Vin Publications Internationales (Bordeaux, France)

4-inaki 24/06/09 17:18 Page 90

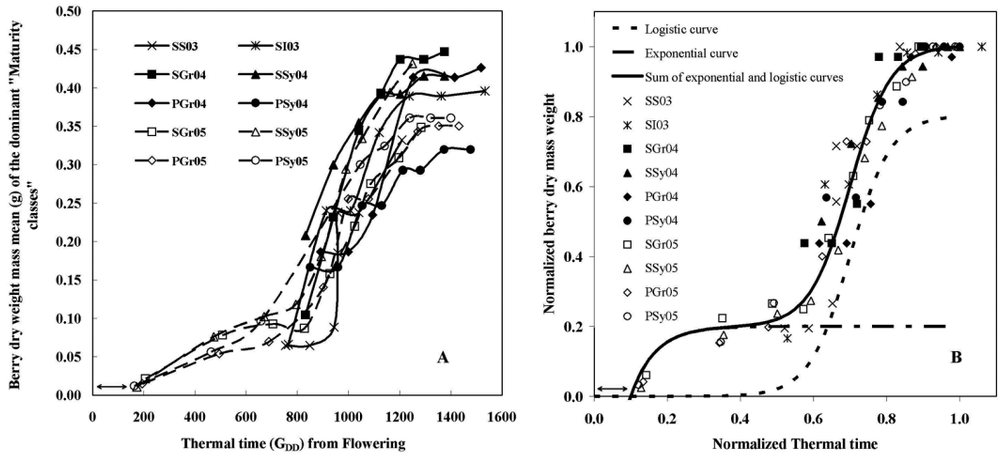


Figure 6A - Curve of dry matter of the dominant « Maturity class » from flowering as a function of thermal time (G_{DD}).

Figure 6B - Normalisation of the various curves and estimation of a curve to describe the dynamics.

Description of the exponential curve (cell multiplication) and of the logistic curve (enlargement and cell elongation).
RMSE = 0.026. R^2 = 0.99.

a) Phenological stages

As for the phenological development of the berry, the four stages identified (flowering, fruit setting, veraison and maturity) were converted to GDD and summarised in Table 3 for the two varieties Grenache N and Syrah. It appears that all the periods are significantly different for the two varieties studied. « Fruit set » (stage 27) was estimated from a non-linear extrapolation to the origin of the relationship between berry weight and degree days, fruit setting being calculated for each dataset as the abscissa at zero weight (figure 6).

b) Dry weight

Berry dry weight recorded over the three years was plotted as a function of thermal time (GDD) (figure 6 A). Data were collected before veraison in 2005 only. Dry weight increases rapidly after veraison, and then seems to reach a plateau before harvest. If one normalises the X-axes by the variety-dependent flowering-maturity period duration in GDD (1446 °C.d for Grenache N and 1338 °C.d for Syrah) (table 3) and the Y-axes by the maximal dry weight reached at harvest, the measurements can be represented by a single curve, regardless of the year, plot and variety (figure 6 B). This curve could clearly be described as a classical double sigmoid with two complementary dynamics: (1) an exponential curve and (2) a logistic curve. The summation of these two equations enables to describe the double sigmoid curve as a function of development and dry matter using the following equation:

$$M_{dn} = E_{mg}\left(1 - e^{-(E_c\ (NG_{DDn} - 0.096))}\right) + \frac{A_{fx}}{1 + e^{-(L_c\ (NG_{DDn} - L_{mg}))}} + B_{fx} \quad (4)$$

$$A_{fx} = \frac{1 - E_{mg}\left(1 - e^{-(E_c\ (0.904))}\right)}{\left(\frac{1}{1 + e^{-(L_c\ (1 - L_{mg}))}} - \frac{1}{1 + e^{-(L_c\ (0.096 - L_{mg}))}}\right)} \quad (5)$$

$$B_{fx} = -\frac{A_{fx}}{1 + e^{-(L_c\ (0.906 - L_{mg}))}} \quad (6)$$

where M_{dn} is the fraction of the harvest berry dry weight (g); NG_{DDn} is the fraction of the total thermal time since flowering; L_c and L_{mg} are the curvature and the point of maximum growth of the logistic, respectively; E_c and E_{mg} are the curvature and point of maximum growth of the exponential, respectively; and A_{fx} and B_{fx} are coefficients useful for M_{dn} remains in the [0, 1] normalized interval (equations 5 and 6). The value of 0.096 indicates the « fruit set » stage, in equation 4. This value was obtained by averaging all estimated « Fruit set » data. Non-linear fitting of these equations to the data from the experiments enabled the estimation of the values of the parameters E_c (15), E_{mg} (0.2), L_c (18) and L_{mg} (0.7) (figure 5 B).

c) Water amount

Amount of water per berry was plotted against thermal time (figure 7 A). Its dynamic is more erratic than dry weight dynamics because it was heavily dependent on the variety, plot and year. However, if water content is expressed as a percentage (figure 7 B), the trend was more

©Vigne et Vin Publications Internationales (Bordeaux, France)

4-inaki 24/06/09 17:18 Page 91

regular. Water content was characterized by a decrease from fruit set to harvest.

d) Water content

In order to test the possibility of using the same developmental scale to describe dry matter and water content, the relationship between berry water content as function of thermal time (G_{DD}) was further investigated. Water content dynamic was broken down into two components, one of which is related to the berry phenological stage (in number of days or in thermal time) and the other to the water status of the plant. It was assumed that the first component corresponds to the upper envelope of the curves relating water content per berry (%) to development scale, and would describe the maximal berry water content. The second component was linked to the difference between the crop canopy temperature (simulated by STICS crop model) and the

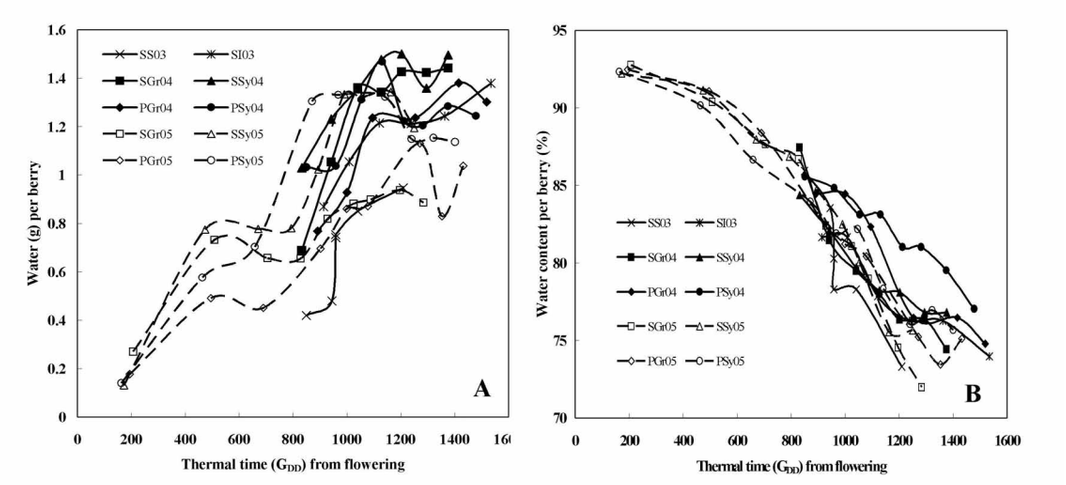


Figure 7A - Accumulation of water (g) of the dominant « Maturity class » as a function of thermal time (G_{DD}) for the various treatments.
Figure 7B - Water content (%) in a berry as a function of thermal time (G_{DD}).

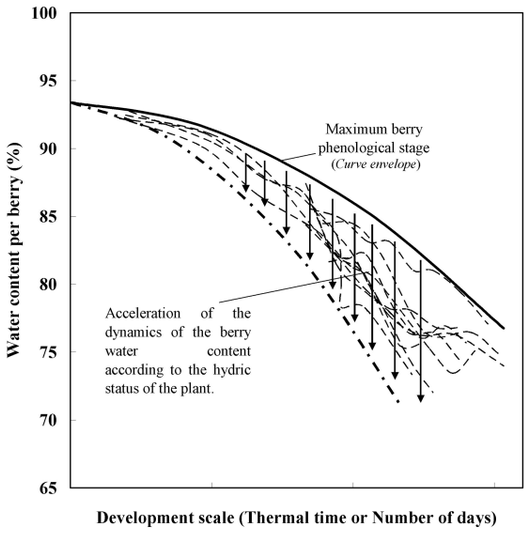


Figure 8 - Water content per berry as a function of a development scale (thermal time or number of days) and water status of the plant.
The water status is evaluated by the difference between the crop canopy temperature (simulated by STICS crop model) and the mean air temperature.

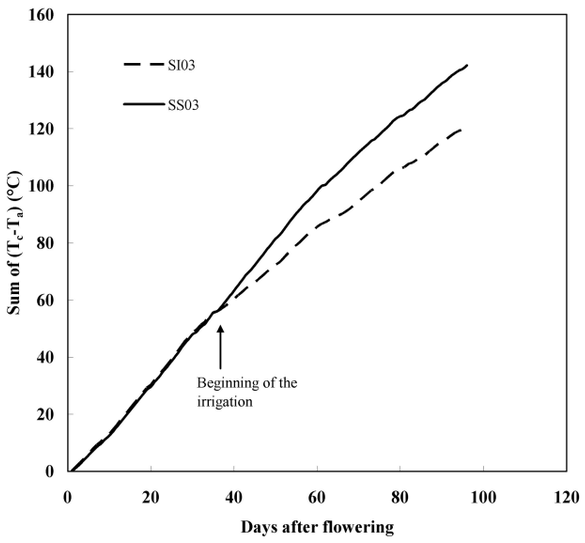


Figure 9 - Graphical representation of the cumulative difference between the crop temperature (T_c) and the air temperature (T_a) for the plots SS03 and SI03, from flowering to harvest.

J. Int. Sci. Vigne Vin, 2009, **43**, n°2, 83-97
©Vigne et Vin Publications Internationales (Bordeaux, France)

4-inaki 24/06/09 17:18 Page 92

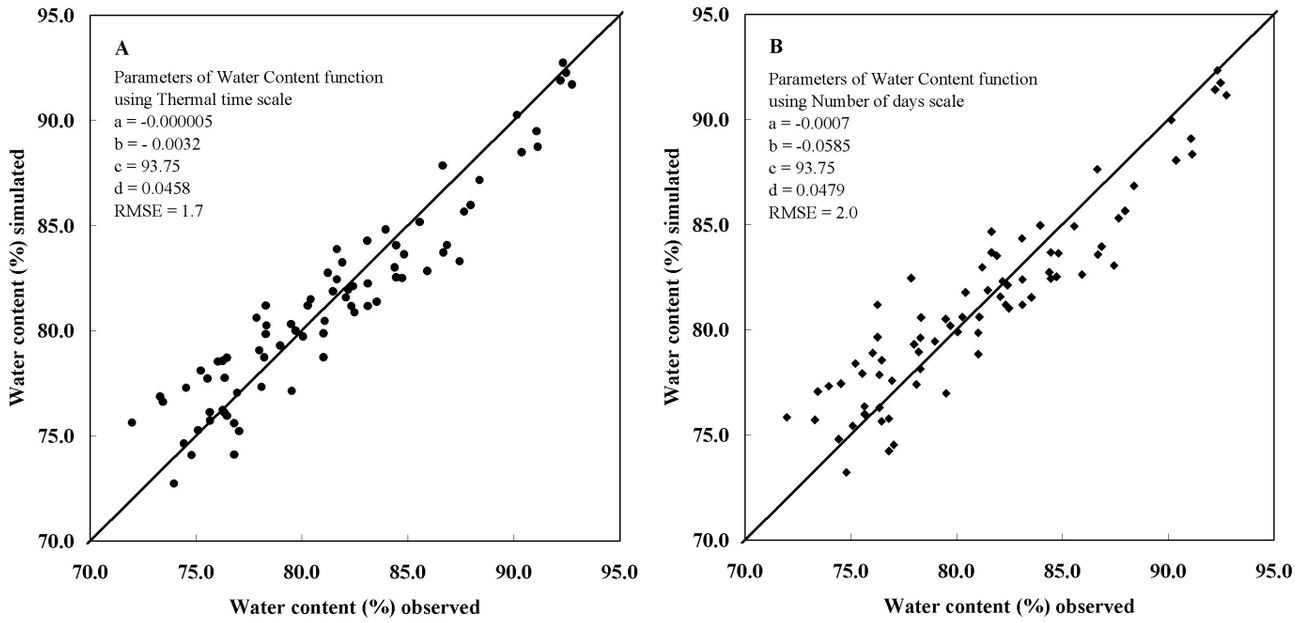


Figure 10 - Comparing simulated water content (%) using equation 6 with two developmental scales A: Thermal time – RMSE = 1.7; B: Number of days – RMSE = 2.0, with water content observations.

mean air temperature (figure 8). Figure 9 shows the cumulative temperature difference between the crop and the air for the conditions SS03 (non-irrigated system) and SI03 (irrigated system) from flowering to harvest. The curve envelope was determined by non-linear fitting of a second degree polynomial to the highest observed values. The relationship with the temperature elevation of the canopy is found by linear regression of the residues against the values of the curve envelope. The resulting relation allowing the calculation of the berry water content is as follows: (7)

$$W_c = a * (\sum_{F}^{N} S_d(n))^2 + b * (\sum_{F}^{N} S_d(n)) + c - [d * (\sum_{F}^{N} (T_c(n) - T_a(n)))]$$

where W_c is the berry water content (%); *a, b, c* and *d*, are the parameters determined by fitting; *N* is the number of days at harvest date at maturity; S_d is the scale of development: thermal time (base 10) or number of days on day n since flowering; T_c is the crop temperature (°C) on day *n* calculated by STICS ; and T_a is the air temperature (°C) on day *n*.

Furthermore, if equations 3 and 7 are combined, we obtain a new equation which will enable to simulate °Brix dynamics:

$$C_s = -\left(\frac{a * (\sum_{F}^{N} S_d(n))^2 + b * (\sum_{F}^{N} S_d(n)) + c - [d * (\sum_{F}^{N} Tc(n) - Ta(n))] - 94.40}{0.82} \right) \quad (8)$$

The correlation coefficient was calculated to evaluate the performance of the two development scales tested (thermal time and number of days) to simulate berry water content. Figure 10 shows the values of different parameters and the comparison between observed and simulated data. Highly significant correlations were obtained in both cases (Thermal time Pearson's $r = 0.95$, $p < 0.001$; number of days Pearson's $r = 0.93$, $p < 0.001$).

DISCUSSION

1. Asynchrony of ripening

These results confirm the heterogeneous character of berry maturation (Singleton *et al.,* 1966; Coombe, 1992; May, 2000; Pool, 2004). According to our data, the number of « Maturity classes » at a given moment is relatively constant. Pool (2004) showed that high crop load and thinning type increase berry density distribution and improve wine quality at the lower densities. However these effects cannot be observed in this study because of big differences in thinning practices. The range of 8.2 ± 0.5 °Brix on average obtained in this work, could allow quantifying harvest homogeneity. Results of this study show that variability in the °Brix value of the studied grapes was high, but without any apparent damage to the wine quality (personal communications from the property managers). However, wine quality is not only linked to high °Brix values; other components influence it (i.e. acidity, flavours) (Pool, 2004). These results raise the following questions about the concept of homogeneity:

4-inaki 24/06/09 17:18 Page 93

what is a homogeneous harvest? What level of homogeneity is required to reach the best quality and complexity of one type of wine? Careful characterisation of the variability of the harvest and the wines made from the different « Maturity classes » obtained according to the methodology described in this paper, might provide material for this debate.

However, too much variability within the berry population may be a sign of maturation problems linked, for example, to nutritional deficiencies or hydric/trophic stress. In other experiments (data not shown) the expected intervals for the majority « maturity classes » did not appear clearly (some days presented variations from 9 to 11.5 °Brix). This anomaly was explained by potassium deficiency, revealed by regular leaf analysis. Potassium deficiency is known to delay berry growth (Champagnol, 1984; Coombe and Dry, 1988), causing berries to become stuck in certain « maturity classes ». This results in a broader duration of the maturity.

2. Berry dry weight estimation using the relationship between sugar concentration and water content

A very stable and robust relationship between sugar concentration (°Brix) and water content (% water) was obtained for the period veraison-harvest, regardless of year, geographical location, plot and variety. When fresh weight is known, dry matter accumulation and water content, both pre-requisites for modelling the growth of the berry, may be determined at any stage of maturation. This relationship is a powerful way to estimate experimentally berry dry weight for a range of varieties (Grenache, Syrah, Pinot noir and Chardonnay) during the veraison-harvest period.

Usually, dry weight is determined only in small-scale growth studies (Staudt *et al.*, 1986; Ollat, 1997). Otherwise, it is estimated from the value of °Brix measured with a refractometer (McCarthy and Coombe, 1999) or from volume determination (Coombe, 1980). However if the relation between water content and °Brix is extrapolated up to 0 % value (figure 4), 5.6% of the dry matter remained unexplained. This 5.6% could correspond to the structural dry matter (skin, pedicel and seeds). It means that the determination of dry weight using refractometric data does not account for 100% of the berry. Consequently this methodology should be revised to study berry growth development accurately.

3. Thermal time scale to describe berry development and dry matter modelling

Every stage from flowering to harvest day (at 24 °Brix) could be predicted using the thermal time since flowering (table 3). These data collected were in agreement with those obtained from PHENOCLIM (Chuine and Seguin, 2008), an important database which includes phenological and meteorological data (minimal and maximal daily temperatures) from different orchards and vineyards. The differences observed between Syrah and Grenache confirm the varietal character of berry development (Huglin and Schneider, 1998). Syrah is characterized by an earlier veraison than Grenache N, although the latter shows the shorter veraison-maturity period. The variability of thermal time measured for different periods was low (C.V. 4%-17%). However, variability of veraison-harvest period was about twice as high as at other periods, which could show the effect of other factors in the duration of this phase (Coombe, 1980; McCarthy, 1999, 2000).

Thermal time (G_{DD}) was also very efficient in explaining variation in berry dry weight dynamics in variable weather (figures 5A and 5B). Moreover by normalizing the berry dry weight growth by its final value, a standard curve similar for all Grenache N and Syrah varieties under various field conditions is obtained (soils, years, with or without irrigation). This result could be explained by the strong relation between temperature, especially before veraison, and berry growth (Jona and Botta, 1988; Ebadi *et al.*, 1996), which is in agreement with other types of model using the same hypothesis to calculate fruit dry weight evolution for other species (Grossman and Dejong, 1994; Lescourret and Genard, 2005).

4. Berry water content and development scales

Berry water content was characterized by a continuous decrease, from fruit set to harvest, as mentioned previously by Matthews and Anderson (1988). It was largely dependent on soil and weather conditions, and could not be predicted simply from thermal time. For water content, two factors seem to be superimposed, the first being linked to the age of the berries and the second to the moisture conditions prevailing during maturation. Furthermore, the relationship obtained between water content and °BRIX (equation 8), made it possible to compute the dynamics of the latter. However the need to use a model (in this case STICS) to estimate the crop temperature makes it difficult to use the established formulation routinely. Similar estimates of water content are obtained when time is expressed as thermal time (G_{DD}) or number of days (figure 10). Results obtained in this work do not allow discrimination between models. This is probably due to the strong correlation between the measured thermal time and the numbers of days between flowering and harvest in this region. This formalism was introduced into the STICS 6.0 crop model, adapted for the grapevine (García de Cortázar-Atauri, 2006). The study was done for different regions in France (Rhone Valley, Languedoc, Burgundy, Champagne, Loira Valley, Cognac and Bordeaux), with different soils, climates and cultural

J. Int. Sci. Vigne Vin, 2009, **43**, n°2, 83-97
©Vigne et Vin Publications Internationales (Bordeaux, France)

4-inaki 24/06/09 17:18 Page 94

practices, and for 8 varieties: Grenache, Syrah, Pinot noir, Chardonnay, Ugni blanc, Merlot, Chenin and Cabernet franc. This study showed better results using the number of days scale (García de Cortázar-Atauri, 2006, Valdes *et al.*, 2009). These results are in agreement with those obtained by several authors who have shown a greater stability using the number of days to study sugar content dynamics (Coombe, 1980; McCarthy, 1999, 2000; Roby and Matthews, 2004). The idea that berry water accumulation is not under the control of temperature, but it could respond to a cicardian system or to berry metabolism as in the eco-physiological models could be proposed.

5. Berry growth modelling

This work provides interesting algorithms and methodology to predict berry dry weight and water content at any stage from flowering to maturity.

For the dry weight, normalization has shown very interesting results. The model presented is similar to that presented in other studies (Ollat *et al.*, 2002; Fanizza and Colonna, 1996). The model uses a double sigmoid curve which easily describes in a mathematical formalism the two main physiological processes supporting berry growth (Pavel and Dejong, 1993): (1) the exponential part to describe cell multiplication and (2) the logistic part to describe cell elongation. From a mathematical point of view, the use of continuous functions enables easier parameter estimation and simpler integration into more complex models, even if starting berry growth at the « fruit set » stage using an exponential curve may limit its biological interpretation (dry matter values before « fruit set » are negatives).

The normalization of thermal time by a varietal maximum GDD value showed a good unification of the dynamics in this axis, considering this dynamic as variety-dependent and environment-independent. On the other hand, dry weight at harvest varies considerably with cultivars and environmental conditions (figure 6A) and for this reason dry weight was normalized using the maximum dry weight measured in each situation. This double normalization, figure 6B shows that it is possible to assess a proportion of final dry weight at any time (proportion of flowering-maturity period duration that is varietal dependent), for all Grenache N and Syrah varieties under various field conditions (soils, years, with or without irrigation) (figures 6A, B). These results show as this dynamic was earlier predetermined. Thus, there are two possibilities using this model:

1) According to these results, this equation cannot be used without knowledge of the potential final dry weight. But if dry weight at a given moment during growth and the varietal duration of the flowering – maturity period is known, the normalized model could be used to predict it. Thus, the relationship established could be used as a predictive tool using the berry weight at veraison, which is about 25% of the final potential dry weight. The final dry weight of the berry is reached before maturity (at 90% of the flowering-maturity period), at 1301 and 1204 G_{DD} for Grenache N and Syrah respectively. After this date the fluctuations in the fresh weight of the berry are mainly due to variation in its water content. These results provide several insights about the berry potential growth: the final weight of the berry could be determined before veraison as shown by some authors (Ollat *et al.*, 2002; McCarthy, 1997; Ojeda *et al.*, 2001).

2) The second possibility is to include this model in more complex crop models (Brisson *et al.*, 2003, 2009) which could simulate berry growth taking into account information about soil (water balance), plant (trophic competition) and weather. For example, results using this formalism, showed its ability to accurately simulate grapevine yield (dry matter) in many different conditions (in the same study mentioned above for different French vineyards) (Pearson's $r = 0.8$; $p < 0.001$; RMSE = 0.87*t*/ha; data not shown) and using different varieties (García de Cortázar-Atauri, 2006, Valdes *et al.*, 2009).

This algorithm did not fit data collected for Pinot noir and Chardonnay in Burgundy (not presented). In cooler regions, it is difficult to reach maximal berry size and impossible to calculate the thermal time needed to reach maturity (as defined previously, i.e. 24 °Brix) because of low temperatures at the end of September and at the beginning of October. In order to check this model over a wide range of varieties, data used to calculate the parameters of the equations (maximal berry dry weight and thermal time - G_{DD} to reach 24 °Brix) should be collected under climatic conditions which are non-limiting for berry growth and development.

This work shows that dry matter accumulation in the berry was closely linked to temperature, whereas the water content was associated with time and plant water status. The fact that different environmental parameters control these physiological mechanisms need to be better known (Coombe and McCarthy, 2000; Ollat *et al.*, 2002; Matthews and Shackel, 2005). Only a few fruit ecophysiological models consider dry matter and water accumulation together (tomato: Bussieres, 1993, 1995; peach: Fishman and Genard, 1998). It could be interesting to establish such a model for the grape berry in order to study the physiological mechanisms underlying growth (Wu Dai *et al.*, 2009). However, while existing models require the estimation or measurement of many parameters in order to be used in a practical way, the model proposed in this study is very simple. After confirming these results under various conditions (varieties, climatic conditions,

©Vigne et Vin Publications Internationales (Bordeaux, France)

4-inaki 24/06/09 17:18 Page 95

soil, technical practices), it might be possible to predict veraison date, yield and sugar content.

In the context of global climate change (IPCC, 2007), this result raises important considerations. Although the results of this study do not allow us to determine whether dry matter and water or dry matter content have the same development scale, a difference in the development function could have significant consequences. García de Cortázar-Atauri (2006) using different development scales for dry matter growth and water content (°Brix), show that while higher temperatures will accelerate dry matter accumulation, the number of days needed to reach a given sugar content (°Brix) remain the same, leading to variations in typical harvest berry composition. By testing this hypothesis in the vineyard under controlled conditions (e.g. at higher temperatures), it might be possible to obtain experimental data for predicting these complex modifications. This could provide valuable information to describe the possible scenarios of climatic change (Jones *et al.*, 2005) and assist in the development of new practices to manage these changes.

CONCLUSIONS

This study provides an experimental framework to study the dynamics of the dry matter and water content of a population of grape berries. Results obtained using densimetry allowed the evaluation of the asynchronous nature of grapevine maturation. This methodology allowed us to determine different relations between water and sugar content, but also between dry matter and water content with different development scales. Berry dry weight accumulation followed a double sigmoid curve, as was previously shown for fresh weight. By using a double normalisation, a simple equation allows calculating berry dry weight growth during maturity. Use of a water stress indicator, represented by the difference between crop temperature (Tc) and air temperature, to simulate water content evolution in a berry, gives good results. This work show the possibility to use two different developmental scales (thermal time and number of days) to manage dry matter accumulation and berry water content. This possibility, not yet reported for fleshy fruits, underlines the importance of studying these dynamics in detail.

Moreover, this model could be used to better identify and understand the key factors and processes in the field until detailed processes of berry are better understood and can be incorporated into the model. A predictive model could be developed which could be applied under other field conditions or to study the possible effects of climate change on the grapevine. Although the model has already been introduced into a generic crop model (STICS) and tested under rather broad conditions, with satisfactory results (García de Cortázar-Atauri, 2006; Valdes *et al.* 2009), it is important to test this formalism under new climatic conditions and with other varieties.

Acknowledgements: We thank various members of the Vaucluse Chamber of Agriculture and all the technicians and assistants in the CSE-INRA Avignon laboratory, Elian Salançon of ITV Nîmes, Jean-Claude Fournioux of the Institut Jules Guyot of the Burgundy University, Jean-Pierre Ramel of CIRAME, the station Ferme Saint Victor, the Bolchet estate, and Christine Monamy of BIVB, for their availability and their help throughout the experiment. Authors thank reviewers for their useful comments and suggestions.

BIBLIOGRAPHY

BAGGIOLINI M., 1952. Les stades repères dans le développement annuel de la vigne et leur utilisation pratique. *Rev. romande Agric. Vitic. Arboric.*, **8**, 4–6.

BONHOMME R., 2000. Bases and limits to using degree.day units. *Europ. J. Agr.*, **13**, 1–10.

BRISSON N., ITIER B., L'HOTEL J. C., AND LORENDEAU, J.Y., 1998. Parameterisation of the Shuttleworth-Wallace model to estimate daily maximum transpiration for use in crop models. *Ecological Modelling*, **107**, 159-169.

BRISSON N., GARY C., JUSTES E., ROCHE R., MARY B., RIPOCHE D., ZIMMER D., SIERRA J., BERTUZZI P., BURGER P., BUSSIERE F., CABIDOCHE Y.M., CELLIER P., DEBAEKE P., GAUDILLÈRE J.P., MARAUX F., SEGUIN B. and SINOQUET H., 2003. An overview of the crop model STICS. *Eur. J. Agronomy,* **18**, 309-332.

BRISSON N., LAUNAY M., MARY B., and BEAUDOIN N., 2009. *Conceptual basis, formalisations and parameterization of the STICS crop model*, Quae ed., Paris.

BUSSIÈRES P., 1993. Potential dry matter and water import rates in the tomato fruit in relationship to fruit size. *Annals Botany,* **72**, 63–72.

BUSSIÈRES P., 1994. Water import rate in Tomato fruit. *Annals Botany,* **73**, 75–82.

BUSSIÈRES P., 1995. Dry matter and water import rates in the tomato fruit: a model incorporating the changes in sap viscosity and osmotic potential with temperature. *Annals Botany,* **75**, 469 – 476.

CARBONNEAU A., RIOU C., GUYON D., RIOM J. and SCHNEIDER C.. 1992. *Agrométéorologie de la vigne en France*. Office des Publications Officielles des Communautés Européennes, Luxembourg.

CHAMPAGNOL F., 1984. *Éléments de physiologie de la vigne et viticulture générale*. Ed. Champagnol F., Saint-Gely-du-Fesc, France.

CHUINE I., YIOU P., VIOVY N., SEGUIN B., DAUX V. and LADURIE E.L., 2004. Historical phenology: Grape ripening as a past climate indicator. *Nature*, **432**, 289-290.

CHUINE I. and SEGUIN B., 2008. The History and current status of the French Phenology Networks, pp 76 – 79. *In : The History and current status of plant phenology in Europe*. ed. COST Office, Vammalan Kirjapaino Oy.

©Vigne et Vin Publications Internationales (Bordeaux, France)

4-inaki 24/06/09 17:18 Page 96

COOMBE B.G., 1980. Development of the grape berry. I Effects of time of flowering and competition. *Austr. J. Agric. Research*, **31**,125-131.

COOMBE B.G., 1992. Research on development and ripening of the grape berry. *Am. J. Enol. Vitic*., **43**, 101-110.

COOMBE B.G., 1995. Growth stages of the grapevine. *J. Grape Wine Res.*, **1**, 100-110.

COOMBE B.G. and McCARTHY M.G., 2000. Dynamics of grape berry growth and physiology of ripening. *Aust. J. Grape Wine Res.*, **6**, 131-135.

DAI Z.W., GENARD M., LI S.H. and VIVIN P., 2009. Analyzing the functional association among seed traits, berry growth and chemical composition in Cabernet-Sauvignon berry (*Vitis vinifera* L.) using a mathematical growth function. *J. Int. Sci. Vigne Vin*, **43**, 35-44.

DRY P.R. and COOMBE B.G., 1988. *Viticulture. Vol: 1 Ressources. Winetitles*, Adelaide.

EBADI A., MAY P. and COOMBE B.G., 1996. Effect of short-term temperature and shading on fruit-set, seed and berry development in model vines of *Vitis vinifera*, cvs Chardonnay and Shiraz. *Aust. J. Grape Wine Res.*, **2**, 2-9.

FANIZZA G. and COLONNA G., 1996. A mathematical function to study berry growth variability in grapes (*Vitis vinifera*), *J. Wine Res*., **7**, 117-123.

FISHMAN S. and GENARD M., 1998. A biophysical model of fruit growth: simulation of seasonal and diurnal dynamics of mass. *Plant, cell, Environnment*, **21**, 739-752.

FREEMAN B.M., LEE T.H. and TURKINGHAM CR. 1980. Interaction of irrigation and pruning level on grape and wine quality of Shiraz vines. *Am. J. Enology Vitic*., **31**, 124-135.

GARCÍA DE CORTÁZAR-ATAURI I., 2006. Adaptation du modèle STICS à la vigne (*Vitis vinifera* L.). Utilisation dans le cadre d'une étude du changement climatique à l'échelle de la France. *Phd Thesis*, École Supérieure Nationale d'Agronomie de Montpellier. [Thesis is available in URL: http://www.inra.fr/ea/sources/index.php?page=detail_these&id=200].

GROSSMAN Y.L. and DEJONG T.M., 1994. PEACH: A simulation model of reproductive and vegetative growth in peach trees. *Tree physiology*, **14**, 329-345.

HOLT H.E., FRANCIS I.L., FIELD J., HERDERICH M.J. and ILAND P.G., 2008a. Relationships between berry size, berry phenolic composition and wine quality scores for Cabernet-Sauvignon (*Vitis vinifera* L.) from different pruning treatments and different vintages. *Aust J. Grape Wine Res.*, **14**, 191-202.

HOLT H.E., FRANCIS I.L., FIELD J., HERDERICH, M.J. and ILAND, P.G. 2008b. Relationships between wine phenolic composition and wine sensory properties for Cabernet Sauvignon (*Vitis vinifera* L.). *Aust J. Grape Wine Res.*, **14**, 162-176.

HUGLIN P. and SCHNEIDER C., 1998. *Biologie et écologie de la vigne*, 2nd edn., Paris: Tech and Doc, Lavoisier eds.

IPCC, 2007. *Climate Change 2007 – Impacts, adaptation and vulnerability*. Contribution of working group II to the fourth assessment report of the IPCC. Cambridge University Press, Cambridge.

JANSSEN P.H.M. and HEUBERGER P.S.C., 1995. Calibration of process-oriented models. Ecological Modelling. 83, 55–56.http://aob.oxfordjournals.org.gate1.inist.fr/cgi/external_ref?access_num=10.1016/0304-3800%2895%2900084-9&link_type=DOI.

JONA R. and BOTTA R., 1988. Fruit set and early berry development in two grapevine cultivars. *Israel J. Botany*, **37**, 203-216.

JONES G.V., WHITE M.A., COOPER O.R. and STORCHMANN K., 2005. Climate change and global wine quality. *Climatic Change*, **73**, 319-343.

LECHAUDEL M., GENARD M., LESCOURRET F., URBAN L. and JANNOYER M., 2005. Modeling effects of weather and source-sink relationships on mango fruit growth. *Tree Physiology*, **25**, 583–597.

LECHAUDEL M., VERCAMBRE G., LESCOURRET F., NORMAND F. and GENARD M., 2007. An analysis of elastic and plastic fruit growth of mango in response to various assimilate supplies. *Tree Physiology*, **27**, 219–230.

LESCOURRET F. and GÉNARD M., 2005. A virtual peach fruit model simulating changes in fruit quality during the final stage of fruit growth. *Tree Physiology*, **25**, 1303–1315.

MATTHEWS M.A. and ANDERSON M.M., 1988. Fruit ripening in *Vitis vinifera* L.: Responses to seasonal water deficits. *Am. J. Enol. Vitic*., **39**, 313-320.

MATTHEWS M.A. and SHACKEL K.A., 2005. Growth and water transport in fleshy fruit. *In: Holbrook NM, Zwieniecki MA, eds. Vascular Transport in Plants*, 181-197.

MAY P., 2000. From bud to berry, with special reference to inflorescence and bunch morphology in *Vitis vinifera* L. *Aust. J. Grape Wine Res*., **6**, 82-98.

McCARTHY M.G., 1997. The effect of transient water deficit on berry development of cultivar Shiraz (*Vitis vinifera* L.). *Aust. J. Grape Wine Res.*, **3**, 102-108.

McCARTHY M.G., 1999. Weight loss from ripening berries of Shiraz grapevines (*Vitis vinifera* L. cv. Shiraz). *Aust. J. Grape Wine Res.*, **5**, 10-16.

McCARTHY M.G., 2000. Developmental variation in sensitivity of *Vitis vinifera* L. (Shiraz) berries to soil water deficit. *Aust. J. Grape Wine Res.*, **6**, 136-140.

McCARTHY M.G. and COOMBE B.G., 1999. Is weight loss in ripening grape berries cultivar Shiraz caused by impeded phloem transport? *Aust. J. Grape Wine Res.*, **5**, 17-21.

OJEDA H., DELOIRE A. and CARBONNEAU A., 2001. Influence of water deficits on grape berry growth. *Vitis*, **40**, 141-145.

OJEDA H., ANDARY C., KRAEVA E., CARBONNEAU A. and DELOIRE A., 2002. Influence of pre- and postveraison water deficit on synthesis and concentration of skin phenolic compounds during berry growth of *Vitis vinifera* L. cv. Shiraz. *Am. J. Enol. Vitic.*, **53**, 261-267.

OJEDA H., CARRILLO N., DEIS L., TISSEYRE B., HEYWANG M. and CARBONNEAU A., 2005. Précision viticulture and water status II : quantitative and qualitative performance of different within field zones, defined from water potential mapping. *In: Proceedings of 4th Gesco*. Vol II. Germany p. 741-748.

©Vigne et Vin Publications Internationales (Bordeaux, France)

4-inaki 24/06/09 17:18 Page 97

OLLAT N., 1997. Bases physiologiques et anatomiques de la croissance des baies de *Vitis vinifera* cv Cabernet-Sauvignon. *PhD Thesis*, Ecole Nationale Supérieure Agronomique de Montpellier.

OLLAT N. and GAUDILLERE J.P., 1998. The effect of limiting leaf area during stage I of berry growth on development and composition of berries of *Vitis vinifera* L. cv. Cabernet Sauvignon. *Am. J. Enol. Vitic*., **49**, 251-258.

OLLAT N., DIAKU-VERDIN P., CARDE J.P., BARRIEU F., GAUDILLERE J.P. and MOING A., 2002. Grape berry development: a review. *J. Int. Sci. Vigne Vin*, **36**, 109-131.

ORTEGA-FARIAS S., CARRASCO M., OLIOSO A., ACEVEDO C., and POBLETE C., 2008. Latent heat flux over Cabernet Sauvignon vineyard using the Shuttleworth and Wallace model. *Irrigation science*, **25**, 161-170.

PAVEL E.W. and DEJONG T.M., 1993. Relative growth rate and its relationship to compositional changes of non-structural carbohydrates in the mesocarp of developing peach fruits. *J. Amer. Soc. Hortic. Sci.*, **118**, 503-508.

PIERI P. and FERMAUD M., 2005. Effects of defoliation on temperature and wetness of grapevine berries. *Acta Horticulturae*, **689**, 109-116.

POOL R. M., 2004. Vineyard balance - What is it? - Can it be achieved? Viticulture - Living with Limitations. *Acta Horticulturae*, **640**, 285-302.

RIOU C., 1994. *Le déterminisme climatique de la maturation du raisin : application au zonage de la teneur en sucre dans la Communauté Européenne*. Office des Publications Officielles des Communautés Européennes, Luxembourg.

RIPOCHE D., WEISS M. and PREVOT L., 2001. Driving the STICS application to remote sensing. *In: Proceed. 2nd Int. Symp. on Modelling Cropping System*, Italy, p. 169-170.

ROBY G. and MATTHEWS M.A., 2004. Relative proportions of seed, skin and flesh, in ripe berries from Cabernet-Sauvignon grapevines grown in a vineyard either well irrigated or under water deficit. *Aust. J. Grape Wine Res.*, **10**, 74-82.

SANTESTEBAN L.G. and ROYO J.B., 2006. Water status, leaf area and fruit load influence on berry weight and sugar accumulation of cv. Tempranillo under semiarid conditions. *Scientia Horticulturae*, **109**, 60-65.

SINCLAIR T.R. and SELIGMAN N., 2000. Criteria for publishing papers on crop modeling. *Field Crops Research*, **68**, 165-172.

SINGLETON V.L., OUGH C.S. and NELSON K.E., 1966. Density Separations of Wine Grape Berries and Ripeness Distribution. *American J. Enol. Vitic*. **17**, 95-105.

STAUDT G., SCHNEIDER W. and LEIDEL J., 1986. Phases of berry growth in *Vitis vinifera*. *Annals of Botany*. **58**, 789-800.

TARARA J.M., FERGUSON J.C., HOHEISEL G.A. and PEREZ PEÑA J.E., 2005. Asymmetrical canopy architecture due to prevailing wind direction and row orientation creates an imbalance in irradiance at the fruiting zone of grapevines. *Agricult. Forest Meteorology*, **135**, 144-155.

VALDES-GOMEZ H., CELETTE F., GARCIA DE CORTAZAR-ATAURI, I., JARA-ROJAS F., ORTAGA-FARIAS S. and GARY C., 2009. Modelling soil water content and grapevine growth and development with the stics crop-soil model under two different water management strategies. *J. Int. Sciences Vigne Vin*, **43**, 13-28.

WILLIAMS D.W., ANDRIS H.L., BEEDE R.H., LUVISI D.A., NORTON M.V.K. and WILLIAMS L.E., 1985. Validation of a model for the growth and development of the Thompsom Seedless grapevine. II. Phenology. *Amer. J. Enol. Vitic*., **36**, 283-289.

WINKLER A.J., COOK J.A., KLIEWER W.M. and LIDER L.A., 1962. *General Viticulture*. University of California Press, Berkeley, LA: University of California.

 ©Vigne et Vin Publications Internationales (Bordeaux, France)