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Growth kinetics of grape berry density (*Vitis vinifera* L. 'Black Corinth')

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Summary

Density is a significant physical property of grape berries depending on their mass, volume and chemical composition - mass concentrations of sugar, water or other chemical compounds. The current research studies the changes of grape berry density for the seedless grape cultivar 'Black Corinth' from anthesis to maturity. It has been found that the change of grape berry density during the growth follows the double sigmoid curve and consists of two growth cycles divided by a lag phase. During the first growth cycle, between anthesis and lag phase, berry density increases from 800 mg·cm^{-3} to 1020 mg·cm^{-3}. During the lag phase berry growth is delayed and berry density remains almost a constant. At the end of véraison, berry density rose quickly, and during the technological maturity it reached ~ 1120 mg cm^{-3}. The rate of change of berry density has two local maxima coinciding with the middle of the first and second growth cycles of berry development.

K e y w o r d s : grape berry density; double sigmoid growth model; seedless vine cultivars; 'Black Corinth'; phenology.

Introduction

The development of grape berries is a dynamic process, which includes a complex sequence of molecular genetics and biochemical changes (Conde *et al*. 2007, Roubelakis-Angelakis 2009). There is vast research on the relationship between changes in diameter, length, mass and volume of berries and the processes shaping berry chemical composition. As a result of these studies, it has been found that grape berry development passes through two principal cycles following the double sigmoid growth curve (Coombe 1960, 1995, Harris *et al*. 1968, Staudt *et al*. 1986, Xu *et al*. 1995, Coombe and McCarthy 2000, Dokoozlian 2000, Ollat *et al.* 2002). The two growth periods are separated by a lag phase. During the first growth cycle, berry sizes increase due to cell division followed by enlargement of cells. Tannins and organic acids (malic and tartaric acids, hydroxycinnamic) are accumulated in this stage. During the lag phase, characterized by a delay in growth, cell sizes almost stop increasing, acids' concentrations progressively increase in berry and reach their highest levels near véraison. The véraison (beginning of berry colouring) launches the second growth cycle when berries continue to grow, as a consequence of the enlargement of mesocarp cells. During this cycle berries soften, sugars – glucose and fructose – reach maximum values, a decrease in the amount of organic acids is observed, anthocyanin pigments responsible for berry colour, and aroma and flavour compounds are accumulated in berry skin.

Berry density integrates the main biophysical growth parameters – diameter, length, volume and mass of berries, and depends on their biochemical composition. In the second cycle of berry development, relations have been established between berry density and the amount of soluble solids SSC (°Brix), pH, SSC:acid ratio, reducing sugars:tartaric acid ratio, phenolic composition and the aromatic profile (linalool, nerol and geraniol), mechanical properties of the whole berry and berry skin (Lanier and Morris 1978, 1979, Walker *et al*. 2001, Matthews and Nuzzo 2007, Rolle *et al.* 2011, 2012, 2015, Río Segade *et al.* 2013, Liu *et al.* 2016). These results lead to two principal questions: whether berry density reflects the main stages of berry development, and to what extent it allows a differentiation to be made in berry composition based on berry density during the separate stages of their development.

The purpose of the current research is to study the changes of berry density during the period anthesis – technological maturity in seedless varieties, and to verify the hypothesis that grape berry density during this period follows the double sigmoid growth pattern. This would allow the introduction of a new metric of growth - the grape berry density that brings new information about growth processes. For a more accurate description and better understanding of the seasonal growth of berries, a double sigmoidal model of berry density changes was developed, from which multiple stages of grape development can be inferred. Accurate identification of these stages is important for producers and processors as it can affect the quality and management of the grape crop (Price *et al.* 2008). For the grapevine, Fanizza and Colonna (1996) have developed a double logistic growth function model to fit berry diameter of table grape varieties. Double logistic functions model of berry weight has also been applied by Ollat and Gaudillere (1998) in study of the effects of limiting leaf area on development and composition of berries ('Cabernet Sauvignon'), but they used different mathematical expressions to simulate the double sigmoid. To describe berry growth in the 'Chardonnay' grape

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variety, PRICE *et al*. (2008) developed a two- component mixture model based on normal distribution functions. Recently a combination of monomolecular and logistic functions has been applied to analyse the dependencies between the function parameters and berry quality features (DAI *et al.* 2009). In a study of dry matter growth GARCIA DE CORTAZAR *et al.* (2009) have proposed a classical double sigmoid model based on thermal time (GDD) and final potential dry weight with two complementary dynamics: exponential growth and logistic growth. Using thermal time scale is very efficient in explaining berry growth dynamics as it allows a comparison of growth at different weather conditions. The model developed in the present study follows the growth function approach too and is close to the OLLAT and GAUDILLERE'S (1998) model, as the model parameters have good biological relevance and interpretation (THORNLEY and JOHNSON 2000).

Material and Methods

The study was conducted during 2015 and 2016 on the *Vitis vinifera* L. seedless cultivar 'Black Corinth' with stimulative parthenocarpy, a part of the Ampelographic Collection of the Department of Viticulture, Agricultural University of Plovdiv, grown in the vicinity of the Brestnik village, Bulgaria (42.05N, 24.77E; 300 m a.s.l.) under a regulated water regime. The annual sums of precipitation R were 313 mm (2015) and 358 mm (2016), and they were ~ 40 % lower than the annual mean R between 2010 and 2016. The mean annual temperatures T were 12.7 °C (2015) and 14.0 °C (2016) and they were close to the annual mean 13.6 °C during the 2010-2016 period. Precipitation and temperatures (Fig. 1a and b) were measured with an iMETOS electronic weather station (Pessl Instruments GmbH), near the vineyard.

The density ρ of a substance is its mass per unit volume and is usually expressed in grams per cubic centimeter ($g \cdot cm^{-3}$) at some definite temperature. It can be determined indirectly as ρ = m/V by measuring the mass m of berries and the berry volume V. Berry mass m was measured by laboratory balances, while berry volume was measured by means of two methods. From the beginning until the end of anthesis, volume was measured by a pycnometer (HIDNERT and PEFFER 1950). After that, berry volume was measured by a graduated cylinder. In order to reduce the error, the mass and volume of samples were measured, instead of the mass and volume of a single berry. The random samples of berries were comprised after the berries were removed from the clusters.

Berry density was measured once a week from anthesis until technological maturity. In the anthesis the mass m of 20 samples each with 5 to 7 g of grape flower buttons, were weighed by laboratory balances with accuracy 0.01 g. Volume was measured by means of a pycnometer, 50 cm^3 capacity, and glycerol was used as wetting liquid. The volume of berries V is equal to the volume of the displaced liquid of the pycnometer:

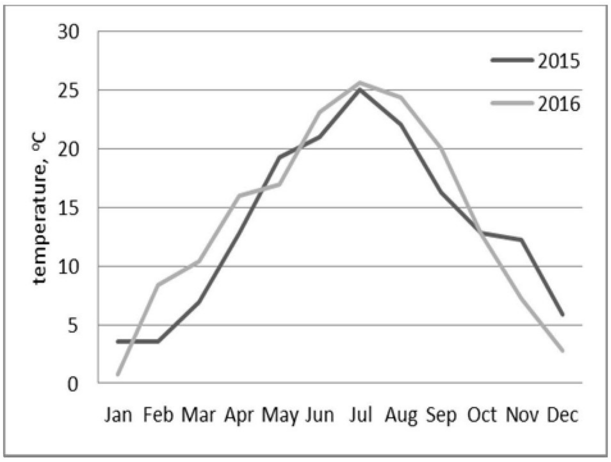
$$(1) \quad V = \frac{m_1 + m - m_2}{\rho'}$$

where: m – berries sample mass, m_1 – mass of the pycnometer after its filling only with glycerol, m_2 – mass of the pycnometer after the immersion of berries in it and ρ' – wetting liquid density. The masses m_1 and m_2 were measured after the pycnometer was placed in a constant temperature water bath at 20 °C and thermal equilibrium was attained. The percentage error in density measurements was 0.5 % for all samples.

After the end of flowering, the density of about 20 samples of berries was measured weekly. In the period following anthesis until the end of véraison, the berry sample mass was (75 ± 15) g. During technological maturity sample mass was (100 ± 14) g. The mass m was measured by laboratory balances with accuracy 0.01 g, and berry volume V was measured by a graduated cylinder with accuracy 5 mL, so the percentage error was 0.02 %. Berry density was determined by dividing the mean mass m by the mean volume V of grape berry samples.

During the growth period, regular phenological observations were carried out concerning the initiation and duration of the separate phenological phases in the studied vine cultivar. Since within the change of berry density two growth cycles have been distinguished, the current research builds a double sigmoid model of the type (PRICE *et al*. 2008)

$$(2) \quad \rho(t) = \rho_1(t; a_1, b_1, \mu_1) + \rho_2(t; a_2, b_2, \mu_2)$$



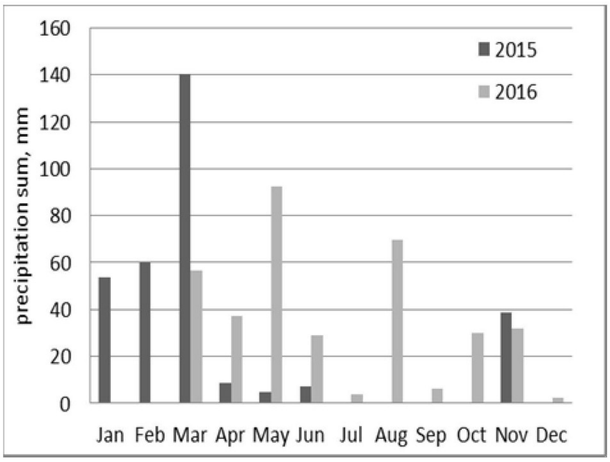


Fig. 1: Mean monthly temperature (**a**) and precipitation sums (**b**), village Brestnik, Plovdiv region.

where: ρ_1 and ρ_2 are the functions showing the density changes, respectively during the first and the second growth cycles. Assuming that the growth rate of grape berry density at the moment t is proportional to the density at this moment, and that growth is an irreversible process, then the growth function for a given cycle is of the logistic type (Thornley and Johnson 2000):

(3) $$\rho_i(t) = \frac{a_i.b_i}{a_i + (b_i - a_i).\exp(-\mu_i.t)} + d_i \text{ , } i=1,2 \text{ , } i=1,2$$

where: the coefficient μ is the specific growth rate of berry density at the beginning of the cycle and $\mu = \frac{1}{\rho}\left(\frac{d\rho}{dt}\right)$.

It should be noted that the parameters a, b, μ, d of the model (2) and (3) have a direct biophysical meaning. The parameter a represents the density of the new substrate at the initiation of a cycle, and it usually tends to zero since the new substrate is still at the very beginning of formation, the parameter d shows the density of the available substrate accumulated during previous stages, b is the densification of berries during the given cycle. The parameters a, b, μ, d of the growth functions ρ = ρ(t; a, b, μ, d) have been determined minimizing the residual sum of squares, between the measured values $\rho_i(t_i)$ and the values of the growth function $\rho(t_i; a, b, \mu, d)$, determined by means of the sigmoid model in the time moments t_i:

(4) $$\sum_{i=1}^{n} \left(\rho(t_i; a, b, \mu, d) - \rho_i(t_i)\right)^2 \text{ n – number of measurements.}$$

Results and Discussion

Berry density change (anthesis - maturity): The duration of the period of berry development from the beginning of anthesis until technological maturity was approximately 120 d. The results from the measurements clearly outline two growth cycles in the grape berry density changes (Fig. 2). The first cycle lasted for approximately 5 weeks, starting in the middle of May with the beginning of anthesis and finishing two weeks after the end of anthesis, in the middle of June (June 18). During this transition berry density increases by about 221 mg·cm^{-3} at an average rate of 6.14 mg·cm^{-3}·d^{-1}, as at the end of the cycle it reaches values of 1026 mg·cm^{-3}.

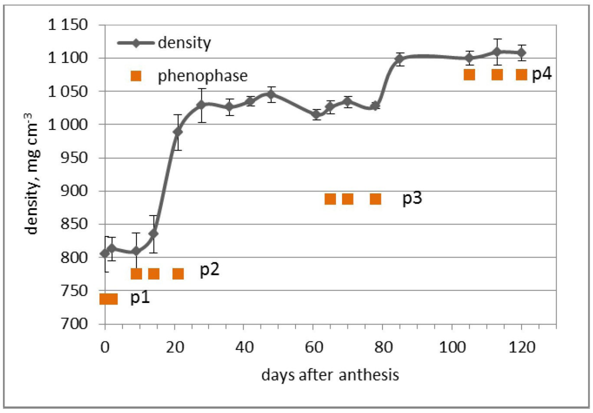


Fig. 2: Berry density changes during the period anthesis – technological maturity. Phenological phases: **p1** (bud break – anthesis), **p2** (full bloom), **p3** (véraison), **p4** (maturity). Seedless grape cultivar 'Black Corinth'. Density is represented by sample mean value and the standard deviation.

During the first cycle berries are shaped as a result of the accelerated cell division, followed by an enlargement of their sizes, *i.e.* an increase of the biomass and volume of berries. The changes in berry density during this stage are due to ongoing biochemical processes of accumulation of malic acid (ρ = 1790 mg·cm^{-3}) in the mesocarp and tartaric acid (ρ = 1610 mg·cm^{-3}) in the skin, as well as the varying water content of berries (Etchebarne *et al.* 2009) and other compounds entering the fruit. The processes of biomass accumulation were more intense in comparison to the increase in volume since there was a significant growth in density.

The lag phase was characterized by a decline in growth processes, as a result of which berry density remained almost constant ~ (1030.23 ± 12.69) mg·cm^{-3}. The lag phase in terms of berry density covered a period of one month and it ended in the middle of July (July 17) with the initiation of véraison.

The second cycle began with the start of véraison and continued until the technological maturity of the berries was reached. It lasted for a month and a half, until the end of August and the beginning of September (August 28 - September 3). During the véraison (Fig. 2), from July 17 to July 30, berry density increased by 10 mg cm^{-3}, which was probably due to the onset of sugar accumulation in the mesocarp. After the end of véraison until the beginning of technological maturity (Fig. 2), intense growth of berry density was observed by another 84 mg cm^{-3}, at an average rate of ~ 1.75 mg·cm^{-3} d^{-1}, and it reached values of 1118 ± 21 mg·cm^{-3}. Compared to the first cycle, during the second cycle berry density increased 3.5 times more slowly. During the second cycle berry density is determined by the growing sugar content in the mesocarp (Matthews and Nuzzo 2007, Barbagallo *et al.* 2011). The processes of berry drying as a result of the decrease of their water content, also contributed to the increase in density during this stage.

Double sigmoid model of berry density change: The double sigmoid function (2) described well the processes of grape berry densification in 'Black Corinth' during the period anthesis – technological maturity, as R^2 = 0.9614, SE = 19.36 mg cm^{-3} (standard error), n = 20 (Fig. 3). The parameters a, b, μ, d of the growth functions

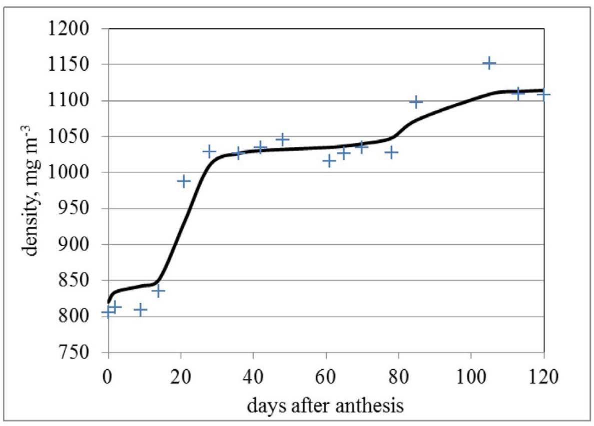


Fig. 3: Double sigmoid model of grape berry density changes, during the period anthesis – technological maturity.

$\rho = \rho(t; a, b, \mu, d)$ for the two cycles of berry density change and 95 % confidence bounds are presented in Tab. 1. The differences between measured and modeled basic characteristics of the first and second growth cycles of berry density were small (Tab. 2). During the lag phase there was no increase in measured density and it varies slightly around the average (standard deviation $\sigma = 12.65$ mg·cm^{-3}), while in this stage the modelled density showed a gradual increase at an average rate of 0.35 mg cm^{-3}·d^{-1}. However, as a result of this growth the density increased slightly, less than the standard deviation σ of measured ρ for the period. The end of the lag phase was related to the triggering of véraison. During the first two weeks of véraison, the average rate of increase in density ρ was 0.85 kg·m^{-2}d^{-1}, and after the end of véraison until reaching technological maturity, the rate of berry densification rose sharply and reached values close to the measured ones.

The rate of grape berry density change during the berry development was characterized by two maximums which coincide with the middle of the first and second cycles (Fig. 4). During flowering an acceleration of the berries' densification processes was observed, and a week after the end of flowering, the calculated rate of density change increase reached a maximum value of 11.44 mg·cm^{-3}·d^{-1}. This is due to the accelerated biomass accumulation at a slower increase of berry volume. The calculated maximum rate of change was two times smaller than the maximum rate of 21.78 mg·cm^{-3}·d^{-1} measured at the same time. One week before the beginning of the lag phase, when cell division ended (HARRIS *et al*. 1968), the rate of density change rapidly dropped to zero, indicating the beginning of the lag phase. A week after the end of flowering dρ/dt reached a local maximum again. This was the second local maximum in the berry density change rate (Fig. 4). Also, the rate of density change of 3.59 mg cm^{-3} d^{-1} computed by double logistic model at the second local maximum underestimated the measured density rate of 10 mg·cm^{-3}·d^{-1} (Fig. 4). Similar results for growth rate were obtained by FANIZZA and COLONNA (1996) for berry diameter of table grape varieties and by OLLAT and GAUDILLERE (1998), for fresh berry mass of 'Cabernet Sauvignon'. After reaching the second maximum, the density rate decreased to 0.2-0.3 mg·cm^{-3}·d^{-1} at the beginning of maturity. During the technological maturity berry density varied slightly mainly due to changes in the

Table 1

Parameters of the double sigmoid model of berry density changes during the two growth processes in the periods (anthesis – véraison) and (véraison – maturity)

Parameters	anthesis – véraison	véraison – maturity
a, mg·cm^{-3}	0.00658	0.00261
b, mg·cm^{-3}	258.3 (241.2, 275.4)	92.79 (71.57, 114)
d, mg·cm^{-3}	782.5 (770.3, 794.8)	1023 (1005, 1040)
μ, d^{-1}	0.1886 (0.1281, 0.2491)	0.1136 (0.0712, 0.1561)
Goodness of fit		
R^2	0.9749	0.8994
RMSE	18.78	15.45

Note: 95% confidence intervals are given in parentheses; μ is measured in d^{-1}.

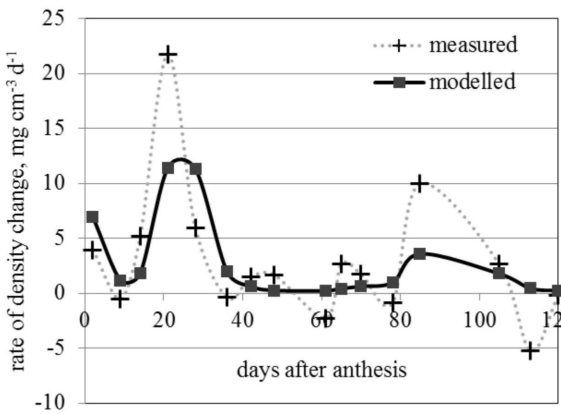


Fig. 4: Rate of berry density changes during the growth period.

Table 2

Grape berry density changes during anthesis – véraison and véraison – maturity growth cycles

Growth characteristics	Measurements	Double sigmoid model
1st growth cycle		
Cycle duration	36 days	
Berry density at the end of the cycle	1026 mg·cm^{-3}	1026 mg·cm^{-3}
Density change Δρ	221 mg·cm^{-3}	206 mg·cm^{-3}
Average rate of density change	6.14 mg·cm^{-3}·d^{-1}	5.73 mg·cm^{-3}·d^{-1}
lag phase		
Stage duration	30 days	
Berry density	1030 ± 12.65 mg·cm^{-3}	1026 mg·cm^{-3} at the beginning
Density change Δρ	-	10 mg·cm^{-3}
Average rate of density change	-	0.349 mg·cm^{-3}·d^{-1}
2nd growth cycle		
Cycle duration	48 days	
Berry density at the end of the cycle	1110 mg·cm^{-3}	1112 mg·cm^{-3}
Density change Δρ	84 mg·cm^{-3}	76 mg·cm^{-3}
Average rate of density change	1.75 mg·cm^{-3}·d^{-1}	1.57 mg·cm^{-3}·d^{-1}

water content of the berry.The double sigmoid model also made possible to calculate the specific rate μ of densification at the beginning of each of the growth cycles. The specific rate determined the duration of each cycle, and the higher μ was, the shorter the densification cycle. At the beginning of the first cycle μ was 0.1886 d^{-1}, and it was 1.5 times higher than the specific rate at the beginning of the second cycle starting immediately after véraison.

Conclusion

The results from the current research show that during the period anthesis – maturity, berry density change follows the double sigmoid curve, with clearly outlined two growth cycles divided by a phase of relative latency (lag phase). Since density integrates in itself the other growth parameters – mass, volume and linear dimensions as length, diameter, then berry density can be successfully used in studies of berry growth processes instead of them. Furthermore, density depends on the composition of grape berries and it could also serve as an indicator of the changes in their composition.

The developed double sigmoid model of density growth allows the performance of a more detailed quantitative analysis of growth processes and defining objective metrics for determination of the timing and duration of berry development stages.

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