A double-sigmoid model
for grapevine bunch compactness development

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Abstract

Aim: Bunch compactness results from a complex dynamic process in which many bunch, berry and rachis features interact during the whole grapevine reproductive cycle. The aim of this work is to identify the different developmental stages involved in bunch compactness determination during the second growing season, from berry set to harvest time.

Methods and results: In this work, bunch features from ten wine grapevine cultivars with diverse bunch compactness (including very loose and very compact bunches) have been periodically described. Experimental data allowed us to quantify changes in bunch compactness from berry set until harvest time in an objective manner. Our results indicate that bunch compactness development follows a double-sigmoid model, characterized by two consecutive cycles, each one with a growing stage followed by a latent one. Differences in the slope factor of the growing stages and in the extension of each developmental phase can explain part of the bunch compactness variation observed at harvest time in our set of cultivars.

Conclusions: Bunch compactness development after berry set is mainly driven by berry growth, and differences in compactness between loose and compact bunches can be majorly attributed to variation in berry number and rachis length. Accordingly, bunch architecture before véraison plays an important role in bunch compactness at harvest time.

Significance and impact of the study: The double-sigmoid model for bunch compactness development, and the four different stages identified, will aid in future analyses aimed to unravel the underlying mechanisms affecting this complex trait.

Keywords: berries per bunch, berry volume, bunch density, grapevine inflorescence, rachis length

Introduction

Botrytis bunch rot outbreaks (caused by the rot-inducing organism *Botrytis cinerea* Pers. ex. Fr.) cause important economic drops for the grape and wine industry, especially under the humid climate conditions of certain winemaking regions (Molitor *et al.*, 2016). Botrytis bunch rot reduces crop yield and grape quality, and it also worsen the quality of wines by generating off-flavors, oxidative damage, premature aging and difficulties in clarification during the winemaking process (Ribéreau-Gayon, 1983). *Botrytis cinerea* epidemiology and Botrytis bunch rot disease expression can be affected by a great number of factors (Gabler *et al.*, 2003; Molitor *et al.*, 2016), and different studies indicate the strong link between bunch compactness and their predisposition to rot infestation (Hed *et al.*, 2009; Vail *et al.*, 1998). Consequently, growers are sometimes forced to collect grapes before ripening is complete (Molitor *et al.*, 2016). In addition, berry illumination and ripeness homogeneity differ between loose and compact bunches (Silvestre *et al.*, 2017), affecting fruit composition and wine quality.

As a result, bunch compactness is becoming an important trait for clonal selection and grapevine breeding programs (Blaich *et al.*, 2007; Regner, 2015), so a better understanding of this trait is needed. Tello *et al., 20*15) have recently identified three traits (rachis architecture, berry number and berry dimensions) as the main factors affecting bunch compactness variation in a multi-cultivar framework, whose developmental determination is controlled by diverse genetic and metabolic pathways (Deluc *et al.*, 2007; Diaz-Riquelme *et al.*, 2014; Grimplet *et al.*, 2017; Li-Mallet *et al.*, 2016). Differences in rachis architecture between loose and compact cultivars are mainly determined during the period of inflorescence development prior to anthesis (Shavrukov *et al.*, 2004). Berry number is a consequence of flower number and fruit set rate (Carmona *et al.*, 2008), and it is definitively determined one or two weeks after flowering (Bessis and Fournioux, 1992). Major differences in berry dimensions are due to differences in cell division rate before and after anthesis and/or to differences in cell expansion after anthesis (Houel *et al.*, 2013). In addition, different works suggest the interconnection in the determination of these traits, like the inverse correlation between berry size and berry number (May, 2004), and between flower (or berry) number and rachis development (Gourieroux *et al.*, 2017; Gourieroux *et al.*, 2016; Theiler and Coombe, 1985). Altogether, bunch compactness is the result of a complex dynamic process in which many bunch, berry and rachis factors interact for its final determination.

The identification of the different stages taking place during this process might aid in improving vineyard management practices, as well as to perform more detailed analyses of this complex trait. In a previous study on a set of bunches of the wine grapevine cv. Syrah, Igounet *et al.* (1995) identified three different stages in the determination of bunch compactness during the berry maturation process: a first stage where bunch compactness increases slightly, a second stage where a rapid increment can be observed (bunch closure), and a third stage of stabilization where a slight decline in bunch compactness might appear. Nonetheless, the proposal of a general model needs the periodical measurement of inflorescence/bunch architecture related traits in a higher diverse sample of grapevine bunches.

Aware of the relevance that pre-véraison bunch architecture might play on final bunch compactness and bunch rot epidemics (Molitor *et al.*, 2015), and considering the usefulness of modeling grapevine inflorescence growth and development processes to improve our knowledge of plant functioning (Fourcaud *et al.*, 2008), the purpose of this work is to analyze how bunch compactness varies in different grapevine cultivars from berry set to harvest time. As a proof of concept study, ten wine grape cultivars commonly grown in Austria and with diverse bunch morphology (including very loose and very compact bunches) have been periodically described, providing the basis of a developmental model of easy interpretation and practical relevance.

Materials and methods

1. Plant material

Ten black and white wine grapevine (*Vitis vinifera* L.) cultivars that differ in bunch compactness and related traits were selected for this study: Blauer Portugieser, Blaufränkisch, Grüner Veltliner, Müller Thurgau, Neuburger, Roter Veltliner, Rotgipfler, Saint Laurent, Zierfandler and Zweigelt. These cultivars are part of the Experimental Grapevine Collection of the Universität für Bodenkultur Wien (BOKU), in Tulln an der Donau (Niederösterreich, Austria), and they were described in 2017. Plants are maintained following common conditions in terms of training system, row orientation and cultural practices. In this work, the modified Eichhorn and Lorenz (EL) system (Coombe, 1995) has been used for identifying the major grapevine phenological stages. Two shoots at a similar developmental stage from three plants per cultivar were selected at shoot length of 10 cm (EL-

12; five leaves separated and inflorescence clearly visible). The basal inflorescence of each shoot was then tagged for phenotyping assays, so six inflorescences/bunches were analyzed per cultivar (60 inflorescences/bunch in total). Whole canopy nets were used from véraison (EL-35) to harvest time (EL-38) to protect selected bunches from birds/insects.

2. Measurement of phenotypic characters

Peduncle and main rachis lengths were measured every three-four days from EL-12 until harvest time (EL-38). Berry width was measured on the widest section of five random berries from the middle part of the bunch every three-four days, starting two weeks after berry setting [EL-29; berries pepper-corn size (4mm diam), bunch at right angles to stem] and finishing at harvest time (EL-38). Average berry volume was then estimated considering a spherical volume (1). At harvest time, bunches were collected for the manual counting of berry number. Measurements were done using a digital caliper (Lux Tools, mod. 572587) as previously detailed (Tello and Ibáñez, 2014).

$$\text{Average berry volume (cm}^3) = \frac{4 \times \pi \times (\text{Average berry radius (cm)})^3}{3} \quad (1)$$

The quantitative compactness index CI13 (Tello and Ibáñez, 2014) was used to obtain an estimation of trait variation during inflorescence/bunch growth. This index estimates the trait as the ratio between bunch volume (cm^3) to rachis length squared (cm^2). For its calculation, bunch volume was derived from final berry number and berry volume estimation, and rachis length was directly used from experimental data (2). In addition, bunch compactness was visually rated at harvest time according to the OIV descriptor 204 (O.I.V., 2007).

$$\text{CI13} = \frac{\text{Average berry volume (cm}^3) \times \text{Berry number}}{(\text{Rachis length (cm)})^2} \quad (2)$$

3. Model fitting and statistical analyses

The relationship between bunch compactness (CI13) and time (days) was fitted using the non-linear growth/sigmoidal models available in the Origin software package (v. 9.4, OriginLab Co. MA, USA), using experimental data from all grapevine bunches. The best fitting model was selected according to R^2 associated values. Accordingly, experimental data best fitted a double-sigmoid model that follows the equation shown in (3), where CI13$_{min}$ and CI13$_{max}$ are the minimal and maximal CI13 values, respectively; p is the fraction of the curve comprising

the more potent phase; logSt$_1$ and logSt$_2$ are the midpoint potency parameters for the two different growing stages, respectively; x represents time (in days); and h$_1$ and h$_2$ are unitless slope factors of growing stages 1 and 2, respectively.

$$\text{CI13} = \text{CI13}_{min} + (\text{CI13}_{max} - \text{CI13}_{min}) \times$$

$$\left[\frac{p}{1 + 10^{(\log St_1 - x) \times h1}} + \frac{1 - p}{1 + 10^{(\log St_2 - x) \times h2}} \right] \quad (3)$$

Once the model was selected, the fitting procedure was individually repeated on each bunch (and set of bunches with the same value of visual compactness) to obtain curve fitting parameters and the goodness-of-fit, described using R^2 values. Bivariate correlations between traits, visual compactness, CI13 and curve fitting parameters were estimated using Kendall's τb coefficients by means of SPSS v. 21.0 (IBM, Chicago, IL, USA). The correlation plot was obtained using *corrplot*, a package for R (v. 3.2.5).

Results and discussion

Date and intervals between the main phenological events (budburst, flowering, véraison and harvest) are important factors to understand grapevine developmental processes (Tomasi *et al.*, 2011). Considering our set of cultivars, the earliest symptoms of budburst were observed for the cultivar Saint Laurent (on 4th April), and the latest for Blauer Portugieser (on 18th April) (Figure 1). Contrasting with this long time lapse between cultivars (14 days), EL-12 (shoots 10 cm) and full flowering stages took place in just three days. Consequently, and due to the consistency between cultivars, results in this work are shown as days after EL-12 stage. As it is generally accepted for grapevine (Keller, 2010), a period of favorable temperature over 18°C was needed to trigger flowering. Véraison (evaluated by the beginning of berry softening in white and black cultivars and supported by changes in berry color in black cultivars) occurred as early as 26th July (Saint Laurent, Blauer Portugieser and Zweigelt) and as late as 4th August (Blaufränkisch). Harvest took place from 28th August (Neuburger) to 1st September (Blauer Portugieser, Blaufränkisch) except for cv. Zierfandler, whose bunches had to be harvested before reaching maturity (16.6°Brix) due to evident rot symptoms (Botrytis bunch rot) probably favored by their high compactness (Figure 2). In addition, two bunches (one from Müller Thurgau and the other from Saint Laurent) were discarded from final description because they showed some structural damage.
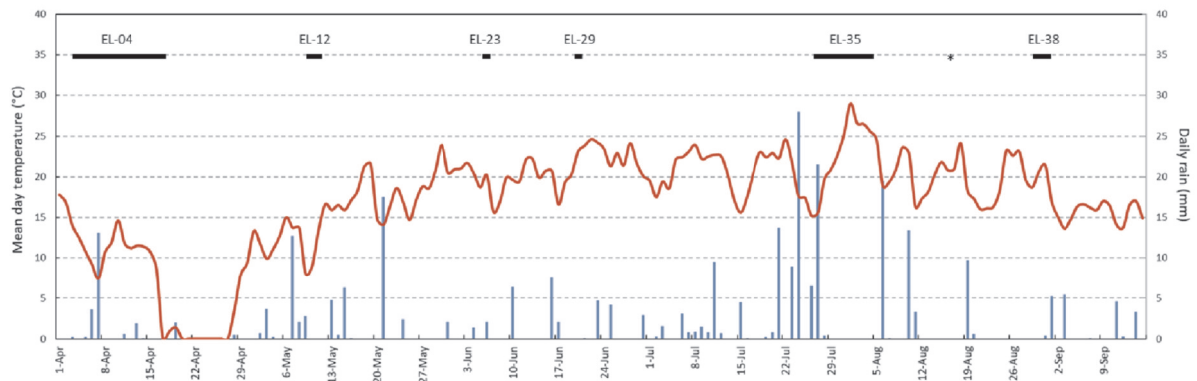
Figure 1. Climate conditions at the Experimental Grapevine Collection of the Universität für Bodenkultur Wien, in Tulln an der Donau (Niederösterreich, Austria) in 2017 (1-Apr to 15-Sep).

Figure 2. Grapevine bunches differing in compactness at harvest time.
1: Very loose bunch ('Saint Laurent'); 3: Loose bunch ('Müller Thurgau'); 5: Medium bunch ('Blauer Portugieser');
7: Dense/Compact bunch ('Rotgipfler'); 9: Very dense/Very compact bunch ('Zierfandler').
Bunch compactness was rated at harvest time according to the OIV descriptor 204 (O.I.V., 2007). Squares in the background have 1 cm².

Time lapses for the major developmental stages are indicated as black bars (EL-04: Budburst; EL-12: Shoots 10 cm; EL-23: Full flowering; EL-29: Berries pepper-corn size; EL-35: Véraison; EL-38: Berries harvest-ripe). *: Zierfandler bunches were harvested at an incomplete status of maturity due to evident rot symptoms. Data were obtained from a weather station located at the experimental plot (https://dnw-web.boku.ac.at/dnw/wetter_form_uft.php).

Significant differences (p<0.01) were observed for bunch compactness and related traits between the different cultivars here evaluated (Table 1). Nonetheless, the aim of this work was not to compare differences for this variable between cultivars, but to use them to quantify changes in bunch compactness. Supporting the usefulness of our sample, we observed a wide range of diversity for compactness at harvest time, including very loose and very compact bunches (Table 1 and Figure 2). Peduncle and rachis lengths were measured for each bunch from EL-12 (shoots 10 cm, inflorescence clearly visible) until harvest time (Figure 3A). Confirming

previous observations on Red Chasselas grapevines (Theiler and Coombe, 1985), peduncle growth stopped after an initial rapid increase, reaching its definitive length around 10 days before flowering. In contrast, and agreeing with previous works (Coombe, 1995; Gourieroux et al., 2016; Shavrukov et al., 2004; Theiler and Coombe, 1985), rachis grew progressively up to the post-flowering period (ca.15 days afterwards), when it reached its maximum length. It has been recently suggested a differential development on the vascular system of both structures, including significant higher number of lignified phloem fibers in the peduncle compared with the main axis of the rachis (Gourieroux et al., 2017), which are known to provide mechanical strength and support to the inflorescence. In contrast, phloem conducting area is rather constant all along the rachis main axis (Gourieroux et al., 2016). Altogether, these findings suggest that inflorescence peduncle might be under distinct genetic, hormonal and physiological control compared to the rest of the inflorescence (Gourieroux et al., 2016), and so it

Table 1 - Phenotypic values (mean±S.D.) obtained at harvest time.

Cultivar	Peduncle length (mm)	Rachis length (cm)	Berries per bunch	Berry width (cm)	Bunch compactness (OIV rating)*	Bunch compactness (CI13)
Blauer Portugieser	22.8± 3.2	17.5± 2.1	155.3± 32.9	1.5± 0.1	5	1.43± 0.27
Blaufränkisch	17.1± 3.9	18.1± 2.7	142.8± 63.7	1.5± 0.1	1-5	0.85± 0.31
Grüner Veltliner	32.7± 10.9	14.2± 2.2	181.3± 56.4	1.3± 0.0	3	1.32± 0.29
Müller Thurgau	18.3± 3.0	12.5± 1.2	83.2± 20.9	1.3± 0.1	3-5	0.57± 0.09
Neuburger	21.6± 8.1	10.6± 1.1	90.0± 18.7	1.4± 0.0	5-7	1.92± 0.27
Roter Veltliner	30.2± 11.4	13.5± 1.0	182.8± 28.4	1.3± 0.1	5-7	1.86± 0.22
Rotgipfler	12.9± 3.7	13.2± 0.5	210.3± 37.6	1.3± 0.1	7-9	2.80± 0.51
Saint Laurent	13.8± 1.8	14.5± 0.5	139.4± 77.2	1.3± 0.1	1-7	0.93± 0.52
Zierfandler	26.8± 4.3	17.5± 1.2	285.2± 99.2	1.4± 0.1	9	2.13± 0.53
Zweigelt	19.4± 2.9	12.7± 1.1	134.8± 32.5	1.5± 0.1	3-5	1.15± 0.26

All traits showed significant differences between cultivars (p<0.001, one-way ANOVA). * For bunch compactness, the range of variation according to the OIV descriptor 204 is given for each cultivar (1: Very loose bunch; 3: Loose bunch; 5: Medium bunch; 7: Dense/Compact bunch; 9: Very dense/Very compact bunch).
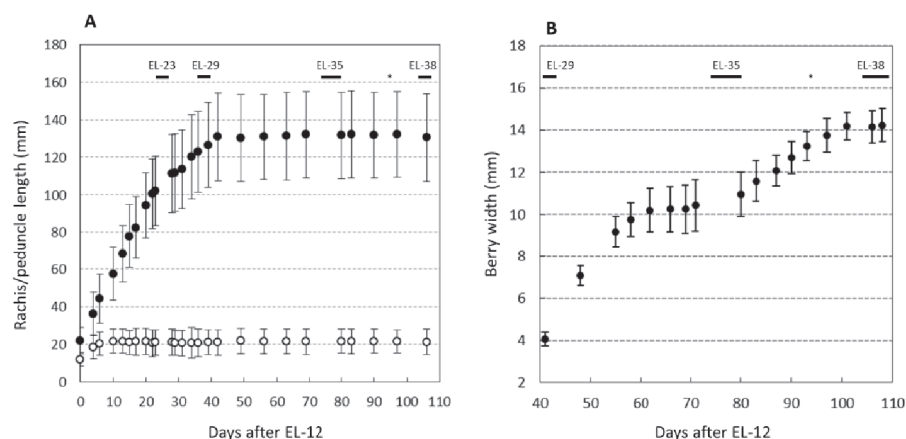

Figure 3. Rachis, peduncle and berry growth. In A, peduncle (empty dots) and rachis (full dots) growth is shown between EL-12 (shoots 10 cm) and EL-38 (harvest time). In B, berry size (width) is shown between EL-29 (berries pepper-corn size, 4mm diameter) and EL-38 (harvest time).
Data are mean values between bunches (in A) or berries (in B), whereas whiskers indicate standard deviations. EL-23: Full flowering; EL-35: Véraison. *: Zierfandler bunches were harvested at an incomplete status of maturity due to evident rot symptoms.

should be considered as an independent inflorescence structure.

Similarly, berry development was periodically monitored between EL-29 and EL-38 stages (Figure 3B). Berry growth followed a double-sigmoid curve, corresponding to the three developmental stages largely described: (I) a first stage of berry growth by cell division and expansion, (II) a lag phase of slow growth that ends with the onset of véraison, and (III) a final stage of berry growth through cell enlargement (Coombe and McCarthy, 2000; Ojeda *et al.*, 2001). Interestingly, berries reached their maximum size in a short period of time, with a second growth period shorter than those previously reported (Coombe and

McCarthy, 2000). Considering Austrian cool climate conditions, cultivars with short ripening periods are preferred for grape production, which increases the chance of obtaining early-ripen berries whilst reducing the risk of grapes exposition to events like rain, cold, frost or bunch rots. As a result, traditional cultivars like Blauer Portugieser, Neuburger and Roter Veltliner are known to ripen quite early, likely shaped through their long history of development and adaptation to Central Europe conditions (Sefc *et al.*, 1998). Similarly, early ripeness (combined with adequate yields and pathogen resistance) was a key parameter for the breeding of the most successful Austrian bred cultivars (Regner, 2015). This is the case of cv. Zweigelt, a cross between Saint Laurent

and Blaufränkisch, commonly found nowadays in the Austrian winemaking regions of Niederösterreich, Burgenland and Steiermark, and in several winemaking regions from neighboring countries with similar climate conditions like Hungary, Slovakia and the Czech Republic (Regner, 2015).

Bunch formation and architecture unfolds in two consecutive seasons. During the first season (in the bud until dormancy), processes related to inflorescence primordia initiation and differentiation occur. During the second one, flowering and fruit development (berry formation and ripening) processes take place (Carmona *et al.*, 2008; Li-Mallet *et al.*, 2016). Here, we focused on the quantitative analysis of bunch compactness during the second season, so the use of a nondestructive metric that could be used under field conditions throughout this period was paramount. In a previous work, Molitor *et al., 20*15) estimated this trait at pre-véraison through the use of the so-called 'density index', providing a value with high correlation with bunch rot severity at harvest time. Despite its interest, this index is an ordinal descriptor that classifies bunches into five predefined categories, considering two bunch compactness-related attributes (proximity between berries and bending of the stem), so it did not provide the quantitative data needed for our work. Considering the diverse quantitative methods available for bunch compactness evaluation (Tello and Ibáñez, 2018), we used the compactness index CI13, defined as the ratio of bunch volume (cm^3) to bunch length squared (cm^2) and calculated as detailed in Material and Methods. As reported in different grapevine cultivars (Khalil *et al.*, 2017; Tello *et al.*, 2016), this metric correlated significantly with the visual OIV rating obtained at harvest time in our sample ($\tau_b = 0.67$; $p \leq 0.01$), supporting its usefulness for our aim (Figure 4). The use of this index proved to be helpful to monitor bunch compactness variation from EL-29 until EL-38 stages through the direct measurement of berry diameter, berry number and rachis length. We chose EL-29 as the first measurement time point because berry abscission normally finishes two weeks after flowering (Bessis and Fournioux, 1992), and earlier measurements could have stimulated flower/berry drop processes and so altered final bunch architecture. Bunch compactness at harvest time correlated significantly with the number of berries per bunch ($\tau_b = 0.43$; $p \leq 0.01$), and the length of the rachis ($\tau_b = -0.25$; $p \leq 0.01$), but no significant correlation was observed with berry width (Figure 4). It is in agreement with previous findings that indicate the leading role of the total number of berries per bunch and the architecture of the rachis on bunch compactness variation at

Figure 4. Correlation plot based on Kendall's τ_b correlation values obtained between the traits (harvest time) included in this study.

Only significant ($p \leq 0.01$) correlations are shown, in blue (positive correlations) or in orange (negative correlations).

harvest time, as well as the minor role of berry dimensions on this trait in a multi-cultivar framework (Tello *et al.*, 2015).

Changes in bunch compactness from EL-29 to EL-38 are shown in Figure 5a. Considering the whole set of samples, the double-sigmoid model described in (3) fitted individual measurements with an overall R^2 value of 0.48 ($p \leq 0.01$). In contrast to the three-stage model proposed by Igounet *et al.* (1995), our data supports a four-stage model for bunch compactness determination. Accordingly, this process follows two consecutive cycles, each one with a growing and a lag phase. The first cycle starts after berry set, once the final number of berries is determined (Bessis and Fournioux, 1992). During the growing phase of this first cycle (phase I in Figure 5b), berries grow due to a combination of cell division and cell expansion (Coombe and McCarthy, 2000), which produces an increment in the solid component of the bunch. Although some growth in rachis length is still appreciated during the first days of this stage (which will ultimately produce an increment in the morphological volume of the bunch, and so a reduction of bunch compactness), bunch compactness increases progressively as berries grow. After that, berry growth stops and so does bunch compactness, showing a first stationary phase in the developmental process (phase II in Figure 5b). The second cycle starts with the onset of ripening (véraison), when berries start growing again by cell expansion processes (Coombe, 1995). This berry growth corresponds to the growing phase of the second cycle of bunch compactness determination (phase III in Figure 5b). As berries grow, a rearrangement of the

berries is observed, which drives to the filling of the empty holes present in the morphological structure in compact bunches. At the end of this phase, bunches reach their final value of compactness. After that, a second phase of bunch compactness stabilization is observed (phase IV in Figure 5b).

Bunch compactness is highly variable between different cultivars (Tello *et al.*, 2015), and so it might be its developmental determinism. Here, we observed that the extension of each developmental phase and the slope factor of the growing stages in both cycles (phase I and III, in Figure 5b) varies between the grape bunches analyzed in this work, which affects final bunch architecture and compactness. In this regard, we observed that bunches with higher slope factors and/or longer growing phases (I and III) and/or shorter first lag phase (II) present higher final compactness values and vice versa. Consequently, we individually fitted our model to five sets of bunches, grouped according to the OIV descriptor 204 (O.I.V., 2007): very loose, loose, medium, compact and very compact. The double-sigmoid model significantly fitted all type of bunches (p≤0.01), with R^2 values ranging from 0.53 to 0.89 (for very loose and very compact bunches, respectively) (Figure 5c). Interestingly, significant differences between different classes of bunch compactness were already observable at the beginning of our experimental period, especially for the most extreme categories (very loose and very compact bunches, data not shown). In addition, significant positive correlations between initial and final measurements were obtained (i.e.: τ_b= 0.67; p≤0.01 between bunch compactness estimation 48 days after EL-12 and visual compactness at harvest time), suggesting the role of early bunch architecture on final bunch compactness. Lastly, the double-sigmoid model was individually fitted to each bunch to obtain model parameters ($CI13_{min}$, $CI13_{max}$, p, $logSt_1$, $logSt_2$, h_1 and h_2). Correlation analysis showed that the slopes of both growing cycles are significantly correlated (p≤0.01) with the final visual value of compactness. Interestingly, the correlation of bunch compactness with the slope of the first growing cycle was higher than that of the second cycle (τ_b= 0.60 and 0.48, for h_1 and h_2, respectively), reinforcing the relevance of bunch architecture prior to véraison on final bunch compactness (Molitor *et al.*, 2015).

In fine, our results indicate that, whilst bunch compactness development after berry set is mainly driven by berry growth, differences in bunch compactness between loose and compact bunches can be attributed to pre-véraison developmental events, which include the determination of berry number
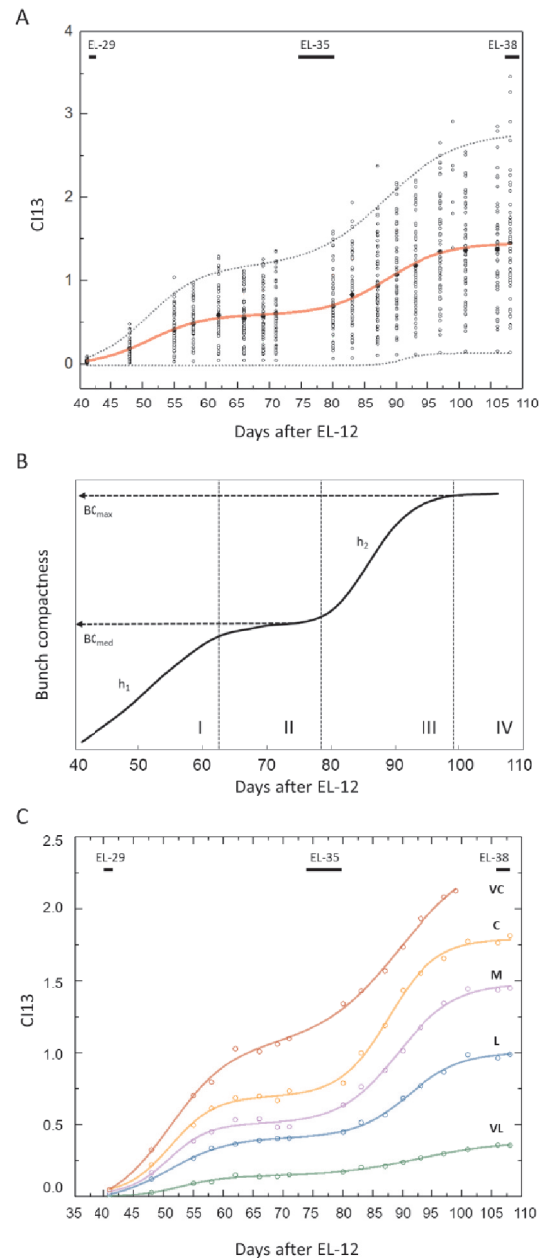

Figure 5. Bunch compactness evolution between EL-29 (berries pepper-corn size) and EL-38 (harvest time) growth stages.

Changes in bunch compactness (CI13) are shown in A, where empty dots indicate individual measurements and black dots average values per day. Model fitting curve is shown as a continuous red line, whereas ranges of standard deviation are indicated as discontinuous black lines. In B, an idealized diagram of the double-sigmoid model of bunch compactness for the same period is shown. BC_{max} and BC_{med} indicate the maximal values of bunch compactness reached in each growing cycle, and h_1 and h_2 represent slope factors. I, II, III and IV represent the four different developmental stages identified for bunch compactness determination. In C, the same model was individually fitted to very loose (VL, green; n=3), loose (L, blue; n=16), medium (M, violet; n=19), compact (C, orange; n=9) and very compact bunches (VC, red; n=11). Empty dots indicate average values, and fitted curve is shown as a continuous line (R²= 0.53, 0.57, 0.72, 0.77 and 0.89 for VL, L, M, C and VC data, respectively). Since Zierfandler bunches (very compact) were early harvested, the last two datapoints were excluded for modeling VC bunches' compactness development.

(Bessis and Fournioux, 1992), rachis length (Shavrukov *et al*., 2004) and most of the factors involved in the genetic variation for berry size (Houel *et al.*, 2013). Here, and for the sake of simplicity, only three factors were used for model construction, but the inclusion of other traits not considered (like pedicel length, or the number of ramifications of the bunch) might improve its accuracy. In addition, and considering the divergent selection and breeding targets followed for table and wine grapes in terms of bunch architecture (Migicovsky *et al.*, 2017), it would be of great interest to validate the model in grape cultivars with different origin and use.

From a practical point of view, the reduction of the slope of the first growing cycle (phase I in Figure 5b) arises as the most promising approach to reduce bunch compactness in highly compact cultivars. This reduction can be achieved by pre-véraison viticultural practices that reduce the solid component of the bunch (by reducing berry number and/or berry size) and/or by those that promote rachis elongation, which will increase the available space for the spreading of the berries in a looser conformation. As some examples, pre-flowering leaf removal has been suggested to reduce berry number in different cultivars (Gatti *et al.*, 2015; Sternad-Lemut *et al.*, 2015), and the pre-bloom application of gibberellic acid can stimulate rachis growth (Molitor *et al.*, 2012). Both strategies might reduce bunch compactness and bunch susceptibility to rots, but their recommendation would require case-by-case experimental studies.

Conclusion

Our results indicate that grapevine bunch compactness determination follows a double-sigmoid process characterized by two consecutive cycles, each one with a growing stage followed by a latent one. After berry set, bunch compactness determination mainly reflects changes in berry dimensions, whilst differences between loose and compact bunches can be majorly attributed to pre-véraison differences in rachis length and/or berry number. Consequently, bunch compactness at harvest time is highly impacted by early bunch architecture, suggesting that pre-véraison viticultural practices will be more effective than later strategies to reduce bunch compactness in highly compact cultivars.

Once validated in a wider sample of grapevine bunches of different origin and use (table and wine cultivars), the proposed model and the different stages identified in this work will be useful for further studies aimed to analyze the underlying mechanisms affecting grapevine inflorescence/bunch growth and bunch compactness diversity.

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