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Chilling requirements and dormancy evolution in grapevine buds

Requerimentos de frio e evolução da dormência em gemas de videiras

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ABSTRACT

Fluctuations in winter chilling availability impact bud dormancy and budburst. The objective of this work was to determine chilling requirements to induce and overcome endodormancy (dormancy controlled by chilling) of buds in different grape cultivars. 'Chardonnay', 'Merlot' and 'Cabernet Sauvignon' shoots were collected in Veranópolis-RS vineyards in 2010, and submitted to a constant 3 °C temperature or daily cycles of 3/15 °C for 12/12h or 18/6h, until reaching 1120 chilling hours (CH, sum of hours with temperature ≤ 7.2 °C). Periodically, part of the samples in each treatment was transferred to 25 °C for budburst evaluation (green tip). Chilling requirements to induce and overcome endodormancy vary among cultivars, reaching a total of 136 CH for 'Chardonnay', 298 CH for 'Merlot' and 392 CH for 'Cabernet Sauvignon'. Of these, approximately 39, 53 and 91 CH are required for induction of endodormancy in the three cultivars, respectively. The thermal regimes tested (constant or alternating) do not influence the response pattern of each cultivar to cold, with 15 °C being inert in the CH accumulation process. In addition, time required to start budburst reduces with the increase in CH, at a rate of one day per 62 CH, without significant impacts on budburst uniformity.

Index terms: Chilling hours; endodormancy; budburst; *Vitis vinifera*.

RESUMO

Flutuações na disponibilidade de frio hibernal afetam a dormencia e brotação de gemas. O objetivo deste trabalho foi determinar requerimentos de frio para indução e superação da endodormência (dormência controlada pelo frio) de gemas em diferentes cultivares de videira. Estacas de 'Chardonnay', 'Merlot' e 'Cabernet Sauvignon' foram coletadas em vinhedos de Veranópolis-RS em 2010 e submetidas à temperatura de 3 °C constante ou ciclos diários de 3/15 °C por 12/12h ou 18/6h, até 1120 horas de frio (HF, soma de horas com temperatura ≤ 7.2 °C). Periodicamente, parte das estacas de cada tratamento foi transferida para 25 °C, para avaliação da brotação (ponta verde). Requerimentos de frio para indução e superação da endodormência variam entre cultivares, alcançando um total de 136 HF para 'Chardonnay', 298 HF para 'Merlot' e 392 HF para 'Cabernet Sauvignon'. Destes, aproximadamente 39, 53 e 91 HF, respectivamente, são necessárias para indução da endodormência. Os regimes térmicos testados (constante ou alternado) não afetam o padrão de resposta de cada cultivar ao frio, sendo 15 °C inerte no processo de acúmulo de HF. O tempo necessário para iniciar a brotação diminui com o aumento de HF, à taxa de um dia para cada 62 HF, sem impactos significativos na uniformidade de brotação.

Termos para indexação: Horas de frio; endodormência; brotação; *Vitis vinifera*.

INTRODUCTION

Grapevines and other temperate fruit species may undergo dormancy, a period of temporary suspension of visible growth of plant tissue (Keller, 2015). Bud dormancy may occur in three forms: paradormancy, endodormancy and ecodormancy (Hawerroth et al., 2010). Paradormancy is the inhibition of bud growth by influence of another organ of the plant (e.g. apical dominance). Ecodormancy is caused by a temporary environmental restriction (e.g. lack of high temperatures). Endodormancy occurs during colder months, when bud development is hindered by biochemical and physiological events in the meristem or nearby tissues, triggered by environmental stimuli, such as low temperatures or changes in photoperiod. Endodormancy varies in intensity and duration and, once triggered, will remain in effect until a certain number of chilling hours (CH, sum of hours with air temperature below 7.2 °C) is reached. Although the exact biochemical mechanisms controlling endodormancy are still unknown, they vary among species and cultivars (Bruckner et al., 2010; Biasi; Carvalho; Zanette, 2010; Campoy et al., 2011; Anzanello et al., 2014). Satisfaction of chilling requirements during endodormancy is essential to avoid phenological disorders, such as insufficient or nonuniform budburst (Alldermann; Steyn; Cook, 2011; Atkinson; Brennan; Jones, 2013; Malagi et al., 2015).

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In the South of Brazil, temperature fluctuations during the winter can be considered as the main problem to overcome endodormancy in temperate fruit trees (Hawerroth et al., 2010). Guo et al. (2011) reported the adverse effect of high cyclic temperatures on endodormancy. According to Anzanello et al. (2014), elevated temperatures alternating with cold periods can cause considerable delays and irregularities in budburst, due to high temperatures reversing the effect of accumulated chilling. These thermal effects on dormancy metabolism have been observed mainly in peach and apple trees (Luedeling; Brown, 2011; Campoy; Ruiz; Egea, 2011; Melke, 2015). In grapes, the temperature effect on dormancy tends to be aggravated by the worldwide expansion of growing areas, mainly in subtropical regions. The perspective of global temperature elevation due to climate changes tends to worsen this scenario, with currently adequate areas becoming susceptible to marginal temperature conditions (Luedeling, 2012). In Rio Grande do Sul, a reduction in yearly chilling hours has been observed (Cardoso et al., 2012), directly impacting the endodormancy state and budburst ability of grapevines and other temperate fruit species.

Historically, modeling dormancy overcome has been related to the accumulation of CH (Weinberger, 1950). Other models have also been used to estimate the amount of chilling to overcome endodormancy and consequent induction of budburst, such as the Utah Model (Richardson; Seeley; Walker, 1974) and the North Carolina Model (Shaltout; Unrath, 1983), which evaluate quality of accumulated chill during autumn and winter by assigning differing weights to different temperatures. However, these models were adjusted in North American climatic conditions (Richardson; Seeley; Walker, 1974; Shaltout; Unrath, 1983), marked by regular autumns and winters, and none were fitted to grapevines. This makes them unreliable and imprecise when applied to grape producing regions in Brazil (Felippeto et al., 2013). Thus, the effect of temperature on dormancy should be better studied in grapevines, in order to adjust or develop better adapted models to predict budburst, especially in regions with mild winters.

This work evaluated the effect of chilling regimes on bud endodormancy of grapevine cultivars, in order to determine the chilling requirements to induce and overcome dormancy in different genotypes. In addition, the response of buds to cycling temperatures and to cold beyond the chilling requirement was assessed.

MATERIAL AND METHODS

The middle portions of annual shoots formed during the previous cycle of *Vitis vinifera* cvs. ‘Chardonnay’, ‘Merlot’ and ‘Cabernet Sauvignon’ were collected from a commercial vineyard located in Veranópolis, RS (29°01’44”S, 51°35’00”W, 590 m), in the Serra Gaúcha region, in 5 May 2010 (before any field CH had occurred) and 7 July 2010 (with 62 field CH). A total of 1780 shoots were collected, each measuring approximately 40-60 cm in length, 1 cm in diameter, and containing 5 compound axillary buds, without leaves. Plants were 8-years old, grafted on Paulsen 1103 rootstock, and conducted in a vertical trellis system spaced 1.50 x 3.50 m.

Shoots collected in the field were wrapped in bundles with moist newspaper, placed in plastic bags and transported on the same day to the lab. They were cleaned with 70% ethanol for 45-60 seconds, followed by 2.5% sodium hypochlorite for 20 min, rinsed three times with distilled water, and dried in the shade for 30 min. Samples of 10 shoots each were packed in black plastic film, and submitted to thermal regimes in Eletrolab EL202 climate incubators chambers, in the dark. Treatments were: I) constant 3 °C; II) 3/15 °C in 12/12 h daily cycles (12 hours in 3 °C and 12 hours in 15 °C); III) 3/15 °C in 18/6 h daily cycles (18 hours in 3 °C and 6 hours in 15 °C). The 3/15 °C regimes were defined based on climatic conditions of the main grapevine producing region of Rio Grande do Sul (Serra Gaúcha). Samples were kept in the chambers for up to 840 CH for ‘Chardonnay’ and 1120 CH for ‘Merlot’ and ‘Cabernet Sauvignon’.

Periodically (every 24 to 96 CH), samples were unwrapped, cut at the upper and lower extremities (leaving the three middle buds), had the upper tip dipped in paraffin and were set in an upright position with the lower tip kept in water. Shoots were supported by a double layer of braided screen (1 x 1 cm) laid over a 3 cm water blade, inside a Percival Boone 50036 growth chamber set at 25±1.5 °C and 12 h photoperiod, for induction and evaluation of budburst. For each combination of treatment and chilling time, three 10-shoot samples were evaluated. The experiment also included a control treatment, in which unchilled shoots were submitted directly to 25 °C in the growth chamber. Growth chamber air temperature and humidity (RH) were monitored by a hygrothermograph, keeping RH between 70 and 80%.

Field meteorological conditions were monitored with an automatic station, located approximately 16 km away (29°09’53”S, 51°32’03”W, 605 m) from the commercial vineyard where samples were collected. Pre-sampling field CH were added to experimental CH.

Budburst was evaluated daily in the growth chamber for 56 days, considering the date when the green-tip stage (Carvalho et al., 2010) was reached. Maximum budburst, precocity and uniformity data were estimated using a reparameterized Gompertz function (Fialho, 1999), as shown in Figure 1. For each treatment, the three parameters were expressed as functions of the number of chilling hours. Maximum budburst was modeled as a double sigmoid, accounting for both dormancy induction and overcoming. Precocity and uniformity were modeled as decreasing exponential functions. The difference between the resulting curves was tested using the F-test to compare nested models. All statistical analysis was performed using the R software (R Development Core Team, 2018).

RESULTS AND DISCUSSION

Experimental conditions were successful in inducing and overcoming dormancy. This may be seen in Figure 2 as a reduction in maximum budburst (inducing), followed by an increase to normal levels (overcoming). Initial budburst percentage in May (58 to 75%, depending on the cultivar) indicated that grapevine cultivars were not fully dormant in the field, although some part of the dormancy process may have already started prior to the occurrence of low temperatures in the field, specially in ‘Chardonnay’ and ‘Merlot’. Grapevine buds respond to short days prior to the low temperature stimulus, allowing them to initiate the changes involved in cold acclimation, which characterize endodormancy (Wake; Fennell, 2000; Garris et al., 2009; Fenell et al., 2015).

Thermal regimes (constant, 18/6 h and 12/12 h cycles) did not affect budburst response ($p>0.1$) in both sampling dates and all cultivars (Figure 2). This suggests that, within the thermal amplitude tested, the response of each genotype is based only on chilling time (3 °C) and is insensitive to the higher temperature period (15 °C) within the daily cycle. Similar results were observed in peach buds by Richardson et al. (1974) and in apple buds by Shaltout and Unrath (1983) and Anzanello et al. (2014), with 3 °C contributing to meet chilling requirements, but 15 °C having no effect. Erez and Fishman (1990) also found that moderate temperatures (15 °C) within a 6 °C cold treatment were not harmful, but helped to overcome dormancy in peach buds. The importance of alternating heat (15-20 °C) with cold (3-6 °C) in overcoming dormancy was also observed in other works with apricot, apple and peach trees (Guerriero; Indiogine; Scalabrelli, 1985; Naor et al., 2003; Sugiura et al., 2010). However, this beneficial effect of cycling temperatures was not observed with grapevine cultivars in the present work (Figure 2).

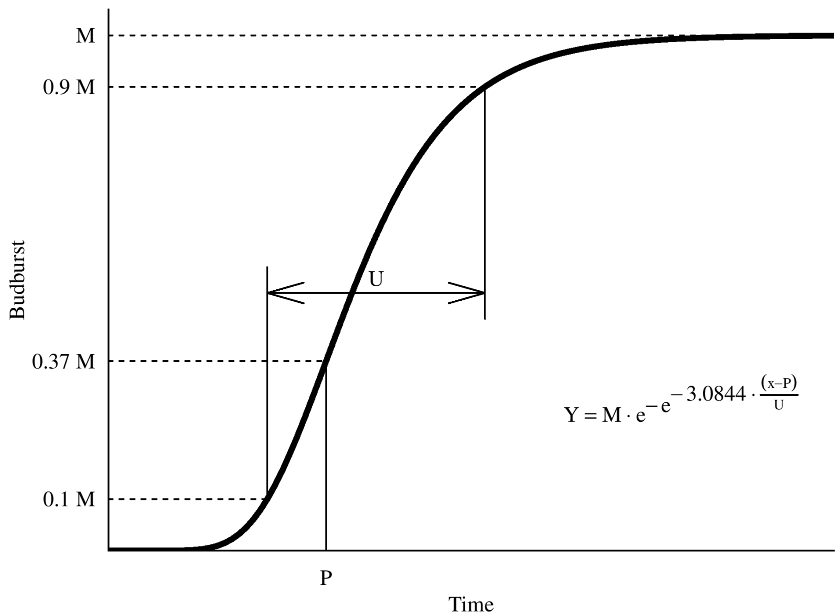

Figure 1: Model used to evaluate budburst in the growth chamber, after chilling treatments. The model uses a reparameterized Gompertz function (Fialho, 1999), in order to obtain parameters of biological significance: M = Maximum budburst (total percentage of sprouted buds); P = Precocity (number of days to reach the inflection point of the curve, at 37% of maximum budburst); U = Uniformity (time period between 10 and 90% of maximum budburst).

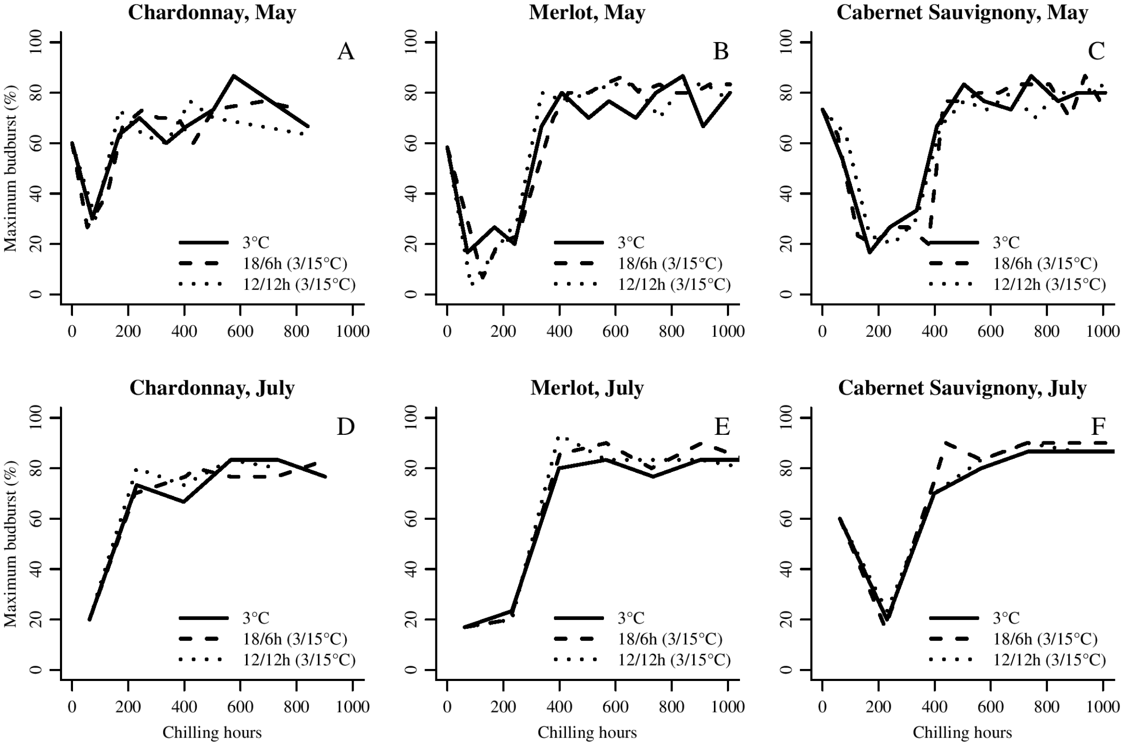

Figure 2: Maximum budburst of cultivars Chardonnay (A, D), Merlot (B, E) and Cabernet Sauvignon (C, F), sampled in May and July/2010, and submitted to a constant temperature of 3 °C or daily cycles of 18/6 h or 12/12 h at 3 °C and 15 °C, during dormancy. No significant difference between treatments was observed within each combination of cultivar and sampling date (P>0.1).

Dormancy evolution differed among cultivars. In 'Chardonnay' and 'Merlot', deep dormancy was rapidly induced in May, and buds collected in July were already fully dormant. In 'Cabernet Sauvignon', the rate of decrease in maximum budburst was smaller, and July buds were not yet completely dormant. The results observed in the July samples of all three cultivars were compatible with those of the May samples. Specifically, the same effect of 62 CH in the field suffered by the July samples was observed in the May samples submitted to a similar amount of artificial cold (Figure 2). These compatible results observed in May and July and the lack of effect of cycling vs. constant temperatures allowed all data within each cultivar to be grouped together to determine chilling requirements.

Fitted values of initial budburst, before the onset of dormancy, were 60% in 'Chardonnay', 59% in 'Merlot' and 71% in 'Cabernet Sauvignon' (Figure 3). Dormancy onset in grapevines is a complex process which may involve both photoperiod and temperature (Fenell et al., 2015). *Vitis vinifera* is relatively short-day tolerant, compared to other *Vitis* species, although not entirely insensitive to photoperiod (Lavee; May, 1997). Contrasts between cultivars may be common, and the lower initial budburst observed in 'Chardonnay' and 'Merlot' may have been due to a higher sensitivity to photoperiod, compared to 'Cabernet Sauvignon'. After chilling accumulation induced dormancy, minimum budburst levels of 25% in 'Chardonnay', 15% in 'Merlot' and 23% in 'Cabernet Sauvignon' were reached. When the chilling requirements were completely met, budburst levels were raised to 73%, 81% and 82%, respectively, characterizing a complete overcome of dormancy. Although there is a marked genotype contrast, these three values were similar among cultivars.

The main result observed in the data was a marked difference among cultivars in the number of chilling hours required to induce and, especially, to overcome dormancy. It is generally accepted that, once endodormancy is induced, chilling is essential to its termination (Lavee; May, 1997). 'Chardonnay' dormancy was induced with only 39 CH (the inflection point of the first sigmoid, in Figure 3), while 'Merlot' required 53 CH. In contrast, 'Cabernet Sauvignon' needed 91 CH to induce dormancy, more than double that of ‘Chardonnay’. The contrast is even greater on the number of CH required to overcome dormancy, estimated by the inflection point of the second sigmoid in each curve. ‘Chardonnay’ required a total of only 136 CH, while ‘Cabernet Sauvignon’ required 392 CH, nearly three times as much. ‘Merlot’ has an intermediate requirement of 298 CH, closer to that of ‘Cabernet Sauvignon’ than to ‘Chardonnay’.

According to Melke (2015), dormancy in temperate fruit cultivars can be divided into three levels: light, intermediate and deep. Cultivars with light dormancy, such as ‘Chardonnay’, halt bud growth superficially during the period of endodormancy. In cultivars with intermediate to deep dormancy, such as ‘Merlot’ and ‘Cabernet Sauvignon’, there is total or almost total paralysis of bud growth. Dormancy levels are directly related to genotype budburst dates commonly observed on the field, where ‘Chardonnay’, ‘Merlot’ and ‘Cabernet Sauvignon’ are known to have early, intermediate and late cycle, respectively (Giovaninni, 2008). Similar relations were observed in apples, in which earlier budburst is associated with smaller chilling requirements (El Yaacoubi et al., 2016).

In general, uniformity was not significantly affected by thermal regime or cultivar. Mean observed uniformity, measured as the time period between 10% and 90% of maximum budburst, was 21.7 days. Budburst precocity, however, increased with chilling exposure time in all cultivars, but was also not affected by the daily temperature cycles. This may be observed in Figure 4 as a reduction in the number of days between the onset of warm conditions (25 °C) and budburst. The effect of chilling hours on precocity can be clearly seen, with a reduction of about one day for every 62 CH, within the limits of the experiment (up to around 1000 CH). A similar pattern was observed in apple (Noar et al., 2003), pear (Herter et al., 2001), grapevine (Dokoozlian, 1999), peach (Bruckner et al., 2010; Sugiura et al., 2010), apricot (Campoy et al., 2011) and cherry (Shi et al., 2017) trees, in which reduced budburst time was observed with increased chilling exposure time.

Although the curves were slightly different among cultivars (Figure 4), precocity data had much more variation than maximum budburst, as seen by the coefficient of variation (CV = 24.1% and 8.9%) and the model fit ($R^2 = 0.508$ and 0.946, respectively), especially with a small number of CH. Nevertheless, ‘Chardonnay’ seems to sprout about 3 days earlier than the other cultivars. This association between lower chilling and lower heat requirements has also been observed in grapevines (Mohamed; El-Sese, 2009), apples (Guo et al., 2014; Malagi et al., 2015), which reinforces a hypothesis of similar and conserved budburst mechanisms in temperate fruit species.

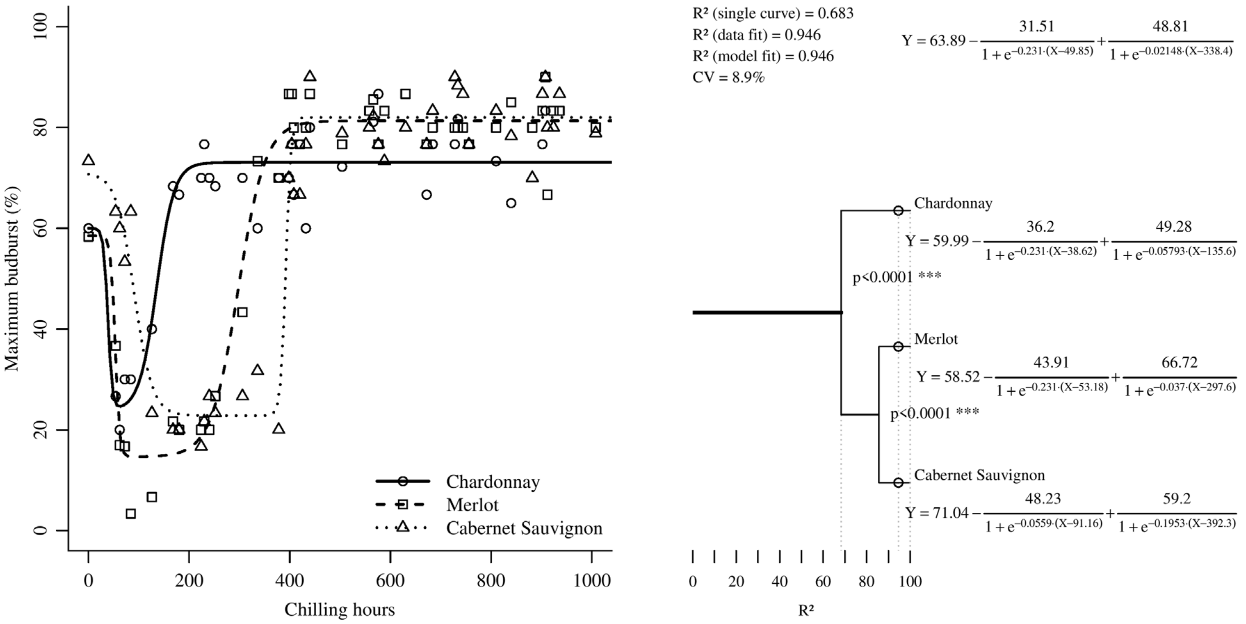

Figure 3: Maximum budburst of grapevines, grouped by cultivars, modeled as double sigmoid functions of chilling hours (left), and graphical representation of the statistical analysis comparing curves with the F-test, and resulting model equations (right). The top equation represents a general model of all data in a single curve, and the bottom three equations represent the individual models for each cultivar.

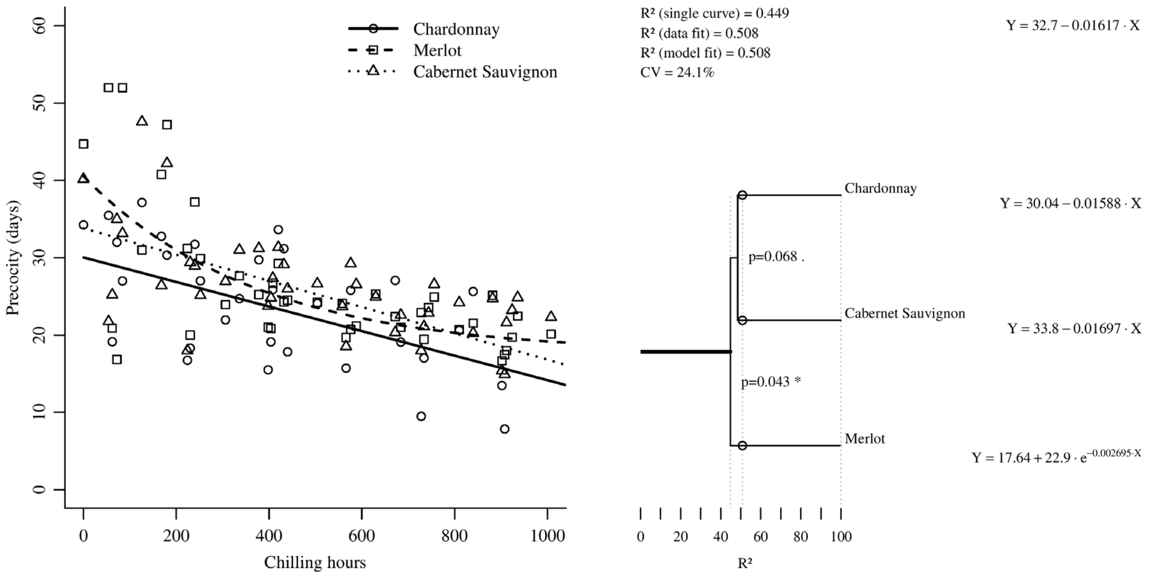

Figure 4: Precocity of grapevines, grouped by cultivars, modeled as decreasing exponential or linear functions of chilling hours (left), and graphical representation of the statistical analysis comparing curves with the F-test, and resulting model equations (right). The top equation represents a general model of all data in a single curve, and the bottom three equations represent the individual models for each cultivar.

CONCLUSIONS

The total chilling requirements to induce and overcome endodormancy in grapevines are 136 CH for 'Chardonnay', 298 CH for 'Merlot' and 392 CH for 'Cabernet Sauvignon', while the requirements to only induce dormancy are 39 CH, 53 CH and 91 CH, respectively. Dormancy evolution is associated with the number of hours in cold temperature (3 °C), regardless if they are interspersed with mild temperature periods (15 °C) or not. The time required for budburst is reduced as the number of CH increases, at the rate of approximately one day for every 62 CH, in 'Chardonnay', 'Merlot' and 'Cabernet Sauvignon'.

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