

Bud dormancy in apple trees after thermal fluctuations

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Abstract – The objective of this work was to evaluate the effect of heat waves on the evolution of bud dormancy, in apple trees with contrasting chilling requirements. Twigs of 'Castel Gala' and 'Royal Gala' were collected in orchards in Papanduva, state of Santa Catarina, Brazil, and were exposed to constant (3°C) or alternating (3 and 15°C for 12/12 hours) temperature, combined with zero, one or two days a week at 25°C. Two additional treatments were evaluated: constant temperature (3°C), with a heat wave of seven days at 25°C, in the beginning or in the middle of the experimental period. Periodically, part of the twigs was transferred to 25°C for daily budburst evaluation of apical and lateral buds. Endodormancy (dormancy induced by cold) was overcome with less than 330 chilling hours (CH) of constant cold in 'Castel Gala' and less than 618 CH in 'Royal Gala'. A daily 15°C-temperature cycle did not affect the endodormancy process. Heat waves during endodormancy resulted in an increased CH to achieve bud requirements. The negative effect of high temperature depended on the lasting of this condition. Chilling was partly cancelled during dormancy when the heat wave lasted 36 continuous hours or more. Therefore, budburst prediction models need adjustments, mainly for regions with mild and irregular winters, such as those of Southern Brazil.

Index terms: *Malus domestica*, budburst, chilling hours, climate change, dormancy models, endodormancy.

Dormência de gemas em macieira após flutuações térmicas

Resumo – O objetivo deste trabalho foi avaliar o efeito de ondas de calor sobre a evolução da dormência de gemas de macieiras com necessidades contrastantes de frio hibernal. Brindilas de macieiras 'Castel Gala' e 'Royal Gala' foram coletadas de pomares em Papanduva, SC, e expostas à temperatura constante (3°C) ou alternada (3 e 15°C, por 12/12 horas), combinadas com zero, um ou dois dias por semana a 25°C. Dois outros tratamentos foram avaliados: temperatura constante (3°C), com onda de calor de sete dias a 25°C, no início ou no meio do período experimental. Periodicamente, parte das brindilas era transferida para 25°C, para avaliação da brotação das gemas apicais e laterais. A endodormência (dormência induzida pelo frio) foi superada com menos de 330 horas de resfriamento (HF) constante em 'Castel Gala' e menos de 618 HF em 'Royal Gala'. Um ciclo diário de temperatura a 15°C não afetou o processo de endodormência. Ondas de calor de 25°C durante a endodormência resultaram em aumento de HF para atender à necessidade das gemas. O efeito negativo da alta temperatura dependeu da duração desta condição. O resfriamento foi parcialmente anulado durante a dormência, quando a onda de calor durou 36 horas contínuas ou mais. Portanto, os modelos de previsão da brotação necessitam de ajustes, principalmente para regiões com invernos amenos e irregulares, como os do Sul do Brasil.

Termos para indexação: *Malus domestica*, brotação, horas de frio, mudanças climáticas, modelos de dormência, endodormência.

Introduction

Apple trees need to be exposed to low temperatures during fall and winter, in order to overcome endodormancy (dormancy controlled by chilling) and to start a new growth cycle in the spring (Rohde & Bhalerao, 2007). If the chilling requirement is not met,

delays and irregularities in budburst and flowering occur, affecting fruit production.

The required amount of chilling to overcome endodormancy differs among species and cultivars (Putti et al., 2006; Horvath, 2009). The accumulation of chilling hours (CH) has been related to the sum of hours for plants under conditions below or equal to

7.2°C, a generic temperature for fruit trees (Luedeling & Brown, 2011). Other models have been used to estimate the amount of chilling required to overcome endodormancy and induce budburst, such as the Utah model (Richardson et al., 1974) and the North Carolina model (Shaltout & Unrath, 1983), which evaluate the quality of accumulated chill during fall and winter, by attributing different weights to different temperature ranges.

In the climatic conditions of Southern Brazil, there are large temperature fluctuations during the winter period. However, the most common dormancy models were adjusted to North American weather conditions (Luedeling & Brown, 2011), characterized by relatively regular falls and winters. When used to predict budburst under the conditions of the apple producing regions in Brazil, these models proved to be inaccurate and unreliable (Anzanello et al., 2014). Thus, the importance of heat and cold in the evolution of dormancy should be better understood, in order to adjust or develop best suited models to predict budburst potential.

The importance of dormancy characterization has increased in view of the current and future scenarios of global climate change. Climate models predict a significant reduction of winter chill in the traditional apple producing regions of Brazil (Cardoso et al., 2012). Three possible scenarios predict increases in minimum temperature of 1°C (optimistic), 3°C (pessimistic), and 5.8°C (very pessimistic) in the South of Brazil (Solomon et al., 2007). Biological response models (including dormancy status), adjusted to unstable temperatures during fall and winter, are important to predict scenarios and to minimize impacts of increasing temperatures. Accurate models may be used as decision support tools for orchard management, and to predict adequacy of genotypes to the future climate of a particular region.

Heat waves during dormancy generate anomalies in plants, such as the absence of budburst, or delay and lengthening of the flowering period (Petri & Leite, 2004). In sprouted and flowered material, anomalies such as shoot growth paralysis, small leaves, and small fruit appear during the vegetative cycle (Petri & Leite, 2004). Therefore, it is very important to study the effect of heat waves during the winter period, in order to suggest measures to minimize problems of reduced cold or increased temperatures during dormancy.

The objective of this work was to evaluate the effect of heat waves on the evolution of bud dormancy, in apple trees with contrasting chilling requirements.

Materials and Methods

Dormancy was evaluated in twigs of two apple genotypes, 'Royal Gala' and 'Castel Gala', respectively with medium and low chilling requirements (Denardi & Seccon, 2005; Petri et al., 2006). Twigs with about 25 cm length were sampled from a commercial orchard in Papanduva, SC (26°26'68"S, 50°05'47"W, at 788 m altitude), in June 2011. Until the collection date, 162 hours of chilling, below or equal to 7.2°C, were recorded, and plants had already shed their leaves. Seven-year old 'Royal Gala' plants were grafted on rootstock 'Marubakaido' with 'M9' filter, with 1.25 m between plants and 4.0 m between rows. Five-year old 'Castel Gala' plants were grafted on 'M9' rootstock, with 0.80 m between plants and 3.50 m between rows. The collected material was selected based on bud maturity (fully closed), health (no damage by *Grapholita molesta* or other causes), and size (approximately 5 mm diameter). Twigs were wrapped in moist newspaper inside plastic bags and were transported to Embrapa Uva e Vinho, in Bento Gonçalves, RS, Brazil, for bud dormancy evaluation under controlled conditions.

Twigs were cut 20 cm below the apical bud, retaining approximately 6–10 lateral buds; then, they were cleaned with ethanol at 70% for 45–60 s and sodium hypochlorite at 2.5% for 20 min, and finally they were rinsed thrice with distilled water and dried in the shade for about 30 min. Groups of 20 twigs were packed with black plastic film, vertically set inside incubator chambers Eletrolab EL202 (Eletrolab, São Paulo, SP) in the dark, and subjected to different thermal regimes.

Eight thermal regimes were used with 'Royal Gala': constant (C = 3°C) or alternating (A = 3 and 15°C for 12/12 hours) temperatures, combined with zero (C0 and A0), one (C1 and A1), or two (C2 and A2) days per week at 25°C, which formed the first six treatments. Two additional regimes were evaluated, with constant temperature (3°C) and 7-day heat wave (25°C) at the beginning (HB) or in the middle (HM) of the experimental period. For 'Castel Gala', only regimes C0, C1, C2 and HB were used, due to the reduced availability of gems and the large number of field

chilling hours (162 CH below 7.2°C) at the beginning of the experiment.

After the periods of 330, 426, 522, and 714 chilling hours (CH, below 7.2°C), for 'Castel Gala', and 330, 618, 714, 810, and 1,002 CH, for 'Royal Gala' (which included 162 field CH), two groups of 20 twigs per combination of cultivar, thermal regime, and chilling hours were transferred to a plant growth chamber Percival Boone model 50036, (Percival Scientific Inc., Perry, IA, USA). The one-centimeter bottom was cut off to unblock vascular bundles, and the twigs were planted upright in moistened phenolic foam 3.75 cm high. A 1x1 cm metal mesh was used on the top of the phenolic foam to help the organization and identification of treatments. Temperature in the growth chamber was kept at 25±1.5°C, with 70–80% humidity, and 12-hour photoperiod by day

One additional treatment per cultivar consisted in planting the gems directly in the growth chamber in order to evaluate the budburst, without putting them into the incubator chambers, nor applying any additional thermal regime to them, apart from field chilling hours.

Budburst date of each gem was recorded, and the date when gems reached the green tip stage was noted (Iuchi, 2006), with daily evaluations, for 56 days at 25°C in each treatment. Maximum budburst was expressed as a function of the number of chilling hours; the resulting curves were modeled as sigmoids and were compared by the F-test, using the R software (R Development Core Team, 2013).

Results and Discussion

In the C0 thermal regime, with 3°C constant temperature, less than 618 CH were required to overcome dormancy (budburst larger than 50%) in 'Royal Gala' apical buds, and less than 330 CH, in 'Castel Gala' (Figures 1 A and 1 C). These results are compatible with those of Anzanello (2012), who determined the chilling requirements of these two cultivars, under the same conditions, to be about 600 and 300 CH, respectively. Moreover, they agree with field results by Denardi & Seccon (2005) for 'Castel Gala', and Petri et al. (2006) for 'Royal Gala'. The alternating daily temperatures used in regime A0 (3 and 15°C, in a 12/12-hour cycle) did not affect the

chilling requirements of 'Royal Gala', which remained under 618 CH (Figure 1 A).

The effect of brief periods of heat (25°C) on chilling requirements was variable, depending on the thermal regime applied. Under constant temperature (3°C), the condition of 24 hours per week at 25°C (regime C1) did not change the chilling requirement. However, 48 hours per week at 25°C (regime C2) increased chilling requirements for both cultivars to over 618 CH ('Royal Gala') and over 330 CH ('Castel Gala') (Figures 1 A and 1 C). Under cycling temperatures (3°C/15°C cycle), the exposure of 'Royal Gala' to 25°C for 24 (regime A1) and 48 (regime A2) hours per week increased chilling requirements to over 618 CH and over 714 CH, respectively (possibly increasing the requirement in about 100 and 200 CH, compared to C0). Longer heat waves (regimes HB and HM, with 25°C for one week) increased the chilling requirement of both cultivars in more than 96 CH (possibly around 200 CH), compared to C0, and also seem to have reduced the maximum budburst.

The statistical analysis of the 'Royal Gala' curves was able to separate three distinct groups (Figure 1 B). Thermal regimes C0, A0 and C1 formed the first group, requiring less than 618 CH on average to overcome dormancy. The common factor in these three regimes, which differed from the other treatments, was that the heat period never lasted more than 24 hours. The second group consisted of regimes A1 and C2, which had heat periods of 36 and 48 hours, respectively (A1 ranged from 3°C to 15°C for 6 hours, to 25°C for 24 hours, and to 15°C for 6 hours, before going back to 3°C). This group differed ($p=0.0068$) from the first group, requiring between 618 and 714 CH to overcome dormancy. The third group was formed by regimes A2, HB and HM, and had heat periods of 60 hours or more. This group's curves differed from the other regimes ($p<0.0001$) and required over 714 CH to overcome dormancy.

Although 'Castel Gala' curves were not subjected to all the thermal regimes, their statistical analysis also separated the treatments into three groups, in a similar manner to that observed for 'Royal Gala' (Figure 1 D). Treatments C0 and C1 were in the first group, with a chilling requirement under 330 CH. This group differed ($p=0.04$) from regime C2, which had a chilling requirement between 330 and 426 CH, and they all

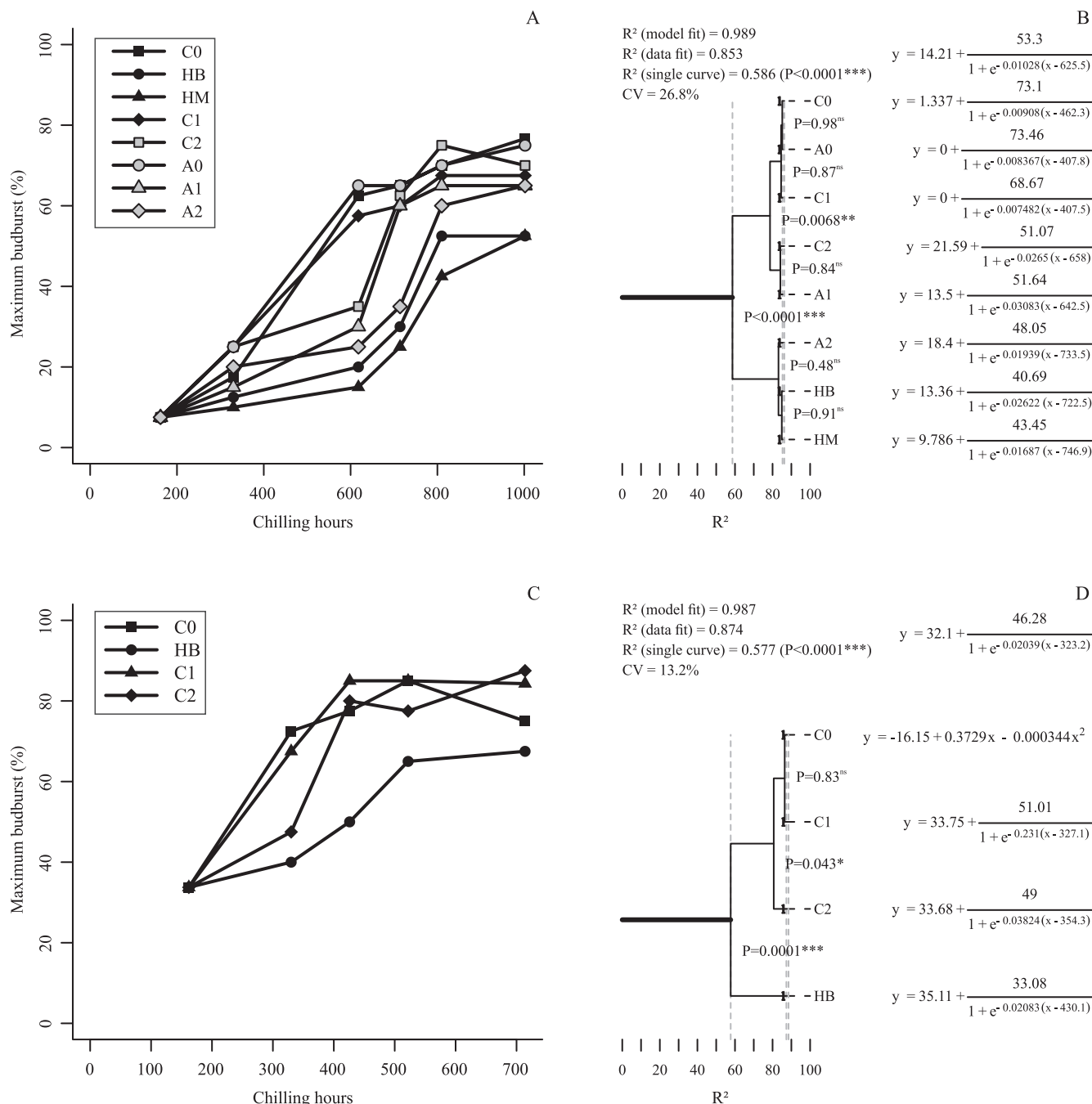


Figure 1. Maximum budburst of apical buds of 'Royal Gala' (A and B) and 'Castel Gala' (C and D) apples at 25°C, as a function of the number of chilling hours (under 7.2°C) during the dormancy period, under various thermal regimes after 162 chilling hours in the field. Observed values are plotted in A and C, while a graphical representation of the analysis of variance is shown in B and D. Thermal regimes were: C0, constant 3°C; C1, weekly cycles of 6 days at 3°C, and 1 day at 25°C; C2, weekly cycles of 5 days at 3°C, and 2 days at 25°C; A0, alternating daily temperature cycles of 3°C for 12 hours, and 15°C for 12 hours; A1, alternating daily temperatures (3°C/15°C), with 1 day per week at 25°C; A2, alternating daily temperatures (3°C/15°C), with 2 days per week at 25°C; HB, simulated heat wave of 7 days at 25°C, at the beginning of the experiment, followed by constant 3°C; HM, constant 3°C for 7 days, followed by a simulated heat wave of 7 days at 25°C, in the middle of the experimental period, followed by constant 3°C thereafter. ^{ns}Nonsignificant. *, **, and ***Significant at 5, 1, and 0.1% of probability, respectively.

differed ($p=0.0001$) from regime HB, which required more than 426 CH.

A direct relationship between heat duration and budburst capacity was observed for both cultivars (Figures 1 A and 1 C). Plants subjected to brief heat periods (1 or 2 days per week at 25°C) were able to recover their maximum budburst potential. However, longer periods (7 days at 25°C) inhibited budburst, even after longer periods of cold.

Alternating warm and cool temperatures can have a synergistic effect, promoting better or faster dormancy overcome, compared to the effect of low temperatures alone, in some apple cultivars (Guak & Neilsen, 2013). However, high temperatures for long periods during dormancy affect thermal requirements, resulting in irregular budburst (Campoy et al., 2011). For Ruiz et al. (2007), long heat periods increase the chilling requirements of temperate fruit trees. According to Perez et al. (2008) and Chavarria et al. (2009), the regularity and intensity of low temperatures, after dormancy induction, are critical because large temperature fluctuations may increase dormancy duration and result in insufficient and uneven budburst and flowering, thus affecting the production cycle.

Lateral buds were not affected by chilling and remained dormant after the period of heat exposure (Figures 2 A and 2 C). This dormancy status is associated mainly to paradormancy, in which lateral budburst is inhibited by apical dominance (Anzanello et al., 2014). Lauri (2007) states that the influence of apical dominance is coordinated by basipetal transport of auxin, which exerts direct inhibition on the growth of axillary buds. For Maguylo et al. (2012), the growth of lateral buds is controlled mainly by paradormancy, rather than by the intrinsic state of endodormancy. Given this effect of apical buds on lateral buds, and the observation that lateral budburst was low for all treatments, the significant differences eventually observed between thermal regimes become unimportant (Figures 2 B and 2 D). Maintaining 'Castel Gala' and 'Royal Gala' twigs upright, during the experiment, maximizes the apical dominance (Hawerth et al., 2013), which justifies the low rates of budburst, even after a long period of exposure to cold.

Maximum requirements of chilling hours varied between 330 and 522 CH for, 'Castel Gala', and

between 618 and 1,002 CH, for 'Royal Gala', depending on the thermal regime (Table 1). For Petri et al. (2006) and Campoy et al. (2011), the CH model has not yield satisfactory results because it does not consider the effect of a wider range of temperatures, making it difficult to establish the number of chilling hours required to overcome dormancy in years with unusual temperature regimes. The CH model is also considered by Luedeling & Brown (2011) as inadequate to estimate the number of chilling hours to reach budburst because it oversimplifies the biochemical process of dormancy to a simple function of temperature.

The limitations of CH models resulted in the development of more accurate models, which consider a wider effective temperature range and the negative effects of high temperatures (Luedeling & Brown, 2011). The chilling unit (CU) models of Utah (Richardson et al. 1974) and North Carolina (Shaltout & Unrath, 1983) consider high temperatures (25°C) to have a negative effect of -1 CU or -2 CU, per hour, respectively. These models have been tested and compared, under different climatic conditions, in cherry (Albuquerque et al., 2008), walnut (Luedeling et al., 2009), apricot (Viti et al., 2010), grapevine (Cortázar-Atauri et al., 2009), and other crops. The Modified Utah and Modified North Carolina models (Ebert et al., 1986) consider that the negative effect occurs only during the first 96 hours of continuous heat. All the four models proved to be inaccurate when the thermal regime included heat waves (Table 1). An ideal model would estimate the same requirement, no matter what thermal regime is used. However, the models did not appear to behave better than the chilling hour method and, in some cases, behaved much worse, as may be verified by the estimates with a negative number of chilling units to overcome dormancy. Chilling unit models, considered effective by some authors (Ebert et al., 1986; Erez, 2000; Legave et al., 2008), appear to be unreliable and mostly inaccurate in the presence of heat waves, and their use is therefore inappropriate in the conditions of Southern Brazil, unless some fundamental change occurs in the modeling process.

Luedeling & Brown (2011) state that the negative effect of high temperature depends on its intensity and duration. This was initially reported by Erez & Lavee

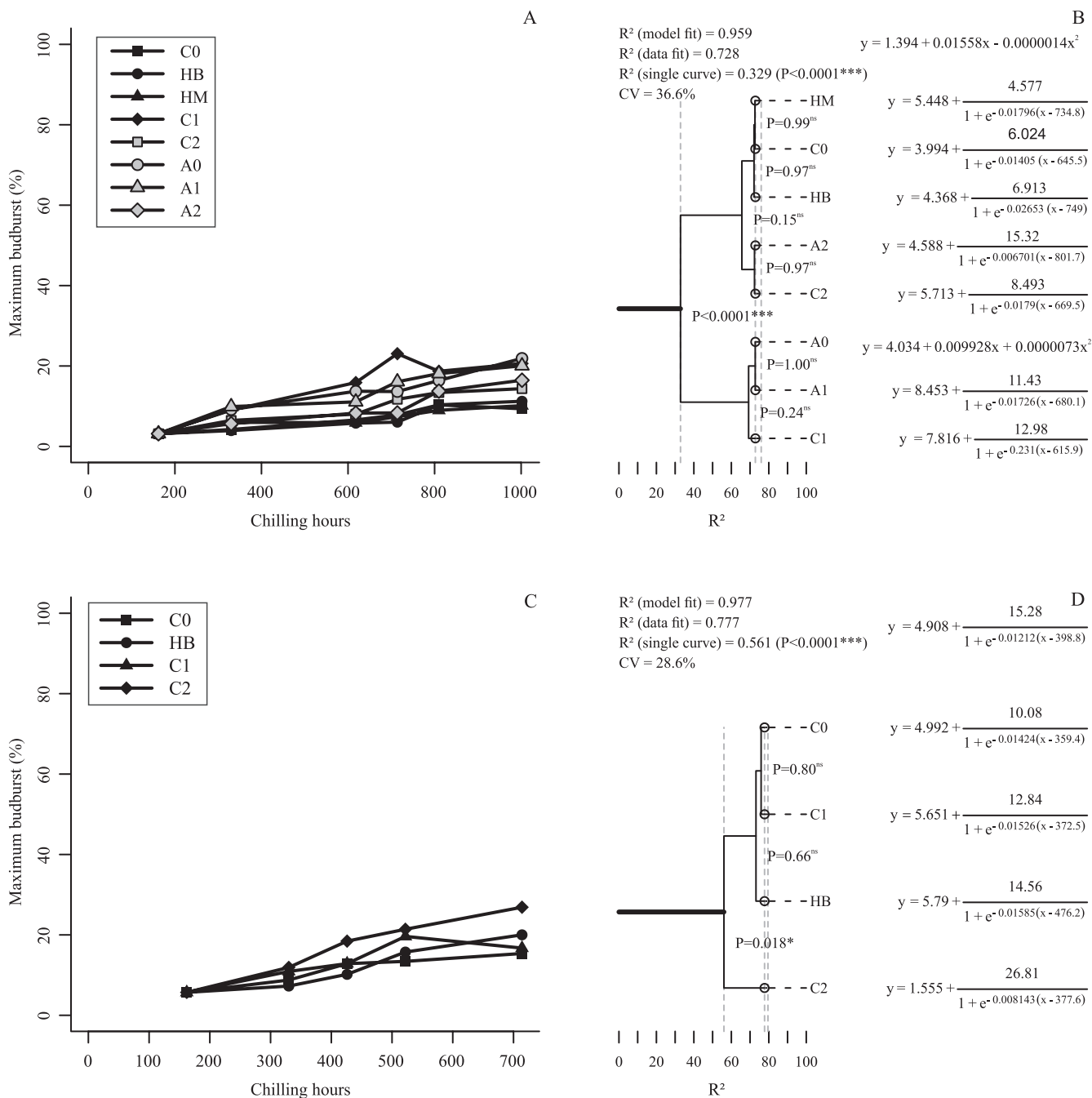


Figure 2. Maximum budburst of lateral buds of 'Royal Gala' (A and B) and 'Castel Gala' apples (C and D) at 25°C, as a function of the number of chilling hours (under 7.2°C) during the dormancy period, under various thermal regimes after 162 chilling hours in the field. Observed values are plotted in A and C, while a graphical representation of the analysis of variance is shown in B and D. Thermal regimes were: C0, constant 3°C; C1, weekly cycles of 6 days at 3°C, and 1 day at 25°C; C2, weekly cycles of 5 days at 3°C, and 2 days at 25°C; A0, alternating daily temperature cycles of 3°C for 12 hours, and 15°C for 12 hours; A1, alternating daily temperatures (3°C/15°C), with 1 day per week at 25°C; A2, alternating daily temperatures (3°C/15°C), with 2 days per week at 25°C; HB, simulated heat wave of 7 days at 25°C, at the beginning of the experiment, followed by constant 3°C; HM, constant 3°C for 7 days, followed by a simulated heat wave of 7 days at 25°C, in the middle of the experimental period, followed by constant 3°C thereafter. ^{ns}Nonsignificant. *, **, and ***Significant at 5, 1, and 0.1% of probability, respectively.

(1971), who claimed that only after 8 hours of exposure to 21°C the effect of chilling hours on dormancy was partially cancelled. They also sustain that, at higher temperatures (24°C), a mere 2 hours of exposure might cancel chilling hours. The present study suggests that only after 24 to 36 hours does heat cancel part of the effect of accumulated chilling. In the alternating temperature regimes, 24 or 48 hours at 25°C were always accompanied by 12 hours at 15°C, totaling 36 or 60 hours of absence of chilling. These conditions reversed the process of dormancy and increased the chilling requirement of the cultivars (Figures 1 A and 1 C), reinforcing the need for adjustments in the usual dormancy models. Models should partially cancel the effect of chilling only after over 24 hours of heat, with the dormancy process being immune to the influence of high temperatures in the period of a single day. One of the main deficiencies of current dormancy models is that they fail to adequately estimate cold requirements under heat wave conditions, such as the ones tested in the present work.

Table 1. Maximum chilling units required for overcoming dormancy, as estimated by the number of chilling hours (CH) under 7.2°C, Utah (UT), North Carolina (NC), Modified Utah (UTm), and Modified North Carolina (NCm) models, for 'Royal Gala' (G) and 'Castel Gala' (K) apples.

Treatment ⁽¹⁾	Cultivar	Models				
		CH<7.2°C	UT	NC	UTm	NCm
C0	K	330	330	330	330	330
C0	G	618	618	618	618	618
A0	G	618	618	618	618	618
C1	K	330	306	283	306	283
C2	K	426	330	234	330	234
HB	K	522	354	186	450	378
C1	G	618	546	474	546	474
C2	G	714	474	234	474	234
A1	G	714	522	330	522	330
A2	G	810	282	-246	282	-246
HB	G	810	642	474	738	666
HM	G	1002	834	666	930	858

⁽¹⁾C0, constant 3°C; C1, weekly cycles of 6 days at 3°C, and 1 day at 25°C; C2, weekly cycles of 5 days at 3°C, and 2 days at 25°C; A0, alternating daily temperature cycles of 3°C for 12 hours, and 15°C for 12 hours; A1, alternating daily temperatures (3°C/15°C), with 1 day per week at 25°C; A2, alternating daily temperatures (3°C/15°C), with 2 days per week at 25°C; HB, simulated heat wave of 7 days at 25°C, at the beginning of the experiment, followed by constant 3°C; HM, constant 3°C for 7 days, followed by a simulated heat wave of 7 days at 25°C in the middle of the experimental period, followed by constant 3°C thereafter.

Conclusions

1. Daily temperature cycles ranging from 3°C to 15°C do not affect the process of overcoming endodormancy.

2. Heat waves of 25°C during dormancy result in an increase in the number of the necessary chilling hours to achieve the chilling requirements of apple buds.

3. The negative effect of high temperature depends on its duration, and heat partially cancels chilling during dormancy only if it lasts 36 or more hours.

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