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What Is Wrong with Winter Chill Models in Warm Climates?

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Abstract. **Bud dormancy is an evolutionary strategy that protects temperate fruit trees from low temperatures during winter. With adequate winter chilling, it is a process consisting of a rapid entrance phase where growth inhibition increases to a maximum and is then released via an exit phase. This progression is, however, different in areas with insufficient winter chill. In such areas, the dormancy entrance phase is protracted, and the exit phase is often incomplete. Several chill models have been designed to describe the plants' response to chill accumulation to match cultivar and site. Although it is known that these models are less accurate in warm winter areas, their accuracy during the two dormancy phases has always been assumed equal. The aim of this study was to investigate the accuracy of four chill models during the entrance and exit phases of bud dormancy of 'Royal Gala' buds from two contrasting climatic areas. One-year-old shoots were collected from commercial orchards and forced to determine their bud dormancy level. Before forcing, the shoots received varied amounts of chill additional to the field chill. The bud dormancy progression was represented as joint two- or three-line models to determine the entrance and exit phases. For each phase, the dormancy level of every sample was plotted against its chill accumulation based on four chill models (Chilling Hours, Utah, Positive Utah, and Dynamic Model). Results were compared to determine the ability of each model to predict the linearity of the dormancy progression. The results indicated that although all the models were able to describe the exit phase of bud dormancy successfully, none could describe a linear entrance phase. This suggests that during the onset of dormancy, buds respond to temperature differently to what is measured by the chill models making the models unreliable when winter chill is inadequate.**

Temperate zone fruit trees exhibit annual growth cycles consisting of periods of growth in spring and early summer, cessation of growth in midsummer and autumn and an inactive resting state in winter, they then resume growth the following spring (Romberger 1963). Although this growth cycle is an evolutionary strategy to protect plant tissue against dehydration stress caused by subzero temperatures, it also reorganizes the growth potential in the bud meristems to allow for synchronized bud burst in spring. This coordinated start to the growing season affects tree architecture (Cook and Jacobs 1999), making the dormancy period a morphogenetic factor.

The inability of bud meristems to grow during the annual cycle is well defined by commonly used nomenclature (Lang 1987; Rohde and Bhalerao 2007) that describes the dormant state according to the origin of the growth inhibition trigger. *Paradormancy* is where the trigger for growth inhibition resides outside of the bud tissue itself, that is, caused by other plant organs. This state typically includes phenomena such as apical dominance and the restriction of growth due to overriding sink–source relationships. Although apical dominance is common throughout the annual cycle, sink–source competition is often associated with growth cessation in midsummer and autumn. The term *endodormancy* is used when the inhibition trigger is located within the bud itself; although not well understood, it is believed that the meristem is not able to expand due to a physiological block within the bud tissue despite ideal growing conditions. This growth inhibition is released by the accumulation of sufficient low temperatures during the winter period (Naor et al. 2003). The amount of chilling required for growth resumption is known as the chill requirement and is genotype and bud type specific (Erez 2000; Hauagge and Cummins 1991). A bud is under *ecodormancy* when the trigger for growth inhibition is external, that is, from the environment outside of the plant. In the annual growth cycle, this is mostly associated with early spring when endodormancy has been released but the bud is prevented from growing due to low environmental temperatures (Fishman et al. 1987). Once the air temperature increases sufficiently, the meristem resumes growth.

The different dormancy types are, however, not exclusive to specific phases of the annual cycle. Faust et al. (1997) indicated overlap of endodormancy with both paradormancy and ecodormancy, and Saure (1985) illustrated how this overlap can change in areas with a lack of winter chill. This redefines the intensity of dormancy during the winter period as "the sum of the inhibitions" and the time to growth resumption is a cumulative result of these inhibitive components (Champagnat 1983; Cook and Jacobs 1999; Faust et al. 1995). During mild winter conditions, the contribution of the inhibitive components becomes even more convoluted. The paradormant component (apical dominance/correlative inhibition) is thought to continue throughout the winter and early spring (Cook and Jacobs 1999). In these climates, warm winters protract the entrance into endodormancy as temperatures are warm enough for growth to continue, making ecodormancy nonexistent or very short. For this reason, we refer only to correlative inhibition and bud dormancy as the two concurrent physiological processes contributing to dormancy and growth resumption in warm winter areas.

The bud dormancy component of a tree can be quantified by exposing excised 1-year-old shoots (no correlative inhibition from

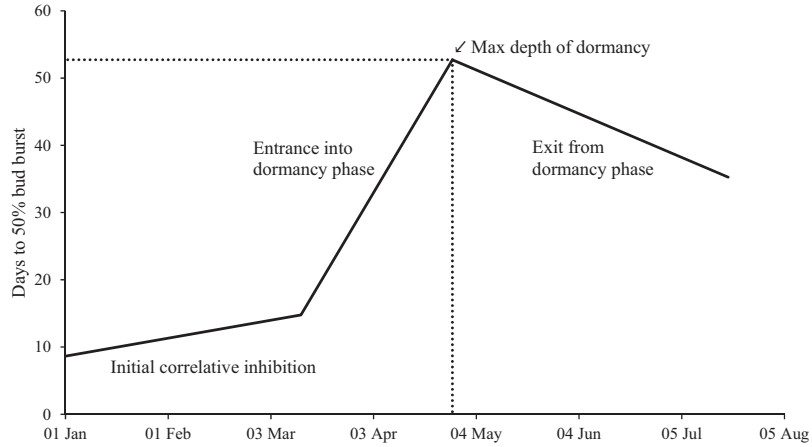

Fig. 1. A typical dormancy progression model using the joint three-line linear relationship indicating the two phases of dormancy.

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other plant parts) to ideal growing conditions and using the time to bud burst of the terminal buds (no correlative inhibition from shoot material) as an indication of the depth of bud dormancy. The longer the time to bud burst (growth resumption), the higher the physiological block within the buds and therefore the higher the dormancy level. This method has been used successfully to generate dormancy progression curves and to illustrate how dormancy patterns change under different climatic conditions (Cook and Jacobs 2000; Cook et al. 2017). In such studies, bud dormancy progression is typically illustrated as a two- or three-line model where the induction of dormancy is recognized as a linear increase (entrance) in dormancy until a maximum level is reached, followed by a negative linear relationship indicating a decrease (exit) in dormancy as the physiological block is broken down by the accumulation of chill (Fig. 1).

Quantifying chill accumulation and chill requirements have been the aim of many research groups, with the objective of better understanding and matching fruit crops to growing areas. Of late, chill accumulation research in warm winter climates has also gained attention, as climate change indicates that future temperatures will increase (International Panel on Climate Change 2022) and current sufficiently chilled areas might become less suitable for production of traditional varieties, and even, crop types (Luedeling and Brown 2011; Luedeling et al. 2011; Parkes et al. 2020). Many models have been developed and compared with quantify chill accumulation (Luedeling 2012). The earliest and simplest model is the Chilling Hours Model (Chandler 1942; Weinberger 1950), which defines a chilling hour as 1 h of temperatures between 0 and 7.2 °C. All such hours are summed, and the total is used to represent the accumulated chilling hours. The Utah Chill Model (Richardson et al. 1974) recognizes the most effective temperatures for chill accumulations as 2.5 to 9.1 °C and assigns a weighting of 1 chill unit (CU) per hour to it. Temperatures flanking this range (1.5 to 2.4 °C and 9.2 to 12.4 °C) are rated as less effective and weighted at 0.5 CU per hour. Temperatures lower and higher are considered ineffective for chill accumulation and temperatures higher than 16 °C are weighted negatively, thus negating the accumulated CU. All the CU are summed to tally the accumulated chill. Linsley-Noakes et al. (1994) modified the Utah model and claimed that it is more suitable for warm winter areas where chill negation is more likely. This modified Utah model is known as the Positive Utah Model because it ignores any negative daily sum of higher temperatures and as a result gives higher chill unit accumulation in warm areas compared with the Utah model, but somewhat equal results in colder areas with little to no chill negation. The Dynamic Chill Model (Fishman et al. 1987) is called a "process-based" model (Luedeling 2012) where it is assumed that chill accumulation is a reversible two-step system that produces a "dormancy breaking factor" via the formation of an intermediate product when exposed to low temperatures (similar range as Utah Model). The intermediated product is thermally unstable and is reversible when exposed to heat. When cycled with moderate temperatures, it will fixate the accumulated chill as a chill portion and thus acknowledges the dual effect of warm temperatures (Fishman et al. 1987). The Dynamic model is believed to be a more accurate chill model (Luedeling et al. 2021) but is by far the most complex.

It is worth noting that all the well-known chill models have a few general aspects in common: 1) they all use an isometric curve of temperature effectivity (within 0 to 12 °C) to calculate chill accumulation; 2) all the models assume that buds react similarly to temperature changes during the entrance and the exit of dormancy progression and that chill hours, chill units, or chill portions are accumulated equally regardless of the endodormancy phase; 3) although progress has been made,

Table 1. Description of the control and the four treatment groups in terms of chill accumulation before forcing.

Group	Chill exposure	Additional chill units according to models			
		Chilling hours	Utah	Positive Utah	Dynamic
Control	Field chill	0	0	0	0
Treatment 1 (T1)	Field chill + 4 d at 1 °C	96	0	0	0.73
Treatment 2 (T2)	Field chill + 4 d at 4 °C	96	96	96	2.54
Treatment 3 (T3)	Field chill + 4 d at 10 °C	0	48	48	3.04
Treatment 4 (T4)	Field chill + 14 d at 4 °C	336	336	336	9.62

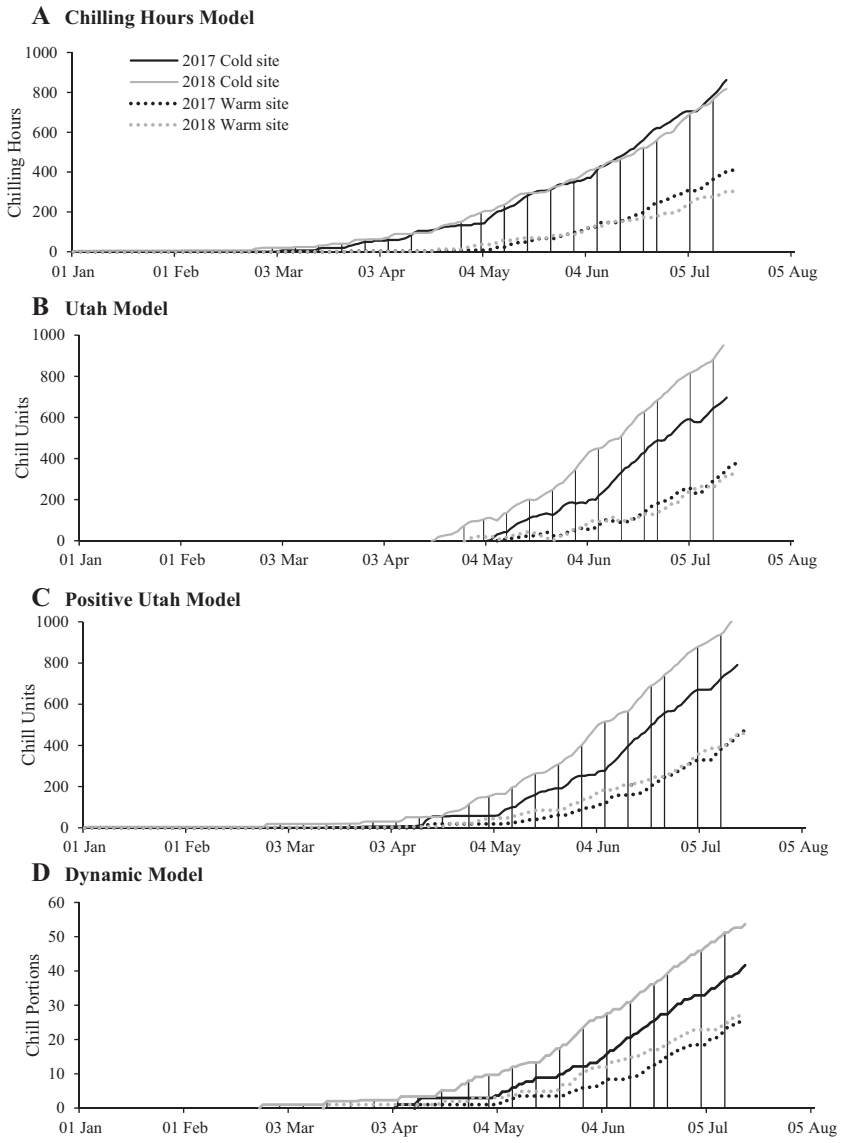

Fig. 2. The accumulated chill (both trial sites, both years), according to the (**A**) chilling hours, (**B**) Utah, (**C**) Positive Utah, and (**D**) Dynamic models. Vertical lines indicate the field chill accumulated on the respective sampling dates.

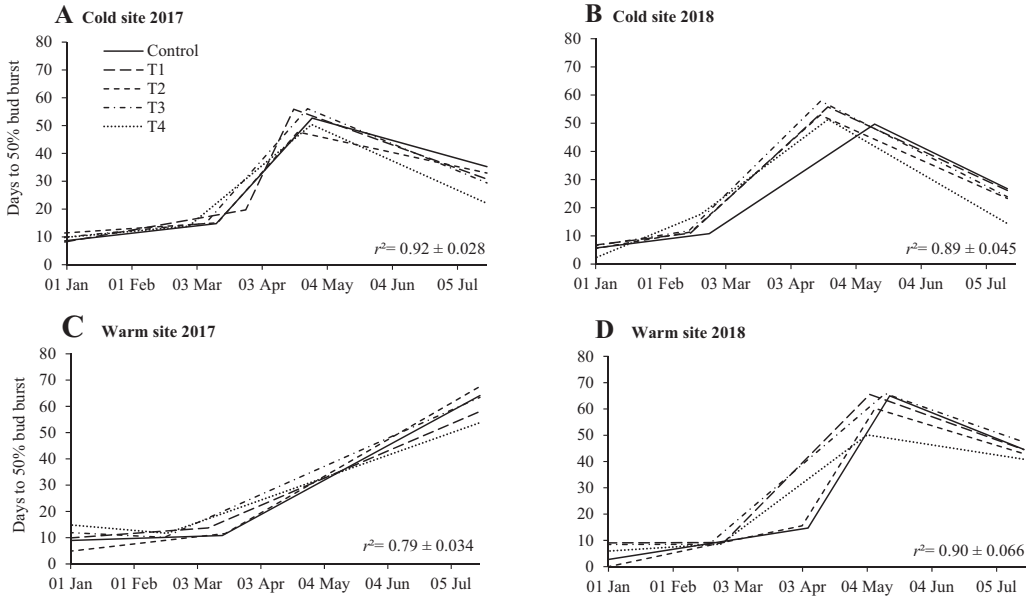

Fig. 3. Joint two- and three-line models of the dormancy progression plots for the control and treatment groups of the cold (Esperanto farm) and warm (Molteno farm) sites during the two seasons. r^2 values indicate the average fit across all linear relationships.

especially with the introduction of the Positive Utah and the Dynamic models, all the models are less effective and reliable when used in warm winter climates.

The aim of this study was to investigate the accuracy of four chill models during the entrance and exit phases of bud dormancy by comparing their respective chill accumulation values to the dormancy levels of buds that received natural and controlled chilling conditions.

Materials and Methods

Plant material and site description. In two consecutive years (2017 and 2018), shoots from mature, bearing 'Royal Gala' apple trees (grafted on M793 rootstocks) were sourced from two climatically contrasting commercial farms representing the two main apple growing regions of South Africa. The colder Esperanto farm, situated in the Koue Bokkeveld (33°10′04.8″S, 19°20′09.6″E; 1023 meters above sea level), received an average of 1505 Utah CU during the 2017 and 2018 winters. The warmer Molteno farm in the Elgin region (34°08′31.2″S, 19°02′42.0″E; 307 meters above sea level) received an average of 671 Utah CU.

One hundred and fifty 1-year-old shoots (35 cm in length) were randomly collected weekly from orchards on each site throughout both winters. Shoot harvesting commenced at bud set and was ended before the start of the manipulation of spring bud burst through the use of rest-breaking chemicals as part of standard production practices. To prevent dehydration, the shoots were defoliated in the orchard, sealed in plastic bags, and transported to the laboratory.

Temperature data and chill modeling. Temperature data were obtained from Tinytag Plus 2 data loggers (Gemini Data Loggers, UK) that recorded the hourly temperature of the respective orchards during both winter

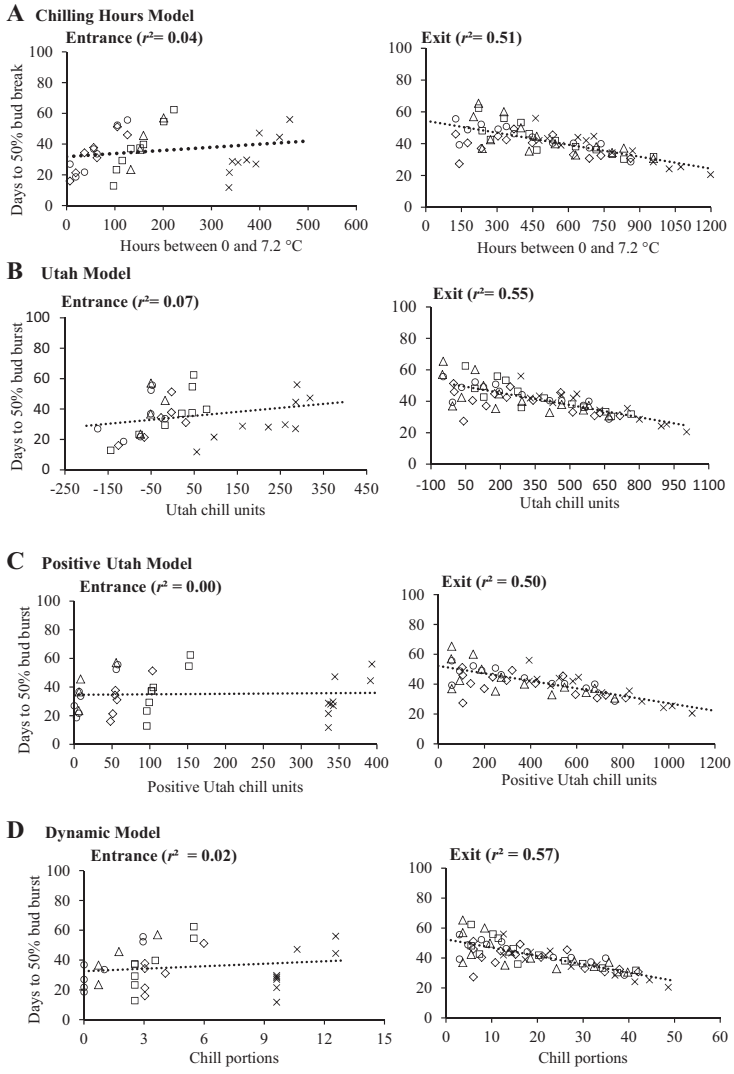

Fig. 4. Dormancy levels relative to the chill accumulation for the entrance and exit phases for the 2017 Cold site according to the (**A**) chilling hours and (**B**) Utah, (**C**) Positive Utah, and (**D**) Dynamic models. ○ = Control, Δ= T1, ◊ = T2, □ = T3, × = T4. r^2 values indicate the average fit across all linear relationships.

seasons. Temperature logging commenced early in January before any chilling occurred and loggers were removed from the orchards at the end of the trial. The respective chill accumulation was calculated according to the following models: Chilling Hours Model (Weinberger 1950), Utah Model (Richardson et al. 1974), Positive Utah Model (Lindsley-Noakes et al. 1994), and the Dynamic Model (Fishman et al. 1987).

Forcing experiments. In the laboratory, the shoots were immediately cut to 30 cm by removing the excess proximal shoot piece. The shoots were divided into four treatments and a control group, each consisting of 30 shoots. Each group was further divided into three replicates of 10 shoots each. All the shoots were forced to grow under conditions as described by Cook et al. (2017). Before forcing, the treatment groups were wrapped in damp newspaper, sealed in plastic bags, and exposed to additional chill according to Table 1 and then moved to forcing conditions; the control group did not receive any additional chill. Under forcing conditions, the number of days to 50% bud burst of each replicate was recorded by monitoring the shoots every 2 to 3 days until a single bud (either terminal or lateral in the distal 10 cm of the shoot) on five of the 10 shoots in each replicate had reached green tip stage. The time interval between the shoots being subjected to forcing conditions and 50% bud burst was used as an indication of the depth of bud dormancy (Cook and Jacobs 2000; Cook et al. 2017).

Dormancy progression modeling. The progression of bud dormancy of each treatment and the control was determined by plotting individual graphs of the depth of dormancy (days to 50% bud burst) of the mean of the replicates relative to the weekly harvest date for each treatment for each site and year (data not shown). A typical dormancy progression plot (Fig. 1) consisted of three distinct parts: an initial period of correlative inhibition in the field followed by two bud dormancy phases: a rapid increase or entrance into dormancy that reaches a maximum dormancy level and an exit from dormancy where the depth of dormancy decreases again. The joining points of the first two lines (of a three-line model) represented the start of the entrance into dormancy and the joining of the second and third lines indicated the maximum dormancy level as well as the start of the exit from dormancy phase (Fig. 1). In cases where the dormancy level had not yet decreased by the end of the trial (Warm site 2017) a joined two-line linear model was fitted, representing the initial correlative inhibition phase and the entrance into dormancy. Modeling was performed using the NLIN procedure of SAS statistical software (version 9.4; SAS Institute Inc., Cary, NC, USA, 2000), employing the Gauss–Newton iterative method. This method uses the entire data set for each treatment to fit lines and determines their convergence points (if any). The reported r^2 values represent the average fit across all the treatments and the control.

To compare the reaction of each sample to their respective chill exposure the depth of dormancy (time to 50% bud burst) at each collection date was plotted against its total amount of chill units/portions accumulated according to the four chill models. Samples from the entrance and exit phases were plotted separately and the initial correlative inhibition phase was not included. The number of samples included in the entrance and the exit phases was determined by the model and varied between treatments and as a result the number of samples used to construct these plots differed. The reported r^2 values represent the average fit across all the linear relationships.

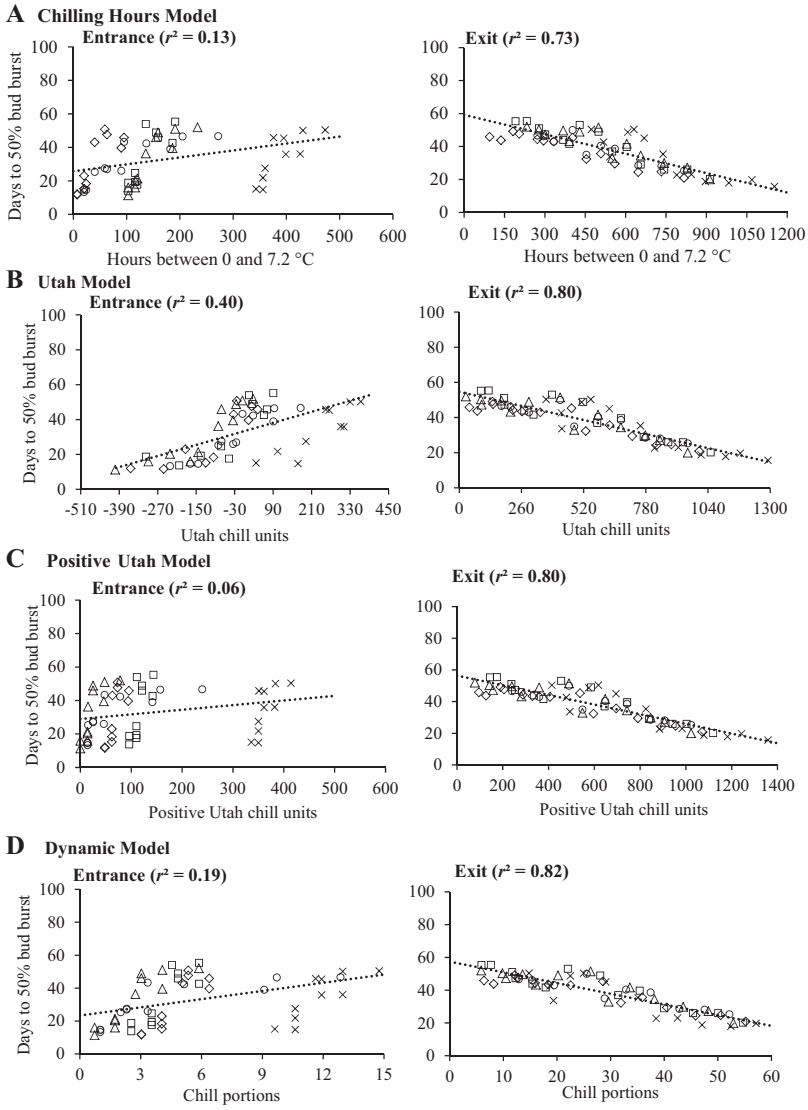

Fig. 5. Dormancy levels relative to the chill accumulation for the entrance and exit phases for the 2018 Cold site according to the (**A**) chilling hours and (**B**) Utah, (**C**) Positive Utah, and (**D**) Dynamic models. ○ = Control, Δ= T1, ◊ = T2, □ = T3, × = T4. r^2 values indicate the average fit across all linear relationships.

Results

Chill accumulation. As expected, all four chill models indicate that Esperanto was colder than Molteno in both winter seasons with chill accumulation values, on average, almost double that of Molteno (Fig. 2). The 2018 winter was colder in both areas compared with 2017 and the chill difference between the two years was greater in the colder (Esperanto) site than the warmer (Molteno) site. The start date of the 2018 winter season was earlier compared with 2017 (Fig. 2). For the remainder of the paper the Esperanto and Molteno farms are referred to as the Cold and Warm sites, respectively.

Dormancy progression. The two phases of dormancy were successfully illustrated by the joined three-line model for all the data sets (average r^2 >0.89), except for the 2017 Warm site data where a joined two-line model was used (average r^2 >0.79) (Fig. 3). All the models showed an initial correlative inhibition period where the dormancy level (days to 50% bud burst) remained low (on average <15 d). This was followed by a two-phase dormant period. First, a distinct entrance phase, where the dormancy levels of all the models increased rapidly and reached a maximum dormancy level (Fig. 3), was

found. For the Cold site maximum dormancy levels of the treatments were reached toward the end of April in both years (Fig. 3A and B). In 2017, no maximum dormancy level could be determined for any of the treatments nor the control from the Warm site as dormancy continued to increase by the end of the trial despite additional chill. For this data set, only two lines were fitted (Fig. 3C). In 2018, a maximum dormancy level could be determined for the Warm site samples and was on average a week later compared with the Cold site results (Fig. 3D). The maximum dormancy level of all the three-line models indicated the start of the dormancy exit phase characterized by a sudden decline in the number of days to 50% bud burst, signifying a decrease in dormancy until the end of the trial. In the colder 2018 season, the additional chill received by the treatments showed an earlier entrance into dormancy compared with the control except for T2 in the Warm site 2018, which showed levels similar to the control (Fig. 3B and D). In both sites and years, T4 (which received the most additional chill) had the lowest dormancy level at the end of the trial.

Dormancy levels relative to chill accumulation. The chill accumulation (all four chill models) of all the individual samples from the entrance and exit phases are presented relative to their dormancy levels in Figs. 4–7. For all the results, regardless of trial site, year or chill model, the entrance into dormancy showed a poor positive linear trend (average $r^2 = 0.15$; range: 0.00–0.49) with little difference between the Warm and Cold sites and the 2 years. In all cases, the linearity over time was weak, and most data points were scattered far from the trend line. Although poorly correlated, the Utah Chill model showed higher r^2 values (average $r^2 = 0.30$) compared with the other models. Contrary to this, the individual data points for the exit phase showed a strong negative linear trend (average $r^2 = 0.58$; range: 0.36 to 0.82). The chill models all appeared to perform similarly within the respective sites but differed across the years. The highest coefficients of determination were achieved in the coldest winter season (Cold site 2018) with a value of 0.73 for the Chilling Hours Model and values ≥0.80 for the other three models. The lowest values (average $r^2 = 0.36$ and 0.39) were obtained for the Chilling Hours and Utah models of the Warm site in 2018, here the Positive Utah and Dynamic models respectively obtained average r^2 values of 0.44 and 0.45. When considering these values, it should be kept in mind that no exit phase was detected for any of the treatments nor the control for the 2017 Warm site season. The general exit trend across sites and years indicated that time to bud burst decreased with increasing chill accumulation and samples with comparable chill accumulation showed similar dormancy levels.

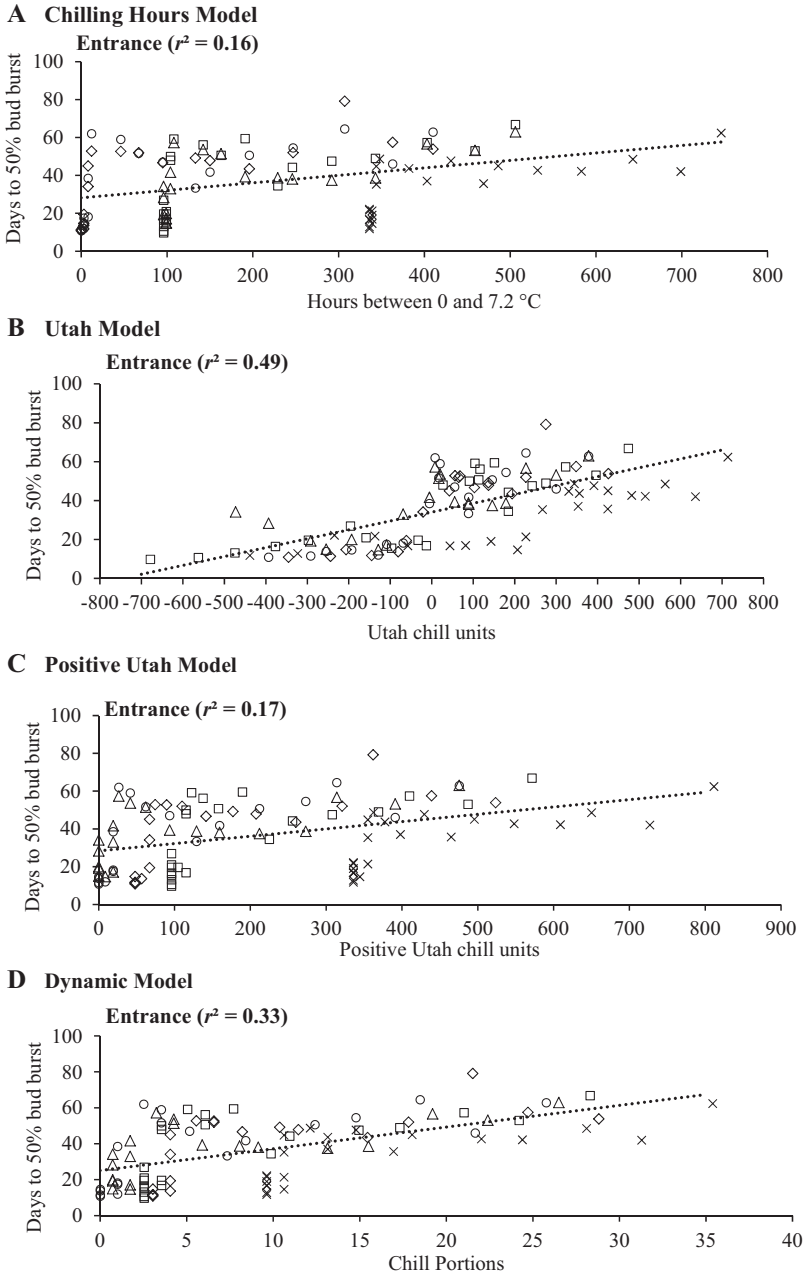

Fig. 6. Dormancy levels relative to the chill accumulation for the entrance phases for the 2017 Warm site according to the (**A**) chilling hours and (**B**) Utah, (**C**) Positive Utah, and (**D**) Dynamic models. ○ = Control, Δ= T1, ◊ = T2, □ = T3, × = T4. r^2 values indicate the average fit across all linear relationships.

Discussion

The chill requirement of 'Royal Gala' has been reported to be 800 to 1000+ Positive Utah CU (Sheard 2001) or between 1064 to 1200 Utah CU (Ghariani and Stebbins 1994; Hauagge and Cummins 1991; Ogundeji and Jordaan 2017) putting it in the medium to high chill range. Comparing this to the chill accumulation at the two sites, it is clear that chilling was inadequate at the Warm site and marginal at the Cold site. Although it is known that chill requirement quantification methods differ drastically and can produce variable results (Parkes et al. 2020), we believe from personal experience that the chill requirement for 'Royal Gala' is seldom met locally, necessitating the application of chemical rest-breaking agents to combat prolonged dormancy symptoms. The dormancy progressions produced in this trial were generally similar to that found by Cook and Jacobs (2000) and Cook et al. (2017) for apple cultivars in similar growing regions showing later, protracted entrance phases and longer exit phases in warmer years and areas.

When considering dormancy levels of individual bud samples relative to their accumulated chill, the data clearly show that the entrance phase does not have a positive linear trend as expected. Samples that received the same or similar amounts of chill (natural or artificial) behaved differently from one another. In fact, one would expect to find that control samples (orchard chill only) and samples with additional chilling that are ineffective for chill accumulation (according to the models) to have the same dormancy level at

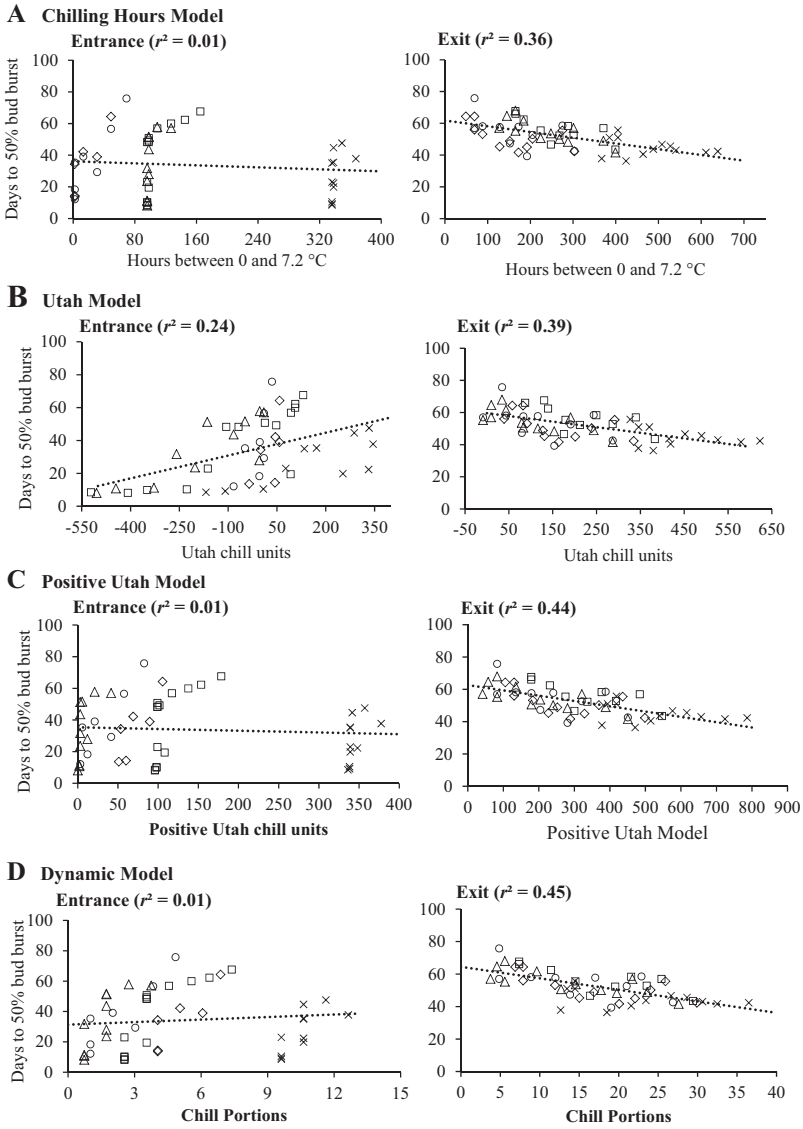

Fig. 7. Dormancy levels relative to the chill accumulation for the entrance and exit phases for the 2018 Warm site according to the (**A**) chilling hours and (**B**) Utah, (**C**) Positive Utah, and (**D**) Dynamic models. ○ = Control, Δ= T1, ◊ = T2, □ = T3, × = T4. r^2 values indicate the average fit across all linear relationships.

the same sampling date, but this is indeed not the case. Samples with similar amounts of accumulated chill often showed very different dormancy levels regardless of which chill model was used. This indicates that the buds did not react as the chill models predict and that temperatures that are, according to the chill models, not effective at contributing to chill accumulation are indeed capable of inducing dormancy. This was, however, only observed for samples during the dormancy entrance phase. Once the maximum dormancy level was reached and the chill started to release the buds from dormancy, their performance was more aligned and showed a much improved linear negative trend regardless of trial site, season, or chill model used. During the exit from dormancy, buds responded as predicted by the chill models.

Cook and Jacobs (2000) suspected this anomaly during their study on apple buds in similar trial sites. In their discussion on the entrance into dormancy, they suggested that "temperatures, other than those used to calculate chill units" are capable of inducing dormancy. It seems that the isometric temperature curve, which is used by all the chill models to determine chill accumulation, may be failing during the entrance into dormancy as buds show an "autonomous" and unpredictable behavior during this phase.

Potential reasoning why the inaccuracy of chill models in the early stages of bud dormancy has gone undetected in the past could be that not many studies focus on the entrance into dormancy. Autumn temperatures are much lower in high chill areas (where most of the initial chill model research was conducted) causing the dormancy entrance phase to be rapid. Therefore, the miscalculation of chill accumulation is only in a small part of the model compared with warm winter areas where the entrance phase is much more protracted allowing for a greater margin for error. In fact, our 2017 Warm site data showed that the entire dormancy progression only consisted of an entrance phase and no maximum level or exit phase could be detected. This is similar to what Cook and Jacobs (2000) found in warm areas where buds continued to accumulate chill although effective chilling should release the buds from dormancy. It seems that in climates where dormancy cannot be avoided completely, buds must reach a turning point or "maximum" dormancy before temperatures described by the current chill models can elicit a release from dormancy. It is possible that the negative linear trend would have developed if the sampling had continued for longer. In the current trial, sampling stopped because a chemical rest-breaker was applied as part of standard commercial practices in warm winter areas. A chemical rest-breaker is typically applied when it is assumed that the buds are in a shallow dormancy, which was evidently not the case considering that the buds were still accumulating chill and have not reached a turning point in the warmer season. This plasticity could explain why chemical rest-breaking has differing degrees of success in warm winter areas.

Conclusion

The current chill models are effective in quantifying bud dormancy release but do not explain the behavior of buds in the early stages of dormancy when growth inhibition intensifies. Because the entrance into dormancy is slower (and longer) in warmer climates, the current chilling models are poor indicators of the progression of dormancy. The processes associated with the entrance into bud dormancy are poorly understood, and although chilling temperatures are probably involved, these processes are not described by the current concepts of chill hours, units, or portions.

The anomaly observed in this data set undoubtedly creates more questions than answers and calls for an alternative way of thinking about the concept of a chill hour/unit/portion during the entrance phase of bud dormancy. The current quantification of chill accumulation during dormancy release cannot be transferred to the entrance phase as buds seem to be governed by different parameters, albeit temperature, of different magnitude than described thus far.

References Cited

Champagnat P. 1983. Bud dormancy, correlation between organs, and morphogenesis in woody plants. Soviet Plant Physiol. 30:458–471.

Chandler WH. 1942. Deciduous orchards. Lea & Febiger, Philadelphia, PA, USA.

Cook NC, Calitz FJ, Allderman L, Steyn WJ, Louw ED. 2017. Diverse patterns in dormancy progression of apple buds under variable winter conditions. Scientia Hortic. 226:307–315. https://doi.org/10.1016/j.scienta.2017.08.028.

Cook NC, Jacobs G. 1999. Sub-optimal winter chilling impedes development of acrotony in apple shoots. HortScience. 34:1213–1216. https://doi.org/10.21273/HORTSCI.34.7.1213.

Cook NC, Jacobs G. 2000. Progression of apple (*Malus x domestica* Borkh.) bud dormancy in two mild winter climates. J Hortic Sci Biotechnol. 75:233–236. https://doi.org/10.1080/14620316.2000.11511229.

Erez A. 2000. Bud dormancy; phenomenon, problems and solutions in the tropics and subtropics, p. 17–48. In: Erez A (ed.). Temperate fruit crops in warm climates. Kluwer Academic Publishers, Dordrecht, The Netherlands. https://doi.org/10.1007/978-94-017-3215-4_2.

Faust M, Erez A, Rowland LJ, Wang SY, Norman HA. 1997. Bud dormancy in perennial fruit trees: Physiological basis for dormancy induction, maintenance, and release. HortScience. 32:623–629. https://doi.org/10.21273/HORTSCI.32.4.623.

Faust M, Liu D, Wang S, Stutte GW. 1995. Involvement of apical dominance in winter dormancy of apple buds. Acta Hortic. 395:47–56. https://doi.org/10.17660/ActaHortic.1995.395.4.

Fishman S, Erez A, Couvillon GA. 1987. The temperature dependence of dormancy breaking in plants—mathematical analysis of a two-step model involving a cooperative transition. J Theor Biol. 124:473–483. https://doi.org/10.1016/S0022-5193(87)80221-7.

Ghariani K, Stebbins RL. 1994. Chilling requirements of apple and pear cultivars. Fruit Var J. 48:215–222.

Hauagge R, Cummins JN. 1991. Genetics of length of dormancy period in *Malus* vegetative buds. J Am Soc Hortic Sci. 116:121–126. https://doi.org/10.21273/JASHS.116.1.121.

Intergovernmental Panel on Climate Change. 2022: Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Pörtner HO, Roberts DC, Tignor M, Poloczanska ES, Mintenbeck K, Alegría A, Craig M, Langsdorf S, Löschke S, Möller V, Okem A, Rama B (eds.). Cambridge University Press, Cambridge, UK, and New York, NY, USA. https://doi.org/10.1017/9781009325844.

Lang GA. 1987. Dormancy: A new universal terminology. In: Proceedings of the symposium: Mechanisms of rest and dormancy. HortScience. 22(5):817–820. https://doi.org/10.21273/HORTSCI.22.5.817.

Linsley-Noakes GC, Allan P, Matthee G. 1994. Modification of rest completion prediction models for improved accuracy in South African stone fruit orchards. J South Afr Soc Hortic Sci. 4:13–15. https://doi.org/10.1016/0304-4238(94)90077-9.

Luedeling E. 2012. Climate change impacts on winter chill for temperate fruit and nut production: A review. Scientia Hortic. 144:218–229. https://doi.org/10.1016/j.scienta.2012.07.011.

Luedeling E, Brown PH. 2011. A global analysis of the comparability of winter chill models for fruit and nut trees. Int J Biometeorol. 55:411–421. https://doi.org/10.1007/s00484-010-0352-y.

Luedeling E, Girvetz EH, Semenov MA, Brown PH. 2011. Climate change affects winter chill for temperate fruit and nut trees. PLoS One. 6:E20155. https://doi.org/10.1371/journal.pone.0020155.

Luedeling E, Schiffers K, Fohrmann T, Urbach C. 2021. PhenoFlex—An integrated model to predict spring phenology in temperate fruit trees. Agr For Meteorol. 307:108491. https://doi.org/10.1016/j.agrformet.2021.108491.

Naor A, Flaishman N, Stern R, Moshe A, Erez A. 2003. Temperature effects on dormancy completion of vegetative buds in apple. J Am Soc Hortic Sci. 128(5):636–641. https://doi.org/10.21273/JASHS.128.5.0636.

Ogundeji AA, Jordaan HA. 2017. Simulation study on the effect of climate change on crop water use and chill unit accumulation. S Afr J Sci. 113:1–7. https://doi.org/10.17159/sajs.2017/20160119.

Parkes H, Darbyshire R, White N. 2020. Chilling requirements of apple cultivars grown in mild Australian winter conditions. Scientia Hortic. 260:108858. https://doi.org/10.1016/j.scienta.2019.108858.

Richardson EA, Seeley SD, Walker DR. 1974. A model for estimating the completion of rest for 'Redhaven' and 'Elberta' peach trees. HortScience. 9:331–332. https://doi.org/10.21273/HORTSCI.9.4.331.

Rohde A, Bhalerao RP. 2007. Plant dormancy in the perennial context. Trends Plant Sci. 12:217–223. https://doi.org/10.1016/j.tplants.2007.03.012.

Romberger JA. 1963. Meristems, Growth, and Development in Woody Plants. Technical Bulletin No. 1293, Forest Service, U.S. Dept. Of Agriculture. 214 p.

Saure MC. 1985. Dormancy release in deciduous fruit trees. Hortic Rev. 7:239–300. https://doi.org/10.1002/9781118060735.ch6.

Sheard AG. 2001. Measuring winter chilling in the South West region of KwaZulu-Natal during 2001 and its implications for deciduous fruit production, p. 16. In KZN Agri-Report No. N/A/2002/02.

Weinberger JH. 1950. Chilling requirements of peach varieties. Proc Am Soc Hortic Sci. 56:122–128.