

A biologically based approach to modeling spring phenology in temperate deciduous trees

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ABSTRACT

Prediction of the timing of spring phenological events such as bloom and leaf-out has important uses in agricultural and ecological management and modeling. However, after decades of model comparison there remains no consensus model to predict the date of spring phenological events in perennial temperate trees across species and locations. This lack of consensus may be due to over-fitting resulting from high model complexity, use of parameters that have not been adequately validated, or omission of parameters that are sound biological indicators of dormancy breaking. The aim of this study was to construct spring phenology candidate models with biologically-based parameters and starting values to test hypotheses regarding chill accumulation duration and the impact of pre-bloom conditions. Bloom data for three cultivars of *Prunus dulcis* (almond) from three decades in California were analyzed. Across all three cultivars, models which accumulated chill until approximately 75% of the heat requirement had been met, and did not integrate pre-bloom conditions, were substantially supported by the data. This suggests cold temperatures affect dormancy breaking well after the chilling requirement has been met and bud break timing is not substantially impacted by environmental conditions just prior to bud break. Fitting spring phenology using biologically based starting values estimated from bud break records may allow for the development of improved predictive models and improved approximations of critical phenological thresholds.

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1. Introduction

1.1. Previous model structures

Predicting the timing of bud break has important application in agriculture and forestry, from planning bee hive delivery to modeling carbon dioxide fluxes (Hemming et al., 2013; Richardson et al., 2013). The buds of temperate perennial plants become dormant in the late fall, suspending growth and undergoing a number of physiological changes. Buds remain dormant during the winter and part of spring (Lang et al., 1987). The timing of bud break (bloom or leaf-out) depends on exposure to winter chill to exit endodormancy (Westwood, 1993) and spring heat to exit ecodormancy (Cannell, 1989). The minimum amount of chill necessary to exit

endodormancy is known as the chilling requirement, hereafter C_r . The minimum heat necessary to exit ecodormancy is known as the heat requirement, hereafter H_r . Both requirements are specific to species and cultivar (Westwood, 1993).

Modeling in agriculture and ecology requires balancing the complexity of physiological reality with the simplicity necessary to attain biologically interpretable parameter values (Burnham and Anderson, 2002b). Numerous models relating chill and heat accumulation have been developed and compared (Chuine, 2000; Chuine et al., 1999; Hanninen, 1990; Hanninen and Kramer, 2007; Kramer, 1994a; Linkosalo et al., 2008), but there remains no consensus model which accurately predicts the date of spring phenological events across locations, species or cultivars. This may be due in part to the over-fitting that can result when a large number of parameters are fit with limited data (Richardson et al., 2013). Nonlinear models can be particularly vulnerable to over-fitting, potentially resulting in biologically unrealistic temperature thresholds as well as chill and heat requirements (Richardson et al., 2013).

Kramer (1994b) delineated six spring phenology model types, four of which have persisted in the literature. The *thermal time* model is based solely on spring heat accumulated after a set date

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(Cannell and Smith, 1983). The *sequential* model consists of an accumulation of chill up to C_r followed by heat up to H_r with no accumulation overlap between the chilling and heating phases. C_r and H_r are consistent year to year for the species or cultivar modeled (Ashcroft et al., 1977; Sarvas, 1974). The *parallel* model accumulates chill and heat in the same time period, with the rate of heat accumulation dependent on the amount of chill accumulated (Landsberg, 1974). The *alternating* model also integrates overlap in chill and heat accumulation (hereafter “chill overlap”), however an hour or day can only count toward accumulation of chill or of heat, depending on whether the temperature is below or above a threshold (Cannell and Smith, 1983). In the *parallel* and *alternating* models, H_r and the *heat accumulation* that results in bloom are not necessarily the same. H_r is the minimum amount of heat accumulation at which bloom is possible given preceding chill accumulation above C_r . The heat accumulation necessary for bloom in any given year can be more than H_r , depending on the amount of chill accumulated in that year. The same is true for C_r and chill accumulation.

Neither the *thermal time* model nor the *sequential* model are well-suited for a Mediterranean climate such as California's, with winters occasionally mild enough to not meet the C_r of some species or cultivars (Brown, 1952; Crane and Takeda, 1979; Griggs et al., 1972), nor for a changing climate of warming winters (Luedeling et al., 2011). The *thermal time* model is inappropriate because it assumes C_r is met every year. *Sequential* models do not include the partially compensatory relationship between chill and heat accumulation, by which some chill beyond the minimum requirement can reduce the amount of heat necessary for bloom (Cannell and Smith, 1983; Chuine et al., 1999; Harrington et al., 2010). As such, *sequential* models reflect the more frequent combinations of chill and heat accumulation, not the bare minimums necessary for bloom, and can over-estimate C_r and H_r . The *parallel* and *alternating* models are the only types of models from Kramer (1994b) that allow for the compensatory relationship between chill and heat and the chill overlap reported in both controlled and observational studies (Cannell and Smith, 1983; Landsberg, 1974; Murray et al., 1989).

1.2. Chill and heat accumulation overlap

The amount of chill overlap remains unresolved in spring phenology modeling. The *parallel* model assumes chill and heat accumulation begin at the same time (Landsberg, 1974). However, a number of changes in dormant buds only occur once C_r is met, e.g. unblocking of plasmodesmata and resumption of intracellular communication and transport (Faust et al., 1997). Similarly, recent research indicates that on the genetic level chill breaks dormancy by inhibiting the expression of dormancy-related (DAM) genes which otherwise inhibit expression of FLOWERING LOCUS T (FT) (Horvath, 2009; Leida et al., 2012). This would indicate C_r must be met first for heat accumulation to be able to trigger the expression of genes that result in the promotion of flowering. Given that there are physiological and genetic changes that only occur once C_r has been met, changes that must take place for heat accumulation to be able to trigger further changes, it seems biologically disadvantageous that a mechanism in the bud would “count” heat accumulation before C_r was met. Why start counting heat accumulation without certainty that such an accumulation could affect change?

The extent to which chill accumulation continues after C_r has been met has not been quantified. The *parallel* and *alternating* models assume chill accumulates until bud break (Cannell and Smith, 1983; Landsberg, 1974). Recent work on chromatin modification, the remodeling of chromatin architecture to expose DNA segments for transcription, indicates that exposure to chill beyond the C_r may facilitate long-term inactivation of the FT-inhibiting gene DAM6

(Leida et al., 2012). This indicates that chill may only accumulate briefly after the C_r is met, up until the chromatin modification has been ‘fixed’. On the other hand, numerous works have found expression of DAM genes to decrease with chill exposure well after the C_r has been met, nearly until bloom (Cooke et al., 2012; Yamane et al., 2011), suggesting that there is a large chill overlap.

1.3. Additional parameters

Beyond chill and heat accumulation, there may be additional environmental factors that delay or hasten the termination of dormancy and the beginning of bud break (Linkosalo et al., 2006). Both Saure (1985) and Faust et al. (1997) proposed there may be a third stage of dormancy following sufficient heat accumulation. This stage would be broken after heat accumulation removes limitations to growth, when a final environmental cue signals that conditions are not only safe but *ideal* for flowering, pollination and photosynthesis. While photoperiod plays a role in dormancy induction in some species, there is little indication it is involved in dormancy breaking (van der Schoot and Rinne, 2011). The final cue for bud break may be prompted by the environmental conditions (hereafter “pre-bloom parameters”) that are favorable during bloom or leaf-out, such as warm temperatures that would promote pollinators, dry air that would promote wind-borne pollen circulation or high solar radiation that would allow for production of photosynthates by new leaves.

The objective of this study was to develop a model framework to test the importance of a variety of parameters in predicting the timing of spring phenological events, balancing the complexity of biological processes with the simplicity necessary to avoid overfitting and to produce biologically interpretable values. The bloom timing of *Prunus dulcis* (almond) in three locations in California's Central Valley ranging from the valley's coldest to mildest winter climates were used to fit and validate the candidate models. To test the adaptability of the models, the bloom records for three commonly grown cultivars were used: the earliest to bloom in the records, ‘Sonora’, one of the latest, ‘Mission’ (elsewhere known as ‘Texas’), and ‘Nonpareil’, which is the most commercially valuable cultivar in California and blooms between the time of the other two cultivars. A cultivar-specific horticultural dataset such as this eliminates the eco-type noise inherent to analysis on the species level. The exponentially declining curve framework of the *alternating* model was used as the starting point for the candidate models. Numerous models were compared to test (1) the amount of chill overlap and (2) whether including pre-bloom parameters would improve the predictive capabilities of spring phenological models.

2. Materials and methods

2.1. Phenology and climate

2.1.1. Bloom records

Bloom records from the University of California Almond Regional Variety Trials from 1983 to 2011 were used, with sites in the north, center and south of California's Central Valley near the towns of Chico (39.69, -121.83), Manteca (37.83, -121.22) and Shafter (35.45, -119.23). The first trials were planted in 1974. The second trials were planted in 1993 and observed from 1996 to 2008. Bloom stages recorded were the average for 20 or more trees. The timing of first bloom, here 10%, was modeled instead of full bloom (e.g. 50% or 80%) because the timing of bloom stages relative to first bloom varies with temperature during bloom and preceding chill accumulation (Degrandi-Hoffman et al., 1996; NeSmith and Bridges, 1992). For Shafter, the date of 10% bloom was not recorded, so was estimated by linear interpolation of records for

1% and 80% bloom. Records from 1996 to 2008 for all sites excepting Shafter, 2007, were used to parameterize the models. The first trials' datasets were limited by accessibility and weather records quality. Records from 1984 to 1995 for Chico and 1991–1994 for Manteca were used to validate the best models.

2.1.2. Weather records

Hourly temperature, average daily solar radiation and daily precipitation data were retrieved from the California Irrigation and Management Information System (CIMIS, www.cimis.water.ca.gov) for October, 1983 through March 2008 for the stations closest to each site. The second closest weather station was used to supplement missing data. Durham station (39.61, -121.82) was used for Chico (back-up: Orland; 39.69, -122.15), Manteca station (37.84, -121.22) for Manteca (back-up: Modesto; 37.65, -121.19) and Shafter station (35.53, -119.28) for Shafter (back-up: Kettleman City 1995–1997; 35.87, -119.89 and Famoso 1997–2005; 35.6, -119.21). Temperature data were screened following Pope et al. (2013). Pre-bloom solar radiation and precipitation were calculated as the sum of average daily solar radiation and daily precipitation, respectively, for ten days prior to bloom.

2.2. Model components

2.2.1. Model framework

The partially compensatory relationship between chill and heat has been modeled as exponentially declining curves with heat necessary for bloom dependent on chill accumulation (Eq. (1), Cannell and Smith, 1983; Eq. (2), Chuine et al., 1999). C_a and H_a represent the accumulation of chill and heat prior to bloom, respectively. The parameters a , b and r were fit based on the data.

$$H_a = a + b \times e^{r \times C_a} \quad (1)$$

$$H_a = a \times e^{b \times C_a} \quad (2)$$

Eq. (1) was found to be easier to relate to the biological parameters of thresholds associated with chill and heat accumulation. Because values for r in Cannell and Smith (1983) and b in Chuine et al. (1999) were fitted as negative values, for heuristic purposes the model was reformatted as¹

$$H_a = \beta_1 + \frac{\beta_2}{e^{(\beta_3 \times C_a)}} \quad (3)$$

¹ Equivalent to $H_a = \beta_1 + \beta_2 e^{(-\beta_3 \times C_a)}$

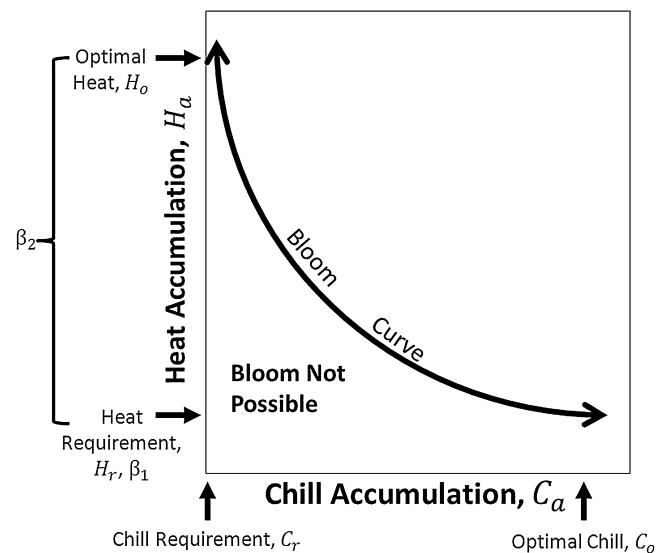


Fig. 1. Curve representing the relationship between chill accumulation and heat accumulation necessary for bloom. Harrington et al. (2010) provide the framework of the curve representing the possible combinations of C_a and H_a that result in bud-break and locating C_r and C_o , chill that requires heat only to H_r for bloom. Expanding on this framework, the present model locates H_r and optimal heat, H_o , heat necessary when chill only accumulates to C_r , on the curve to facilitate interpreting the model parameters.

where H_a represents heat accumulation from the hour after C_r is met through the day before bloom and C_a represents chill accumulation following the chilling requirement being met.

Harrington et al. (2010) provided a useful framework for understanding this exponential relationship. The curve represents the possible combinations of C_a and H_a that result in bud-break. On the model curve they located C_r , and optimal chill, C_o . Optimal chill is the amount of chill that, once accumulated, requires heat to only accumulate to H_r for bloom. Expanding on their framework, it is possible to decipher H_r and optimal heat, H_o , the amount of heat necessary when chill only accumulates to C_r (Fig. 1). Locating these thresholds on the curve facilitates interpreting the model parameters.

2.2.2. Interpreting and estimating parameters

In Eq. (3), when all other parameters remain equal, changing the value of β_1 moves the curve up or down the heat axis. Thus β_1 sets the curve's horizontal asymptote, the lowest heat accumulation at which bloom is possible. As such, β_1 is equivalent to H_r (Fig. 2a). With a large enough dataset in a climate that at least occasionally experiences high chill, it can be assumed that C_a approached C_o at

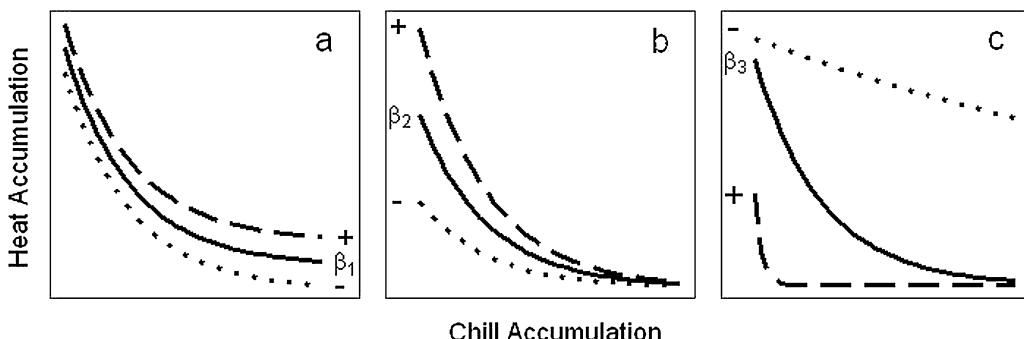


Fig. 2. Framework of changing parameter values of exponentially declining model. (a) Increasing β_1 (dashed line, +) shifts the curve up the y axis. Decreasing β_1 (dotted line, -) shifts the curve down the y axis. (b) Increasing β_2 scales the value of $1/e^{(\beta_3 \times C_a)}$. Lines diverge more at low chill values than high chill values. (c) Decreasing β_3 increases the value of $1/e^{(\beta_3 \times C_a)}$. The horizontal asymptote increases with decreasing β_3 .

Table 1

Models and hypotheses of pre-bloom conditions and chill overlap.

Parameters	Biological hypothesis	Overlap hypotheses
$\beta_1, \beta_2, \beta_3$	$H_a = f(H_r, H_o, C_a)$	25%, 50%, 75%
$\beta_1, \beta_2, \beta_3, \beta_4$	$H_a = f(H_r, H_o, C_a, \text{pre-bloom GDH})$	25%, 50%, 75%
$\beta_1, \beta_2, \beta_3, \beta_4$	$H_a = f(H_r, H_o, C_a, \text{pre-bloom solar radiation})$	25%, 50%, 75%
$\beta_1, \beta_2, \beta_3, \beta_4$	$H_a = f(H_r, H_o, C_a, \text{pre-bloom precipitation})$	25%, 50%, 75%

least once, after which heat would only need to accumulate to H_r . Thus, a starting value for parameterizing β_1 (i.e. H_r) can be approximated using the lowest heat accumulation between C_r being met and bloom.

β_2 scales the value of $1/e^{(\beta_3 \times C_a)}$. Increasing β_2 increases the heat required for bloom at low chill (Fig. 2b). Interpreting and estimating β_2 is simplified by calculating C_a as chill accumulation *after* C_r has been met, instead of total winter chill. At $C_a = 0$, i.e. chill only accumulates to C_r , $e^{(\beta_3 \times C_a)} = 1$ and Eq. (3) becomes $H_a = \beta_1 + \beta_2$. Given that H_o must be accumulated for bloom when chill only accumulates to C_r , at $C_a = 0$, $H_a = H_o$. Given $\beta_1 = H_r$, then $\beta_2 = H_o - H_r$. With a dataset large enough to capture very mild occasional winters, it can be assumed that H_o is approached at least once. As such, a starting value for β_2 can be estimated by approximating H_o and H_r using the highest and lowest heat accumulations in the record.

All other parameters remaining equal, decreasing β_3 decreases $e^{(\beta_3 \times C_a)}$, increasing $1/e^{(\beta_3 \times C_a)}$, resulting in a flatter curve. Lower values of β_3 require more heat for bloom at middle and high amounts of chill. Curves of different β_3 values eventually converge, but well above one winter's possible chill accumulation. In the confines of possible chill accumulation, decreasing β_3 functionally increases the horizontal asymptote. The fact that both β_1 and β_3 can increase the horizontal asymptote illustrates the vulnerability of nonlinear curves to over-fitting.

2.2.3. Chill and heat accumulation sub-models

Chill accumulation was calculated using the Dynamic Model (Fishman et al., 1987), which has been found to model the timing of spring phenological events as well or better than other horticultural models in Mediterranean climates (Alburquerque et al., 2008; Luedeling et al., 2009; Ruiz et al., 2007). Accumulation of chill according to the Dynamic Model is a two-step process. First, a chill intermediate is accumulated based on a bell-shaped relationship of hourly temperature to chill value. This accumulation can be reduced given high temperature. Second, the chill intermediate accumulates to a threshold and is counted as one chill portion (CP), which cannot be negated by later warm temperatures. Accumulation of new chill intermediate starts again from zero (Erez and Fishman, 1998). Chill accumulation was calculated beginning October 1st (Jarvis-Shean et al., 2014).

The C_r for 'Nonpareil' almonds has been estimated as 23 CP (Ramirez et al., 2010). Because this requirement was modeled using the sequential framework for 50% bloom, the value may be overestimated for the present analysis. Thus, 'Nonpareil' models were fit with $C_r = 23$ CP and 17 CP, 25% fewer. 'Mission' models were fit with $C_r = 29$ CP and 21 CP based on previous chill hours requirement quantification as 125% of 'Nonpareil' (Weinbaum et al., 1984; Weinberger, 1950). 'Sonora' models were fit with $C_r = 17$ CP and 13 CP, based on the previous chill hours requirement quantification of 'Ne Plus Ultra', which blooms near the same time as Sonora, as 75% of the C_r of 'Nonpareil' (Weinbaum et al., 1984).

The growing degree hours (GDH) ASYMCUR model of Anderson et al. (1986), was used to quantify heat accumulation. The GDH ASYMCUR model is an asymmetric curvilinear model consisting of two cosine equations defined by an optimum hourly temperature (25°C) that counts for one GDH and minimum (4°C) and maximum

(36°C) temperature above and below which heat accumulates at fractions of a full unit.

2.2.4. Candidate models

The present models assume heat accumulation begins after C_r has been met through the day before bloom. Models compared chill accumulation continuing after C_r through 25, 50 and 75% of H_r . These values test hypotheses of approximations of chill overlap instead of fitting this parameter directly and risking over-fitting or local minima. It was assumed that low GDH, low solar radiation and high precipitation would delay bloom, increasing the amount of heat accumulated prior to bloom in an additive manner. For each cultivar 12 models were compared where β_4 represented pre-bloom GDH, average solar radiation or precipitation, or $\beta_4 = 0$ to not include pre-bloom conditions, with 25%, 50% and 75% chill overlap (Eq. (4), Table 1). Because of the reliance of this framework on some chill overlap, hereafter the generalized form of the model (Eq. (4)) is referred to as the chill overlap model.

$$H_a = \beta_1 + \frac{\beta_2}{e^{(\beta_3 \times C_a)}} + \beta_4 \quad (4)$$

2.2.5. Parameterization

Starting values to fit the models were estimated from the parameterization dataset for each cultivar and C_r (Table 2). β_1 was estimated using the lowest value of H_a . β_2 was estimated by subtracting the lowest H_a from the highest H_a . Given the scale of C_a , and the fact that the value of the term $1/e^{(\beta_3 \times C_a)}$ drops precipitously as C_a increases, it was assumed that the ideal value of β_3 would scale down the value of C_a . This required a value between zero and one. The starting value of 0.01 was used for all cultivars and C_r 's.

The estimated starting value of β_4 depended on the pre-bloom condition. It was hypothesized that because cold or cloudy days (i.e. low pre-bloom GDH or solar radiation) hinder bee flight (Connell, 2000), it would be advantageous for such conditions to delay bloom, meaning β_4 would be negative. For either condition to detectably impact on bloom timing, it was estimated that $\beta_4 \times$ Pre-bloom GDH and $\beta_4 \times$ Pre-bloom solar radiation would be of the same order of magnitude as H_a . Based on the values of H_a and pre-bloom GDH and solar radiation in the parameterizing dataset, a starting value of $\beta_4 = -1$ was used.

It was assumed that because precipitation would hinder bee flight, delayed bloom would be advantageous for nut production as pre-bloom precipitation increased. Delayed bloom would result in higher H_a , thus β_4 would be positive. Given the scale of average precipitation (e.g. 'Nonpareil' averaged 26.34 mm), precipitation was

Table 2

Starting values for β_1 and β_2 used when fitting the chill overlap model for each of three cultivars with two different estimates of the chilling requirement for each cultivar.

Cultivar	C_r	β_1	β_2
Mission	21	5260	3424
Mission	29	4560	3207
Nonpareil	17	5122	2732
Nonpareil	23	4598	2975
Sonora	13	5577	3715
Sonora	17	4732	2934

estimated to be an order of magnitude less than the amount by which it would increase the necessary heat accumulation. Thus a starting value of $\beta_4 = 10$ was used.

2.2.6. Statistical analysis

An information-theoretic approach was used to determine the best model(s) (Burnham and Anderson, 2002a). AICc values were compared within the 12 models of each C_r for each cultivar. AICc allows comparison of models with the same outward structure but different sub-models (e.g. different chill overlap). Models were fit using nonlinear regression and log likelihood values were derived in R v 2.15.1 (R Core Team, 2012) using the nls and logLik functions. Models were fit using the Gauss–Newton algorithm. AICc values were calculated using the AICc function of the nls2 package (Grothendieck, 2013). Assumptions of the correct mean function, homogeneity of variance, normally distributed errors and independent errors were checked for the best models following Ritz and Streibig (2008).

AICc values of models with different C_r could not be compared because lower C_r resulted in earlier heat accumulation, changing the response variable. RMSE was calculated for the error in predicted bloom date compared with actual bloom date for the parameterizing and validating dataset (RMSE_p, RMSE_v respectively) (Linkosalo et al., 2008). To test whether models predicted better than the null hypothesis of average bloom date, RMSE_a was calculated for the validating dataset using the cultivar-specific average bloom date from the parameterizing data.

The Information-Theoretic approach does not seek one ‘best’ model, or classify support for models as significant or not, but rather seeks information from all models which fit the data reasonably well. If a model had an AICc value 3 or more units higher than the lowest value in the set ($\Delta_i > 3$), it was deemed considerably less supported than those with $\Delta_i < 3$ and was excluded from further analysis (Burnham and Anderson, 2002a). If two models differed by $\Delta_i < 3$ and had equivalent log likelihood values (differed by <0.5), but one had an additional parameter, the model with the additional parameter was judged considerably less supported (Burnham and Anderson, 2002a). This comparison was only made within chill overlap groupings (e.g. for models with 25% chill overlap, the model with $\beta_4 = 0$ was compared with the model with $\beta_4 = \text{GDH}$). Models with negative values for β_1 or β_2 were discarded because heat accumulation cannot be negative.

3. Results

The models fit the data to varying degrees (Table 3, Fig. 3a–d). The estimation algorithm failed to achieve convergence for all ‘Mission’ models that assumed $C_r = 29$ CP, all ‘Nonpareil’ models that assumed $C_r = 17$ CP, and all ‘Sonora’ models that assumed $C_r = 17$ CP, except one ‘Sonora’ model that was discarded because $\beta_1 < 0$. Two ‘Mission’ models with $C_r = 21$ CP and 50% chill overlap failed to converge. Two ‘Mission’ models and all 50% overlap ‘Nonpareil’ models assuming $C_r = 23$ CP were excluded from AICc comparison because $\beta_1 < 0$.

All models analyzed for AICc comparison met assumptions for nonlinear analysis. For each cultivar the model that assumed 75% chill overlap without a pre-bloom parameter had the lowest AICc value. The AICc values for ‘Mission’ and ‘Sonora’ models that assumed 25% overlap were well above the Δ_i exclusion threshold (Table 3). For all cultivars, models with 50% chill overlap failed to converge, had negative values for β_1 and β_2 , or had Δ_i values well above the exclusion threshold (Table 3).

For ‘Mission’, the models with 75% chill overlap and either pre-bloom GDH accumulation or pre-bloom precipitation were supported based on AICc, but excluded because log likelihood values were similar to those of the best model, which had one fewer parameter (Table 3). For ‘Nonpareil’, of the five models with $\Delta_i < 3$, two were excluded based on log-likelihood values, leaving the models with 75% chill overlap and pre-bloom GDH accumulation, 25% chill overlap and pre-bloom GDH accumulation and 25% chill overlap with no pre-bloom conditions. According to the information-theoretic approach, these three models are as likely as the model with the lowest AICc value (Table 3). For ‘Sonora’, the three models with pre-bloom conditions and 75% chill overlap had $\Delta_i < 3$ but were discarded based on log likelihood values (Table 3). The best models appeared to fit well irrespective of location. There were no obvious patterns in RMSE values for the parameterizing dataset ranged from 3.46 to 3.90 days from actual bloom depending on cultivar and model (Table 4). There were no obvious patterns in error by location (Fig. 3). When bloom date was estimated with the validating dataset, RMSE ranged from 2.67 to 3.90 days. RMSE values with the validation data were 1.1 days less to 0.81 days more than the RMSE values with the parameterizing data. The performance of predicting bloom based on average bloom date was calculated to compare with the performance of the models. RMSE using average bloom date ranged from 5.47 to 7.73. These

Table 3

Model fit and performance for chilling requirement estimates for which at least some models converged. Values are given for each model for log likelihood, AICc and Δ_i , the difference between the AICc value and the lowest AICc value within a cultivar-chill overlap set.

Models		Mission, $C_r = 21$			Nonpareil, $C_r = 23$			Sonora, $C_r = 13$		
Pre-bloom parameter	Over-lap	Log-like	AICc	Δ_i	Log-like	AICc	Δ_i	Log-like	AICc	Δ_i
Null ¹	25	-296.60	602.41	13.11	-295.08	599.38	2.24 [*]	-297.90	605.01	15.84
GDH	25	-295.63	603.14	13.84	-293.63	599.14	2.00 [*]	-297.36	606.59	17.42
Solar radiation	25	-296.24	604.35	15.05	-294.77	601.41	4.27	-297.89	607.66	18.49
Precipitation	25	-295.70	603.27	13.97	-294.58	601.04	3.90	-297.33	606.53	17.36
Null	50	neg ²	neg	neg	neg	neg	neg	-292.76	594.74	5.57
GDH	50	ftc ³	ftc	ftc	neg	neg	neg	-291.76	595.39	6.22
Solar radiation	50	-292.68	597.24	7.94	neg	neg	neg	-292.68	597.24	8.07
Precipitation	50	ftc	ftc	ftc	neg	neg	neg	-292.59	597.05	7.88
Null	75	-290.04	589.30	0 [*]	-293.96	597.14	0 [*]	-289.98	589.17	0 [*]
GDH	75	-290.00	591.87	2.57 [†]	-293.23	598.34	1.20 [*]	-289.98	591.83	2.66 [†]
Solar radiation	75	neg	neg	neg	-293.69	599.26	2.12 [†]	-289.96	591.80	2.63 [†]
Precipitation	75	-290.04	591.96	2.66 [†]	-293.85	599.57	2.43 [†]	-289.88	591.64	2.47 [†]

¹ Null signifies no pre-bloom parameter.

² Parameter values for β_1 , β_2 were negative. Model was discarded from further analysis.

³ ftc signifies algorithm failed to achieve convergence for these models.

^{*} Substantially supported candidate model ($\Delta_i < 3$).

[†] $\Delta_i < 3$, but log-likelihood value not substantially different from that of same model without pre-bloom parameter.

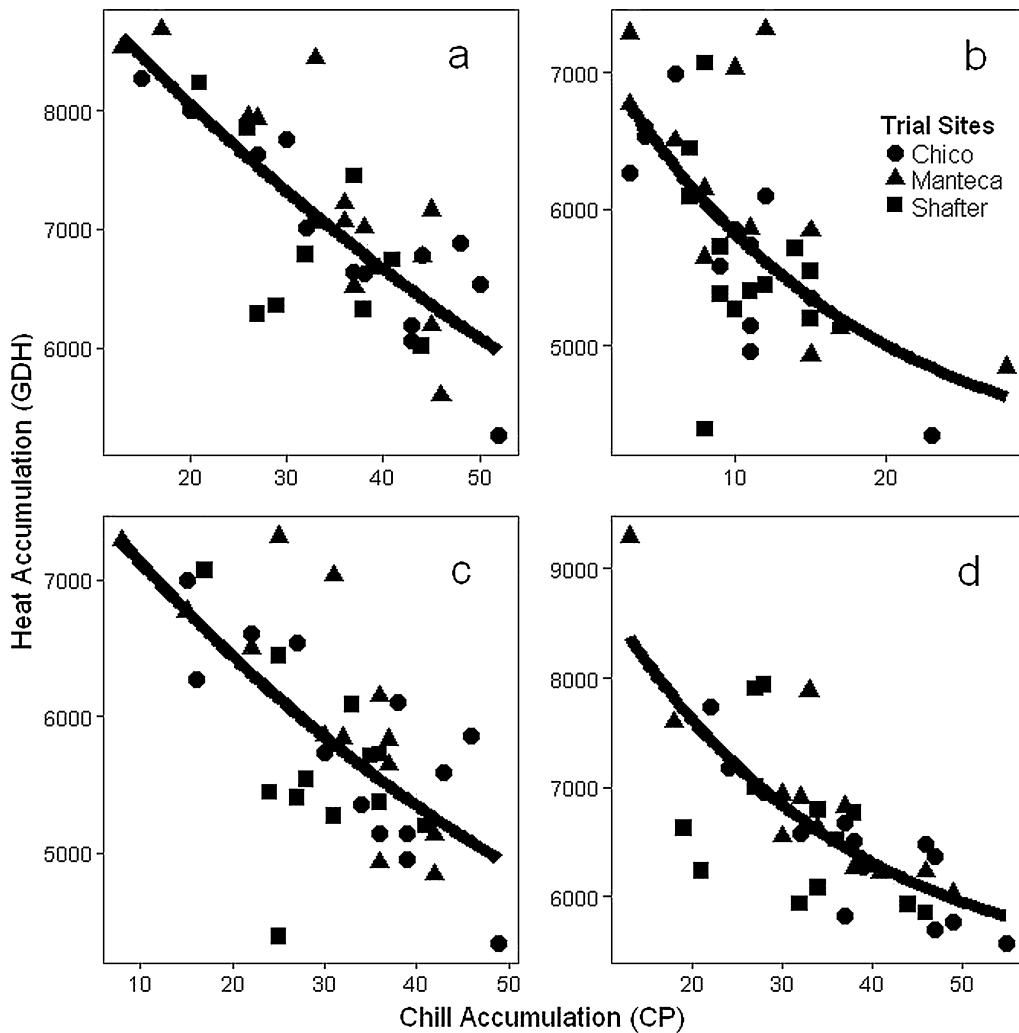


Fig. 3. Model fit for parameterizing data for best models. (a) 'Mission', chill overlap = 75%, $C_r = 21$ CP, (b) 'Nonpareil', chill overlap = 25%, $C_r = 23$ CP, (c) 'Nonpareil', chill overlap = 75%, $C_r = 23$ CP, (d) 'Sonora', chill overlap = 75%, $C_r = 13$ CP

values were 1.63 to 4.27 days more than those of the parameterizing dataset and 0.99 to 3.49 days more than the validating dataset.

4. Discussion

Using starting values based on biological thresholds, models were created that fit both the parameterizing and validation data reasonably well and better than the average bloom date. The data indicate that chill accumulation continued after C_r was met until approximately 75% of H_r had been met. The data further indicated that, with perhaps the exception of pre-bloom GDH accumulation, including pre-bloom conditions did not improve the predictive

power of the spring phenology models. The models with lower C_r estimates fit the data best for 'Mission' and 'Sonora', but the higher chilling requirement estimate fit the data best for 'Nonpareil'.

4.1. Model framework

For the best models, model performance changed little with validation. RMSE_v values were 1.1 days less to 0.81 days more than RMSE_p values (Table 4). In this respect, the *chill overlap* models compare favorably with previous nonlinear spring phenology models. Maximum prediction error increased by 6 days when Kramer (1994b) validated the *parallel* model for *Fagus sylvatica* leaf out.

Table 4

Parameters and evaluation of fit by RMSE of best models of each cultivar.

Cultivar, C_r	Models		Parameter values				RMSE ¹		
	Pre-bloom parameter	Over-lap	β_1	β_2	β_3	β_4	RMSE _p	RMSE _v	RMSE _a
Mission, $C_r = 21$	Null	75	1119	8677	0.01119	–	3.84	4.48	5.47
Nonpareil, $C_r = 23$	Null	75	2308	5624	0.01536	–	3.90	3.89	6.16
	GDH	75	3441	4205	0.0245	0.2782	3.83	3.91	6.16
	Null	25	4010	3305	0.05987	–	3.77	2.67	6.16
	GDH	25	3893	2896	0.07251	0.383	3.85	3.87	6.16
Sonora, $C_r = 13$	Null	75	5180	5259	0.03837	–	3.46	4.27	7.73

¹ RMSE_p = RMSE for parameterizing data (Chico and Manteca, 1996–2008, Shafter 1996–2006, 2008), RMSE_v = RMSE for validating data (Chico 1984–1995, Manteca 1991–1994), RMSE_a = RMSE for validating data predicted based on the average bloom date of the parameterizing data

Comparing fit for a *parallel* model ('Par1Sar') for 15 species in two locations, Chuine et al. (1999) found R^2 decreased by 0.06 to 0.30 from parameterizing to validating data. When Linkosalo et al. (2008) validated the *parallel* model and the exponentially declining *unified* model (Chuine, 2000) for three species, ΔRMSE was -0.12 to +3.41 days for the *parallel* model and -0.84 days to +8.41 days for the *unified* model. When Morin et al. (2009) validated the *unified* model for 22 tree species, ΔR^2 was +0.07 to -0.32. The stability of the predictive power of the *chill overlap* models across locations (Fig. 3), datasets and cultivars indicates that biologically-based starting values create models that are stable outside of the particular circumstances of the dataset used to build them. Modeling with additional species, and in even more varied climates, would be beneficial to further test the value of this approach.

The *chill overlap* model approach to estimating parameters was robust enough to yield well-predicting models, but many of the fitted parameter values differed substantially from the starting values. Some difference was expected for models with a pre-bloom parameter, as these parameters claim some heat accumulation allotted to β_1 and β_2 in the initial framework. The lower the fitted value of β_3 , and thus the more linear the relationship between C_a and H_a , the lower the value of β_1 and the higher the value of β_2 (Table 4, Fig. 3a–d). Consequently, with lower values of β_3 , our approach over-estimated β_1 and under-estimated β_2 (Table 2). The best 'Mission' model is the most extreme example of this, with the lowest value of β_3 and the starter value for β_1 and β_2 that were 4141 GDH more and 5253 GDH less than the fitted values, respectively.

The *chill overlap* framework is based on a curved relationship between chill and heat and the parameterizing dataset containing values that approach C_o , H_o and H_r . It is doubtful the starting and fitted value discrepancies were due to a linear chill–heat relationship, given numerous observational and controlled studies that have shown the curved relationship in temperate perennial species (Cannell and Smith, 1983; Harrington et al., 2010; Landsberg, 1974). The discrepancies may stem from a lack of extreme values in the dataset. Given the geographic range of the dataset, this was not expected, but is possible. A temporally expanded dataset or experimentation in a controlled setting would further elucidate this. Additionally, a more precise estimation of C_r by forcing experiment (Dennis, 2003) could increase model curvature. Until this has been explored, starting values from *chill overlap* models should not be interpreted as the exact H_r or H_o .

4.2. Chill and heat accumulation

The AICc values for the various models that achieved convergence indicate that, of the hypothesized potential chill overlap estimations, 75% chill overlap is the most likely, 25% is much less probable, and 50% is highly unlikely. AICc values for 75% overlap models for all cultivars and for 25% overlap 'Nonpareil' models, Δ_i ranged from 1.2 to 4.27. For all 75% overlap models, $\Delta_i < 3$ (Table 3). There is thus substantial support for the hypothesis that chill continues to accumulate after C_r has been met until approximately 75% of the heat requirement has been met. The fact that the 75% overlap models fit all cultivars well, whereas only two of four 25% overlap 'Nonpareil' models fit comparably well (Table 3) indicates the 25% overlap fit of 'Nonpareil' may have been an aberration. If some 50% overlap models fit moderately well, as opposed to the 25% overlap models, it could be suspected that the overlap may lie between 50% and 75%. The fact the all 50% overlap models failed to converge or were unsupported further corroborates that the good fit of the 25% overlap of 'Nonpareil' was probably anomalous.

In finding a high likelihood of 75% overlap, our best models differ from the *sequential* model that assumes no chill accumulation after C_r (Ashcroft et al., 1977) and indicates *sequential* models are neglecting significant biological processes underlying dormancy

breaking. The superiority of the 75% overlap models supports the idea that chill accumulation has functions beyond short-term chromatin modification (Leida et al., 2012) and is in accordance with studies that have found chill accumulation to decrease expression of DAM genes well after the C_r has been met (Cooke et al., 2012; Yamane et al., 2011). Further analysis in almond fitting the chill overlap using 75% as a starting value, or bracketing possible overlap values around 75% could more exactly quantify this relationship. The present findings support inclusion of substantial chill overlap in modeling spring phenology of other species, though the amount of overlap may vary by species and the bloom stage modeled (e.g. initial bloom, full bloom).

Because this work was aimed at testing the functionality of biologically based starter values for nonlinear model fitting, the overlap in chill accumulation and the inclusion of pre-bloom conditions; chilling requirement estimates were used as opposed to fitting C_r as a parameter. This meant one less parameter vulnerable to over-fitting. Thus, the chilling requirements that achieved convergence should be taken as approximations and conclusions regarding their values should be limited. The estimation algorithm failed to converge for 'Mission' assuming $C_r = 29$ CP, 'Nonpareil' assuming $C_r = 17$ CP and 'Sonora' assuming $C_r = 17$ CP. Thus the C_r of 'Mission' is likely closer to 21 than 29 CP, the C_r of 'Nonpareil' closer to 23 than 17 CP and the C_r of 'Sonora' closer to 13 than 17 CP.

These findings for 'Nonpareil' are in accordance with the chill requirement estimation of Ramirez et al. (2010). The C_r of 'Mission' has been estimated as 125% of the C_r of 'Nonpareil' in chill hours (Weinbaum et al., 1984), whereas the present work found a good fit given a lower C_r than 'Nonpareil'. This discrepancy could be due to these requirements being estimated based on field observations of 'Mission' blooming later than 'Nonpareil' (Weinbaum et al., 1984). 'Mission' may have a higher heat requirement, rather than a higher C_r than 'Nonpareil'. 'Mission' data points are in approximately the same range for chill accumulation as 'Nonpareil' but a higher heat accumulation range (Fig. 3a and c). Alonso et al. (2005) found that, of 44 almond cultivars, many cultivars had lower C_r 's than cultivars that bloomed before them. The C_r of 'Sonora' has not been published in the scientific literature, however, the C_r of 'Ne Plus Ultra', which blooms at nearly the same time, has been estimated as 75% of the C_r of 'Nonpareil' using chill hours (Weinbaum et al., 1984). Given that the C_r of 23 CP fit the 'Nonpareil' data better, the superior fit of the 13 CP 'Sonora' models was surprising. Though almost half the estimated requirement of 'Nonpareil' and 'Mission', this is not unreasonable, as some of the earliest blooming peaches and nectarines have estimated C_r 's of 8–18 CP (Erez, 2000).

4.3. Additional parameters

For all three cultivars, the model with the lowest AICc value assumed 75% chill overlap and did not include a pre-bloom parameter (Table 3). With the exception of 25% and 75% overlap 'Sonora' models, models that included solar radiation or precipitation had higher AICc values than models of the same chill overlap including pre-bloom GDH or no pre-bloom parameter (Table 3). Of the models for which empirical evidence was substantial ($\Delta_i < 3$), only the models for 'Nonpareil' assuming 25% and 75% chill overlap that included GDH before bloom had log-likelihood values that were lower than that of the best model by more than 0.5 and thus shared the status of 'best model' (Table 3).

The 'Nonpareil' pre-bloom GDH models predicted bloom date as accurately or less accurately (depending on the chill overlap) as the no pre-bloom parameter model with the same chill overlap (Table 4). The 75% overlap pre-bloom GDH model RMSE_p was 0.07 days lower than the equivalent model with no pre-bloom parameter, and RMSE_v was 0.02 days higher. The 25% overlap

pre-bloom GDH model's RMSE_p and RMSE_v were both higher than the equivalent overlap model without pre-bloom conditions. The pre-bloom GDH models also contained the mild computational burden of an additional parameter, and, particularly for model utilization by horticultural or forestry managers, the increased conceptual and graphic complication of envisioning a third dimensional. Thus, while fit of the 'Nonpareil' models with and without the pre-bloom GDH parameter may be statistically equivalent, the models that do not include GDH appear to be functionally superior. This indicates against a third stage of dormancy just prior to bloom, as has been suggested by Saure (1985) and Faust et al. (1997), or at least indicates that such a mechanism does not significantly impact bloom timing.

5. Conclusions

The present analysis found one model, $H_a = f(H_r, H_0, C_a)$ with 75% chill overlap to provide the best fit of spring phenological event timing across three diverse locations for cultivars of diverse bloom timing. This chill overlap contrasts with previous models and suggests cold temperatures affect dormancy breaking well after the chilling requirement has been met. Results indicate that the inconsistent fit of previous models was not due to a missing third dormancy stage pre-bloom parameter. We are optimistic that, given the superior performance of the models that only require chill and heat accumulation and the use of starting values that are easily derived from the data, reliable spring phenological models could be easily created for other species with only historical spring phenology records, weather data and an estimate of C_r . Such an approach might be used to quickly, simply and reliably build spring phenology prediction models for horticultural and ecological species that could have significant utility; from improving inter-annual carbon flux models to increasing pollinator management strategies regard to predicting the impacts of climate change. Critical to our approach was a large dataset in a variable, mild temperate climate. In a climate with colder winters, attempting to fit an exponential declining model such as ours may prove less fruitful because the scope of the data could be too narrow. However, as winters continue to warm, this approach could facilitate predictions of phenological responses of agricultural and ecological systems.

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