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Validation of winter chill models using historic records of walnut phenology

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ABSTRACT

Many fruit and nut species require cold temperatures during the dormancy season to initiate flowering and bear fruit. Quantifying these chilling requirements is crucial for identifying appropriate cultivars for a given site, for timing applications of rest-breaking chemicals and for predicting consequences of climate change. We present a new method to test temperature models describing chilling and heat requirements of perennial plants, and use this method to compare the ability of four chilling models (Chilling Hours, Utah Model, Positive Utah Model and Dynamic Model) to explain walnut phenology in California.

When plotting remaining heat before a phenological stage is reached against accumulated winter chill, observational curves for all years should intersect in one common point, assuming fixed chilling and heat requirements and a sequential fulfillment of these requirements. This point defines the chilling and forcing requirements of the plant, and the quality of the chilling/heat model combination is indicated by how well defined the intersection point is.

We used this method on a total of 1297 phenological observations, including four walnut cultivars, seven phenological stages and eight locations in California. Using an hourly temperature record, winter chill was quantified by the four chilling models and remaining heat was estimated using the Growing Degree Hour concept.

The theoretical intersection point was more clearly defined for the Dynamic and Positive Utah Models than for the Chilling Hours and Utah Models in almost all cases, indicating that these are superior in explaining walnut phenology. It was also apparent that chilling models were not equivalent and that chilling requirements determined under constant temperature conditions, when quantified in Chilling Hours, were not representative of chilling requirements in orchards.

1. Introduction

Many perennial trees and shrubs require cool temperatures during the winter, followed by warm spring temperatures to break their winter dormancy (Erez, 2000; Knight, 1801; Samish, 1954; Saure, 1985; Vegis, 1961). This phenomenon is of particular importance in the production of many fruit and nut crops that evolved in temperate or cool subtropical climates, such as peaches, cherries, apples and walnuts, because these species can only be produced, where their winter chilling requirements are fulfilled (Chandler, 1942; Lesley, 1944). At sites where these requirements are not met, such as most tropical locations, production is only possible under certain conditions using labor-intensive cultural practices (Balandier et al., 1993; Denardi and Hough, 1987; Edwards, 1987; Romberger, 1963). Estimating the chilling requirements of fruit and nut species and the amount of winter chill available at a given location has thus been a central theme of horticultural research, ever since the ranges of these species were expanded beyond the traditional growing regions.

Several models have been suggested to calculate winter chill (Bennett, 1949; Fishman et al., 1987b; Linsley-Noakes and Allan, 1994; Richardson et al., 1974), with the development of new models mostly driven by the failure of existing models in a certain growing region. In regions where available models yielded good predictions, or where their failure was not obvious, growers rarely transitioned to a new model, and new chilling models were rarely tested. To date, such tests have mostly entailed the use of competing chilling models to quantify winter chill, the prediction of bloom or leaf out dates with all models, and the comparison of predicted with actual leaf out or bloom dates. The usefulness of this procedure has always been constrained by small numbers of observations and locations, and by a priori assumptions about the chilling or forcing requirements of the cultivars analyzed.

We propose a new method to compare chilling models for fruit and nut trees, which relies on historical observations of phenological stage dates. This method simultaneously estimates

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the cold and heat requirements of the tested cultivar under the climatic conditions of the study location, eliminating the need for experiments under controlled conditions. In order to identify an appropriate chilling model for predicting walnut (*Juglans regia* L.) phenology in California, we compared four different winter chill models: the Chilling Hours Model, the Utah Model, the Positive Utah Model and the Dynamic Model.

The Chilling Hours Model is the oldest and simplest of the evaluated models. It quantifies winter chill as the number of hours during the winter season, when temperatures are between 0 and 7.2 °C (45 °F, often also converted into 7 or 7.22 °C; Bennett, 1949; Weinberger, 1950). The Utah Model (Richardson et al., 1974) was developed to explain studies indicating that these fixed threshold temperatures did not adequately represent the reality of chilling accumulation and that high temperatures had a negative effect on chilling accumulation. This model was adapted in various ways to adjust to varying climatic conditions (Norvell and Moore, 1982; Shaltout and Unrath, 1983). One such adaptation for warm subtropical climates is the Positive Utah Model, which does not contain the chill negation mechanism of the original Utah Model (Linsley-Noakes and Allan, 1994). The Dynamic Model (Fishman et al., 1987a; Fishman et al., 1987b) was developed to reflect the results of controlled temperature experiments in Israel, indicating that the sequence of cool and warm temperatures was important for describing chilling accumulation (Erez and Couvillon, 1987; Erez et al., 1979a; Erez et al., 1979b) and that moderate temperatures had a chill-enhancing effect (Erez and Couvillon, 1987).

To date, the Dynamic Model has not been widely adopted, and most fruit and nut growers in subtropical climates still base their choice of cultivars and cultural practices either on the Utah Model or on one of two versions of the Chilling Hour concept. In California, only cherry growers, who depend on the precisely timed application of rest-breaking chemicals to induce bloom of this high-chill species, have started using the Dynamic Model. For most other species, such as almonds, peaches, grapes and apricots, winter chill has so far been sufficient to allow good production, even in low-chill years. A recent study on the impacts of climate change on California fruit production, however, indicates that this might change in the near future, soon enough to affect orchards that are being planted today (Baldocchi and Wong, 2008). Baldocchi and Wong (2008) calculated the number of Chilling Hours for weather stations throughout California from long-term climatic records, finding dramatic decreases at several sites. Extending their analysis to predicted temperature changes for California indicated that conditions for the production of temperate and cold-loving subtropical fruit trees might deteriorate within a few decades. For interpreting these results and for converting them into advice to fruit and nut growers, it is crucial to know how well the estimates reflect the reality of winter chill accumulation in California. An analysis of the sensitivity of the four chilling models investigated in this study to climate change revealed large differences between the models, with the Chilling Hours Model predicting a much faster decline of winter chill than the other models (Luedeling et al., 2009a).

We present a new method for evaluating chilling models for a given region, and compare the four most important models with respect to their ability to explain walnut phenology under California conditions.

2. Materials and methods

2.1. Theoretical framework

In spite of decades of research on the breaking of dormancy, the processes leading eventually to leaf out and bloom of perennial species are as yet not well understood. One of the major uncertainties in predicting the influences of cold and heat in this process is during what stages of a tree's dormancy cold and heat are effective. An often unstated assumption in most studies on chilling and heat requirements is that trees have more or less fixed chilling and forcing requirements, which have to be fulfilled one after the other. Evidence has also been found, however, for certain effects of actual winter temperatures on chilling and forcing requirements (Couvillon and Erez, 1985; Gariglio et al., 2006), indicating that a purely sequential interpretation might be a simplification. In spite of the risk of such a simplification, we adopt a purely sequential approach with fixed chilling and forcing requirements in this study. This is not only the most common approach taken to date; it also appears to be the only one that can realistically be tested, and the most likely to produce useful results with practical implications.

According to this framework, the dormancy season can be divided into two parts. During the first phase, often termed dormancy (Romberger, 1963) or endodormancy (Lang et al., 1985), the chilling requirement has not been fulfilled, and all heat that is accumulated during this phase is ineffective (Fig. 1). After the chilling requirement is fulfilled, in the quiescence (Romberger, 1963) or ecodormancy (Lang et al., 1985) phase, the tree no longer accumulates chilling, and leaf out or bloom will occur after the respective forcing or heat requirements for these stages have been fulfilled (Fig. 1).

Under the assumptions stated above, the lengths of these two phases are well defined. The first phase is determined by the time it takes to accumulate the cold units necessary to fulfill the chilling requirement, while the length of the second phase reflects the time between the end of endodormancy and the fulfillment of the heat requirement. Plotting the accumulated units of chilling against the units of heat that still remain to be accumulated to reach a given phenological stage illustrates the point in the tree's physiological time at which endodormancy is broken (Fig. 2). The dashed lines in Fig. 2 indicate hypothetical observations of chilling and heat accumulation during different dormancy seasons. Since during the first dormancy phase, heat is ineffective, and during the second phase, chilling is ineffective, the curves representing such observations would all pass through one well-defined point, if chilling and heat accumulations were described by perfect models.

While there is no indication that any of the existing models accurately describe the complex physiological processes involved in breaking dormancy, the degree to which the theoretical intersection point is defined gives a good indication of how well a given combination of a chilling and a forcing model describes reality.

2.2. Phenological observations

Observations of walnut phenology have been conducted in experimental orchards at the University of California at Davis since 1954 and at various other locations in California for variable periods of time. Researchers and farm advisors have recorded the dates of distinct phenological stages, such as leaf out, and first, peak and last male and female bloom. For identifying the most suitable winter chill model for walnuts in California, we used 1297 phenological dates comprising all seven stages for the walnut cultivars Chandler, Hartley, Payne and Scharsch Franquette observed at up to eight locations in California for varying numbers of years (Table 1). Only seven people were involved in collecting this dataset, with one of us (C. Leslie) responsible for 59% of all observations. All cultivars were grafted on either Northern California Black Walnut (*Juglans hindsii* (Jeps.) Jeps. ex R.E. Sm.) or Paradox (*J. hindsii* × *J. regia* L.) rootstocks. In those orchards

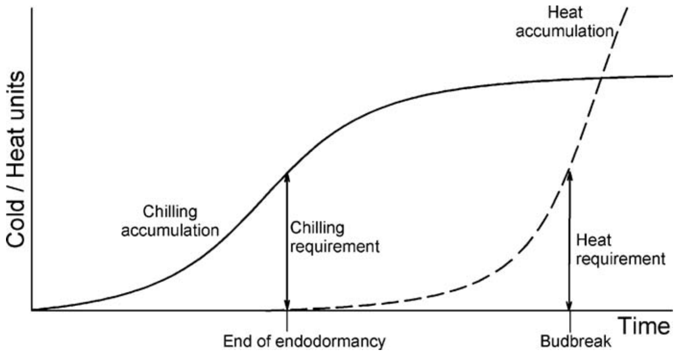

Fig. 1. Schematic illustration of chilling and heat accumulation during the dormancy period as a function of time, under the assumption that chilling and heat are accumulated sequentially.

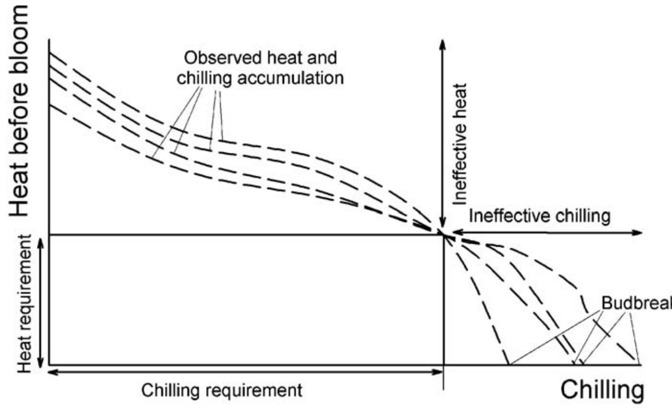

Fig. 2. Schematic illustration of heat units remaining until budbreak, as a function of accumulated chilling during the winter season, under the assumption that the chilling and heat requirements are fulfilled sequentially. Heat occurring before the chilling requirement is fulfilled and chilling occurring after the chilling requirement is fulfilled are considered ineffective. Under the given assumptions, all seasonal observations of chilling vs. remaining heat should pass through a common intersection point.

where both rootstocks were used (at Davis and Parlier), no detectable impact of rootstock on phenological dates was observed. All observations were done on mature trees.

2.3. Temperature records

The Central Valley of California is covered by a dense network of weather stations, pertaining to the California Irrigation Management Information System (CIMIS; http://www.cimis.water.ca.gov/), which record temperatures at hourly intervals and make the records available to the public. Since this system was only initiated in 1982, its records do not cover the full range of phenological observations available. For extending the record back in time, we used Partial Least Squares regression between hourly temperatures of the CIMIS record and daily minimum and maximum temperatures recorded by a different weather station network maintained by the National Climatic Data Center (NCDC; downloaded from UC IPM Online at http://www.ipm.ucdavis.edu). As a further independent variable, modeled daylength was also included in the regression. Such temperature estimates have been shown to be suitable for describing the daily temperature curve at a given location and for calculating winter chill (Luedeling et al., in press, 2009a,b).

Table 1
Number of years, for which phenological stages were observed for each stage of each cultivar at the eight study locations.

	Chico	Davis	Hollister	Madison	Parlier	Rumsey	Wheatland	Winters	Total
Chandler (376 observations)									
Leaf out	6	20	–	4	5	3	3	9	50
1st male bloom	6	20	6	4	5	2	3	9	55
Peak male bloom	6	19	6	3	5	2	3	9	53
Last male bloom	6	20	6	3	5	2	3	9	54
1st female bloom	6	20	6	3	5	3	3	9	55
Peak female bloom	6	20	6	3	5	3	3	9	55
Last female bloom	6	20	6	3	4	3	3	9	54
Hartley (271 observations)									
Leaf out	6	15	–	–	5	–	–	12	38
1st male bloom	3	13	5	–	5	–	–	9	35
Peak male bloom	3	12	5	–	5	–	–	9	34
Last male bloom	3	13	5	–	5	–	–	9	35
1st female bloom	6	15	5	–	5	–	–	12	43
Peak female bloom	6	15	5	–	5	–	–	12	43
Last female bloom	6	15	5	–	5	–	–	12	43
Payne (482 observations)									
Leaf out	6	54	–	–	5	–	–	12	77
1st male bloom	6	54	6	–	5	–	–	11	82
Peak male bloom	6	18	6	–	5	–	–	11	46
Last male bloom	6	53	6	–	5	–	–	11	81
1st female bloom	6	28	6	–	5	–	–	12	57
Peak female bloom	6	53	6	–	5	–	–	12	82
Last female bloom	6	28	6	–	5	–	–	12	57
Scharsch Franquette (168 observations)									
Leaf out	–	20	–	–	–	–	2	12	34
1st male bloom	–	11	–	–	–	–	1	9	21
Peak male bloom	–	10	–	–	–	–	1	9	20
Last male bloom	–	11	–	–	–	–	1	9	21
1st female bloom	–	12	–	–	–	–	–	12	24
Peak female bloom	–	12	–	–	–	–	–	12	24
Last female bloom	–	12	–	–	–	–	–	12	24
Total	117	613	102	23	104	18	26	294	1297

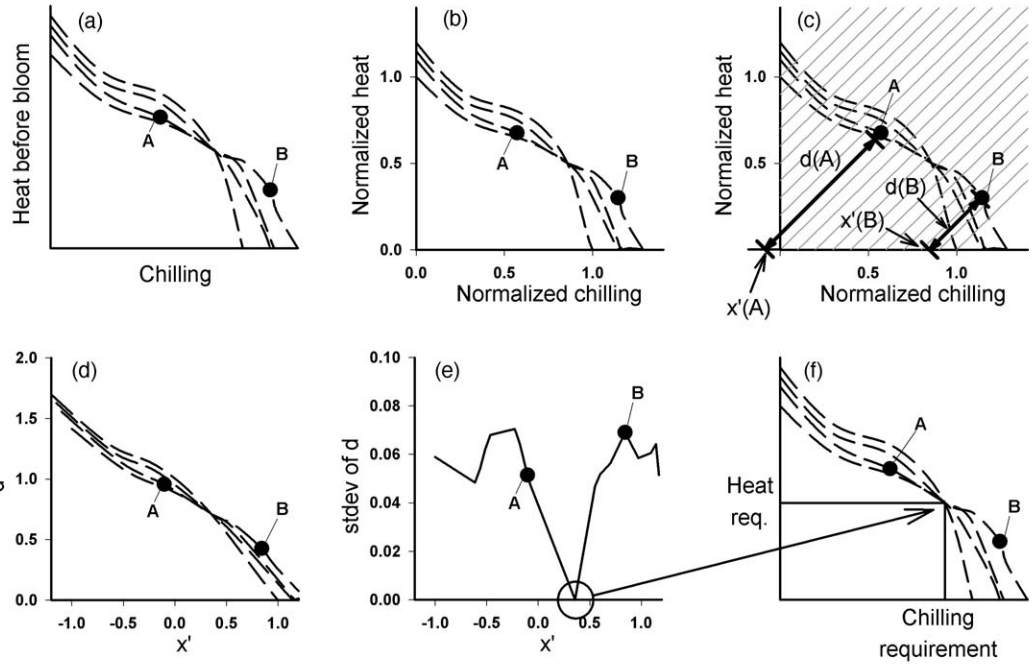

Fig. 3. Illustration of the chilling model testing procedure. (a) Remaining heat before reaching the phenological stage is plotted against accumulated chilling for all observed phenological dates; (b) the curves are normalized by dividing by the minimum axis intercepts; (c) the curves are projected onto a tilted coordinate system, resulting in (d); (e) the minimum standard deviation of d denotes the best approximation of an intersection point; (f) converting the x' and d values back to the original units yields the chilling and forcing requirements. Points A and B were added to the graphs to illustrate the effect of the transformations on individual data points. x'(A), x'(B), d(A) and d(B) in (c) indicate the coordinates of the points in the projected coordinate system.

2.4. Chilling models

We compared the predictive performance of the Chilling Hours Model, the Utah Model, the Positive Utah Model and the Dynamic Model. The equations used for calculating winter chill with these model are given in Luedeling et al. (2009a).

For each of these models, accumulated chilling was calculated for each hour of the temperature record, with the beginning of the chilling season set to November 1st for the Chilling Hours, Utah and Positive Utah Models. For the Dynamic Model, winter chill was assumed to start accumulating in July, but because of the chill-inhibiting effect of warm temperatures in the model, winter chill effectively did not start accruing before October. For each phenological observation, accumulated winter chill was calculated for every hour until reaching the phenological stage.

2.5. Forcing model

Since the focus of this study was on testing chilling models rather than forcing models, we only used a single forcing model in our analyses. This model uses the concept of Growing Degree Hours (GDH; Anderson et al., 1986), calculated from hourly temperatures (T_h), as a function of a base (T_b), an optimum (T_u) and a critical (T_c) temperature. The underlying assumption is that heat accumulates, when temperatures range between T_b and T_c, with maximum accumulation at T_u. For temperatures between T_b and T_u, the corresponding equation is:

$$\mathrm{GDH} = F\frac{T_u - T_b}{2}\left(1 + \cos\left(\pi + \pi\frac{T_h - T_b}{T_u - T_b}\right)\right),$$

whereas for temperatures between T_u and T_c, heat accumulates as

$$\mathrm{GDH} = F(T_u - T_b)\left(1 + \cos\left(\frac{\pi}{2} + \frac{\pi}{2}\frac{T_h - T_u}{T_c - T_u}\right)\right)$$

In both equations, F is a plant stress factor that is commonly set to 1, if no particular stresses are assumed. T_b, T_u and T_c were set to 4, 25 and 36 °C, respectively, as suggested by Anderson et al. (1986) for fruit trees.

Since our method requires knowledge of the amount of heat that is still required to reach the phenological stage in question, we converted Growing Degree Hours (GDH) into remaining Growing Degree Hours (GDHr). For doing this, we first determined the seasonal maximum of GDH ($\mathrm{GDH_{max}}$) as the number of GDH accumulated between November 1 and the time a certain phenological stage was reached (t_p):

$$\mathrm{GDH_{max}} = \sum_{i=1}^{t_p}\mathrm{GDH}_i.$$

For each hour during the season, the number of growing degrees remaining was then calculated as:

$$\mathrm{GDHr}_t = \mathrm{GDH_{max}} - \sum_{i=1}^{t}\mathrm{GDH}_i$$

This calculation can also be implemented iteratively as:

$$\mathrm{GDHr}_t = \mathrm{GDHr}_{t-1} - \mathrm{GDH}_t, \quad \text{with}\ \mathrm{GDHr}_0 = \mathrm{GDH_{max}}$$

For all chilling models, the number of GDHr was then plotted against the number of chill units for each hour of each dormancy season.

2.6. Determining the intersection point

For each chilling model that was tested, the procedure outlined above yielded sets of curves for each cultivar and phenological stage (Fig. 3a). According to the theoretical considerations above (Figs. 1 and 2), the chilling model, for which the intersection point of these curves is most clearly defined, should be considered superior for explaining the timing of the respective phenological stage for the tested cultivar. Since none of the chilling models is absolutely accurate, not all curves of a set will intersect in one point. A statistical approach was therefore necessary to determine the best approximation of the intersection point.

To allow comparison between different chilling models, all observations first had to be normalized. For this normalization, we selected from among all observational curves of a given set the minimum remaining heat on the first day of the winter season (November 1st), and the minimum accumulated winter chill, at which the phenological stage was reached. Division by these factors projected all curves onto a common scale (Fig. 3b). Since the temperature requirements for reaching a certain phenological stage consist of a combination of a chilling and a heat requirement, we projected all data points of each observational curve onto a new coordinate system, in which the *y*-axis was tilted by 45° (Fig. 3c). In the new coordinate space, each data point is defined by an x'-coordinate (x' = normalized chilling − normalized heat), and the distance d of the unprojected data point from the unprojected *x*-axis at a 45° angle (*d* = normalized heat/sin 45°) (Fig. 3d). Some data points (such as point A in Fig. 3) were assigned negative x' values, whereas all *d* values were positive. Analyzing the variation of the *d* coordinate in the new coordinate system allowed an estimate of how well a combination of chilling and heat requirements was defined (Fig. 3e). We used the standard deviation to evaluate the variation in *d*. The closest approximation of the theoretical intersection point of the observational curves was interpreted to be located where the standard deviation was minimized. Calculating the mean d value at this x' position and converting both coordinates back to the original data scale yielded the chilling and heat requirements of the cultivar for the tested phenological stage (Fig. 3f). Because of the prior normalization of the observational curves, the standard deviation of *d* could be compared across chilling models, and the model with the lowest value for this metric was considered superior to the other models for explaining the tested phenological stage date.

2.7. Verification of calculated requirements

Several indicators were calculated to verify whether the calculated heat and chilling requirements were suitable for explaining the phenological stages of the tested walnut cultivars. Modeled chilling and heat requirements were used to predict all phenological dates in the database based on observed hourly temperatures. Modeled dates were then compared to observed phenological dates, and the difference between the two was calculated. The mean and the standard deviation of the resulting distribution of prediction errors were used as indicators of prediction accuracy. We also counted the number of phenological observations that occurred before the fulfillment of the calculated chilling requirements.

Another evaluation criterion was the variation in the amount of heat that was accumulated between the fulfillment of the chilling requirement and the observed phenological dates. We expressed this error as a percentage of the predicted heat requirements and calculated means and standard deviations of the resulting distributions. In a similar calculation, we counted accumulated heat backwards from the phenological dates, and evaluated the amounts of chilling that had accumulated at the time of rest completion, as predicted by the heat requirement. This amount of chilling was expressed as a percentage of the calculated chilling requirements and evaluated by the mean and standard deviation of the distribution. Finally, we calculated the predicted date of rest completion, starting both from the beginning and from the end of the dormancy period.

2.8. Equivalence of chilling models

For arguing that a certain winter chill model is superior to another one, the models must be shown to not be equivalent. We examined the relationship between accumulated units of chilling at all study locations, as calculated by all four models. We used all available temperature records for all years between 1951 and 2008 for all stations, obtained as described above. As an additional study site, we added a hypothetical location (Constant6), where temperatures were a constant 6 °C throughout the entire study period. This site represents conditions often used, when chilling requirements are determined in temperature-controlled experiments.

For each model, we quantified winter chill accumulated by every hour between November 1st and March 31st of each year on record. For each site and pair of two chilling models, we then compared accumulated winter chill by linear regression, with the intercept of the regression line constrained to zero. The correlations were characterized by the slope of the regression line and the goodness of fit by the coefficient of determination. We also calculated the same metrics separately for each year on record for each of the locations.

2.9. Data processing

Because of the large number of phenological observations processed in this study, we implemented all analysis steps using the JMP Scripting Language (JSL) of the statistics package JMP 8 (SAS Institute, Cary, NC, USA). First, we created modeled temperature records for each site and converted these into units of chilling and heat. Subsequently, we separately matched these records with the phenological observations for each cultivar and phenological stage, and converted accumulated heat into remaining heat before the phenological date. For each phenological observation, a data file containing all temperature metrics for a given year, cultivar and phenological stage was stored in a database.

The database was then screened for all observations with a common cultivar and phenological stage, and all such records were jointly analyzed. In screening for the best defined value of d, it was necessary for all observational curves to have a d value for each x'. All x' values were thus rounded to three digits, and the d values corresponding to a unique rounded x' were averaged. For rounded x' values that did not have any corresponding d values in an observational curve, the d value was linearly interpolated from the closest existing d values of the same curve. To ensure that all available observational curves were evaluated, we restricted the screening for the minimum standard deviation of d to the x' range between −0.7 and 1. In defining this range, the lower limit was not set to −1, because many observational curves had the best defined points very early in the season, when almost no chilling had accumulated.

3. Results

3.1. Model performance

Based on the minimum standard deviation in the x'–*d* diagram, the success of the four chilling models in explaining walnut phenology for the seven phenological stages differed substantially. The Chilling Hours Model and the Utah Model averaged minimum standard deviations of 0.099 over all cultivars and phenological stages, compared to 0.078 and 0.077 for the Positive Utah Model and the Dynamic Model, respectively (Table 2). When comparing model performance for each combination of cultivar and phenological stage separately, both the Dynamic Model and the Positive Utah Model offered the best explanation for walnut phenology in 14 cases, while the other two models were never superior. The average rank in this classification was 1.50 for the Dynamic Model, 1.54 for the Positive Utah Model, 3.46 for the Utah Model and 3.50 for the Chilling Hours Model. Except for the peak

Table 2
Minimum standard deviations (Stdev.) of the *d* values for each set of curves (cultivar/phenological stage combination), and rank of the respective chilling model in the model comparison. The lower the standard deviation, the more successful the chilling model at explaining the date, when the phenological stage was reached.

Cultivar	Stage	Chilling Hours		Utah Model		Positive Utah		Dynamic Model	
		Stdev.	Rank	Stdev.	Rank	Stdev.	Rank	Stdev.	Rank
Chandler	1st female	0.113	3	0.132	4	0.088	1	0.092	2
	Peak female	0.108	3	0.119	4	0.083	2	0.079	1
	Last female	0.121	4	0.117	3	0.085	2	0.080	1
	Leaf out	0.119	4	0.107	3	0.071	1	0.076	2
	1st male	0.096	3	0.119	4	0.085	2	0.083	1
	Peak male	0.087	3	0.112	4	0.077	2	0.076	1
	Last male	0.093	3	0.112	4	0.079	2	0.069	1
Hartley	1st female	0.094	4	0.091	3	0.076	1	0.081	2
	Peak female	0.075	4	0.074	3	0.070	2	0.066	1
	Last female	0.082	3	0.082	4	0.072	2	0.069	1
	Leaf out	0.073	3	0.082	4	0.071	1	0.072	2
	1st male	0.103	4	0.095	3	0.079	1	0.087	2
	Peak male	0.081	4	0.080	3	0.067	1	0.076	2
	Last male	0.079	3	0.086	4	0.065	1	0.070	2
Payne	1st female	0.122	4	0.110	3	0.091	2	0.080	1
	Peak female	0.105	4	0.089	3	0.079	2	0.075	1
	Last female	0.090	4	0.077	3	0.063	2	0.057	1
	Leaf out	0.118	4	0.085	3	0.073	1	0.073	2
	1st male	0.115	4	0.093	3	0.089	2	0.074	1
	Peak male	0.092	4	0.091	3	0.079	2	0.071	1
	Last male	0.109	4	0.091	3	0.077	2	0.073	1
Scharsch Franquette	1st female	0.102	3	0.106	4	0.077	1	0.084	2
	Peak female	0.072	2	0.088	4	0.073	3	0.066	1
	Last female	0.089	3	0.104	4	0.073	1	0.073	2
	Leaf out	0.104	4	0.090	3	0.069	1	0.070	2
	1st male	0.107	3	0.109	4	0.084	1	0.098	2
	Peak male	0.089	3	0.098	4	0.082	1	0.089	2
	Last male	0.138	4	0.134	3	0.097	1	0.106	2
Mean		0.099	3.50	0.099	3.46	0.078	1.54	0.077	1.50

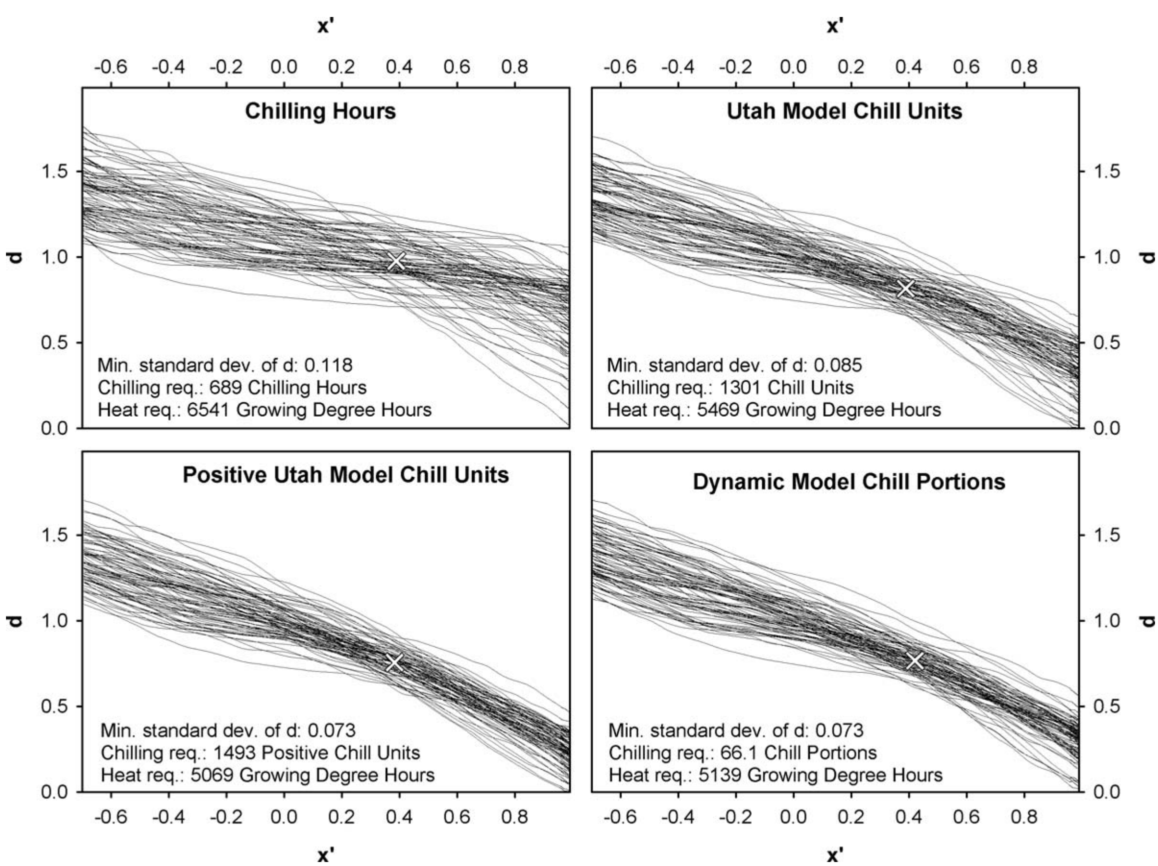

Fig. 4. Sets of observational curves for leaf out of the walnut cultivar Payne for all four chilling models and all 77 observations processed in this study plotted in the x'–d diagram.

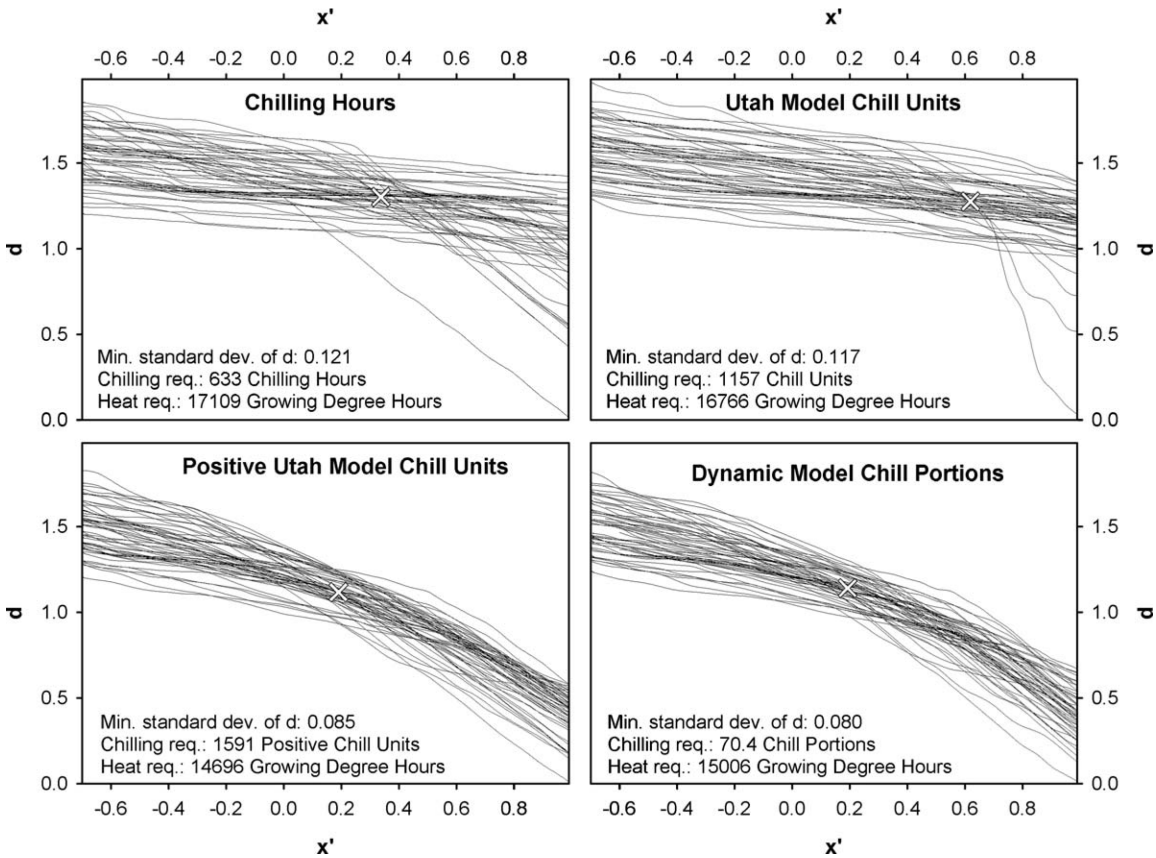

Fig. 5. Sets of observational curves for last female bloom of the walnut cultivar Chandler for all four chilling models and all 54 observations processed in this study plotted in the x'–d diagram.

female bloom of Scharsch Franquette, where Chilling Hours was the second most successful model, the Chilling Hours and the Utah Models were always inferior to both the Positive Utah Model and the Dynamic Model.

Figs. 4 and 5 show the x'–d plots for the leaf out dates of the cultivar Payne and for the last female bloom of Chandler. In both cases, the Dynamic and Positive Utah Models produced a much more compact set of curves than the other two models, indicating that they provide better measures of the progression of the trees through the dormancy season. Both the plots for the Chilling Hours and Utah Models contained outlier seasons, which were very poorly explained by the models.

Chilling and heat requirements derived from our algorithm appeared reasonable (Table 3), but are difficult to evaluate, given the lack of reference information for all but the Chilling Hours Model. For this model, chilling requirements were at the lowest end of the range typically given for walnuts (700 Chilling Hours), with some requirements substantially lower, especially the requirement for the first female bloom of Hartley. Surprisingly, the widely different chilling requirements often assumed for different cultivars did not manifest themselves in our analysis. For Scharsch Franquette, commonly used estimates of the chilling requirement reach up to 1500 Chilling Hours (e.g. http://grounds.stanford.edu/topics/cur_hort_subjects.html), which is more than twice our estimate. It should be noted, however, that chilling requirements often take into account not simply the occurrence of bloom or other stages, but also their extent. For example, an experimentally determined chilling requirement might be the amount of cold needed for 50% budbreak. Since such information was not included in our datasets, our study does not consider quantitative aspects of phenology.

3.2. Predictive capacity of modeled climatic requirements

For all chilling models analyzed, substantial variation occurred in the accuracy of predicted bloom dates. For the Chilling Hours, Utah and Dynamic Models, 50% of predicted phenological dates were within 4 days of observed dates, whereas for the Positive Utah Model, 50% were within 6 days. Ninety percent of predicted dates were within 12 days of observed dates for the Chilling Hours Model, within 13 days for the Utah and Dynamic Models, and within 15 days for the Positive Utah Model. Expressed by the mean and standard deviations of the distribution, predictions using the Chilling Hours Model were most accurate, followed by the Utah and Dynamic Models and the Positive Utah Model (Table 4). Maximum errors of the predictions were between 40 and 46 days for all models. In 31 cases, phenological stages occurred before one of the models predicted that the chilling requirement was fulfilled. This happened 5 times for the Positive Utah Model, 6 times for the Utah Model, 8 times for the Dynamic Model and 12 times for the Chilling Hours Model.

Starting the evaluation from the phenological date, and defining the date of rest completion as the date when exactly the amount of heat corresponding to the calculated heat requirement remained to be accumulated, produced different results. Measuring the accuracy of the model predictions by the variation in the amount of chilling accumulated at this time showed the smallest variation for the Positive Utah Model (mean error of 10% of the calculated chilling requirement), followed by the Dynamic Model (12%), the Utah Model (20%) and the Chilling Hours Model (31%).

The dates predicted by the four models as the dates of rest completion differed widely, with the Chilling Hours Model predicting rest to be completed on January 14, on average over

Table 3
Chilling and heat requirements for all tested cultivar and phenological stages and each chilling model, as derived from the algorithm presented in this study. All heat requirements are given in Growing Degree Hours, whereas the chilling requirements are given in the respective units of the chilling model.

Cultivar	Stage	Chilling Hours		Utah Model		Positive Utah		Dynamic Model	
		Chill	Heat	Chill	Heat	Chill	Heat	Chill	Heat
Chandler	1st female	631	13,162	1,142	12,952	1,580	10,773	71.2	10,966
	Peak female	635	15,041	1,168	14,683	1,594	12,708	70.6	12,941
	Last female	633	17,109	1,157	16,766	1,591	14,696	70.4	15,006
	Leaf out	629	10,545	1,126	10,380	1,545	8,660	70.2	8,573
	1st male	638	10,762	1,195	10,130	1,576	8,473	70.9	8,536
	Peak male	664	12,306	1,175	12,013	1,597	10,047	71.5	10,212
	Last male	661	14,690	1,171	14,451	1,597	12,424	71.7	12,473
Hartley	1st female	312	15,640	1,026	13,826	2,010	5,103	56.4	13,230
	Peak female	529	16,231	1,052	15,460	1,189	15,394	53.3	15,362
	Last female	654	16,970	1,065	16,858	2,002	8,745	64.8	15,391
	Leaf out	633	10,644	1,029	10,602	1,548	8,453	68.4	8,551
	1st male	600	11,570	1,081	11,197	1,952	3,877	57.2	10,761
	Peak male	578	13,383	1,054	13,012	1,877	7,214	53.8	12,896
	Last male	638	15,191	1,110	14,945	1,667	12,160	72.1	12,566
Payne	1st female	640	9,576	1,240	8,498	1,568	7,264	69.5	7,402
	Peak female	613	11,450	1,083	11,000	1,481	9,602	67.4	9,481
	Last female	617	13,162	1,095	12,601	1,538	10,832	70.1	10,687
	Leaf out	689	6,541	1,301	5,469	1,493	5,069	66.1	5,139
	1st male	570	8,844	1,123	8,025	1,349	7,541	64.6	7,031
	Peak male	610	10,184	1,026	10,024	1,454	8,353	68.2	8,032
	Last male	649	11,591	1,270	10,436	1,553	9,482	67.1	9,840
Scharsch Franquette	1st female	740	16,195	1,437	14,020	2,012	7,613	74.9	13,257
	Peak female	671	18,375	1,078	18,221	2,019	9,209	71.0	15,673
	Last female	679	20,654	1,322	19,028	2,019	11,588	69.5	18,229
	Leaf out	688	12,734	1,361	11,114	1,941	6,403	70.2	10,705
	1st male	704	12,800	1,360	11,384	2,011	4,542	69.0	10,999
	Peak male	703	14,762	1,389	13,062	2,020	6,213	69.7	12,806
	Last male	728	18,167	1,449	16,146	2,063	8,275	79.5	14,032

Table 4
Predictive capacity of the combinations of each tested chilling model with the Growing Degree Hours forcing model (Anderson et al., 1986). Errors are quantified using the predicted phenological dates, the number of years when chilling requirements were not fulfilled, and the variation in accumulated chilling and remaining heat at the predicted dates of rest completion. Mean and standard deviation are given for each error metric.

	Chilling Hours	Utah Model	Positive Utah Model	Dynamic Model
Forward calculation[a]				
Error of predicted phenological date (days)	5.4 ± 5.2	5.7 ± 5.8	7.2 ± 6.2	5.8 ± 5.9
Chilling requirement not fulfilled (# years)	12	6	5	8
Heat remaining at Creq (% off calculated heat requirement)	9.4 ± 9.1	11.4 ± 12.2	18.0 ± 19.5	12.5 ± 12.2
Date of rest completion (chill based)	1/15 ± 18 d	1/27 ± 15 d	2/20 ± 21 d	2/11 ± 14 d
Backward calculation[b]				
Heat requirement not fulfilled	0	0	0	0
Chilling at Hreq (% off calculated chilling requirement)	31.4 ± 25.5	20.4 ± 18.4	10.0 ± 9.6	11.7 ± 11.0
Date of rest completion (heat based)	1/14 ± 26 d	1/25 ± 23 d	2/20 ± 24 d	2/10 ± 18 d

[a] In the forward calculation method, chill accumulation starts at the beginning of the dormancy season; and the date of rest completion (Creq) is assumed to occur when the calculated chilling requirement has been fulfilled.
[b] In the backward calculation method, the date of rest completion (Hreq) is assumed to occur, when the remaining heat before bloom corresponds exactly to the heat requirement.

all cultivars, stages and sites, compared to January 25 for the Utah Model, February 10 for the Dynamic Model and February 20 for the Positive Utah Model. This date varied least for the Dynamic Model (Table 4).

3.3. Equivalence of chilling models

Testing the four models for equivalence clearly indicated that the relationship between the models is not constant in time or space (Fig. 6), meaning that the models are not equivalent. While all correlations were highly significant due to the large number of data points, the slope of the linear regressions between winter chill calculated with different models varied substantially between years, in particular for comparisons involving the Chilling Hours Model (top row in Fig. 6). In different years, one accumulated Chilling Hour at Chico corresponded to between 1.0 and 3.0 Utah Chill Units, between 1.3 and 3.2 Positive Utah Chill Units and between 0.06 and 0.15 Chill Portions. For the other three model comparisons, slopes also varied substantially (Fig. 6).

The correlation between winter chill calculated with different models also significantly varied with location (Fig. 6). The lowest slopes consistently occurred for the Constant6 location, with often substantial differences to slopes observed at any of the other sites. This observation strongly indicates that chilling estimates with the various models differ in a very different way under controlled than under orchard conditions. The choice of chilling model is thus a major determinant of how closely winter chill calculated in constant-temperature experiments corresponds to winter chill under orchard conditions.

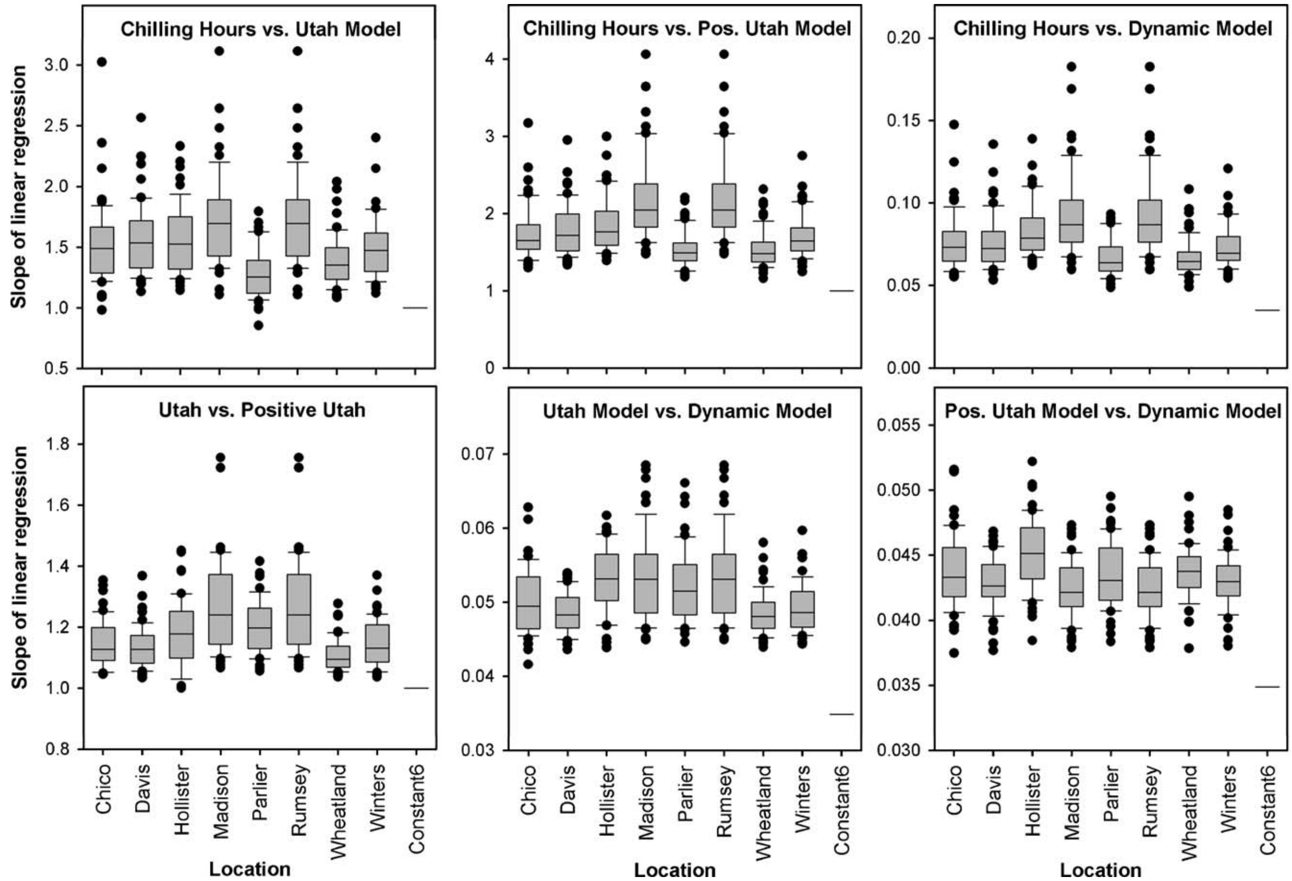

Fig. 6. Comparison between winter chill quantified with all possible combinations of two chilling models. Boxplots show the distribution of slopes of the corresponding linear regression lines for all years between 1952 and 2008. In boxplots, the central line marks the median, the edges of the boxes indicate the 25% and 75% quantiles, the error bars are the 10% and 90% quantiles and all dots are outliers.

4. Discussion

Based on the theoretical considerations outlined in the introduction and the assumptions stated therein, the Dynamic Model and the Positive Utah Model were clearly more successful in explaining walnut phenology in California than the Utah Model and especially the Chilling Hours Model, though not necessarily better at predicting phenological dates. The standard deviations of the *d* values were lower for the Dynamic Model and the Positive Utah Model than for the other two for all phenological stages of all cultivars, with only one exception, where the Chilling Hours Model was superior to the Positive Utah Model (but not the Dynamic Model).

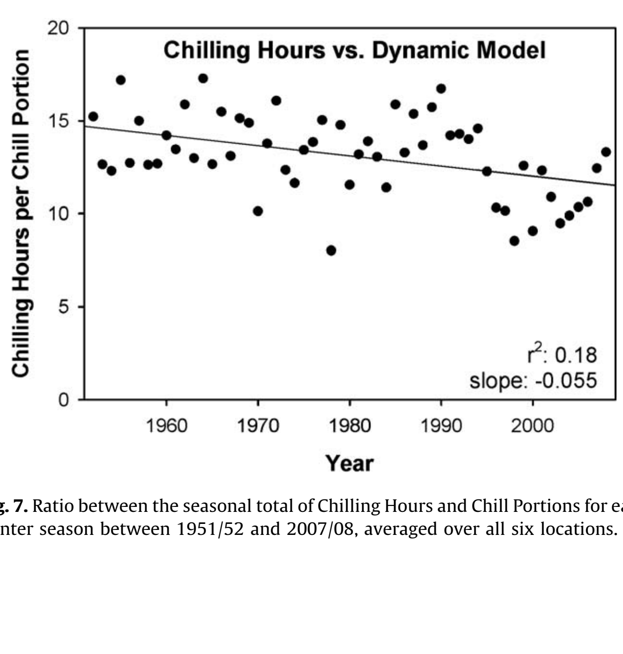

Fig. 7. Ratio between the seasonal total of Chilling Hours and Chill Portions for each winter season between 1951/52 and 2007/08, averaged over all six locations.

Due to its slight edge in the overall comparison over the Positive Utah Model, its more convincing theoretical background (Erez et al., 1990; Fishman et al., 1987a; Fishman et al., 1987b) and its capability for explaining all experimentally derived results from systematic studies in Israel (Erez and Couvillon, 1987; Erez et al., 1979a; Erez et al., 1979b), we recommend the Dynamic Model for explaining walnut phenology.

It should be noted that there is no reason to believe that this model perfectly explains the accumulation of winter chill, because the biological processes involved are as yet poorly understood (Dennis, 2003; Erez, 2000; Kozlowski and Pallardy, 2002; Saure, 1985). Among the models available today, it appears to be the most promising candidate, and for the purposes of this discussion, we will assume that it approximates accumulated winter chill with sufficient accuracy. If our conclusion is true, growers of walnuts and likely other fruit and nut trees would benefit from the adoption of the Dynamic Model for quantifying winter chill.

Nevertheless, growers in California and other growing regions have successfully used the Chilling Hours Model in the past, without adverse consequences in most years, indicating that this model might be a good proxy for winter chill. A proxy is a metric that can be used to infer information about a process or phenomenon without measuring the process or phenomenon itself. The very high correlations between Chilling Hours and Chill Portions (the units of the Dynamic Model) in each year at each location indicate that the Chilling Hours Model is indeed such a proxy. The slope of the regression line between Chilling Hours and

Chill Portions (Fig. 6) can be used to infer real accumulated winter chill from accumulated Chilling Hours. The same procedure can be applied for the Utah and the Positive Utah Models. As shown in Fig. 6, however, these conversion factors differ between years and between locations, making the comparison of winter chill between years and sites questionable, when Chilling Hours are used as a proxy. Unfortunately, this is exactly what these metrics are routinely used for, since growers need to know how much chilling has been accumulated relative to their experience from the past, or relative to chilling requirements determined elsewhere. In addition to these uncertainties, the relationship between winter chill as quantified by different models appears to be shifting as climate changes (Luedeling et al., 2009a). The slopes of the annual regression equations between winter chill quantified with the Chilling Hours and Dynamic Models, averaged over all natural locations (excluding Constant6) already showed a shift over the 57 years, for which we calculated winter chill (Fig. 7).

As long as the role of relatively inaccurate chilling models as mere proxies for winter chill is acknowledged, however, they can be useful for informing orchard management decisions, as has been shown impressively by growers in California over the past 70 years, during which the Chilling Hours Model was applied. Unfortunately, the Chilling Hours Model has often been used in contexts where the actual number of Chilling Hours was interpreted as biologically meaningful. This tacit assumption might underlie much of the research on winter chill that has been done in the past. It is also implicit in all studies that have determined chilling requirements under controlled constant temperature conditions, corresponding to our site Constant6. Fig. 6 shows that the correlations of winter chill calculated with different chilling models under such conditions dramatically differ from those observed in the orchards. Consequently, when an inaccurate chilling model or a mere proxy for winter chill is used for quantifying chilling requirements under controlled conditions, the results are likely to be invalid outside the controlled environment (Dennis, 2003).

The commonly stated chilling requirement of 1500 Chilling Hours for the walnut cultivar Scharsch Franquette illustrates this point. This cultivar has successfully been grown around the towns of Winters and Davis in Northern California, where 1500 Chilling Hours occur rarely to never. Assuming that this requirement was determined under a constant temperature regime of 6 °C (such information is unfortunately very hard to find), the chilling requirement would correspond to roughly 52 Chill Portions of the Dynamic Model. This amount of winter chill is easily exceeded in these two towns, as well as in most other parts of Northern California, explaining the presence of this cultivar. According to our calculations, the chilling requirement of this cultivar under orchard conditions should be around 700 Chilling Hours, or 70 Chill Portions (Table 3). While our estimate in Chill Portions is still 35% higher than what was (probably) derived under experimental conditions, the requirement in Chilling Hours appeared to be less than half of what is commonly assumed. It should be noted again, however, that these estimates are not necessarily comparable, because under controlled conditions, quantitative indicators of budbreak, such as percentage budbreak, are often considered. Nevertheless, the large discrepancy between the amounts of winter chill likely represented by one Chilling Hour under controlled vs. orchard conditions makes chilling requirements determined in this manner appear of relatively limited use to growers, unless they are first converted into Chill Portions.

The predictive capability of all combinations of chilling and heat models was limited, with errors of predicted dates varying widely. This confirms the cautionary note by Dennis (2003), who stated that our understanding of the rest-breaking process is not sufficient for this task. Phenological dates predicted with the Chilling Hours Model were most accurate, and this model also showed the least variation in remaining heat at the time it predicted the chilling requirement to be fulfilled. When assuming a fixed heat requirement, however, the accumulated chilling at the inferred time of rest-completion varied least in the Positive Utah and Dynamic Models. The Dynamic Model produced the most precise estimate of rest-completion dates (Table 4). The Dynamic Model and the Positive Utah Model predicted much later mean dates of rest-completion (February 10 and February 20, respectively) than the Chilling Hours (January 14) and Utah Models (January 25). Given the large variation in observed bloom dates and the straggly bloom during years with relatively warm late winters (e.g. 2009), it seems unlikely that the estimates of the latter two models are accurate. Unfortunately, data on rest-completion of walnuts under California orchard conditions is unavailable, making it impossible to decide which estimates are most exact. For walnuts, there is also no information on the interaction between accumulated chilling and remaining heat that has been reported for other species (Gariglio et al., 2006). For predicting phenological dates in low-chilling winters, inclusion of such a mechanism in the phenological model might be necessary for obtaining accurate predictions.

5. Conclusions

Our analysis clearly made the Dynamic Model stand out as the most accurate tool available for quantifying winter chill. It also appeared most likely to be valid across space and time, with the correspondence between winter chill and the Chilling Hours proxy likely to vary substantially between locations and years. The biological significance of Chilling Hours is likely weak compared to Chill Portions, which in turn are unlikely to perfectly represent actual winter chill. While many chilling models might have some use for approximating winter chill, many applications of these models tacitly assume generally applicable biological significance of the models. The transferability of chilling requirements or other research results determined under a given climatic regime to different temperature conditions is probably limited, if an inappropriate chilling model is used. This caveat might affect much of the chilling research done in the past.

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