



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

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