Int J Biometeorol
DOI 10.1007/s00484-013-0714-3

ORIGINAL PAPER

Chilling and heat requirements for flowering in temperate fruit trees

Liang Guo · Junhu Dai · Sailesh Ranjitkar · Haiying Yu · Jianchu Xu · Eike Luedeling

Received: 25 April 2013 / Revised: 8 July 2013 / Accepted: 25 July 2013
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Abstract Climate change has affected the rates of chilling and heat accumulation, which are vital for flowering and production, in temperate fruit trees, but few studies have been conducted in the cold-winter climates of East Asia. To evaluate tree responses to variation in chill and heat accumulation rates, partial least squares regression was used to correlate first flowering dates of chestnut (*Castanea mollissima* Blume) and jujube (*Zizyphus jujube* Mill.) in Beijing, China, with daily chill and heat accumulation between 1963 and 2008. The Dynamic Model and the Growing Degree Hour Model were used to convert daily records of minimum and maximum temperature into horticulturally meaningful metrics. Regression analyses identified the chilling and forcing periods for chestnut and jujube. The forcing periods started when half the chilling requirements were fulfilled. Over the past 50 years, heat accumulation during tree dormancy increased significantly, while chill accumulation remained relatively stable for both species. Heat accumulation was the main driver of bloom timing, with effects of variation in chill accumulation negligible in Beijing's cold-winter climate. It does not seem likely that reductions in chill will have a major effect on the studied species in Beijing in the near future. Such problems are much more likely for trees grown in locations that are substantially warmer than their native habitats, such as temperate species in the subtropics and tropics.

Keywords Chilling requirement · Climate change · Flowering · Fruit trees · Heat requirement · Partial least squares regression

L. Guo · J. Xu (✉)
Centre for Mountain Ecosystem Studies, Kunming Institute of Botany, Chinese Academy of Sciences, Lanhei Road 132, Heilongtan, Kunming 650201, Yunnan, China
e-mail: J.C.Xu@cgiar.org

L. Guo
University of Chinese Academy of Sciences, Beijing 100049, China

J. Dai
Institute of Geographical Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China

S. Ranjitkar · H. Yu · J. Xu
World Agroforestry Centre, East-Asia Node, Kunming 650201, China

E. Luedeling (✉)
World Agroforestry Centre, Nairobi 00100, Kenya
e-mail: e.luedeling@cgiar.org

Introduction

Long-term phenological observations at species level and at specific sites can provide direct evidence of the impacts of climatic variation and change (Rosenzweig et al. 2008). Obvious responses of plant phenology to climate warming have been reported across the globe. While the majority of published studies have focused on phenological changes in natural vegetation, relatively few reports are available on the response of fruit trees to climate change despite the high economic and agricultural values of these crops (Chmielewski et al. 2004). For fruit trees, flowering phenology has vital impacts on pollination, fruit set and production (Legave et al. 2008). Impacts of climate change on the flowering of fruits have aroused worldwide interest. Earlier flowering events have occurred for some fruits in many countries due to global warming (Chmielewski et al. 2004; Grab and Craparo 2011; Guédon and Legave 2008; Legave and Clauzel 2006; Wolfe et al. 2005). However, some fruit trees grown in areas that are substantially warmer than their native habitat have displayed delayed flowering (Elloumi et al. 2013; Legave et al. 2013). The most likely reason for the advance or delay of flowering is the impact of climate change on plant dormancy.

Published online: 21 August 2013

Fruit trees in temperate regions fall dormant in autumn and winter, as an adaptive strategy to protect sensitive growing tissue from unfavorable conditions (Jones et al. 2013; Luedeling et al. 2012). It is commonly assumed that dormancy is composed of an endodormancy phase, followed by an ecodormancy period (Lang et al. 1987). The chilling and forcing temperatures during the two periods are perceived by the floral primordial (Legave et al. 2008), and the corresponding chilling and heat requirements are generally considered to be the main driving factors in the breaking of both dormancy stages (Campoy et al. 2011b; Luedeling 2012). Varied rates of chilling and heat accumulation caused by climate changes could influence the fulfillment of chilling and heat requirements, leading to advanced or delayed spring phenological events.

Climate warming has affected chilling and heat accumulation rates for fruit trees in recent decades (Baldocchi and Wong 2008; Luedeling et al. 2011a). Historic declines in winter chill have been detected in many warm fruit growing regions, and this trend will likely be exacerbated by future temperature increases (Baldocchi and Wong 2008; Darbyshire et al. 2011; Farag et al. 2010; Luedeling et al. 2009a, c). Insufficient chilling can lead to uneven leafing and bloom, and can cause varying fruit sizes and maturity times, both of which can reduce the quantity and quality of fruits (Lang et al. 1987; Luedeling et al. 2009c). However, warming during the forcing period could increase the rate of heat accumulation, which could compensate for any phenology-delaying effects of reduced chilling (Ruiz et al. 2007). Compared to studies on the effects of variation in winter chill, studies on heat are scarce, and the effects of heat accumulation rates on flowering dates are reported less frequently (Citadin et al. 2001).

Horticultural scientists have developed several models for quantifying the chilling and heat requirements of trees, which vary by species, cultivar and region. Among many approaches used to quantify chill and heat, the Dynamic Model has almost always emerged as the most robust chilling model (Campoy et al. 2011b; Luedeling et al. 2009e; Luedeling and Gassner 2012; Ruiz et al. 2007; Zhang and Taylor 2011), while the Growing Degree Hour Model (Anderson et al. 1986; Luedeling et al. 2009e) has been used widely as a forcing model. We therefore adopt these two models in this study. Many previous assessments of chilling and forcing periods have used rather arbitrary delineations of the phases during which chill and heat accumulated. This has made it difficult to evaluate the impacts of climatic changes on chill and heat accumulation for particular species and thus to project impacts of climate change on tree phenology (Campoy et al. 2011b; Dennis 2003; Luedeling 2012). Reliable quantification of the chilling and heat accumulation periods is critical to close these knowledge gaps.

When long-term temperature and phenology records are available, partial least squares (PLS) regression has been used recently to derive the chilling and forcing period of cherry in Germany statistically based on daily temperatures and bloom dates (Luedeling et al. 2012). PLS regression—a procedure commonly used in chemometrics (Wold et al. 2001) and hyperspectral remote sensing (Luedeling et al. 2009b)—is a regression technique that can be used reliably in situations where independent variables are highly auto-correlated and where the number of independent variables exceeds the number of observations. Recent studies have shown that PLS regression can be used effectively to analyze relationships between phenology and climate variation (Luedeling et al. 2012; Luedeling and Gassner 2012; Ranjitkar et al. 2013; Yu et al. 2010, 2012).

In this analysis, we refined the PLS regression procedure such that the flowering phenology dates of two temperate fruit trees were related not directly to temperatures, but to daily chill and heat accumulation rates calculated with chilling and forcing models. Based on regression results, chilling and heat requirements of chestnut and jujube were estimated. The objectives of the present study were to assess the response of winter chill and heat accumulation to climate change, and—more importantly—to clarify the relative importance of chilling and heat requirements for explaining variation in temperate fruit flowering in a cold-winter climate.

Materials and methods

Study site

Located on the North China Plain, Beijing has the longest and most abundant records of phenology in China (Zhang et al. 2005). Compared to American and European regions at similar latitude, climatic variation in Beijing is substantially greater, leading to greater variation in the timing of phenological events and providing valuable data for elucidating climate responses of species (Lu et al. 2006). In Beijing, species-level phenological observations of plants were conducted mainly at the Summer Palace (40°01′N, 116°20′E, 50 m a.s.l.), a former royal garden with a long history. Both phenological data series used in this study were obtained from this park.

Phenology and climate data

Phenological data of chestnut (*Castanea mollissima* Blume) and jujube (*Zizyphus jujube* Mill.) collected at the Beijing Summer Palace between 1963 and 2008 were acquired from the Chinese Phenological Observation Network (CPON)—a nationwide system of monitoring stations that has conducted standardized, systematic and comprehensive phenological observations of plants and animals across China since 1963. Detailed phenological observation methods have been described by Wan and Liu (1979) and Lu et al. (2006). In the analysis, the first flowering phase was registered when 10 % of flowers were open, corresponding to stage 61 on the BBCH ('Biologische Bundesanstalt Bundessortenamt und Chemische Industrie') scale (Meier et al. 1994).

Daily minimum and maximum temperatures in Beijing during 1963–2008 were obtained from the Beijing Meteorological Station, which is only 2.5 km from the Summer Palace, so that temperatures recorded there should closely mirror conditions at the observation site. Since most common chilling and forcing models require hourly temperature data, idealized daily temperature curves with an hourly resolution were constructed from daily temperature extremes as proposed by Linvill (1989, 1990). Required inputs for these calculations were sunrise and sunset time, as well as daylength, which were computed according to procedures used by Spencer (1971) and Almorox et al. (2005).

Chilling and forcing models

Horticultural scientists have developed several chilling models to quantify the chilling requirement of plants. Among them, three chilling models are used widely around the world: the Chilling Hours Model (Weinberger 1950), the Utah Model (Richardson et al. 1974), and the Dynamic Model (Fishman et al. 1987a, b). Many studies have tested and compared which chilling model is best for different species and cultivars in different regions of the world. The Dynamic Model has almost always emerged as the most robust model, and is often considered as the current milestone model due to its rigorous theoretical structure as well as its ability to explain phenological observations (Campoy et al. 2011b; Luedeling et al. 2009e; Luedeling and Gassner 2012; Ruiz et al. 2007; Zhang and Taylor 2011). Thus, the Dynamic Model was applied in our analyses.

The Dynamic Model assumes that chilling accumulation occurs as a two-step process. In the first step, low temperatures lead to the formation of an intermediate chill product. This product can be destroyed by heat. Once a certain quantity of the intermediate product has been accumulated, moderate temperatures facilitate its conversion into a permanent Chill Portion. Chill Portions are then summed up until the end of the dormancy period. The mathematical functions of the Dynamic Model are given in Luedeling et al. (2009d).

The forcing model used in the analysis is the Growing Degree Hour (GDH) Model (Anderson et al. 1986; Luedeling et al. 2009e). The GDH Model assumes that heat accumulates when hourly temperature (T_i) ranges between a base temperature (T_b) and a critical temperature (T_c), with maximum heat accumulation at optimum temperature (T_u). The function to calculate GDH is described below:

$$GDH = \begin{cases} F\left(\frac{T_u - T_b}{2}\right)\left(1 + \cos\left(\pi + \pi\frac{T_i - T_b}{T_u - T_b}\right)\right), T_u \geq T_i \geq T_b \\ F(T_u - T_b)\left(1 + \cos\left(\frac{\pi}{2} + \frac{\pi}{2}\frac{T_i - T_u}{T_c - T_u}\right)\right), T_c \geq T_i \geq T_u \\ 0, \quad T_i > T_c \, or \, T_i < T_b \end{cases}$$

F is a plant stress factor that is commonly set to 1, if no particular stress exists. 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.

Chilling and forcing periods and chill and heat requirements

Based on the hourly temperature data, the Dynamic Model and the GDH Model were used to calculate daily chill and heat accumulation during 1963–2008. To ensure the emergence of recognizable response patterns between the chill/heat units and the first flowering data of fruit trees in subsequent statistical analyses, daily chill and heat values were subjected to a 15-day running mean (Luedeling et al. 2012; Luedeling and Gassner 2012).

PLS regression analysis was used to identify the chilling and forcing periods by relating the first flowering dates of fruit trees to daily chill and heat accumulation during 1963–2008. For each year, 365 daily chill and heat values (excluding data for 31 December in leap years) were thus used as independent variables, while the single bloom date of chestnut or jujube, respectively, was used as dependent variable.

The two major outputs of PLS analysis are the variable importance in the projection (VIP) and standardized model coefficients. The VIP values reflect the importance of all independent variables for explaining variation in the dependent variables, with 0.8 often used as threshold for determining importance (Wold 1995). The standardized model coefficients indicate the strength and direction of the impact of each variable in the PLS model (Luedeling et al. 2012).

Theoretically, high rates of chilling and heat accumulation should accelerate the fulfillment of chilling and forcing requirements, leading to early flowering. In the output of PLS regression analysis, periods during which the VIP values are greater than 0.8 and model coefficients are negative can be interpreted as chilling and forcing periods. During these phases, high daily chilling and heat accumulation rates are correlated with early dormancy release and early bloom. The chilling period was combined with the forcing period to display the entire dormancy period of chestnut and jujube.

Chilling and heat requirements of chestnut and jujube were then estimated as the total numbers of chilling and heat units accrued during the corresponding chilling and forcing periods.

Response of chilling and heat accumulation during relevant periods to climate warming

Linear regression was used to analyze temporal trends of chilling and heat accumulation during respective periods for chestnut and jujube during 1963–2008. Trends were tested for statistical significance using the Mann-Kendall test (Tao et al. 2006), a tool commonly used for time series analysis. Relationships between chilling and heat accumulation and mean temperature variations during the corresponding chilling and forcing periods were also analyzed by linear regression. Results were assessed for significance using analysis of variance.

Response of fruit tree flowering to chilling and heat accumulation during relevant periods

PLS regression indicated that plant bloom timing was related to chilling and heat accumulation during the chilling and forcing periods, but the relative strength of these factors was not initially clear. To clarify this relationship, we plotted tree bloom dates in relation to chilling and heat accumulation during the chilling and forcing periods. Surfaces of the response of flowering dates were interpolated using the Kriging technique. Default settings of the Kriging procedure in the R package 'fields' (Furrer et al. 2012) were used in the interpolation.

All analyses were implemented in the R 2.15.2 programming language (R Development Core Team 2012). All procedures used in this study are included in the package 'chillR' (Luedeling 2013), which relies heavily on the 'pls' package (Mevik et al. 2011).

Results

Chilling and forcing periods for chestnut

Between 1963 and 2008, the average first flowering date of chestnut at Beijing Summer Palace was 2nd June. Daily chilling and heat accumulation rates between the previous July and June were used as independent variables in the PLS regression, while dependent variables were chestnut first flowering dates, expressed in day of the year. Based on the VIP values and standardized model coefficients of the PLS regression, chilling and forcing periods for chestnut were identified (Fig. 1).

Two periods with important and negative relationships between chill accumulations and flowering dates were visible in September–October and January–March (left part of Fig. 1), indicating the initiation and end of the chilling period, during which high chill accumulation rates had an advancing effect on first flowering. However, the chilling period included a spell with positive model coefficients and high VIP values, showing an opposite effect on flowering. This indicated that chilling accumulation likely occurred discontinuously or was slowed substantially during part of the chilling period. Periods with positive model coefficients between October and December should also be considered to delineate the chilling

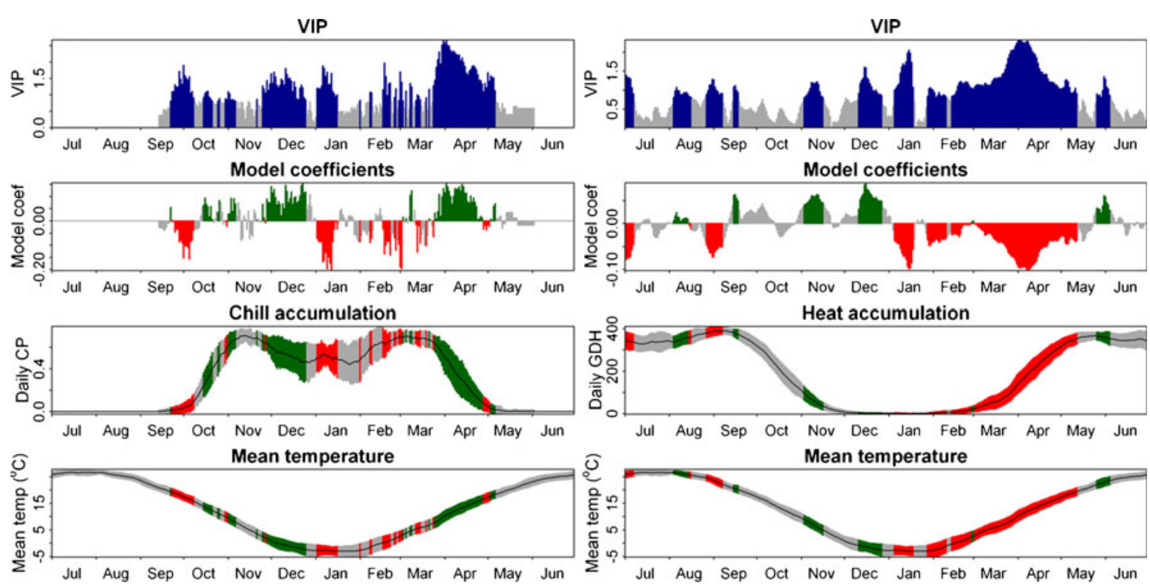


Fig. 1 Results of the partial least squares (PLS) regression analysis for chestnut in Beijing, China using the Dynamic Model and the Growing Degree Hour (GDH) Model. *Blue bars* in the *top row* mean that VIP is above 0.8, the threshold for variable importance. In the *second row*, *red bars* mean that model coefficients are negative (and important), while *green bars* indicate positive (and important) relationships between flowering and daily chilling and heat accumulation. In the *third* and *bottom rows*, the *grey*, *red* and *green bars* indicate the standard deviation of daily chilling and heat accumulation and mean temperature, respectively. The *left* part of Fig. 1 is the PLS analysis result for the chilling period, while the *right* part is for the forcing period. *CP* Chill portions

period. Thus the chilling phase likely extended from 14 September to 24 March for chestnut. For heat accumulation (right part of Fig. 1), between 4 January and 23 May, model coefficients were consistently negative and almost always significant (VIP>0.8), justifying consideration of the entire period as the forcing period, during which daily heat accumulation was correlated with early chestnut flowering. It showed some overlap with the period identified as effective for chilling.

Chilling and forcing periods for jujube

Between 1963 and 2008, the average first flowering date of jujube at Beijing Summer Palace was 28 May. Similar to the analyses for chestnut, the chilling period for jujube was from 17 September to 19 March, and the forcing period was from 9 January to 13 May (Fig. 2). Also for jujube, the chilling period was interrupted by certain phases with negative impacts on the dormancy breaking and early flowering. Overlap between the chilling and forcing period also occurred.

Chilling and heat requirements for chestnut and jujube

Accumulated chilling and heat units during the chilling and forcing periods provided rough approximations of chilling and heat requirements of chestnut and jujube at Beijing Summer Palace (Table 1). Both requirements were slightly higher for chestnut than for jujube. According to the Dynamic Model for chilling and the GDH Model for heat, chilling and heat requirements of chestnut at Beijing Summer Palace were 93± 6 Chill Portions (CP) and 17,418±1,983 GDH respectively. For jujube, we found a chilling requirement of 89±6 CP and a heat requirement of 13,619±2,033 GDH.

Response of chilling and heat accumulation during relevant periods to climate warming

Heat accumulation during the forcing period for chestnut in Beijing showed a significant trend, increasing by 97.8 GDH per year ($P<0.01$) during 1963–2008 (Fig. 3). The increase of heat accumulation was related significantly to rising mean temperatures during the forcing period, with heat accumulation increasing by 1,463.2 GDH/°C ($P<0.01$). Rising mean temperatures during the chilling period increased chilling accumulation by 2.5 CP/°C ($P<0.01$). However, chilling accumulation of chestnut did not show a significant trend during the past 50 years ($P>0.1$).

A similar response of chilling and heat accumulation occurred for jujube. A significant increase of heat accumulation over time was explained mainly by rising mean temperatures during the forcing period (1427.1 GDH/°C, $P<0.01$). Although no obvious trend was apparent for chilling accumulation of jujube over time, rising temperatures increased the amount of chilling accumulation by 2.8 CP/°C ($P<0.01$).

Response of fruit tree bloom to chilling and heat accumulation during relevant periods

Plotting first flowering dates of chestnut and jujube as a function of chilling and heat accumulation during the relevant periods clearly showed that chestnut and jujube bloom dates were determined primarily by heat accumulation during the forcing period (Figs. 4, 5). More heat during this phase advanced first flowering of both species. The limited influence of chilling accumulation during the chilling period was indicated by almost horizontal contour lines in Figs. 4 and 5.

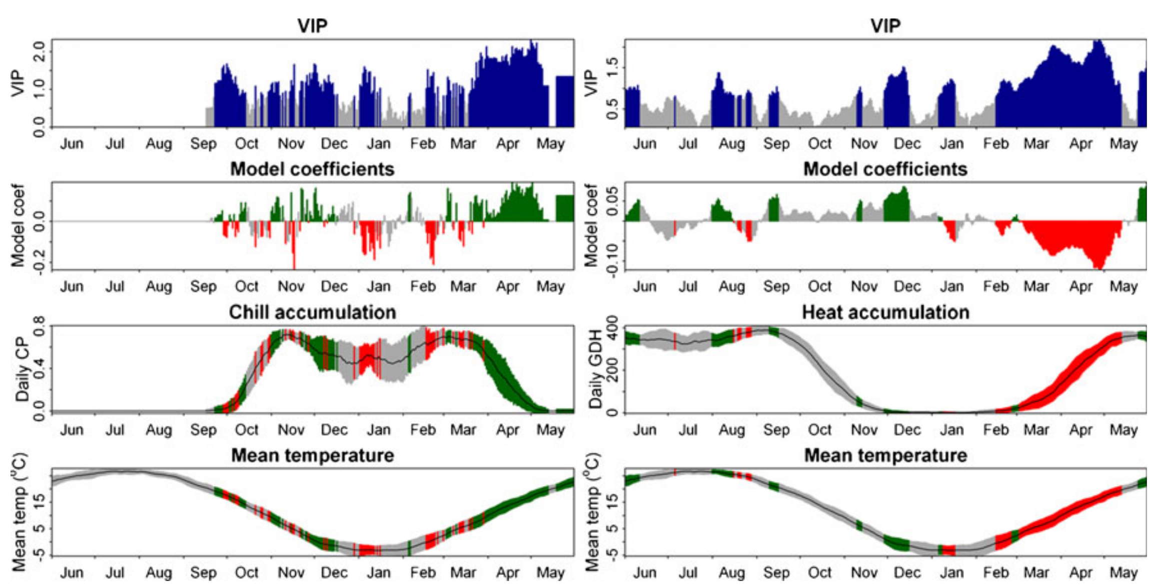


Fig. 2 Results of PLS regression analysis for jujube in Beijing, China using the Dynamic Model and the GDH Model. See caption of Fig. 1 for full explanation

Table 1 Estimates of the chilling and heat requirements of chestnut and jujube at Beijing Summer Palace, using the Dynamic Model, and the Growing Degree Hour (GDH) Model. *CP* Chill portions

Species	Chilling period			Forcing period		
	Start	End	Requirement	Start	End	Requirement
Chestnut	14 September	24 March	93±6 CP	4 January	23 May	17,418±1,983 GDH
Jujube	17 September	19 March	89±6 CP	9 January	13 May	13,619±2,033 GDH

Discussion

Identification of chilling and forcing periods and usefulness of the PLS analysis procedure

Three different approaches were applied to identify the chilling and forcing periods of fruit trees. The simplest approach, commonly used in modeling studies, was the selection of a fixed date for the beginning of chill accumulation based on researcher intuition (Baldocchi and Wong 2008; Darbyshire et al. 2011; Luedeling et al. 2009a, c, d, e; Luedeling and Brown 2011). Controlled experiments involving exposure of individual buds, detached twigs, or plants in containers to different cold and warm conditions have also been used to identify these periods (Aslamarz et al. 2009; Jones et al. 2013; Naor et al. 2003; Ruiz et al. 2007). Recently, long time series of phenological records have been exploited for identifying chill and heat periods using

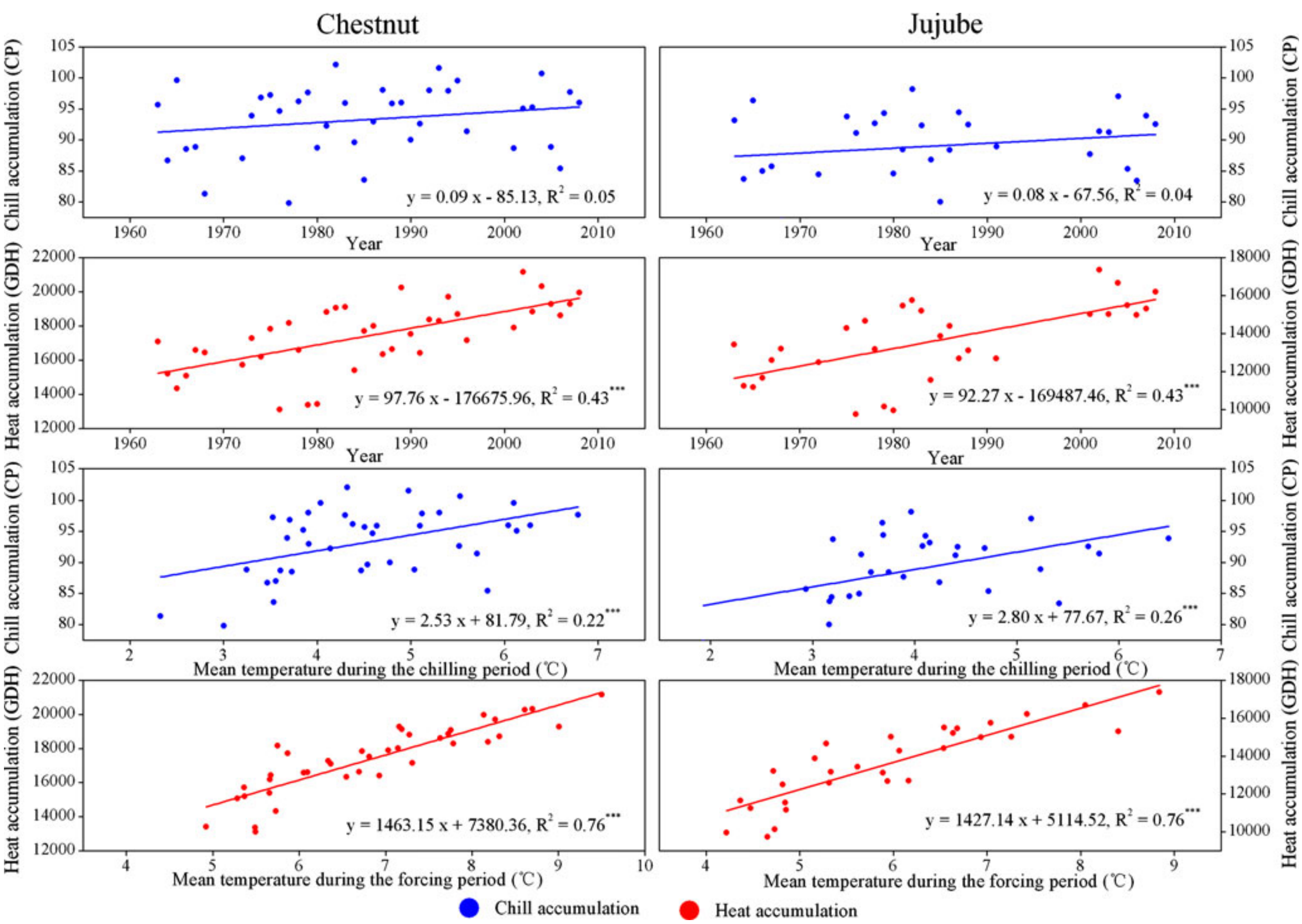


Fig. 3 Trends of chilling and heat accumulation of chestnut and jujube during chilling and forcing periods from 1963 to 2008, and relationships between chilling and heat accumulation and mean temperature during relevant periods. *Blue dots* Chill accumulation, *red dots* heat accumulation. Trends are significant with $^{*}P<0.1$, $^{**}P<0.05$, $^{***}P<0.01$

Fig. 4 Response of flowering dates of chestnut to chilling and heat accumulation during the chilling and forcing periods. Variation in *color* reflects variation in first flowering dates, *black dots* phenological observations between 1963 and 2008

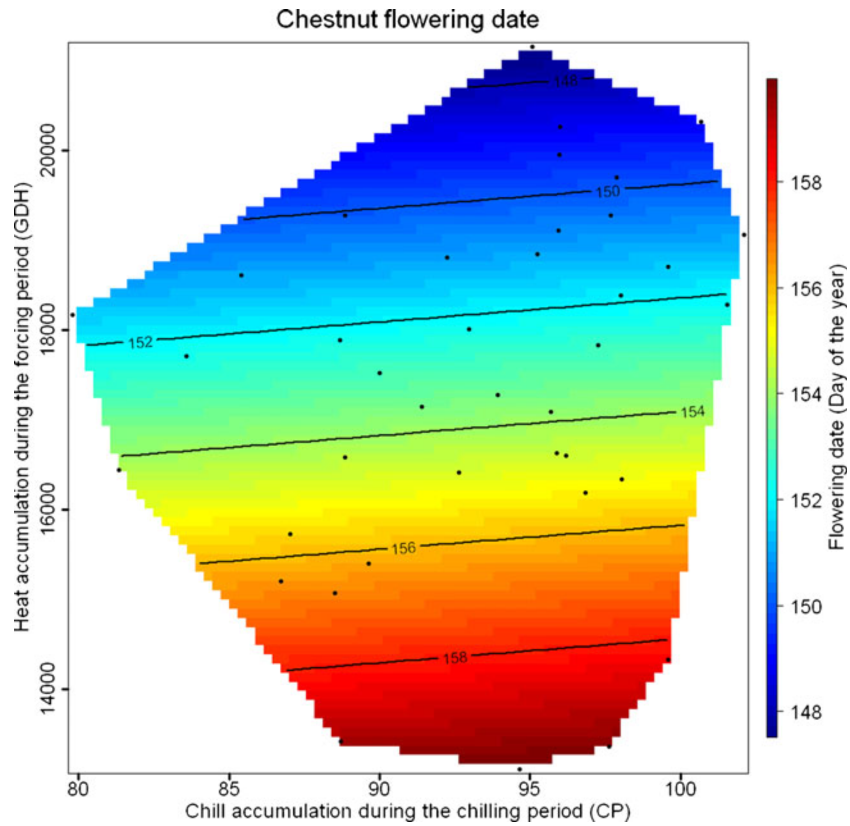
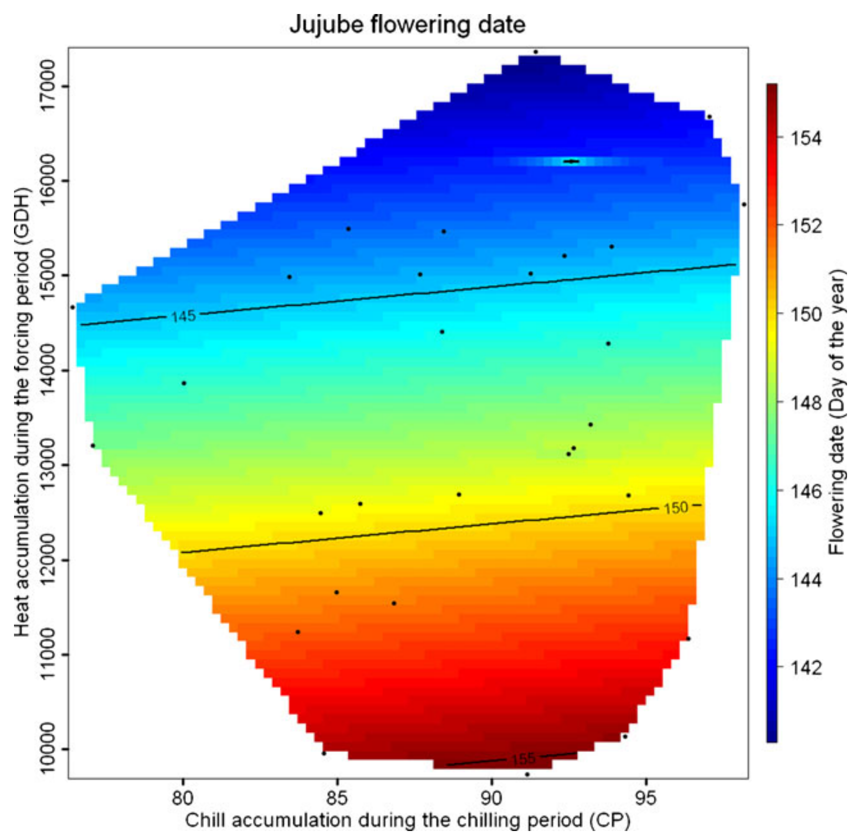


Fig. 5 Response of flowering dates of jujube to chilling and heat accumulation during the chilling and forcing periods. See Fig. 4 for explanation



statistical correlations between phenological dates and temperatures. Based on long-term cherry flowering data and daily temperatures in Klein-Altendorf, Germany, Luedeling et al. (2012) determined the start and end dates of chilling and forcing periods using PLS regression analysis. This statistical method is based on the natural response of flowering to temperature. PLS regression promises to be an efficient strategy for delineating temperature response phases of trees, wherever long phenology records are available.

In our analysis, substitution of daily temperatures with measures of chill and heat allowed clearer delineation of chilling and forcing periods. A significant improvement of our method over an earlier application of PLS on the chestnut data from Beijing (Guo et al. 2013) was the effective detection of chill effects during the cold part of the year. Mean temperatures in Beijing during January and early-February are frequently below 0 °C. Warming during this phase should accelerate chill accumulation, since freezing temperatures are commonly assumed to not be effective for chill accumulation (Luedeling and Brown 2011). While the earlier analysis did not show this effect, it clearly emerged in the present analysis such that the cold period during January and February was included in the chilling phase.

A second interesting result of the PLS analysis was that chilling appeared to accumulate in phases rather than continuously throughout the entire chilling period. This observation has been made before (Afshari et al. 2009), and our results indicate that the common assumption of one continuous chilling period is likely a simplification of a more complex chilling accumulation process. This could have implications for modeling studies on phenology responses to temperature change, none of which, to our knowledge, currently include variation in chill accumulation responses to temperature throughout the winter. While the occurrence of freezing conditions in Beijing offers a possible explanation for variation in chill effectiveness in the present study, such variation has also been observed in studies on walnuts in California (Luedeling and Gassner 2012; Luedeling et al. 2013), where temperatures rarely drop below 0 °C and such effects can be ruled out.

A major advantage of PLS analysis over previous approaches is that the method relies on fewer assumptions about the dormancy breaking process than previous methods. Where phenology models were fitted to historic bloom data, researchers have normally had to select either a parallel or a sequential structure for their model (Darbyshire et al. 2013a). Several studies have also used both structures to decide which one is more appropriate (Chmielewski et al. 2011). In the application of PLS regression, the timing of plant responses to temperature emerges from the analysis results, so that such assumptions are not needed. However, when using unprocessed temperatures as independent variables in the regression, parallel accumulation of chill and heat cannot emerge, because effects of chill and heat accumulation cannot easily be disentangled. Separation of chill and heat accumulation in the set of independent variables, as done in the present study, overcomes this limitation and allows emergence of different temperature response patterns: sequential, parallel or, as observed in this study, a mixture of both. On the flip side of this gained opportunity, however, the method now relies on horticultural chill and heat models, which are relatively coarse approximations of the physiological processes. This introduces a new source of error, which is difficult to quantify.

Temporal succession of chilling and forcing periods

It is commonly assumed that chilling and forcing requirements are fulfilled sequentially, with heat only being effective after sufficient chill has accumulated (Cannell and Smith 1983; Cesaraccio et al. 2004; Fuchigami and Nee 1987; Rea and Eccel 2006). However, parallel models with overlapping chilling and forcing phases have also been suggested (Hänninen 1990, 1987; Kramer 1994). The decision about which type of model to use is often made a priori in phenology modeling studies, and models are then fitted to available data. In PLS regression, the model structure is an emerging property resulting from the timing of plant responses to temperature cues. Selection of parallel or sequential structure is thus not necessary. On the contrary, results from PLS regression may help clarify which structure is more appropriate for a particular cultivar in a specific place.

In our analysis, chilling and forcing periods appeared to overlap. The chilling period for chestnut was from 14 September to 24 March, while the forcing period was from 4 January to 23 May. The overlap occurred after 3 January and continued until the end of the chilling period, implying that heat accumulation started being effective when only about 50 % of the chilling requirement had been fulfilled. For jujube, the forcing phase appeared to begin when 55 % of chilling requirements were fulfilled. It seemed that parallel accumulation of both chill and heat occurred after a tree's critical chilling requirement had been satisfied (Campoy et al. 2011a).

Our statistical method offers no explanation about the physiological mechanisms involved in the overlap between chilling and forcing, but our results may provide information for dormancy management in orchards. Where growers aim to produce fruits as early in the season as possible, as is common in protected cultivation in China, better knowledge on the earliest time when tree buds become responsive to heat can be useful. Management practices such as warming of tree canopies by covering or heating may start being effective at this time. Our results indicate that for chestnut and jujube, this strategy may show effects well before the chilling period is over.

Climate change impacts on chilling and heat accumulation during relevant periods

Climate change has affected winter chill accumulation in recent decades. Studies at different scales have been conducted to examine these responses. In a fruit growing area in high-altitude oases of Oman, Luedeling et al. (2009a) detected decreases in the number of chilling hours by 1.2–9.5 h per year between 1983 and 2008. Decreasing winter chilling hours (5–26 h per year) were also found for the Central Valley of California (Baldocchi and Wong 2008). Luedeling et al. (2009c, d) also observed and projected substantial decreases in winter chill for this region with different chilling models and climate change scenarios, and pointed out that production of some fruits might no longer be possible in the future. Declining winter chill was also reported in Australia (Hennessy and Clayton-Greene 1995; Darbyshire et al. 2011, 2013b), Egypt (Farag et al. 2010), Southern Brazil (Wrege et al. 2010), the United Kingdom (Sunley et al. 2006), and the Western Cape region of South Africa (Midgley and Lötze 2011). In the cooler growing regions of Germany, in contrast, winter chill has been relatively stable in the past (Luedeling et al. 2011b). In a global context, warm growing regions might experience severe reductions in winter chill as global temperatures increase. In temperate zones, winter chill is likely to remain relatively stable, while cold climate might see increasing chill due to lower incidence of freezing temperature events, which the chill model does not consider effective for chill accumulation (Luedeling et al. 2011a). Trends in available heat accumulation have, to our knowledge, not been studied.

In our analysis, warming during the chilling period apparently led to an increasing tendency in chill accumulation of chestnut and jujube over the past 50 years, which was, however, not statistically significant. The lack of a decline in chill may be caused by the low winter temperatures in Beijing, which often drop below freezing point. Since all chilling models assume that temperatures below 0 °C are not effective for chilling, warming during cold months can increase chill. This appears to have occurred in Beijing. Rising temperatures during the forcing period significantly increased heat accumulation of trees in Beijing. During 1963–2008, heat accumulation of chestnut and jujube significantly increased by 97.8 and 92.3 GDH per year. Since surprisingly little attention has been paid in the scientific literature to past and future trends in heat accumulation, more research on this aspect would be desirable.

Impacts of chilling and heat accumulation on flowering

Flowering is under the control of both chilling and heat. While these two processes are often believed to be independent, there is evidence of correlation between accumulated chilling and heat requirements (Couvillon and Erez 1985). Lower heat requirements have been reported, when abundant chill was accumulated (Alburquerque et al. 2008), and more heat could compensate for insufficient chilling (Harrington et al. 2010; Murray et al. 1989). Some contrary findings have also been reported, indicating no or even a positive correlation between chill and heat requirement (Gao et al. 2012).

We did not find a strong influence of chilling accumulation rates on flowering dates of chestnut or jujube. Our results thus differ from many studies in warmer climates, where chill has been shown to be a main driver of phenology. Egea et al. (2003) reported that the flowering time of some almond cultivars in Spain was determined mainly by chilling requirements, with heat requirements contributing little. Studies involving apricot, almond, pistachio and sweet cherry cultivars showed similar results (Alburquerque et al. 2008; Campoy et al. 2012; Rahemi and Pakkish 2009; Ruiz et al. 2007). However, Alonso et al. (2005) demonstrated that the heat requirements of almond were more important for regulation of flowering than chilling requirements in the cool climate of Zaragoza in northeast Spain. Sparks (1993) reported that bud break of pecan might even occur with no chill accumulated, as long as heat requirements are satisfied. In the cold-winter climate of Beijing, forcing effects were much stronger than those of chilling, in line with previous studies that have attributed changes of flowering dates in Germany and the United Kingdom mainly to variation of heat accumulation in spring (Chmielewski and Rötzer 2001; Fitter and Fitter 2002). It appears that temperature conditions in Beijing were close to optimal for chilling accumulation in much of the winter, with slight warming during some parts of the dormancy season even increasing chill accumulation rates. Since chilling requirements of both species are easily met in all winters under present climate conditions, changes in winter chill are unlikely to cause delays in spring phases in the near future. Impacts due to climate change are thus likely to arise from increased rates of heat accumulation rather than from changes in chill. Consequently, further advances in spring phases seem likely. In some species, such changes have been associated with increased frost risk, but both chestnut and jujube flower so late in the year that this risk should be small. While there is a possibility that an increased rate of heat accumulation could have other negative implications, we currently do not see particular reasons to be concerned about climate change impacts on chestnut and jujube in Beijing.

Conclusions

Wherever long-term temperature and phenology data are available, PLS regression between phenological dates and daily chilling and heat accumulation can be used effectively to delineate chilling and forcing periods and to estimate chilling and heat requirements of temperate trees.

For chestnut and jujube, the forcing periods started when half the chilling requirements were fulfilled. Climate warming affected both chilling and heat accumulation rates during the periods identified as relevant for chilling and heat accumulation. During the past 50 years, heat accumulation of chestnut and jujube increased by 97.8 and 92.3 GDH per year, respectively. Winter chill showed a tendency to increase, but this trend was not strong enough to reject the null hypothesis of no change over time. Flowering dates of chestnut and jujube were determined by heat accumulation, with chilling accumulation contributing a small effect on bloom timing. The most likely reason for this is that chilling requirements of both species were fulfilled easily every year. However, for trees with high chilling requirement, for trees grown in places that are warmer than their original habitat (e.g., species originating from temperate regions that are cultivated in the subtropics and even in the tropics), and for trees exposed to significant temperature increases, future warming may reduce chilling accumulation to the point where spring phenology gets delayed. This may then lead to production losses and even crop failures in temperate fruits and nuts.

Acknowledgments This research was supported by the National Natural Science Foundation of China (NSFC)'s project on "Response of *Rhododendron arboreum* Smith to climate change in Eastern Himalaya" (No: 31270524) and another Key Project of NSFC (No: 41030101). Further support was supplied by the Consultative Group on International Agricultural Research Program 6: Forests, Trees and Agroforestry, and Research Program 7: Climate Change, Agriculture and Food Security. We greatly appreciate the staff in the Institute of Geographic Sciences and Natural Resource Research at the Chinese Academy of Sciences for organizing, collecting and publishing phenology data across China over several decades. We also thank the field editor from the International Journal of Biometeorology and two anonymous reviewers provided constructive comments on earlier drafts of this paper.

References

Afshari H, Tajabadipour A, Hossein H, Mohamadi moghadam M (2009) Determining the chilling requirements of four Pistachio cultivars in Semnan province (Iran). Afr J Agric Res 4:55–59

Alburquerque N, García-Montiel F, Carrillo A, Burgos L (2008) Chilling and heat requirements of sweet cherry cultivars and the relationship between altitude and the probability of satisfying the chill requirements. Environ Exp Bot 64:162–170

Almorox J, Hontoria C, Benito M (2005) Statistical validation of daylength definitions for estimation of global solar radiation in Toledo, Spain. Energy Convers Manag 46:1465–1471

Alonso JM, Ansón JM, Espiau MT, Company RSI (2005) Determination of endodormancy break in almond flower buds by a correlation model using the average temperature of different day intervals and its application to the estimation of chill and heat requirements and blooming date. J Am Soc Hortic Sci 130:308–318

Anderson JL, Richardson EA, Kesner CD (1986) Validation of chill unit and flower bud phenology models for "Montmorency" sour cherry. Acta Hortic 184:71–78

Aslamarz AA, Vahdati K, Rahemi M, Hassani D (2009) Estimation of chilling and heat requirements of some Persian walnut cultivars and genotypes. HortScience 44:697–701

Baldocchi D, Wong S (2008) Accumulated winter chill is decreasing in the fruit growing regions of California. Clim Chang 87:153–166

Campoy JA, Ruiz D, Cook N, Allderman L, Egea J (2011a) High temperatures and time to budbreak in low chill apricot "Palsteyn". Towards a better understanding of chill and heat requirements fulfilment. Sci Hortic 129:649–655

Campoy JA, Ruiz D, Egea J (2011b) Dormancy in temperate fruit trees in a global warming context: a review. Sci Hortic 130:357–372

Campoy JA, Ruiz D, Allderman L, Cook N, Egea J (2012) The fulfilment of chilling requirements and the adaptation of apricot (*Prunus armeniaca* L.) in warm winter climates: an approach in Murcia (Spain) and the Western Cape (South Africa). Eur J Agron 37:43–55

Cannell MGR, Smith RI (1983) Thermal time, chill days and prediction of budburst in Picea sitchensis. J Appl Ecol 20:951–963

Cesaraccio C, Spano D, Snyder RL, Duce P (2004) Chilling and forcing model to predict bud-burst of crop and forest species. Agric For Meteorol 126:1–13

Chmielewski F-M, Rötzer T (2001) Response of tree phenology to climate change across Europe. Agric For Meteorol 108:101–112

Chmielewski F-M, Müller A, Bruns E (2004) Climate changes and trends in phenology of fruit trees and field crops in Germany, 1961–2000. Agric For Meteorol 121:69–78

Chmielewski F-M, Blümel K, Henniges Y, Blanke M, Weber RWS, Zoth M (2011) Phenological models for the beginning of apple blossom in Germany. Meteorol Z 20:487–496

Citadin I, Raseira MCB, Herter FG, Baptista da Silva J (2001) Heat requirement for blooming and leafing in peach. HortScience 36:305–307

Couvillon GA, Erez A (1985) Influence of prolonged exposure to chilling temperatures on bud break and heat requirement for bloom of several fruit species. J Am Soc Hortic Sci 110:47–50

Darbyshire R, Webb L, Goodwin I, Barlow S (2011) Winter chilling trends for deciduous fruit trees in Australia. Agric For Meteorol 151:1074–1085

Darbyshire R, Webb L, Goodwin I, Barlow EWR (2013a) Evaluation of recent trends in Australian pome fruit spring phenology. Int J Biometeorol 57:409–421

Darbyshire R, Webb L, Goodwin I, Barlow EWR (2013b) Impact of future warming on winter chilling in Australia. Int J Biometeorol 57:355–366

Dennis FG (2003) Problems in standardizing methods for evaluating the chilling requirements for the breaking of dormancy in buds of woody plants. HortScience 38:347–350

Egea J, Ortega E, Martinez-Gomez P, Dicenta F (2003) Chilling and heat requirements of almond cultivars for flowering. Environ Exp Bot 50:79–85

Elloumi O, Ghrab M, Kessentini H, Ben Mimoun M (2013) Chilling accumulation effects on performance of pistachio trees cv. Mateur in dry and warm area climate. Sci Hortic 159:80–87

Farag AA, Khalil AA, Hassanei MK (2010) Chilling requirement for deciduous fruits under climate change in Egypt. Res J Agric Biol Sci 6:815–822

Fishman S, Erez A, Couvillon GA (1987a) The temperature dependence of dormancy breaking in plants: computer simulation of processes studied under controlled temperatures. J Theor Biol 126:309–321

Fishman S, Erez A, Couvillon GA (1987b) The temperature dependence of dormancy breaking in plants: mathematical analysis of a two-step model involving a cooperative transition. J Theor Biol 124:473–483

Fitter AH, Fitter RSR (2002) Rapid changes in flowering time in British plants. Science 296:1689–1691

Fuchigami LH, Nee C (1987) Degree growth stage model and rest-breaking mechanisms in temperate woody perennials. HortScience 22:836–845

Furrer R, Nychka D, Sain S (2012) Fields: tools for spatial data. R package version 6.7. http://cran.r-project.org/web/packages/fields/

Gao Z, Zhuang W, Wang L, Shao J, Luo X, Cai B, Zhang Z (2012) Evaluation of chilling and heat requirements in Japanese apricot with three models. HortScience 47:1826–1831

Grab S, Craparo A (2011) Advance of apple and pear tree full bloom dates in response to climate change in the southwestern Cape, South Africa: 1973–2009. Agric For Meteorol 151:406–413

Guédon Y, Legave JM (2008) Analyzing the time-course variation of apple and pear tree dates of flowering stages in the global warming context. Ecol Model 219:189–199

Guo L, Dai J, Ranjitkar S, Xu J, Luedeling E (2013) Response of chestnut phenology in China to climate variation and change. Agric For Meteorol 180:164–172

Hänninen H (1987) Effects of temperature on dormancy release in woody plants: implications of prevailing models. Silva Fenn 21:279–299

Hänninen H (1990) Modelling bud dormancy release in trees from cool and temperate regions. Acta For Fenn 213:1–47

Harrington CA, Gould PJ, St. Clair JB (2010) Modeling the effects of winter environment on dormancy release of Douglas-fir. For Ecol Manag 259:798–808

Hennessy K, Clayton-Greene K (1995) Greenhouse warming and vernalisation of high-chill fruit in Southern Australia. Clim Chang 30:327–348

Jones HG, Hillis RM, Gordon SL, Brennan RM (2013) An approach to the determination of winter chill requirements for different Ribes cultivars. Plant Biol 15:18–27

Kramer K (1994) Selecting a model to predict the onset of growth of *Fagus sylvatica*. J Appl Ecol 54:172–181

Lang GA, Early JD, Martin GC, Darnell RL (1987) Endo-, para-, and ecodormancy: physiological terminology and classification for dormancy research. HortScience 22:371–377

Legave JM, Clauzel G (2006) Long-term evolution of flowering time in apricot cultivars grown in southern France: which future impacts of global warming? Acta Horticult 717:47–50

Legave JM, Farrera I, Almeras T, Calleja M (2008) Selecting models of apple flowering time and understanding how global warming has had an impact on this trait. J Hortic Sci Biotechnol 83:76–84

Legave J, Blanke M, Christen D, Giovannini D, Mathieu V, Oger R (2013) A comprehensive overview of the spatial and temporal variability of apple bud dormancy release and blooming phenology in Western Europe. Int J Biometeorol 57:317–331

Linvill DE (1989) Using maximum and minimum temperatures to determine chilling completion. Acta Horticult 254:249–254

Linvill DE (1990) Calculating chilling hours and chill units from daily maximum and minimum temperature observations. HortScience 25:14–16

Lu P, Yu Q, Liu J, Lee X (2006) Advance of tree-flowering dates in response to urban climate change. Agric For Meteorol 138:120–131

Luedeling E (2012) Climate change impacts on winter chill for temperate fruit and nut production: a review. Sci Horticult 144:218–229

Luedeling E (2013) chillR: statistical methods for phenology analysis in temperate fruit trees. R package version 0.54. http://cran.r-project.org/web/packages/chillR/

Luedeling E, Brown PH (2011) A global analysis of the comparability of winter chill models for fruit and nut trees. Int J Biometeorol 55:411–421

Luedeling E, Gassner A (2012) Partial least squares regression for analyzing walnut phenology in California. Agric For Meteorol 158–159:43–52

Luedeling E, Gebauer J, Buerkert A (2009a) Climate change effects on winter chill for tree crops with chilling requirements on the Arabian Peninsula. Clim Chang 96:219–237

Luedeling E, Hale A, Zhang M, Bentley WJ, Dharmasri LC (2009b) Remote sensing of spider mite damage in California peach orchards. Int J Appl Earth Obs Geoinf 11:244–255

Luedeling E, Zhang M, Girvetz EH (2009c) Climatic changes lead to declining winter chill for fruit and nut trees in California during 1950–2099. PLoS ONE 4:e6166

Luedeling E, Zhang M, Luedeling V, Girvetz EH (2009d) Sensitivity of winter chill models for fruit and nut trees to climatic changes expected in California's Central Valley. Agric Ecosyst Environ 133:23–31

Luedeling E, Zhang M, McGranahan G, Leslie C (2009e) Validation of winter chill models using historic records of walnut phenology. Agric For Meteorol 149:1854–1864

Luedeling E, Girvetz EH, Semenov MA, Brown PH (2011a) Climate change affects winter chill for temperate fruit and nut trees. PLoS ONE 6:e20155

Luedeling E, Kunz A, Blanke MM (2011b) More winter chill for fruit trees in warmer winters?—Mehr Chilling für Obstbäume in wärmeren Wintern? Erwerbs-Obstbau 53:145–155

Luedeling E, Kunz A, Blanke MM (2012) Identification of chilling and heat requirements of cherry trees—a statistical approach. Int J Biometeorol. doi:10.1007/s00484-012-0594-y

Luedeling E, Guo L, Dai J, Leslie C, Blanke MM (2013) Differential responses of trees to temperature variation during the chilling and forcing phases. Agric For Meteorol 181:33–42

Meier UH, Graf H, Hack H, Hess M, Kennel W, Klose R, Mappes D, Seipp D, Stauss R, Streif J, Van den Boom T (1994) Phänologische Entwick-lungsstadien des Kernobstes (*Malus domestica* Borkh. Und *Pyrus communis* L.), des Steinobstes (Prunus-Arten), der Johannisbeere (Ribes-Arten) und der Erdbeere (*Fragaria x ananassa* Duch.). Nachrichtenbl Dtsch Pflanzenschutzdienstes 46:141–153

Mevik B-H, Wehrens R, Liland K (2011) PLS: partial least squares and principal component regression. R package version 2.3.0. http://cran.r-project.org/web/packages/pls/

Midgley SJE, Lötze E (2011) Climate change in the western cape of South Africa: trends, projections and implications for chill unit accumulation. Acta Hortic 903:1127–1134

Murray MB, Cannell MGR, Smith RI (1989) Date of budburst of fifteen tree species in Britain following climatic warming. J Appl Ecol 26:693–700

Naor A, Flaishman M, Stern R, Moshe A, Erez A (2003) Temperature effects on dormancy completion of vegetative buds in apple. J Am Soc Hortic Sci 128:636–641

R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. ISBN 3-900051-07-0. http://www.r-project.org/

Rahemi M, Pakkish Z (2009) Determination of chilling and heat requirements of Pistachio (*Pistacia vera* L.) cultivars. Agric Sci China 8:803–807

Ranjitkar S, Luedeling E, Shrestha KK, Guan K, Xu J (2013) Flowering phenology of tree rhododendron along an elevation gradient in two sites in the Eastern Himalayas. Int J Biometeorol 57:225–240

Rea R, Eccel E (2006) Phenological models for blooming of apple in a mountainous region. Int J Biometeorol 51:1–16

Richardson EA, Seeley SD, Walker DR (1974) A model for estimating the completion of rest for Redhaven and Elberta peach trees. HortScience 9:331–332

Rosenzweig C, Karoly D, Vicarelli M, Neofotis P, Wu Q, Casassa G, Menzel A, Root TL, Estrella N, Seguin B, Tryjanowski P, Liu C, Rawlins S, Imeson A (2008) Attributing physical and biological impacts to anthropogenic climate change. Nature 453:353–357

Ruiz D, Campoy JA, Egea J (2007) Chilling and heat requirements of apricot cultivars for flowering. Environ Exp Bot 61:254–263

Sparks D (1993) Chilling and heating model for pecan budbreak. J Am Soc Hortic Sci 118:29–35

Spencer JW (1971) Fourier series representation of the position of the sun. Search 2:172

Sunley RJ, Atkinson CJ, Jones HG (2006) Chill unit models and recent changes in the occurrence of winter chill and spring frost in the United Kingdom. J Hortic Sci Biotechnol 81:949–958

Tao F, Yokozawa M, Xu Y, Hayashi Y, Zhang Z (2006) Climate changes and trends in phenology and yields of field crops in China, 1981–2000. Agric For Meteorol 138:82–92

Wan MW, Liu XZ (1979) Method of phenology observation of China. Science Press, Beijing, pp 1–22

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

Wold S (1995) PLS for multivariate linear modeling. In: van der Waterbeemd H (ed) Chemometric methods in molecular design: methods and principles in medicinal chemistry. Verlag-Chemie, Weinheim, pp 195–218

Wold S, Sjöström M, Eriksson L (2001) PLS-regression: a basic tool of chemometrics. Chemom Intell Lab Syst 58:109–130

Wolfe DW, Schwartz MD, Lakso AN, Otsuki Y, Pool RM, Shaulis NJ (2005) Climate change and shifts in spring phenology of three horticultural woody perennials in northeastern USA. Int J Biometeorol 49:303–309

Wrege MS, Caramori PH, Herter FG, Steinmetz S, Reisser Júnior C, Matzenauer R, Braga HJ (2010) Impact of global warming on the accumulated chilling hours in the sourthern region of Brazil. Acta Hortic 872:31–40

Yu H, Luedeling E, Xu J (2010) Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. Proc Natl Acad Sci USA 107:22151–22156

Yu H, Xu J, Okuto E, Luedeling E (2012) Seasonal response of grasslands to climate change on the Tibetan Plateau. PLoS ONE 7:e49230

Zhang J, Taylor C (2011) The dynamic model provides the best description of the chill process on “Sirora” Pistachio trees in Australia. HortScience 46:420–425

Zhang X, Ge Q, Zheng J, Zhang F (2005) Responses of spring phenology to climate changes in Beijing in last 150 years. Chin J Agrometeorol 26:263–267