

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology



journal homepage: www.elsevier.com/locate/agrformet

Distribution margins as natural laboratories to infer species' flowering responses to climate warming and implications for frost risk



Liang Guo^{a,1}, Jinghong Wang^{b,1}, Mingjun Li^c, Lu Liu^b, Jianchu Xu^{d,e}, Jimin Cheng^a, Chengcheng Gang^a, Qiang Yu^{a,f}, Ji Chen^g, Changhui Peng^{a,h,*}, Eike Luedelingⁱ

^a State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Northwest A&F University, Yangling, 712100, China

^b Shaanxi Meteorological Service Observatory For Economical Crops, Xi'an, 710015, China

^c State Key Laboratory of Crop Stress Biology for Arid Areas, Shaanxi Key Laboratory of Apple, College of Horticulture, Northwest A&F University, Yangling, 712100,

^d Centre for Mountain Ecosystem Studies, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, 650201, China

e World Agroforestry Centre, Nairobi, 00100, Kenya

^f School of Life Sciences, University of Technology Sydney, NSW, 2007, Australia

⁸ Centre for Circular Bioeconomy, Department of Agroecology, Aarhus University, Tjele, 8830, Denmark

^h Department of Biology Science, Institute of Environment Sciences, University of Quebec at Montreal, Montreal, H3C 3P8, Canada

ⁱ INRES- Horticultural Sciences, University of Bonn, Bonn 53121, Germany

ARTICLE INFO

Keywords: Apple flowering phenology Chilling period Climate warming Distribution margin Late frost Partial least squares regression

ABSTRACT

The timing of flowering phenology in most temperate trees results from the interplay of winter chilling and spring heat. As global warming progresses, reduced chilling may gain increasing importance in regulating flowering dates, and eventually offset flowering advances in response to warmer springs. Later onset of flowering events may arise, with negative effects on plant fitness. However, delayed flowering in trees may also reduce the risk from late frosts. Different temperature conditions at both margins of the apple growing areas of Shaanxi in China provide a natural laboratory to examine the responses of trees' flowering phenology and late frost risk to climate warming. We identified the chilling and heat accumulation periods for apples by Partial Least Squares regression of first flowering dates against daily chilling and heat accumulation rates during 2001–2016. We then analyzed the impacts of temperatures during these periods on flowering timing, and evaluated the frost risk for each site. Results indicated increasing importance of chilling temperatures from north to south, with greatest effects determined for the warmest site, where delayed blossom has been observed during the past 16 years. Since late frosts mostly occurred before tree flowering, only minor frost damage was detected for our study areas, with future delays in flowering likely to reduce the frost risk even further. The redistribution of apple trees to nearby locations with cold winters, either northward or uphill, could be a promising strategy to reduce the risk of insufficient chilling and ensure that production remains viable in a warming future.

1. Introduction

Flowering phenology is sensitive to environmental change and therefore a good indicator of changing climate. It has been widely used to track or reconstruct climate changes in both natural and agricultural ecosystems (Aono, 2015; Dunnell and Travers, 2011; Fitter and Fitter, 2002; Mo et al., 2017). Flowering time is a key life-history stage for individual plants, determining reproductive success and hence fitness (Fitter et al., 1995). Changes in flowering timing can also have profound impacts on interactions between different trophic levels of organization within an ecosystem (Thackeray et al., 2016), potentially influencing population dynamics, community composition, and ecosystem service provision (Franks, 2015; Walther et al., 2002). Thus, flowering phenology has emerged recently as a hotspot of ecological and agrometeorological research, especially in the context of global warming.

Temperature is commonly regarded as the primary driver of flowering phenology (Badeck et al., 2004; Chmielewski et al., 2004), especially for trees at middle and high latitudes of the Northern Hemisphere (Hänninen and Kramer, 2007). Many deciduous trees

* Corresponding author.

https://doi.org/10.1016/j.agrformet.2019.01.038

Received 14 July 2018; Received in revised form 26 November 2018; Accepted 26 January 2019 Available online 01 February 2019

0168-1923/ © 2019 Elsevier B.V. All rights reserved.

China

E-mail addresses: changhui_peng@163.com, peng.changhui@uqam.ca (C. Peng).

¹ Both authors contributed equally to this work.

require cold winter temperatures (chilling) to break endodormancy, and warm spring temperatures (forcing) to initiate flower bud unfolding (Chuine, 2000; Guo et al., 2015; Luedeling et al., 2013). Temperature increases in winter might reduce effective chilling accumulation and therefore delay spring flowering. By contrast, warmer conditions in early spring could advance the fulfillment of heat requirements, leading to earlier onset of flowering (Cook et al., 2012; Murray et al., 1989; Shi et al., 2017). In consequence, flowering timing should be expected to respond to temperature variation during both the chilling and forcing periods (Chen et al., 2017; Guo et al., 2015; Luedeling et al., 2013).

In addition to an abundance of reports of advancing flowering events (Ahas et al., 2002; Bock et al., 2014; Fujisawa and Kobayashi, 2010; Ge et al., 2015; Menzel et al., 2006; Miller-Rushing et al., 2007; Templ et al., 2017), some studies have also demonstrated stationary or delayed flowering phenology in response to warming (Fitchett et al., 2014; Jochner and Menzel, 2015; Legave et al., 2015). This indicates that forcing temperatures have so far dominated species' flowering responses to warming, but the observed and predicted decline in chilling (Atkinson et al., 2013; Funes et al., 2016; Luedeling et al., 2011; Vitasse et al., 2011) may gain increasing importance in influencing spring events and eventually buffer or even reverse the advancing trend in plant flowering. More phenological observations at the warm edges of a certain species' distribution area (usually the southern edge in the Northern Hemisphere), where suboptimal chilling conditions frequently prevail, may be a promising strategy to test this hypothesis (Fig. 1a).

While the bloom-delaying effect of insufficient chilling is of high relevance for tree survival and production at the southern edge, it is less likely to be a threat for plants at the northern margin, since chilling requirements are easily fulfilled by current cold-winter conditions (Fig. 1b), and this situation is unlikely to change in the short term. However, advances in flowering times may increase the risk of damage by late frosts (Cannell and Smith, 1986; Chmielewski et al., 2004). Widespread spring frost injuries to natural vegetation and crops have recently been reported (Gu et al., 2008; Hufkens et al., 2012; Vitasse et al., 2018). While it is very likely that overall frost frequency has decreased and will continue to decline in the future (IPCC, 2013), this does not necessarily mean that the risk of late frost damage to trees is decreasing. Frost risk depends on both changes of flowering phenology and the timing of frost occurrences (Schwartz, 1993). If the last occurrence of spring frost advances at a faster rate than flowering time, frost risk is likely to decrease (Ge et al., 2013; Scheifinger et al., 2003). However, increased risk may arise, if flowering advances more quickly than late frosts retreat (Kaukoranta et al., 2010; Vitasse et al., 2018). Given the severe damage that frost during flowering can inflict on trees, evaluations of how changes in late frost occurrence and flowering



timing will play out in the future are worthy of special attention, especially for plants at the cold/northern margin of ecological suitability (Fig. 1b).

Most published studies have focused on phenological changes in natural vegetation (Guo et al., 2013; Legave et al., 2015). Relatively few reports are available on the response of fruit trees to climate warming despite the substantial economic and agricultural significance of such species (Chmielewski et al., 2004). Apple (Malus pumila var. domestica) presents itself as an appropriate study plant due to its worldwide cultivation, sensitivity to frost, and relatively high chilling requirements, which may result in divergent responses of flowering phenology to warming in different climatic regions (Legave et al., 2015). In China, by far the largest apple producer in the world, the highest apple yields are obtained in Shaanxi province (National Bureau of Statistics of China, 2017). In the present study, we observed flowering phenology and investigated spring frost risk in four orchards two located at the northern and southern margins, and two in the central part of the Shaanxi apple growing region, between 2001 and 2016. The long-term and site-specific observations provide a unique opportunity for exploring tree responses to temperature variation. Partial Least Squares (PLS) regression correlating flowering dates with daily chilling and heat accumulation rates was applied to identify the chilling and forcing periods. Our objectives were (i) to test whether chilling temperatures are gaining importance in regulating flowering dates from north to south of the growing region, and (ii) to evaluate the risk of spring frost during the flowering period across different locations, especially for trees at the northern margin. While the sites selected for the present study do not cover the entire gradient of apple production climates found globally, conclusions derived from our limited data can contribute to the development of effective ways to manage and adapt this fruit crop to future warming.

2. Materials and methods

2.1. Site description

In Shaanxi province, 30 counties (outlined in Fig. 2) accounted for 94% of the province's total apple production in 2016 (Shaanxi Provincial Bureau of Statistics, 2017). Among them, four orchards were chosen for this study – two in the central part of the growing areas (i.e., Baishui and Tongchuan) and one each at the northern and southern margins (i.e., Yan'an and Liquan, respectively). Temperature regimes differ between these four sites, especially between the two marginal locations (Fig. 2). From 2001 to 2016, Liquan recorded a mean annual temperature that was 2.5 °C higher than at Yan'an, with the greatest differences observed in winter (3.7 °C). These different temperature

Fig. 1. Hypotheses on how chilling and forcing temperatures affect tree flowering dates, and how late frost damage to trees may change under future warming between the southern and the northern margins of a species' distribution. Red arrows show flowering dates, while blue arrows indicate the timing of late frost occurrences. At the warm margin, reduced chilling would gain increasing importance in controlling tree flowering and delay plant flowering dates in a warmer future. The relative speed of the advancing trends between tree flowering and late frost has profound impacts on plant fitness at the cold margin, where chilling requirements can easily be satisfied. The black bold lines are time axes from left to right (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).



Fig. 2. Location of the study sites within the apple growing region of Shaanxi province in China. Mean monthly temperatures at the four locations are shown in the inset. "T" stands for mean annual temperature between 2001 and 2016.

conditions, combined with the two intermediate sites, provided a unique opportunity for exploring tree responses along a wide temperature gradient.

2.2. Phenology and climate data

For all the locations, first flowering events of apple (*Malus pumila* var. *domestica*) variety "Fuji" were recorded between 2001 and 2016. The day of first flowering was registered when 10% of flowers were open, corresponding to stage 61 on the international BBCH ("Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie") scale for pome fruits (Meier et al., 1994). At all four sites, phenology of the same five trees was observed throughout the study period. The trees were more than 12 years old and of good health, and they had been subjected to similar cultivation measures, when we began the observations in 2001. Thus, the flowering records in this study should be free from anomalies that may affect observations during the juvenile stages of apple trees (Fujisawa and Kobayashi, 2010).

For each site, daily minimum and maximum temperatures during 2001–2016 were obtained from weather stations located closest to the phenological observation site (Table A.1), so that temperatures recorded there should closely mirror conditions within the apple orchards. All daily weather data were provided by the Shaanxi Province Meteorological Bureau. Since most chilling and forcing models require hourly rather than daily temperature inputs, hourly temperatures were generated with the sine-log equations proposed by Linvill (1990). These

equations are based on the premise that the daytime temperature cycle follows a sine curve from sunrise to sunset, while nighttime cooling follows a logarithmic decline:

Daytime:
$$T(t) = (T_{max} - T_{min}) \cdot \sin\left(\frac{\pi \cdot t}{DL + 4}\right) + T_{min}$$
 (1)

Nighttime:
$$T(t) = T_s - \left(\frac{T_s - T_{min}}{\ln (24 - DL)}\right) \cdot \ln(t)$$
 (2)

where T(t) is the temperature at time t; T_{max} and T_{min} represent the maximum and minimum temperature, respectively; DL is day length in hours, and T_s indicates the sunset temperature. Sunrise and sunset time, as well as day length (DL) were calculated using an algorithm described in Almorox et al. (2005) and Spencer (1971).

2.3. Identification of the chilling and forcing periods for apple flowering

Based on the hourly temperature data generated through the above procedure, we calculated daily chilling and heat accumulation at each site for the period 2001–2016. Daily chilling accumulation was quantified using the Dynamic Model (Fishman et al., 1987a, 1987b), which has shown a better performance than other chilling models across a wide range of conditions (Campoy et al., 2011; Guo et al., 2015; Luedeling and Gassner, 2012; Ruiz et al., 2007). The Dynamic Model assumes that chilling accumulation involves two steps. First, an intermediate chilling substance is formed by cool temperatures. Then, moderate temperatures convert this intermediate product into a permanent Chill Portion (CP). CPs are then summed up until the end of the dormancy period. The detailed mathematical functions of the Dynamic Model can be found in Luedeling and Brown (2011). The widely used Growing Degree Hour (GDH) Model (Anderson et al., 1986) was applied to calculate daily heat accumulation. The function to caculate GDH is described below:

$$GDH = \begin{cases} F \cdot \left(\frac{T_u - T_b}{2}\right) \cdot \left(1 + \cos\left(\pi + \pi \cdot \frac{T_i - T_b}{T_u - T_b}\right)\right), \ T_u \ge T_i \ge T_b \\ F \cdot (T_u - T_b) \cdot \left(1 + \cos\left(\frac{\pi}{2} + \frac{\pi}{2} \cdot \frac{T_i - T_u}{T_c - T_u}\right)\right), \ T_c \ge T_i \ge T_u \\ 0, \ T_i > T_c \text{ or } T_i < T_b \end{cases}$$
(3)

where F is a plant stress factor that is commonly set to 1, if no particular stress exists. T_i is the hourly temperature for hour i; T_b , T_u and T_c are the base, optimum, and critical temperatures for tree development, respectively, and set to 4, 25 and 36 °C, as suggested by Anderson et al. (1986); Darbyshire et al. (2013) and Guo et al. (2014).

Partial Least Squares (PLS) regression was used to identify the chilling and forcing periods for apple flowering. Application of this method permitted us to correlate daily chilling and heat accumulation for the 12 months preceding the latest flowering date at each site with annual first flowering timing (the response variable in the PLS regression). In our earlier analyses, the effects of using original vs. smoothed daily chilling/heat accumulation data on PLS outputs have been compared (e.g., Guo et al., 2015; Luedeling and Gassner, 2012). Based on these experiences, a 15-day moving average of daily chilling/heat accumulation was constructed, in which daily accumulation data were replaced by the mean chilling/heat values of the period starting 7 days before and ending 7 days after the respective date. Results indicated that the running average treatment facilitated the delineation of recognizable chilling and forcing stages compared to the use of raw data (Fig. A.1). Thus, in the present study, we first subjected all daily chilling and heat values to a 15-day running average procedure, before feeding them into the PLS model.

The two major outputs of PLS analysis are the variable importance in the projection (VIP) and standardized model coefficients. The VIP indicates how important variation in the value of a particular variable (daily chilling/heat accumulation) is for explaining variation in the dependent variable (i.e., first flowering date in the present study), with the threshold for considering a variable important often set to 0.8 (Wold, 1995). The standardized model coefficients reflect the strength and direction of impacts of daily chilling and heat accumulation on tree flowering dates.

Theoretically, high rates of chilling and heat accumulation during the chilling and forcing periods could advance tree flowering, and these negative correlations should be detected by the PLS analysis. Thus, in the outputs of the PLS procedure, periods with high VIP scores and negative model coefficients, for chilling and heat accumulation respectively, can be regarded as the chilling and forcing periods (Luedeling et al., 2013; Martinez-Lüscher et al., 2017).

2.4. Response patterns of apple flowering to chilling and forcing temperatures between the northern and southern margin

To illustrate the dependency of apple flowering on temperature variation during the chilling and forcing periods at each site, we delineated response surfaces of flowering dates using the Kriging interpolation method in the R package "fields" (Furrer et al., 2013). Kriging, which is a Gaussian regression technique frequently used in spatial analysis, can estimate values at sites where no data are available (Oliver and Webster, 1990). These response surfaces were plotted as contour lines to illustrate the relative importance of chilling and forcing temperatures for tree flowering timing at different sites within the Shaanxi apple growing region.

2.5. Spring frost risk evaluation across different sites

In order to assess the frost risk in the Shaanxi apple growing area, we recently conducted field observations (including surveys of frozen inflorescences and the following yields) and controlled experiments (Fig. A.2). Different levels of freezing treatments (-5 °C⁻0 °C) with different durations were applied to blooming apple flowers (Fig. A.2b), followed by anatomical and morphological analysis of reproductive organs (e.g., petal, stigma, anther and ovary). Results indicated that for Fuji apple in Shaanxi, "frost" conditions are associated with a minimum temperature of -2 °C or lower. More detailed information can be found in Table A.2.

Daily minimum temperatures during 15 March-15 May at each site were used to calculate the frequency of frost events for the period 2001–2016, using -2 °C as a threshold for frost in our analyses. The reasons for the choice of such a time period were that (i) it allowed encompassing all flower durations, and (ii) it includes weeks before and after flowering events, which represent an important time window during which dehardened buds, emerging leaves or developing ovaries are still vulnerable to spring frost (Rodrigo, 2000; Vitasse et al., 2018). Daily minimum temperatures and the duration of low-temperature phases were combined to evaluate frost severity (Table A.2). The hourly temperature values reconstructed above were used to quantify the duration of low temperatures for each location.

All data analyses were performed using R 3.5.0 programming language (R Core Team, 2018). PLS analysis was mainly based on the "pls" and "chillR" packages (Luedeling, 2017; Mevik et al., 2016). Codes used in the present study are provided as supplementary materials to this manuscript.

3. Results

3.1. Chilling and forcing periods for apple flowering across the study sites

In Tongchuan, the latest flowering date during the past 16 years was 19 April. Daily chilling and heat accumulation rates between previous 1 May and 19 April were used as predictor variables in the PLS regression, while response variables were the first flowering dates of apples, expressed in day of the year. Based on the VIP values and standardized model coefficients of the PLS regression, chilling and forcing periods for apple in Tongchuan were clearly delineated (Fig. 3). We interpreted the period between 24 September and 19 February as the chilling accumulation phase, since during this period, most model coefficients were negative and VIP values mostly exceeded 0.8 (Fig. 3a), indicating that high chilling accumulation rates during this period advanced flowering dates. It should be noted that some periods with positive model coefficients or low VIP scores occurred during this phase. Such discontinuities within the chilling accumulation period, which have been reported in several earlier studies (e.g., Guo et al., 2015; Martinez-Lüscher et al., 2017), may be related to occurrence of different physiological processes during the dormancy period, which may be triggered by varying levels of dormancy-associated gene expression during the dormant season (Benmoussa et al., 2017a; Leida et al., 2012). Thus, we considered the entire period (24 September to 19 February) as the chilling stage. In comparison, the delineation of the forcing period was clearer. An almost uninterrupted period of negative model coefficients and high VIP values occurred between 9 February and 10 April (Fig. 3b).

The chilling and forcing periods for apple flowering at the other locations were identified in the same manner, and similar chilling and forcing periods were found among all four sites. For instance, in Liquan, the chilling period extended from 25 September to 10 February, and the forcing period was between 29 January and 9 April (Fig. A.3). For apple trees in the Baishui orchard, chilling occurred during 23 September-19 February, while forcing happened between 9 February and 9 April (Fig. A.4). In Yan'an, the chilling and forcing phases were 28 September until



Fig. 3. Results of Partial Least Squares regression between daily (a) chilling and (b) heat accumulation rates and first flowering dates in Tongchuan during 2001–2016. Blue bars in the top row indicate VIP above 0.8, the threshold for considering variables important. In the second row, red and green bars represent, besides importance, negative and positive model coefficients, respectively. In the third row, bars show the standard deviation of daily chilling and heat accumulation, with colors following the same pattern as for the model coefficients. Shaded areas and dashed lines in the last row indicate the range and the median of first flowering dates, respectively, during the past 16 years. The identified chilling and forcing periods are marked in this figure. "GDH" means Growing Degree Hours (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

20 February, and 7 February to 21 April, respectively (Fig. A.5). Generally, in our four study areas, chilling accumulation started at the end of September, and lasted until mid-to-late February. The forcing period was mostly between early-February and mid-April, showing some overlap with the chilling period.

3.2. Response of flowering phenology to chilling and forcing temperatures along the temperature gradient

Plotting flowering dates of apple trees as a function of mean temperatures during the chilling and forcing periods for each site revealed important differences in the response patterns of flowering dates to both factors (Fig. 4).

In Yan'an, the northern/cold margin of apple growing areas in Shaanxi, with mean chilling temperatures of 2.6 °C, flowering date was almost completely determined by forcing conditions, as indicated by nearly horizontal contour lines in the left part of Fig. 4. Increasing forcing temperatures had a significant bloom-advancing effect. However, temperature increases during the chilling period had negligible impacts on flowering in the Yan'an orchard. Towards the southern/ warm edge of the growing region, the effect of chilling temperatures on tree flowering increased in importance, reaching its greatest influences in Liquan, as was clearly shown by the steeper contour lines in the right part of Fig. 4.

3.3. Spring frost risk assessment across different locations

Daily minimum temperatures during 15 March-15 May at each location were investigated for the period 2001–2016, using -2 °C as the threshold for potential freezing risk. The frequency of freezing events and the extent of frost injury decreased significantly from north to south (Fig. 5). It is worth noting that low temperatures (less than -2 °C) mainly happened before tree flowering. Taking the Yan'an orchard as an instance, only 5 freezing events occurred during all recorded flowering periods (10 April-3 May) of the past 16 years.

Since frost occurring after flowering can severely damage apple reproductive organs and reduce yields, we compared the dates of the above mentioned 5 freezing events with the flowering dates in the corresponding year. Results indicated that between 2001 and 2016, flowers were only exposed to frost once, in 2013 for apples in the Yan'an orchard (Fig. 5). During the other four frost events, flowers opened after the events, so that no frost damage on the inflorescence could arise. These findings indicate that the risk of late frost during the apple flowering period in Shaanxi is relatively small. However, freezing temperatures might cause severe injuries to the emerging or expanding leaves, which appear before the trees bloom.

4. Discussion

4.1. Usefulness of the distribution margin analysis

Temperate fruit trees and ornamental plants are widely grown in environments that are warmer than their traditional ranges (Guy, 2014), motivated by economic benefits and market demands. Only on a few occasions (e.g., Benmoussa et al., 2017a, 2017b; Luedeling and Gassner, 2012) has the performance of trees in such environments been systematically evaluated through long-term site-specific observations. Following the principles of latitude and altitude gradient analyses (e.g., Cornelius et al., 2013; De Frenne et al., 2013), evaluating differences in temperature responses between individuals or populations at the northern and the southern margins of a species' distribution area can generate insights into their climatic sensitivity (e.g., Fig. 4). For instance, the future response pattern of flowering phenology at the northern/cold edge may be similar to what is presently happening at the warm margin of the distribution region. While the detailed physiological processes and genetic mechanisms of plant flowering responses to global warming remain uncertain, systematic evaluation of such "climate analogue locations" (Luedeling, 2012), especially based on long-term site-specific observations may provide valuable insights into future temperature responses and allow collecting data that can be



Fig. 4. Response of flowering dates to mean chilling and forcing temperatures from the northern to the southern margin of the Shaanxi apple growing region. For each location (distinguished by colors), dots indicate the observed combinations of mean chilling and forcing temperatures, while the contour lines illustrate the distribution of flowering dates. The gradient of these lines shows the relative importance of chilling and forcing temperature on flowering dates. Horizontal lines imply an exclusive effect of forcing temperatures, while vertical lines indicate a dominant impact of chilling temperatures on tree flowering dates. "CTmean" stands for mean temperature during the chilling period. "FTmean" denotes the mean forcing temperature.

used to extend the validity of data-driven phenology models into a warmer future. Therefore, we recommend extended observations of phenology responses at the warm margins of species' distributions.

4.2. Rising importance of chilling temperatures for tree flowering

Systematic analyses of climate change impacts on plants have long neglected the consequences of declining chilling accumulation, since most plants have shown advanced spring phenology (Ahas et al., 2002; Bock et al., 2014; Fujisawa and Kobayashi, 2010; Ge et al., 2015; Menzel et al., 2006; Miller-Rushing et al., 2007; Templ et al., 2017). To some extent, it also seems possible to compensate insufficient winter chilling by greater heat accumulation (Harrington et al., 2010). Nevertheless, in the past two decades, field observation records (Cook et al., 2012; Fu et al., 2015; Pope et al., 2013), satellite remote sensing (Jeong et al., 2011; Wang et al., 2011), controlled experiments (Laube et al., 2014) and modelling approaches (Funes et al., 2016; Morin et al., 2009) have suggested that these phenology-advancing trends have slowed, or even been reversed in some warmer regions due to decreasing winter chilling. We also observed increasing importance of chilling temperatures for tree flowering from the northern to southern locations (Fig. 4), while delayed flowering has already occurred in the two southernmost sites during the past 16 years (Fig. A.6).

The most effective temperatures for chilling accumulation are expected to range between 2 °C and 4 °C (Basler and Körner, 2014; Battey, 2000), which is lower than the current mean temperature during chilling accumulation in Liquan (about 6 °C, Fig. 4). In the near future, such as during 2040–2060, mean chilling temperature in most of Shaanxi's apple growing areas may exceed 6 °C, and could be even higher than 8 °C for the southern region (Fig. A.7). Future temperatures during the chilling period may thus be too high to fulfill the chilling requirement of apple trees, which may lead to later bloom or even failure to flower in the future. Thus, chilling may be of primary ecological and production relevance as warming continues. Efforts should thus be made to

breed cultivars with lower chilling requirements, and to develop appropriate measures (e.g., rest breaking chemicals, shading, irrigation and fertilizer application) to cope with insufficient winter chilling. Some alternatives to manage this situation could involve the redistribution of cultivars to locations with colder winters, both northward and uphill. Species' distribution shifts to higher elevations and latitudes in response to climate warming have also been observed in natural ecosystems, both in the distant past and more recently (Davis and Shaw, 2001; Halbritter et al., 2013). This could have large impacts on community composition and ecosystem stability, especially on the survival and growth of trees which depend on winter chilling to initiate flowering, but are located at the southern edge. While the upward and northward expansion of apple orchards may be a necessary strategy to ensure that apple production remains viable in a warming future, some agricultural and ecological consequences induced by this expansion (e.g., the re-distribution of land use patterns, decreases in biodiversity, and loss of valuable habitats) also need careful considerations.

4.3. Risk of late frost in Shaanxi's apple growing region

Spring frost damage is generally associated with a threshold temperature that is common across different species, ranging from -4 °C to 0 °C (Lenz et al., 2016). For instance, -2.2 °C was adopted to evaluate frost risk across the Northern Hemisphere (Schwartz et al., 2006), while -1.7 °C was used to assess the risk of freezing damage in 20 woody species in Illinois, USA (Augspurger, 2013). Our field observations and controlled experiments (Fig. A.2) suggested -2 °C as a reasonable threshold value. This is in line with other apple frost studies, in which daily minimum temperature below -2 °C was set as the condition for frost during the flowering period (Eccel et al., 2009; Kaukoranta et al., 2010). While most studies, especially modeling analyses, have mainly focused on the effects of temperature extremes, other factors influencing the extent of cold injury may be of equal importance. Analyses of the combined effects of the duration of low temperature and different



Fig. 5. Frequency of freezing events and frost severity during 15 March-15 May in 4 locations for the period 2001-2016, with -2 °C regarded as the threshold for frost damage. Red shaded areas mark the flowering period from the earliest first flowering date to the latest last flowering date recorded during the past 16 years. Black and blue dashed lines represent the medians of all the first and last flowering dates, respectively. Dots with different colors indicate different levels of frost severity, as indicated by the minimum temperature and the duration of low-temperature phases (see Table A.2 for more information). Red, vellow and black dots stand for heavy, moderate and slight frost injury, respectively. Frost happening after bloom can cause flower damage, thus the frost events which actually damaged inflorescences are marked by red circles. "Y" means year. "F" and "B" stand for the date of late frost occurrence and the first flowering, respectively (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

levels of freezing temperature (Table A.2) could provide additional insights into the impacts of spring frost on tree flowering and fitness. Additionally, factors including temperature decrease rates (Rodrigo, 2000), the temperature of previous periods (Hufkens et al., 2012), spring temperature variation (Rigby and Porporato, 2008), and other climatic conditions such as wind speed, relative humidity, and cloud cover during the flowering stage, as well as the tree's nutritional status (Rodrigo, 2000), may also affect the extent of frost injuries. The processes and mechanisms involved in frost injury appear to be complex, and more efforts should be undertaken to narrow these knowledge gaps.

Advanced dates of the last spring frost have been widely reported, with a rate of 1.5 days per decade for Northern Hemisphere temperate areas between 1955 and 2002 (Schwartz et al., 2006), and about 0.2 days year⁻¹ in Central Europe during 1951–1997 (Scheifinger et al., 2003). To assess trends in frost risk to plants, the direction and magnitude of phenology shifts should be evaluated in conjunction with such advances (or delays) in the onset of the frost-free period. The combination of these effects can play out in different ways, with different studies reporting increases (Augspurger, 2013; Gu et al., 2008; Vitasse et al., 2018) or decreases in frost risk (Dai et al., 2013; Eccel et al., 2009; Scheifinger et al., 2003), while others have found no changes (Eccel et al., 2009; Schwartz et al., 2006). In our study, frost events mostly occurred before flowering, indicating that the risk of frost damage to apple trees is currently small. Regarding the future suitability of this crop, we showed that the increased importance of declining chilling might partially counteract advances in response to warmer springs, resulting in later onset of flowering phenology (which has already been observed in the two southernmost sites during the past 16

years; Fig. A.6) or warmer conditions before and after tree flowering. If this trend continues, future warming may further reduce the frost risk for apple production in Shaanxi, and allow northward and uphill expansion of the current growing region.

4.4. The role of photoperiod in determining apple trees' flowering phenology

Temperate trees employ sophisticated mechanism to attune flowering to appropriate seasonal conditions. Temperature (including winter chilling and spring forcing) and photoperiod are believed to be the most important cues to drive spring phenology (Duputie et al., 2015; Flynn and Wolkovich, 2018; Körner and Basler, 2010; Laube et al., 2014; Tooke and Battey, 2010). Across studies, temperature is often believed to be the dominant factor that controls spring events (Badeck et al., 2004; Laube et al., 2014); however, some authors have argued that temperature and photoperiod both drive spring phenology (Flynn and Wolkovich, 2018). An extreme case is beech (Fagus), which is controlled by photoperiod, with temperature only exerting a limited effect (Körner and Basler, 2010). In the present study, daily day length among all four sites almost completely overlapped (Fig. A.8a). Comparatively, daily temperature, especially winter chilling temperatures, varied significantly, with a mean difference of 3.5 °C for daily temperature between the southern and the northern site during the chilling period (Fig. A.8b). This indicates that photoperiod cannot explain variation in flowering patterns among these four sites, while variation in temperature regimes is likely to play the primary role.

5. Conclusions

Different temperature regimes between the northern and the southern margin of the apple growing region in Shaanxi provide a natural laboratory to better understand apple flowering response patterns to temperature. Results demonstrated that at the cold and northern margin, the timing of flowering phenology was almost entirely determined by forcing temperatures, with a negligible effect of chilling conditions on tree flowering. However, for apples at the warm/southern edge, flowering dates were controlled by both factors. Chilling temperatures gained increasing importance from north to south. This finding indicates that as warming continues, especially warming in winter, declining chilling accumulation might counteract or even reverse flowering advances that have dominated plant responses to warming so far. To ensure the sustainability of apple production in this region, adaptation strategies to delayed flowering should be developed, including breeding cultivars with low chilling requirements, improving dormancy management measures, and expanding the current growing region northward and uphill. Additionally, analysis of spring frost risk also deserves more attention, despite only minor damage during the past 16 years. Given the severe implications of frost injury for plant fitness and economic viability of orchards, development and dissemination of effective frost protection techniques would likely produce benefits, especially for new orchards established at higher altitudes or latitudes.

Acknowledgements

We greatly appreciate the staff at each phenology observation site for recording apple flowering phenology since 2001, and Shaanxi Province Meteorological Bureau for providing daily climatic data. This research was supported by the National Natural Science Foundation of China (41701606), the National Key Research Program of China (2016YFC0500700), the Project funded by China Postdoctoral Science Foundation (2018T111100), the West Light Foundation of the Chinese Academy of Sciences (K318021507), and the Natural Science Basic Research Plan in Shaanxi Province (2017JQ3015), as well as the program from Northwest A&F University (2452016108). Further support was supplied by the Key Cultivation Project of the Chinese Academy of Sciences. We also thank Dr. Aud Halbritter and an anonymous reviewer who provided constructive comments on an earlier draft of this paper. The authors have no conflicts of interest to declare.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agrformet.2019.01. 038.

References

- Ahas, R., Aasa, A., Menzel, A., Fedotova, V.G., Scheifinger, H., 2002. Changes in European spring phenology. Int. J. Climatol. 22, 1727–1738.
- Almorox, J., Hontoria, C., Benito, M., 2005. Statistical validation of daylength definitions for estimation of global solar radiation in Toledo. Spain. Energ. Convers. Manage. 46, 1465–1471.
- Anderson, J.L., Richardson, E.A., Kesner, C.D., 1986. Validation of chill unit and flower bud phenology models for' Montmorency' sour cherry. Acta Hortic. 184, 71–78.
- Aono, Y., 2015. Cherry blossom phenological data since the seventeenth century for Edo (Tokyo), Japan, and their application to estimation of March temperatures. Int. J. Biometeorol. 59, 427–434.
- Atkinson, C.J., Brennan, R.M., Jones, H.G., 2013. Declining chilling and its impact on temperate perennial crops. Environ. Exp. Bot. 91, 48–62.
- Augspurger, C.K., 2013. Reconstructing patterns of temperature, phenology, and frost damage over 124 years: spring damage risk is increasing. Ecology 94, 41–50.
- Badeck, F.W., Bondeau, A., Bottcher, K., Doktor, D., Lucht, W., Schaber, J., Sitch, S., 2004. Responses of spring phenology to climate change. New Phytol. 162, 295–309. Basler, D., Körner, C., 2014. Photoperiod and temperature responses of bud swelling and
- bud burst in four temperate forest tree species. Tree Physiol. 34, 377–388. Battey, N.H., 2000. Aspects of seasonality. J. Exp. Bot. 51, 1769–1780.

- Benmoussa, H., Ghrab, M., Ben Mimoun, M., Luedeling, E., 2017a. Chilling and heat requirements for local and foreign almond (*Prunus dulcis Mill.*) cultivars in a warm Mediterranean location based on 30 years of phenology records. Agric. For. Meteorol. 239, 34–46.
- Benmoussa, H., Luedeling, E., Ghrab, M., Ben Yahmed, J., Ben Mimoun, M., 2017b. Performance of pistachio (*Pistacia vera* L.) in warming Mediterranean orchards. Environ. Exp. Bot. 140, 76–85.
- Bock, A., Sparks, T.H., Estrella, N., Jee, N., Casebow, A., Schunk, C., Leuchner, M., Menzel, A., 2014. Changes in first flowering dates and flowering duration of 232 plant species on the island of Guernsey. Glob. Change Biol. 20, 3508–3519.
- Campoy, J.A., Ruiz, D., Egea, J., 2011. Dormancy in temperate fruit trees in a global warming context: a review. Sci. Hortic. 130, 357–372.
- Cannell, M.G.R., Smith, R.I., 1986. Climatic warming, spring budburst and forest damage on trees. J. Appl. Ecol. 23, 177–191.
- Chen, X., Wang, L., Inouye, D., 2017. Delayed response of spring phenology to global warming in subtropics and tropics. Agric. For. Meteorol. 234, 222–235.
- Chmielewski, F.M., Muller, 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.
- Chuine, I., 2000. A unified model for budburst of trees. J. Theor. Biol. 207, 337-347.
- Cook, B.I., Wolkovich, E.M., Parmesan, C., 2012. Divergent responses to spring and winter warming drive community level flowering trends. Proc. Natl. Acad. Sci. U.S.A. 109, 9000–9005.
- Cornelius, C., Estrella, N., Franz, H., Menzel, A., 2013. Linking altitudinal gradients and temperature responses of plant phenology in the Bavarian Alps. Plant Biol. 15, 57–69.
- Dai, J., Wang, H., Ge, Q., 2013. The decreasing spring frost risks during the flowering period for woody plants in temperate area of eastern China over past 50 years. J. Geogr. Sci. 23, 641–652.
- Darbyshire, R., Webb, L., Goodwin, I., Barlow, E.W.R., 2013. Evaluation of recent trends in Australian pome fruit spring phenology. Int. J. Biometeorol. 57, 409–421.
- Davis, M.B., Shaw, R.G., 2001. Range shifts and adaptive responses to Quaternary climate change. Science 292, 673–679.
- De Frenne, P., Graae, B.J., Rodriguez-Sanchez, F., Kolb, A., Chabrerie, O., Decocq, G., De Kort, H., De Schrijver, A., Diekmann, M., Eriksson, O., Gruwez, R., Hermy, M., Lenoir, J., Plue, J., Coomes, D.A., Verheyen, K., 2013. Latitudinal gradients as natural laboratories to infer species' responses to temperature. J. Ecol. 101, 784–795.
- Dunnell, K.L., Travers, S.E., 2011. Shifts in the flowering phenology of the northern Great Plains: patterns over 100 years. Am. J. Bot. 98, 935–945.
- Duputie, A., Rutschmann, A., Ronce, O., Chuine, I., 2015. Phenological plasticity will not help all species adapt to climate change. Glob. Change Biol. 21, 3062–3073.
- Eccel, E., Rea, R., Caffarra, A., Crisci, A., 2009. Risk of spring frost to apple production under future climate scenarios: the role of phenological acclimation. Int. J. Biometeorol. 53, 273–286
- Fishman, S., Erez, A., Couvillon, G.A., 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, G.A., 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.
- Fitchett, J.M., Grab, S.W., Thompson, D.I., Roshand, G., 2014. Spatio-temporal variation in phenological response of citrus to climate change in Iran: 1960-2010. Agric. For. Meteorol. 198, 285–293.
- Fitter, A.H., Fitter, R.S.R., 2002. Rapid changes in flowering time in British plants. Science 296, 1689–1691.
- Fitter, A.H., Fitter, R.S.R., Harris, I.T.B., Williamson, M.H., 1995. Relationships between first flowering date and temperature in the flora of a locality in central England. Funct. Ecol. 9, 55–60.
- Flynn, D.F.B., Wolkovich, E.M., 2018. Temperature and photoperiod drive spring phenology across all species in a temperate forest community. New Phytol. 219, 1353–1362.
- Franks, S.J., 2015. The unique and multifaceted importance of the timing of flowering. Am. J. Bot. 102, 1401–1402.
- Fu, Y.H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., Ciais, P., Huang, M., Menzel, A., Uelas, J.P., Song, Y., Vitasse, Y., Zeng, Z., Janssens, I.A., 2015. Declining global warming effects on the phenology of spring leaf unfolding. Nature 2015 (526), 104–107.
- Fujisawa, M., Kobayashi, K., 2010. Apple (Malus pumila var. domestica) phenology is advancing due to rising air temperature in northern Japan. Glob. Change Biol. 16, 2651–2660.
- Funes, I., Aranda, X., Biel, C., Carbó, J., Camps, F., Molina, A.J., de Herralde, F., Grau, B., Savé, R., 2016. Future climate change impacts on apple flowering date in a Mediterranean subbasin. Agric. Water Manage. 164, 19–27.
- Furrer, R., Nychka, D., Sain, S., 2013. Fields: Tools for Spatial Data. R Package Version 6.7. http:// cran.r-project.org/package=fields.
- Ge, Q., Wang, H., Dai, J., 2013. Shifts in spring phenophases, frost events and frost risk for woody plants in temperate China. Clim. Res. 57, 249–258.
- Ge, Q., Wang, H., Rutishauser, T., Dai, J., 2015. Phenological response to climate change in China: a meta-analysis. Glob. Change Biol. 21, 265–274.
- Gu, L., Hanson, P.J., Mac Post, W., Kaiser, D.P., Yang, B., Nemani, R., Pallardy, S.G., Meyers, T., 2008. The 2007 eastern US spring freezes: increased cold damage in a warming world? Bioscience 58, 253–262.
- 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.
- Guo, L., Dai, J., Ranjitkar, S., Yu, H., Xu, J., Luedeling, E., 2014. Chilling and heat requirements for flowering in temperate fruit trees. Int. J. Biometeorol. 58, 1195–1206.
- Guo, L., Dai, J., Wang, M., Xu, J., Luedeling, E., 2015. Responses of spring phenology in

temperate zone trees to climate warming: a case study of apricot flowering in China. Agric. For. Meteorol. 201, 1–7.

Guy, R.D., 2014. The early bud gets to warm. New Phytol. 202, 7-9.

- Halbritter, A.H., Alexander, J.M., Edwards, P.J., Billeter, R., 2013. How comparable are species distributions along elevational and latitudinal climate gradients? Glob. Ecol. Biogeogr. 22, 1228–1237.
- Hänninen, H., Kramer, K., 2007. A framework for modelling the annual cycle of trees in boreal and temperate regions. Silva Fenn. 41, 167–205.
- Harrington, C.A., Gould, P.J., St Clair, J.B., 2010. Modeling the effects of winter en-

vironment on dormancy release of Douglas-fir. For. Ecol. Manage. 259, 798-808. Hufkens, K., Friedl, M.A., Keenan, T.F., Sonnentag, O., Bailey, A., O'Keefe, J., Richardson,

A.D., 2012. Ecological impacts of a widespread frost event following early spring leafout. Glob. Change Biol. 18, 2365–2377.

IPCC, 2013. Climate Change 2013: The Physical Science Basis. Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, USA.

- Jeong, S.J., Ho, C.H., Gim, H.J., Brown, M.E., 2011. Phenology shifts at start vs. end of growing season in temperate vegetation over the Northern Hemisphere for the period 1982-2008. Glob. Change Biol. 17, 2385–2399.
- Jochner, S., Menzel, A., 2015. Does flower phenology mirror the slowdown of global warming? Ecol. Evol. 5, 2284–2295.
- Kaukoranta, T., Tahvonen, R., Ylämäki, A., 2010. Climatic potential and risks for apple growing by 2040. Agric. Food Sci. 19, 144–159.
- Körner, C., Basler, D., 2010. Phenology under global warming. Science 327, 1461–1462. Laube, J., Sparks, T.H., Estrella, N., Hoefler, J., Ankerst, D.P., Menzel, A., 2014. Chilling outweighs photoperiod in preventing precocious spring development. Glob. Change
- Biol. 20, 170–182.
 Legave, J.M., Guédon, Y., Malagi, G., El Yaacoubi, A., Bonhomme, M., 2015.
 Differentiated responses of apple tree floral phenology to global warming in contrasting climatic regions. Front. Plant Sci. 6, 1054.
- Leida, C., Conesa, A., Llácer, G., Luisa Badenes, M., Ríos, G., 2012. Histone modifications and expression of DAM6 gene in peach are modulated during bud dormancy release in a cultivar-dependent manner. New Phytol. 193, 67–80.

Lenz, A., Hoch, G., Körner, C., Vitasse, Y., 2016. Convergence of leaf-out towards minimum risk of freezing damage in temperate trees. Funct. Ecol. 30, 1480–1490.

Linvill, D.E., 1990. Calculating chilling hours and chill units from daily maximum and minimum temperature observations. Hortscience 25, 14–16.

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

- Luedeling, E., 2017. chillR: Statistical Methods for Phenology Analysis in Temperate Fruit Trees. R Package Version 0.66. http://cran.r-project.org/package = chillR.
- Luedeling, E., Brown, P.H., 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, 43–52.

- Luedeling, E., Girvetz, E.H., Semenov, M.A., Brown, P.H., 2011. Climate change affects winter chill for temperate fruit and nut trees. PLoS One 6, e20155.
- Luedeling, E., Guo, L., Dai, J., Leslie, C., Blanke, M.M., 2013. Differential responses of trees to temperature variation during the chilling and forcing phases. Agric. For. Meteorol. 181, 33–42.
- Martinez-Lüscher, J., Hadley, P., Ordidge, M., Xu, X., Luedeling, E., 2017. Delayed chilling appears to counteract flowering advances of apricot in southern UK. Agric. For. Meteorol. 237, 209–218.
- Meier, U.H., 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. Deut. Pflanzenschutzd 46, 141–153.
- Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Küebler, K., Bissolli, P., Braslavská, O.G., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, A., Defila, C., Donnelly, A., Filella, Y., Jatcza, K., Måge, F., Mestre, A., Nordli, Ø., Peñuelas, J., Pirinen, P., Remišová, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wielgolaski, F.E., Zach, S., Zust, A., 2006. European phenological response to climate change matches the warming pattern. Glob. Change Biol. 12, 1969–1976.
- Mevik, B.H., Wehrens, R., Liland, K., 2016. PLS: Partial Least Squares and Principal Component Regression. R Package Version 2.6.0. http://cran.r-project.org/ package = pls.

- Miller-Rushing, A.J., Katsuki, T., Primack, R.B., Ishii, Y., Lee, S.D., Higuchi, H., 2007. Impact of global warming on a group of related species and their hybrids: Cherry tree (Rosaceae) flowering at Mt. Takao, Japan. Am. J. Bot. 94, 1470–1478.
- Mo, F., Zhang, J., Wang, J., Cheng, Z.G., Sun, G.J., Ren, H.X., Zhao, X.Z., Cheruiyot, W.K., Kavagi, L., Wang, J.Y., Xiong, Y.C., 2017. Phenological evidence from China to address rapid shifts in global flowering times with recent climate change. Agric. For. Meteorol. 246, 22–30.
- Morin, X., Lechowicz, M.J., Augspurger, C., O' Keefe, J., Viner, D., Chuine, I., 2009. Leaf phenology in 22 North American tree species during the 21st century. Glob. Change Biol. 15, 961–975.

Murray, M.B., Cannell, M.G.R., Smith, R.I., 1989. Date of budburst of fifteen tree species in Britain following climatic warming. J. Appl. Ecol. 26, 693–700.

- National Bureau of Statistics of China, 2017. China Statistical Yearbook. China Stitistical Press, Beijing.
- Oliver, M.A., Webster, R., 1990. Kriging: a method of interpolation for geographical information systems. Int. J. Geogr. Inf. Syst. 4, 313–332.
- Pope, K.S., Dose, V., Da Silva, D., Brown, P.H., Leslie, C.A., Dejong, T.M., 2013. Detecting nonlinear response of spring phenology to climate change by Bayesian analysis. Glob. Change Biol. 19, 1518–1525.
- R Core Team, 2018. R: A Language And Environment For Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rigby, J.R., Porporato, A., 2008. Spring frost risk in a changing climate. Geophys. Res. Lett. 35, 150–152.
- Rodrigo, J., 2000. Spring frosts in deciduous fruit trees morphological damage and flower hardiness. Sci. Hortic. 85, 155–173.
- Ruiz, D., Campoy, J.A., Egea, J., 2007. Chilling and heat requirements of apricot cultivars for flowering. Environ. Exp. Bot. 61, 254–263.
- Scheifinger, H., Menzel, A., Koch, E., Peter, C., 2003. Trends of spring time frost events and phenological dates in Central Europe. Theor. Appl. Climatol. 74, 41–51.
- Schwartz, M.D., 1993. Assessing the onset of spring: a climatological perspective. Phys. Geogr. 14, 536–550.
- Schwartz, M.D., Ahas, R., Aasa, A., 2006. Onset of spring starting earlier across the Northern Hemisphere. Glob. Change Biol. 12, 343–351.
- Shaanxi Provincial Bureau of Statistics, 2017. Shaanxi Statistical Yearbook. China Stitistical Press, Beijing.
- Shi, P., Chen, Z., Reddy, G.V.P., Hui, G., Huang, J., Xiao, M., 2017. Timing of cherry tree blooming: contrasting effects of rising winter low temperatures and early spring temperatures. Agric. For. Meteorol. 240, 78–89.
- Spencer, J.W., 1971. Fourier Series Representation of the Position of the Sun. Search 2,172.
- Templ, B., Templ, M., Filzmoser, P., Lehoczky, A., Bakšienè, E., Fleck, S., Gregow, H., Hodzic, S., Kalvane, G., Kubin, E., Palm, V., Romanovskaja, D., Vučetic, V., Žust, A., Czúcz, B., Team, N.S.P., 2017. Phenological patterns of flowering across biogeographical regions of Europe. Int. J. Biometeorol. 61, 1347–1358.
- Thackeray, S.J., Henrys, P.A., Hemming, D., Bell, J.R., Botham, M.S., Burthe, S., Helaouet, P., Johns, D.G., Jones, I.D., Leech, D.I., Mackay, E.B., Massimino, D., Atkinson, S., Bacon, P.J., Brereton, T.M., Carvalho, L., Clutton-Brock, T.H., Duck, C., Edwards, M., Elliott, J.M., Hall, S.J.G., Harrington, R., Pearce-Higgins, J.W., Høye, T.T., Kruuk, L.E.B., Pemberton, J.M., Sparks, T.H., Thompson, P.M., White, I., Winfield, I.J., Wanless, S., 2016. Phenological sensitivity to climate across taxa and trophic levels. Nature 535, 241–245.
- Tooke, F., Battey, N.H., 2010. Temperate flowering phenology. J. Exp. Bot. 61, 2853–2862
- Vitasse, Y., Francois, C., Delpierre, N., Dufrêne, E., Kremer, A., Chuine, I., Delzon, S., 2011. Assessing the effects of climate change on the phenology of European temperate trees. Agric. For. Meteorol. 151, 969–980.
- Vitasse, Y., Schneider, L., Rixen, C., Christen, D., Rebetez, M., 2018. Increase in the risk of exposure of forest and fruit trees to spring frosts at higher elevations in Switzerland over the last four decades. Agric. For. Meteorol. 248, 60–69.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416, 389–395.
- Wang, X., Piao, S., Ciais, P., Li, J., Friedlingstein, P., Koven, C., Chen, A., 2011. Spring temperature change and its implication in the change of vegetation growth in North America from 1982 to 2006. Proc. Natl. Acad. Sci. U.S.A. 108, 1240–1245.
- 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, Germany, pp. 195–218.