Responses of spring phenology in temperate zone trees to climate warming: A case study of apricot flowering in China

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ABSTRACT

The timing of spring phenology in most temperate zone plants results from the combined effects of both autumn/winter cold and spring heat. Temperature increases in spring can advance spring phases, but warming in autumn and winter may slow the fulfilment of chilling requirements and lead to later onset of spring events, as evidenced by recent phenology delays in response to warming at some locations. As warming continues, the phenology-delaying impacts of higher autumn/winter temperatures may increase in importance, and could eventually attenuate – or even reverse – the phenology-advancing effect of warming springs that has dominated plant responses to climate change so far. To test this hypothesis, we evaluated the temperature responses of apricot bloom at five climatically contrasting sites in China. Long-term records of first flowering dates were related to temperature data at daily resolution, and chilling and forcing periods were identified by Partial Least Squares (PLS) regression of bloom dates against daily chill and heat accumulation rates. We then analyzed the impacts of temperature variation during the chilling and forcing periods on tree flowering dates for each site. Results indicated that in cold climates, spring timing of apricots is almost entirely determined by forcing conditions, with warmer springs leading to earlier bloom. However, for apricots at warmer locations, chilling temperatures were the main driver of bloom timing, implying that further warming in winter might cause delayed spring phases. As global warming progresses, current trends of advancing phenology might slow or even turn into delays for increasing numbers of temperate species.

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1. Introduction

Variation in the phenology of plants and animals is one of the most sensitive ecological responses to climate change (Menzel et al., 2006; Stenseth et al., 2002; Walther et al., 2002). Changes to species' phenology can have a wide range of impacts on ecological processes, agriculture, forestry, food supply, human health, and the global economy (Peñuelas and Filella, 2001). Temperature is the major driver of such changes, as confirmed by numerous experimental studies (Menzel and Fabian, 1999; Price and Waser, 1998; Wolkovich et al., 2012) and literature reviews (Chuine and Cour,

1999; Murray et al., 1989; Parmesan and Yohe, 2003; Peñuelas and Filella, 2001; Root et al., 2003; Walther et al., 2002). Most studies that evaluated species responses to global warming have shown progressive advances in spring phenology (Chmielewski and Rötzer, 2001; Chmielewski et al., 2011, 2004; Fitter and Fitter, 2002; Grab and Craparo, 2011; Legave and Clauzel, 2006; Menzel et al., 2006; Parmesan and Yohe, 2003; Parmesan, 2007; Root et al., 2003; Wolfe et al., 2005). However, some physiological and genetic mechanisms of plants in temperate climates may hinder further advances in spring events (Luedeling et al., 2013b). In fact, delayed spring phenology has been reported in recent years for some species and ecosystems, in spite of clear warming trends. For example, Cook et al. (2012) analyzed plant phenological datasets throughout the temperate regions and found that some species exhibited delayed bloom in spring. Trends toward later bloom were also observed for pistachio in Tunisia and apple in Mediterranean regions (Elloumi et al., 2013; Legave et al., 2013). Delayed leaf

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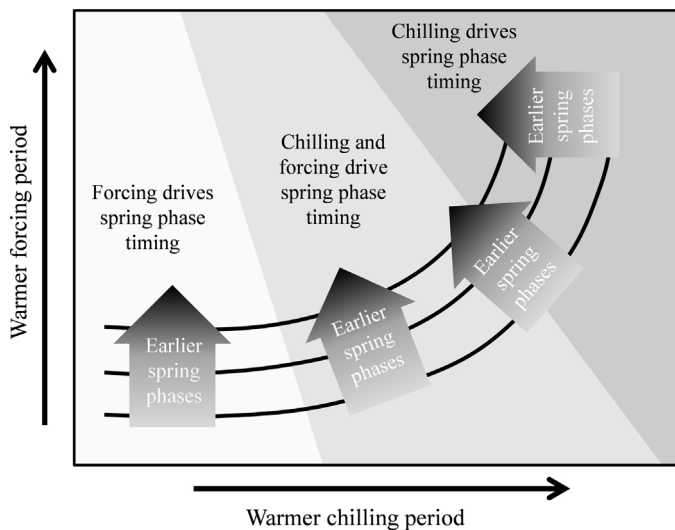
Fig. 1. Theoretical spring phenology responses to warming during the chilling and forcing periods for plants in temperate climates. The slopes of the response curves indicate the relative importance of chilling and forcing temperatures for spring phase timing. Horizontal lines suggest that spring events are dominated by forcing temperatures, with warmer conditions leading to earlier onset of spring phenology. Increasingly steeper slopes indicate that temperature variation during the chilling period gains importance in influencing spring phase timing. Vertical lines mean that the timing of spring phenology is almost exclusively determined by temperatures during the chilling phase.

unrolling in mountain birch and greening of grassland in spring have also been found on the Kola Peninsula in Russia and on the Tibetan Plateau, respectively (Kozlov and Berlina, 2002; Yu et al., 2010).

The timing of spring phenology (e.g. leaf unfolding and flowering) in most temperate zone plants is commonly assumed to respond to two temperature-dependent processes: the accumulation of chilling to the level required for the completion of endodormancy, and the accumulation of heat needed for buds to develop into leaves or flowers in spring (Guo et al., 2014; Luedeling et al., 2013a; Naor et al., 2003). Temperature increases during the latter phase (the forcing period) can advance spring events, but warming during the chilling period may lead to later spring phases due to the delayed fulfilment of chilling requirements (Guo et al., 2013, 2014; Laube et al., 2014; Luedeling et al., 2013a). Nowadays, the abundance of reports on advanced spring phenology (e.g. earlier flowering in Fitter and Fitter, 2002 and Parmesan, 2007; advanced leafing and bloom events in Menzel et al., 2006) indicates that impacts of higher forcing temperatures so far exceed the delaying effect that warming during the chilling period may have. However, as global warming progresses, especially in winter, a point may eventually be reached, where the timing of spring phenology will be dominated by increasing temperatures during the chilling phase, leading to extended chilling periods and in consequence to delayed spring events (Guo et al., 2013; Hart et al., 2014; Luedeling et al., 2013a; Yu et al., 2010). Our research hypothesis is that, as temperatures during plant dormancy increase, the phenology-delaying effect of reduced chill accumulation rates increases in importance relative to the phenology-advancing effect of high temperatures during the forcing phase.

Our hypothesis is illustrated in Fig. 1, where the timing of spring phases is shown as a function of temperatures during the forcing (*y*-axis) and chilling (*x*-axis) phases. Where chilling periods are so cold that temperatures are almost always optimal for chill accumulation (left side of Fig. 1), spring phase timing is entirely driven by variation in temperatures during the forcing phase. However, as the chilling period grows warmer, decreasing chill accumulation

rates begin impacting bloom dates. The phenology-delaying effect of warmer conditions during endodormancy then grows continuously stronger, as temperatures rise further, until the timing of spring phases is determined almost entirely by temperatures during the chilling phase (right side of Fig. 1).

We tested our hypothesis using long-term phenology records of apricots (*Prunus armeniaca* L.) in different climate zones of China. The occurrence of this tree species in locations with widely different climates, where decades of phenological observations coupled with meteorological data at daily resolution have been collected, provides a unique opportunity for exploring tree responses to temperature variation.

2. Materials and methods

2.1. Phenology and temperature records

We analyzed data from five locations in different climatic zones of China. According to China's eco-regional classification, two sites (Jiamusi and Shihezi) were in the mid-temperate zone, two locations (Beijing and Xi'an) in the warm temperate zone and one site (Guiyang) in the mid-subtropical zone (Fig. 2). Temperature regimes at these five sites are shown in Fig. 3.

The Chinese Phenological Observation Network (CPON) has systematically collected extensive data on plant phenology throughout China since the 1960s, using standardized methodologies (Dai et al., 2013; Ge et al., 2011; Wan and Liu, 1979). First bloom data for apricot were collected at all five study locations for between 17 and 39 years during this period (Table 1). First flowering was registered when 10% of flowers were open, corresponding to stage 61 on the BBCH ('Biologische Bundesanstalt Bundessortenamt und Chemische Industrie') scale for stone fruits (Meier et al., 1994). At all study sites, apricots were grown for ornamental purposes and for scientific observation, rather than for production. Tree specimens selected for the botanical gardens at each study site therefore belonged to local provenances rather than common cultivated varieties. Even though no cultivar names have been recorded, it is clear that trees are genetically different, and they very likely differ in chilling and heat requirements as well as in bloom dates. These differences preclude direct comparison of climatic requirements or bloom dates between sites. They should, however, only have a minor impact on the effects of temperatures during the chilling and forcing periods on bloom dates. These effects should vary with temperature during the respective periods according to our initial hypothesis.

Daily minimum and maximum temperatures between 1963 and 2010 for all sites were obtained from the China Meteorological Administration (http://cdc.cma.gov.cn/). Since most common chilling and forcing models require hourly rather than daily temperature data, we constructed idealized daily temperature curves with an hourly resolution from daily temperature extremes as proposed by Linvill (1989, 1990).

2.2. Identification of the chilling and forcing periods

Based on the hourly temperature data, we calculated daily chilling and heat accumulation for each site during the corresponding phenology observation periods. For chill quantification, we chose the Dynamic Model (Fishman et al., 1987a,b), since it has almost always emerged from model comparison studies as the most robust chilling model, and it has shown good capability to explain phenological observations (Campoy et al., 2011; Guo et al., 2014; Luedeling and Gassner, 2012; Luedeling et al., 2009a, 2013a; Ruiz et al., 2007). The widely used Growing Degree Hour (GDH) Model (Anderson et al., 1986) was applied to calculate heat accumulation.
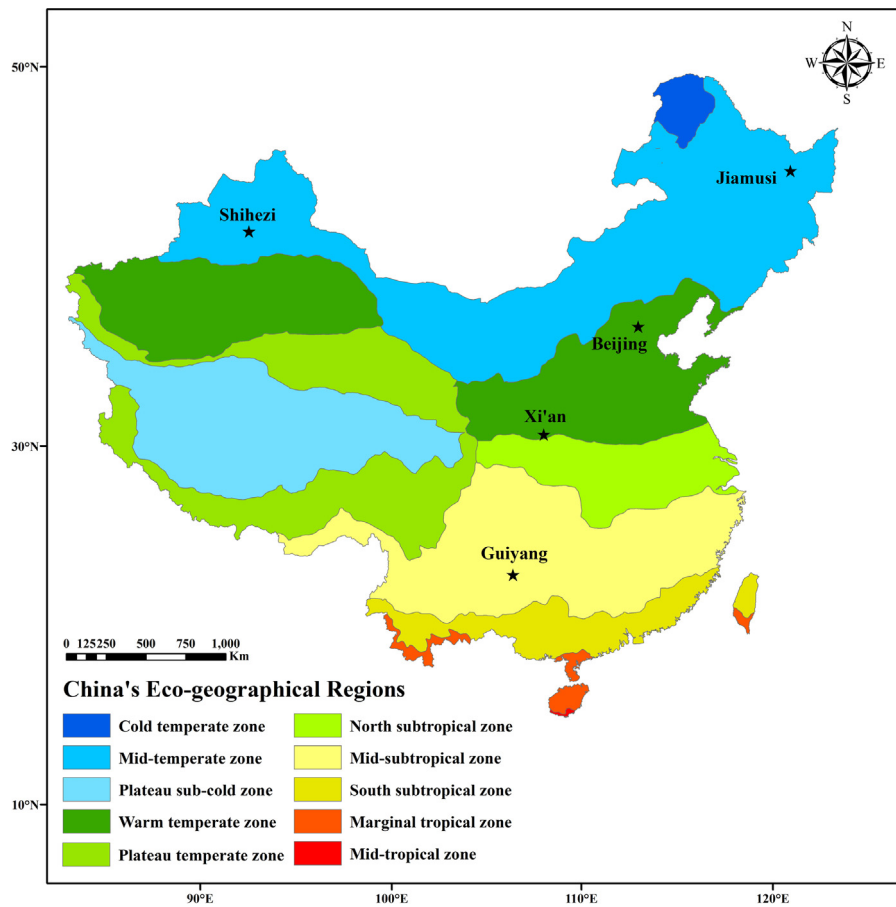
Fig. 2. Locations of observation sites, overlaid on a map of China's eco-geographical regions (issued by the Institute of Geographical Sciences and Natural Resources Research, Chinese Academy of Sciences). The five study locations represent three different climatic regions for apricot cultivation.

Table 1
General information of observation locations in the present study.

Site	Eco-geographical region	Location coordinates	Start year	End year	Observation length
Jiamusi	Mid-temperate zone	46°49′ N, 130°17′ E	1966	1996	23 years
Shihezi	Mid-temperate zone	44°19′ N, 86°03′ E	1963	1996	17 years
Beijing	Warm temperate zone	40°00′ N, 116°16′ E	1963	2010	39 years
Xi'an	Warm temperate zone	34°13′ N, 108°58′ E	1964	2008	28 years
Guiyang	Mid-subtropical zone	26°25′ N, 106°40′ E	1963	2009	23 years

The mathematical functions of these chilling and forcing models were given in Darbyshire et al. (2011, 2013), Guo et al. (2014), Luedeling and Brown (2011) and Luedeling et al. (2009b). Daily chill and heat values were then subjected to a 15-day running mean to ensure emergence of recognizable response patterns between
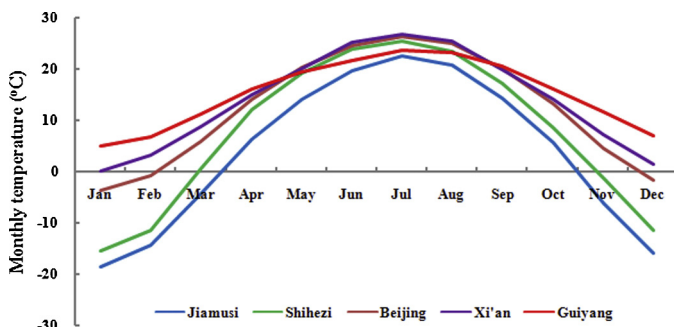

Fig. 3. Mean monthly temperatures at all five observation sites.

the chill/heat units and the first flowering dates of apricot trees in subsequent statistical analyses (Guo et al., 2014; Luedeling et al., 2013a).

Partial Least Squares (PLS) regression analysis was used to identify the chilling and forcing periods (Luedeling and Gassner, 2012; Luedeling et al., 2013a). Unlike many other regression methods, the PLS approach works effectively in situations where the number of independent variables substantially exceeds the number of observations. The common problem of model overfitting is avoided by first constructing a number of latent factors, a kind of principal components, from the predictor variables (and, optionally, from multiple dependent variables) that are then used for fitting the regression model. Application of this method allowed us to correlate daily chill and heat accumulation rates (a total of 730 independent variables) with annual first flowering dates, for which only one data point per location and year was available.

Separate PLS models were fitted for flowering dates at each of the five study locations, using daily chill and heat accumulation for the 12 months preceding typical bloom dates as independent variables. The two major outputs of PLS analysis are the
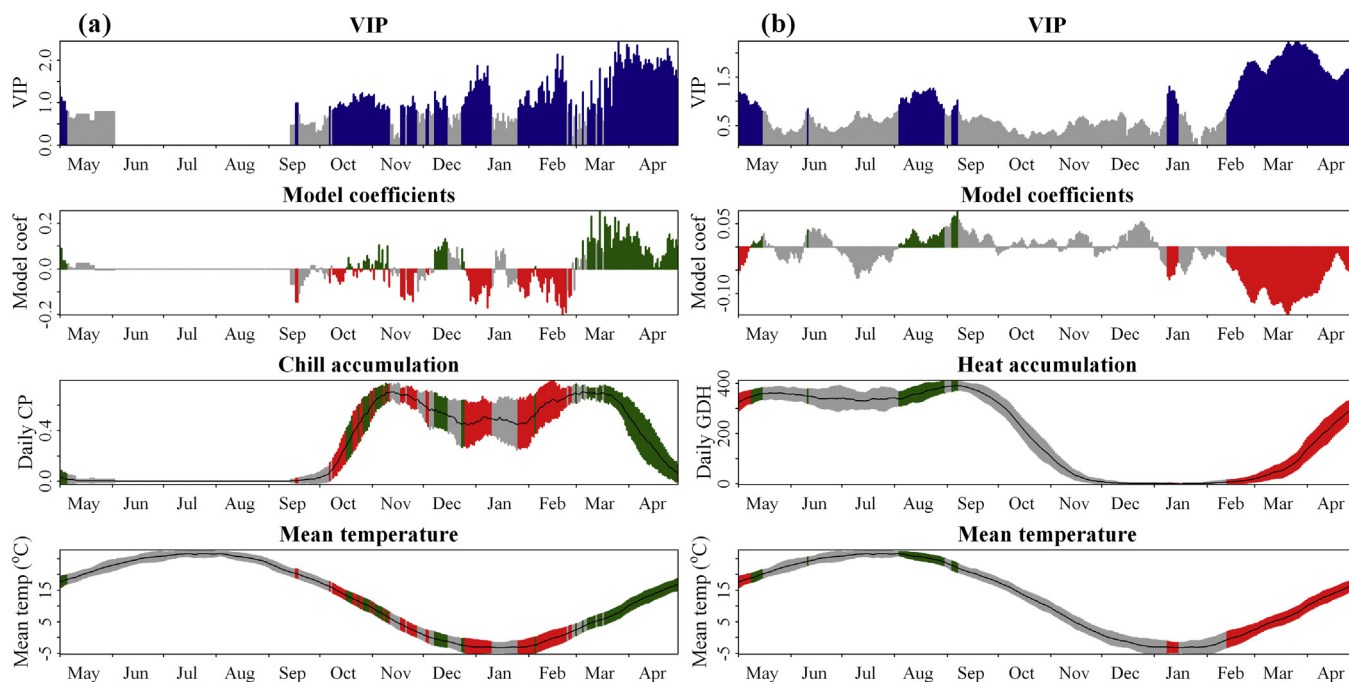
Fig. 4. Results of the Partial Least Squares (PLS) regression analysis for apricot trees in Beijing, China, using the Dynamic Model and the GDH Model for chill and heat accumulation, respectively. Blue bars in the top row indicate that VIP is above 0.8, the threshold value for variable importance. In the second row, red bars signify that model coefficients are negative (and important), while green bars show positive (and important) relationships between flowering, and daily chilling and heat accumulation. In the third and fourth rows, the gray, red and green bars indicate the standard deviation of daily chilling and heat accumulation and mean temperature, respectively. (a) The left half of Fig. 4 is the PLS analysis result for the chilling period and (b) the right half covers the forcing period. "CP" stands for Chill Portions and "GDH" means Growing Degree Hours. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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 a 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 (Guo et al., 2014; Luedeling et al., 2013b).

Interpretation of the PLS output was based on the premise that high rates of chill accumulation during the chilling phase should lead to early bloom, while high rates of heat accumulation during the effective forcing phase should also advance flowering. In the outputs of the PLS procedure, the chilling and forcing phases should thus be marked by high VIP scores and negative model coefficients for the chill and heat accumulation rates, respectively (Guo et al., 2014; Luedeling et al., 2013a). During these phases, high daily chilling and heat accumulation rates are correlated with early dormancy release and bloom timing. This relationship allows delineation of the chilling and forcing phases from the outputs of the PLS procedure.

2.3. Response of apricot flowering to temperature variation during the chilling and forcing periods

To illustrate the impacts of temperature variation during the chilling and forcing periods on apricot flowering at each site, we plotted apricot bloom dates in relation to mean temperatures during both the chilling and forcing periods identified by the PLS procedure. Surfaces of the response of flowering dates were interpolated using the Kriging technique in the R package "fields" (Furrer et al., 2013). Kriging, frequently used in spatial analysis, can estimate unmeasured values and delineate overall trends based on measured data of the relationship between phenological dates and temperatures during both the chilling and forcing phases. Kriging produces a three-dimensional surface, which we show by contour

lines, that expresses the dependency of bloom dates on the two temperature variables. Detailed analysis procedures used in this study are included in the package "chillR" (Luedeling, 2013) for R statistical software (R Core Team, 2013).

3. Results

3.1. Chilling and forcing periods for apricots in different climates

For apricot trees in Beijing, the PLS regression model provided a clear delineation of the chilling and forcing periods (Fig. 4). During the period from September 17 to February 26 (Fig. 4a), most model coefficients were negative and VIP values mostly exceeded 0.8 (the threshold value for variable importance), indicating that high chill accumulation rates during this period were related to early apricot flowering dates. However, this period also contained some short phases with positive model coefficients and high VIP values, during which chill accumulation appeared to be ineffective. Variation in chill effectiveness has been reported before (Guo et al., 2014; Luedeling and Gassner, 2012), and may be related to the occurrence of different physiological processes during the chilling period (Rinne et al., 2011). Since these phases only constituted short interruptions of an overall consistent phase with negative model coefficients, we interpreted the entire period (September 17 to February 26) as the chilling phase for apricots in Beijing. Between January 9 and April 30 (Fig. 4b), model coefficients for heat accumulation rates were consistently negative and almost always important (VIP > 0.8), justifying consideration of this phase as the forcing period, during which daily heat accumulation was correlated with early apricot flowering.

The chilling and forcing periods for apricots at other locations were identified in a similar manner. For apricot trees in Jiamusi, the chilling period extended from August 29 until March 19, and the forcing period was between March 11 and May 12 (Fig. A.1).
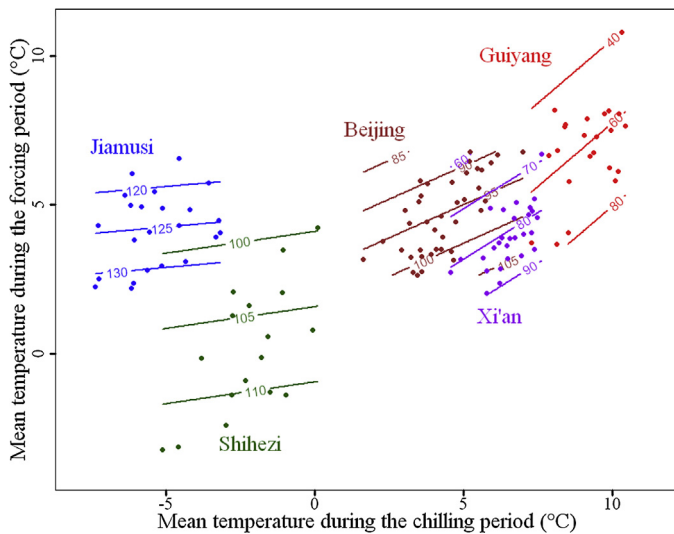
Fig. 5. Response of flowering dates of apricots to chilling and forcing temperatures at five locations in China. Dots indicate the observed flowering dates, while the contour lines describe the overall distribution of apricot bloom dates for each site during the period of the observation record. Slopes of the contour lines indicate the relative importance of chilling and forcing effects (i.e. the steeper the slope, the stronger the bloom-delaying effect of warm chilling phases compared to the bloom-advancing effect of high forcing temperatures). Numbers on the contours indicate the day of the year, on which flowering occurred.

In Shihezi, the chilling and forcing phases were September 1 until March 8, and February 10 to April 18, respectively (Fig. A.2). In Xi'an, chilling occurred between September 23 and February 21, while forcing happened between January 8 and March 22 (Fig. A.3). For Guiyang, the periods of October 25 to February 5 and December 28 to March 12 were identified as the chilling and forcing phases, respectively (Fig. A.4).

3.2. Response of apricot flowering to temperature variation during the chilling and forcing periods

Plotting flowering dates of apricots as a function of mean temperatures during the chilling and forcing periods clearly displayed important differences among apricots grown in different climates, indicating varied responses of apricot flowering to warming (Fig. 5).

In Jiamusi and Shihezi, located in the mid-temperate zone with a cold winter, apricot bloom dates were almost entirely determined by temperatures during the forcing period, as indicated by almost horizontal contour lines in the left part of Fig. 5. Warmer forcing conditions had a significant bloom-advancing effect, while bloom dates were almost completely unrelated to temperature variation during the chilling period at both of these locations.

Tree responses at warmer locations were clearly different. At Beijing, Xi'an, and especially at Guiyang – the warmest site in this study – temperatures during the chilling period showed significant relationships with bloom dates. This is indicated by the slopes of the contour lines for these locations in Fig. 5, which increase with rising temperatures during chill accumulation. Warmer chilling phases were related to later bloom dates for all of these sites, in opposition to the bloom-advancing effect of warmer forcing phases. Along the temperature gradient analyzed, the effect of temperatures during the chilling phase increased in importance, while the relative effect of forcing temperatures gradually declined.

4. Discussion and conclusions

Most studies of the responses of temperate zone plants to temperature increases have shown advancing spring phases

(Chmielewski and Rötzer, 2001; Chmielewski et al., 2011, 2004; Fitter and Fitter, 2002; Grab and Craparo, 2011; Legave and Clauzel, 2006; Menzel et al., 2006; Parmesan and Yohe, 2003; Parmesan, 2007; Root et al., 2003; Wolfe et al., 2005). Only a small number of studies, on a few species and locations, has shown the opposite – delayed spring phases in response to warming (Cook et al., 2012; Elloumi et al., 2013; Kozlov and Berlina, 2002; Legave et al., 2013; Yu et al., 2010). Our results suggest that this apparent contrast can very well be explained by differential responses by plants to warming during the chilling and forcing phases.

According to our research hypothesis, temperate zone plant phenology at cold-winter locations should be determined primarily by temperatures during the forcing period, whereas at sites with warmer winters, temperatures during the chill accumulation period should increase in importance, with warming leading to a delay in spring phases. Our analysis of apricot phenology along a wide temperature gradient supports this hypothesis. While forcing temperatures clearly emerged as the dominant driver of spring phenology in Jiamusi and Shihezi – the coldest locations in our study – spring phase timing at Guiyang was mainly determined by temperatures during the chilling phase. Apricot trees in Beijing and Xi'an showed an intermediate response pattern. Observed responses of apricots to temperature closely resembled the response curves shown in Fig. 1, lending support to our hypothesis.

Earlier results that compared responses of three different combinations of tree species and climate (chestnuts in Beijing, China, cherries in Klein-Altendorf, Germany, and walnuts in Davis, California, United States) showed similar patterns (Luedeling et al., 2013a). Also there, conditions during the chilling phase were much more important in the warm winters of northern California, compared to the colder winters in China and Germany. Near the extreme end of the climatically suitable range of temperate trees, Elloumi et al. (2013) already observed net delays in pistachio phenology in response to warming in Tunisia. Many other studies that have related spring phase timing primarily to spring warming were conducted in cold-winter climates, such as in the United Kingdom (Amano et al., 2010), Germany (Chmielewski et al., 2004), the northeastern United States (Wolfe et al., 2005), Europe (Chmielewski and Rötzer, 2001; Menzel and Fabian, 1999) and Japan (Primack et al., 2009). Net advances in spring phases of temperate zone plants were, on average, 6.0 days $°C^{-1}$ in these studies, with a rate of even 16 days $°C^{-1}$ reported for Japanese apricots in Japan (Doi, 2007). These are faster rates than what has been reported from South Africa, where winters are warmer and phenology of two apple varieties advanced by only 4.2 and 2.4 days $°C^{-1}$ (Grab and Craparo, 2011).

It is important to note that the trees on which phenology was observed were traditional provenances from the respective regions and, thus, not genetically identical. It is likely, and our analysis has confirmed, that they differ in chilling and forcing requirements and in the timing of chilling and forcing periods. Such differences have also been reported for apricots and peaches located in different climatic conditions (Balandier et al., 1993; Campoy et al., 2012). Consequently, bloom dates differed markedly, ranging from early March in Guiyang to early May in Jiamusi. Yet in spite of these differences, the major determinant of the nature of the bloom response to warming (forcing-dominated or chilling-dominated) appeared to be the temperature during the chilling period, with phenology delays in response to warming increasingly likely as autumn and winter temperatures increased.

Our results have implications for interpreting previous studies on the responses of temperate vegetation to increasing temperatures. The non-linear responses to warming that we detected, especially for warming during the chilling phase, imply that the advances in spring phases that currently prevail in most places

might eventually slow or even turn into delays, as warming continues. This seems particularly likely in relatively warm temperate locations, where winter temperatures are already marginal for chill-requiring plants. Observers of temperate phenology should therefore be on the lookout for evidence that advancing spring phase trends could be slowing.

Our study also sheds new light on the considerable number of species that have so far not shown much response to temperature increases (Bai et al., 2011; Bradley et al., 1999; Fitter and Fitter, 2002; Lesica and Kittelson, 2010; McEwan et al., 2011; Menzel et al., 2006). These may either simply be unresponsive to warming–the conventional interpretation – or they may already have exhausted their potential for advancing spring phases, which are now delayed by an equal amount by warmer chilling periods as they are advanced by warmer forcing phases. In the former case, such plants appear at low risk from climate change; in the latter they emerge as the most threatened. More analyses, and ideally some controlled temperature experiments, could help decide which situation is applicable.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agrformet. 2014.10.016.

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