



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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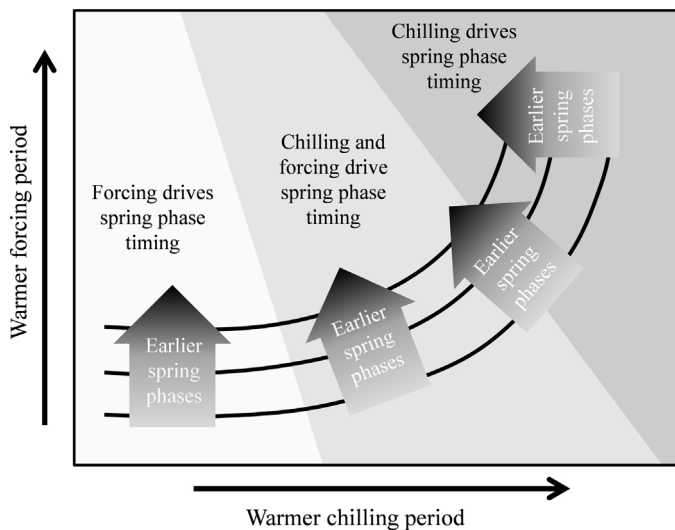


Fig. 1. Theoretical spring phenology responses to warming during the chilling and forcing periods for plants in temperate climates. The slopes of the response curves indicate the relative importance of chilling and forcing temperatures for spring phase timing. Horizontal lines suggest that spring events 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.

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