Spring and Autumn Phenological Patterns of Subtropical Plants and Their Response to Climate Change (Postprint)

Authors: Chen Qin, Tang Xinran, Xue Qianhuai, Wang Xinyang, Du Yanjun

Date: 2022-03-30T21:00:37Z

Abstract

Phenological changes driven by global warming have already exerted significant impacts on biodiversity and ecosystems. Research on subtropical phenology remains relatively limited compared to that in temperate and frigid zones. Studies of autumn phenology are particularly scarce, and whether phenological responses to climate change differ among plant functional groups warrants further investigation. To examine the responses of subtropical plant spring and autumn phenology to climate change and the differences among functional groups, this study utilized 20 years of phenological observation data for 25 woody plant species from Changsha Botanical Garden. Based on the Akaike Information Criterion (AIC), we first selected the optimal temperature and precipitation models for each species, and subsequently employed Wilcoxon rank-sum tests to analyze whether species from different functional groups exhibited consistent responses to temperature. The results showed that: (1) Most species exhibited significant phenological responses to temperature variation in both spring and autumn, with advance rates of leaf unfolding and flowering being 3.76 d/°C and 6.53 d/°C, respectively, and delay rates of leaf coloration and leaf fall being 16.66 d/°C and 3.50 d/°C, respectively. (2) Only a portion of species showed significant responses to precipitation in spring (leaf unfolding phenology: 60%, flowering phenology: 35%) and autumn (leaf coloration phenology: 25%, leaf fall phenology: 13%). (3) Except for leaf unfolding phenology among species with different leaf habits (between evergreen and deciduous), which showed significant differences in climatic responses, no significant differences were found in climatic responses among other functional groups. These findings demonstrate that spring phenology in subtropical regions has advanced significantly, while autumn phenology has been delayed significantly, and that most species from different functional groups in subtropical regions show no significant differences in their temperature responses, suggesting that the impacts of climate change on different functional groups in subtropical regions are largely convergent.

Full Text

Spring and Autumn Phenology Patterns of Subtropical Plants and Their Responses to Climate Change

CHEN Qin, TANG Xinran, XUE Qianhuai, WANG Xinyang, DU Yanjun*

College of Forestry, Hainan University, Haikou 570100, China

Abstract

Phenological changes caused by global warming have already impacted global biodiversity and ecosystems. Compared to temperate and boreal zones, subtropical phenology has been studied relatively less. It remains largely unknown how autumn phenology responds to climate change and how the responses vary among different functional groups. In order to investigate the spring and autumn phenological responses of subtropical plants to climate change and whether the responses vary across different functional groups, we used a 20-year observational phenological dataset for 25 woody species from Changsha Botanical Garden. Based on the Akaike Information Criterion (AIC), we first selected the optimal temperature and precipitation models for each species, then applied Wilcoxon rank-sum tests to analyze whether species' responses to temperature differed among functional groups. The results showed that: (1) Most species exhibited significant responses in both spring and autumn phenology to temperature changes, with leaf-out and flowering advancing at rates of 3.76 d/°C and 6.53 d/°C, respectively, while leaf-coloration and defoliation were delayed by 16.66 d/°C and 3.50 d/°C, respectively. (2) Only some species showed significant responses of spring (leaf-out: 60%, flowering: 35%) and autumn phenology (leaf-coloration: 25%, defoliation: 13%) to precipitation. (3) Except for significant differences in climate responses of leaf-out phenology between species with different deciduousness (evergreen vs. deciduous), no significant differences were found among other functional groups. These results demonstrate that spring phenology in subtropical plants has advanced significantly while autumn phenology has been delayed, and that different functional groups in subtropical regions mostly show convergent responses to temperature, indicating that climate change impacts are largely similar across functional groups.

Keywords: leaf-out, flowering, leaf-coloring, defoliation, functional groups, global warming

---

Plant phenology is widely recognized as one of the most sensitive indicators of ecosystem responses to climate change (Schwartz, 1999; Parmesan, 2006). Phenological changes driven by global warming have profoundly impacted biodiversity and ecosystems worldwide (Jolly et al., 2004; Ahrends et al., 2009). Subtropical regions harbor a substantial proportion of global biodiversity and maintain numerous critical ecological relationships and processes, representing major components of the climate system and global water, carbon, and nutrient cycles (Myers et al., 2000; Bonan, 2008). However, previous research has predominantly focused on temperate plant phenological responses to climate change (Root et al., 2003; Dai et al., 2013; Du et al., 2017), while studies on climate impacts on subtropical plant phenology remain scarce. Understanding phenological changes in subtropical regions is essential for filling critical gaps in scientific knowledge and informing management practices related to climate policy (Peñuelas et al., 2009; Morellato et al., 2016; Du et al., 2019).

Numerous temperate phenology studies have documented earlier spring phenology across the Northern Hemisphere (Morin et al., 2010; CaraDonna et al., 2014; Everill et al., 2014). A meta-analysis of 542 European plant species found that 78% advanced their leaf-out and flowering times (Menzel et al., 2006). In contrast, phenological regulation mechanisms in subtropical regions remain largely unknown (Du et al., 2019). In subtropical zones, temperatures rarely drop below 5 °C, which is considered necessary for fulfilling winter chilling requirements in temperate plants (Zohner & Renner, 2014; Fu et al., 2015; Chuine et al., 2016; Zohner et al., 2016). Consequently, subtropical plants are typically not exposed to winter cold. Recent studies suggest that subtropical woody plants may not be constrained by winter chilling (Qian et al., 2021; Song et al., 2021), and warm autumn-winter temperatures may promote bud development, leading to earlier flowering the following spring (Song et al., 2021).

Precipitation may also influence subtropical plant phenology. Research in the Gutianshan subtropical evergreen broad-leaved forest in Zhejiang found that precipitation can promote spring flowering phenology (Hu et al., 2015). A study of herbarium specimens spanning 116 years on the widespread perennial herb *Spiranthes sinensis* revealed contrasting phenological responses to climate warming between humid and non-humid regions, with flowering advancing in humid areas but delaying in non-humid regions (Song et al., 2020).

Compared to spring phenology, autumn phenology (such as leaf senescence) has received far less attention even in well-studied temperate and polar ecosystems. This gap stems from multiple factors, including the complex drivers of autumn phenology, its prolonged duration, and greater research interest in spring flowering phenology (Gallinat et al., 2015). Nevertheless, autumn phenology holds important ecological and evolutionary significance and represents a critical component of climate warming impacts on ecosystems. In recent years, responses of autumn phenology to climate change have become a research hotspot. Leaf senescence has shown delayed trends with warming temperatures (Gallinat et al., 2015), though the relationship between autumn leaf senescence and autumn temperature appears weaker (Menzel et al., 2003). Drought accelerates leaf-coloration and defoliation, while adequate water conditions delay leaf senescence (Leuzinger et al., 2005). However, studies on subtropical autumn phenology in relation to climate change remain rare (Song et al., 2021). The lack of understanding about environmental drivers of autumn leaf senescence leads to substantial uncertainty in estimating growing seasons in subtropical regions, resulting in inaccurate regional and global carbon uptake and balance estimates (Zani et al., 2020).

Phenological responses to climate change may differ among plant functional groups, yet this aspect remains understudied. Flowering and leaf-out times have been shown to correlate with several important functional traits, including growth form (Molau et al., 2005; Panchen et al., 2014; Du et al., 2015), pollination mode (Du et al., 2015), fruit type (Bolmgren & Lönnberg, 2005; Du et al., 2015), deciduousness (Panchen et al., 2014), and seed dispersal mechanisms (Sargent & Ackerly, 2008; Devaux et al., 2014). However, few studies have reported on differences in phenological responses to climate change among different functional groups.

Based on phenological data from 1963-2008 recorded at the Changsha station of the Chinese Phenology Observation Network, this study addresses three scientific questions: (1) Are subtropical plant spring phenology influenced by temperature and precipitation? (2) Are subtropical plant autumn phenology influenced by temperature and precipitation? (3) Do different functional groups show differential phenological responses to climate change?

1.1.1 Study Area

The Changsha phenological monitoring station in Hunan Province (109.5°E, 24.2°N) is located in the central China plain region. The area has a mean annual temperature of 17.41 °C, with the highest monthly temperature of 29.11 °C in July and the lowest of 5.15 °C in January. Mean annual precipitation is 1,320 mm, concentrated primarily in spring and summer (March–August). The study site belongs to the mid-subtropical humid zone (Zheng et al., 2010).

1.1.2 Phenological Data

We selected phenological observation records from the Chinese Phenology Observation Network (CPON) based on long observation sequences and good continuity. The dataset includes observations of leaf-out onset, first flowering, leaf-coloration, and defoliation periods from 1963-1965, 1973-1974, 1983-1991, and 2003-2007. To meet minimum sample size requirements for statistical analysis, we excluded species with fewer than 8 years of data (Lessard-Therrien et al., 2014; Song et al., 2021). Twenty-five species had sufficient leaf-out data, belonging to 16 families and 24 genera; 20 species had sufficient flowering data (14 families, 20 genera); 16 species had sufficient leaf-coloration data (11 families, 14 genera); and 15 species had sufficient defoliation data (11 families).

1.1.3 Meteorological Data

We used monthly climate data including mean temperature and mean precipitation from 1963-2008, obtained from the Climatic Research Unit 0.5°×0.5° gridded dataset (CRU TS ver. 4.04, <www.cru.uea.ac.uk/>, Harris et al., 2020).

2.1 Research Methods

Phenological observation data were converted to Julian days, transforming annual phenological event dates into the actual number of days since January 1. We performed regression analyses between phenological periods and monthly temperature, 2-month mean temperature, and 3-month mean temperature using time series composed of the 11 months preceding the phenological event and the event month to select the optimal temperature model. This approach follows previous research methods (Beaubien & Freeland, 2000; Miller-Rushing & Primack, 2008; Cook et al., 2012; Mazer et al., 2013; Du et al., 2017). For precipitation, we performed regression analyses between phenological periods and monthly precipitation, 2-month mean precipitation, and 3-month mean precipitation using time series composed of the 2 months preceding the phenological event and the event month to select the optimal precipitation model. Based on the Akaike Information Criterion (AIC), we selected the best models for each species. The slope of the linear regression model between phenological period and temperature was defined as the phenological sensitivity to temperature. Sensitivity to precipitation was defined similarly. We used linear regression to analyze the effects of precipitation and temperature on plant phenology, with steeper slopes indicating stronger phenological responses to climate.

We classified study species into functional groups based on pollination mode (wind vs. insect pollination), fruit type (fleshy vs. dry fruit), and deciduousness (evergreen vs. deciduous). Pollination mode was determined from *Flora of China* (http://frps.eflora.cn/) based on floral morphology: plants with showy perianths were classified as insect-pollinated, while those with reduced or absent perianths, exposed stigmas, abundant pollen, and no nectar were classified as wind-pollinated. Fruit types were divided into fleshy and non-fleshy categories. Non-fleshy fruits included capsules, legumes, nuts, and samaras with dry flesh, while berries, pomes, hesperidia, drupes, and fleshy aggregate fruits were classified as fleshy (Hu et al., 2017). Evergreen species maintain green foliage year-round, whereas deciduous species shed all leaves in autumn-winter or dry seasons. In this study, 18 species were wind-pollinated and 7 were insect-pollinated; 8 species produced fleshy fruits and 13 produced dry fruits; 6 species were evergreen and 19 were deciduous.

We used linear regression to test relationships between phenological event timing and temperature, and Wilcoxon rank-sum tests to analyze whether species' temperature responses differed among functional groups. Because the proportion of species sensitive to precipitation was small, we did not examine differences in precipitation responses among functional groups. All statistical analyses were conducted using R version 4.0.3 (R Core Team, 2020).

3.1 Phenological Patterns

Leaf-out events were concentrated in March and April, with 60% of species leafing out in April. The mean leaf-out date across all species was April 4. The earliest leaf-out species was *Eriobotrya japonica* (March 5) and the latest was *Magnolia grandiflora* (April 27).

Flowering occurred primarily in March (35% of species) and April (50%), with some species flowering in February (15%). The earliest flowering species was *Sassafras tzumu* (February 16) and the latest was *Eriobotrya japonica* (November 9).

Leaf-coloration was concentrated in September and October. The mean leaf-coloration date for 16 species was October 2, with 37.5% changing color in September and 62.5% in October. The earliest leaf-coloration species was *Yulania liliiflora* (September 10) and the latest was *Albizia julibrissin* (October 30).

Defoliation occurred mainly in September, October, and November, with 13% of species shedding leaves in September, 60% in October, and 27% in November. The mean defoliation date for 15 species was October 21. The earliest defoliating species was *Cercis chinensis* (September 22) and the latest was *Ziziphus jujuba* (November 5).

Fig. 1 Phenological patterns. A. Leaf-out; B. Flowering; C. Leaf-coloring; D. Foliage.

2.2 Spring Phenology Responses to Climate Change

For leaf-out phenology, 20 of 25 species (80%) showed significant temperature sensitivity. Only *Firmiana simplex* and *Toona sinensis* exhibited significant positive correlations between leaf-out timing and temperature, while 18 species showed significant negative correlations. The mean temperature sensitivity of leaf-out timing was -3.76 d/°C, ranging from -17.03 d/°C (*Magnolia grandiflora*) to 15.95 d/°C (*Broussonetia papyrifera*). Most species (80%) showed high correlations with January–April temperatures. Fourteen species (60%) showed significant sensitivity to precipitation, all exhibiting significant positive correlations. The mean precipitation sensitivity of leaf-out timing was 0.21 d/mm, ranging from -0.04 d/mm (*Camellia oleifera*) to 0.48 d/mm (*Cunninghamia lanceolata*), with all species showing correlations with January–April precipitation. Sixty percent of species showed sensitivity to the interaction between temperature and precipitation.

For flowering phenology, 17 species (85%) were significantly sensitive to temperature, all showing negative correlations. The mean temperature sensitivity of flowering timing was -6.53 d/°C, ranging from -21.15 d/°C (*Cunninghamia lanceolata*) to 13.38 d/°C (*Sassafras tzumu*), with most species (75%) showing high sensitivity to February–May temperatures. Only 7 species (35%) showed precipitation sensitivity in flowering phenology, and except for *Albizia julibrissin*, all exhibited positive correlations with precipitation. The mean precipitation sensitivity of flowering timing was 0.10 d/mm, ranging from -0.13 d/mm (*Sassafras tzumu*) to 0.51 d/mm (*Cunninghamia lanceolata*), with 75% of species showing correlations with January–April precipitation. Only 35% of species showed sensitivity to temperature-precipitation interactions: *Castanea mollissima*, *Melia azedarach*, *Choerospondias axillaris*, *Cunninghamia lanceolata*, *Yulania denudata*, *Cinnamomum camphora*, and *Cercis chinensis*.

2.3 Autumn Phenology Responses to Climate Change

For leaf-coloration phenology, 12 of 16 species (75%) showed significant temperature sensitivity. Only *Yulania denudata* exhibited a significant negative correlation with temperature, while other species showed significant positive correlations. The mean temperature sensitivity of leaf-coloration timing was 19.90 d/°C, ranging from -11.58 d/°C (*Yulania denudata*) to 37.47 d/°C (*Melia azedarach*). The mean precipitation sensitivity was -0.08 d/mm, with only 4 species (25%) showing significant precipitation sensitivity: *Pterocarya stenoptera*, *Choerospondias axillaris*, *Triadica sebifera*, and *Metasequoia glyptostroboides*. Two species (*Pterocarya stenoptera* and *Yulania liliiflora*) showed sensitivity to temperature-precipitation interactions.

For defoliation phenology, 11 of 15 species (73%) showed significant temperature sensitivity. Five species exhibited significant negative correlations with temperature, while six showed significant positive correlations. The mean temperature sensitivity of defoliation timing was 4.56 d/°C. Only two species (13%) showed precipitation sensitivity in defoliation phenology. Forty-seven percent of species showed sensitivity to temperature-precipitation interactions.

Table 1 Basic information of leaf-out phenology and flowering phenology and parameter estimation of regression model

Table 2 Basic information of leaf-coloring phenology and defoliation phenology and parameter estimation of regression model

2.4 Differences in Phenological Responses Among Functional Groups

No significant relationships were found between leaf-out timing, fruit type, or pollination mode and temperature responses, but species with different deciduousness showed significant differences in temperature responses (Fig. 2). Flowering timing, fruit type, pollination mode, and deciduousness had no significant effects on temperature responses of flowering phenology (Fig. 3). Neither leaf-coloration timing nor defoliation timing showed significant relationships with temperature responses (Fig. 4A, B).

Fig. 2 Response of leaf-out phenology to temperature across different functional groups. A. Earliness of leaf-out date; B. Fruit type; C. Pollination mode; D. Deciduousness.

Fig. 3 Response of flowering phenology to temperature across different functional groups. A. Earliness of flowering date; B. Fruit type; C. Pollination mode; D. Deciduousness.

Fig. 4 Relationship between response of autumn phenology to temperature and earliness of autumn phenology. A. Leaf-coloring phenology; B. Foliage phenology.

3.1 Spring Phenology Responses to Climate Change

Our study found that over 80% of species showed leaf-out and flowering periods regulated by spring temperature, consistent with temperate region studies across Asia (Dai et al., 2014; Chen et al., 2015; Ge et al., 2015), Europe (Menzel et al., 2006; Vitasse et al., 2011; Fu et al., 2014), and North America (Abu-Asab et al., 2001; Miller-Rushing & Primack, 2008; Calinger et al., 2013). The mean flowering response rate in Changsha (-6.53 d/°C) was greater than that in Xi' an at higher latitude (5.99 d/°C) (Dai et al., 2013), contradicting previous understanding that phenological responses are stronger at higher latitudes with more seasonal variation (Jones et al., 2012). Recent studies have found stronger spring phenology response trends in low-latitude woody plants in China compared to high-latitude regions (Chen & Xu, 2012; Dai et al., 2014; Ge et al., 2015), and that phenological responses to climate change weaken with increasing latitude in the widespread herb *Spiranthes sinensis* (Song et al., 2020), supporting our findings.

Our results show that most species' leaf-out and flowering are sensitive to temperatures in the months preceding phenological events, consistent with temperate studies (Menzel et al., 2006; Du et al., 2017; Calinger et al., 2013) and subtropical research (Park & Schwartz, 2015; Wang et al., 2015). This confirms that temperatures in the months preceding phenological events are better predictors than temperatures during the event month (Fitter & Fitter, 2002; Miller-Rushing & Primack, 2008).

We found significant relationships between leaf-out timing and precipitation 1–3 months before the event, consistent with studies in Xi' an showing correlations between leaf-out timing and precipitation one month prior (Bai et al., 2010). However, only one-third of species showed precipitation sensitivity in flowering timing, matching previous findings (Abu-Asab et al., 2001; Sparks et al., 2006). The relationship between phenology and pre-event temperature and precipitation suggests that some species are primarily temperature-driven while others are precipitation-driven, with spring phenology ultimately advancing or delaying depending on whether temperature and precipitation act synergistically or antagonistically (Gordo & Sanz, 2009; Morin et al., 2010).

Our study indicates that most species' leaf-out periods are sensitive to temperature-precipitation interactions, while fewer species show such sensitivity in flowering periods. Temperate studies have found no significant effects of temperature-winter precipitation interactions on leaf-out and flowering phenology (Du et al., 2017). The different response mechanisms between subtropical and temperate plants may explain these discrepancies. Deeper understanding of how temperature-precipitation interactions affect phenology is needed for more effective modeling and prediction, particularly in understudied subtropical ecosystems.

3.2 Autumn Phenology Responses to Climate Change

Over 70% of species showed significant correlations between leaf-coloration/defoliation periods and temperature, with most species exhibiting delayed autumn phenology with warming. Previous studies have documented delayed autumn leaf senescence with temperature increases (Menzel et al., 2006; Piao et al., 2006; Ge et al., 2015), consistent with our results. Precipitation is considered another important factor affecting autumn phenology (Munne-Bosch & Alegre, 2004; Estrella & Menzel, 2006; Anderegg et al., 2013; Dreesen et al., 2014), but our results diverge, showing minimal precipitation effects on leaf senescence phenology in subtropical regions, which appears primarily temperature-driven.

Temperate studies have found that autumn phenology is influenced by combined temperature and precipitation effects (Deng, 2017; Wang & Sang, 2020). We found only a few species showed combined temperature-precipitation effects on leaf-coloration and defoliation, suggesting that environmental drivers may differ in subtropical regions. Our results significantly contribute to understanding relationships between subtropical plant phenology and global climate change.

3.3 Phenological Responses of Different Functional Groups to Climate Change

The relationship between phenological sensitivity to climate and fruit type has rarely been tested. Our study of subtropical species with different fruit types found similar temperature responses between fleshy-fruited and dry-fruited species, though the mechanisms underlying this pattern require further investigation.

This study is the first to examine differences in phenology-temperature sensitivity between insect- and wind-pollinated plants in subtropical regions. Previous studies found that early-flowering species are more sensitive to climate warming (Fitter & Fitter, 2002; Menzel et al., 2006; Calinger et al., 2013), and that wind-pollinated plants typically flower earlier than insect-pollinated plants (Faegri & Pijl, 1979; Du et al., 2015). However, we did not find greater responses in wind-pollinated plants, possibly because pollinator insects experience less extreme low temperatures under climate change, and insect-pollinated plants may have evolved to advance flowering quickly to match pollinator activity and reduce abortion rates (Waser, 1979; Kudo, 2008; Rafferty & Ives, 2011).

Evergreen and deciduous species showed significant differences in leaf-out phenology responses to climate, but no significant differences in flowering phenology responses. In temperate regions, deciduous species leaf out significantly earlier than evergreens (Panchen et al., 2014). In subtropical regions, leaf-out phenology of species with different deciduousness is significantly correlated with temperature (Pan, 2019), consistent with our findings. Both evergreen and deciduous species require stable precipitation before flowering, and when monthly precipitation fluctuates greatly, species may not respond promptly to temperature and other climatic factors (Pan, 2019), resulting in no significant differences in flowering phenology responses among species with different deciduousness.

4 Conclusion

This study provides an important case study of subtropical phenological responses to climate change. Subtropical plants show significantly advanced spring phenology and delayed autumn phenology, changes that will substantially extend the growing season. Research on autumn phenology responses to climate change can deepen understanding of leaf senescence mechanisms and improve predictions of leaf senescence phenology, carbon cycling, and climate change (Zani et al., 2020). Our results demonstrate the importance of both temperature and precipitation for subtropical phenology. Assessing functional group-level variability in plant phenological responses to climate is a critical step toward understanding how climate change alters ecosystems. However, our study shows that most subtropical functional groups do not differ significantly in their temperature responses, indicating largely convergent climate change impacts across functional groups. These results have important implications for future predictions of subtropical phenological events.

References

ABU-ASAB MS, PETERSON PM, SHETLER SG, et al., 2001. Earlier plant flowering in spring as a response to global warming in the Washington, DC, area[J]. Biodivers Conserv, 10(4): 597-612.

AHRENDS HE, ETZOLD S, KUTSCH WL, et al., 2009. Tree phenology and carbon dioxide fluxes: use of digital photography for process-based interpretation at the ecosystem scale[J]. Clim Res, 39(3): 261-274.

ANDEREGG WRL, PLAVCOVÁ L, ANDEREGG LDL, et al., 2013. Drought's legacy: multiyear hydraulic deterioration underlies widespread aspen forest die-off and portends increased future risk[J]. Global Change Biol, 19(4): 1188-1196.

BAI J, GE QS, DAI JH, et al., 2010. Relationship between woody plants phenology and climate factors in Xi'an, China[J]. Chin J Plant Ecol, 34(11): 1274-1282.

BEAUBIEN EG, FREELAND HJ, 2000. Spring phenology trends in Alberta, Canada: links to ocean temperature[J]. Int J Biometeorol, 44(2): 53-59.

BOLMGREN K, LÖNNBERG K, 2005. Herbarium data reveal an association between fleshy fruit type and earlier flowering time[J]. Int J Plant Sci, 166(4): 663-670.

BONAN GB, 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests[J]. Science, 320(5882): 1444-1449.

CALINGER KM, QUEENBOROUGH S, CURTIS PS, 2013. Herbarium specimens reveal the footprint of climate change on flowering trends across north-central North America[J]. Ecol Lett, 16(8): 1037-1044.

CARADONNA PJ, ILER AM, INOUYE DW, 2014. Erratum: Shifts in flowering phenology reshape a subalpine plant community[J]. P Natl Acad Sci USA, 111(13): 4916-4921.

CHEN X, AN S, INOUYE DW, et al., 2015. Temperature and snowfall trigger alpine vegetation green-up on the world' s roof[J]. Global Change Biol, 21(10): 3635-3646.

CHEN X, XU L, 2012. Temperature controls on the spatial pattern of tree phenology in China' s temperate zone[J]. Agr Forest Meteorol, 154: 195-202.

CHUINE I, BONHOMME M, LEGAVE JM, et al., 2016. Can phenological models predict tree phenology accurately in the future? The unrevealed hurdle of endodormancy break[J]. Global Change Biol, 22(10): 3444-3460.

COOK BI, WOLKOVICH EM, PARMESAN C, 2012. Divergent responses to spring and winter warming drive community level flowering trends[J]. P Natl Acad Sci USA, 109(23): 9000-9005.

DAI J, WANG H, GE Q, 2013. Multiple phenological responses to climate change among 42 plant species in Xi' an, China[J]. Int J Biometeorol, 57(5): 749-758.

DAI J, WANG H, GE Q, 2014. The spatial pattern of leaf phenology and its response to climate change in China[J]. Int J Biometeorol, 58(4): 521-528.

DENG LJ, 2017. Response of plant phenology to climate change in North China and Surveillance Camera-based Monitoring of Plant Flowering Phenology[D]. Beijing: China University of Geosciences.

DEVAUX C, LANDE R, PORCHER E, 2014. Pollination ecology and inbreeding depression control individual flowering phenologies and mixed mating[J]. Evolution, 68(11): 3051-3065.

DREESEN FE, DE BOECK HJ, JANSSENS IA, et al., 2014. Do successive climate extremes weaken the resistance of plant communities? An experimental study using plant assemblages[J]. Biogeosciences, 11(1): 109-121.

DU Y, CHEN J, WILLIS CG, et al., 2017. Phylogenetic conservatism and trait correlates of spring phenological responses to climate change in northeast China[J]. Front Ecol Evol, 7(17): 1-10.

DU Y, MAO L, QUEENBOROUGH SA, et al., 2015. Phylogenetic constraints and trait correlates of flowering phenology in the angiosperm flora of China[J]. Global Ecol Biogeogr, 24(8): 928-938.

DU Y, PAN Y, MA K, 2019. Moderate chilling requirement controls budburst for subtropical species in China[J]. Agr Forest Meteorol, 278: 107693.

ESTRELLA N, MENZEL A, 2006. Responses of leaf colouring in four deciduous tree species to climate and weather in Germany[J]. Clim Res, 32(3): 253-267.

EVERILL PH, PRIMACK RB, ELLWOOD ER, et al., 2014. Determining past leaf-out times of New England' s deciduous forests from herbarium specimens[J]. Am J Bot, 101(8): 1293-1300.

FAEGRI K, PIJL L, 1979. The Principles of Pollination Ecology[J]. J Ecol, 3(2).

FITTER AH, FITTER RSR, 2002. Rapid changes in flowering time in British plants[J]. Science, 296(5573): 1689-1691.

FU YH, PIAO S, OP DE BEECK M, et al., 2014. Recent spring phenology shifts in western Central Europe based on multiscale observations[J]. Global Ecol Biogeogr, 23(11): 1255-1263.

FU YH, PIAO S, VITASSE Y, et al., 2015. Increased heat requirement for leaf flushing in temperate woody species over 1980–2012: effects of chilling, precipitation and insolation[J]. Gcb Bioenergy, 21(7): 2687-2697.

GALLINAT AS, PRIMACK RB, WAGNER DL, 2015. Autumn, the neglected season in climate change research[J]. Trends Ecol Evol, 30(3): 169-176.

GE QS, WANG H, RUTISHAUSER T, et al., 2015. Phenological response to climate change in China: a meta-analysis[J]. Global Change Biol, 21(1): 265-274.

GORDO O, SANZ JJ, 2010. Impact of climate change on plant phenology in Mediterranean ecosystems[J]. Gcb Bioenergy, 16(3): 1082-1106.

HARRIS I, OSBORN TJ, JONES P, et al., 2020. Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset[J]. Sci Data, 7(1): 1-18.

HU XL, CHANG ZY, DU YJ, 2017. Effects of pollination mode and fruit type on reproductive phenology of woody plants[J]. Guihaia, 37(3): 315-321.

HU XL, ZHANG YJH, MI XC, et al., 2015. Influence of climate, phylogeny, and functional traits on flowering phenology in a subtropical evergreen broad-leaved forest, East China[J]. Biodivers Sci, 23(05): 601-609.

JOLLY WM, RUNNING SW, 2004. Effects of precipitation and soil water potential on drought deciduous phenology in the Kalahari[J]. Global Change Biol, 10(3): 303-308.

JONES PD, LISTER DH, OSBORN TJ, et al., 2012. Hemispheric and large-scale land-surface air temperature variations: An extensive revision and an update to 2010[J]. J Geophys Res-Planet, 117(D5).

KUDO G, IDA TY, TANI T, 2008. Linkages between phenology, pollination, photosynthesis, and reproduction in deciduous forest understory plants[J]. Ecology, 89(2): 321-331.

LESSARD-THERRIEN M, DAVIES TJ, BOLMGREN K, 2014. A phylogenetic comparative study of flowering phenology along an elevational gradient in the Canadian subarctic[J]. Int J Biometeorol, 58(4): 455-462.

LEUZINGER S, ZOTZ G, ASSHOFF R, et al., 2005. Responses of deciduous forest trees to severe drought in Central Europe[J]. Tree Physiol, 25(6): 641-650.

MAZER SJ, TRAVERS SE, COOK BI, et al., 2013. Flowering date of taxonomic families predicts phenological sensitivity to temperature: implications for forecasting the effects of climate change on unstudied taxa[J]. Am J Bot, 100(7): 1381-1397.

MENZEL A, SPARKS TH, ESTRELLA N, et al., 2006. European phenological response to climate change matches the warming pattern[J]. Global Change Biol, 12(10): 1969-1976.

MENZEL A., 2003. Plant phenological anomalies in Germany and their relation to air temperature and NAO[J]. Climatic Change, 57(3): 243-263.

MILLER-RUSHING AJ, PRIMACK RB, 2008. Global warming and flowering times in Thoreau' s Concord: a community perspective[J]. Ecology, 89(2): 332-341.

MOLAU U, NORDENHÄLL U, ERIKSEN B, 2005. Onset of flowering and climate variability in an alpine landscape: a 10-year study from Swedish Lapland[J]. Am J Bot, 92(3): 422-431.

MORELLATO LPC, ALBERTON B, ALVARADO ST, et al., 2016. Linking plant phenology to conservation biology[J]. Biol Conserv, 195: 60-72.

MORIN X, ROY J, SONIÉ L, et al., 2010. Changes in leaf phenology of three European oak species in response to experimental climate change[J]. New Phytol, 186(4): 900-910.

MUNNÉ-BOSCH S, ALEGRE L, 2004. Die and let live: leaf senescence contributes to plant survival under drought stress[J]. Funct Plant Biol, 31(3): 203-216.

MYERS N, MITTERMEIER RA, MITTERMEIER CG, et al., 2000. Biodiversity hotspots for conservation priorities[J]. Nature, 403(6772): 853-858.

PAN YQ, 2019. The phenological response of woody plants in the evergreen broad-leaved forest of Gutianshan to climate[D]. Chengdu: Chengdu University of Technology.

PANCHEN ZA, PRIMACK RB, NORDT B, et al., 2014. Leaf out times of temperate woody plants are related to phylogeny, deciduousness, growth habit and wood anatomy[J]. New Phytol, 203(4): 1208-1219.

PARK IW, SCHWARTZ MD, 2015. Long-term herbarium records reveal temperature-dependent changes in flowering phenology in the southeastern USA[J]. Int J Biometeorol, 59(3): 347-355.

PARMESAN C., 2006. Ecological and evolutionary responses to recent climate change[J]. Annu Rev Ecol Evol S, 37: 637-669.

PEÑUELAS J, FILELLA I, 2009. Phenology feedbacks on climate change[J]. Science, 324(5929): 887-888.

PIAO S, FANG J, ZHOU L, et al., 2006. Variations in satellite-derived phenology in China' s temperate vegetation[J]. Global Change Biol, 12(4): 672-685.

QIAN S, CHEN X, LANG W, et al., 2021. Examining spring phenological responses to temperature variations during different periods in subtropical and tropical China[J]. Int J Climatol, 41: E3208-E3218.

R Core Team, 2020. R: A Language and Environment for Statistical Computing v. 4.0.3. R Foundation for Statistical Computing, Vienna.

RAFFERTY NE, IVES AR, 2011. Effects of experimental shifts in flowering phenology on plant-pollinator interactions[J]. Ecol Lett, 14(1): 69-74.

ROOT TL, PRICE JT, HALL KR, et al, 2003. Fingerprints of global warming on wild animals and plants[J]. Nature, 421(6918): 57-60.

SARGENT RD, ACKERLY DD, 2008. Plant-pollinator interactions and the assembly of plant communities[J]. Trends Ecol Evol, 23(3): 123-130.

SCHWARTZ MD, 1999. Advancing to full bloom: planning phenological research for the 21st century[J]. Int J Biometeorol, 42(3): 113-118.

SONG Z, DU Y, PRIMACK RB, et al., 2021. Surprising roles of climate in regulating flowering phenology in a subtropical ecosystem[J]. Ecography, 44: 1379-1390.

SONG Z, FU YH, DU Y, et al., 2020. Flowering phenology of a widespread perennial herb shows contrasting responses to global warming between humid and non-humid regions[J]. Funct Ecol, 34(9): 1870-1881.

SONG Z, FU YH, DU Y, et al., 2021. Global warming increases latitudinal divergence in flowering dates of a perennial herb in humid regions across eastern Asia[J]. Agr For Meteorol, 296: 108209.

SPARKS TH, HUBER K, CROXTON PJ, 2006. Plant development scores from fixed-date photographs: the influence of weather variables and recorder experience[J]. Int J Biometeorol, 50(5): 275-279.

VITASSE Y, FRANÇOIS C, DELPIERRE N, et al., 2011. Assessing the effects of climate change on the phenology of European temperate trees[J]. Agr Forest Meteorol, 151(7): 969-980.

WANG H, DAI J, ZHENG J, et al., 2015. Temperature sensitivity of plant phenology in temperate and subtropical regions of China from 1850 to 2009[J]. Int J Climatol, 35(6): 913-922.

WANG M, SANG WG, 2020. The change of phenology of tree and shrub in warm temperate zone and their relationships with climate change[J]. Ecol Sci, 39: 164-175.

WASER NM, 1979. Pollinator availability as a determinant of flowering time in ocotillo (*Fouquieria splendens*)[J]. Oecologia, 39(1): 107-121.

ZANI D, CROWTHER TW, MO L, et al., 2020. Increased growing-season productivity drives earlier autumn leaf senescence in temperate trees[J]. Science, 370(6520): 1066-1071.

ZHENG JY, YIN YH, LI BY, 2010. A new scheme for climate regionalization in China[J]. Acta Geogr Sin, 65(1): 3-12.

ZOHNER CM, BENITO BM, SVENNING JC, et al., 2016. Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants[J]. Nat Clim Change, 6(12): 1120-1123.

ZOHNER CM, RENNER SS, 2014. Common garden comparison of the leaf-out phenology of woody species from different native climates, combined with herbarium records, forecasts long-term change[J]. Ecol Lett, 17(8): 1016-1025.

Note: Figure translations are in progress. See original paper for figures.