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Phenological evidence from China to address rapid shifts in global flowering times with recent climate change

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ABSTRACT

Climate-related flowering phenology has attracted increasing concerns due to its irreplaceable contribution to innovative theory and application of plant phenology at global scale. Most of previous long-term observations were focused on interannual variations in flowering time in Europe and North America, however, very few of them in China were so far reported. Here, we present a meta-analysis through compiling the extended data set from 62 ground-based observations including 136 plant species from 217 observational sites across 8 climatic zones from 1963 to 2013 in China. Quantitative trends in 649 time series (1963–2013) of flowering phases and corresponding temperature changes were analyzed. The results indicated that the beginning, peak and ending of flowering were generally advanced by 2.2, 2.3 and 1.4 days decade^{-1}, respectively, as a result of temperature increase. Flowering duration tended to be prolonged, mainly due to higher temperature sensitivity and greater advancement in the beginning of flowering rather than the ending of flowering. Particularly, the most pronounced advancement in flowering time was observed in east China, up to 3.6 days decade^{-1} as a result of contemporaneous warming. Specifically, flowering time of herbaceous plants displayed an advancing trend by 0.7 day decade^{-1} per degree of increasing latitude. Furthermore, early-flowering species tended to flower earlier than late-flowering ones did. Wind-pollinated and herb species showed greater phenological advancement and temperature sensitivity than insect-pollinated species and other growth forms did. Our results were to some extent different from those in Europe and North America, but played a critical and complementary role at global scale. Our findings and database presented should be powerful complements to address climate-associated flowering shifts and their ecological impacts at global scale.

1. Introduction

Plant phenology, as a sensitive bio-indicator to environmental change, has been widely used to track global climate change in both natural and artificial systems. In most cases, climate-associated plant phenology shifts can serve as a powerful driver in determining the time-sensitive ecological processes and their interactions such as species distribution (Parmesan and Yohe, 2003; Root et al., 2003), population dynamics (Walther et al., 2002), plant-pollinator synchrony (Memmott et al., 2007), and life history evolution (Forrest and Miller-Rushing, 2010). A growing body of literatures confirmed that climate warming has accelerated the onset of spring events such as bud burst, leaf unfolding and first flowering in many terrestrial plant worldwide (Menzel et al., 2001; Ahas et al., 2002; Badeck et al., 2004). In a recent meta-analysis, phenological period was estimated to be advanced by 2.3–2.8 days decade^{-1} in spring events across all the taxa in northern hemisphere (Parmesan, 2007). In southern hemisphere, using terrestrial phenology datasets, Chambers et al. (2013) also detected a consistently earlier spring phenology with increasing temperature.

Flowering time is critical for sexual reproduction of angiosperms, which has been regarded as one of core issues in climate-related phenology (Elzinga et al., 2007). The changes in flowering phases such as timing, duration and abundance will likely affect ecological interactions among plants, pollinators, herbivores, and flower parasites (Memmott et al., 2007; Newnham et al., 2013). For instance, shortened flowering duration may pose a major threat to pollinators, and hence accelerate biodiversity loss, reduce the viability of pollinators and increase seed abortion (Zhao et al., 2013). In contrast, prolonged flowering duration could increase the risk of pollen-related respiratory diseases (Beggs, 2004). Several studies from northern hemisphere

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provided empirical evidences that earlier flowering was closely associated with warming trend over past decades. In England, there existed a strong warming trend in 1990s, and the beginning of flowering was substantially moved up by 15 days in 16% out of 385 plant species in this decade, in comparison with that of earlier decades (Fitter and Fitter, 2002). In Washington region, the beginning of flowering time was significantly advanced by 2.4 days during 1970–2000 when averaged to 100 species (Abu-Asab et al., 2001). Furthermore, Bock et al. (2014) established a 27-year dataset of flowering observations on 232 plant species at the island of Guernsey, and found that mean magnitude of the advancement in first flowering was 5.2 days decade^{-1} since 1985. In the meantime, the whole flowering duration was shortened by 10 days decade^{-1}.

However, another study demonstrated that increased temperature prolonged average length of flowering duration. Miller-Rushing et al. (2007) compiled cherry flowering dataset from 25-year records involving in 97 tree species in Japan, and found that more than 92 out of the 97 individuals had a longer flowering duration in warmer years, while earlier onset of flowering was also observed. Despite some progresses have been achieved in flowering phenology, the relevant efforts were mostly concentrated in the areas of Europe and North America (Ge et al., 2015). The targeted researches to address the responses of flowering phenology to climate change at national scale were largely unavailable in China. Furthermore, most efforts were inclined to illuminate an entire picture on plant phenology via incorporating flowering phenology into spring events. This doing, to most extent, would weaken the importance of flowering phase as a sensitive indicator of ecosystem service and its evolutionary feedback function under climate change. In this case, it is much needed to further explore the coupling relationship between flowering phenology and climate change in China.

Plant phenology is an ancient science in China, and its systematic nationwide observations and explorations can be dated back to 1960s (Chen, 2013). Over last two decades, a large amount of observational data has been reported in various domestic publication agencies such as scientific journals, statistical yearbooks and monographs in Chinese language. To some extent, language barrier greatly restricted the data access to most non-Chinese researchers. This made it difficult to evaluate the responses of plant phenology to changing climate from global perspective, partially due to China's broad geographical coverage and high biodiversity. To eliminate the deficiencies, two recent meta-analyses have been conducted to figure out the phenological trends across China. Ma and Zhou (2012) used phenological dataset in herbs and trees to evaluate the historical changes in spring events during the period from 1980s to 2000s. Ge et al. (2015) explored the spring and autumn phenology shifts in various taxonomic groups including 112 species extracted from 48 case studies across 145 sites. However, these researches were mainly limited within recent 20-year data in meta-analysis, and excluded time series analysis on phenological trends at decadal scale. On the other hand, the solely long time series may mask some significant variations owing to recent stronger warming trend in China. Therefore, to investigate general trends and characteristics of flowering phenology in China, it is necessary to analyze long-term (over five decades) and interdecadal performances. Additionally, an integrated analysis regarding plant species, geographic distribution, pollination type and growth form is also critical and urgent.

In present study, we compiled an extended dataset of all observed flowering phenology records in recent decades (1963–2013) across China. Based on current research progress on flowering phenology, our study was to focus on the following key objectives: 1) to estimate an general trend of the changes in flowering time in China over last five decades; 2) to identify the differences in flowering phenology and its temperature sensitivities across plant species, observation decades and geographical sites; 3) to determine the interspecific variations in flowering shifts in terms of pollination types and seasonality, as well as growth forms; 4) ultimately to enrich the understanding on global rapid shifts of flowering time and their potential ecological effects on the basis of empirical evidences from China.

2. Materials and methods

2.1. Literature search and data collection

To investigate general changes in flowering phenology and their differences in the decades, a database of flowering phenophases was established through systematic review on the historical literatures across temporal and spatial scales, growth forms and pollination types throughout whole China. Online searches using keywords were to identify observational studies on plant flowering times prior to December 2015 in Google Scholar (http://www.scholar.google.com). Three online Chinese databases consisted of China National Knowledge Infrastructure (http://www.cnki.net), Wanfang Data (http://www.wanfangdata.com.cn) and VIP Database for Chinese Technical Periodicals (http://www.cqvip.com). For each database, four key words including phenology; flowering; temperature and anthesis were used to explore and collect a broad inclusive set of studies on flowering phenophases from 1963 to 2015.

2.2. Selection criteria and data extraction

From the article list retrieved above, we first examined each abstract and the results according to the following selection criteria and procedures. 1) The changes in flowering phenophases (i.e. the beginning of flowering, peak of flowering and the ending of flowering) were examined over a span of at least 15 years. 2) The observed historical flowering times were reported in either the calendar date or the relative time, allowing us to reconstruct the phenological database within the targeted years. Flowering phenophases in time series using the slopes of regression between phenophases and years would be included in our database. 3) The studies merely addressing a single phase for one species at one study site would be excluded to minimize potential biases in our database. 4) The time series of flowering phenophases would be statistically fitted for each species. To say, those studies with only a mean or general time trend of flowering phenology among mixed species would be excluded. 5) If there existed multiple time series regarding the same species and phases at the same study site, only the series with the longest duration would be selected in our databases.

Once the papers were deemed suitable for inclusion in the meta-analyses according to above criteria and procedures, the targeted data would be extracted directly from text and tables. On the other hand, the data presented in the form of figures without numeric indication in the context would not be further extracted. Consequently, the information extracted from historical documents consisted of species name, geographic conditions (elevation, latitude and longitude), flowering phenophases (the beginning of flowering, peak of flowering and the ending of flowering), phenological trends (days decade^{-1}) with significance analysis, initial and final years of phenology observations (Table S1). For each species, growth form, life cycle and pollination type would be also identified through the retrieval of biological features (http://www.eflora.cn/). On the basis of biological information collected, all the species would be categorized into four life forms, i.e. herbs, trees, shrubs and other form which was seriously disturbed by human activities. As a whole, the complete database comprised 649 time series of flowering phases from 136 species across 62 ground-based observations (Table S1). In our database, four different growth forms were distributed in 217 locations spanning 8 climatic zones (EC, east China; NCC, north center China; NCP, north China Plateau; NEC, northeast China; NWC, northwest China; SWC, southwest China; SEC, southeast China; TP, Tibet Plateau) in China (Fig. 1). Averaged to all the series, the mean time span was 29.4 years, and the initial and finial years of flowering observations were mostly allocated at 1979 and 2007, respectively (Table S2). Furthermore, the flowering phases mainly fell within the period from March to August across all the sites. To find out

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