Geographical pattern in first bloom variability and its relation to temperature sensitivity in the USA and China

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Abstract Advance in spring plant phenology over the last several decades has been found in all continents of the Northern Hemisphere. Compared to the studies detecting phenological trends, the studies investigating the geographical pattern of phenological variability (including mean date and magnitude of variability) are rather limited. In this study, we analyzed spatial pattern of mean date and standard deviation (SD) of first bloom date (FBD) time series (≥ 15 years) for black locust (*Robinia pseudoacacia*) at 22 stations in China, common lilac (*Syringa vulgaris*) at 79 stations in the Western US and Chinese lilac (*Syringa chinensis*) at 45 stations in the Eastern US. Subsequently, the impact of geographical factors (latitude, longitude, and altitude) on the mean date and SD was quantified by using the multiple regression analysis method. Meanwhile, the relationship between FBD variability and temperature sensitivity of FBD was examined. Results showed that the mean FBD highly depended on geographical factors for all the three species. Compared to the mean date, the dependence of SD of FBD time series on geographical factors was weaker. The geographical factors could only explain 13 to 31 % of spatial variance in SD of FBD. The negative regression coefficients of latitude ($P < 0.05$ except black locust)

indicated that FBD is more variable at lower latitude. At most of stations, significant and negative correlations between FBD and pre-season temperature on interannual scale were found, but the temperature sensitivity varied among different stations. The magnitude of temperature sensitivity decreased with increasing latitude. In general, the locations at lower latitude had earlier and more variable spring phenophase and showed stronger phenological response to climate change than the locations at higher latitude.

Keywords Geographical pattern · Plant phenology · First bloom date · Temperature sensitivity · Climate change · USA · China

Introduction

Plant phenology, as the study of periodical plant life cycle events influenced by environmental factors, can provide useful information about the vegetation dynamics in terrestrial ecosystems (Cleland et al. 2007). The phenological change relating to the start and end of the growing season can affect the vegetation productivity and carbon cycle (Keenan et al. 2014; Richardson et al. 2010, 2013). Also, the shift in plant phenophases would result in mismatches between plants and pollinators, predators and prey, and pests and hosts (DeLucia et al. 2012; Donnelly et al. 2011; Hegland et al. 2008). In addition, human health is affected by plant phenology, through the linkage between flowering phenology and allergenic pollen (Reid and Gamble 2009). Therefore, for the purpose of understanding the impact of climate change on biological systems, it is necessary to study the phenological response to climate change.

Most of the previous studies focus on the temporal change of phenophases in response to climate change

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(Amano et al. 2010; Aono and Kazui 2008; Parmesan and Yohe 2003; Root et al. 2003; Rosenzweig et al. 2007; Rutishauser et al. 2007; Zheng et al. 2013). For example, spring/summer phases of plants advanced by 2.5 days/decade from 1971 to 2000 in Europe (Menzel et al. 2006). Similarly, in China, obvious advancing trend of 2.75 days/decade for spring/summer phenophases over the past 50 years was found (Ge et al. 2014a). Spring phenology in the continental United States (except the southeastern part) became 4–8 days earlier after 1984 compared to proceeding decades (Schwartz et al. 2013a). Except for detecting phenological trends, phenological variability is also noteworthy because some extreme phenological events may lead to critical disturbances and mismatches in ecosystems (Both et al. 2009; Lloret et al. 2012; Schleip et al. 2012).

The phenological variability can be regarded as the way phenophases fluctuates yearly above or below a long-term average value. Thus, the phenological variability includes two aspects: mean date and magnitude of variability. Geographical distribution in mean date of plant phenophases could reflect the dynamics of seasons across space (Rötzer and Chmielewski 2001). Hopkins' bioclimatic law firstly demonstrated the impact of geographical factors on phenology in temperate North America (Hopkins 1918). The phenological maps of several typical plant species were also computed in China and Europe (Dai et al. 2014; Rötzer and Chmielewski 2001). However, to date, the studies about geographical pattern in the magnitude of phenological variability are scarce. The magnitude of phenological variability relative to climate variability determines the sensitivity of phenophases to temperature change. Thus, studying phenological variability across space can help to identify the area where the plants are more responsive to climate change.

In this study, using first bloom date of several typical plant species at many stations in the contiguous United States and China, we analyzed spatial pattern of mean flowering date and then quantified the impact of geographical factors (latitude, longitude, and altitude) on the mean date by applying the multiple regression analysis method. Subsequently, the magnitude of phenological variability, measured as the standard deviation (SD) of phenological time series, was analyzed by applying the same method. Meanwhile, the temperature sensitivity of spring phenology at each station was calculated. At last, the relationship between mean date and SD of phenological time series and temperature sensitivity was examined. Our overall objectives were to explore geographical pattern of phenological variability and illuminate its relationship to the temperature sensitivity of spring phenology.

Material and methods

Phenological and meteorological data

The contiguous United States (US) phenological data (1956–2003) were downloaded from IGBP PAGES/World Data Center for Paleoclimatology (Schwartz and Caprio 2003), including common lilac (*Syringa vulgaris*) first bloom dates (FBD) observed at 96 Western US stations (Cayan et al. 2001), and the same events recorded for cloned Chinese lilac (*Syringa chinensis*) at 61 stations in the Eastern US (Schwartz and Reiter 2000). The first bloom was defined as at least half (50 %) of the flower clusters having at least one open fresh flower for the whole plant. The black locust (*Robinia pseudoacacia*) FBD data from 1963 to 2012 at 22 stations in China were collected by Chinese Phenological Observation Network (CPON) (<http://www.cpon.ac.cn/>). The definition of the first bloom in CPON data (at least one fresh flower opening at any flower cluster for the whole plant) was different with that in the US data. It was worth noting that the number of observation stations changed over the time period for all the plant species (Fig. S1). In addition, using these widespread plant species to study the geographical patterns of phenological variability could reduce the effects of genetic variation among plants as much as possible.

The phenological observation stations being forwarded to further analyses needed to meet the following criteria: (1) they had to contain at least 15 years of FBD data, because only time series with more than 10 or 15 years data would be sufficient for detecting trend or variability (Menzel et al. 2006; Root et al. 2003); (2) for each phenological station, the nearest meteorological station in the US Historical Climatology Network (Menne et al. 2009) or China should be less than 30 km away, and the difference of altitude between these two types of stations should be less than 100 m; (3) the temperature data in the nearest meteorological station covered the same time period with FBD data at corresponding phenological station. As a result, our analyses consisted of 22 phenological stations for black locust in China, 79 stations for common lilac in the Western US, and 45 stations for Chinese lilac in the Eastern US (Fig. 1).

The daily maximum and minimum temperature data at meteorological stations in the US Historical Climatology Network were recorded in Global Historical Climatology Network (GHCN) dataset (Menne et al. 2012), which are available for free download at FTP site of NOAA national climatic data center (<ftp://ftp.ncdc.noaa.gov/pub/data/ghcn/daily/>). The daily mean temperature was calculated as arithmetic mean value of maximum and minimum temperature. Regarding China, the daily mean temperature data were obtained from China Meteorological Data Sharing Service System (<http://cdc.cma.gov.cn/home.do>).

Fig. 1 Locations of phenological observation stations analyzed in this study. First bloom date of three plant species is observed, including **a** black locust (*Robinia pseudoacacia*) in China; **b** common lilac (*Syringa*

vulgaris) in the Western US and Chinese lilac (*Syringa chinensis*) in the Eastern US

Statistical analyses

For each station, mean FBD of specific species for all available years was calculated. The geographical pattern of mean FBD was examined by using the method of multiple regression analysis (Rötzer and Chmielewski 2001):

$$p(x, y, z) = a_x x + a_y y + a_z z + c \quad (1)$$

where $p(x, y, z)$ is the mean date of first bloom at latitude x , longitude y (note that west longitude is expressed as negative number), and altitude z . c is a constant and a_x , a_y , and a_z are regression coefficients.

The magnitude of phenological variability at each station was measured as the SD of FBD time series. Larger SD suggests more dispersed and variable spring phenophases across years. Similarly, the geographical pattern of phenological SD was examined by applying Eq. (1), where $p(x, y, z)$ represents SD of FBD time series.

Following the previous studies (Dai et al. 2013; Fitter and Fitter 2002; Ge et al. 2014b; Rutishauser et al. 2008), temperature sensitivity of spring phenology was computed as a slope coefficient of linear regression between FBD and mean pre-season temperature at the nearest meteorological station on the interannual timescale. Since the temperature sensitivity of FBD based on different pre-season length (e.g., 45 or 90 days) was well correlated with each other ($R > 0.8$, $P < 0.001$, data

Fig. 2 Average first bloom date (day of the year, DOY) of three woody plants. **a** Black locust (*Robinia pseudoacacia*) in China; **b** common lilac (*Syringa vulgaris*) in the Western US and Chinese lilac (*Syringa chinensis*) in the Eastern US

Table 1 Shift of the mean first bloom date (FBD) with latitude (a_x), longitude (a_y), and altitude (a_z)

Phenophase	n value	R^2	a_x (days $^{\circ-1}$)	a_y (days $^{\circ-1}$)	a_z (days m^{-1})	c (days)
Black locust FBD	22	0.83**	1.86**	0.44*	0.006	4.47
Common lilac FBD	79	0.90**	3.81**	−0.05	0.029**	−3.82
Chinese lilac FBD	45	0.92**	4.38**	0.58**	0.013**	−9.91

n number of phenological observation stations; the regression coefficients (a_x , a_y , a_z) and constant (c) of multiple regression model are shown. R^2 : goodness of fit; ** $P<0.01$, * $P<0.05$

not shown), the preseason period lengths had little impact on the results. Here, the preseason period was chosen to be 60 days, which was specified to end at the date that was calculated by mean FBD from all years (Wang et al. 2014a). The geographical pattern of temperature sensitivity was examined through multiple regression analysis (Eq. (1), where $p(x, y, z)$ is the temperature sensitivity of FBD).

At last, to test whether the phenological variability is associated with the temperature sensitivity of spring phenology, Pearson correlation coefficients (Pearson's R) were calculated between mean date and SD of FBD time series and temperature sensitivity of FBD for all species/locations.

Results

Geographical pattern of mean date

The mean FBD for each species/location is shown in Fig. 2. It could be found that FBD of specific species varied widely across locations. In China, black locust FBD occurred from

middle April in Southwest China to middle May in Northeast China (Fig. 2a). The FBD highly depended upon geographical factors (Table 1, $R^2=0.83$, $P<0.01$). The FBD started 1.86 days later per degree of latitude from south to north ($P<0.01$), 0.44 days later per degree of longitude from west to east ($P<0.05$), while the impact of altitude on FBD was insignificant.

In the Western US, average common lilac FBD ranged from middle March in the west coast of California, New Mexico, Arizona, and Texas to early June in Montana and the mountain region of Wyoming (Fig. 2b). The geographical factors were able to explain 90 % of the spatial variance in mean common lilac FBD (Table 1, $P<0.01$). On average, common lilac FBD was delayed by approximately 3.81 days per degree increase in latitude ($P<0.01$), and by 2.9 days per 100-m increase in altitude ($P<0.01$), while the impact of longitude was insignificant.

In the Eastern US, average Chinese lilac FBD ranged between early April in Tennessee and late May in North Dakota, Wisconsin, and Vermont (Fig. 2b). The geographical factors were able to explain 92 % of the spatial variance in mean Chinese lilac FBD, and the regression coefficients of latitude (4.38 days per degree), longitude (0.58 days per

Fig. 3 The standard deviation (SD) of first bloom date of three woody plants. **a** Black locust (*Robinia pseudoacacia*) in China; **b** common lilac (*Syringa vulgaris*) in the Western US and Chinese lilac (*Syringa chinensis*) in the Eastern US

Table 2 Shift of standard deviation (SD) of first bloom date (FBD) time series with latitude (a_x), longitude (a_y) and altitude (a_z)

Phenophase	n value	R^2	a_x (days $^{\circ}$ $^{-1}$)	a_y (days $^{\circ}$ $^{-1}$)	a_z (days m^{-1})	c (days)
Black locust FBD	22	0.25	−0.068	−0.007	0.002	8.82
Common lilac FBD	79	0.13*	−0.141*	−0.117*	0.000	0.571
Chinese lilac FBD	45	0.31**	−0.245**	−0.046	0.001	13.7

n number of phenological observation stations; the regression coefficients (a_x , a_y , a_z) and constant (c) of multiple regression model are shown. R^2 : goodness of fit; ** $P<0.01$, * $P<0.05$

degree), and altitude (1.3 days per 100 m) were all statistically significant ($P<0.01$, Table 1).

Geographical pattern of phenological SD

Figure 3 displays the SD of FBD time series for each species/location. The SD of black locust FBD in China ranged from 3.4 to 9.1 days (Fig. 3a). Maximum variability was found in Southwest China. The geographical factors could only explain 25 % of the spatial variance in phenological SD and no significant influencing factors were found (Table 2). The SD of common lilac FBD in the Western US ranged from 4.2 to 15.1 days with a mean of 8.3 days. Centers of maximum variability were found in Northern California and Nevada (Fig. 3b). Through multiple regression analysis, the regression coefficients of latitude and longitude were both negative and significant ($P<0.05$), suggesting the SD of common lilac FBD is greater at lower latitude and in areas closer to the west coast (Table 2). In the Eastern US, the SD of Chinese lilac FBD varied from 4.8 to 12.6 days with a mean of 7.2 days. The maximum variability was found at two stations in Tennessee and one station in North Dakota (Fig. 3b). Geographical factors could explained 31 % of the spatial variance in the SD of Chinese lilac FBD (Table 2, $P<0.01$). The only significant influencing factor was latitude ($P<0.01$). The negative regression coefficient of latitude indicated that the phenological SD is greater at lower latitude.

Geographical pattern of temperature sensitivity

In most of stations, the preseason temperature was the dominant factor affecting interannual change in FBD (Fig. 4). In China, the Pearson's R between black locust FBD and preseason temperature was significant ($P<0.05$) at all of the 22 stations (Fig. 4a). Similarly, common lilac and Chinese lilac FBD in the contiguous US showed a significant correlation to preseason temperature in 60 of 79 stations (75.9 %) and 38 of 45 stations (84.4 %), respectively (Fig. 4b, c). The insignificant correlations between FBD and preseason temperature in some stations may be due to the influence of other unknown factors, for example, the plant conditions, the plant age, and the micro-climate of the location. Therefore, when analyzing the geographical pattern of temperature sensitivity, we did not

consider the stations showing insignificant temperature–FBD relationship.

The geographical factors could explain 27 to 39 % of spatial variance in temperature sensitivity of FBD for the three plant species (Table 3, $P<0.05$). The temperature sensitivity of black locust FBD ranged between −6.5 and −2.7 days $^{\circ}$ C (Fig. 5a). Only the regression coefficient of latitude was significant ($P<0.05$, Table 3), and the positive coefficients

Fig. 4 The frequency distribution of Pearson's R between first bloom date and preseason (60 days) temperature. **a** Black locust (*Robinia pseudoacacia*) at 22 stations in China; **b** common lilac (*Syringa vulgaris*) at 79 stations in the Western US; and **c** Chinese lilac (*Syringa chinensis*) at 45 stations in the Eastern US

Table 3 Shift of temperature sensitivity of first bloom date (FBD) with latitude (a_x), longitude (a_y), and altitude (a_z)

Phenophase	n value	R^2	a_x (days $^{\circ}\text{C}^{-1}$)	a_y (days $^{\circ}\text{C}^{-1}$)	a_z (days $^{\circ}\text{C}^{-1} \text{ m}^{-1}$)	c (days $^{\circ}\text{C}^{-1}$)
Black locust FBD	22	0.39*	0.093**	0.027	0.000	−10.3
Common lilac FBD	60	0.32**	0.072	0.164**	0.000	10.5
Chinese lilac FBD	38	0.27*	0.209*	0.028	0.003	−11.5

n number of phenological observation stations; the regression coefficients (a_x , a_y , a_z) and constant (c) of multiple regression model are shown. R^2 : goodness of fit; ** $P < 0.01$, * $P < 0.05$

suggested weaker temperature sensitivity at higher latitude. The temperature sensitivity of common lilac FBD in the Western US varied from −12.5 to −1.2 days $^{\circ}\text{C}$ and showed its maximum absolute value along the north western coast (Fig. 5b). The positive and significant regression coefficient of longitude implied that the temperature sensitivity became weaker from west to east. For Chinese lilac FBD in the Eastern US, the temperature sensitivity revealed similar spatial pattern with black locust FBD in China (Fig. 5b, Table 3).

Relationship between phenological variability and temperature sensitivity

Figure 6 shows the relationship between mean date and temperature sensitivity of FBD for the three plant species. The mean FBD correlated positively with the temperature sensitivity ($P < 0.05$ except common lilac), which suggested that stations with earlier flowering time had stronger phenological responsiveness to temperature (Fig. 6). Furthermore, the SD of FBD time series was correlated significantly and negatively with the temperature sensitivity ($P < 0.05$, Fig. 7). This implied

that a greater magnitude of phenological variability was associated with stronger temperature sensitivity.

Discussion

The impact of geographical factors on the spring plant phenophases, which is known as Hopkins' bioclimatic law, has been described in an early study (Hopkins 1918). The law states that in temperate North America, weather-related events, such as bloom time, shift linearly with latitude, longitude, and altitude. In this study, we found a 1.86 to 4.38 days delay in FBD per degree of latitude from south to north, which is consistent with Hopkins' law. Similar latitudinal patterns in spring phenophase were also found in Europe (Rötzer and Chmielewski 2001). Thus, strong dependences on latitude for spring plant phenophases exist in all continents of the Northern Hemisphere. Furthermore, in the eastern parts of the continents (e.g., Eastern China and US), the flowering time is earlier at stations farther from the coast, which caused by the asymmetric heating of land and sea. In the western parts of the

Fig. 5 Temperature sensitivity for first bloom date (FBD) of three woody plants. **a** Black locust (*Robinia pseudoacacia*) in China; **b** common lilac (*Syringa vulgaris*) in the Western US and Chinese lilac (*Syringa chinensis*) in the Eastern US. Temperature sensitivity of FBD is calculated

as the slope coefficient of linear regression between annual FBD and mean pre-season (60 days) temperature. Note that only stations showing significant temperature–FBD relationship are shown ($P < 0.05$)

Fig. 6 The relationship between the mean date and the temperature sensitivity of FBD. **a** Black locust in China ($R=0.62$, $P<0.01$); **b** common lilac in the Western US ($R=0.22$, $P=0.1$); **c** Chinese lilac in the Eastern US ($R=0.41$, $P<0.05$)

continents, the impact of longitude is significant in Europe, where the FBD delayed from the maritime regions in West Europe to the continental regions in East Europe (Rötzer and Chmielewski 2001). However, the impact of longitude on FBD is not obvious in the Western US (Table 2), which may be because the mountain range in the Western US blocked the warm maritime airflow (Fig. 1b). The impact of altitude on FBD is significant for two plant species in the contiguous US, but insignificant for black locust in China. This may be due to the frequency distribution of the station altitude. For black locust in China, 15 of the 22 stations (68 %) have an altitude between 0 and 100 m (Fig. S2a). Oppositely, frequency distribution of station altitude in the USA is relatively dispersive. For 11 and 31 % of stations, the altitudes are lower than 100 m for common lilac and Chinese lilac, respectively (Fig. S2b, c). Therefore, there is a high probability that the sample size along the altitude gradient is insufficient to detect significant altitude impact in China.

Fig. 7 The relationship between the standard deviation (SD) and the temperature sensitivity of FBD. **a** Black locust in China ($R=-0.55$, $P<0.01$); **b** common lilac in the Western US ($R=-0.59$, $P<0.01$); and **c** Chinese lilac in the Eastern US ($R=-0.39$, $P<0.05$)

Our study highlighted that the magnitude of phenological variability is highly spatially heterogeneous: geographical factors can only explain 13 to 31 % of spatial variance in the SD of FBD time series. Even so, latitude is a significant factor influencing the SD of FBD time series for common lilac and Chinese lilac (Table 2). Negative regression coefficient of latitude suggests that the FBD is more variable at lower latitude. Oppositely, based on the temperature dataset in this study, the SD of spring temperature (March–May) time series is stronger at higher latitude. Therefore, although the interannual change in FBD follows the climate variability closely, the magnitude of phenological variability does not match the magnitude of temperature variability across different locations. This can be ascribed to varying temperature sensitivity across space.

Temperature sensitivity of spring phenophases at low latitude is stronger than that at high latitude (Fig. 5, Table 3). This could lead to higher magnitude of phenological variability at low latitude even though the magnitude of temperature

variability is relatively weaker there. The latitudinal pattern of temperature sensitivity found in this study is in accord with other studies using different spring phenophases or indicators in China (Dai et al. 2014; Wang et al. 2014b). In Europe, the rate of advance in leaf unfolding of most species per 1 °C temperature rise is higher in warmer countries (Menzel et al. 2006). Therefore, all continents of the Northern Hemisphere show consistent latitudinal pattern of temperature sensitivity. This pattern may results from the local adaptation of plant species to regional climate (Chen and Xu 2012). However, the Chinese lilac observed in this study is a cloned species, which means that the genotypic difference has little influence on phenological responses across different locations. Therefore, more modeling or experimental studies are needed to explain such spatial pattern of phenological responsiveness.

The temperature sensitivity of FBD can be linked to mean date of FBD time series at species-level (Fig. 6). At ecosystem scale, the temperature sensitivity of the onset of spring greenness based on satellite data showed negative relationship with mean green-up onset date in the whole Northern Hemisphere (Shen et al. 2014). Thus, the result in this study is robust at broad scale. Moreover, greater magnitude of phenological variability is associated with stronger temperature sensitivity (Fig. 7). Therefore, phenological variability is a considerable factor impacting phenological response to temperature. The greater advancing trend in spring phenophases is not simply impacted by stronger warming trend. The phenological variability and its associated temperature sensitivity also play an important role in shaping the response of the spring phenophases to warming temperature (Matsumoto 2010; Wang et al. 2014b).

In general, low latitude region exhibits earlier and more variable spring phenophase and stronger phenological response to climate change than high latitude region. However, higher latitude has warmed more than lower latitude over the past half century (IPCC 2013; Jones et al. 2012). Therefore, at high latitude, the contribution of stronger warming to advancing trend in spring phenophases can be partly or totally offset by the weaker temperature sensitivity there. This explains why the latitude is not an important predictor of the strength of phenological trends, as suggested by previous studies (Ge et al. 2014a; Matsumoto 2010; Parmesan 2007).

Conclusions

This study explored the geographical patterns of phenological variability (including mean date and SD) and temperature sensitivity using the FBD data of three widespread plant species (black locust, common lilac, and Chinese lilac) in the USA and China. We found that the mean FBD highly depends on geographical factors (latitude, longitude, and altitude) for all the three plant species. Compared to the mean

date, the dependence of SD of FBD time series on geographical factors was weaker, but negative regression coefficient of latitude (significant except black locust) indicates that FBD is more variable at lower latitude. Although most of the stations show significant correlations between FBD and pre-season temperature on interannual scale, the temperature sensitivity varied among different stations. Overall, the locations at lower latitude have earlier and more variable spring phenophase and show stronger phenological response to climate change than that at higher latitude.

Phenological research has traditionally been identified with studies of mid-latitude plants (mostly trees and shrubs) in seasonal climates (Schwartz 2013b), but the results of this study urge researcher to pay more attention to plant phenology in low-latitude ecosystems. Moreover, further study should make progress on phenological models for simulating and predicting phenological variation across time, space, and species. Then the temperature sensitivity of plant phenology could be parameterized from phenological model, which can help us to answer the question that why phenological response to temperature is greater at lower latitude.

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