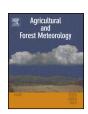
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Continuous but diverse advancement of spring-summer phenology in response to climate warming across the Qinghai-Tibetan Plateau



Zhoutao Zheng ^{a,b,c}, Wenquan Zhu ^{a,b,c,*}, Guangsheng Chen ^d, Nan Jiang ^{a,b,c}, Deqin Fan ^{a,b,c}, Donghai Zhang ^{a,b,c}

- ^a State Key Laboratory of Earth Surface Processes and Resource Ecology, Beijing Normal University, Beijing 100875, China
- ^b Joint Center for Global Change Studies (JCGCS), Beijing 100875, China
- ^c College of Resources Science and Technology, Beijing Normal University, Beijing 100875, China
- ^d Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831, USA

ARTICLE INFO

Article history: Received 30 November 2015 Received in revised form 1 April 2016 Accepted 16 April 2016

Keywords: Climate change Spring-summer phenology Phenology shift Climatic sensitivity Qinghai-Tibetan Plateau

ABSTRACT

The Qinghai-Tibetan Plateau (QTP) is more vulnerable and sensitive to climate change than many other regions worldwide because of its high altitude, permafrost geography, and harsh physical environment. As a sensitive bio-indicator of climate change, plant phenology shift in this region has been intensively studied during the recent decades, primarily based on satellite-retrieved data. However, great controversy still exists regarding the change in direction and magnitudes of spring-summer phenology. Based on a large number (11,000+ records) of long-term and continuous ground observational data for various plant species, our study intended to more comprehensively assess the changing trends of spring-summer phenology and their relationships with climatic change across the QTP. The results indicated a continuous advancement $(-2.69 \,\mathrm{days}\,\mathrm{decade}^{-1})$ in spring-summer phenology from 1981 to 2011, with an even more rapid advancement during 2000–2011 (-3.13 days decade⁻¹), which provided new field evidence for continuous advancement in spring-summer phenology across the QTP. However, diverse advancing rates in spring-summer phenology were observed for different vegetation types, thermal conditions, and seasons. The advancing trends matched well with the difference in sensitivity of spring-summer phenology to increasing temperature, implying that the sensitivity of phenology to temperature was one of the major factors influencing spring-summer phenology shifts. Besides, increased precipitation could advance the spring-summer phenology. The response of spring-summer phenology to temperature tended to be stronger from east to west across all species, while the response to precipitation showed no consistent spatial pattern.

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1. Introduction

Plant phenology is the timing and duration of recurring phenological events during plant growth and development. It is a sensitive bio-indicator of climate and natural environment change (Cong et al., 2012; Morisette et al., 2009; Penuelas and Filella, 2001) and plays an important role in adjusting biogeochemical cycles (Running and Nemani, 1991; Sellers et al., 1996; White et al., 1997). The extensive changes in plant phenology in response to recent climate change have been observed worldwide (Cleland et al., 2007; Jeong et al., 2011; Menzel and Fabian, 1999; Parmesan and Yohe,

E-mail address: zhuwq75@bnu.edu.cn (W. Zhu).

2003; Piao et al., 2006; Root et al., 2003; Schwartz et al., 2006; Zhu et al., 2012 Piao et al., 2006; Root et al., 2003; Schwartz et al., 2006; Zhu et al., 2012). The phenological change in the Qinghai-Tibetan Plateau (QTP) has caused increasing concerns in recent years in particular (Piao et al., 2011; Yu et al., 2010; Zhang et al., 2013a,b). The unique vegetation composition (i.e., typical alpine meadow and steppe) and climate features (e.g., a harsh physical environment as the Earth's third pole), along with low levels of human disturbance (Piao et al., 2011), make this region an ideal study example for climate change effects on ecosystem dynamics. Several recent studies based on remote sensing time-series data have reported varying or even opposite change trends in spring phenology in the QTP. For example, using the normalized difference vegetation index (NDVI) from the advanced very high resolution radiometer (AVHRR) global inventory modeling and mapping studies (GIMMS) dataset, Yu et al. (2010) found that spring phenology in the QTP initially showed an

 $[\]ast\,$ Corresponding author at: College of Resources Science and Technology, Beijing Normal University, Beijing 100875, China.

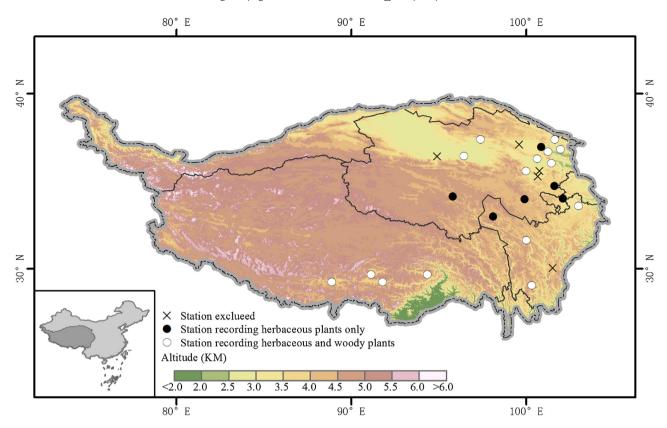


Fig. 1. The study region and locations of the observational sites in the Qinghai-Tibetan Plateau (QTP).

advancing trend since 1982 but started to level off in the mid-1990s. Piao et al. (2011) obtained a similar conclusion that spring phenology advanced significantly before 2000 and was delayed after 2000 based on the same dataset. However, Zhang et al. (2013b) found that the start of the vegetation growing season (SOS) experienced a continuous advancing trend during 1982-2011, and no turning point occurred, through merging AVHRR-based SOSs from 1982 to 2000 with SPOT-VGT-based SOSs from 2001 to 2011. These varying results aroused wide controversies about the actual plant phenology patterns in the QTP (Chen et al., 2011; Shen, 2011; Shen et al., 2013; Wang et al., 2013; Yi and Zhou, 2011). These controversies have been partly attributed to the lack of sufficient and precise ground-based observations and remote sensing data issues, including low data quality, indistinct phenometrics, ill-defined mixture of target (or signal) and background (or noise) objects, length of time series, and phenology retrieving methods (Chen et al., 2011; Hanes et al., 2013; Wang et al., 2013; White et al., 2009; Yi and Zhou, 2011).

Compared to remote sensing methods, ground-based observations often provide first-hand, more accurate phenology dates at point scale and thus can serve as validations of remote sensing products. A few studies have reported different or even opposite phenological trends among plant species and observational sites based on few scattered ground-observed phenological data in the QTP. For example, Li et al. (2010) reported advancing green-up onset dates at the Huangyuan, Menyuan and Qumarleb stations but delayed green-up onset dates at the Delingca station. Xu et al. (2014) reported that the onset date of blossoming for *Elymus nutans* delayed at the Gade station, while it advanced at the Henan station. Owing to the diverse reported phenological trends at individual or groups of few sites, it is hard to make an accurate evaluation about the phenological trend across the whole QTP. It is necessary to collect more field observation data and synthesize them with the

existing data to obtain a comprehensive assessment of the actual phenology changes in the QTP.

Thanks to the long-term and continuous observations from the phenology network established by the China Meteorological Administration (CMA), we were able to collect a large number of continuous and long-term, ground-observed phenology events and weather data from the QTP. Based on these data, this study aimed to conduct a comprehensive and synthetic evaluation of changes in spring-summer phenology over the period 1981–2011. We hypothesized that there existed continuous but diverse advancing trends in spring-summer phenological events among different vegetation types, thermal conditions and seasons in response to recent climate warming across the QTP. In addition, we hypothesized that the difference in sensitivity to climate warming was the major contributor to the diverse responses.

2. Materials and methods

The phenological data for the OTP were collected from the nation-wide phenological observation network established by the CMA (Chen, 2013; Ge et al., 2015). The CMA phenological observation network was established in 1980 and is the largest network for observing meteorological conditions and phenological events synchronously in China. At present, there exist 446 stations, and 26 of them are located in the QTP (Fig. 1). Because the phenological and meteorological observations are conducted at the same locations, these observational data are especially useful and consistent for understanding phenology-climate relationships (Chen, 2013). We only selected the sites with at least 10 years of continuous observation during 1981-2011 to explore the changes in springsummer phenology across the QTP. As a result, only 21 out of the 26 stations were selected (Fig. 1). There were a total of 32 species (22 herbaceous plants and 10 woody plants) and 642 phenological time series (11,000+ records), including 8 phenological events

Table 1The phenological events and observational numbers for different vegetation types.

Taxa	Phenological events	$N_{\rm ts}$	N _{spe}	ecies N _{site}
Herbaceous pl	ants BB, FLU, 50LU, FH, 50H, FF, 50F, EF	371	22	21
Woody plants	FBS, LBS, FB, LB, FLU, 50LU, FBIA, FF, 50	F, EF 271	10	15

Note: Phenological events: BB, bud burst; FLU, first leaf unfolding; 50LU, 50% leaf unfolding; FH, first heading; 50H, 50% heading; FF, first flowering; 50F, 50% flowering; EF, end of flowering; FBS, flower bud swelling; LBS, leaf bud swelling; FB, flower budburst; LB, leaf budburst; FBIA, flower bud or inflorescence appearance. $N_{\rm ts}$: number of time series. $N_{\rm species}$: number of species. $N_{\rm site}$: number of sites.

for herbaceous plants and 10 phenological events for woody plants (Table 1). More details about the geographical coordinates, altitude and plant species for each station can be found in Table S1.

The overall phenological trend was computed using a metaanalysis method (Parmesan and Yohe, 2003; Root et al., 2003 Root et al., 2003). Three investigated periods (1981-1999, 2000-2011 and 1981-2011) were determined to analyze the overall phenological trends. For each period, only those phenological time series with at least 10 years of continuous observations were selected to calculate the overall change trend. For each phenological event of each species at each station, the mean onset date, its linear change trend and the standard error were calculated for the three periods. The statistical significance of the change trends was examined using the F-test. A negative value for the trend indicated an earlier occurrence of this phenological event, whereas a positive value represented a later occurrence. An overall effect is considered to be significant if the confidence interval (CI) at the 0.05 level did not include zero (Gurevitch et al., 2000). In order to investigate the differences in phenological trends among vegetation types, thermal conditions and seasons, the phenological time series were further divided into more groups. Specifically, (1) to investigate the differences among vegetation types, the phenological time series were divided into herbaceous and woody plants; (2) to analyze the phenological trends at different thermal conditions, the phenological data were divided into two groups: multi-year (1981-2011) spring-summer mean temperature > 10 °C and \leq 10 °C; (3) to investigate the differences in the response of phenology to warming trends, the phenological data were divided into two groups: the trends in spring-summer temperature > 0.5 °C decade⁻¹ and ≤ 0.5 °C decade⁻¹; and (4) to reveal the seasonal differences, phenological events that occurred from February to May were treated as spring phenological events, and those from June to August were treated as summer phenological events.

The monthly mean temperature, minimum temperature and precipitation for each phenological station from 1981 to 2011 were obtained from the China Meteorological Data Service System (http://data.cma.cn/). The spring-summer mean temperature was calculated as the average of monthly temperatures from March to August for each year. The change trends in the spring-summer mean temperature were computed using a simple linear regression between the mean temperature and year for each station, and the significance of the trend was evaluated with the F-test at the 0.05 level. The spring-summer mean temperature and its trend at each station are listed in Table S2. With the same method used for calculating the overall phenological trend (Parmesan and Yohe, 2003; Root et al., 2003 Root et al., 2003), we also calculated the overall spring-summer temperature trend for different time periods (1981–1999, 2000–2011 and 1981–2011) and overall temperature trend for different seasons (spring and summer) during 1981-2011 (Tables S3 and S4). The temperature (precipitation) sensitivity was computed as the slope of the linear regression of the onset date of a given phenological event against the mean temperature (total precipitation) of three selected months (current month of the mean onset date and its two preceding months).

The one-way analysis of variance (ANOVA) was used to compare the significant differences in change trends and climatic sensitivity among groups. The level of P < 0.05 indicated significant difference, while P < 0.01 indicated very significant difference.

The mean temperature/precipitation sensitivity for each station for different vegetation types during 1981–2011 was calculated to explore the spatial distribution of climatic sensitivity. The spatial patterns of climatic sensitivity were examined by a multiple linear regression:

$$S_{\text{cli}} = S_{\text{lat}}x + S_{\text{lon}}y + S_{\text{alt}}z + S_{\text{int}}$$
 (1)

where $S_{\rm cli}$ is the climatic sensitivity; x,y and z are latitude, longitude and altitude, respectively; $S_{\rm int}$ is the intercept; and $S_{\rm lat}$, $S_{\rm lon}$ and $S_{\rm alt}$ are the parameters that describe the impact of geographic factors on the climatic sensitivity of spring-summer phenology.

3. Results

3.1. Overall phenological trends

The observed phenological changes across the QTP are summarized in Table 2. Combining all of the phenological events, the spring-summer phenology across the QTP advanced at a significant (P<0.05) rate of 2.69 days decade⁻¹ (n=642, median = -2.52 days decade⁻¹) during 1981–2011 (Table 2a, Fig. S1). Significant advancing trends in spring-summer phenology were also observed both before and after 2000 (Table 2a). The magnitude of the advancing trend during 2000–2011 was 3.13 days decade⁻¹, which was significantly greater (one-way ANOVA, d.f. = 487, F = 11.771, P<0.001) than that during 1981–1999 (-2.73 days decade⁻¹). This implied that the spring-summer phenology experienced a more rapid advancement during the more recent period.

The signal of shifts towards earlier spring-summer events was evident during 1981-2011. Among all 18 phenological events of herbaceous and woody plants, significant advancing trends were found in 11 phenological events. Except for the event of EF (end of flowering) for herbaceous plants, the proportions for the advancing trends were greater than those for the delaying trends during 1981-2011 (Table 2b). For the phenological events of leaf unfolding (first leaf unfolding and 50% leaf unfolding) of both herbaceous and woody plants, 66% of the time series showed an advancing trend (29% were significant at P < 0.05) and 34% showed a delaying trend (10% were significant). For the phenological events of flowering (first flowering, 50% flowering and end of flowering), 61% of the observational data showed an advancing trend (24% were significant), while 39% showed a delaying trend (11% were significant). During 1981-2011, the mean overall advancing trends for leaf unfolding and flowering were 1.56 and 2.48 days decade⁻¹ (Table 2b), respectively.

3.2. Phenological trends for different vegetation types

Phenological trends varied greatly for different vegetation types (Table 2a). During 1981–2011, the spring-summer phenology for herbaceous plants showed an overall advancing signal, and 60% of the phenological time series showed an advancing trend (19% were significant), while 40% of those showed a delaying trend (12% were significant). In comparison, the advancing signals for woody plants were much stronger, and 73% of the phenological time series shifted earlier (35% were significant), while 27% of them shifted later (6% were significant). Overall, the spring-summer phenology for the herbaceous plants advanced significantly by $1.32 \, \text{days} \, \text{decade}^{-1}$ (n = 371, median = $-1.44 \, \text{days} \, \text{decade}^{-1}$), while the woody plants showed a more significant advancing trend of $4.90 \, \text{days} \, \text{decade}^{-1}$ (n = 271, median = $-4.10 \, \text{days} \, \text{decade}^{-1}$) during

Table 2
Summaries of phenological trends across the Qinghai-Tibetan Plateau (QTP). (a) Phenological trends for different vegetation types and different periods, (b) Phenological trends for different phenological events during 1981–2011, (c) Phenological trends for different thermal conditions during 1981–2011, (d) Phenological trends for different seasons during 1981–2011.

Vegetation type	Trend (days decade-1)	95% confidence interval	$N_{ m ts}$	$A_{\rm all}$	A_{sig}	$D_{ m all}$	D_{sig}
1981–1999	,				3.5		348
Herbaceous plants	-1.93	[-3.24, -0.63]	164	0.57	0.16	0.43	0.0
Woody plants	-4.55	[-6.45, -2.65]	66	0.79	0.42	0.21	0.1
J 1	-4.33 -2.73	[-3.84, -1.62]	230	0.63	0.24	0.21	0.0
All species	-2.73	[-3.64, -1.62]	230	0.05	0.24	0.57	0.0
2000–2011	1.46	[2.42 0.40]	250	0.50	0.12	0.42	0.0
Herbaceous plants	-1.46 5.60	[-2.43, -0.49]	356	0.58	0.13	0.42	0.0
Woody plants	-5.68	[-7.25, -4.12]	255	0.69	0.23	0.31	0.0
All species	-3.13	[-3.98, -2.29]	611	0.63	0.17	0.37	0.0
1981–2011	4.00	[4.04 0.70]	254	0.00	0.10	0.40	0.4
Herbaceous plants	-1.32	[-1.91, -0.72]	371	0.60	0.19	0.40	0.1
Noody plants	-4.90	[-5.86, -3.94]	271	0.73	0.35	0.27	0.0
All species	-2.69	[-3.23, -2.16]	642	0.65	0.26	0.35	0.0
b) Phenological trends	for different phenological events o	luring 1981–2011					
Phenological event	Trend (days decade-	95% confidence inter	al N _{ts}	A _{all}	A _{sig}	$D_{ m all}$	D_{sig}
Herbaceous plants							
BB	-1.12	[-2.38, 0.15]	69	0.64	0.14	0.36	0.1
TLU	-1.09	[-3.06, 0.87]	45	0.60	0.22	0.40	0.1
50LU	-0.61	[-2.58, 1.37]	45	0.53	0.20	0.47	0.1
H	-2.62	[-4.80, -0.45]	17	0.59	0.24	0.41	0.0
50H	-2.02 -3.39	[-4.80, -0.43] [-6.14, -0.64]	17			0.29	
F	-3.39 -1.91			0.71 0.65	0.24		0.0
		[-3.19, -0.62]	68		0.19	0.35	0.0
iOF	-1.38	[-2.68, -0.08]	67	0.58	0.19	0.42	0.1
EF	0.75	[-1.83, 3.32]	43	0.47	0.16	0.53	0.2
Noody plants							
BS	-9.20	[-13.97, -4.44]	25	0.80	0.40	0.20	0.0
LBS	-8.81	[-14.43, -3.19]	26	0.81	0.38	0.19	0.0
EB.	-6.31	[-10.25, -2.37]	25	0.76	0.32	0.24	0.0
.B	-3.34	[-5.75, -0.94]	28	0.71	0.25	0.29	0.0
·LU	-4.58	[-6.39, -2.77]	28	0.82	0.43	0.18	0.0
50LU	-5.39	[-7.02, -3.77]	28	0.82	0.43	0.18	0.0
BIA	-5.07	[-9.37, -0.77]	27	0.63	0.26	0.37	0.0
F	-2.50	[-5.35, 0.35]	28	0.71	0.36	0.29	0.1
50F	-2.84	[-5.70, 0.02]	28	0.68	0.36	0.32	0.1
F	-1.93	[-4.91, 1.05]	28	0.61	0.32	0.39	0.0
Herbaceous and woody	plant						
eaf unfolding (FLU, 50L	U) — 1.56	[-2.35, -0.77]	146	0.66	0.29	0.34	0.1
flowering (FF, 50F, EF)	-2.48	[-3.50, -1.46]	262	0.61	0.24	0.39	0.1
c) Phenological trends f	for different thermal conditions d	ıring 1981–2011					
Thermal condition	Trend (days decade ⁻¹)	95% confidence interval	N _{ts}	A _{all}	A _{sig}	$D_{\rm all}$	$D_{\rm sig}$
Spring-summer mean te	emperature (°C)						
≤ 10	- 2.04	[-2.73, -1.34]	333	0.61	0.23	0.39	0.1
≥10 ≥10	-3.58	[-4.39, -2.77]	309	0.71	0.29	0.29	0.0
	r mean temperature (°C decade ⁻¹)		303	0.71	0.23	0.23	0.0
≤ 0.5		[-2.48, -0.39]	247	0.57	0.11	0.43	0.0
0.5	-3.18	[-3.80, -2.55]	395	0.70	0.35	0.30	0.1
	for different seasons during 1981-						
, 0		25% confidence interval	N _{ts}	A _{all}	A .	$D_{ m all}$	D_{si}
	,				A _{sig}		
1 0	-	-3.97, -2.62]	464	0.68	0.28	0.32	0.0
ummer -1	1.35	-2.16, -0.54	178	0.59	0.20	0.41	0.1

Note: The bold black numbers indicate significant (P<0.05) change trends. Phenological event: BB, bud burst; FLU, first leaf unfolding; 50LU, 50% leaf unfolding; FH, first heading; 50H, 50% heading; FF, first flowering; 50F, 50% flowering; EF, end of flowering; FBS, flower bud swelling; LBS, leaf bud swelling; FB, flower budburst; LB, leaf budburst; FBIA, flower bud or inflorescence appearance. N_{ts} : number of time series. A_{all} and D_{all} : proportions of advancing and delaying trends, respectively. A_{sig} and D_{sig} : proportions of significant (P<0.05) advancing and delaying trends, respectively.

1981–2011 (Table 2a, Fig. S1). This difference in the advancing trends between herbaceous and woody plants was found to be statistically significant during 1981–2011 (one-way ANOVA, d.f. = 640, F = 11.771, P < 0.001).

The phenology of herbaceous plants advanced by 1.93 days decade⁻¹ during 1981–1999 and 1.46 days decade⁻¹ during 2000–2011 (Table 2a), but there was no significant dif-

ference between the two periods (one-way ANOVA, d.f. = 518, F = 0.149, P = 0.897). For the woody plants, the average magnitude of the advancing trend was 4.55 days decade⁻¹ during 1981–1999 and 5.68 days decade⁻¹ during 2000–2011 (Table 2a), but again there was no significant difference between the two periods (one-way ANOVA, d.f. = 319, F = 2.475, P = 0.127).

3.3. Phenological trends under different thermal conditions

The magnitude of advance in spring-summer phenology was $2.04\,\mathrm{days}\,\mathrm{decade^{-1}}$ at the stations with spring-summer mean temperatures $\leq 10\,^\circ\mathrm{C}$ during 1981-2011 (Table 2c). In contrast, the advancing trend ($-3.58\,\mathrm{days}\,\mathrm{decade^{-1}}$) was significantly greater (one-way ANOVA, d.f.= $547,\,F=10.434,\,P=0.007$) at the stations with spring-summer mean temperatures >10 °C. The mean phenology trend ($-3.18\,\mathrm{days}\,\mathrm{decade^{-1}}$) at the stations with the trend of the spring-summer mean temperature >0.5 °C decade $^{-1}$ was significantly greater than that ($-1.44\,\mathrm{days}\,\mathrm{decade^{-1}}$) at the stations with the trend of the spring-summer mean temperature $\leq 0.5\,^\circ\mathrm{C}\,\mathrm{decade^{-1}}$ (one-way ANOVA, d.f. = $640,\,F=3.483,\,P<0.001$).

3.4. Phenological trends for different seasons

The mean onset dates of spring-summer phenological events mainly occurred between March and July in the QTP (Fig. S2). Spring phenology advanced significantly at a mean rate of $3.29 \, \mathrm{days} \, \mathrm{decade^{-1}}$, while summer phenology advanced significantly at a mean rate of $1.35 \, \mathrm{days} \, \mathrm{decade^{-1}}$ during 1981-2011 (Table 2d). Moreover, the difference in the advancing rates between spring and summer phenology was significant (one-way ANOVA, $\mathrm{d.f.} = 640, F = 2.101, P = 0.003$), indicating a more rapid advancement for spring onset date.

3.5. Climatic sensitivity of spring-summer phenology

The spring-summer phenology advanced by 3.48 days per °C increase of the mean temperature across the QTP during 1981–2011 (Table 3a). However, the temperature sensitivity was significantly stronger for woody plants than herbaceous plants (one-way ANOVA, d.f. = 595, F = 0.459, P < 0.001) (Table 3b). Furthermore, earlier phenological events showed stronger temperature sensitivity (Fig. 2). Overall, the temperature response in the spring was significantly stronger than that in the summer during 1981–2011 (one-way ANOVA, d.f. = 595, F = 3.770, P = 0.033) (Table 3c). Temperature response during 2000-2011 was significantly stronger than that during 1981-1999 (one-way ANOVA, d.f. = 730, F = 3.790, P = 0.029) (Table 3a). Similar results were also found in the sensitivity of spring-summer phenology to the minimum temperature (Table S5), but the phenological responses to the minimum temperature were much weaker than those to the mean temperature.

The spring-summer phenology advanced 2.4 days in response to 100 mm increase of precipitation across the QTP during 1981–2011 (Table 4a). Although the proportions of time series with significant advancing trends were small, significant sensitivities of spring-summer phenology to precipitation were found for all time periods (Table 4a) and vegetation types (Table 4b). Among different seasons, the sensitivity to precipitation was significant for spring phenology, but not for summer phenology (Table 4c). The precipitation sensitivity of woody plants was significantly stronger (one-way ANOVA, d.f. = 387.161, F = 17.451, P = 0.03) than that of herbaceous plants, but no significant difference was found between different periods or seasons.

3.6. Spatial patterns of climatic sensitivity of spring-summer phenology

By applying the multiple linear regression analysis method between climatic sensitivity and geographic factors, we found that the regression slope of temperature sensitivity against longitude $(0.30\,\mathrm{days}\,^\circ\mathrm{C}^{-1}\,^\circ\mathrm{-1})$ was significant across all species, which suggested that the overall temperature sensitivity of spring-summer phenology tended to be stronger from east to west. Overall, geo-

graphic factors could only explain 39% (P<0.05) of variation in temperate sensitivity of spring-summer phenology for all species. However, for herbaceous plants or woody plants alone, no consistent spatial patterns of the temperature sensitivity were found. Moreover, there were no consistent patterns between precipitation sensitivity and geographic factors.

4. Discussion

4.1. Comparisons of the spring-summer phenological trends with previous studies

Our results showed that 65% of the 642 spring-summer phenological time series across the QTP exhibited an advancing trend during 1981-2011, and the mean advancing rate was 2.69 days decade⁻¹ (Table 2a). In a meta-analysis of herbaceous and woody plant phenological observations from the published literatures, Ma and Zhou (2012) reported a greater advancing rate of 6.13 days decade⁻¹ in spring phenology in China during the 1980s-2000s compared to our estimate $(3.29 \, days \, decade^{-1})$ in spring phenology during 1981-2011. However, based on a metaanalysis of plant and animal phenological observations, a more recent study by Ge et al. (2015) reported a mean advancing rate of 2.75 days decade⁻¹ in spring-summer phenology in China from the 1960s to the 2000s. Our estimate $(2.69 \,\mathrm{days}\,\mathrm{decade}^{-1})$ in the QTP is generally consistent with that from Ge et al. (2015), which focused on the entire China and only used three phenological stations in the QTP. The spring-summer phenology change trend in the QTP has been shown to be comparable to that in Europe $(-2.5 \,\mathrm{days}\,\mathrm{decade}^{-1})$ (Menzel et al., 2006) and the Northern Hemisphere $(-2.8 \, days \, decade^{-1})$ (Parmesan, 2007). These comparisons implied that the overall phenology shifts in the permafrost of the QTP kept a similar pace with other regions worldwide, although a more rapid climate warming trend was found in this region (Duan and Xiao, 2015; Liu and Chen, 2000).

Our study found that the spring-summer phenology maintained a continuous advancing trend in the OTP during 1981–2011. We did not observe a slowdown or turnover for the change trends after 2000. For herbaceous plants, the advancing trend during 2000–2011 (-1.46 days decade⁻¹) was smaller, but nonsignificantly, than that during $1981-1999(-1.93 \text{ days decade}^{-1})$. In contrast, for woody plants, the advancing trend during 2000-2011 $(-5.68 \,\mathrm{days}\,\mathrm{decade}^{-1})$ was greater, although still non-significantly, than that during 1981-1999 (-4.55 days decade⁻¹). For all vegetation types, the advancement was significantly greater during $2000-2011 (-3.13 \, days \, decade^{-1})$ than that during 1981-1999(-2.73 days decade⁻¹) (Table 2a). This continuous advancement in spring-summer phenology was consistent with the result of Zhang et al. (2013b), who also found a continuous advancing trend in green-up phenology of the plateau by combining multi-source remote sensing data. However, it disagreed with the results of Yu et al. (2010) and Piao et al. (2011), who reported a delaying spring phenology after 2000 based on the AVHRR GIMMS NDVI data. As noted by Zhang et al. (2013b), the GIMMS NDVI data had worsened quality for the western Plateau, which might skew the phenological change trends based on this NDVI dataset (Kobayashi and Dye, 2005; Shen et al., 2014b).

4.2. Diverse responses of phenology advancement to climate warming

Our study observed significant differences in the magnitudes of advancement in spring-summer phenology for different vegetation types, thermal conditions and seasons. The advancing trend of woody plants was significantly stronger than that of herba-

Table 3Summaries of temperature sensitivities of spring-summer phenology across the Qinghai-Tibetan Plateau (QTP). (a) Temperature sensitivities of spring-summer phenology for different time periods, (b) Temperature sensitivities of spring-summer phenology for different vegetation types during 1981–2011, (c) Temperature sensitivities of spring-summer phenology for different seasons during 1981–2011.

(a) Tamparatura	consitivities of enring summer phonology for e	lifferent time periods					
(a) remperature s	sensitivities of spring-summer phenology for d	interent time periods					
Period	Temperature sensitivity (days $^{\circ}C^{-1}$)	95% confidence interval	N	$P_{\rm all}$	$P_{\rm sig}$	$N_{ m all}$	$N_{\rm sig}$
1981–1999 –2.83		[-3.36, -2.31]	160	0.21	0.03	0.79	0.23
2000-2011 - 3.15		[-3.43, -2.86]	[-3.43, -2.86] 572		0.01	0.84	0.23
1981-2011	-3.48	[-3.75, -3.21]	597	0.14	0.00	0.86	0.33
Vegetation type	sensitivities of spring-summer phenology for c Temperature sensitivity (days °C ⁻¹		N N	P_{all}	P_{sig}	N _{all}	N _{sig}
Herbaceous plant	ts -2.58	[-2.91, -2.24]	332	0.2	0	0.8	0.24
Woody plants	-4.42	[-4.78, -4.06]	265	0.07	0	0.93	0.45
	sensitivities of spring-summer phenology for d						
Season	Temperature sensitivity (days ° C ⁻¹)	95% confidence interval	N	$P_{\rm all}$	P_{sig}	$N_{\rm all}$	$N_{\rm sig}$
Spring	-3.56	[-3.86, -3.26]	442	0.1 3	0.00	0.87	0.37
Summer	-3.18	[-3.76, -2.60]	155	0.19	0.01	0.81	0.21

Note: The bold black numbers indicate significant (P < 0.05) temperature sensitivities. N: number of data. P_{all} and N_{all} : proportions of positive and negative trends, respectively. P_{sig} and N_{sig} : proportions of significant (P < 0.05) positive and negative trends, respectively.

Table 4Summaries of precipitation sensitivities of spring-summer phenology across the Qinghai-Tibetan Plateau (QTP). (a) Precipitation sensitivities of spring-summer phenology for different time periods, (b) Precipitation sensitivities of spring-summer phenology for different vegetation types during 1981–2011, (c) Precipitation sensitivities of spring-summer phenology for different seasons during 1981–2011.

(a) Precipitation	n sensitivities of spring-summer phenology for diffe	rent time periods					
Period	Precipitation sensitivity (0.1 days mm ⁻¹)	95% confidence interval	N	$P_{\rm all}$	$P_{\rm sig}$	$N_{\rm all}$	$N_{\rm sig}$
1981–1999 –0.11 2000–2011 –0.20 1981–2011 –0.24		[-0.22, -0.01] 160 [-0.26, -0.13] 572 [-0.31, -0.16] 597		0.46 0.39 0.39	0.01 0.02 0.03	0.54 0.61 0.61	0.03 0.04 0.05
(b) Precipitation	n sensitivities of spring-summer phenology for diffe	rent vegetation types during 1981-	2011				
Vegetation type	Precipitation sensitivity (0.1 days mm ⁻¹) 95% confidence interval	N	P_{all}	P_{sig}	N _{all}	$N_{\rm sig}$
Herbaceous plants -0.20 Woody plants -0.35		[-0.29, -0.11] [-0.49, -0.21]	332 265	0.38 0.40	0.03 0.02	0.62 0.60	0.06 0.03
(c) Precipitation	n sensitivities of spring-summer phenology for diffe	rent seasons during 1981–2011					
Season	Precipitation sensitivity (0.1 days mm ⁻¹)	95% confidence interval	N	$P_{\rm all}$	$P_{\rm sig}$	$N_{\rm all}$	$N_{\rm sig}$
Spring Summer	- 0.45 -0.02	[-0.58, -0.31] [-0.08, 0.04]	442 155	0.36 0.48	0.03 0.01	0.64 0.52	0.05 0.03

Note: The bold black numbers indicate significant (P < 0.05) precipitation sensitivities. N: number of data. P_{all} and N_{all} : proportions of positive and negative trends, respectively. P_{sig} and N_{sig} : proportions of significant (P < 0.05) positive and negative trends, respectively.

ceous plants ($-4.90 \text{ } vs -1.32 \text{ days} \text{ decade}^{-1}$) in the QTP during 1981–2011 (Table 2a), which is consistent with the finding that the advancing trend of trees was significantly stronger than that of herbs and grasses ($-3.3 \text{ } vs. -1.1 \text{ days} \text{ decade}^{-1}$) in the Northern Hemisphere (Parmesan, 2007). However, there were also some other studies reporting a stronger advancement for herbs than trees. For example, Ge et al. (2015) found that the mean spring advancement of trees was significantly weaker than herbs ($-2.29 \text{ } vs. -5.71 \text{ days} \text{ decade}^{-1}$) in China during 1960s–2000s, and Root et al. (2003) reported that the advancement in spring phenology of trees was significantly weaker than non-trees ($-3.0 \text{ } vs. -5.2 \text{ days} \text{ decade}^{-1}$) in the Northern Hemisphere. The difference in estimated advancing trends might be due to differences in the study area and selected plant species.

Temperature is an important factor influencing the change trend in spring-summer phenology. Our study showed that the advancing trend in spring-summer phenology was significantly greater under warmer climate condition (Table 2c). Moreover, the advancement was significantly stronger in areas with a greater warming trend. As a result, the advancement in spring phenology was significantly

stronger than that in summer phenology (Table 2d) because the warming trend in the spring was significantly greater than that in the summer in the QTP(Table S3). Similar results were also reported in other studies. For example, Piao et al. (2011) found that spring phenology advanced more in areas with a greater warming trend in the QTP based on remote sensing data. Chen and Xu (2012) found that in the temperate zone of China, the change trends of the spring start date correlated negatively with the trend of spring temperature during the optimum length period, and the negative response of the start date to temperature was stronger at warmer locations. Ge et al. (2015) found that sites with a greater increasing trend in the March-August mean temperature had significantly earlier spring-summer phenophases for woody plants in China. Similarly, in Europe, most of the spring phenophases showed a stronger response to temperature in warmer countries (Menzel et al., 2006).

4.3. Climatic sensitivity of spring-summer phenology

Our results showed that the spring-summer phenology advanced 3.48 days as the mean temperature increased by $1\,^\circ\text{C}$

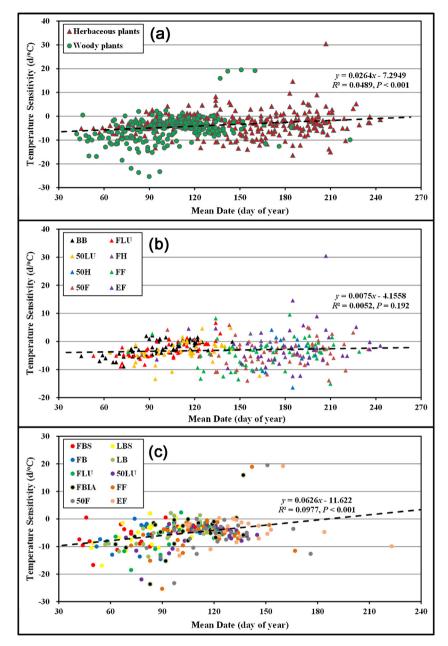


Fig. 2. Temperature sensitivity for the onset dates of different phenological events during 1981–2011. (a) All species, (b) herbaceous plants, and (c) woody plants. Phenological events: BB, bud burst; FLU, first leaf unfolding; 50LU, 50% leaf unfolding; FH, first heading; 50H, 50% heading; FF, first flowering; 50F, 50% flowering; FBS, flower bud swelling; LBS, leaf bud swelling; FB, flower budburst; LB, leaf budburst; FBIA, flower bud or inflorescence appearance.

across the QTP during 1981-2011 (Table 3a). The response of spring-summer phenology to the mean temperature was more sensitive than that to the minimum temperature $(-1.17 \,\mathrm{days}\,^{\circ}\mathrm{C}^{-1})$ (Table S5). However, there were significant differences in temperature sensitivity for different vegetation types, time periods, thermal conditions and seasons (Table 3a,b,c; Fig. 2). Similar results were also reported by previous studies in China. For example, Chen and Xu (2012) found that the sensitivity of the SOS date to air temperature changes during the optimum spring length period ranged from $-1.02\,days\,^{\circ}C^{-1}$ to $-7.63\,days\,^{\circ}C^{-1}$ for the Ulmus pumila tree species in the temperate zone of China during 1986-2005, depending on thermal conditions. Dai et al. (2014) found that the temperature sensitivity of the first leaf date for four woody plant species ranged from −3.30 days °C⁻¹ to −3.93 days °C⁻¹ in China during 1960-1990. Wang et al. (2015) reported that the mean sensitivity of the spring phenology index (SPI) to spring temperature

in the subtropical region $(-3.7 \, \text{days} \,^{\circ} \, \text{C}^{-1})$ was stronger than that in the temperate region $(-2.5 \, \text{days} \,^{\circ} \, \text{C}^{-1})$ of China during 1850–2009. The temperature sensitivity of SPI varied among consecutive 30-year periods, up to $-4.6 \, \text{days} \,^{\circ} \, \text{C}^{-1}$ and $-6.2 \, \text{days} \,^{\circ} \, \text{C}^{-1}$ in temperate and subtropical regions, respectively, during the most recent 30 years (i.e., 1975–2009), which exceeded all recorded temperature sensitivities in previous periods.

Except for the temperature change trend, the temperature sensitivity of phenophases is also a key factor in determining phenological trends (Ge et al., 2015; Shen et al., 2014a; Wang et al., 2015). The warming trend in mean spring-summer temperature throughout 2000–2011 was significantly weaker than that during 1981–1999 in the QTP (Table S4). However, the advancement in spring-summer phenology during 2000–2011 was significantly stronger than that during 1981–1999 (Table 2a). This contradiction could be explained by the stronger temperature sensitivity

Table 5The spatial patterns of climatic sensitivities. (a) Temperature sensitivity, (b) Precipitation sensitivity.

(a) Temperature sensitivity									
N		S_{lat} (days \circ C ⁻¹ \circ -1)	S_{lon} (days \circ C ⁻¹ \circ -1)	S _{alt} (days °C ⁻¹ km ⁻¹)	S _{int} (days °C ⁻¹)	R^2			
All species	20	0.106	0.300*	1.625	-42.024	0.388*			
Herbaceous plants	20	0.196	0.126	0.859	11.472	0.141			
Woody plant	15	0.097	0.370	2.166	-50.846	0.195			
(b) Precipitation sensiti	vity								
	N	S_{lat} (days mm ⁻¹ °-1)	S _{lon} (days mm ⁻¹ ∘ −1)	$S_{\rm alt}$ (days mm ⁻¹ km ⁻¹)	S _{int} (days mm ⁻¹)	R^2			
All species	20	-0.013	-0.011	-0.002	1.476	0.090			
Herbaceous plants	20	-0.014	-0.008	-0.002	1.306	0.193			
Woody plant	15	0.007	-0.020	0.127	1.316	0.074			

Note: N: number of sites. S_{lat} , S_{lon} , S_{alt} and S_{int} : parameters in Eq. (1). R^2 : explained variance of Eq. (1).

of spring-summer phenology during 2000–2011 (Table 3a), which was also observed in the temperate and subtropical regions of China (Wang et al., 2015). The spring phenology of vegetation might have higher temperature sensitivity in warmer areas in the Northern Hemisphere (Shen et al., 2014a). Moreover, the temperature sensitivity of spring-summer phenology was stronger at lower latitudes or altitudes (warmer locations) than at higher latitudes or altitudes (colder locations) in our study, although the relationship was not significant (Table 5a). It was consistent with the findings of previous studies (e.g., Dai et al., 2014; Menzel et al., 2006).

Our results showed the spring-summer phenology advanced 2.4 days in response to 100 mm increase of precipitation across the QTP during 1981–2011 (Table 4a). In a previous study based on remote sensing data, Piao et al. (2006) suggested that the onset date of green-up postponed with an increase in precipitation of the preceding months for the alpine meadow in China, which is mostly distributed in the QTP. However, Shen et al. (2011) found that increased preseason precipitation tended to advance the onset of green up at many stations. In our study, we found the precipitation sensitivity of spring-summer phenology varied among different periods, vegetation types and seasons, but overall, increased precipitation would advance the spring-summer phenology.

5. Conclusions

Plant phenology is a sensitive indicator of the effect of climate change on vegetation dynamics. Because of the higher vulnerability and sensitivity to climate change, phenology shifts in the Qinghai-Tibetan Plateau (QTP) have been receiving more and more attention. However, great controversy still exists regarding the change in direction and magnitudes of spring-summer phenology. Most previous studies were based on remote sensing data but lacked sufficient ground observational data to reveal the actual phenology shifts. With continuous and long-term ground observational data, our study found a continuous advancing trend in spring-summer phenology across all the species with a mean rate of 2.69 days decade⁻¹ during 1981–2011. However, diverse advancing rates in spring-summer phenology were observed for different vegetation types, thermal conditions and seasons. The diverse advancing trends matched well with the differences in sensitivity of spring-summer phenology to increasing temperature, implying that different responses to temperature change was one of the major factor controlling the varied spring-summer phenology shifts across the QTP. Besides, increased precipitation could advance the spring-summer phenology. The response of springsummer phenology to temperature tended to be stronger from east to west for all species, while the response to precipitation showed no consistent spatial pattern.

Since a stronger temperature sensitivity of spring-summer phenology in the OTP was found in the warmer locations or locations with a greater warming trend, future climate warming may enhance the sensitivity of plant phenological response to temperature (Chen and Xu, 2012) and further promote the advancement of spring-summer phenology, especially in colder regions like the QTP where a greater rate of climate warming is anticipated. However, large uncertainties still exist when estimating the future change trend in spring-summer phenology across the QTP. Although enhanced sensitivity of plant phenological response to temperature could increase the advancement of spring-summer phenology under projected climate warming scenarios, reduced chilling fulfillment and possible reduced rainfall might delay spring-summer phenology (Chen et al., 2015; Yu et al., 2010). Therefore, a series of controlled experiments, along with simulated results, is still required to further investigate the change in spring-summer phenology across the QTP under projected climate warming scenarios.

Acknowledgements

This work was supported by the National Natural Science Foundation of China (No. 41371389) and the State Key Laboratory of Earth Surface Processes and Resource Ecology (No. 2013-ZY-14).

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.2016. 04.012.

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^{*} P < 0.05

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