Plant phenological sensitivity to climate change on the Tibetan Plateau and relative to other areas of the world

JI SUONAN [ID],[1,2,3] AIMÉE T. CLASSEN,[3,4,5] NATHAN J. SANDERS,[3,4,5] AND JIN-SHENG HE[1,6],†

[1]Department of Ecology, College of Urban and Environmental Sciences, Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, 5 Yiheyuan Road, Beijing 100871 China
[2]Key Laboratory of Alpine Ecology and Biodiversity, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, No. 16 Lincui Road, Beijing 100101 China
[3]The Center for Macroecology, Evolution, and Climate, Natural History Museum of Denmark, University of Copenhagen, Copenhagen DK-2100 Denmark
[4]Rubenstein School of Environment & Natural Resources, University of Vermont, Burlington, Vermont 05405 USA
[5]The Gund Institute for Environment, University of Vermont, Burlington, Vermont 05405 USA
[6]State Key Laboratory of Grassland Agro-Ecosystems, College of Pastoral Agriculture Science and Technology, Lanzhou University, Lanzhou 730000 China

Abstract. Global warming and changes in precipitation are altering the phenology of plants that significantly impact the functioning and services of ecosystems. Although a number of studies have addressed responses of plant phenology to warming and altered precipitation individually, their interactions can alter plant phenology differently than either does independently. To explore how the interactions between global change drivers alter alpine ecosystems, we conducted a factorial experiment manipulating warming (ambient and +2°C) and altered precipitation (50% decrease, control, and 50% increase) simultaneously in an alpine meadow on the Tibetan Plateau. Over two years, we monitored plant phenological events, leaf-out day and first flowering day, for 11 common plant species that account for 74.4% of the total above biomass. Surprisingly, there was no interaction between warming and changes in precipitation on community plant phenology, but warming advanced leaf-out and first flowering day by 7.10 and 9.79 d, respectively. Unlike the community response, plant functional groups had a variety of direct and interactive responses to the experimental climate drivers. While the phenology of legumes was most influenced by temperature, temperature and precipitation interacted to alter the phenology of grasses and forbs. To explore how plant phenological sensitivity on the Tibetan Plateau is compared with other meadow ecosystems, we combined our dataset with a global plant phenology dataset. Interestingly, the phenological sensitivity of leaf-out day and first flowering day on the Tibetan Plateau is 7.3 and 37.8 times greater than global phenological sensitivity, respectively. This result highlights that a meta-analysis of global phenological sensitivity may significantly underestimate change in some regions—even regions as large as the Tibetan Plateau. Together, our results suggest that the Tibetan Plateau may experience rapid change as temperatures warm and that these changes will likely be more rapid than in other regions of the world. Further, our study highlights that if we are to make accurate predictions of how plant phenology may change with warming, we need to understand the specific environmental cues that drive phenological responses across different areas.

Key words: alpine meadow; altered precipitation; climate change; global warming; phenological sensitivity; plant functional groups; Tibetan Plateau.

† **E-mail:** jshe@pku.edu.cn

INTRODUCTION

Global changes, such as accumulating atmospheric carbon dioxide (CO_2), are directly associated with elevated global temperatures and altered precipitation regimes (Stocker et al. 2013). While global temperatures are rising steadily, changes in precipitation are more variable and both increases and decreases have been observed at regional scales (Wu et al. 2011, Beier et al. 2012, Jamieson et al. 2012, Stocker et al. 2013). Because temperature and precipitation are the main drivers of plant phenology, warming and altered precipitation regimes shift important stages in plant life history, such as leaf-out and flowering time (Arft et al. 1999, Abu-Asab et al. 2001, Fitter and Fitter 2002, Parmesan and Yohe 2003, Peñuelas et al. 2004, Menzel et al. 2006, Cleland et al. 2007). Such shifts in plant phenology may lead to changes in plant reproduction, population-level interactions, community dynamics, and even plant evolution and adaptation—impacts that may ultimately influence important ecosystem functions and services (Peñuelas and Filella 2001, Parmesan 2006, Cleland et al. 2012, Peñuelas et al. 2013).

High-latitude and alpine ecosystems are sensitive to changes in temperature and precipitation (Bliss 1971, Inouye and Wielgolaski 2013, Wielgolaski and Inouye 2013, Panchen and Gorelick 2017, Prevéy et al. 2017) and especially in different forms of precipitation such as snowfall (Chen et al. 2015a); thus, they can act as early-warming ecosystems when attempting to understand the consequences of global changes. The Tibetan Plateau covers 2.5 million km^2, is located at ~4000 m elevation, and has been called "the third pole" of the world (Qiu 2008). Substantial climate changes on the Tibetan Plateau have been observed in recent decades (Liu and Chen 2000, Qin et al. 2009). For example, the mean annual temperature has increased by about 0.4°C per decade over the past 50 yr (Dong et al. 2012), which is more than twice the rate of global temperature rise (Stocker et al. 2013). At the same time, precipitation regimes are also changing across the Tibetan Plateau (Chen et al. 2015b, Shen et al. 2015b). In some regions on the Tibetan Plateau, annual precipitation has increased, but precipitation has decreased in other regions (Chen et al. 2013). These climate changes on the Tibetan Plateau will likely alter plant phenology.

Warming on the Tibetan Plateau advances both leaf-out day and first flowering day of alpine meadow plants (Wang et al. 2014, Suonan et al. 2017). Climate changes like warming and altered precipitation can interact to alter plant phenology differently than either does independently. For example, warming can increase drought stress (Knapp et al. 2008, Overpeck and Udall 2010, Williams et al. 2013) and this stress can alter plant growth, leaf and floral expansion, and leaf and flower turgor maintenance under evapotranspiration demand (Bouchabké et al. 2006, Turc et al. 2016). Therefore, the combined effects of warming and precipitation could be additive, antagonistic, or even synergistic (Beier et al. 2012, Kreyling and Beier 2013, Carón et al. 2015). In addition, different plant functional groups (e.g., grasses, forbs, legumes, and shrubs) can vary in their responses to climate change based on differences in their physiology and life history (Fay et al. 2002, Cleland et al. 2006). For example, some legume species prefer dry environments, while grasses can prefer wet conditions; hence, different local ecophysiological environments can result in variation of reproductive phenology among functional groups (Dorji et al. 2013). In addition, the capacity to use mobilized nutrients differs among plant functional types, which could be why functional groups show different phenological responses to environmental changes such as warming and precipitation, and their interactions between precipitation and warming (Ehleringer et al. 1991, Golluscio et al. 1998, Hu et al. 2013). For example, if warming and increasing precipitation caused soil nitrogen mineralization to increase, nitrogen-fixing legumes could decline while non-legume plants could benefit (Temperton et al. 2007). However, we know little about how the interactive effects of warming and altered precipitation will influence the phenology of alpine plants in general as well as the phenology of different functional groups, or the mechanisms that might be driving the observed patterns.

In addition to absolute changes in phenology, the temperature sensitivity of phenology (change in phenology per °C, hereafter referred to as "phenological sensitivity") is a commonly used metric to quantifying the responses of plant phenology to climate change (Cleland et al. 2012, Wolkovich et al. 2012, Mazer et al. 2013, Friedl et al. 2014, Wang et al. 2015, Li et al. 2016). Phenological

sensitivity is especially useful when comparing results among diverse phenology studies—studies conducted using different methods and at different spatial and temporal scales. A recent global synthesis of short-term warming experiments and long-term observations of phenological sensitivity of plant species found that relative to observations, experiments underestimated the phenological sensitivity (Wolkovich et al. 2012). However, spatial variation in phenological shifts has been less explored. For example, the phenological sensitivity of alpine plants on the Tibetan Plateau could be large relative to other regions in the world because the growing season is short and the temperatures are low. Thus, adding the phenological response of alpine meadow plants on the Tibetan Plateau would add another data point to our global understanding of how plants will respond to climate warming. More crucially, these data and comparisons will help with conservation and rangeland management decisions under projected climate change such as identification and selection of conservation priority areas.

To explore how the direct and interactive effects of warming and changes in precipitation altered alpine plant phenology, we established a multifactorial manipulative experiment with two levels of warming (ambient and warming) and three levels of precipitation change (50% decrease, control, and 50% increase) in an alpine meadow on the Tibetan Plateau. Over two years, we recorded leaf-out day and first flowering day for eleven common species from four functional groups. In addition, in order to explore how our results are compared with studies from other regions and other systems, we extracted the phenological sensitivity of short-term warming experiments from a recent meta-analysis (Wolkovich et al. 2012) and compared those results with the phenological sensitivity we recorded on the Tibetan Plateau. We tested three specific predictions:

1. Warming and altered precipitation would interactively impact the phenology of alpine meadow plants on the Tibetan Plateau. While warming would advance leaf-out day and first flowering day, increased precipitation would decrease soil temperature and slow the phenology. Decreased precipitation would lead to even drier soils under warm conditions and further retard plant development.

2. The phenological responses of plants to warming and altered precipitation would vary among functional groups. For example, grasses will benefit from wetter environments, legumes will advance their phenology in drier treatments, and non-legume plants will benefit from environments relatively rich in nutrients.

3. Because of generally low temperatures and short growing seasons, we predicted that the phenological sensitivity (temperature) of alpine plants on the Tibetan Plateau would be greater than the reported global phenological sensitivity of plants.

MATERIALS AND METHODS

Study site and experiment design

We conducted this experiment at the Haibei Alpine Grassland Ecosystem Research Station managed by the Chinese Academy of Sciences (Haibei Station, 101°12′ E, 37°30′ N, 3200 m asl). The experimental area is dominated by alpine grassland and has a continental monsoon climate, with cold, long winters and short, cool summers. From 1983 to 2013, the mean annual air temperature was 1.1°C and the mean annual precipitation was 485 mm. Over 84% of the precipitation falls during the short summer-growing season from May to September (Zhao and Zhou 1999). Soils at the site are classified as Mat-Gryic Cambisols (Chinese Soil Taxonomy) and as borolls (USDA Soil Taxonomy). Detailed information for our experimental site can be found in previously published papers (Zhao and Zhou 1999, Wang et al. 2014, Suonan et al. 2017).

We established a multifactor warming × precipitation experiment in July 2011 (for details of the experimental setup, see Ma et al. 2017, Suonan et al. 2017, Liu et al. 2018, and Xu et al. 2018). Briefly, we used a randomized block design with two levels of temperature (ambient and +2°C) and three levels of precipitation (50% reduction, control, and 50% addition). Each experimental plot was 2.2 × 1.8 m with at least a 2.5 m buffer zone among treatment plots distributed in six blocks. Therefore, the six treatments in our study were control, drought (50% decrease in precipitation), water addition (50% increase in precipitation), warmed (+2°C), warmed and drought, and warmed and water addition.

An infrared heating structure was established above all the plots as a control, but only the warmed plots were warmed. Two medium-wave infrared heaters (1200 W, 220 V, 1 m long, and 0.22 m wide) or their light-free control boxes were fixed 1.5 m above the ground within each plot with stainless steel stakes. Above the drought zone, a rainout shelter with 20 cm wide clear polycarbonate slats spaced 20 cm apart removed 50% of incoming precipitation from the drought treatments. During the non-freezing months, this water drained into storage bucket and was manually transferred to the wet section in each rainfall event, to achieve a 50% increase in water addition plots. Ambient and wet treatment plots had similar infrastructure that controlled for shading from the rainout shelters. In two plots within each treatment, temperature and moisture probes (EM50; Decagon Devices, Pullman, Washington, USA) were installed. Air temperature probes were installed 30 cm above the soil surface, and soil temperature and moisture probes were installed at 5, 10, and 20 cm in the soil profile; all data were automatically recorded hourly and stored in a data logger. We only used soil moisture data during the growing season (12 April–19 October 2013; 4 April–17 October 2014; the definition of the start and end of the growing season; Suonan et al. 2017) because the soil moisture probes did not give accurate readings when the soil was frozen. Hourly soil temperature and moisture data were averaged to daily level in this study.

Phenology measurements

We used a pool of 11 common plant species to explore how warming altered plant phenology. Each species was monitored every three to four days during the growing season from March to September in 2013 and 2014. In total, we observed the phenology of three grasses, one sedge, two legumes, and five forbs (Table 1). Combined, the selected pool of eleven species made up 70–80% of the relative cover and 74% of the total biomass in the plant community (Table 1). To track leaf-out day, individuals in each plot were marked when the first leaf was observed. Once all the plants had leafed out, six individuals for forbs and legumes and six stems for grasses and sedges were randomly selected, marked, and monitored for the duration of the

growing season. We were unable to identify the leaves of *Stipa alinea* and *Poa pratensis* grass species during their leaf-out phase; thus, we tracked nine out of the 11 species for leaf-out day over the course of the study. The first date a flower was observed for each of the marked individuals was recorded as the first flowering day. Flowering rates were low for two out of the 11 species monitored (*Saussure superba* and *Aster diplostephioides*); thus, we monitored first flowering day for nine species across the 2 yr. Leaf-out day and first flowering day events were averaged for six individuals of each species within each plot.

Phenological sensitivity

We calculated the phenological sensitivity using the experimental control and the warmed treatment approach outlined by Wolkovich et al. (2012):

$$\big(\text{Phenological event date}_{i,\text{warm}} - \\ \text{Phenological event date}_{i,\text{control}}\big)/\Delta T$$

where ΔT is the change in the air temperature between warmed-only and control treatments. We calculated the average phenological sensitivity for each of the species monitored in this study and used these data to represent the phenological sensitivity of the community at the site.

Table 1. Functional group and biomass information on the species examined in this study.

Species	Abbreviation	Functional group	Contribution to community biomass (%)
Stipa alinea	Sa	Grass	44.62
Elymus nutans	En	Grass	3.13
Poa pratensis	Pp	Grass	2.75
Kobresia humilis	Kh	Sedge	3.59
Tibetia himalaica	Th	Legume	4.73
Melilotoides archiducis-nicolai	Ma	Legume	1.53
Gentiana lawrencei	Gl	Forb	4.60
Aster diplostephioides	Ad	Forb	3.65
Potentilla saundersiana	Ps	Forb	3.54
Gentiana straminea	Gs	Forb	1.24
Saussurea superba	Ss	Forb	0.97

Note: The 11 species accounted for over 74.4% of community aboveground biomass.

Statistical analysis

We used linear mixed-effects models (restricted maximum likelihood (REML) estimation) to test the separate and interactive effects of temperature and precipitation on soil temperature (5 cm) and soil moisture (5 cm). We set temperature × precipitation as fixed factor and time nested within plot within block as a random effect in each model to account for variation among repeated measurements of temperature or moisture (time represents the date that the soil temperature and moisture were measured). Next, we used Tukey's tests to conduct pairwise comparisons of differences in soil temperature and moisture between ambient and warming treatments at three precipitation levels (drought, control, and wet), and among drought, control, and wet at two warming levels (ambient and warming) within each year. Linear mixed-effects models were used to examine the separate and interactive effects of year, temperature, and precipitation on plant phenology (leaf-out day and first flowering day). We set year × temperature × precipitation as fixed factor and species nested within plot within block as random factor to account for variation among species within plot within block. All the species we studied were pooled together to test the community-level phenology. In addition, we used Tukey's tests to conduct pairwise comparisons of differences in plant phenology between ambient and warming treatments, and among drought, control, and wet treatments in each year. We also used linear mixed-effects models to examine the separate and interactive effects of temperature, precipitation, year, and species on plant phenology (leaf-out day and first flowering day). We set temperature × precipitation × year × species as fixed factor and plot within block as random factor to account for variation among plot within block.

For each functional group (grass, sedge, legume, and forb), we used linear mixed-effects models to test the separate and interactive effects of temperature and altered precipitation on the phenology (leaf-out day and first flowering day) in each year (2013 and 2014). We used two different variables as fixed factors to test the effects more accurately. First, we used temperature and precipitation as categorical variables to test the effects of temperature and precipitation. Second, we used soil moisture collected during the growing season and soil temperature as a continuous variable to test the effects of soil temperature and moisture. "Species" was used as a random factor in all analyses to account for variation among species. For functional groups with single species, we used generalized least squares models to test the effects of temperature and altered precipitation on the phenology within each year. These analyses made sure that the results found for single species functional groups were comparable with the results of linear mixed-effects models used for functional groups with more than one species in our study. All analyses were performed in R 3.3.1 (R Development Core Team, 2016) using the lme and gls function in package nlme (Pinheiro et al. 2007).

In addition, we calculated the average phenological sensitivity (leaf-out day and first flowering day) for each of the 11 species in our study and then averaged them to get a site-level measurement. Additionally, a global dataset (Wolkovich et al. 2012) presented the average phenological sensitivity of worldwide warming experiments (36 experimental sites) for both leaf-out day and flowering day. We then compared our site-level phenological sensitivity with the global-level phenological sensitivity in the global dataset to see how the phenological response of alpine plants on the Tibetan Plateau varies from other places. Furthermore, we extracted plant phenology sensitivity data from two additional studies conducted at high-latitude arctic areas (Panchen and Gorelick 2017, Prevéy et al. 2017), to compare our results with other cold and climate-sensitive ecosystems.

To put our results into a global context, we extracted the phenological sensitivity of plants at 24 experimental sites (leaf-out day; the global dataset includes 36 sites totally, data for only 24 study sites were available). To explain the variation of phenological sensitivity among different areas, we extracted a series of abiotic factors. Using the coordinates of the 24 sites and our own site, we extracted the mean monthly temperature of each site from the WorldClim database (www.worldclim.org). We used these data to calculate the mean annual temperature (MAT) and the temperature range (*T* range: temperature of the warmest and the coldest month) for each site. In addition, we extracted the degree of warming in each experiment (Δ*T*) and calculated the

percentage of the degree of warming in mean annual temperature for each site (ΔT/MAT). Next, we explored a regression relationship between the phenological sensitivity of 25 sites and each of the abiotic factors: MAT, T range, ΔT, and ΔT/MAT. Lastly, all the focal plant species included in each of the 24 study sites were extracted. With the addition of the 11 species in our study, we constructed a phylogenetic tree for the complete set of taxa using the software program Phylomatic (Webb and Donoghue 2005). All these analyses were performed using R 3.3.1 (R Development Core Team 2016).

RESULTS

Treatment effects on soil temperature and moisture

As expected, warming elevated soil temperatures (Fig. 1a). Specifically, on average across two years, warming increased soil temperatures at 5 cm depth by 1.77°C relative to ambient plots (temperature: $F_{1,5} = 156.523$, $P < 0.001$; precipitation: $F_{2,5} = 2.709$, $P = 0.160$; temperature × precipitation: $F_{2,5} = 4.269$, $P = 0.083$; Fig. 1a). Soil temperatures (5 cm) in drought and wet treatments were 0.15°C and 0.04°C lower than in ambient plots across two years, respectively (Fig. 1a). Relative to the ambient plots, soil temperature (5 cm) in the warmed and drought plots was 0.68°C warmer and 0.40°C lower in warmed and wet plots (Fig. 1a). Furthermore, increased and decreased precipitation led to wetter and drier soil, respectively (Fig. 1b). On average across two years, soil moisture (5 cm) during the growing season was 6.0% lower in drought plots relative to control plots, while wet plots had 2.7% more moisture relative to control treatments (temperature: $F_{1,5} = 20.005$, $P = 0.007$, precipitation: $F_{2,5} = 66.458$, $P < 0.001$; temperature × precipitation: $F_{2,5} = 3.190$, $P = 0.128$; Fig. 1b). Relative to control plots, soil moisture (5 cm) during the growing season was 1.7% higher in warmed and wet plots, and 5.3% and 8.9% lower in warmed plots and warmed and drought plots, respectively, across two years (Fig. 1b).

Phenological responses at the community level

Unexpectedly, we found no interactive effects of temperature and precipitation on either leaf-out day ($F_{2,20} = 0.102$; $P = 0.904$; Table 2, Fig. 2a, b) or first flowering day ($F_{2,20} = 0.002$; $P = 0.998$; Table 2, Fig. 2c, d) at the community level. However, there were direct effects of temperature and
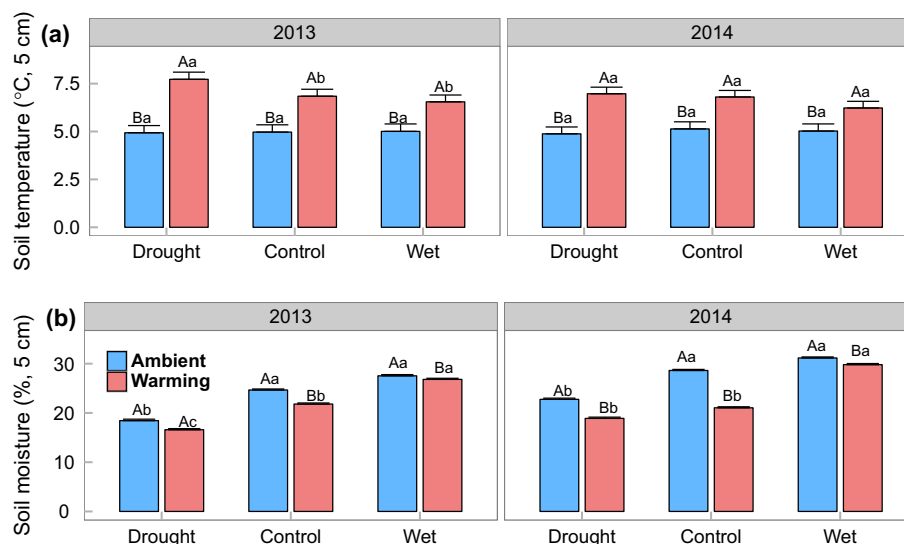

Fig. 1. Average soil temperature (a) and soil moisture in growing season (b) at 5 cm depth of all temperature and altered precipitation treatments in two years (2013 and 2014). Mean ± SE is shown in the figures. Different capital letters indicate significant differences between ambient and warming treatments at 0.05 level, and different lowercase letters indicate significant differences among drought, control, and wet treatments at 0.05 level.

Table 2. Linear mixed-effects models showing the independent and interactive effects of year, temperature, and precipitation on leaf-out day and first flowering day at community level.

	Leaf-out day			First flowering day		
Treatments	df	F	P	df	F	P
Year	1, 243	509.004	**<0.001***	1, 247	12.749	**<0.001***
Temp	1, 20	8.985	**0.007**	1, 20	8.457	**0.009**
Precip	2, 20	2.496	0.108	2, 20	0.327	0.725
Year × Temp	1, 243	0.271	0.603	1, 247	5.817	**0.017***
Year × Precip	2, 243	4.455	**0.013***	2, 247	3.328	**0.038***
Temp × Precip	2, 20	0.102	0.904	2, 20	0.002	0.998
Year × Temp × Precip	2, 243	0.044	0.957	2, 247	0.909	0.404

Notes: Species nested within plot nested within block was used as a random factor to account for variation among species within plot within block. Temp and Precip indicate temperature and precipitation, respectively. The bold numbers denote significant effects.
F values are shown, and the asterisks denote significance at *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.
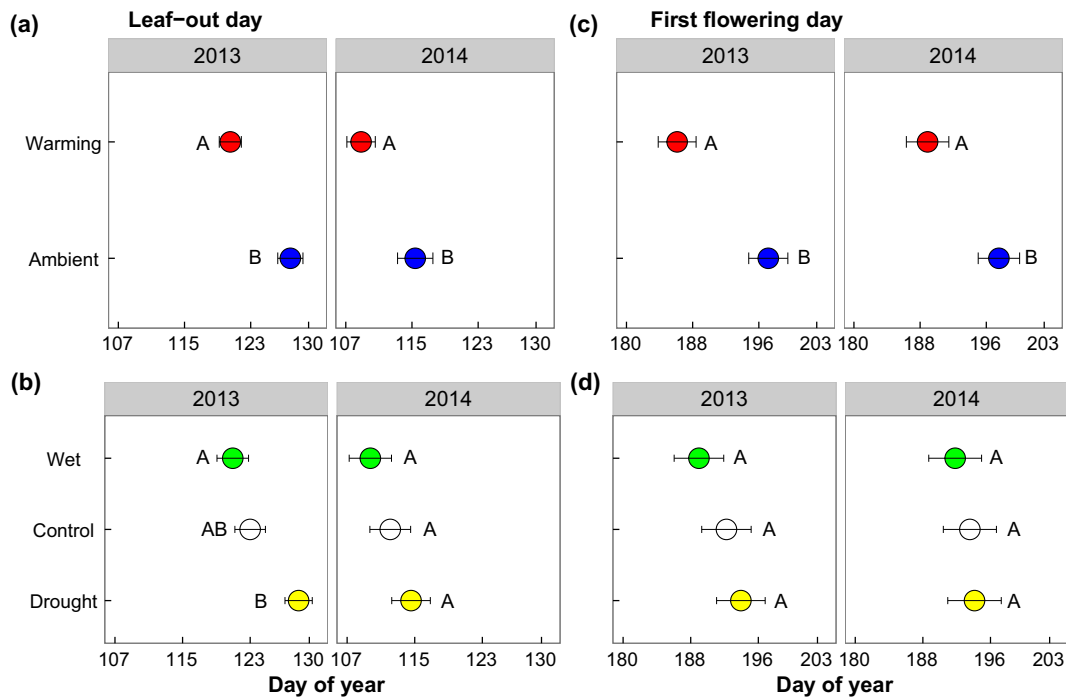

Fig. 2. Average leaf-out day and the first flowering day for all species monitored in two years (2013 and 2014). (a) Leaf-out day in temperature treatments: ambient and warming; (b) leaf-out day in precipitation treatments: drought, control, and wet; (c) first flowering day in temperature treatments: ambient and warming; (d) first flowering day in precipitation treatments: drought, control, and wet; ambient in (a) and (c) is the average of control (no temperature and precipitation treatment), water decreasing, and water addition; warming in (a) and (c) is the average of warmed, warmed with water decreasing, and warmed with water addition; drought in (b) and (d) is the average of water decreasing and warmed with water decreasing; control in (b) and (d) is the average of control (no temperature and precipitation treatment) and warmed; wet in (b) and (d) is the average of water addition and warmed with water addition. Mean ± SE is shown in the figures. Different letters indicate significant differences among treatments at 0.05 level.

precipitation on phenology. Across two years, warming significantly advanced leaf-out day by 7.10 d relative to ambient plots (Table 2, Fig. 2a). In contrast, drought delayed leaf-out day by 4.39 d, while water addition advanced leaf-out day by 1.88 d relative to control treatments (Table 2, Fig. 2b). Similarly, across two years, first flowering day was advanced by 9.79 d in warmed plots relative to ambient plots (Table 2, Fig. 2c). Again, drought treatments delayed first flowering day by 1.12 d while water addition advanced first flowering day by 2.48 d (Table 2, Fig. 2d). Moreover, phenology patterns were often species-specific and variations were found between years (Table 2; Appendix S1: Table S1; Figs. S1, S2).

Phenological responses of functional groups

As predicted, functional groups varied in their response to the warming and precipitation treatments. To test the responses of each functional groups independently, we performed a more extensive analysis of the explanatory variables (temperature and precipitation as categorical variables; soil temperature and moisture as continuous variables). We found that the phenology of grass and forb was controlled by both temperature and precipitation; however, the phenology of legumes was related to temperature (Figs. 3 and 4, Table 3). In addition, the leaf-out day and first flowering day of each functional groups showed similar results (Figs. 3 and 4, Table 3). Unlike community phenological response in this study, we found significant interactive effects of temperature and precipitation on first flowering day for some of functional groups (Table 3). However, the interactive effects on first flowering day were inconsistent between years (Table 3).

Phenological sensitivity

The phenological sensitivity of leaf-out day and first flowering day at our site are −11.7 and −18.9 d/°C, respectively (Fig. 5), indicating that phenological sensitivity at the site was greater than at other sites around the world (leaf-out day: −1.6 d/°C; first flowering day: −0.5 d/°C; Wolkovich et al. 2012). Specifically, the phenological sensitivity of leaf-out day and first flowering day on the Tibetan Plateau is 7.3 and 37.8 times greater than global phenological sensitivity, respectively. More interestingly, in contrast to the meta-analysis, phenological sensitivity of the first flowering day in our study showed a greater response than leaf-out day. Furthermore, leaf-out day and first flowering day at our site were more sensitive to
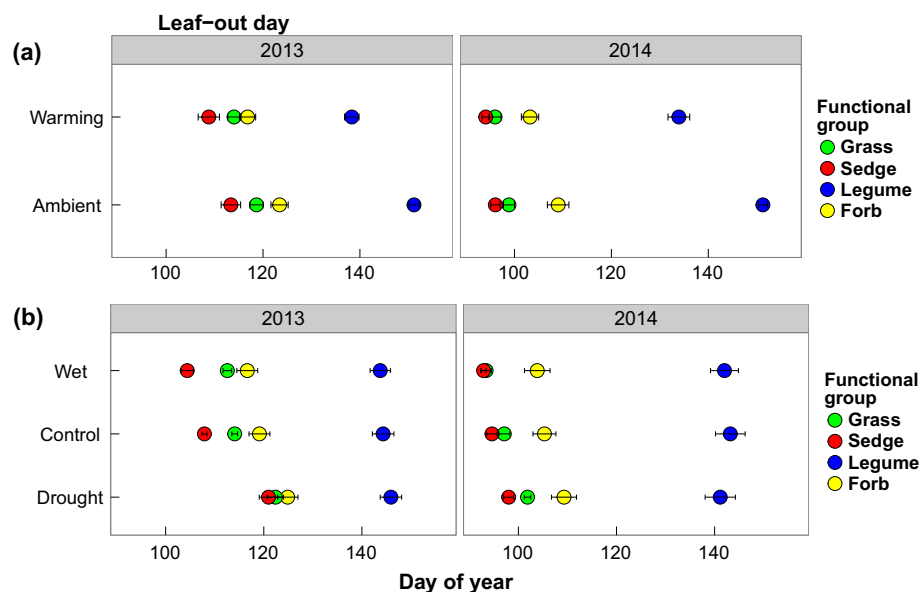

Fig. 3. The effects of temperature and altered precipitation on leaf-out day of four functional groups (grass, sedge, legume, and forb) in two years (2013 and 2014). (a) The effects of temperature treatments: ambient and warming; (b) the effects of precipitation treatments: drought, control, and wet. Means ± SE is shown in the figures.
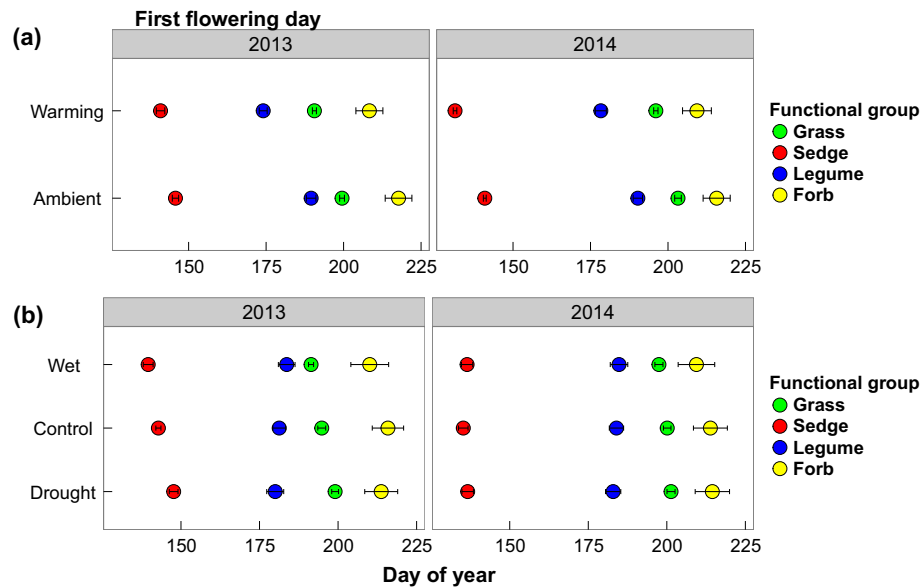
First flowering day

Fig. 4. The effects of temperature and altered precipitation on first flowering day of four functional groups (grass, sedge, legume, and forb) in two years (2013 and 2014). (a) The effects of temperature treatments: ambient and warming; (b) the effects of precipitation treatments: drought, control, and wet. Mean ± SE is shown in the figures.

Table 3. Linear mixed-effects models showing the separate and interactive effects of temperature and precipitation on leaf-out day and first flowering day of four functional groups (grass, sedge, legume, and forb) in 2013 and 2014.

	2013				2014			
Variable	Grass	Sedge	Legume	Forb	Grass	Sedge	Legume	Forb
Leaf-out day								
Temp	**22.945*****	**12.769****	**224.786*******	**42.843*****	**7.204***	3.959	**97.276*****	**21.458*****
Precip	**39.851*****	**62.544*****	2.397	**34.761*****	**19.597*****	**8.410***	0.483	**11.046*****
Temp × Precip	1.136	1.765	0.055	1.068	0.763	0.630	0.644	0.860
ST	0.372	0.001	**109.012*****	**6.137***	3.297	0.269	**38.381*****	**4.730***
SM	**13.236****	**10.680***	**6.034***	**24.264*****	**47.906*****	3.475	0.000	**16.534*****
ST × SM	0.000	0.107	3.748	3.958	2.936	0.025	3.005	1.733
First flowering day								
Temp	**208.587*****	**16.275*****	**167.385*****	**219.891*****	**100.124*****	**168.130*****	**100.255*****	**71.512*****
Precip	**51.986*****	**15.592*****	2.216	**5.740****	**10.131*****	1.392	1.417	**5.249****
Temp × Precip	**4.174*****	0.947	1.186	0.115	1.109	0.566	2.203	**5.748***
ST	**18.270*****	0.087	**36.632*****	**78.192*****	**31.808*****	**21.680****	**56.681*****	**33.647*****
SM	**28.285*****	**10.216***	0.000	**13.411****	**19.806*****	1.147	0.436	1.862
ST × SM	**5.875***	**6.130***	1.553	2.470	3.063	4.147	0.560	**8.168****

Notes: The results from two different methods for fixed factor are shown: First, temperature and precipitation were used as categorical variables; second, soil temperature and soil moisture were used as continuous variables. Species was used as a random factor to account for variation among species. To make sure the results of single species functional groups are comparable with the results of linear mixed-effects models that were used for functional groups with more than one species in our study, we used generalized least squares models for functional groups with single species to test the effects of explanatory variables on the phenology in each year. Temp and Precip indicate temperature and precipitation, respectively. ST and SM indicate soil temperature and moisture, respectively. ST and SM were measured at 5 cm soil depth. The bold numbers denote significant effects.

F values are shown, and the asterisks denote significance at $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.
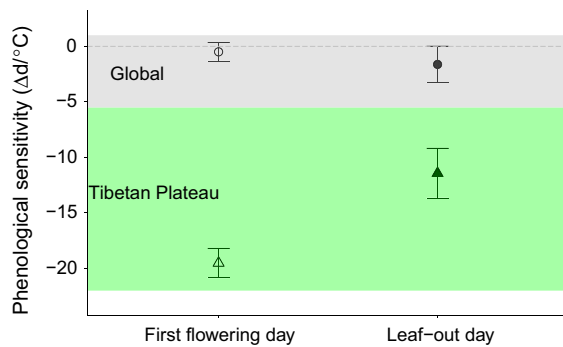
Fig. 5. Comparison of average phenological sensitivity (Δ days/°C) of leaf-out day and first flowering day of all species monitored in our study and average global phenological sensitivity.

warming than the plant phenology observed in a meta-analysis of 18 arctic sites (greening: −0.15 to −3.96 d/°C; flowering: −0.09 to −4.49 d/°C; Prevéy et al. 2017), and a study was conducted in the Canadian Arctic using historical records (flowering: −1.7 to −9.6 d/°C; Panchen and Gorelick 2017). It should be noted that both of these studies used summer mean temperature in their phenological sensitivity calculation. This suggests their results underestimated phenological sensitivity because they did not make their calculations using mean annual temperature.

To explain the variation of phenological sensitivity among different areas, we extracted data on phenological sensitivity (leaf-out day) and a series of abiotic factors at 24 experimental sites from the global dataset (Wolkovich et al. 2012), as well as all plant species included at each site (see details in *Materials and Methods*). With the addition of data from our own study, we found that phenological sensitivity varied extensively among 25 experimental sites, but the Tibetan Plateau was the most sensitive site (Appendix S1: Fig. S3a). However, mean annual temperature (MAT) at our site was not the lowest nor was the temperature range (*T* range) the narrowest across the 25 sites (Appendix S1: Fig. S3b). Moreover, the degree of warming in our experiment (Δ*T*) was lower than most of other sites (Appendix S1: Fig. S3c). Lastly, the percent of the degree of warming in mean annual temperature (Δ*T*/MAT) at our site was not the highest across all sites (Appendix S1: Fig. S3d). We further tested the regression relationship between phenological

sensitivity and each of the abiotic factors mentioned above. None of the abiotic factors (MAT, *T* range, Δ*T*, Δ*T*/MAT) were significantly related to phenological sensitivity (Appendix S1: Fig. S4a–d). In addition, we tested whether biotic factors explained our observed results by constructing a phylogenetic tree that included all the plant species involved in the global dataset and in our study. We did not find any evidence of a phylogenetic effect on the responses of the 11 taxa at our site (Appendix S1: Fig. S5).

Discussion

Contrary to our predictions, warming and altered precipitation did not interact to alter community plant phenology in this alpine system. Warming significantly advanced both leaf-out day and first flowering day, a result that has been observed in numerous other studies (Schwartz 1998, Peñuelas and Filella 2001, Peñuelas et al. 2002, Dunne et al. 2003, Norby et al. 2003, Cleland et al. 2007, Miller-Rushing and Primack 2008, Morin et al. 2010, Han et al. 2014). While more modest an impact, increases and decreases in precipitation also altered plant phenology in contrasting ways. Specifically, increased precipitation advanced phenology while decreased precipitation delayed it. Wet conditions on the Tibetan Plateau enable plants to develop more quickly, while dry conditions clearly delayed alpine plant development. Further, remote sensing studies on the Tibetan Plateau also find that phenology is more sensitive to temperature in wetter areas and more sensitive to precipitation in drier areas (Shen et al. 2015*a*). Given our study site is located in the wet, northeast area of Tibetan Plateau, our experimental findings support previous satellite studies that temperature is the most important driver of plant phenology in wetter areas. In sum, while there is inter-annual variation, temperature is clearly the major global change driver impacting plant phenology in temperature-limited (cold) areas, such as Tibetan Plateau (Bliss 1971, Polgar and Primack 2011, Inouye and Wielgolaski 2013).

Exploring the interactive effects of warming and precipitation on phenology is uncommon, even though these global changes can interact with one another to shape plant development (Cleland et al. 2006). We predicted that water addition treatments

would decrease soil temperature in warm plots and thus slow plant leaf-out and flowering time. Similarly, we predicted that decreased precipitation would lead to even drier soils under warm conditions and further retard plant development (Adams et al. 2015). However, we found no interactive effects of warming and altered precipitation on plant phenology. A warming and double precipitation experiment in an Oklahoma grassland also found that increases in precipitation did not additively increase the impact of warming on plant phenology (Sherry et al. 2007). However, not surprisingly, different results were found in drier semiarid alpine meadows on the Tibetan Plateau. Warming delayed the phenology of *Kobresia pygmaea*, but snow addition as precipitation inputs reversed the response (Dorji et al. 2013). It is noteworthy that the two study years differed in terms of weather, 2013 was dry and 2014 was wet (Liu et al. 2018), which may have caused the significant interactive effects of precipitation and year on plant phenology in this study. While warming had the largest effect on phenology in our study, precipitation influenced the response of functional groups to warming.

Temperature clearly advanced the phenology of all the functional groups we measured, but the groups interacted with precipitation change in a variety of ways. While legumes were most influenced by temperature, both temperature and precipitation altered grasses and forbs. Variation among functional groups may result from the different local ecophysiological environments the group inhabit, such as xerophytic or mesic environments (Dorji et al. 2013). The variability in functional group responses may also arise due to increased temporal overlap among groups, decreased phenological complementarity, and increased water and nutrient resource competition (Cleland et al. 2006, Temperton et al. 2007). Each of these factors may have been important in our study; however, they were beyond the scope of the current study. Notably, studies carried out in the same experiment revealed that the biomass of grasses was improved by increased precipitation and biomass of legume was enhanced by warming (Ma et al. 2017, Xu et al. 2018), both results that might be induced by earlier phenology. In addition, warming-induced community shifts to legumes (due to higher forage quality in legumes) and precipitation-induced forage production (due to a strong increase of grass production), improving the rangeland quality of this alpine ecosystem (Xu et al. 2018). These findings indicate that future climate change may result in shifts in community composition and biodiversity, thus impacting ecosystem function and services. Given the important role of livestock husbandry for the livelihood of native nomads on the Tibetan Plateau (Qiu 2016), the variability in functional group responses should be considered when coping with challenges and opportunities of future climate change in this high-elevation grassland ecosystem.

Phenological sensitivity (leaf-out day) on Tibetan Plateau was 7.3 times greater than in other areas on the world. Further analysis showed that neither abiotic nor biotic factors explain this result. That is, no relationship was found between phenological sensitivity and abiotic factors (mean annual temperature, temperature range, the amount of temperature increased, the percent of temperature increased of mean annual temperature) at each site. Moreover, no clustered phylogenetic pattern of 11 species at our site was seen over the phylogenetic tree with all the plant species involved in the global dataset and in our study. Other factors (e.g., chilling requirements, photoperiod, plant life form) that we cannot quantify here may have led to the differences in phenological sensitivity among areas on the world. For example, key explanatory variables are likely to differ from one ecosystem type to another; while phenology is controlled by snowmelt timing in some areas (Price and Waser 1998, Inouye 2008), photoperiod is the main driving factor in other areas (Körner and Basler 2010). However, meta-analysis of the global dataset used warming as the key explanatory variable for all the areas, which may fail to address explicitly the differences among data sources (Harte and Kueppers 2012).

On the one hand, our result implies that predicted climate change will likely have large impacts on the Tibetan Plateau: Plant phenology might occur earlier in the spring in this alpine meadow than in other ecosystems under future warmer climates, which could cause problems for migratory animals, such as herbivores or pollinators (McKinney et al. 2012). Therefore, priority attention should be paid on the conservation of alpine ecosystems on the Tibetan Plateau. On the other hand, our findings also suggest that

previous meta-analyses of global phenological sensitivity may have neglected variation of key explanatory variables that drive plant phenology in different areas (Harte and Kueppers 2012). In addition, meta-analyses should carefully consider the appropriate explanatory variables across experimental studies (Harte and Kueppers 2012, Lapenis et al. 2014). Therefore, more caution should be paid to the factors that govern, or do not govern, phenological sensitivity in global datasets from many corners of the world.

Our study results highlight the importance of understanding the specific environmental cues that drive phenological responses when forecasting phenology over the coming decades. As demonstrated here, there were no interactive effects of warming and precipitation on plant phenology; temperature alone is the main driver of plant phenology. In addition, the response of different plant functional groups to climate drivers varied among functional groups. While grasses and forbs grew earlier in warmer and wetter conditions, legumes did better under drier conditions. When compared to a recent global dataset, we showed that phenological sensitivity on the Tibetan Plateau is much greater than it is in other areas in the world. Thus, previous meta-analyses of global phenological sensitivity may have neglected variation of key driving variables from different areas. As the most likely future scenario on the Tibetan Plateau, warmer and wetter climates will likely accelerate the phenology of alpine meadow plants, especially of grasses and forbs. In addition, it is likely that alpine ecosystems such as ours will be more sensitive to future, warmer climate than other ecosystems. Our study provides detailed predictions for the causes of phenological shifts in this particular system, and it suggests that other multifactor experiments in other ecosystem types around the world might be necessary in order to understand the implications of ongoing climate change, for understanding not only the biodiversity, but also its conservation and relationship to ecosystem function and sustainability.

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