Received: 25 October 2023 | Accepted: 6 November 2023

DOI: 10.1002/ecs2.4761

ARTICLE

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

Growing-season climate as an explanation of spatial variations in temperature sensitivity of green-up on Tibetan Plateau

Zhiyong Yang[1] | **Nan Jiang**[2] | **Yan Huang**[3] | **Miaogen Shen**[2] | **Wenquan Zhu**[2] | **Yongshuo Fu**[4] | **Yanhong Tang**[5] | **Ivan Janssens**[6]

[1]Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing, China

[2]State Key Laboratory of Earth Surface Processes and Resource Ecology, Faculty of Geographical Science, Beijing Normal University, Beijing, China

[3]Qian Xuesen Laboratory of Space Technology, China Academy of Space Technology, Beijing, China

[4]College of Water Sciences, Beijing Normal University, Beijing, China

[5]College of Urban and Environmental Sciences, Peking University, Beijing, China

[6]Research Group Plants and Ecosystems, University of Antwerp, Antwerp, Belgium

Correspondence
Miaogen Shen
Email: shen.miaogen@gmail.com

Funding information
Science and Technology Innovation Base Free Research Program of Tibetan Autonomous Region of China; National Natural Science Foundation of China, Grant/Award Number: 42001108; Top-Notch Young Talents Program of China

Handling Editor: Scott Ferrenberg

Abstract

Temperature sensitivity (TS) of the green-up date (GUD) of plants is crucial for the prediction of grassland phenology that is important for animal husbandry and pasture management. Spatial variations in the TS are known to reflect interannual temperature variability and/or accumulated precipitation preceding the GUD (pre-GUD). However, whether spatial TS variations are related to the interaction between pre-GUD temperature variability and precipitation, which is a potential indicator of frost risk, remains unclear. Furthermore, because the interaction between interannual temperature variability and accumulated precipitation following the GUD (post-GUD) can exert selection pressure on the plant life cycle, it may also be involved in shaping the spatial TS pattern. Using long-term ground observations of GUD on the Tibetan Plateau, we show that TS is more negative (greater GUD advance per unit temperature increase) in areas with more pre-GUD precipitation and low pre-GUD interannual temperature variability, but less negative in areas with more pre-GUD precipitation and high pre-GUD interannual temperature variability. This result is likely because more pre-GUD precipitation facilitates sprout and leaf development under stable temperature conditions, whereas it increases frost risk when the temperature variability is high. In contrast, TS magnitude decreases with increases in post-GUD precipitation in areas where post-GUD interannual temperature variability is low, but increases with post-GUD precipitation in areas where post-GUD interannual temperature variability is high. We speculate that because hydrothermal demands for leaf growth from the onset of green-up to maturity are more easily fulfilled when interannual temperature variability is lower and precipitation is higher, green-up need not be sensitive to pre-GUD temperature. In contrast, high post-GUD precipitation likely aggravates low-temperature constraints on leaf growth when temperature variability is high, resulting in greater TS to maximize growing season length. These results suggest that spatial TS variations on the Tibetan Plateau are likely associated with adaptations of leaf-out phenology to background pre-GUD climatic conditions together with selection pressure from post-GUD conditions.

KEYWORDS
alpine ecosystem, climate change, dryland, spring phenology, temperature sensitivity, temperature variability

INTRODUCTION

Global surface temperature has been increasing at a rate of approximately 0.2°C per decade since the 1970s, and the warming rate has been even faster at higher altitudes (Pepin et al., 2015; Yun et al., 2019; Zeng et al., 2015). Changes in plant spring phenology, which are among the most sensitive indicators of ecosystem responses to global warming, have substantial implications for community assemblies and ecosystem functions (Buermann et al., 2018; CaraDonna et al., 2014; Prevey et al., 2019; Yang & Rudolf, 2010). Generally, the plant green-up date (GUD) has advanced as a result of climate warming in temperate, alpine, and boreal ecosystems of the Northern Hemisphere (Menzel et al., 2020; Piao et al., 2019). However, the magnitude and even the direction of shifts in the GUD differ among regions (Chen et al., 2015; Menzel et al., 2020; Sun et al., 2021). Alongside differences in warming trends among regions, spatial differences in phenological temperature sensitivity (TS; changes in the GUD per unit temperature increase) are another important determinant of warming-induced shifts in the GUD (Chmura et al., 2019; Shen, Cong, & Cao, 2015; Zhang, Yuan, Liu, & Dong, 2015). Hence, exploring the determinants of spatial variation in the TS of the GUD is essential for understanding and predicting the effects of climate warming on the GUD.

Most studies of plant phenology have been conducted in humid, mid-latitude regions, especially in Europe (Menzel et al., 2020; Schwartz, 2013). In such regions, which are characterized by climate seasonality, temperature is the most important environmental driver of the plant GUD (Cleland et al., 2007; Piao et al., 2019), with photoperiod affecting the GUD to a lesser degree (Fu et al., 2019). TS of the GUD is closely related to the interannual variability of the background temperature through local adaptation to reduce frost risk (Körner & Basler, 2010; Zohner et al., 2017). In temperate regions (Peaucelle et al., 2019), and especially in arid and semiarid regions, the GUD and its TS are also affected by water conditions (Chen et al., 2015; Cleverly et al., 2016; Du et al., 2019; Shen, Cong, & Cao, 2015; Zhang, 2005). Compared to humid temperate regions, plant phenology has received much less attention in arid and semiarid regions (Piao et al., 2019; Schwartz, 2013), even though they cover about 41% of the Earth's land surface (Reid et al., 2005; Reynolds et al., 2007). Hence, phenological studies in arid and semiarid regions can enhance understanding of the response mechanisms of terrestrial ecosystem phenology to climate change and facilitate the development of plant phenology models.

Background climatic conditions are involved in shaping the spatial pattern of the TS of spring leaf-out phenology (Park et al., 2018; Peaucelle et al., 2019). Intuitively, the TS of the GUD should be regulated by climatic conditions before the GUD (pre-GUD) (Du et al., 2019; Shen, Cong, & Cao, 2015; Zohner et al., 2017). Indeed, in arid and semiarid regions, TS of the GUD has been shown to be regulated by pre-GUD precipitation (Du et al., 2019; Shen, Cong, & Cao, 2015), because, in addition to temperature, water availability is an important factor limiting plant development (Cleverly et al., 2016). The trade-off between the benefit derived from an advance of the GUD under warmer conditions and drought risk due to leaf-out before the rainy season explains a part of the spatial variation in the TS of the GUD across the Tibetan Plateau (Shen, Cong, & Cao, 2015). Thus, to maximize the thermal benefit, the GUD generally displays greater TS in areas with more pre-GUD precipitation if other factors allow. However, in areas with less pre-GUD precipitation, warming potentially increases drought risk, and plants adapt to this risk by reducing the TS of their GUD (Du et al., 2019; Ganjurjav et al., 2020; Shen, Cong, & Cao, 2015). Pre-GUD interannual temperature variability is another determinant of the TS of spring phenology (Zohner et al., 2017). In areas with high pre-GUD interannual temperature variability, frost events occur more frequently, and in these areas, the GUD tends to show weaker TS to minimize the risk of frost damage (Zohner et al., 2017). However, the fact that frost damage is also related to water status should not be ignored. Liquid water plays an important role as both a solvent and reactant in biochemical reactions, and it is also the primary medium via which plants absorb and transport nutrients (Gurevitch et al., 2006). However, frozen water cannot participate in biochemical reactions, and it can damage plant cells (Kawamura & Uemura, 2014). In regions with higher pre-GUD interannual temperature variability, an increase in pre-GUD precipitation may aggravate the risk of frost damage due to the crystallization of water, to which plants again adapt by reducing the TS of their GUD (Figure 1a). In contrast, when pre-GUD interannual temperature variability is lower, higher pre-GUD precipitation may not increase the frost risk; rather, it may ease the constraint of low water availability on spring development and allow a higher TS of the GUD. It is thus necessary to assess the interaction effects of precipitation and temperature variations on the TS of the GUD.

On the other hand, climatic conditions after the GUD (post-GUD) can impose selection pressures on the leaf life cycle and plant fitness, thereby inducing spatial variation in the TS of the GUD (Bennie et al., 2010; Peaucelle et al., 2019). In regions where post-GUD climatic conditions are more favorable for plant growth, plant leaves mature faster (Klosterman et al., 2018), and under such conditions, plants likely profit more from the better post-GUD thermal conditions and avoid frost damage by not leafing out earlier in years with warm springs; thus, they adopt a conservative leaf-out strategy (i.e., smaller TS of the GUD). By contrast, where post-GUD climatic conditions are suboptimal, plant leaf growth is slower, and under such conditions, plants may profit from a warm spring by lengthening their growing season (advancing leaf-out) despite the increased frost risk; therefore, their GUD is more likely to exhibit high TS. In cold arid and semiarid regions such as the Tibetan Plateau, higher post-GUD precipitation combined with low post-GUD interannual temperature variability implies more favorable thermal and water conditions for leaf growth. In these regions, therefore, such conditions can be expected to favor a conservative GUD strategy to minimize frost risk (i.e., smaller TS of the GUD). Hence, spatially, an increase in post-GUD precipitation can be expected to coincide with decreased TS of the GUD when post-GUD interannual temperature variability is low (Figure 1b). By contrast, higher post-GUD precipitation combined with high post-GUD interannual temperature variability may aggravate the low-temperature constraint on leaf growth and impose higher risk of frost damage, which can deplete carbon reserves and delay the buildup of leaf area (Cong et al., 2017; Shen et al., 2016). This combination of high post-GUD precipitation and temperature variability would be expected to force plants to invest more in frost resistance (Muffler et al., 2016), which in turn would allow greater TS of the GUD to maximize growing season length. Therefore, a spatial increase in post-GUD precipitation may be expected to lead to an increase in the TS of the GUD to maximize growing season length whenever temperature allows. Therefore, the interaction between post-GUD precipitation and post-GUD interannual temperature variability may also explain part of the spatial variation in the TS of spring phenology, although this interaction has rarely been studied.

The Tibetan Plateau, which has an area of more than 2.5 million km^2, ranges from 2000 m to higher than 6000 m in altitude; thus, it is the highest and largest

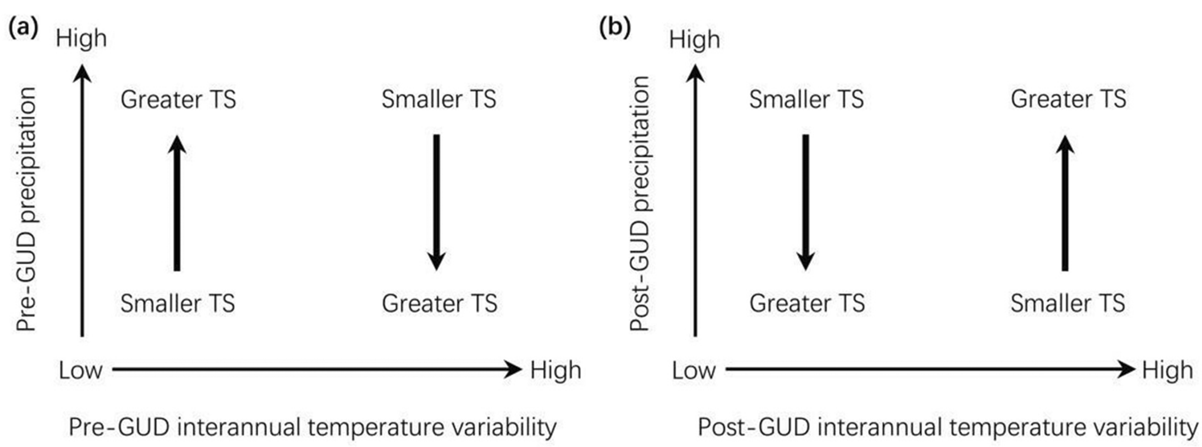

FIGURE 1 Schematic diagrams showing how temperature sensitivity (TS) of the green-up date (GUD) varies with background climatic conditions in arid and semiarid alpine regions. (a) Variability in TS in relation to pre-GUD accumulated precipitation and pre-GUD interannual temperature variability; the TS magnitude increases with an increase in pre-GUD precipitation when pre-GUD interannual temperature variability is low, whereas it decreases with increased pre-GUD precipitation when pre-GUD interannual temperature variability is high. (b) Variability in TS in relation to post-GUD accumulated precipitation and post-GUD interannual temperature variability; the TS magnitude increases as post-GUD precipitation decreases when post-GUD interannual temperature variability is low, but it increases with an increase in post-GUD precipitation when post-GUD interannual temperature variability is high.

plateau in the world (Lu et al., 2011; Tang et al., 2009). The Tibetan Plateau has been warming by more than 0.35°C decade^{-1} since the early 1980s, faster than the global average (He et al., 2021; Wang et al., 2008). Satellite remote sensing has well documented a general advance in the vegetation GUD across the Tibetan Plateau, but the magnitude of this advance exhibits large spatial variability (Sun et al., 2020, 2021; Yang et al., 2015; Zheng et al., 2016). The TS of the vegetation GUD across the Tibetan Plateau ranges from −6 to 6 days °C^{-1} (Shen, Piao, et al., 2015). In most of the Tibetan Plateau, the TS of the GUD is negative (i.e., GUD advance per unit pre-GUD temperature increase), whereas positive TS (i.e., GUD delay per unit pre-GUD temperature increase) is found mainly in the southwestern Tibetan Plateau, where it has been attributed in part to limited pre-GUD cumulative precipitation (Shen, Cong, & Cao, 2015). However, how pre-GUD and post-GUD background climate conditions contribute to spatial variations in TS of GUD in the Tibetan Plateau remains an open question. The Tibetan Plateau is also the world's largest alpine dryland, with highly heterogeneous hydrothermal conditions: mean annual temperature ranges from −15 to 10°C (Qin et al., 2016; You et al., 2013), and annual cumulative precipitation ranges from less than 100 mm to more than 1000 mm, although it is less than 600 mm in most areas (Fang et al., 2019; Gao & Liu, 2013). Moreover, in most of the Tibetan Plateau, because precipitation is far less than potential evapotranspiration (Chen et al., 2006; Wang et al., 2013, 2018), the climate is dry. These features make the Tibetan Plateau an ideal region for exploring the impacts of interactions between precipitation and interannual temperature variability on the TS of spring phenology across geographical spaces.

In this study, we used in situ phenological observations across the Tibetan Plateau to test whether spatial variability in the TS of the GUD is related to the interaction between cumulative precipitation and interannual temperature variability. Specifically, we tested the following two hypotheses: First, we hypothesized that under low pre-GUD interannual temperature variability, the TS of the GUD is greater (more negative) in areas with higher pre-GUD cumulative precipitation across the Tibetan Plateau, whereas under high pre-GUD interannual temperature variability, the TS of the GUD is smaller (less negative) in areas with higher pre-GUD precipitation (Figure 1a). Second, we hypothesized that under low post-GUD interannual temperature variability, the TS of the GUD is smaller in areas with higher post-GUD accumulative precipitation, whereas under high post-GUD interannual temperature variability, the TS of the GUD is greater in areas with higher post-GUD accumulative precipitation across the Tibetan Plateau (Figure 1b).

MATERIALS AND METHODS

Phenology observations and meteorology data

We obtained field records of the GUD on the Tibetan Plateau for the period from 1981 to 2012 recorded by the nationwide phenological observation network, which was established in 1980 by the China Meteorological Administration (1993) (Chen, 2013). For woody species, the GUD was defined as the date when the first leaves of more than half of the observed individuals were fully unfolded. For herbaceous species, it was defined as the date when more than half of the observed individuals displayed green leaves (China Meteorological Administration, 1993; Sun et al., 2020). The phenological status of the plants was recorded once every two days at the species level at each phenological site (referred to as a site–species hereafter). For each woody species, 3–5 middle-aged individuals were selected, and for each herbaceous species, 10 individuals were marked for phenological observation. We removed site–species combinations with less than 10 years of observations from our analyses. The final dataset for analyses included 77 site–species (i.e., 77 GUD time series) comprising 29 different species at 18 sites (Appendix S1: Table S1). The 18 sites were distributed across the Tibetan Plateau; during 1981–2012, mean annual temperature at the sites ranged from −1.7 to 9.1°C, and annual cumulative precipitation ranged from 51 to 686 mm. Most precipitation occurred during May–September, and winters were typically dry.

Daily mean temperature and daily cumulative precipitation at the exact locations of 14 phenological sites were provided by the China Meteorological Data Service System (http://data.cma.cn/). For the remaining four phenological sites, data from the nearest meteorological station, located 6, 21, 33, and 46 km away from the site, were used. The geographical coordinates and altitude of each phenological site and meteorological station and the plant species observed at each phenological site are given in Appendix S1: Table S1.

TS of the GUD

The GUD on the Tibetan Plateau was found to be driven mainly by the temperature during a period before GUD (referred to as the preseason), but precipitation also played a role in controlling the GUD (Chen et al., 2015; Shen, Cong, & Cao, 2015; Sun et al., 2018). The TS (in days per degree Celsius) of the GUD is defined as the change in the GUD per unit increase in the mean temperature of the preseason. As in previous studies, we estimated TS as the coefficient of preseason mean temperature in multiple interannual linear regression results of GUD against preseason mean temperature and cumulative precipitation (Fu, Zhao, et al., 2015; Panchen & Gorelick, 2017; Wu et al., 2018). The length of the preseason for each site–species combination was determined as follows: we performed temporal partial correlation analyses of GUD against preseason mean temperature while controlling for preseason cumulative precipitation (Fu, Zhao, et al., 2015; Jeong et al., 2011; Matsumoto et al., 2003). Here, the candidate preseason length was varied from 20 to 120 days preceding the multiyear average GUD, with a step of five days, yielding 21 values of the partial correlation coefficients. The preseason length with the highest absolute value of the partial correlation coefficient was selected and used as the preseason length in the analysis.

Analyses of spatial variations in TS

To explore the roles of background climatic temperature and precipitation conditions in the spatial variation of the TS of the GUD, we defined four climate variables: as indicated in the *Introduction* section, the interannual SD of mean temperature and the multiyear average of cumulative precipitation in the period before the multiyear average GUD (T_{SD}^{pre} and P_{mean}^{pre}, respectively), and the interannual SD of mean temperature and the multiyear average of cumulative precipitation in the period following the multiyear average GUD (T_{SD}^{post} and P_{mean}^{post}, respectively). To determine the period length for T_{SD}^{pre} and P_{mean}^{pre}, we performed spatial linear regression analyses of TS against T_{SD}^{pre}, P_{mean}^{pre}, and their interaction ($P_{mean}^{pre} \times T_{SD}^{pre}$) by varying the period length from 20 to 120 days at intervals of five days among the site–species combinations. Then we used the period length for which the R^2 value of the regression was highest as the final period length for T_{SD}^{pre} and P_{mean}^{pre}. We constrained the period lengths for T_{SD}^{pre} and P_{mean}^{pre} to be identical, considering their interaction. To avoid the effects of different period lengths on the values of T_{SD}^{pre} and P_{mean}^{pre} and thus on the quantification of the spatial variability of background climatic conditions, the period length was not allowed to vary among the site–species combinations. The period lengths for T_{SD}^{post} and P_{mean}^{post} were determined in a similar way.

To assess how spatial variations in TS were related to pre-GUD climatic factors, we linearly regressed TS against P_{mean}^{pre}, T_{SD}^{pre}, and their interaction ($T_{SD}^{pre} \times P_{mean}^{pre}$). Similarly, we assessed the spatial relationship between TS and post-GUD climatic factors by linearly regressing TS against T_{SD}^{post}, P_{mean}^{post}, and $T_{SD}^{post} \times P_{mean}^{post}$. The relative importance of each independent variable was quantified by hierarchical partitioning to calculate its contribution to R^2 (Chevan & Sutherland, 1991); this procedure was implemented by using the R package "relaimpo" (Grömping, 2006; Yin et al., 2020).

RESULTS

GUD and its TS

The multiyear average of each site–species GUD ranged from day of year (DOY) 54 to DOY 144 across the plateau (mean DOY 120, SD 18 days). TS ranged from −9.4 to +2.6 days $°C^{-1}$ with a mean (±SD) of -3.4 ± 2.3 days $°C^{-1}$. TS was negative for 71 site–species (statistically significant for 49 site–species at $p < 0.05$). TS values for six site–species were positive, but none of these differed significantly from zero ($p > 0.05$).

Spatial relationships between TS and background climatic conditions

One-way ANOVA results showed that the TS of the GUD did not differ significantly among species (df $= 28$, $F = 1.24$, $p = 0.25$).

Based on the largest R^2 values of the spatial linear regression analysis results (see *Analyses of spatial variations in TS*), the period length for T_{SD}^{pre} and P_{mean}^{pre} was 105 days, and that for T_{SD}^{post} and P_{mean}^{post} was 80 days.

When the interaction between T_{SD}^{pre} and P_{mean}^{pre} was not considered, TS was significantly more negative at sites with smaller T_{SD}^{pre} or less P_{mean}^{pre} (Figure 2a,b). When the interaction between T_{SD}^{post} and P_{mean}^{post} was not considered, TS significantly decreased toward sites with higher T_{SD}^{post}; thus opposite to its relation with T_{SD}^{pre} (Figure 2a,c). The relation between TS and P_{mean}^{post}, however, was similar to that between TS and P_{mean}^{pre} (Figure 2b,d).

When the interaction between pre-GUD temperature variability and cumulative precipitation was considered, the spatial linear regression between TS and T_{SD}^{pre}, P_{mean}^{pre}, and $T_{SD}^{pre} \times P_{mean}^{pre}$ showed that the separate role of T_{SD}^{pre} on TS of the GUD was not statistically significant ($p > 0.10$; Appendix S1: Table S2), and thus was ruled out in subsequent analyses. However, spatial differences in TS were significantly affected by both P_{mean}^{pre} and $T_{SD}^{pre} \times P_{mean}^{pre}$ (Table 1). Using only the preseason climate data, we obtained the following linear regression model (Table 1): $TS = 0.2618 \times (T_{SD}^{pre} - 0.9828) \times P_{mean}^{pre} - 4.0079$. The relation between TS and P_{mean}^{pre} is thus regulated by T_{SD}^{pre}. Where T_{SD}^{pre} was small (i.e., less than 0.9828°C), TS increased toward sites with higher P_{mean}^{pre}, whereas where T_{SD}^{pre} was large (i.e., more than 0.9828°C), TS decreased

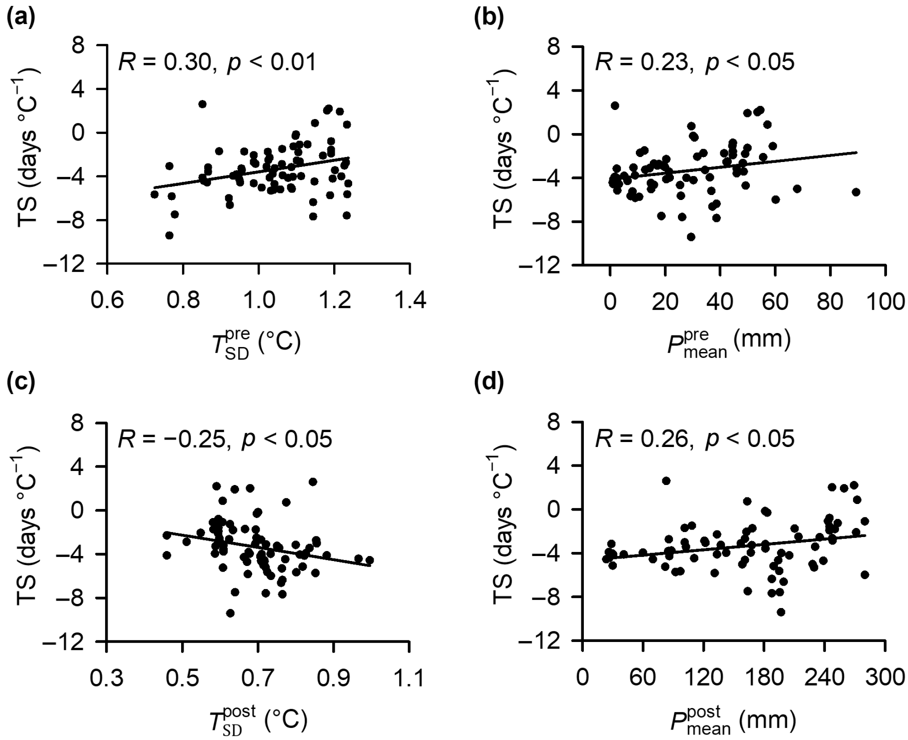

FIGURE 2 Changes in temperature sensitivity (TS) of the green-up date (GUD) in relation to background climatic factors: (a) pre-GUD interannual temperature variability (T_{SD}^{pre}); (b) pre-GUD precipitation (P_{mean}^{pre}); (c) post-GUD interannual temperature variability (T_{SD}^{post}); and (d) post-GUD precipitation (P_{mean}^{post}). R is the linear correlation coefficient between TS and each factor.

TABLE 1 Linear regression analysis results for quantifying the spatial relationship between temperature sensitivity (TS) of the green-up date (GUD) and pre-GUD cumulative precipitation (P_{mean}^{pre}) and the interaction between pre-GUD interannual temperature variability (T_{SD}^{pre}) and P_{mean}^{pre} ($T_{SD}^{pre} \times P_{mean}^{pre}$) across the Tibetan Plateau.

Predictive variable	Coefficient	T	p
Intercept	−4.0079	−9.7572	<0.0001
P_{mean}^{pre}	−0.2573	−3.5573	0.0007
$T_{SD}^{pre} \times P_{mean}^{pre}$	0.2618	3.9898	0.0002

Note: For the linear regression model, $R^2 = 0.22$ and $p < 0.01$.

toward sites with higher P_{mean}^{pre} (Figure 3). Further, TS was smallest (i.e., least negative; fluctuating around 0 days °C^{-1}) at sites with the highest P_{mean}^{pre} and highest T_{SD}^{pre} values, and greatest (i.e., most negative) at sites with the highest P_{mean}^{pre} and lowest T_{SD}^{pre} values (Figure 3).

Similarly, when only the post-season climatic data were used, the linear regression model did not select T_{SD}^{post} as a significant explainer of the spatial variations in TS of the GUD (Appendix S1: Table S3), whereas P_{mean}^{post} and the interaction between T_{SD}^{post} and P_{mean}^{post} ($T_{SD}^{post} \times P_{mean}^{post}$) were again selected by the model (Table 2). However, the regulatory role of T_{SD}^{post} in the relation between TS and P_{mean}^{post} was opposite to the

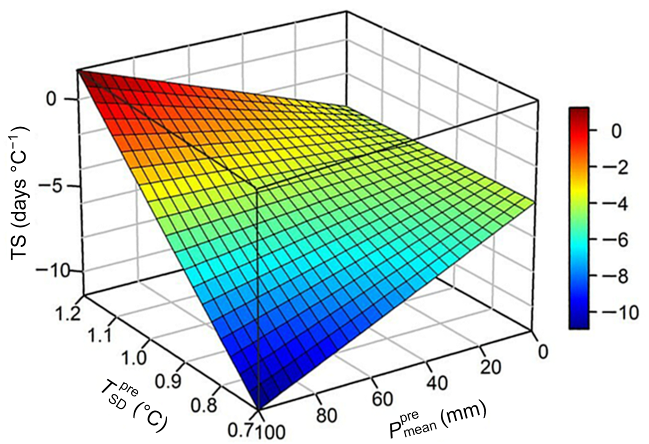

FIGURE 3 Spatial variation in temperature sensitivity (TS) of the green-up date (GUD) in relation to pre-GUD cumulative precipitation (P_{mean}^{pre}) and pre-GUD interannual temperature variability (T_{SD}^{pre}) (drawn from the linear regression model described in Table 1). Color scale indicates TS values.

regulatory role of T_{SD}^{pre} observed in the relation between TS and P_{mean}^{pre}. The obtained linear regression model was $TS = 0.0554 \times \left(0.7599 - T_{SD}^{post}\right) \times P_{mean}^{post} - 4.1615$ (Table 2). Where T_{SD}^{post} was less than 0.7599°C, TS decreased toward sites with higher P_{mean}^{post}, whereas where T_{SD}^{post} was higher than 0.7599°C, TS increased toward sites with higher

TABLE 2 Linear regression analysis results for quantifying the spatial relationship between temperature sensitivity (TS) of the green-up date (GUD) and post-GUD cumulative precipitation (P^{post}_{mean}) and the interaction between post-GUD interannual temperature variability (T^{post}_{SD}) and P^{post}_{mean} ($T^{post}_{SD} \times P^{post}_{mean}$) across the Tibetan Plateau.

Predictive variable	Coefficient	T	p
Intercept	−4.1615	−6.7306	<0.0001
P^{post}_{mean}	0.0421	3.3642	0.0012
$T^{post}_{SD} \times P^{post}_{mean}$	−0.0554	−2.8142	0.0063

Note: For the linear regression model, $R^2 = 0.16$ and $p < 0.01$.

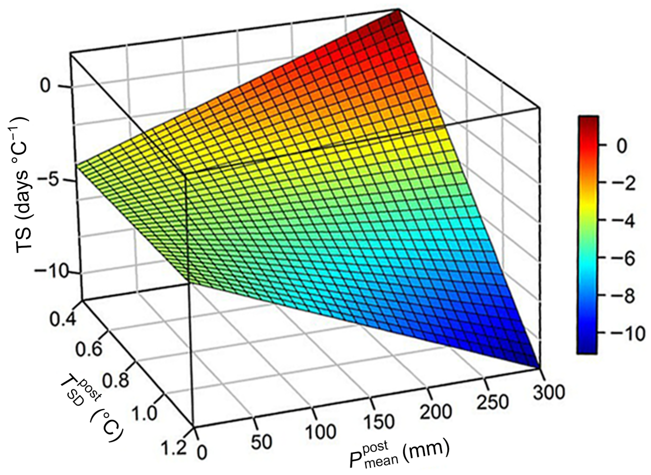

FIGURE 4 Spatial variation in temperature sensitivity (TS) of the green-up date (GUD) in relation to post-GUD interannual temperature variability (T^{post}_{SD}) and post-GUD precipitation (P^{post}_{mean}) (drawn from the linear regression model described in Table 2). Color scale indicates TS values.

P^{post}_{mean} (Figure 4). Further, TS was smallest (i.e., least negative; around 0 days °C^{-1}) at the sites with highest P^{post}_{mean} and lowest T^{post}_{SD}, and greatest (i.e., most negative) at the sites with highest P^{post}_{mean} and highest T^{post}_{SD} (Figure 4).

When all of the selected pre-GUD and post-GUD climatic factors (P^{pre}_{mean}, $T^{pre}_{SD} \times P^{pre}_{mean}$, P^{post}_{mean} and $T^{post}_{SD} \times P^{post}_{mean}$) were included in a linear regression model to explain spatial TS variations (Table 3), all four of these factors were found to be significant determinants ($p < 0.01$). This model explained 32% of the spatial variation in TS, substantially more than that explained by the models based solely on either pre- or post-GUD climatic factors (22% and 16% for pre-GUD climate and post-GUD climate, respectively). The relative importances of P^{pre}_{mean}, $T^{pre}_{SD} \times P^{pre}_{mean}$, P^{post}_{mean} and $T^{post}_{SD} \times P^{post}_{mean}$ in the model were 25%, 36%, 20%, and 19%, respectively.

To evaluate the robustness of our results, we repeated the above analyses under the condition that the pre-GUD and post-GUD period lengths were determined simultaneously by the linear regression results for TS against T^{pre}_{SD}, P^{pre}_{mean}, $T^{pre}_{SD} \times P^{pre}_{mean}$, T^{post}_{SD}, P^{post}_{mean}, and $T^{post}_{SD} \times P^{post}_{mean}$ with the largest R^2. This analysis yielded similar results (Appendix S1: Tables S4–S6; Appendix S1: Figures S1 and S2) to those described above. In addition, we repeated these analyses under the condition that neither the T^{pre}_{SD} and P^{pre}_{mean} period lengths nor the T^{post}_{SD} and P^{post}_{mean} period lengths were constrained to be identical. Again, the analyses yielded similar results (Appendix S1: Tables S7–S9 and Figures S3 and S4). The similar results obtained under these conditions support the robustness of this study.

TABLE 3 Linear regression analysis results for quantifying the spatial relationship between temperature sensitivity (TS) of the green-up date (GUD) and pre-GUD precipitation (P^{pre}_{mean}), the interaction between pre-GUD interannual temperature variability (T^{pre}_{SD}) and P^{pre}_{mean} ($T^{pre}_{SD} \times P^{pre}_{mean}$), post-GUD precipitation (P^{post}_{mean}), and the interaction between post-GUD interannual temperature variability (T^{post}_{SD}) and P^{post}_{mean} ($T^{post}_{SD} \times P^{post}_{mean}$) across the Tibetan Plateau.

Predictive variable	Coefficient	p	Contribution to R^2 (%)
Intercept	−3.5349	<0.0001	
P^{pre}_{mean}	−0.2531	0.0005	25.01
$T^{pre}_{SD} \times P^{pre}_{mean}$	0.2604	0.0001	36.29
P^{post}_{mean}	0.0355	0.0050	19.90
$T^{post}_{SD} \times P^{post}_{mean}$	−0.0580	0.0021	18.80

Note: For the linear regression model, $R^2 = 0.32$, $p < 0.01$. R^2 contribution metrics are normalized to sum to 100%. The R^2 contribution indicates the relative importance of each independent variable to the spatial variation in TS.

DISCUSSION

The individual effects of T^{pre}_{SD} and P^{pre}_{mean} on spatial variation of the TS of the GUD have been previously explored (Du et al., 2019; Fu, Piao, et al., 2015; Shen, Cong, & Cao, 2015; Zohner et al., 2017). In agreement with these studies, our results show that the magnitude of TS increases across sites with increasing P^{pre}_{mean} or decreasing T^{pre}_{SD}. However, no previous studies have assessed the impact of the interaction between T^{pre}_{SD} and P^{pre}_{mean} on TS. This study revealed a significant interactive effect between T^{pre}_{SD} and P^{pre}_{mean} on spatial variations in the TS of the GUD on the Tibetan Plateau: namely, the magnitude of TS increases (i.e., more negative) with P^{pre}_{mean} where T^{pre}_{SD} is low, but decreases with P^{pre}_{mean} where T^{pre}_{SD} is high (Figure 3).

Warming across the Northern Hemisphere (latitude >30° N) has been shown to advance the GUD more than the last spring frost date, implying that global warming is increasing the risk of frost damage (Liu et al., 2018). Moreover, this risk is most pronounced where T_{SD}^{pre} is high and late frost events are more common (Zohner et al., 2017). Thus, in areas with high T_{SD}^{pre}, an advance of the GUD can subject plant leaves to a sharply increased risk of frost damage, and in the long run, it is likely not beneficial to plants for the TS of their GUD to be high. Precipitation during frost events may further aggravate the frost damage to young leaves due to the crystallization of water (Muffler et al., 2016). Thus, where both T_{SD}^{pre} and P_{mean}^{pre} are high, adopting a conservative phenology with low TS of the GUD appears to be the best option for plants to maximize survival, productivity, and competitiveness. By contrast, in areas with low T_{SD}^{pre} (and thus a lower occurrence frequency of frost events before the GUD), higher P_{mean}^{pre} does not increase the potential frost damage when the GUD is advanced; instead, it facilitates plant development because water is a scarce resource in arid and semiarid regions. In this case, higher P_{mean}^{pre} allows the GUD of plants to have greater TS and maximize the growing season length during warm springs. In support of our first hypothesis, our results illustrate for the first time how T_{SD}^{pre} and P_{mean}^{pre} interactively shape the spatial variability of the TS of the GUD across the Tibetan Plateau.

In our results, the magnitude of TS was generally inversely related to T_{SD}^{pre}, a finding consistent with the conclusion of other studies (Körner & Basler, 2010; Wang et al., 2014; Zohner et al., 2017). However, we found that the individual effect of T_{SD}^{pre} on the TS of the GUD was not significant across the Tibetan Plateau when the effects of P_{mean}^{pre} and the interaction between T_{SD}^{pre} and P_{mean}^{pre} were considered simultaneously (Table 1). This result suggests that the relation between TS and T_{SD}^{pre} depends on P_{mean}^{pre}. Interestingly, we found no relation between TS and T_{SD}^{pre} across the driest study sites (Figure 3). There are three possible reasons for that. First, the GUD is not sensitive to the pre-GUD temperature in the driest areas of the Tibetan Plateau (Shen, Piao, et al., 2015), and as a result, TS values are close to zero, which reduces drought risk at sites with high T_{SD}^{pre} and dryness. Second, frost events damage plant tissues and cells by changing the phase of water. Low amounts of water would nullify the potential damage from frost events to plant tissues and cells. Third, greater dryness might also increase plant cell sap concentrations, which would increase their tolerance to low temperatures. Thus, the impact of frost events on plants with high drought tolerance may be less severe in extremely dry areas (Muffler et al., 2016; Walter et al., 2013).

Previous studies mostly focusing on spring leaf-out phenology in humid mid-latitude regions have attributed spatial TS variations to T_{SD}^{pre}, reasoning that T_{SD}^{pre} is an indicator of spring frost risk (Körner & Basler, 2010; Wang et al., 2014; Zohner et al., 2017). Such attribution is reasonable, because low temperatures can easily lead to freezing injury under water sufficiency. However, our results showed that T_{SD}^{pre} is likely not a determinant of spatial TS variations in arid and semiarid regions, possibly because T_{SD}^{pre} is a good indicator of frost risk only when water availability is high and temperature is low. Although this study was conducted in the Tibetan Plateau, which is characterized by a cold, dry climate, our results provide reference data for understanding the effect of frost risk on leaf-out phenology in other arid and semiarid ecosystems in climates with seasonality. Moreover, a considerable fraction of the Earth's surface is projected to become more arid under future climate scenarios (Huang et al., 2016; Koutroulis, 2019). This study may thus provide a foundation for better models of leaf-out phenology in these future (semi)arid regions with cold winter.

A few studies have shown that in addition to the pre-GUD climate, the post-GUD climate also affects the TS of GUD (Bennie et al., 2010; Peaucelle et al., 2019). Our study revealed that not T_{SD}^{post} by itself, but both P_{mean}^{post} and the interaction between P_{mean}^{post} and T_{SD}^{post} are involved in shaping spatial TS variations across the Tibetan Plateau. The magnitude of TS decreased spatially with an increase in P_{mean}^{post} where T_{SD}^{post} was low, but increased with an increase in P_{mean}^{post} where T_{SD}^{post} was high (Figure 4). This result indicates that post-GUD hydrothermal conditions likely exert selection pressure on the TS of the GUD by modifying the balance between maximization of carbon gain and minimization of frost risk (Bennie et al., 2010; Cannell, 1997; Zohner et al., 2017). On the one hand, leaves grow to maturity faster under favorable hydrothermal conditions (Klosterman et al., 2018), and they can achieve sufficient carbon uptake without increasing the pre-GUD frost risk by substantially advancing the GUD whenever the pre-GUD temperature is high, resulting in smaller TS of the GUD (i.e., more conservative leaf-out strategy) with higher P_{mean}^{post} where T_{SD}^{post} was low. On the other hand, in cold areas such as the Tibetan Plateau, plants generally grow under less-than-optimal temperature conditions, and vegetation activity is therefore expected to increase with higher temperature (Chen et al., 2021; Huang et al., 2019). However, given the high specific heat capacity of water, wetter conditions imply a greater energy requirement to warm up the soil after the more frequent cold spells under high-temperature variability. Therefore, high P_{mean}^{post} can aggravate the negative impact of low temperatures on leaf growth under high T_{SD}^{post}. If soil warming is slow after the GUD, plants would likely profit from leafing out earlier (i.e., from the GUD's being more sensitive to pre-GUD temperature to lengthen the growing season whenever possible), thereby gaining time for developing a mature canopy. These new findings challenge our intuitive notion that spatial variations in the TS of spring phenology are dominantly determined by pre-GUD climatic conditions (Du et al., 2019; Matthews & Mazer, 2016; Shen, Cong, & Cao, 2015; Zohner et al., 2017). This study shows for the first time how $T_{\mathrm{SD}}^{\mathrm{post}}$ and $P_{\mathrm{mean}}^{\mathrm{post}}$ interactively shape the spatial variability of the TS of the GUD across the Tibetan Plateau, with implications for interpreting spatial variations in leaf-out responses to temperature in other arid and semi-arid ecosystems in climates with seasonality.

Although our analyses revealed $P_{\mathrm{mean}}^{\mathrm{pre}}$, $T_{\mathrm{SD}}^{\mathrm{pre}} \times P_{\mathrm{mean}}^{\mathrm{pre}}$, $P_{\mathrm{mean}}^{\mathrm{post}}$, and $T_{\mathrm{SD}}^{\mathrm{post}} \times P_{\mathrm{mean}}^{\mathrm{post}}$ to be significant determinants of spatial variations in TS ($R^2 = 0.32$), more than half of the spatial variation in the TS of the GUD were not explained by these four variables (Table 3). This result may be related to a suite of confounding factors. First, TS, defined here as the change in the GUD per degree of change in the preseason temperature, does not directly reflect the physiological sensitivity of plants to temperature, although it is widely used as a proxy for it (Cook et al., 2012; Fu, Zhao, et al., 2015; Gao et al., 2020; Prevéy et al., 2017; Wolkovich et al., 2012). Second, climatic factors alone may not explain all of the spatial variations in the TS of the GUD; biotic factors, such as interspecific interactions, may also affect TS (Liang et al., 2016; Singer et al., 2013). The impact of species interactions on TS should be explored in future studies conducted in plant communities for which comprehensive information about species composition, relative abundances, and phenology of each species is available. Third, other factors, such as photoperiod (Fu et al., 2019; Huang et al., 2020; Rollinson & Kaye, 2012), soil properties (Ata-Ul-Karim et al., 2020), nutrient availability (Falk et al., 2020; Xi et al., 2015), carbon dioxide concentration (Inoue et al., 2020), and microbes (O'Brien et al., 2021; Van Nuland et al., 2021), may explain part of the spatial variation in the TS of the GUD. Fourth, the spatial variability of TS may be related to species and phenotypes, although the ANOVA results showed that the TS of the GUD did not significantly differ among species in this study. Lastly, the spatial relationship between TS and pre- and post-GUD climatic factors may be nonlinear, a possibility that should be addressed in further studies. These possibilities mentioned above require further analysis with more data to be determined. In fact, the 32% of explained variance is not small if we compare it with the 15 models concerning spatial variation in TS of spring phenology whose R^2 values ranged from 0.03 to 0.37 with the mean and SD of 0.19 ± 0.09 in five previous studies (Dai et al., 2014; Kopp et al., 2020; Lapenis et al., 2013; Zhang, Yuan, Liu, & Dong, 2015; Zhang, Yuan, Liu, Dong, & Fu, 2015). More importantly, the fact that the effects of the background climate variables we have considered are statistically significant (Table 3) indicates that the model in this study is valid, and our qualitative inferences in the introduction hold true. In addition, the models in previous studies were generally univariate linear regression in which the environment variable included annual precipitation, annual temperature, SD of annual temperatures or SD of monthly temperatures, and so on (Dai et al., 2014; Kopp et al., 2020; Lapenis et al., 2013; Zhang, Yuan, Liu, & Dong, 2015; Zhang, Yuan, Liu, Dong, & Fu, 2015). Thus, we have done similar tests using univariate linear regression with very small R values, which was suggested to be inapplicable in the Tibetan Plateau (Figure 2). To verify the progressiveness of our model, we also used the data in this study to compare our model to those in previous studies based on the Akaike information criterion (AIC). Our model had larger R^2 and smaller AIC values than the univariate linear regression models in previous studies (Appendix S1: Table S10), suggesting a significant improvement irrelevance to the additional complexity. In addition, it should be noted that the threshold of pre-GUD temperature variability (0.9828°C for $T_{\mathrm{SD}}^{\mathrm{pre}}$) for reversing the effect of pre-GUD precipitation on TS variations was based on a limited sample size (77 GUD time series) and thus should be interpreted with caution. Similarly, the threshold of post-GUD temperature variability ($T_{\mathrm{SD}}^{\mathrm{post}} = 0.7599°\mathrm{C}$) needs to be interpreted cautiously.

CONCLUSIONS

Using ground-based phenological records across the Tibetan Plateau, we showed that the interaction between $T_{\mathrm{SD}}^{\mathrm{pre}}$ and $P_{\mathrm{mean}}^{\mathrm{pre}}$ and the interaction between $T_{\mathrm{SD}}^{\mathrm{post}}$ and $P_{\mathrm{mean}}^{\mathrm{post}}$ shaped the spatial variability of the TS of the GUD. We found that in areas with low $T_{\mathrm{SD}}^{\mathrm{pre}}$, a spatial increase in $P_{\mathrm{mean}}^{\mathrm{pre}}$ led to an increase in the magnitude of TS, probably owing to a greater availability of liquid water for plant physiological processes. In areas with high $T_{\mathrm{SD}}^{\mathrm{pre}}$, a spatial increase in $P_{\mathrm{mean}}^{\mathrm{pre}}$ led to a decrease in the magnitude of TS, likely because precipitation can aggravate the damage of frost events to plant tissues and cells due to the crystallization of water. Opposite to the interactive effect between $T_{\mathrm{SD}}^{\mathrm{pre}}$ and $P_{\mathrm{mean}}^{\mathrm{pre}}$, in areas with low $T_{\mathrm{SD}}^{\mathrm{post}}$, high $P_{\mathrm{mean}}^{\mathrm{post}}$ can help plant leaves reach maturity faster and obviate the need to closely track temperature changes to reduce frost risk. Therefore, a spatial increase in $P_{\mathrm{mean}}^{\mathrm{post}}$ led to a decrease in the magnitude of TS in areas with low T_{SD}^{post}. In areas with high T_{SD}^{post}, high P_{mean}^{post} can slow plant leaf growth and maturation by aggravating low temperature constraints. As a result, plants need to closely track temperature changes to lengthen the growing season. Therefore, a spatial increase in P_{mean}^{post} led to an increase in the magnitude of TS in areas with high T_{SD}^{post}. The results of this study deepen the understanding of spatial TS variation by showing the interactive effects of pre-GUD temperature variability and precipitation, shedding new light on the frost risk hypothesis in spring leaf-out phenology. Moreover, our results suggest that post-GUD precipitation and interactions between post-GUD precipitation and temperature variability might be involved in shaping spatial TS variability. Our findings provide a reference for understanding leaf-out phenology in other arid and semiarid ecosystems in seasonally cold regions.

ACKNOWLEDGMENTS

This work was funded by the Science and Technology Innovation Base Free Research Program of Tibetan Autonomous Region of China (to Zhiyong Yang), the National Natural Science Foundation of China (42001108), and the Top-Notch Young Talents Program of China (to Miaogen Shen).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The raw in situ phenological observations were purchased from the China Meteorological Administration (CMA). Contact the China Meteorological Data Service Centre for data purchase (http://data.cma.cn/en/?r=article/getLeft&id=349&keyIndex=30). The meteorology data are freely available online for real-name registered users at the Meteorological Science Knowledge Service System (http://data.cma.cn/). The processed data used for graphing and statistical analyses (Yang et al., 2023) are available from Figshare: https://doi.org/10.6084/m9.figshare.21455922.v1.

ORCID

Zhiyong Yang https://orcid.org/0000-0001-5552-2672
Nan Jiang https://orcid.org/0000-0001-5151-5715
Yongshuo Fu https://orcid.org/0000-0002-9761-5292

REFERENCES

Ata-Ul-Karim, S. T., L. Cang, Y. Wang, and D. Zhou. 2020. "Effects of Soil Properties, Nitrogen Application, Plant Phenology, and Their Interactions on Plant Uptake of Cadmium in Wheat." *Journal of Hazardous Materials* 384: 121452. https://doi.org/10.1016/j.jhazmat.2019.121452.

Bennie, J., E. Kubin, A. Wiltshire, B. Huntley, and R. Baxter. 2010. "Predicting Spatial and Temporal Patterns of Bud-Burst and Spring Frost Risk in North-West Europe: The Implications of Local Adaptation to Climate." *Global Change Biology* 16(5): 1503–14. https://doi.org/10.1111/j.1365-2486.2009.02095.x.

Buermann, W., M. Forkel, M. O'Sullivan, S. Sitch, P. Friedlingstein, V. Haverd, A. K. Jain, et al. 2018. "Widespread Seasonal Compensation Effects of Spring Warming on Northern Plant Productivity." *Nature* 562(7725): 110–14. https://doi.org/10.1038/s41586-018-0555-7.

Cannell, M. G. R. 1997. "Spring Phenology of Trees and Frost Avoidance." *Weather* 52(2): 46–52. https://doi.org/10.1002/j.1477-8696.1997.tb06268.x.

CaraDonna, P. J., A. M. Iler, and D. W. Inouye. 2014. "Shifts in Flowering Phenology Reshape a Subalpine Plant Community." *Proceedings of the National Academy of Sciences of the United States of America* 111(13): 4916–21. https://doi.org/10.1073/pnas.1323073111.

Chen, A., L. Huang, Q. Liu, and S. Piao. 2021. "Optimal Temperature of Vegetation Productivity and Its Linkage with Climate and Elevation on the Tibetan Plateau." *Global Change Biology* 27(9): 1942–51. https://doi.org/10.1111/gcb.15542.

Chen, S., Y. Liu, and T. Axel. 2006. "Climatic Change on the Tibetan Plateau: Potential Evapotranspiration Trends from 1961–2000." *Climatic Change* 76(3–4): 291–319. https://doi.org/10.1007/s10584-006-9080-z.

Chen, X., S. An, D. W. Inouye, and M. D. Schwartz. 2015. "Temperature and Snowfall Trigger Alpine Vegetation Green-Up on the World's Roof." *Global Change Biology* 21(10): 3635–46. https://doi.org/10.1111/gcb.12954.

Chen, X. 2013. "East Asia." In *Phenology: An Integrative Environmental Science*, edited by M. D. Schwartz, 9–22. Dordrecht: Springer.

Chevan, A., and M. Sutherland. 1991. "Hierarchical Partitioning." *The American Statistician* 45(2): 90–96. https://doi.org/10.1080/00031305.1991.10475776.

China Meteorological Administration. 1993. *Observation Criterion of Agricultural Meteorology*. Beijing: China Meteorological Press.

Chmura, H. E., H. M. Kharouba, J. Ashander, S. M. Ehlman, E. B. Rivest, and L. H. Yang. 2019. "The Mechanisms of Phenology: The Patterns and Processes of Phenological Shifts." *Ecological Monographs* 89(1): e01337. https://doi.org/10.1002/ecm.1337.

Cleland, E., I. Chuine, A. Menzel, H. Mooney, and M. Schwartz. 2007. "Shifting Plant Phenology in Response to Global Change." *Trends in Ecology & Evolution* 22(7): 357–365. https://doi.org/10.1016/j.tree.2007.04.003.

Cleverly, J., D. Eamus, N. R. Coupe, C. Chen, W. Maes, L. Li, R. Faux, et al. 2016. "Soil Moisture Controls on Phenology and Productivity in a Semi-Arid Critical Zone." *Science of the Total Environment* 568: 1227–37. https://doi.org/10.1016/j.scitotenv.2016.05.142.

Cong, N., M. Shen, W. Yang, Z. Yang, G. Zhang, and S. Piao. 2017. "Varying Responses of Vegetation Activity to Climate Changes on the Tibetan Plateau Grassland." *International Journal of Biometeorology* 61(8): 1433–44. https://doi.org/10.1007/s00484-017-1321-5.

Cook, B. I., E. M. Wolkovich, T. Jonathan Davies, T. R. Ault, J. L. Betancourt, J. M. Allen, K. Bolmgren, et al. 2012. "Sensitivity of Spring Phenology to Warming across Temporal and Spatial Climate Gradients in Two Independent Databases." *Ecosystems* 15(8): 1283–94. https://doi.org/10.1007/s10021-012-9584-5.

Dai, J., H. Wang, and Q. Ge. 2014. "The Spatial Pattern of Leaf Phenology and Its Response to Climate Change in China." *International Journal of Biometeorology* 58(4): 521–28. https://doi.org/10.1007/s00484-013-0679-2.

Du, J., Z. He, K. B. Piatek, L. Chen, P. Lin, and X. Zhu. 2019. "Interacting Effects of Temperature and Precipitation on Climatic Sensitivity of Spring Vegetation Green-Up in Arid Mountains of China." *Agricultural and Forest Meteorology* 269–270: 71–77. https://doi.org/10.1016/j.agrformet.2019.02.008.

Falk, M. A., J. R. Donaldson, M. T. Stevens, K. F. Raffa, and R. L. Lindroth. 2020. "Phenological Responses to Prior-Season Defoliation and Soil-Nutrient Availability Vary among Early- and Late-Flushing Aspen (*Populus tremuloides* Michx.) Genotypes." *Forest Ecology and Management* 458: 117771. https://doi.org/10.1016/j.foreco.2019.117771.

Fang, J., W. Yang, Y. Luan, D. Juan, A. Lin, and L. Zhao. 2019. "Evaluation of the TRMM 3B42 and GPM IMERG Products for Extreme Precipitation Analysis over China." *Atmospheric Research* 223: 24–38. https://doi.org/10.1016/j.atmosres.2019.03.001.

Fu, Y. H., S. Piao, Y. Vitasse, H. Zhao, H. J. De Boeck, Q. Liu, H. Yang, U. Weber, H. Hanninen, and I. A. Janssens. 2015. "Increased Heat Requirement for Leaf Flushing in Temperate Woody Species over 1980-2012: Effects of Chilling, Precipitation and Insolation." *Global Change Biology* 21(7): 2687–97. https://doi.org/10.1111/gcb.12863.

Fu, Y. H., H. Zhao, S. Piao, M. Peaucelle, S. Peng, G. Zhou, P. Ciais, et al. 2015. "Declining Global Warming Effects on the Phenology of Spring Leaf Unfolding." *Nature* 526(7571): 104–7. https://doi.org/10.1038/nature15402.

Fu, Y. H., S. Piao, X. Zhou, X. Geng, F. Hao, Y. Vitasse, and I. A. Janssens. 2019. "Short Photoperiod Reduces the Temperature Sensitivity of Leaf-out in Saplings of *Fagus sylvatica* but Not in Horse Chestnut." *Global Change Biology* 25(5): 1696–1703. https://doi.org/10.1111/gcb.14599.

Ganjurjav, H., E. S. Gornish, G. Hu, M. W. Schwartz, Y. Wan, Y. Li, and Q. Gao. 2020. "Warming and Precipitation Addition Interact to Affect Plant Spring Phenology in Alpine Meadows on the Central Qinghai-Tibetan Plateau." *Agricultural and Forest Meteorology* 287: 107943. https://doi.org/10.1016/j.agrformet.2020.107943.

Gao, M., X. Wang, F. Meng, Q. Liu, X. Li, Y. Zhang, and S. Piao. 2020. "Three-Dimensional Change in Temperature Sensitivity of Northern Vegetation Phenology." *Global Change Biology* 26(9): 5189–5201. https://doi.org/10.1111/gcb.15200.

Gao, Y. C., and M. F. Liu. 2013. "Evaluation of High-Resolution Satellite Precipitation Products Using Rain Gauge Observations over the Tibetan Plateau." *Hydrology and Earth System Sciences* 17(2): 837–849. https://doi.org/10.5194/hess-17-837-2013.

Grömping, U. 2006. "Relative Importance for Linear Regression in R: The Package Relaimpo." *Journal of Statistical Software* 17(1): 1–27.

Gurevitch, J., S. Scheiner, and G. Fox. 2006. *The Ecology of Plants*, 2nd ed., Vol. 14. Sunderland, MA: Sinauer Associates.

He, J.-S., S. Dong, Z. Shang, M. K. Sundqvist, W. Gaolin, and Y. Yang. 2021. "Above-Belowground Interactions in Alpine Ecosystems on the Roof of the World." *Plant and Soil* 458(1–2): 1–6. https://doi.org/10.1007/s11104-020-04761-4.

Huang, J.-G., Q. Ma, S. Rossi, F. Biondi, A. Deslauriers, P. Fonti, E. Liang, et al. 2020. "Photoperiod and Temperature as Dominant Environmental Drivers Triggering Secondary Growth Resumption in Northern Hemisphere Conifers." *Proceedings of the National Academy of Sciences of the United States of America* 117(34): 20645–52. https://doi.org/10.1073/pnas.2007058117.

Huang, J., H. Yu, X. Guan, G. Wang, and R. Guo. 2016. "Accelerated Dryland Expansion under Climate Change." *Nature Climate Change* 6(2): 1661–2171. https://doi.org/10.1038/nclimate2837.

Huang, M., S. Piao, P. Ciais, J. Peñuelas, X. Wang, T. F. Keenan, S. Peng, et al. 2019. "Air Temperature Optima of Vegetation Productivity across Global Biomes." *Nature Ecology & Evolution* 3(5): 772–79. https://doi.org/10.1038/s41559-019-0838-x.

Inoue, S., Q.-L. Dang, R. Man, and B. Tedla. 2020. "Photoperiod, CO_2 and Soil Moisture Interactively Affect Phenology in Trembling Aspen: Implications to Climate Change-Induced Migration." *Environmental and Experimental Botany* 180: 104269. https://doi.org/10.1016/j.envexpbot.2020.104269.

Jeong, S.-J., C.-H. Ho, H.-J. Gim, and M. E. Brown. 2011. "Phenology Shifts at Start vs. End of Growing Season in Temperate Vegetation over the Northern Hemisphere for the Period 1982-2008." *Global Change Biology* 17(7): 2385–99. https://doi.org/10.1111/j.1365-2486.2011.02397.x.

Kawamura, Y., and M. Uemura. 2014. "Plant Low-Temperature Tolerance and Its Cellular Mechanisms." In *Plant Abiotic Stress*, edited by M. A. Jenks and P. M. Haseegawa, 1091–2132. Ames, IA: John Wiley & Sons, Inc.

Klosterman, S., K. Hufkens, and A. D. Richardson. 2018. "Later Springs Green-Up Faster: The Relation between Onset and Completion of Green-Up in Deciduous Forests of North America." *International Journal of Biometeorology* 62(9): 1645–55. https://doi.org/10.1007/s00484-018-1564-9.

Kopp, C. W., B. M. Neto-Bradley, L. P. J. Lipsen, J. Sandhar, and S. Smith. 2020. "Herbarium Records Indicate Variation in Bloom-Time Sensitivity to Temperature across a Geographically Diverse Region." *International Journal of Biometeorology* 64(5): 873–880. https://doi.org/10.1007/s00484-020-01877-1.

Körner, C., and D. Basler. 2010. "Phenology under Global Warming." *Science* 327(5972): 1461–62. https://doi.org/10.1126/science.1186473.

Koutroulis, A. G. 2019. "Dryland Changes under Different Levels of Global Warming." *Science of the Total Environment* 655: 482–511. https://doi.org/10.1016/j.scitotenv.2018.11.215.

Lapenis, A., H. Henry, M. Vuille, and J. Mower. 2013. "Climatic Factors Controlling Plant Sensitivity to Warming." *Climatic Change* 122(4): 723–734. https://doi.org/10.1007/s10584-013-1010-2.

Liang, E., Y. Wang, S. Piao, X. Lu, J. J. Camarero, H. Zhu, L. Zhu, A. M. Ellison, P. Ciais, and J. Peñuelas. 2016. "Species Interactions Slow Warming-Induced Upward Shifts of Treelines on the Tibetan Plateau." *Proceedings of the National Academy of Sciences of the United States of America* 113(16): 4380–85. https://doi.org/10.1073/pnas.1520582113.

Liu, Q., S. Piao, I. Janssens, Y. Fu, S. Peng, X. Lian, P. Ciais, R. Myneni, J. Penuelas, and T. Wang. 2018. "Extension of the Growing Season Increases Vegetation Exposure to Frost." *Nature Communications* 9: 426. https://doi.org/10.1038/s41467-017-02690-y.

Lu, H., N. Wu, K.-b. Liu, L. Zhu, X. Yang, T. Yao, L. Wang, et al. 2011. "Modern Pollen Distributions in Qinghai-Tibetan

Plateau and the Development of Transfer Functions for Reconstructing Holocene Environmental Changes." *Quaternary Science Reviews* 30(7–8): 947–966. https://doi.org/10.1016/j.quascirev.2011.01.008.

Matsumoto, K., T. Ohta, M. Irasawa, and T. Nakamura. 2003. "Climate Change and Extension of the *Ginkgo biloba* L. Growing Season in Japan." *Global Change Biology* 9(11): 1634–42. https://doi.org/10.1046/j.1365-2486.2003.00688.x.

Matthews, E. R., and S. J. Mazer. 2016. "Historical Changes in Flowering Phenology Are Governed by Temperature × Precipitation Interactions in a Widespread Perennial Herb in Western North America." *New Phytologist* 210(1): 157–167. https://doi.org/10.1111/nph.13751.

Menzel, A., Y. Yuan, M. Matiu, T. Sparks, H. Scheifinger, R. Gehrig, and N. Estrella. 2020. "Climate Change Fingerprints in Recent European Plant Phenology." *Global Change Biology* 26: 2599–2612. https://doi.org/10.1111/gcb.15000.

Muffler, L., C. Beierkuhnlein, G. Aas, A. Jentsch, A. H. Schweiger, C. Zohner, and J. Kreyling. 2016. "Distribution Ranges and Spring Phenology Explain Late Frost Sensitivity in 170 Woody Plants from the Northern Hemisphere." *Global Ecology and Biogeography* 25(9): 1061–71. https://doi.org/10.1111/geb.12466.

O'Brien, A. M., N. A. Ginnan, M. Rebolleda-Gomez, and M. R. Wagner. 2021. "Microbial Effects on Plant Phenology and Fitness." *American Journal of Botany* 108(10): 1824–37. https://doi.org/10.1002/ajb2.1743.

Panchen, Z. A., and R. Gorelick. 2017. "Prediction of Arctic Plant Phenological Sensitivity to Climate Change from Historical Records." *Ecology and Evolution* 7(5): 1325–38. https://doi.org/10.1002/ece3.2702.

Park, D. S., I. Breckheimer, A. C. Williams, E. Law, A. M. Ellison, and C. C. Davis. 2018. "Herbarium Specimens Reveal Substantial and Unexpected Variation in Phenological Sensitivity across the Eastern United States." *Philosophical Transactions of the Royal Society B: Biological Sciences* 374(1763): 20170394. https://doi.org/10.1098/rstb.2017.0394.

Peaucelle, M., I. A. Janssens, B. D. Stocker, A. Descals Ferrando, Y. H. Fu, R. Molowny-Horas, P. Ciais, and J. Penuelas. 2019. "Spatial Variance of Spring Phenology in Temperate Deciduous Forests Is Constrained by Background Climatic Conditions." *Nature Communications* 10(1): 5388. https://doi.org/10.1038/s41467-019-13365-1.

Pepin, N., R. S. Bradley, H. F. Diaz, M. Baraer, E. B. Caceres, N. Forsythe, H. Fowler, et al. 2015. "Elevation-Dependent Warming in Mountain Regions of the World." *Nature Climate Change* 5(5): 424–430. https://doi.org/10.1038/nclimate2563.

Piao, S., Q. Liu, A. Chen, I. A. Janssens, Y. Fu, J. Dai, L. Liu, X. Lian, M. Shen, and X. Zhu. 2019. "Plant Phenology and Global Climate Change: Current Progresses and Challenges." *Global Change Biology* 25(6): 1922–40. https://doi.org/10.1111/gcb.14619.

Prevey, J. S., C. Rixen, N. Ruger, T. T. Hoye, A. D. Bjorkman, I. H. Myers-Smith, S. C. Elmendorf, et al. 2019. "Warming Shortens Flowering Seasons of Tundra Plant Communities." *Nature Ecology & Evolution* 3(1): 45–52. https://doi.org/10.1038/s41559-018-0745-6.

Prevéy, J., M. Vellend, N. Rüger, R. D. Hollister, A. D. Bjorkman, I. H. Myers-Smith, S. C. Elmendorf, et al. 2017. "Greater Temperature Sensitivity of Plant Phenology at Colder Sites: Implications for Convergence across Northern Latitudes." *Global Change Biology* 23(7): 2660–71. https://doi.org/10.1111/gcb.13619.

Qin, Y., T. Wu, R. Li, W. Yu, T. Wang, X. Zhu, W. Wang, G. Hu, and L. Tian. 2016. "Using ERA-Interim Reanalysis Dataset to Assess the Changes of Ground Surface Freezing and Thawing Condition on the Qinghai–Tibet Plateau." *Environmental Earth Sciences* 75(9): 1–13. https://doi.org/10.1007/s12665-016-5633-2.

Reid, W., H. Mooney, A. Cropper, D. Capistrano, S. Carpenter, and K. Chopra. 2005. *Millennium Ecosystem Assessment. Ecosystems and Human Well-Being: Synthesis*. Washington, DC: World Resources Institute.

Reynolds, J. F., D. M. S. Smith, E. F. Lambin, B. L. Turner, M. Mortimore, S. P. J. Batterbury, T. E. Downing, et al. 2007. "Global Desertification: Building a Science for Dryland Development." *Science* 316(5826): 847–851. https://doi.org/10.1126/science.1131634.

Rollinson, C. R., and M. W. Kaye. 2012. "Experimental Warming Alters Spring Phenology of Certain Plant Functional Groups in an Early Successional Forest Community." *Global Change Biology* 18(3): 1108–16. https://doi.org/10.1111/j.1365-2486.2011.02612.x.

Schwartz, M. D. 2013. *Phenology: An Integrative Environmental Science*. Dordrecht: Springer.

Shen, M., S. Piao, N. Cong, G. Zhang, and I. A. Jassens. 2015. "Precipitation Impacts on Vegetation Spring Phenology on the Tibetan Plateau." *Global Change Biology* 21(10): 3647–56. https://doi.org/10.1111/gcb.12961.

Shen, M., N. Cong, and R. Cao. 2015. "Temperature Sensitivity as an Explanation of the Latitudinal Pattern of Green-Up Date Trend in Northern Hemisphere Vegetation during 1982-2008." *International Journal of Climatology* 35(12): 3707–12. https://doi.org/10.1002/joc.4227.

Shen, M., S. Piao, X. Chen, S. An, Y. H. Fu, S. Wang, N. Cong, and I. A. Janssens. 2016. "Strong Impacts of Daily Minimum Temperature on the Green-Up Date and Summer Greenness of the Tibetan Plateau." *Global Change Biology* 22(9): 3057–66. https://doi.org/10.1111/gcb.13301.

Singer, A., J. M. J. Travis, and K. Johst. 2013. "Interspecific Interactions Affect Species and Community Responses to Climate Shifts." *Oikos* 122(3): 358–366. https://doi.org/10.1111/j.1600-0706.2012.20465.x.

Sun, Q., B. Li, Y. Jiang, X. Chen, and G. Zhou. 2021. "Declined Trend in Herbaceous Plant Green-Up Dates on the Qinghai-Tibetan Plateau Caused by Spring Warming Slowdown." *Science of the Total Environment* 772: 145039. https://doi.org/10.1016/j.scitotenv.2021.145039.

Sun, Q., B. Li, Y. Yuan, Y. Jiang, T. Zhang, X. Gao, J. Ge, F. Li, and Z. Zhang. 2018. "A Prognostic Phenology Model for Alpine Meadows on the Qinghai–Tibetan Plateau." *Ecological Indicators* 93: 1089–1100. https://doi.org/10.1016/j.ecolind.2018.05.061.

Sun, Q., B. Li, G. Zhou, Y. Jiang, and Y. Yuan. 2020. "Delayed Autumn Leaf Senescence Date Prolongs the Growing Season Length of Herbaceous Plants on the Qinghai–Tibetan Plateau." *Agricultural and Forest Meteorology* 284: 107896. https://doi.org/10.1016/j.agrformet.2019.107896.

Tang, Y., S. Wan, J. He, and X. Zhao. 2009. "Foreword to the Special Issue: Looking into the Impacts of Global Warming from the Roof of the World." *Journal of Plant Ecology* 2(4): 169–171. https://doi.org/10.1093/jpe/rtp026.

Van Nuland, M. E., I. M. Ware, C. W. Schadt, Z. Yang, J. K. Bailey, and J. A. Schweitzer. 2021. "Natural Soil Microbiome Variation Affects Spring Foliar Phenology with Consequences for Plant Productivity and Climate-Driven Range Shifts." *The New Phytologist* 232(2): 762–775. https://doi.org/10.1111/nph.17599.

Walter, J., A. Jentsch, C. Beierkuhnlein, and J. Kreyling. 2013. "Ecological Stress Memory and Cross Stress Tolerance in Plants in the Face of Climate Extremes." *Environmental and Experimental Botany* 94: 3–8. https://doi.org/10.1016/j.envexpbot.2012.02.009.

Wang, B., Q. Bao, B. Hoskins, G. Wu, and Y. Liu. 2008. "Tibetan Plateau Warming and Precipitation Changes in East Asia." *Geophysical Research Letters* 35(14): L14702. https://doi.org/10.1029/2008gl034330.

Wang, T., C. Ottle, S. Peng, I. A. Janssens, X. Lin, B. Poulter, C. Yue, and P. Ciais. 2014. "The Influence of Local Spring Temperature Variance on Temperature Sensitivity of Spring Phenology." *Global Change Biology* 20(5): 1473–80. https://doi.org/10.1111/gcb.12509.

Wang, W., J. Li, Z. Yu, Y. Ding, W. Xing, and W. Lu. 2018. "Satellite Retrieval of Actual Evapotranspiration in the Tibetan Plateau: Components Partitioning, Multidecadal Trends and Dominated Factors Identifying." *Journal of Hydrology* 559: 471–485. https://doi.org/10.1016/j.jhydrol.2018.02.065.

Wang, W., W. Xing, Q. Shao, Z. Yu, S. Peng, T. Yang, B. Yong, J. Taylor, and V. P. Singh. 2013. "Changes in Reference Evapotranspiration across the Tibetan Plateau: Observations and Future Projections Based on Statistical Downscaling." *Journal of Geophysical Research: Atmospheres* 118(10): 4049–68. https://doi.org/10.1002/jgrd.50393.

Wolkovich, E. M., B. I. Cook, J. M. Allen, T. M. Crimmins, J. L. Betancourt, S. E. Travers, S. Pau, et al. 2012. "Warming Experiments Underpredict Plant Phenological Responses to Climate Change." *Nature* 485(7399): 494–97. https://doi.org/10.1038/nature11014.

Wu, C., X. Wang, H. Wang, P. Ciais, J. Peñuelas, R. B. Myneni, A. R. Desai, et al. 2018. "Contrasting Responses of Autumn-Leaf Senescence to Daytime and Night-Time Warming." *Nature Climate Change* 8(12): 1092–96. https://doi.org/10.1038/s41558-018-0346-z.

Xi, Y., T. Zhang, Y. Zhang, J. Zhu, G. Zhang, and Y. Jiang. 2015. "Nitrogen Addition Alters the Phenology of a Dominant Alpine Plant in Northern Tibet." *Arctic, Antarctic, and Alpine Research* 47(3): 511–18. https://doi.org/10.1657/aaar0014-054.

Yang, L. H., and V. H. Rudolf. 2010. "Phenology, Ontogeny and the Effects of Climate Change on the Timing of Species Interactions." *Ecology Letters* 13(1): 1–10. https://doi.org/10.1111/j.1461-0248.2009.01402.x.

Yang, Y., H. Guan, M. Shen, W. Liang, and L. Jiang. 2015. "Changes in Autumn Vegetation Dormancy Onset Date and the Climate Controls across Temperate Ecosystems in China from 1982 to 2010." *Global Change Biology* 21(2): 652–665. https://doi.org/10.1111/gcb.12778.

Yang, Z., N. Jiang, Y. Huang, M. Shen, W. Zhu, Y. Fu, Y. Tang, and I. A. Janssens. 2023. "Growing-Season Climate as an Explanation of Spatial Variations in Temperature Sensitivity of Green-Up on Tibetan Plateau." Figshare. Dataset. https://doi.org/10.6084/m9.figshare.21455922.v1.

Yin, L., X. Feng, B. Fu, Y. Chen, X. Wang, and F. Tao. 2020. "Irrigation Water Consumption of Irrigated Cropland and Its Dominant Factor in China from 1982 to 2015." *Advances in Water Resources* 143: 103661. https://doi.org/10.1016/j.advwatres.2020.103661.

You, Q., K. Fraedrich, G. Ren, N. Pepin, and S. Kang. 2013. "Variability of Temperature in the Tibetan Plateau Based on Homogenized Surface Stations and Reanalysis Data." *International Journal of Climatology* 33(6): 1337–47. https://doi.org/10.1002/joc.3512.

Yun, X., B. Huang, J. Cheng, W. Xu, S. Qiao, and Q. Li. 2019. "A New Merge of Global Surface Temperature Datasets since the Start of the 20th Century." *Earth System Science Data* 11(4): 1629–43. https://doi.org/10.5194/essd-11-1629-2019.

Zeng, Z., A. Chen, P. Ciais, Y. Li, L. Z. X. Li, R. Vautard, L. Zhou, H. Yang, M. Huang, and S. Piao. 2015. "Regional Air Pollution Brightening Reverses the Greenhouse Gases Induced Warming-Elevation Relationship." *Geophysical Research Letters* 42(11): 4563–72. https://doi.org/10.1002/2015gl064410.

Zhang, H., W. Yuan, S. Liu, and W. Dong. 2015. "Divergent Responses of Leaf Phenology to Changing Temperature among Plant Species and Geographical Regions." *Ecosphere* 6(12): 250–58. https://doi.org/10.1890/es15-00223.1.

Zhang, H., W. Yuan, S. Liu, W. Dong, and Y. Fu. 2015. "Sensitivity of Flowering Phenology to Changing Temperature in China." *Journal of Geophysical Research: Biogeosciences* 120(8): 1658–65. https://doi.org/10.1002/2015jg003112.

Zhang, X. 2005. "Monitoring the Response of Vegetation Phenology to Precipitation in Africa by Coupling MODIS and TRMM Instruments." *Journal of Geophysical Research* 110(D12): D12103. https://doi.org/10.1029/2004jd005263.

Zheng, Z., W. Zhu, G. Chen, N. Jiang, D. Fan, and D. Zhang. 2016. "Continuous but Diverse Advancement of Spring-Summer Phenology in Response to Climate Warming across the Qinghai-Tibetan Plateau." *Agricultural and Forest Meteorology* 223: 194–202. https://doi.org/10.1016/j.agrformet.2016.04.012.

Zohner, C. M., B. M. Benito, J. D. Fridley, J. C. Svenning, and S. S. Renner. 2017. "Spring Predictability Explains Different Leaf-Out Strategies in the Woody Floras of North America, Europe and East Asia." *Ecology Letters* 20(4): 452–460. https://doi.org/10.1111/ele.12746.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Yang, Zhiyong, Nan Jiang, Yan Huang, Miaogen Shen, Wenquan Zhu, Yongshuo Fu, Yanhong Tang, and Ivan Janssens. 2024. "Growing-Season Climate as an Explanation of Spatial Variations in Temperature Sensitivity of Green-Up On Tibetan Plateau." *Ecosphere* 15(2): e4761. https://doi.org/10.1002/ecs2.4761