

GEOSCIENCES

Special Topic: The Tibetan Plateau

Plant phenological responses to climate change on the Tibetan Plateau: research status and challenges

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ABSTRACT

Phenology studies the cycle of events in nature that are initiated and driven by an annually recurring environment. Plant phenology is expected to be one of the most sensitive and easily observable natural indicators of climate change. On the Tibetan Plateau (TP), an accelerated warming since the mid-1980s has resulted in significant environmental changes. These new conditions are accompanied by phenological changes that are characterized by considerable spatiotemporal heterogeneity. Satellite remote sensing observed widespread advance in the start of the plant growing season across the plateau during the 1980s and 1990s but substantial delay over 2000–2011 in the southwest although it continued to advance in the northeast regions of the TP. Both observational studies and controlled experiments have revealed, to some extent, the positive role of higher pre-season temperature and even more precipitation in advancing the leaf onset and first flowering date of the TP. However, a number of rarely visited research issues that are essential for understanding the role of phenology in ecosystem responses and feedback processes to climate change remain to be solved. Our review recommends that addressing the following questions should be a high priority. How did other phenological events change, such as flowering and fruiting phenology? What are the influences from environmental changes other than temperature and precipitation, including human activities such as grazing? What are the genetic and physiological bases of plants phenological responses? How does phenological change influence ecosystem structure and function at different scales and feedback to the climate system? Investigating these research questions requires, first of all, new data of the associated environmental variables, and consistent and reliable phenological observation using different methodologies (i.e. *in situ* observations and remote sensing).

Keywords: climate change, plant phenology, Tibetan Plateau

INTRODUCTION

Phenology studies the timing of the annual cycle of biological events and how they respond to inter-annual changes in the biotic and abiotic environment, particularly changes in meteorological conditions [1]. Plant phenology is expected to be the simplest process with which to track changes in the ecology of species in response to interannual changes in climate [2]. Traditional plant phenology makes field observations of the annual cycle of budburst, leaf unfolding, flowering, fruiting, leaf coloring, and leaf fall of individual plants, but

now satellite-mounted instruments can also be used. Satellite observations have the advantage of measuring spatiotemporally continuous spectral features of the vegetation with global coverage but a resolution down to hundreds of square meters; this is often termed ‘remote sensing phenology’ or ‘landscape phenology’ [3]. Typically, satellite data are used to determine the start and end of the vegetation growing season (SOS and EOS) [4] (sometimes termed ‘green-up’ and ‘dormancy onset’, respectively [5]).

Timing the annual cycle of plant development to match the seasonal change in climate is essential for individual survival, particularly in an era with a rapid

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rate of climatic change [6]. Shifts in phenological events may also affect the interplay between different species within a community and trophic levels, and even community composition [7–9]. At large scale, variations in vegetation phenology can alter vegetation activity and ecosystem functions [10–12], with implications for the land surface energy and carbon budgets [13–15] and even regional climate [16,17]. Understanding phenological responses to climate is thus a prerequisite for the realistic modeling and evaluation of ecosystem dynamics in climate change studies [18–20]. Furthermore, phenological changes are also relevant for human activities such as agriculture, forestry, and wildlife management, and even in health care (e.g. allergies) and tourism [21–23] and thus for mitigating the impacts of global climate change. On the Tibetan Plateau (TP), in particular, plant phenology could affect the forage production on which livestock feed, and thus the livelihoods of local residents living the traditional nomadic lifestyle [24,25].

The unique TP has an average altitude higher than 4000 m and extends over more than 2.5×10^6 km². It is the largest and highest plateau in the world, and is often called as ‘the third pole’ of the Earth [26]. As a part of the land climate system, the TP makes a significant impact on large-scale atmospheric circulations such as the Asian monsoon system [27–30]. The ratio of the surface heat fluxes, which regulates the timing of the start of the Asian summer monsoon and its interannual variability [31], is strongly influenced by the vegetation dynamics [32]. In this context, data on changes in the springtime phenology not only give us insight into how ecosystems respond to changing climate, but also provide information to help us understand the year-to-year variations in the onset of the Asian summer monsoon.

Within the TP, the weakening moisture-bearing monsoon and varying topography shape a variety of climate regimes. Annual precipitation decreases northwestward from more than 1000 mm in the southeast to less than 100 mm in the northwest [33,34]. Mean annual temperature decreases from the edges of the plateau towards the center and from low to high altitudes, ranging from -15°C to 10°C [35]. The daily mean temperature remains below freezing point for nearly half of the year, and ranges from 10°C to 20°C in summer [35]. The precipitation falls mainly between May and September, and thus the winter and spring are drier. The low latitude and high altitude of the TP results in high levels of solar radiation, and this in combination with the cold temperature creates a range of unique ecosystems, such as the alpine meadow, alpine steppe, and alpine desert distributed from

southeast to northwest [36]. Because of the relatively late onset of the spring green-up, the TP alpine vegetation has a much shorter growing season compared with other ecosystems at the same latitude [37,38].

Substantial climate changes on the TP have been observed in recent decades [39,40]. The mean annual temperature has increased by about 0.4°C per decade during the past 50 years [41], which is more than twice the rate of global temperature rise [42], and global climate models project that it will continue to increase over this century [43,44]. The temperature increases have exhibited spatiotemporal heterogeneity, being greater in winter and autumn than in spring and summer, in nighttime than in daytime, and in the western parts of TP than in the eastern parts [45,46]. On the other hand, the winter and spring precipitation has significantly increased but summer and autumn non-significantly decreased [45]. Spatially, the annual precipitation increase has been greater in the central-eastern and southeastern regions, while the northwest region and east edge received decreasing annual precipitation [45]. The mean annual temperature increase has accelerated since the early 1980s [47]. In the first decade of 21st century, in contrast to the observed climatic warming hiatus in most of world’s other regions [48], the temperature on the TP continued to increase [49]. Nevertheless, in the same period, precipitation declined in the southwestern region [49]. This combination of climatic change acting on a diverse range of vegetation types should have resulted in complex responses in phenology. However, there had been contradictory evidences regarding changes in spring vegetation phenology.

In this paper, we first review recent progress in the study of the plant phenology of the TP during the past few decades and the links with climatic change. We then briefly discuss the challenges in phenology observations, understanding the mechanisms through which the phenology responds to climatic change, and quantifying the effects of phenological changes on other ecosystem and climate processes.

PHENOLOGY CHANGE ON THE TP

Evidences from *in situ* observations

Ground-based phenological observations on the TP date back to the early 1980s. Until now, only a few studies have addressed changes in plant green-up onset date using *in situ* observations on the TP [50]. Chen *et al.* [50] collected phenological records with lengths of at least 10 years between 1981 and 2011 for 22 herbaceous plant species at 23 sites, mostly

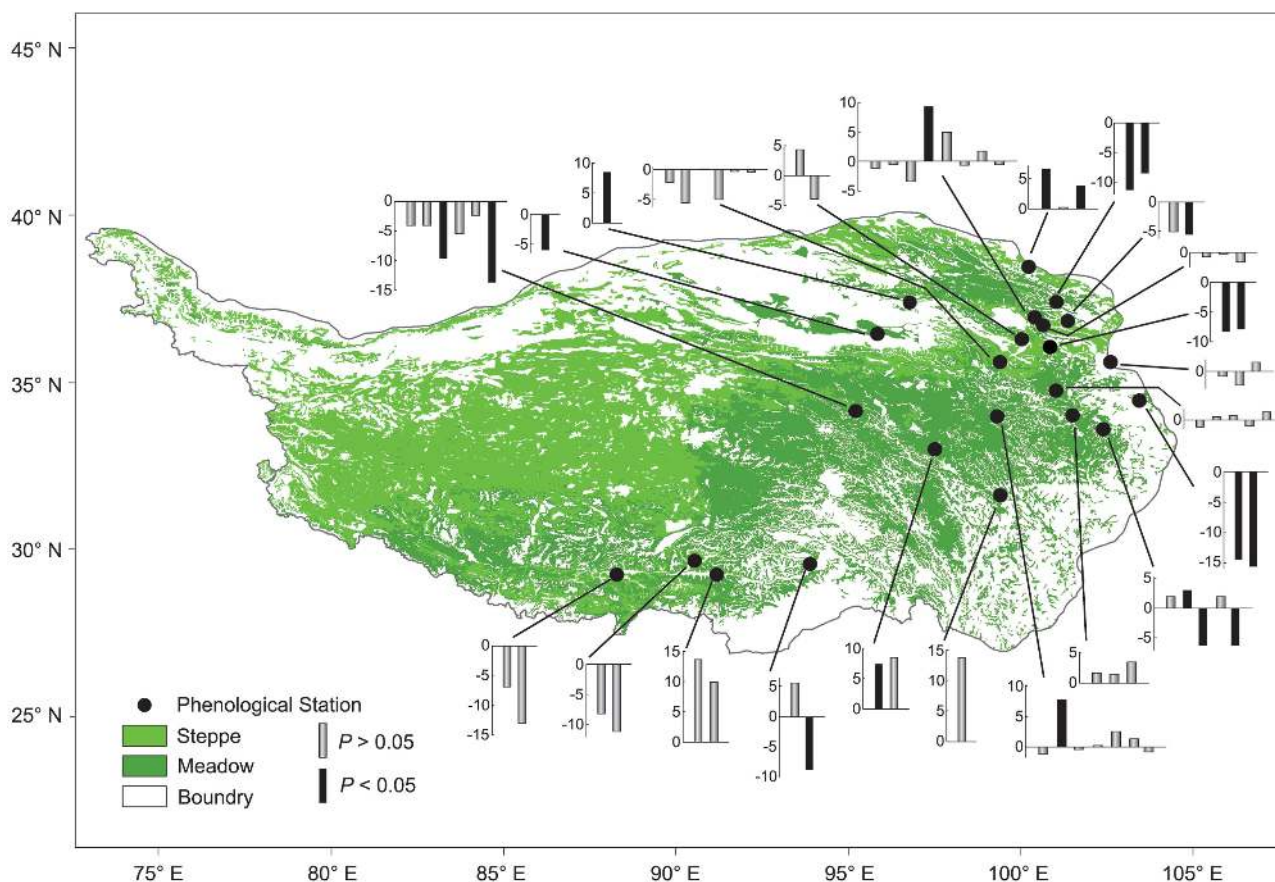


Figure 1. Temporal trends of plant green-up onset date (in days per decade) observed at 23 phenological stations, within the period 1982–2011. Each bar chart stands for one station (black dot within the map) and each bar indicates temporal trends for one species. Details are given by Chen *et al.* [50].

distributed over the eastern region of the TP. It is worth noting that the number of observed species varies among the different sites; for most of the sites, the phenology of only a few species was recorded (Fig. 1). Nevertheless, a total of 72 time series of green-up onset date were recorded. Of those time series, 18% showed significant ($P < 0.05$) advance of green-up onset, averaging -9.4 days per decade; these were mostly in the northeast of the TP. On the other hand, significant delay of green-up onset was observed in 11% of the time series, averaging 7.5 days per decade. In terms of species, 7 out of the 22 species showed a significant advancing trend and 6 species a significant delaying trend. There are slightly more significant trends at lower than at higher altitudes [50]. Based on those observations, the proportion of spring phenology with significant advance is less than that reported in a meta-analysis of 481 plant species collected over the globe [51]. Such a difference does not indicate that the phenology of the TP is less responsive to climatic warming than the rest of the world, because the observations in both studies are insufficient and there are substantial

differences in the observation periods, species, and locations [50,51]. This seems inevitable because traditional field observations relying on direct human observations of discrete phenological events are typically limited to a small number of individual organisms, across a limited geographic area [52].

Evidences from satellite observations

Satellite remote sensing provides a valuable way of retrieving large-scale vegetation phenology, with consistent temporal resolution. On the TP in particular, the changes in vegetation phenology are mostly being assessed using SOS and EOS derived from satellite observations of vegetation greenness, indicated by the Normalized Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI). NDVI was designed to reflect vegetation activity by observing radiation absorption by chlorophyll in the red band and radiation scattering by mesophyll in the near-infrared (NIR) band:

$$\text{NDVI} = (R_{\text{NIR}} - R_{\text{red}}) / (R_{\text{NIR}} + R_{\text{red}})$$

where R_{NIR} and R_{red} are reflectance in the NIR and red bands, respectively [53]. EVI is a modification of NDVI, designed to minimize background interference from the soil and atmospheric noises:

$$\text{EVI} = 2.5 (R_{\text{NIR}} - R_{\text{red}}) / (R_{\text{NIR}} + 6R_{\text{red}} - 7.5R_{\text{blue}} + 1)$$

where R_{blue} is the reflectance in the blue band [54,55]. Both NDVI and EVI, if used correctly, can effectively indicate variations in vegetation activity such as photosynthesis and aboveground green biomass [12,56–59], and thus reflect changes in SOS and EOS.

The earliest study of vegetation phenological changes reported interannual changes in SOS averaged over the TP from 1982 to 2006 [60]. They derived SOS from an NDVI dataset produced from

observations by the Advanced Very High Resolution Radiometer (AVHRR) [61], and found that the regionally averaged SOS at first showed a significant advance from 1982 to the mid-1990s, but thereafter showed a delaying trend for the rest of that period [60]. As a result, the regionally averaged SOS showed no significant trend over the whole period 1982–2006 (Fig. 2) [60,62]. This non-significance was due to a delayed SOS in the center of the TP and an advanced SOS in the southwest, east and northeast of the TP [63]. These changes cancelled each other out. During 1982–1999, different studies showed the regionally averaged SOS advanced by rates ranging from 4.5 days per decade to 10.2 days per decade (Fig. 2) [49,62,64], i.e. a region-wide advancing trend of SOS (Fig. 3A).

The AVHRR sensor was renewed in late 2000 and it has been suggested that the delaying trend from the mid-1990s to 2006 is caused by the reduced quality of the AVHRR NDVI data from 2001 onwards [64]. Zhang *et al.* [64] retrieved SOS over 2000–11 from two other independent NDVI datasets with higher fidelity during the growing season [NDVI from the Système Pour l'Observation de la Terre (SPOT), and from the Moderate Resolution Imaging Spectroradiometer (MODIS)]. Their results suggested that the advancing trend of SOS since the earlier 1980s has continued for the past 30 years, with an SOS advance of 16 days during 2000–2011. This magnitude of SOS advance over 2000–2011, however, was cast into doubt by a later study [65] investigating SOS sensitivity to interannual variations in temperature. Wang *et al.* [65] attributed the large magnitude of SOS advance to the decline in snow coverage during the non-growing season. This is because, according to the method proposed by Piao *et al.* [66] to determine SOS from NDVI, decline in non-growing season snow coverage should lead to NDVI increase and thus to negative bias (i.e. 'advance') in the retrieved SOS [67]. After calibrating the impacts of snow coverage on NDVI [67], it was found that the SOS averaged over the TP showed no significant trend over 2000–2011. This lack of significance, which was also found by three other studies [68–70], resulted from substantial spatial heterogeneity of trends in green-up date, with a notable delay in the southwest region, and widespread advancing trend in the other areas of the TP (Fig. 3B). Over the past three decades, SOS is 1–10 days per decade later in the southwest, but 1–10 days per decade earlier in most of the other regions of the TP (Fig. 3C).

The advancing trend of SOS on the TP over the past 30 years, even according to the most conservative estimate (i.e. advance by 4.5 days per decade during 1982–1999, and no significant trend over

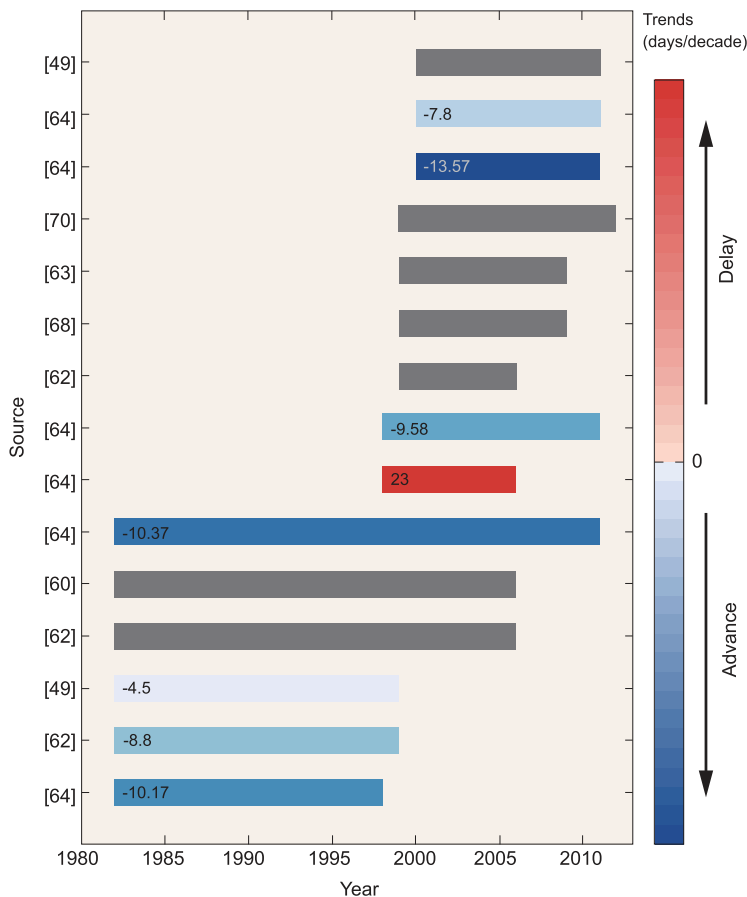


Figure 2. Gantt Chart showing temporal trends in regionally averaged SOS for various periods, as given by published studies. The numbers in the colored bars indicate the trends for the periods as given by the horizontal axis. For instance, the bottom color bar indicates that the temporal trend of SOS was -10.17 days per decade for the period 1982–1998 as given in [64]. SOS was retrieved from satellite-derived vegetation greenness indices (NDVI and EVI). The colored bars indicate significance at $P < 0.05$ level, and the gray bars, insignificance ($P > 0.05$). In the right color bar, deeper blue and red indicate greater SOS advancement and delay, respectively.

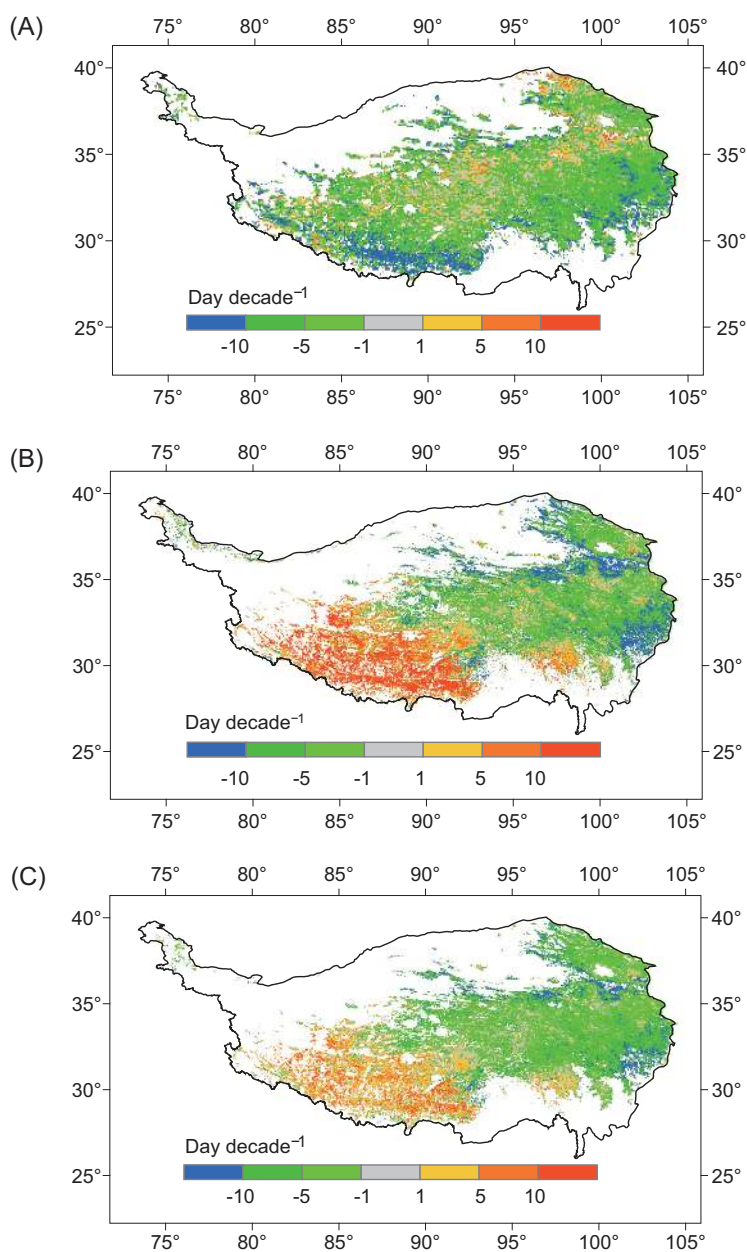


Figure 3. Spatial distribution of temporal trends of satellite-derived SOS over (A) 1982–1999, (B) 2000–2011 (modified from [49]) and (C) 1982–2011. For 1982–1999, the SOS was determined from the AVHRR NDVI using five methods described by Shen *et al.* [49], and for 2000–2011, the SOS on the NDVIs observed by AVHRR, MODIS and SPOT and on the MODIS EVI.

2000–2011), was greater than the SOS trends for high and middle latitudes. In detail, SOS averaged over the TP advanced by 3.7 days decade ($P < 0.01$) over 1982–2011, while SOS advanced by 1.5 days per decade and 1.7 days per decade (both $P < 0.01$) for boreal and arctic vegetation (north to 55°N), and temperate grasslands (30°N to 55°N), respectively (Fig. 4). Given that the similar magnitude of increase in spring temperature was observed between those three regions in the last 30 years (Fig. 4), the spring

vegetative phenology of the TP could be more sensitive to climate warming than that of the other two regions. However, whether the greater advancement of TP can be only ascribed to the difference in SOS sensitivity to spring temperature requires further investigations. It could also result from differences in vegetation traits, and/or may be due to the environmental changes themselves, in particular to the changes of climatic system such as variations in precipitation and winter temperature.

Compared with SOS, few studies have focused on changes in EOS on the TP. Those studies that did consistently found that, at regional scale, EOS showed no significant trends over the past three decades [68,71,72]. Regarding the spatial pattern, significant ($P < 0.05$) delaying trend of EOS from 1982 to 2011 was found only in about 9% of the TP areas, mostly observed in the eastern TP [72]. Therefore, changes in growing-season length were mainly from the shifting SOS. This pattern is different from that found in North America [73] and in Europe [74] where delay in EOS substantially contributed to extension of the growing season.

CLIMATIC IMPACT ON PHENOLOGY

In this section, we review the findings on the climatic controls on leafing phenology, which were gained mainly by using statistical analyses between remote-sensing retrievals of phenology and certain climatic variables. We then discuss how further findings were explored using field experiments in which environmental conditions were artificially altered.

Impacts of climatic change on the leafing phenology

In any region that experiences a cold winter or dormant season, SOS of vegetation in the spring requires that a certain threshold of forcing temperature has been reached to break ecodormancy [75,76]. Here the forcing temperature refers to the temperature in the period preceding SOS that initiates vegetative growth. On the TP, the intensive increase in forcing temperature during 1982–1999 (Fig. 5A) has been shown to result in evident advance of SOS [60,62,64]. It has also been suggested that before entering the period of ecodormancy, vegetation first experiences a period of endodormancy. Endodormancy is induced by a decreasing photoperiod and/or the low temperatures that occur naturally in the fall; it is broken after a chilling period at low temperature typically lower than 0°C during the dormant season [75,77]. Therefore, climate warming in late autumn and winter could potentially lead to insufficient chilling and thus a tendency of delaying SOS. On the TP, no direct

delaying effect of autumn and winter warming on the SOS of the steppe and meadow has yet been observed [49,67]. This is because, the mean daily temperature is always lower than 0°C from November to the following April on the TP and such low temperature is sufficient to meet the chilling requirement of the herbaceous plants [50]. As to EOS, a recent study found positive interannual partial correlation between EOS and growing-season temperature for the alpine steppe and meadow, suggesting

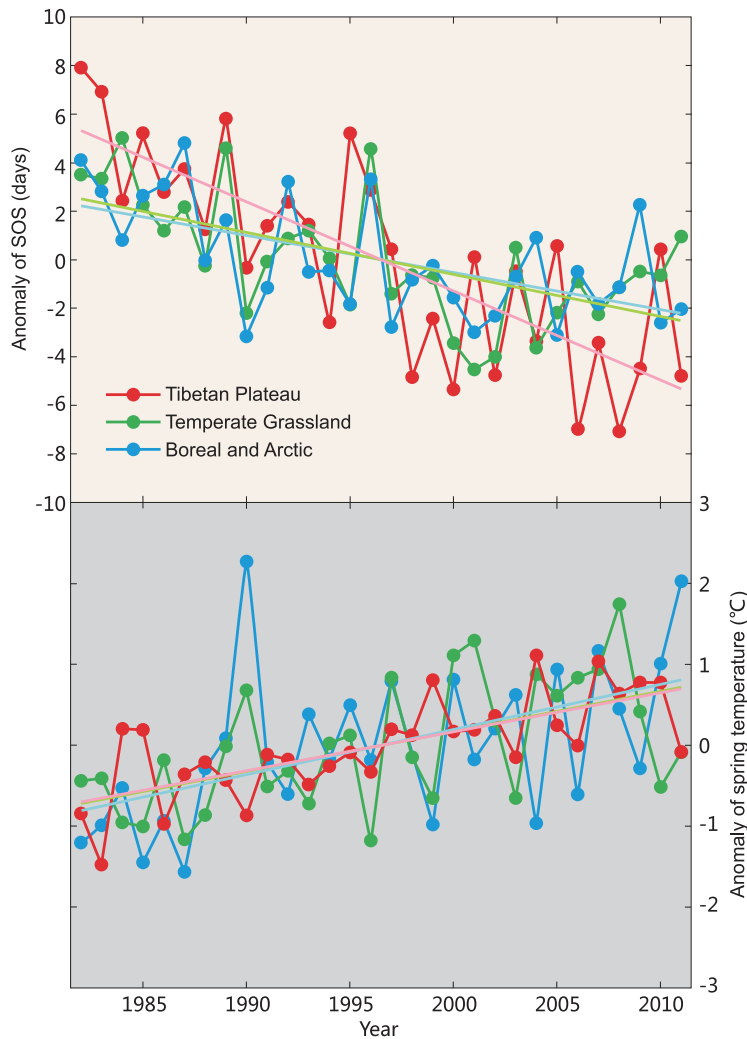


Figure 4. Interannual anomalies in satellite retrieval of SOS and mean spring (March–May) temperature averaged for the TP, temperate grassland, and boreal and arctic vegetation, respectively. SOS for the TP is the same as in Fig. 3, and SOS for temperate grassland, and for boreal and arctic vegetation was determined from AVHRR NDVI using the methods described by Cong *et al.* [128]. The spatial extent of temperate grassland was described by [129] between 30°N and 55°N, and the boreal and arctic vegetation refers to the vegetation in the region from the North Pole to 55°N. Temperature was extracted from the dataset provided by the Climatic Research Unit (CRU) [130]. The linear trends of SOS and spring temperature: for the TP are -3.7 days per decade and 0.48°C per decade respectively; for temperate grassland are -1.7 days per decade and 0.49°C per decade, respectively; and for the boreal and arctic vegetation are -1.5 days per decade and 0.55°C per decade respectively. $P < 0.01$ for all the six trends.

that warming during the growing season tends to delay EOS on the TP [78].

On the TP, however, the increasing forcing temperature did not necessarily advance SOS. For example, during the period 2000–11, there was region-wide increase in the forcing temperature (Fig. 5B), but the SOS in the southwestern region of TP was substantially delayed (Fig. 3B). Such mismatch between the warming and SOS trends was attributed to the impact of a decline in pre-season precipitation during this period (Fig. 5D). A recent study found that increasing pre-season precipitation could directly advance SOS in most areas of the TP, and the SOS was more sensitive to pre-season precipitation in more arid areas [79]. Moreover, the pre-season precipitation also regulated the SOS response to forcing temperature, with the SOS being more sensitive to forcing temperature in wetter areas [79]. Therefore, the extensive SOS advance during 1982–99 should be attributed to both increasing pre-season temperature and precipitation (Fig. 5A and C), and the slight decrease in precipitation might be responsible for the weak advancing trend of SOS in the northeastern region (Fig. 3A). Moreover, precipitation could also affect EOS on the TP, with increasing growing-season precipitation delaying EOS [78]. The positive effects of higher temperature and more precipitation on plant leafing phenology were also revealed by *in situ* observations [50]. Based on those findings, we might expect that the projected warmer and wetter climate [44] would advance the SOS and postpone the EOS, and thus expand the growing season on the TP in the future.

Effects of experimental conditions on phenology

Remote sensing can only detect plant leafing phenology changes at large scale—pixels have a length scale of dozens to thousands of meters. Remote sensing cannot, therefore, detect changes in flowering phenology (except for the rare case of a strong flower signal, see [80]), and flowering is one of most important plant phenological events. We now review the findings from field experiments that have focused on flowering phenology.

There are a limited number of field manipulative experimental studies that have reported on the effect of controlled conditions, such as temperature [81–84], precipitation [83,85–87], and nutrient additions [88–90], on flowering phenology on the TP. Those studies found that plant phenological responses to simulated environmental conditions were species specific. Under warming conditions, early-flowering plant species, from both central [83] and eastern [91] TP, consistently showed

delayed flowering dates, while shrubs tended to advance their flowering date across the TP [82,83]. It is also evident that precipitation, in the form of snow [83,85] or rainfall [86], seemed to play important roles in regulating plant phenology of species found in both the central TP area [83] and its eastern margin [64,85]. Early spring snow addition advanced first flowering dates of *Kobresia pygmea*, an absolute-dominant species with shallow roots and early flowering, on an alpine meadow ecosystem in central TP [83], while higher total rainfall amount significantly increased flowering duration of *K. pygmea* on the eastern TP [64]. A one-year manipulative experimental study conducted in eastern TP showed that extreme drought events can also significantly change the phenology of alpine plants and the responses are species-specific [87]. In addition, Xi *et al.* [90] recently reported that nitrogen addition significantly advanced the date of budding in

K. pygmea growing on an alpine meadow ecosystem in central TP.

Despite observing different signs (positive or negative) and various magnitudes (strong to weak) of phenological responses of different plant species to environmental conditions, a simple meta-analysis of data reported in the published literatures (Table S1, Supporting Information) shows that plants with similar functional traits, such as rooting depth, early or late flowering, woody or herbaceous, and life-forms, seem to respond in similar ways to the same environmental condition (Fig. 6). These results indicate that the resource acquisition properties of different traits may be more important in allowing plants to adapt to changes in environmental condition under future climate scenarios. For example, plants with shallow rooting depth may be more sensitive to droughts, either caused by warming chambers [83] or actual drought

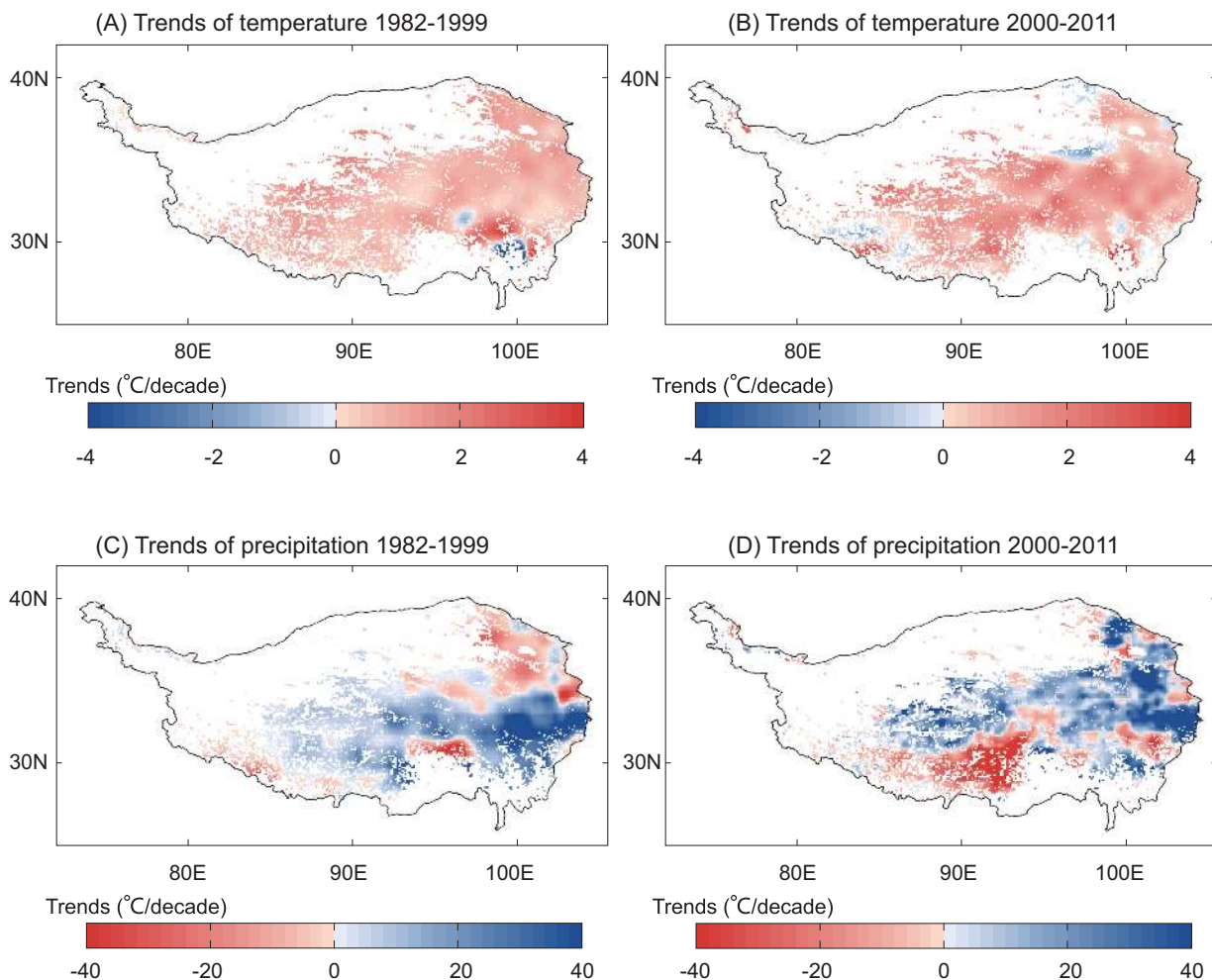


Figure 5. Spatial pattern of the temporal trends in spring (March–May) temperature and precipitation over the periods 1982–1999 (A and C) and 2000–2011 (B and D), respectively. Information on the climate data source is given by Shen *et al.* [79].

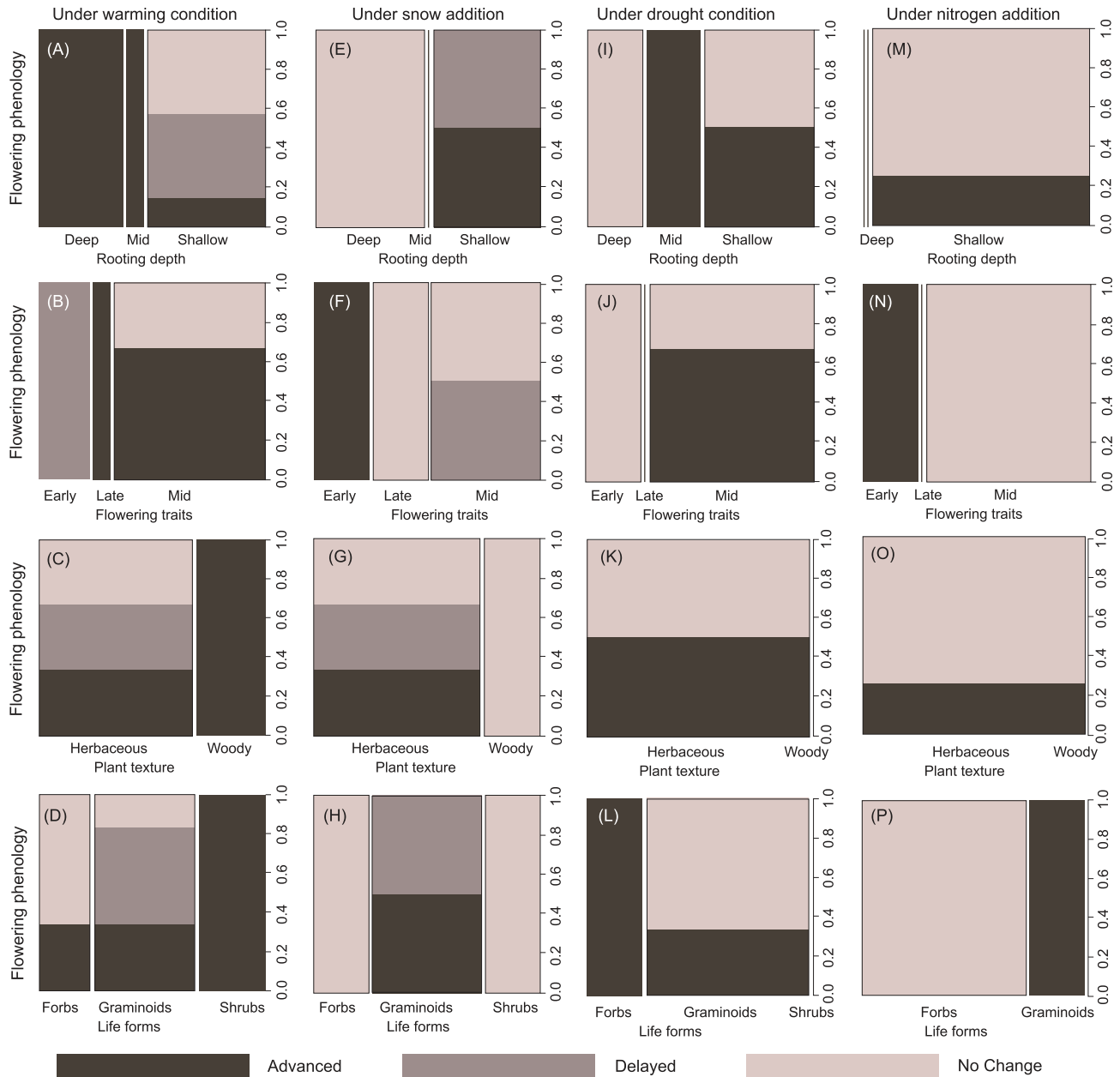


Figure 6. The fraction of flowering phenology changes (advanced, delayed, or no change, indicated by the height of each single-colored rectangle in each plate) of plant species with different functional traits under warming (A–D), snow addition (E–H), drought (I–L), and nitrogen addition (M–P) treatments, respectively. In each plate, width of the rectangle indicates the proportion of number of observed species in each trait (e.g. deep-, mid-, and shallow- rooted plant species), vertical line indicates no species with corresponding trait was observed. More information is given in Table S1 (Supporting Information).

events [87], while deep-rooted plant species, such as those shrub species studied by Xu *et al.* [82] and Dorji *et al.* [83], will show lower sensitivity to reduced precipitation, particularly those that can access deep groundwater. While the growth, distribution, and abundance of woody plants are mostly reported to be temperature- limited across the globe [92–95], they have also been shown to be

phenologically sensitive to warming on the TP [82,83,96]. As also indicated elsewhere [95,97,98], early-flowering plants seem sensitive to early spring warming and snow addition, although the sign of responses (positive or negative) may depend on the other traits, such as rooting depth or leaf structure, of the early-flowering species [81,83].

REMAINING ISSUES AND FURTHER TASKS

Deficiencies in phenological observations

The findings regarding the impacts of temperature and precipitation on spring leafing phenology are to some extent consistent between the remote sensing and *in situ* observations. However, there are considerable differences in the temporal trends in SOS between satellite measurements and field observations. These differences have several causes. Satellite remote sensing can only capture the leaf phenology of those species with high coverage in a community at the time of observation. If the sequence of leaf unfolding of different species within a community were to be altered by changing environmental conditions, then the species with the highest coverage at any particular time could change. Second, satellite-derived SOS relies on the greenness of a pixel, while *in situ* observation is based on the morphological changes of individual plants. Different species at the same leafing stage could exhibit different greenness because of differences in the characteristic area of individual leaves. Thus, because the flowering and fruiting phenology can currently only be obtained by *in situ* observation, satellite and *in situ* observations are complementary and both are needed. However, considerable deficiencies exist in both types of observations for the TP.

In assessing the satellite remote sensing of leafing phenology, the first issue concerns the data quality of NDVI. Satellite images are usually taken around noon, but such images are likely to be contaminated by clouds, which frequently occur at that time on the TP [99]. Validation of satellite-derived phenology is usually conducted by using *in situ* phenology observations in cropland and deciduous forest at the species level. In comparison, the satellite-derived phenology in natural grassland is difficult to validate by using such species-level observations because of coexistence of a large number of species within a pixel that exhibiting diverse phenological stage [63]. We recommend that *in situ* recording of landscape-level observations of leaf area index or greenness (such as NDVI and vegetation coverage), which is spatially and ecologically compatible with satellite-derived phenology, be used for validation. Fortunately, such an observation network is under construction by the Chinese Academy of Sciences. Only after that can the phenology of individual plants be scaled up to population-level phenology, then to community phenology, and finally to landscape phenology. Traditional phenological observations, which up until now have been mainly located only in the eastern part of the TP (Fig. 1) and been con-

ducted for leaf unfolding, are still insufficient, given the various species, vegetation types, climate gradients, and geographic extent of the TP. Moreover, field observations of flowering and fruiting phenology under natural condition should also be included. After that can climate effects on the phenological sequences be assessed.

Impacts of multiple environmental factors and plant response strategies

Previous studies mainly investigated the impact of mean temperature and the amount precipitation on the phenology of the TP. Yet, there could be many other factors that affect the phenology and these should be addressed in future research. First, given the large diurnal temperature range and greater nighttime warming than daytime warming on the TP, one may expect different impacts [100] of daytime and nighttime temperature change on phenology. Second, the cumulated precipitation is not a direct indicator of water availability for plants. The timing and intensity of precipitation, soil freezing/thawing, snowmelt, evaporation, and permafrost degradation could also affect the water availability and thus the phenology. For example, climate warming may reduce water availability by increasing evaporation [101–103], or by deepening the active layer and thus enhancing soil water loss [104–107]. In addition, the characterization of water availability could be further complicated by the complex and diverse soil properties found on the TP [108]. Third, process-based modeling indicates that the herbaceous plant phenology may be triggered by a diverse range of interactions between air temperature and precipitation/snowfall [50], although the evidence for this is still limited. Fourth, photoperiod has been suggested an important regulator of plant phenology [109–112], but its impacts on phenology have not been assessed on the TP. Fifth, although no statistical relationship was found between spring phenology and winter warming, we could not rule out the possible requirement of chilling and the potential effects of future winter warming on spring phenology on the TP. Sixth, vegetation phenology could also be affected by changes in species composition of the vegetation community which could be caused by climate warming but also by human activities such as overgrazing [113–116].

The diverse environmental conditions and plant functional traits that characterize the TP result in a range of phenological cycles occurring in parallel. Plants adapt these cycles in response to new conditions. Although experiment-based studies have provided important insights into how some plants would respond, it is still premature to reach any solid

and robust conclusions. First of all, most of the available experiments were short term, thus the reported results may not accurately predict the plants' future phenological adaptation strategies, in the long run. Other studies conducted elsewhere have indicated that plant phenological responses to experimental warming changed with the time scale of the experiment [95,97]. Second, many of these studies only focused on a single aspect of environmental change. Because environmental changes are complex and multifactorial, it is hard to predict how the interactions between different environmental factors will affect changes in plant phenology as plants adapt to new conditions. Most of these previous experiments only attempted to represent change in one environmental factor, and thus, are not likely able to capture the effects of the multilevel non-linear nature of environmental conditions on plant phenology. Future controlled experimental studies should, therefore, be longer termed and multifactorial. Third, genetic and physiological bases [117] of plants phenological responses should also be explored.

Influences of phenological changes on ecosystem structure and function

If the various species within a community have different phenological responses to climate change, the community-level rank order of phenological events could change. Such changes would then lead to variations in competition for abiotic resources such as light and water and changes to the interactions between different plant species. In the long run, the species composition of a certain community could also be changed. Such effects have been observed elsewhere [19,118,119], but have not yet been discovered for the TP. The phenological changes could also have consequences for adjacent ecosystem trophic levels, including trophic mismatch in consumer-resource dynamics and pollinator-host mismatch in mutualistic relationships [120,121]. Particular attention should be paid to this aspect of the TP vegetation, which provides the habitat for many Tibetan animal species (e.g. *Grus nigricollis*, *Ursus arctos pruinosus*, *Pantholops hodgsonii*), some of which are endangered.

Changes in the vegetation growing season at broad scale could further impact ecosystem functions such as carbon cycling and energy flows [15]. These impacts could in turn affect the climate system [122]. In particular, changes in the timing of SOS and EOS make a considerable impact on the annual carbon budget of Northern Hemisphere vegetation [11,14,123,124] and thus to the atmospheric CO₂ concentration. For example, it is suggested that

warming-induced advance in spring leaf unfolding will increase net carbon uptake [124], while delayed leaf senescence in the fall is found to lead to either increase [11,124] or decrease in net carbon uptake [14]. However, little is known about how the rapid phenological changes on the TP contribute to the variations in the regional energy and carbon balances. In the short term, phenological changes could directly modify land surface biophysical parameters and processes, such as albedo, sensible heat flux and evaporation, and boundary-layer turbulence, producing changes in the land surface energy and water budgets and thus in local climate [16,17,99,125,126]. The observations from a network of eddy-covariance flux towers on the TP could be helpful in addressing those issues. In particular, on the TP it is still unknown how the surface heat source strength, which is expected to influence the Asian summer monsoon, is affected by changes in the spring plant phenology.

Despite the extensive influences of plant phenology changes on ecosystem structure and function, no phenological models are specifically designed for the TP. Therefore, most of the current land surface models (or terrestrial ecosystem models) cannot realistically simulate the current seasonal cycle of vegetation growth [127], or its interannual variation on the TP. Further modeling work, which should address the phenological characteristics of the TP such as impacts of water availability on phenology, is challenging because we only have limited mechanistic understanding of phenological responses to environmental changes.

SUPPLEMENTARY DATA

Supplementary Data is available at NSR Online.

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