Responses of net primary productivity to phenological dynamics in the Tibetan Plateau, China

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A B S T R A C T
Quantifying the response of vegetation Net Primary Productivity (NPP) to phenological dynamics is critical to study climate change effects on ecosystem dynamics in the high-latitude, so investigating responses of NPP to phenological dynamics is becoming an increasing important way to identify and predict global ecosystem dynamics. In this study, we intend to quantify the temporal trends and spatial variations of vegetation phenology and NPP across the Tibetan Plateau by calibrating and analyzing time series of the MODIS-derived normalized difference vegetation index (NDVI) during 2002–2012, and examining the mechanisms of vegetation NPP response to phenological dynamics over the plateau. Our results indicated that most of the plateau experienced a continuous advancing trend in the beginning of vegetation growing season (BGS) and a delaying trend in the end of vegetation growing season (EGS), consequently a prolonged length of vegetation growing season (LGS). Accordingly, NPP also substantially increased in most parts of the plateau. Meanwhile, the spatial patterns of the BGS, EGS, LGS and NPP varied in accordance with the heat and water gradient across the plateau. The response modes of the NPP to phenological shifts varied within different climatic regimes, and the spatiotemporal response patterns were primarily controlled by the local climatic and topographic conditions. Moreover, temperature and precipitation played different roles in diverse responses of NPP to phenological dynamics, implying a profound effect of climate on response mechanism of the NPP to phenological changes.

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1. Introduction

Since the 1950s, global warming has increased by 0.6 °C, and the warming trend was more rapid at higher latitudes in the Eurasian continent (IPCC, 2007). Vegetation phenology is highly sensitive to climate change, as a result of the recent increase in surface temperature, earlier spring phenological events have been observed in the high latitudes (Piao et al., 2007; Geerken, 2009; Jeong et al., 2011). Changes in plant phenology will affect future ecosystem structure and functions since they affect surface energy exchange, water cycling, and terrestrial carbon cycling (Richardson et al., 2010; Steven et al., 2011). Increasing attentions have been paid in how these phenological shifts may affect net primary productivity (NPP) (Day and Monk, 1977; Richardson et al., 2010), which is an important indicator of an ecosystem’s potential for storage of nutrients and energy. So improving our ability to accurately describe the response of NPP to phenological shifts will advance our understanding of terrestrial ecosystems respond to global change.

The Tibetan Plateau (TP), the highest plateau of the earth, located in the central part of the troposphere in the mid-latitude westerlies, is regarded as the Earth’s third pole. The mean annual temperature on the plateau is only 1.6 °C, more than 60% of the plateau is covered by alpine grasslands (alpine steppe and meadow). TP has a large variety of ecosystem types, from subtropical rain forest in southeast to alpine desert in the northwest. TP is one of the most sensitive regions to climate change, over the past three decades the plateau has experienced significant warming trends (0.13 °C/year in winter, 0.04 °C/year in annual mean) (Liu and Chen, 2000; Du et al., 2004), and this warming is predicted to continue in the 21st century (IPCC, 2007). Thus, the plateau’s ecosystems and natural environment are inherently fragile and instable, making them especially vulnerable to global warming and leading diverse phenological responses to warming across the plateau. In recent years some studies applied time-series of the satellite-derived vegetation index (VI) to investigate phenological events and their connection to climate change in the TP (Piao et al., 2011; Shen et al., 2011). However, these stud-
ies revealed that the timing phenological events under the current climate warming differed in magnitude and even in direction (i.e., advance vs. delay in the date). Especially, due to the lack of 'in situ' observing data, vegetation phenology change and its linkage with NPP over the plateau remain poorly understood.

In this study, we aimed to investigating the temporal trends and spatial variability of vegetation phenology and NPP dynamics, as well as examining the mechanisms of NPP response to phenological shifts in the Tibetan Plateau during 2002–2012. Our purposes were to address the following key scientific questions: (1) What are the vegetation phenology and NPP pattern over the Tibetan Plateau during the recent decade? (2) How do relationships between vegetation phenology and NPP across the plateau? And (3) What are the driving mechanisms of NPP and phenological changes, especially, how do the driving factors control NPP and do the effects of phenology on NPP? Answers to these questions will improve our understanding of the relationships between vegetation phenology and NPP, help to quantify the magnitude and direction of NPP changes caused by phenological shifts, and thus provide an important scientific basis for the sustainable development.

2. Materials and methods

2.1. Data source and pre-processing

2.1.1. NDVI Dataset from MODIS

The Moderate Resolution Imaging Spectroradiometer (MODIS) onboard the Terra and Aqua satellites provide near-daily repeated coverage of the earth's surface with 36 spectral bands and a swath width of approximately 2330 km. For this study we selected the MOD 13C1 for vegetation-related information extraction. The MODIS products are distributed through NASA's Earth Observing System Data and Information System (EOSDIS). The MODIS product (MOD 13C1), with a 0.05° spatial resolution and 16-d intervals from 2002 to 2012, were generated based on atmospheric correction using bi-directional surface reflectance functions, and masked out water, clouds, heavy aerosols, and shadows (Huete et al., 1999, 2002).

2.1.2. Climate, vegetation cover and topography datasets

To estimate NPP and evaluate the climate conditions related to vegetation phenology and NPP changes, the climate data was used in this study. The climate data set was acquired from the China Meteorological Data Sharing Service System of the China Meteorological Administration. The climate data are available at 6h intervals (4-times daily). Three climate variables were acquired: mean daily air temperatures, daily rainfall and sunshine hours. To analyse the phenology variations at the biome level, the vegetation cover characteristics data were acquired from a digitized 1:100,000 vegetation map of Tibetan Plateau (Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, 1992). The plateau's vegetation types were regrouped into the following 10 types: evergreen broadleaf forest, deciduous broadleaf forest, mixed forest, shrubland, swamp and barren land, steppe, brushwood, alpine meadow and tundra, sparse alpine vegetation and cultivated land (Fig. 1). The topography data were obtained from the United States Geological Survey (USGS) global digital elevation model (DEM) with a horizontal grid spacing of 30 second (approximately1 km) resolution (GTOPO30, available at https://lta.cr.usgs.gov/GTOPO30).

2.1.3. Preprocessing of NDVI time-series data

MODIS NDVI datasets are processed to reduce the cloud and atmospheric effects before using them. The cloud filtering function of the maximum value composition (MVC) was applied to the MODIS NDVI data time series. However, there is still some cloud contamination existing under some cases. To eliminate errors caused by clouds, snow and ice contamination, we further applied a Savitzky-Golay filtering procedure to each annual NDVI cycle for smoothing and reconstrucing the NDVI time series, as described by Chen et al. (2004). For MODIS MOD13C1 product, a summary pixel reliability layer has been included in the MOD13C1, we first use the reliability layer information to locate the cloud or ice/snow pixels (where the pixel value equals 2 or 3 in the reliability layer) in the NDVI time-series. Then these cloud or ice/snow pixels can be replaced by a linear interpolation method using the adjacent NDVI data. The new NDVI values can be calculated as follows:

\[
\text{NDVI}^\text{N}(i, t) = \frac{a \text{NDVI}(i, t - 1) + b \text{NDVI}(i, t + 1)}{N(i, t)}, \quad \text{PR} = 2 \text{or} \text{PR} = 3
\]

Where PR is pixel reliability and NDVI\((i, t)\) is the NDVI of the pixel \(i\) at the time \(t\).

To further minimize the influence of soil and non-vegetated signals in NDVI time series, we choose areas with a multiyear average NDVI greater than 0.2 in the plateau as the study region based on the eleven years (2002–2012) NDVI data.

2.2. Determination of phenological metrics

Several methods have been developed to detect the phenophases (greenup, maturity, senescence, and dormancy) of vegetation phenology based on NDVI data, such as NDVI thresholds (Lloyd, 1990; White et al., 1997), largest NDVI increase (Kaduk and Heimann, 1996), backward-looking moving averages (Reed et al., 1994), and fitting logistic functions (Zhang et al., 2003, 2006). Comparative studies have indicated that the dynamic threshold method is one of the simplest and most effective methods for phenological study (Richardson et al., 2010; Hufkens et al., 2012). Thus, for the determination of phenological metrics based on NDVI, we also used this method to estimation of the beginning of vegetation growing season (BGS), end of vegetation growing season (EGS) and length of vegetation growing season (LGS) over the Tibetan Plateau. Firstly, we calculated the averaged annual NDVI ratio time series curve during 2002–2012. Then, we applied 20% and 50% as two dynamic thresholds which had been used widely for satellite-based phenology detection in previous studies (Jonsson and Eklundh, 2002; Hufkens et al., 2012). Consequently, we calculated the phenology date according to the 20% and 50% dynamic thresholds and a linear regression model. Fig. 2 showed the general scheme of the method for determining the phenological metrics. The NDVI ratio (ranges between 0 and 1) can be calculated by using the following formula:

\[
\text{NDVI}_{\text{ratio}} = \frac{\text{NDVI} - \text{NDVI}_{\text{min}}}{\text{NDVI}_{\text{max}} - \text{NDVI}_{\text{min}}} = \frac{\text{NDVI}}{\text{NDVI}_{\text{max}} - \text{NDVI}_{\text{min}}}
\]

where \(\text{NDVI}_{\text{ratio}}\) is the output ratio, ranging from 0 to 1; \(\text{NDVI}\) is the daily NDVI; \(\text{NDVI}_{\text{max}}\) and \(\text{NDVI}_{\text{min}}\) are the annual maximum and minimum NDVI, respectively. Thus the phenological metrics can be extracted with a NDVI dynamic threshold model for each pixel.

2.3. NPP estimation using CASA model

NPP is a key variable in investigating vegetation productivity, terrestrial ecosystem and global carbon cycle. Since it is difficult to directly measure NPP at the regional scale, process-based models are considered as a cost-effective alternative for NPP estimation. In recent years, a number of models have been developed to quantify NPP at the regional or global scale. Among these models, the CASA (Carnegie-Ames-Stanford Approach) model is an excellent process-based model for NPP estimation based on the plant growing mechanism (Monteith, 1977; Potter et al., 1993; Running et al., 2004). In this study, we applied CASA model to estimate vegeta-
Fig. 1. Distribution of vegetation types in the Tibetan Plateau (adopted from the Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, 1992). The 156 meteorological stations used in this study are also plotted.

Fig. 2. Schematic illustration for the method determining beginning of growing season (BGS), end of growing season (EGS) and length of growing season (LGS).

The CASA model can be summarized in the following equations:

\[ NPP(x, t) = APAR(x, t) \times \varepsilon(x, t) \]  \hspace{1cm} (3)

where, \( NPP \) is net primary productivity (gC/m²), \( APAR \) is the absorbed photosynthetically active radiation, \( \varepsilon \) is the light-use efficiency variable (gC/MJ), which is set as 0.389 gC/MJ in this study. \( T(x, t) \) and \( W(x, t) \) are multipliers of temperature and moisture effects on light use efficiency of vegetation, respectively. \( R \) stands for the fraction of solar active radiation (0.4–0.7 µm) that can be used by vegetation \((R=0.5)\).

Further details about the theoretical background of the CASA model can be found in the literatures (Monteith, 1977; Potter et al., 1993; Nemani et al., 2003).

Due to the complexity of the terrain, in order to obtain more accurate surface radiation, surface solar radiation value was estimated based on latitude, elevation, average daily sunlight hours, relative humidity and rainfall of 156 meteorological stations using stepwise regression method. Final solar radiation was calculated with the following formulas:

\[ Q = b_0 + \sum_{i=1}^{m} \left( \sum_{j=1}^{s} b_{ij} x_{ij} + \sum_{k=i+1}^{m} c_{ik} x_{ik} \right) \]  \hspace{1cm} (6)

where \( Q \) is the total solar radiation; \( m \) is the total number of factors; \( x_{ij} \) and \( x_{ik} \) represent the \( i \)th and \( k \)th factors (i.e. latitude, elevation, etc.), respectively; \( b_0, b_{ij}, c_{ik} \) represent factor coefficients.
fPAR can be calculated as:

\[ fPAR = a \times NDVI + b \]  

where \( a = 1.24 \) and \( b = 0.169 \) are empirical parameters. fPAR also can be obtained from MODIS fPAR products (MOD15). In this study, we used MODIS-Terra 1 km 16-day fPAR products during 2002–2012.

Using CASA model, we calculated monthly NPP of the plateau from 2002 to 2012. To evaluate the NPP estimates, an intercomparison between field measured observation and model simulation was carried out at Namco Observation Station, and a linear regression technique was used to identify the differences between observed and modeled NPP (Fig. 3). The CASA model reasonably reconstructed NPP at the site in both magnitude and temporal variability. The linear relationship between the estimated and measured NPP is \( Y = 0.862X + 6.930 \) (\( R^2 = 0.715, P<0.001 \)), which indicates that the CASA model can successfully capture changes in NPP in study area.

2.4. Correlation analysis between NPP and Phenology

Correlation coefficients and significance tests were used to examine the relationships between NPP and phenological shifts over 2002–2012. We analyzed the effects of vegetation phenological shifts on the trends of NPP based on Pearson correlation analysis. In addition, a t-test was used to test the significance of the correlations, with \( p \) values <0.1, 0.05 and 0.01 are considered to be low, middle and high significance levels, respectively.

3. Results and analyses

3.1. Spatial patterns and interannual variations of phenology and NPP

The spatial patterns of phenological metrics (BGS, EGS, LGS) and NPP were depicted in Fig. 4(a–d). The BGS date gradually decreased from west to east in the TP, while LGS and NPP gradually increased from west to east. These characteristics reflected the spatial heterogeneity of climate and terrain, and are in accordance with the gradients in humidity, temperature and elevation in the plateau. The BGS dates ranged from approximately 111 days for forests to approximately 122 days for steppe; EGS dates ranged from approximately 297–308 days; LGS dates ranged from 183 days to 193 days; the mean annual NPP ranged from approximately 219.802–242.543 g C m\(^{-2}\) yr\(^{-1}\). Furthermore, the analysis of relationships between phenological metrics and NPP for individual vegetation types indicated that alpine meadow and tundras, which are located in the southeast, had the earliest BGS and longest LGS, while alpine grassland located in the southwest had the latest BGS and shortest LGS. The spatial distribution of NPP was similar to that of phenological metrics, and was also in line with the heat and water gradients from southeast to northwest across the TP. The climate on the plateau gradually shifts from semi-moist in the east, semi-arid in the central, to arid regimes in the western plateau, which regulates the spatial pattern of phenological indicators and NPP.

The spatial patterns of the change trends of phenological metrics and NPP during 2002–2012 were mapped in Fig. 4(e–h). During 2002–2012, most areas of the plateau experienced an advancing trend in BGS, with more than 24.37% of advanced BGS (> 1 day yr\(^{-1}\)) mainly occurred in the central east (Fig. 5e, red areas in the picture), while most of the plateau (57.53%) experienced a delaying trend in EGS, with some exceptions in the middle of TP showing an earlier EGS. Due to the advanced BGS and delayed EGS, the LGS had been significantly extended for over 55.31% of the study region during the study period, which were consistent with previous studies (Shen, 2011; Jin et al., 2013). Unlike BGS, EGS and LGS, annual NPP showed a decreasing trend in the west and north and an increasing trend in the southeast, this trend is consistent with the previous studies (Chen et al., 2014). There are more areas increased (56.26% of total pixels) in NPP than decreased (33.74%), with the strongest positive trend (>4.0 g C m\(^{-2}\) yr\(^{-1}\)) observed in the Mid-eastern plateau. Consistent with the BGS pattern, more than 20.25% of significantly increased NPP mainly occurred in the mid-eastern plateau.

3.2. Quantitative relationships between NPP and phenological metrics across the plateau

To quantify the influence of spring and autumn phenological shifts on vegetation NPP, we analyzed the quantitative relationships between BGS and spring NPP (March–May), EGS and autumn NPP (August–October), and LGS and annual NPP across the plateau. The relationships between NPP and phenological metrics can be categorized into four groups. The first group belonged to region A of response relationship, in which the NPP decreased and BGS advanced (or EGS advanced or LGS shortened). The second group represents the region B of response relationship where the NPP was decreased and BGS was delayed (or EGS delayed or LGS prolonged), the third group is for the region C with the NPP increased and BGS advanced (or EGS advanced or LGS shortened), and the fourth group belonged to the region D with the NPP increased and BGS delayed (or EGS delayed or LGS prolonged).

3.2.1. Quantitative relationships between NPP and LGS

Fig. 5a and b presented the spatial distribution of response relationship and correlation coefficient between annual NPP and LGS. During 2002–2012, areas that experienced a significant trend in decreased NPP and shortened LGS (Region A) mainly occurred in the southeastern TP, where shrubland is the main vegetation type. Concurrently, over 80% of the areas that experienced a significant trend in decreased NPP and prolonged LGS (Region B) were distributed in the southwestern TP, where belonged to the arid and semi-arid zones of sub-frigid belt, and were sensitive to changing precipitation and vulnerable to climate warming (Qin et al., 2013). The correlation coefficient between NDVI and precipitation was 0.780, which was much higher than that between temperature and NDVI (the correlation coefficient is −0.079), indicating that precipitation is the primary determinant of vegetation growth in these areas. It is noteworthy that a longer LGS was found in these areas, due to most of the areas experienced an advancing trend in BGS (0.942 days yr\(^{-1}\), \( p < 0.01 \)) and a delaying trend in EGS (1.296 days yr\(^{-1}\), \( p < 0.01 \)), indicating that a prolonged LGS might not be necessary to result in increasing NPP. Most of the areas with increased NPP and shortened LGS (Region C) mainly distributed in the central TP, where major vegetation types were steppe, alpine meadow and tundra. We found that temperature was the major determinant of vegetation growth in these areas as the correlation coefficient between NDVI and temperature (the correlation coefficient is 0.673) was significantly higher than that between NDVI and precipitation (the correlation coefficient is 0.269). During 2002–2012, temperature showed a significant increasing trend, and the increases were more significant in autumn than in spring, which lead to advance EGS, LGS shortened, and NPP showed an increasing trend at the rate of 4.957 g C m\(^{-2}\) yr\(^{-1}\). These results are similar to the previous findings of Li et al. (2004), which indicated that climate warming would accelerate growth and maturation of plants, and thus shorten the LGS. The areas with increased NPP and prolonged LGS (Region D) mainly distributed in the semi-arid steppe, alpine meadow and tundra with sub-frigid climate in the central and eastern TP. Compared with the region C, the areas of region D had a better environmental condition. Due to the increased temperature and precipitation, LGS was significantly prolonged and thus
Fig. 3. Comparison of the CASA estimated NPP and field observation at the Namco Observation Station, Tibetan Plateau: (a) Comparison of the CASA estimated NPP and field observation across the same season and different years; b: Comparison of the CASA estimated NPP and field observation across different seasons and different years. The solid black line represents estimated NPP, the black dashed line with circles represents measured NPP.

NPP increased (at a rate of 1.668 g C m\(^{-2}\) with one day prolonging of LGS, \(p < 0.01\)).

3.2.2. Quantitative relationships between NPP and BGS, EGS

Fig. 5c and d presented the spatial distribution of the response relationships and correlation coefficients between spring NPP and BGS. About 54% of the plateau showed a significant negative correlation between spring NPP and BGS, especially in the mid-eastern plateau, the negative correlation was more significant (Fig. 5d). Correspondingly, 36.8% of the plateau showed significant BGS and increased NPP (region C) in the eastern plateau (Fig. 5e). Meanwhile, both of the significant increasing trends in temperature and precipitation were observed across the region C. The increased temperature and precipitation resulted in a significant advance of BGS and increased NPP. The region D, as the second largest region, has fragmented spatial patterns. It showed that temperature was the dominant climatic factor for vegetation growth (\(R = -0.659, p < 0.01\)), and temperature indirectly led to water deficiency. As a result, even the BGS delayed, the spring NPP still showed an increasing trend. This finding is inconsistent with the conclusion drawn by most previous studies, which found that climate warming result in the advance of the green-up date (Menzel, 2000; Piao et al., 2006; Chen et al., 2011a,b). However, precipitation is perhaps the most important factor controlling green-up phenology in arid and semi-arid ecosystems (Ma et al., 2010; Han et al., 2015). These patterns indicated the complex responses of NPP to phenological shifts despite the general warming of climate across the TP.

Fig. 5e and f presented the spatial distribution of response relationships and correlation coefficient between autumn NPP and EGS. The majority of pixels exhibited positive correlations (e.g., 74% pixels were significant at \(p < 0.05\), Fig. 5f), suggesting that a delayed EGS generally caused an increase in autumn NPP. Interestingly, in the region C, we found that although autumn NPP exhibited an increasing trend, but LGS decreased due to the earlier onset of EGS. As we previously mentioned, autumn phenophases occurred earlier due to the increased autumn temperature, which reflected vegetation phenological response to climate warming was more sensitive in these areas. Furthermore, it also reflected NPP response to phenological shifts was more complex in these areas.

As we previously mentioned, during the period of plant growth, spring NPP was primarily determined by the spring climate conditions, and autumn NPP was primarily determined by the autumn climate conditions. In this study, we calculated the correlation coefficients between BGS and spring NPP (March-May), EGS and autumn NPP (August, September and October) for specific vegetation types (Table 1). Mixed forest and sparse alpine vegetation showed a more significant correlation between BGS and annual NPP (\(R = -0.672, R = 0.605\), respectively, \(p < 0.05\)) than the other types. For shrubland, steppe, alpine meadow and tundra, and sparse alpine vegetation, spring NPP showed a significant negative correlation with BGS (\(R = -0.675, -0.778\) and \(-0.802\), respectively, \(p < 0.05\)). However, autumn NPP showed no significant correlation with EGS. For all vegetation types, BGS was found to be negatively correlated with spring NPP (\(R = -0.808, p = 0.003\)) and EGS showed a positive correlation with autumn NPP (\(R = 0.587, p = 0.058\)), indicating that warmer spring tended to increase spring NPP through earlier EGS and a delayed EGS tended to increase autumn NPP by extending the growing season, but the shifts of BGS and EGS were found to have limited impacts on annual NPP, with no significant relationships detected between annual NPP and the two phenological metrics. This result was consistent with previous studies (Richardson et al., 2010; Wu et al., 2013).

3.3. Relationships between NPP and phenology indicators along increasing altitude gradient

Due to the high altitude, exposure to lower temperature and unique physical conditions, and some previous studies reported that altitude had an important effect on phenological response (Inouye, 2008; Crimmins et al., 2010). Therefore, we further investigated the NPP and phenological response across the altitude gradient. Fig. 6 showed the average and standard deviation of the phenological metrics and NPP trends from 2002 to 2012 with an interval of 500 m. The EGS and LGS substantially decreased with increasing altitude, while BGS substantially increased during 2002–2012. Overall, the BGS was significantly advanced by 1.0 days, EGS was advanced by 1.5 days and LGS was shortened by 4.5 days per 500 m increase of altitude. NPP substantially decreased with increasing altitude, with a rate of 78.5 g C m\(^{-2}\) yr\(^{-1}\) per 500 m. However, as shown in Fig. 6A, two distinctly different trends could be identified for BGS date along an altitude gradient. The BGS was significantly advanced (slope = −0.011 day m\(^{-1}\), \(R^2 = 0.773, p < 0.001\)) below 3500 m, but it was significantly delayed (slope = −0.009 day m\(^{-1}\), \(R^2 = 0.824, p < 0.001\)) above 3500 m. Similar trends were also observed for NPP (Fig. 6D). NPP was significantly increased
Fig. 4. Spatial distributions of the annual mean phenological metrics, NPP and their trends over the Tibetan Plateau during 2002–2012. (a) mean Julian day of BGS, (b) mean Julian day of EGS, (c) mean LGS, (d) mean annual NPP, (e) change trends of BGS (days yr\(^{-1}\)), (f) change trends of EGS (days yr\(^{-1}\)), (g) change trends of LGS (days yr\(^{-1}\)), (h) change trends of vegetation NPP (g C m\(^{-2}\)).
Fig. 5. Spatial distribution of response relationships and correlation coefficients between NPP and phenological metrics. (a) response relationship between annual NPP and LCS, (b) correlation coefficient between annual NPP and LCS, (c) response relationship between spring NPP and BCS, (d) correlation coefficient between spring NPP and BCS, (e) response relationship between autumn NPP and EGS, (f) correlation coefficient between autumn NPP and EGS. The insets show the frequency distributions of different response relationships (Region A–D).

4. Discussion

4.1. Role of climate in NPP response to phenological metrics

To examine the role of climate factors in NPP response to phenological changes, we further analyzed the relationship between trends in NPP, phenology and climate within different temperature and precipitation zones determined based on historical climate data. We divided the TP into over 336 hydrothermal zones. The procedures to generate these hydrothermal zones are conducted in two steps. The first step is to divide the plateau’s rainfall into 24 rainfall zones along the annual average precipitation gradient with an interval of 50 mm. The second step is to further divide each rainfall zone into 14 sub-zones along the annual average temperature gradient with an interval of 2°C. Fig. 7 shows the trends in phenology, NPP, and climate over different hydrothermal zones.
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Table 1
Correlation coefficients between annual spring and autumn NPP and phenological metrics (BGS and EGS) for different vegetation types over the Tibetan Plateau.

<table>
<thead>
<tr>
<th>Vegetation Type</th>
<th>Phenological Indicators</th>
<th>Spring NPP</th>
<th>Autumn NPP</th>
<th>Annual NPP</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>( R )</td>
<td>( p )</td>
<td>( R )</td>
</tr>
<tr>
<td>All types</td>
<td>BGS</td>
<td>-0.808(^{**})</td>
<td>0.003</td>
<td>0.257</td>
</tr>
<tr>
<td></td>
<td>EGS</td>
<td>-0.373</td>
<td>0.259</td>
<td>0.587</td>
</tr>
<tr>
<td>Mixed forest</td>
<td>BGS</td>
<td>-0.498</td>
<td>0.119</td>
<td>-0.345</td>
</tr>
<tr>
<td></td>
<td>EGS</td>
<td>-0.032</td>
<td>0.926</td>
<td>0.238</td>
</tr>
<tr>
<td>Shrubland</td>
<td>BGS</td>
<td>-0.650</td>
<td>0.030</td>
<td>0.242</td>
</tr>
<tr>
<td></td>
<td>EGS</td>
<td>-0.251</td>
<td>0.457</td>
<td>0.588</td>
</tr>
<tr>
<td>Steppe</td>
<td>BGS</td>
<td>-0.675</td>
<td>0.023</td>
<td>0.461</td>
</tr>
<tr>
<td></td>
<td>EGS</td>
<td>-0.275</td>
<td>0.413</td>
<td>0.625</td>
</tr>
<tr>
<td>Alpine meadow and tundra</td>
<td>BGS</td>
<td>-0.798</td>
<td>0.030</td>
<td>0.137</td>
</tr>
<tr>
<td></td>
<td>EGS</td>
<td>-0.398</td>
<td>0.226</td>
<td>0.585</td>
</tr>
<tr>
<td>Sparse alpine vegetation</td>
<td>BGS</td>
<td>-0.908(^{*})</td>
<td>0.001</td>
<td>-0.08</td>
</tr>
<tr>
<td></td>
<td>EGS</td>
<td>0.063</td>
<td>0.854</td>
<td>0.48</td>
</tr>
</tbody>
</table>

\( R \): correlation coefficients; \( p \): Significance of the correlation.
\(^{*}\) \( p < 0.05 \).
\(^{**}\) \( p < 0.01 \).

Fig. 6. Changes in mean vegetation NPP and phenological metrics during 2002–2012 along an altitude gradient in the Tibetan Plateau. Error bars showed standard deviation (SD) at each altitude level. Solid lines show regression for the entire elevation gradient from 2500 m to 5500 m, and gray lines show regression for elevation bins below and above 3500 m separately. Slope represents the slope of the regression line.

from 2002 to 2012. There was a strong spatial clustering across the whole plateau, and the roles of climate factors in the response of NPP to phenological shifts varied over the hydrothermal regions. In hydrothermal zones with average annual rainfall between 800 and 1000 mm and the average annual temperature below \(-8\) °C, BGS advanced, while LGS and NPP did not significant changed due to the earlier onset of EGS. We also detected a seldomly reported phenomenon that in hydrothermal zones with average annual rainfall between 500 and 700 mm and the average annual temperature from \(-8\) to \(-4\) °C, NPP increased significantly even though LGS shortened during 2002–2012. Such an opposite trend between NPP and LGS was probably due to the increase in temperature and precipitation and less autotrophic respiration in the autumn. Interestingly, in some areas with good water-heat condition, such as hydrothermal zones with average annual rainfall was more than 900 mm and the average annual temperature above 0 °C, the changing trend of NPP was consistent with the trend of LGS. Our finding was consistent with the results of Klein et al. (2014), who reported different trends of phenology and biomass at broad spatial scales in the TP.

To better illustrate the effects of temperature and precipitation on vegetation productivity and LGS, we further explored the relationship between NPP and LGS along the temperature and precipitation gradients (Fig. 8). As shown in Fig. 8a, we found that NPP responded differently to LGS along the temperature gradient. When temperature was below \(-6\) °C, there was a significant negative correlation between the NPP and LGS (\(R^2 = 0.810, p < 0.05\)). When temperature was between \(-6\) and \(-2\) °C, with the extension of LGS, the trend of NPP was first increased, then decreased, and the turning point went back with the increase of temperature. For example, in temperature belt of \(-4\) to \(-2\) °C, NPP first increased, from about 100 g C m\(^{-2}\) at 145 days to about 250 g C m\(^{-2}\) at 185 days, and then decreased to about 150 g C m\(^{-2}\) at 215 days. When temperature was above 2 °C, with the extension of LGS, the trend of NPP was first slightly decreased, then increased significantly after the turning point of 185 days. Meanwhile, similar to the temperature gradient, NPP also had different responses to LGS along the precipitation gradient at the interval of 100 mm (Fig. 8b). When precipitation was below 400 mm, there was no significant change in NPP. When precipitation was between 400 and 600 mm, with the extension of LGS, NPP significantly increased. However, when the precipitation was above 600 mm, with the extension of LGS, NPP was first decreased, then increased significantly at the turning point of 165 days. Such different trends in NPP and LGS reflected the profound effects of climate on response mechanisms of NPP to phenological changes.

4.2. Other factors influencing NPP response to phenological metrics

Many other factors like permafrost degradation and snowmelt (Yang et al., 2010), photoperiod (Vitasse and Basler, 2013), winter chilling (Clark et al., 2014), human disturbance (Shen et al., 2011), soil moisture (Cramer et al., 1999) and nutrient limitation (LeBauer and Treseder, 2008) may also influence the NPP and phenology dynamics. As we previously mentioned, NPP and phenology were primarily determined by temperature and precipitation in the TP, and alpine plant species were considered to be the most sensitive vegetation ecosystem in response to rising temperature (Jin et al., 2013; Lesica and Kitelson, 2010). On the other hand, permafrost degradation and snowmelt are also important factors...
affecting alpine vegetation phenology, especially in the TP, the timing of snowmelt is often considered to be the observable indicators of growth and reproduction in tundra plants (Chen et al., 2011a,b). In some snow-rich regions, mountain birch may have green leaves before snow melting in spring, and growth in herbaceous plants may also start before snowmelt when there is enough light through the snow (Buus-Hinkler et al., 2006; Reiko and Hiroyuki, 2013; Shutova et al., 2006; Wielgolaskie and Inouye, 2013). Overall, phenology and NPP in plateau snow-rich area are also controlled by timing of snowmelt and temperature.

Fig. 7. Changes in the trends in vegetation's BGS (a), EGS (b), LGS (c), NPP (d), temperature (e) and precipitation (f) with temperature and precipitation gradients in the Plateau from 2002 to 2012.
In addition to snowmelt, the photoperiod and winter chilling also have an influence on vegetation life cycle at the plateau. Although it is commonly assumed that winter chilling plays an important role in regulation of phenological phases, in fact, the interactions between chilling and photoperiod might play a more important role in controlling phenological phases at the high latitudes (Basler and Korner, 2012). Some previous studies found that warmer temperatures during the winter may shorten the chilling period and delay the fulfillment of the chilling requirement, slowing the dormancy breaking process. However, warm temperatures in spring will accelerate heat accumulation and thus advance plant growth (Zhang et al., 2007; Yu et al., 2010; Cook et al., 2012; Shen et al., 2014a, b). Especially for humid extratropical areas, the winter chilling, photoperiod and temperature are the three most important factors controlling phenology (Korner and Basler, 2010; Vitasse and Basler, 2012).

Human activities and nutrient limitation may also influence the NPP and phenology dynamics. The major human activities over the plateau are human-induced land cover changes and grazing (Shen et al., 2011; Chen et al., 2013). Since 1950, the number of human and livestock have increased by almost 300% in the plateau (Du et al., 2004; Fan et al., 2010). Such growth of population and livestock have been considered a major factor leading to phenological changes by affecting plant community (Niu et al., 2009; Song et al., 2009; Chen et al., 2014). Furthermore, during the past two decades, the Chinese central government has paid increasing attention to environmental protection and agricultural sustainable development in the plateau, and a series of larger-scale conservation programs have been implemented across the plateau, including the Natural Forest Conservation Program (initiated in 1998), the Grain for Green Program (initiated in 1999) and Grazing Withdrawal Program (initiated in 2003) (Liu et al., 2008; Chen et al., 2013, 2014). The land cover change that results from three programs can effectively restore grassland and significantly increase vegetation NPP. In addition to human activities, many previous studies have also shown that the nutrient dynamics have an influence on vegetation life cycle and net primary productivity (Cleveland et al., 2011; Fisher et al., 2012). This implied that human activities and nutrient limitation also played a fundamental role in offsetting the impacts of the phenological change on NPP.

4.3. Uncertainties of the results

Satellite-based techniques have been widely used for phenological monitoring and NPP estimation. However, there were many uncertainties in the results due to the spatial, temporal, and ecological complexity of vegetation biochemical processes. In this paper, the uncertainties of the results might be attributed to two aspects: uncertainties associated with the datasets, and uncertainties associated with the methods for determining phenological parameters and estimating NPP.

Uncertainties associated with datasets originate from satellite data and ground observation data. Some previous studies show that the phenology metrics (e.g., BGS, EGS) from the different satellite datasets were significantly different over the northern high latitudes (Delbart et al., 2006; Zeng et al., 2011; Zhang et al., 2013a, b). Furthermore, some studies found that the latest generation of sensors such as MODIS performed better than Advanced Very High Resolution Radiometer (AVHRR) for investigating the phenology in alpine vegetation (Fontana et al., 2008; Zeng et al., 2011; Zhang et al., 2013a, b). In this paper, we selected the MODIS NDVI time-series data to reduce data uncertainty. Due to the harsh physical environment, long-term ground-based observations were very rare in the TP. Such lack of historical in situ observations further limited our understanding on the response of NPP to phenological changes.

Over the past few years, many methods have been developed to detect the phenological parameters and estimate NPP using satellite data. Comparative studies have shown that Midpoint_pixel threshold method based on variations of an NDVI_tchio is one of the most consistent methods for determining phenological parameters over a variety of ecosystems and corroborates well with ground-based phenology data (White et al., 1997, 2009; De Berus and Henebry, 2010). CASA model has also been proved to be an excellent process-based model for NPP estimation based on the plant growing mechanism (Monteith, 1977; Potter et al., 1993; Running et al., 2004). Many previous studies have shown that the CASA model can be successfully used to estimate vegetation NPP in the TP (Piao et al., 2006; Gao et al., 2009; Zhang et al., 2013a, b), our results also confirmed this point. Thus, in order to reduce the bias, we used the Midpoint_pixel threshold method and CASA model in this study. However, due to the absence of in situ observation data, it is difficult to thoroughly evaluate the retrieval results of the Midpoint_pixel threshold method and CASA model. Furthermore, in response to concerns over the validity of satellite-derived phenology and NPP, our research adopted a strict approach to the selection of pixels for analysis through statistical tests of significance at different levels.

5. Conclusion

Considering the importance of quantifying long-term phenological changes and its effects on NPP in the context of global climate changes, this study investigated the spatiotemporal variability of
vegetation NPP and phenological dynamics in the TP, and further examined the response mechanisms of NPP to phenological dynamics. During 2002–2012, most of the plateau experienced significant trends in advancing of BGS, delaying of EGS and prolonging of LGS, and vegetation NPP also substantially increased in most parts of the plateau. The response relationships between NPP and phenological dynamics were more complex in the whole plateau, and the response modes of the NPP to phenological dynamics varied within different climatic regimes. Furthermore, temperature and precipitation play important roles in determining response of NPP to phenological dynamics. Due to the complex terrain and climate conditions in the TP, our study suggests that analysis over climatic regimes and vegetation communities, instead of the whole plateau, may be able to better quantify the response mechanisms of NPP to phenological dynamics.

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