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REGULAR ARTICLE

Early-spring soil warming partially offsets the enhancement of alpine grassland aboveground productivity induced by warmer growing seasons on the Qinghai-Tibetan Plateau

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Abstract

Aims The response of vegetation productivity to global warming is becoming a worldwide concern. While most reports on responses to warming trends are based on measured increases in air temperature, few studies have evaluated long-term variation in soil temperature and its impacts on vegetation productivity. Such impacts are especially important for high-latitude or high-altitude regions, where low temperature is recognized as the most critical limitation for plant growth.

Methods We used Partial Least Squares regression to correlate long-term aboveground net primary productivity (ANPP) data of an alpine grassland on the Qinghai-Tibetan Plateau with daily air and soil temperatures

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during 1997–2011. We also analyzed temporal trends for air temperature and soil temperature at different depths.

Results Soil temperatures have steadily increased at a rate of 0.4–0.9 °C per decade, whereas air temperatures showed no significant trend between 1997 and 2011. While temperature increases during the growing season (May–August) promoted aboveground productivity, warming before the growing season (March–April) had a negative effect on productivity. The negative effect was amplified in the soil layers, especially at 15 cm depth, where variation in aboveground productivity was dominated by early-spring soil warming, rather than by increasing temperature during the growing season.

Conclusions Future warming, especially in winter and spring, may further reduce soil water availability in early spring, which may slow down or even reverse the increases in grassland aboveground productivity that have widely been reported on the Qinghai-Tibetan Plateau.

Keywords Aboveground net primary productivity (ANPP) · Alpine grassland · Climate warming · Qinghai-Tibetan Plateau · Soil temperature

Introduction

Projected increases in global mean temperature by at least 2 °C by the end of the twenty-first century are expected to have profound impacts on vegetation growth and primary productivity in terrestrial ecosystems (IPCC 2013). Compared to air temperature, variation in soil thermal regime and its influences on productivity have received less attention (Helama et al. 2011), partly because soil temperature datasets typically have a much lower spatial and temporal coverage than air temperature records (Qian et al. 2011). However, soil temperature directly controls biological and biochemical processes in the soil, which affect soil organic matter formation and decomposition, nutrient mineralization and uptake, microbial activity, seed germination, and plant development (Zhang et al. 2001; Jacobs et al. 2011). Soil temperature also influences soil respiration and total CO_2 budget (Flanagan et al. 2013), making it a potentially important contributor to global climate change (Luo and Zhou 2010).

Soil temperature has often been regarded as a derivative of atmospheric temperature (García-Suárez and Butler 2006), but recent studies have revealed considerable discrepancies between the two variables, including in the rate of temperature change (Hu and Feng 2003; Zhang et al. 2005; Isard et al. 2007; Jacobs et al. 2011). Soil temperature integrates the effects of various climate variables and environmental factors, including not only air temperature, but also precipitation, evaporation, soil moisture, thawing and freezing processes, surface albedo, and soil thermal conductivity (Zhang et al. 2001). Thus, simple application of the measured or projected warming trends in the atmosphere to the soil is probably too simplistic. Extensive monitoring of soil thermal regimes at multiple depths over an extended period is difficult but urgently needed, since analysis of the long-term variability in soil temperature may contribute to our understanding and prediction of its impacts on the productivity of terrestrial ecosystems.

The Qinghai-Tibetan Plateau, known as the “world’s third pole” for its extremely harsh and fragile ecological environment, has attracted much attention due to its high sensitivity to climate change (Piao et al. 2006; Sun et al. 2013). Low temperature is considered one of the most important limiting factors for vegetative growth in this region (Xu et al. 2015). Temperature increases could ease cold constraints on plant growth and also prolong the length of the growing season (Zhang et al. 2013; Che et al. 2014), leading to higher aboveground productivity for alpine grassland. The production-promoting effects have often been confirmed in correlation studies between atmopheric warming and vegetation productivity (Piao et al. 2006; Gao et al. 2013). In comparison, very few reports are available on responses of grassland productivity to soil warming on the Qinghai-Tibetan Plateau, although evidence is accumulating that soil temperature in cold regions at high latitude or altitude has significantly increased during the past century (Zhang et al. 2001; Hu and Feng 2003), and the increasing trend is even stronger than that of air warming (Zhang et al. 2016).

In the present study, a long-term site-level grassland aboveground productivity dataset linked with air and soil temperature at different depths recorded at the Haibei Grassland Ecological Monitoring Station on the Qinghai-Tibetan Plateau provides a unique opportunity for exploring variation trends of air and soil warming and their impacts on alpine grassland productivity. Additionally, we used Partial Least Squares (PLS) regression, a statistical method that has recently been adopted for climate response studies (Yu et al. 2010; Luedeling et al. 2013), to correlate vegetation aboveground productivity with high-resolution (daily) temperature records, rather than climatic data at monthly or yearly scale. This approach helps identify hidden productivity response characteristics that are easily overlooked by analyses at coarse temporal and spatial resolutions, such as seasonal differences in productivity responses to warming (La Pierre et al. 2011). We hypothesize that (1) variation in air temperature and soil temperature at different depths differs in trend and magnitude, with stronger temperature increases in the soil layers; (2) soil warming has a greater impact on grassland productivity than air warming; and (3) the response of vegetation productivity to warming is season-dependent, and warming during different seasons has different impacts.

Materials and methods

Site description

This study was conducted at the Haibei Grassland Ecological Monitoring Station (36°57’N, 100°51′E, 3140 m a.s.l.) of the China Meteorological Administration. The station is located on an alpine grassland of the Qinghai-Tibetan Plateau, with a typical plateau continental climate. Mean annual temperature during 1997–2011 was 2 °C, with mean monthly temperature extremes of −21 °C in January and 20 °C in July. Annual precipitation averaged 403 mm, and 70% of the rainfall was concentrated during the initial and peak stages of the growing season (i.e. from May to August). The vegetation is dominated by *Stipa sareptana var. krylovii*, *Kobresia humilis*, *Koeleria cristata*, *Poa crymophila*, and *Artemisia scoparia*, all of which are C3 plants. Among them, *Kobresia humilis* and *Artemisia scoparia* belong to the family Cyperaceae and Compositae, respectively, and the other three species are bunchgrasses (Gramineae). The soil is a sandy loam, with soil pH ranging from 7.6 to 7.9 and soil bulk density of 0.94 –1.01 g cm^{-3}. More detailed site information can be found in Chen et al. (2016).

Data collection

Aboveground net primary productivity (ANPP) measurements were conducted in late August of each year, when the standing biomass reached its maximum, from 1997 to 2011. For each biomass harvest in each year, 4 quadrats (1 m × 1 m) were randomly selected within a flat sampling plot (80 m × 80 m). Aboveground plant material was clipped and then oven dried at 65 °C to constant weight to estimate grassland ANPP (Scurlock et al. 2002).

Daily meteorological variables, such as air temperature, precipitation, evaporation and wind speed during 1997–2011 were obtained from a weather station located only 20 m from the surveyed plot. Hourly soil temperature at depths of 10, 15, and 20 cm was measured with thermocouple probes, recorded by a HOBO data logger (Onset Computer Company, Pocasset, MA, USA) and averaged to obtain daily records. Five soil temperature observation sites were placed in the four corners and the center of the sampling plot in order to determine variation in soil thermal conditions across the plot.

Statistical analysis

Partial Least Squares (PLS) regression works well in situations where the number of independent variables far exceeds the number of dependent variables and the independent variables are highly auto-correlated (Wold 1995). It was used to analyze the responses of grassland aboveground productivity to variation in daily air and soil temperature at different depths. In an earlier analysis, the effect of raw and smoothed daily air and soil temperature data on PLS response patterns has been tested by comparing (1) unfiltered daily temperatures, and (2) daily temperatures subjected to a 15-day running mean filter (commonly used in meterological studies; Luedeling and Gassner 2012). Results indicated that running means of temperature produced more recognizable response patterns between temperature variability and aboveground productivity (Fig. S1). Thus, in the present study, all daily temperatures were first subjected to a 15-day running mean filter, before feeding them into the PLS model.

The two major outputs of PLS analysis are the variable importance in the projection (VIP) and standardized model coefficients. The VIP values indicate the importance of all independent variables (i.e. daily temperature) for explaining variation in dependent variables (i.e. grassland aboveground productivity in this study), with the threshold for considering a variable important often set to 0.8 (Wold 1995). The standardized model coefficients reflect the strength and direction of the impacts of daily temperatures in the PLS model. Centering and scaling of dependent and independent variables are necessary to permit comparison between different variables. We calculated the root mean square error (RMSE) to evaluate the accuracy of the PLS model. In the PLS analyses, periods with VIP greater than 0.8 and high absolute values of model coefficients represent the relevant phases influencing grassland aboveground productivity. Positive model coefficients mean that increasing temperature during the respective period increases productivity, while negative ones indicate negative impacts.

Based on the PLS analysis results, we identified relevant periods of time during which temperature impacted aboveground productivity. Warming before and during the growing season (i.e. March–April and May–August) had distinctly opposite effects on aboveground productivity. To clarify the relative importance of these two periods, a three-dimensional surface (visualized by contour lines) illustrating the responses of grassland productivity to mean temperature during both periods was constructed using the Kriging interpolation method in the R package ‘fields’ (Nychka et al. 2017).

All temporal trends in air and soil temperatures in this study were analyzed using linear regression, with trends tested for statistical significance by the Mann-Kendall test (Tao et al. 2006), which is widely used for time series data.

All analyses were implemented in the R 3.4.0 programming language (R Core Team 2017). PLS analysis was mainly based on the ‘pls’ and ‘chillR’ package (Mevik et al. 2016; Luedeling 2017). Codes for reproducing the PLS analyses and all figures in the study are provided as supplementary materials to this paper.

Results

Comparison of change trends in air and soil temperatures

High positive correlation coefficients ($r = 0.69$ and 0.72; Fig. 1) between the mean annual air and soil temperatures (Ta and Ts) at different depths (10–20 cm) were detected in the study region during 1997–2011. However, our results also showed important differences in change trends and magnitudes between soil and air temperatures. Between 1997 and 2011, Ta appeared to increase, but the trend was not statistically significant (Fig. 1a; the insignificant warming is also widely distributed in the northeast of the Qinghai-Tibetan Plateau, see Fig. S2), while Ts at all depths increased steadily at a rate of 0.4–0.9 °C per decade ($P < 0.1$; Fig. 1b-d). Ts at 10–20 cm depth was higher than Ta by approximately 3.2 °C (Fig. 2), with greater difference in winter (3.8 °C) compared to spring (2.4 °C; Fig. S3). In early spring, soil temperatures rose above the freezing point up to 11 days before mean daily air temperature (17 March vs. 28 March in Fig. 2). Note also that daily and monthly soil temperature showed less variation than air temperature, with variation decreasing with increasing soil depth (Figs. 2 and S4).

Response of grassland aboveground productivity to variation in daily air and soil temperature before and during the growing season

Earlier studies indicated that soil and air temperature variation during September and February had negligible impacts on grassland aboveground productivity in our study area (Fig. S5). We therefore only focused on the response of productivity to temperature variation before the growing season (March and April, henceforth referred as preseason) and during the growing season (May–August) in the present study.

The 184 daily air and soil temperature values at different depths recorded between March and August were used as independent variables in the PLS regression, while grassland aboveground productivity during 1997–2011 was the dependent variable. The low root mean square error (RMSE) of 8.43–11.82 g m^{-2} (vs. mean productivity of 129 g m^{-2}) indicated that the PLS model was a good fit for all the data. Based on the VIP and standardized model coefficients of all PLS analyses (Fig. 3), we found that temperature increases during the preseason had an opposite influence on grassland productivity compared with warming during the growing season.

During 28 March-25 April, VIP values mostly exceeded 0.8 (the threshold for variable importance) and model coefficients were consistently negative (Fig. 3a), indicating that increases in air temperature during this period depressed grassland aboveground productivity. However, between 6 May and 26 August, model coefficients were always positive with mostly important VIP values, implying that increasing air temperature during this period increased aboveground productivity, which formed a striking contrast with the

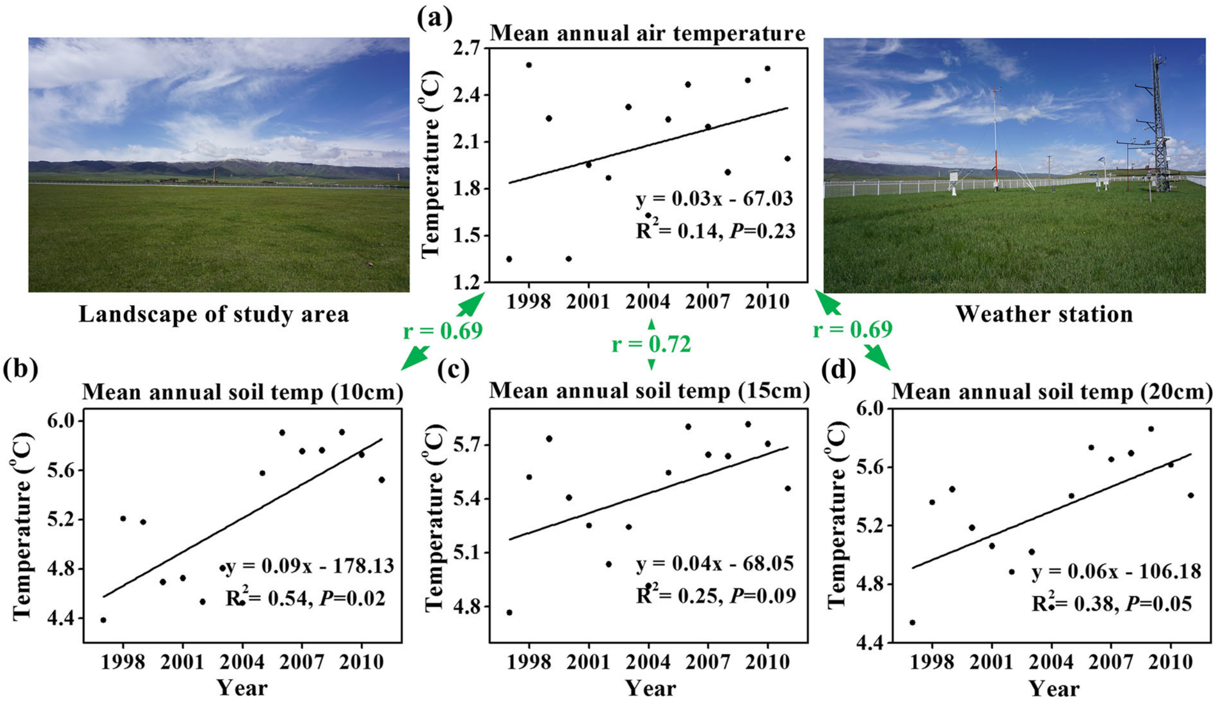


Fig. 1 Correlation between mean annual air and soil temperatures at different depths, and inter-annual variation in air and soil temperatures in our study site during 1997–2011. The correlation coefficients (r) are marked in green color. The landscape and weather station used to provide data for the present study are also shown in the inset pictures

impacts of preseason warming (Fig. 3a). Similarly, PLS analysis detected two important periods during the preseason and the growing season for the correlation between aboveground productivity and soil temperatures at depths of 10, 15 and 20 cm, respectively. Compared to air temperature, the response of grassland aboveground productivity to soil temperature variation during the preseason started earlier (6–16 March; Fig. 3b-d), while phases (early-May to end-August) during which soil warming increased aboveground productivity were similar for all soil layers.

Response of grassland aboveground productivity to mean air and soil temperatures during the preseason and the growing season

Plotting grassland aboveground productivity as a function of mean temperatures during the preseason and the growing season illustrated important differences between the responses to air temperature and soil temperature at different depths (Fig. 4).

In Fig. 4, the slopes of the contour lines show the relative importance of warming preseason and growing season on grassland aboveground productivity. The greater the slope, the stronger the productivity-decreasing effects of warm preseason compared to the productivity-increasing effects of high growing season temperatures. As for the air temperature analysis (Fig. 4a), the low slope of the contour lines indicated that grassland aboveground productivity was almost entirely determined by air temperature variation during the growing season. A productivity-depressing impact of air warming during the preseason was also detected (Fig. 4a). However, productivity was more sensitive to warming during the growing season (Fig. 4a). Additionally, relationships between productivity and mean temperature during each of the two important periods were further explored. A significant positive correlation was found between aboveground productivity and mean temperature during the growing season ($P < 0.01$; Fig. 5a). Mean air temperature increases during the preseason seemed to decrease productivity, but the impacts were not statistically significant ($P = 0.14$), which was consistent with results from Kriging interpolation analysis.

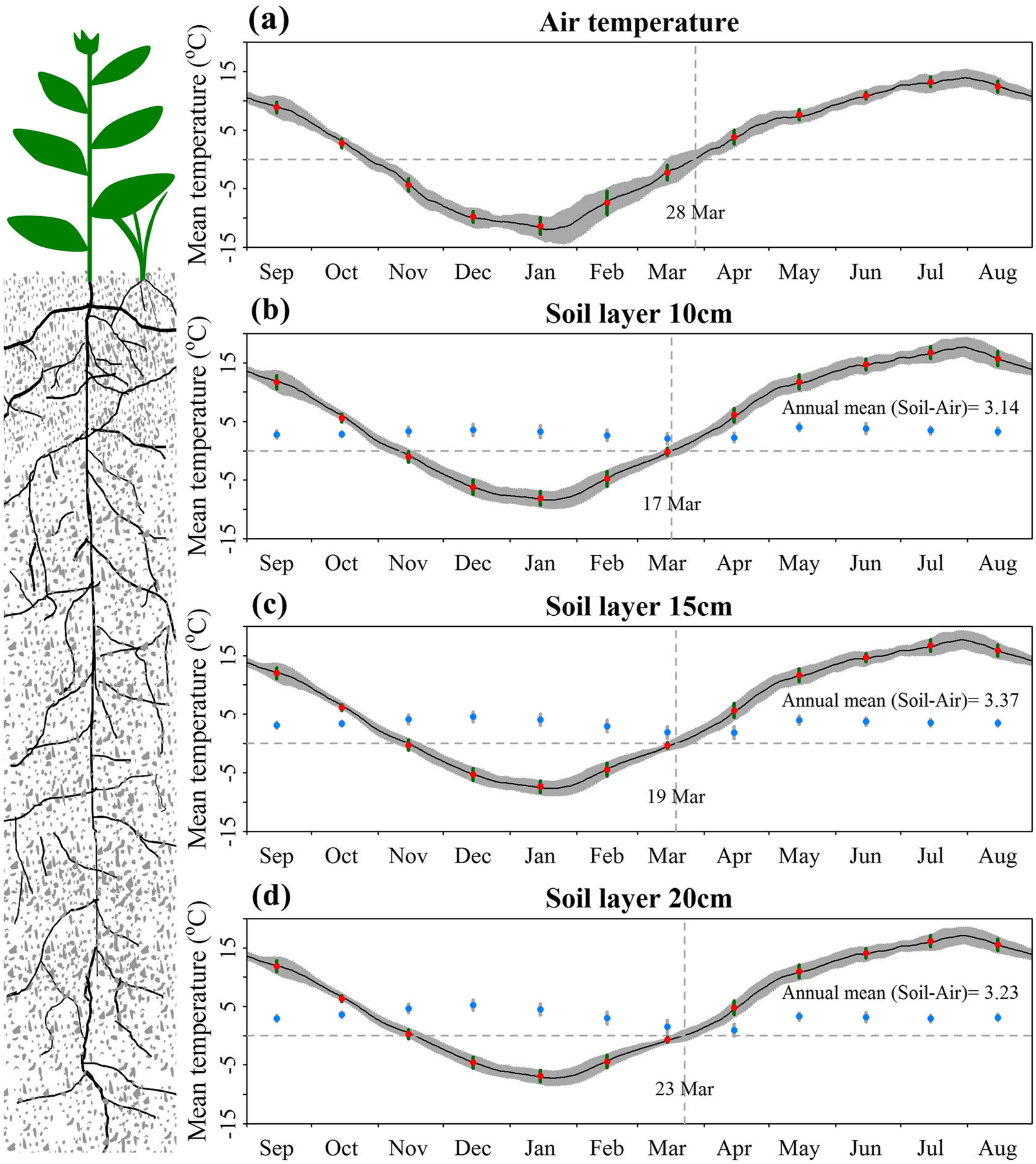
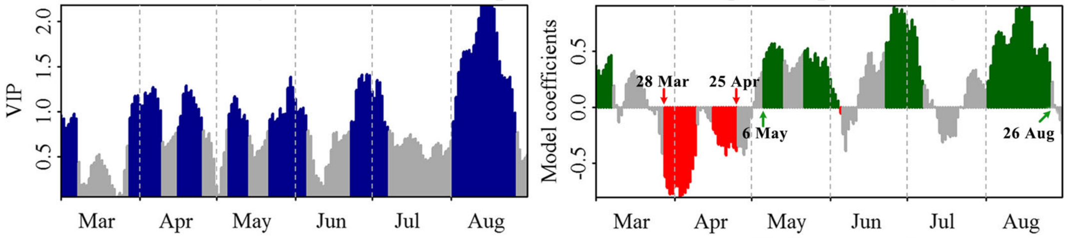


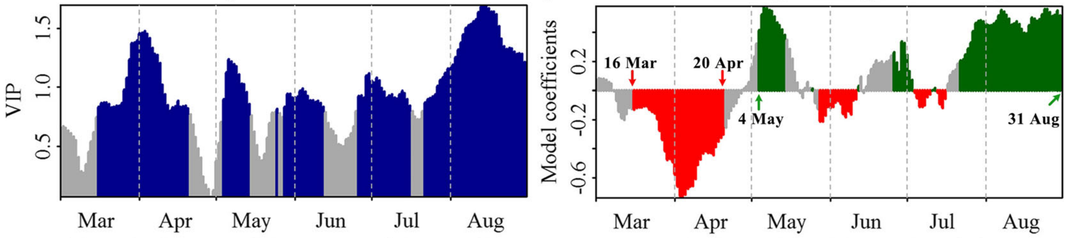
Fig. 2 Air and soil temperature variation at daily and monthly resolution, and monthly differences between soil temperature at different depths and air temperature. The black solid lines in each panel stand for daily mean temperature for air and soil, while grey areas represent the standard deviation (SD). Monthly mean temperature and its corresponding SD are displayed by red dots and green error bars, respectively. Blue dots and grey error bars indicate monthly mean deviations between soil and air temperature, and the SD, respectively. First dates for exceeding the freezing point (0 °C) in early spring and annual mean differences between soil and air temperatures are also shown

The depressing impacts of warming during the preseason on vegetation productivity were amplified in the soil layers (Fig. 4b-d). At the 10 and 20 cm depth soil layers, impacts of mean soil temperature during the preseason and the growing season were almost identical (Fig. 4b, d). However, the greater slope visualized by the nearly vertical contour lines in Fig. 4c indicated that impacts of soil temperature variation during the preseason exceeded the effects of soil warming during the growing season at the 15 cm soil layer, and grassland aboveground productivity decreased by 22.61 g m^{-2} per 1 °C rise of mean temperature during the preseason ($P < 0.01$; Fig. 5c).

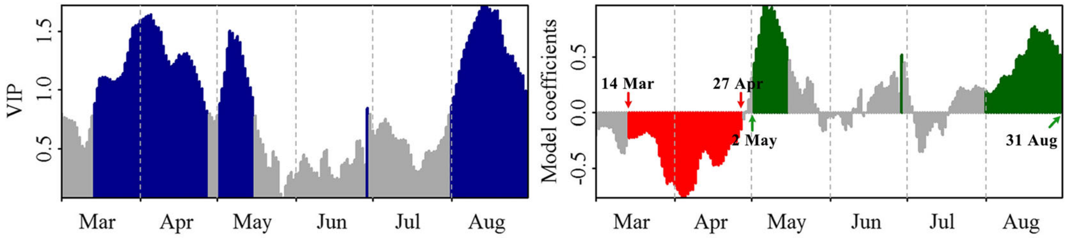
(a) PLS analysis between air temperature and aboveground productivity



(b) PLS analysis between 10cm soil temperature and aboveground productivity



(c) PLS analysis between 15cm soil temperature and aboveground productivity



(d) PLS analysis between 20cm soil temperature and aboveground productivity

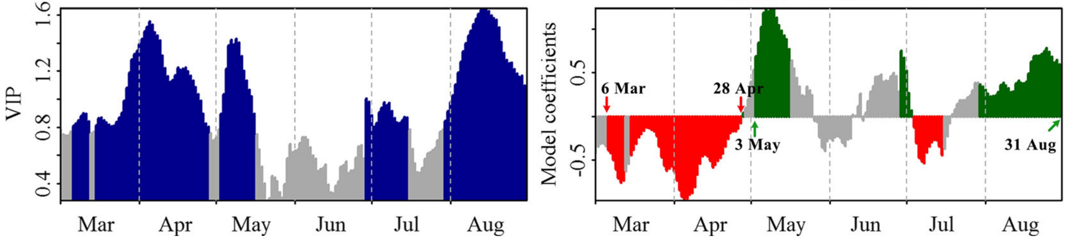


Fig. 3 Results of Partial Least Squares regression correlating grassland aboveground productivity with 15-day running means of daily air and soil temperatures at depths of 10, 15 and 20 cm from March to August. Blue bars in the left part indicated that VIP values are greater than 0.8, the threshold for variable importance. In the right column of this figure, red color means model coefficients are negative and important, with VIP values greater than 0.8. Green color implies an important positive relationship between productivity and daily temperatures, while grey color indicates that no significant correlation was found. The start and end dates of the relevant time periods during which temperature variation had important impacts on grassland aboveground productivity are also marked

Discussion

Differentiation between changes in soil and air temperature

Soil temperature, which has often been regarded to some extent as a derivative of atmospheric temperature, showed a different change trend and amplitude from those observed for air temperature. Mean annual soil temperature (Ts) in our study region has increased by 0.6–1.4 °C during 1997–2011, or about 0.4–0.9 °C per decade, while mean annual air temperature (Ta) did not show a significant upward trend. Similar increases in Ts and greater increase magnitude of Ts vs. Ta have also been observed in Northern Ireland (García-Suárez and Butler 2006) and Irkutsk in Russia (Zhang et al. 2001) over the past century, and reported for most of the 292 U.S. National Weather Service cooperative stations during 1967–2002 (Hu and Feng

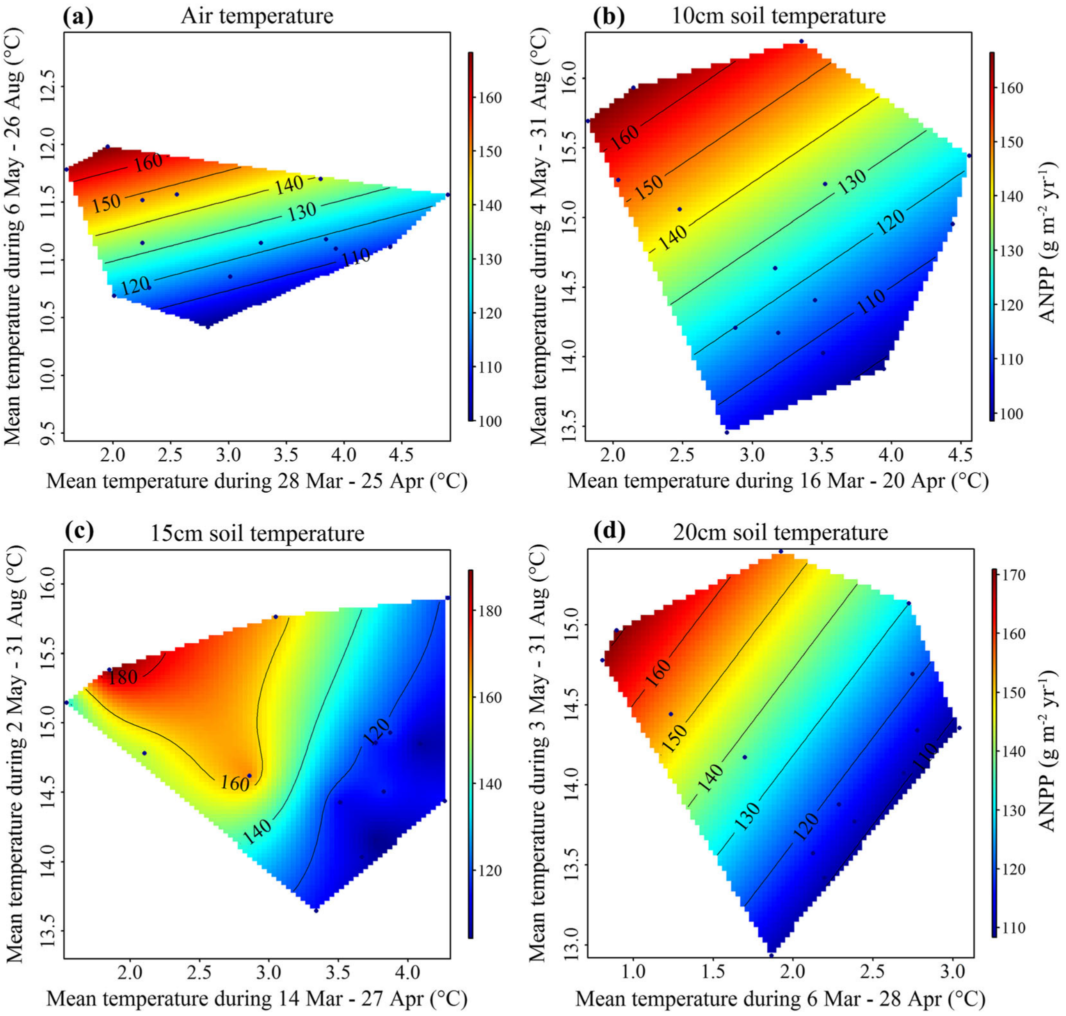


Fig. 4 Response of grassland aboveground productivity to mean air and soil temperatures at different depths during the preseason and the growing season. Variation in color reflects variation in ANPP, while the black dots indicate annual grassland productivity during 1997–2011. The slopes of the contour lines show the relative importance of impacts of temperature increases during the preseason and the growing season on productivity

2003). In contrast, a greater increase rate of Ta was found in the Netherlands (Jacobs et al. 2011), and Canada, where Ts and Ta have, on average, increased by 0.6 °C and 1.0 °C, respectively, during the twentieth century (Zhang et al. 2005). Additionally, Isard et al. (2007) detected decreasing Ts trends in the Great Lakes Region of the United States during 1951–2000, which contrasted with increasing air temperature, especially during the winter. Reduced thermal insulation in winter due to thinner and shorter-duration snow cover is believed to be the major factor explaining the cooling trend of soil (Chen et al. 2003; Isard et al. 2007), which deserves more scientific attention in times of significant winter warming reported worldwide (Fu et al. 2015; Ladwig et al. 2016).

All these reports demonstrate that Ta and Ts can differ in their long-term change trends and magnitudes, and it is difficult to directly infer Ts from Ta or vice versa. Importantly, asymmetric warming between atmosphere and soil might alter the adaptive strategies of plants, with potential ecological and evolutionary implications for the stability of grassland ecosystems.

Warming during the growing season increased grassland aboveground productivity on the Qinghai-Tibetan Plateau

Aboveground net primary production in cool ecosystems has been found to exhibit a stronger positive

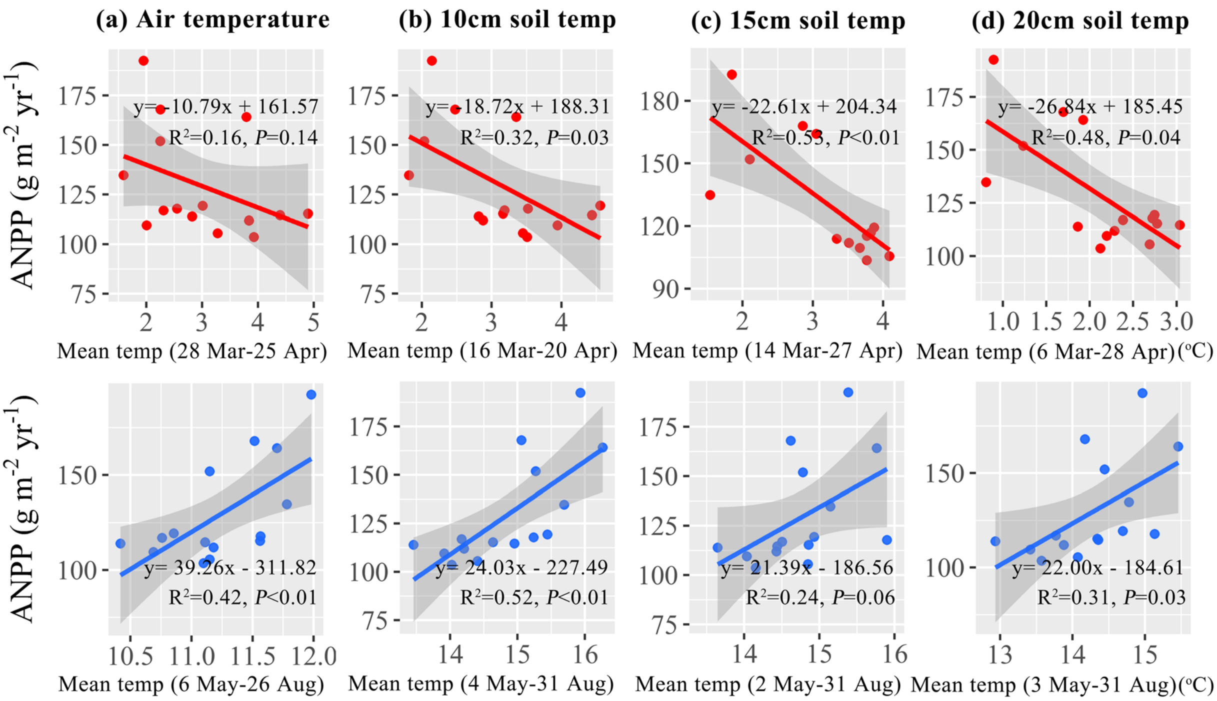


Fig. 5 Relationships between aboveground productivity and mean air and soil temperatures during the preseason and the growing season, which are distinguished by red and blue color, respectively. For each linear regression analysis, 95% confidence intervals are displayed in dark grey color

response to warming compared to warm ecosystems (Rustad et al. 2001), since warming relieves cold stress on biological processes in high-latitude and high-altitude regions. This is consistent with our results, which indicated positive impacts on aboveground productivity for air and soil warming during the growing season. The processes that may have influenced the productivity response to warmer temperatures are discussed below.

First, through biogeochemical feedbacks, warming can stimulate vegetation productivity by enhancing soil nutrient mineralization and the decomposition of soil organic matter (Melillo et al. 2002; Dieleman et al. 2012), resulting in greater nutrient availability, and consequently more rapid plant growth (Rustad et al. 2001). Some studies have demonstrated that the temperature response of nitrification is approximately bell-shaped with an optimum between 20 °C and 35 °C (Barnard et al. 2005), which is higher than the air and soil temperatures (less than 20 °C; Fig. S6a) in our study region. This indicates that nutrient mineralization tends to increase continuously with rising growing season temperature. Additionally, a plentiful supply of substrates constituted by the large amount of labile soil organic matter conserved in the alpine ecosystem (Xu et al. 2015) and increased soil enzyme, microorganism and faunal activity (Jacobs et al. 2011; Gong et al. 2015) triggered by warming could further boost the mineralization reaction and promote grassland productivity on the Qinghai-Tibetan Plateau.

Second, enhanced photosynthesis may lead to earlier spring phenology. An increase in photosynthesis in response to warmer climate has widely been observed in the Northern Hemisphere (Zhou et al. 2001; Lucht et al. 2002). However, some studies also pointed out that experimental warming decreased plant biomass and photosynthesis due to warming-induced moisture stress (De Boeck et al. 2008). This, however, cannot have occurred in our region, where increasing precipitation, with an average of 281 mm, was found during the growing season (Fig. S6a). These warming and wetting trends, also reported in other parts of the Qinghai-Tibetan Plateau (Han et al. 2011), may promote biomass accumulation via increased photosynthesis. Moreover, high soil temperature is essential for seed germination and earlier plant development (Bollero et al. 1996), while an increase in spring air temperature has advanced the onset of green-up around the world in recent decades (Parmesan and Yohe 2003; Menzel et al. 2006).

It is, however, too early to decide whether the impacts of warming on aboveground productivity are transitory or persistent, since some uncertainties still remain, including (1) whether increasing nitrogen mineralization exceeds N uptake and retention by vegetation, and ultimately promotes N losses and reduces N availability over time (Wu et al. 2012); (2) whether increasing temperature weakens the coupling between available nitrogen and phosphorus in soils and triggers more widespread P insufficiency in the Qinghai-Tibetan alpine grasslands (Geng et al. 2017); and (3) whether different species-dependent responses to warming (Cleland et al. 2006) change the community structure and composition, and more productive species are replaced by less productive ones (Harte and Shaw 1995). Thus, the relationship between vegetation productivity and warming during the growing season is not as straightforward as expected. Long-term monitoring and climate change experiments are essential for revealing the complex responses of productivity to future warming, as well as the underlying mechanisms.

Warming during the preseason reduced, and even canceled out the enhancement of aboveground productivity induced by warmer growing season

The majority of published studies have focused on productivity responses to climate variability during the growing season. However, ecologists are beginning to realize the importance of warming during the non-growing season (Fu et al. 2015; Ladwig et al. 2016). Our results indicated that warming during the preseason could reduce grassland aboveground productivity, especially for warming of the soil layers. For example, at 15 cm soil depth, with higher mean temperature than other layers (Fig. 2), the productivity-depressing effects of warming during the preseason even exceeded the growth-promoting impacts of soil temperature increase during the growing season (Figs. 4c and 5c). Warming-induced water stress (Wan et al. 2002) generally explains negative relationships between productivity and warming (Yang et al. 2009), and this theory also provides an explanation for our results. Since early March, the rapid thawing of the seasonally frozen soil of the upper layers (at 0–40 cm depth; Fig. S6b) should improve soil water availability. However, warming coinciding with low precipitation, strong evaporation and high wind speed between March and April (Fig. S6b) substantially decreased available soil water. Water limitations, especially in late April, may influence vegetation spring phenology (i.e. green-up period between end-April and mid-May in our region) responses to warming (Shen et al. 2011), while delayed onset of green-up has already been observed in parts of the Tibetan Plateau, particularly in the relatively dry regions (Yu et al. 2010; Yu et al. 2012; Xu et al. 2014). Postponed and weakened spring growth may cause aboveground productivity decreases. More significant and continuous warming in winter and early spring than during other seasons (IPCC 2013) may further strengthen the growth-depressing effects of warming during the preseason on the Qinghai-Tibetan Plateau. Thus, increased scientific attention should be paid to the direction and magnitude of climate variation during different seasons, and their combined impacts on future service provision and functioning of terrestrial ecosystems.

Conclusions

Soil and air warming differ in change trends and magnitudes, with stronger temperature increases detected in the soil layers and greater productivity impacts of soil warming compared with air warming on the Qinghai-Tibetan Plateau during the past 15 years. PLS regression between grassland aboveground productivity and daily temperature data clearly described the seasonal differences in the productivity response to warming. Rising temperatures during the growing season promoted productivity, but a warmer preseason (March–April) depressed and even offset these productivity increases. The limiting factor for vegetation growth transitioned from soil water availability during the preseason to temperature variation during the growing season, which provided a reasonable explanation for this phenomenon. Future warming, especially strong and continuous warming in winter and spring, which has been projected by IPCC (2013), may further exacerbate soil water scarcity before the growing season, and trigger decreases in productivity. Note also that some uncertainties, including the ratio between nutrient mineralization and uptake, the decoupling between soil available nitrogen and phosphorus, as well as the changes in species composition and richness, seem to contribute to the declining response of productivity to growing season warming. Thus, long-term monitoring and controlled experiments are urgently needed to comprehensively reveal the processes and mechanisms behind the complex responses of grassland ecosystems to warming. These responses are of great importance to other high-latitude and high-altitude regions, which have already experienced or are experiencing disproportionate warming as has been observed on the Qinghai-Tibetan Plateau.

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Compliance with ethical standards

Conflict of interest The authors have no conflicts of interest or ethical issues to declare.

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