Earth's Future

RESEARCH ARTICLE
10.1029/2020EF001837

Key Points:

- There is a universal decrease in aboveground net primary productivity (ANPP) over 30 years across different grassland types, and the magnitude of ANPP decline differed between types
- The air temperature and soil temperature rather than precipitation were the primary drivers of ANPP decline to climate change
- The increased air temperature and soil temperature from increased total solar radiation were the main drivers for ANPP decline

Supporting Information:

Supporting Information may be found in the online version of this article.

Correspondence to:
G.-L. Wu,
gaolinwu@gmail.com

Citation:
Wu, G.-L., Cheng, Z., Alatalo, J. M., Zhao, J., & Liu, Y. (2021). Climate warming consistently reduces grassland ecosystem productivity. *Earth's Future*, *9*, e2020EF001837. https://doi.org/10.1029/2020EF001837

Received 4 OCT 2020
Accepted 1 JUN 2021

Climate Warming Consistently Reduces Grassland Ecosystem Productivity

Gao-Lin Wu[1,2,3], Zhen Cheng[1], Juha Mikael Alatalo[4,5], Jingxue Zhao[1,6], and Yu Liu[1,2]

[1]State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, Northwest A & F University, Yangling, Shaanxi, China, [2]Qinghai Provincial Key Laboratory of Restoration Ecology of Cold Area, Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining, China, [3]CAS Center for Excellence in Quaternary Science and Global Change, Xi'an, China, [4]Department of Biological and Environmental Sciences, College of Arts and Sciences, Qatar University, Doha, Qatar, [5]Environmental Science Center, Qatar University, Doha, Qatar, [6]State Key Laboratory of Grassland Agro-ecosystem, Institute of Innovation Ecology & College of Life Sciences, Lanzhou University, Lanzhou, China

Abstract Future climate may profoundly impact the functioning of terrestrial ecosystems. However, we do not know well how the functioning of different types of grassland ecosystems is associated with variation in temperature and precipitation. Here, we used long-term field measurements to examine how climatic changes between the 1980s and the 2010s (i.e., growing season temperature, precipitation, habitat moisture index, solar radiation, and sunshine duration) have affected aboveground net primary productivity (ANPP) for all major grassland types in northern China. We found that ANPP consistently declined over the 30-year period across all types of grassland, on average by about 6.1%. Warming, associated with increased solar radiation and, hence, soil temperature, was the primary factor driving the decrease of ANPP. We further show that ANPP was more sensitive to climate change in alpine and lowland grasslands than in temperate grasslands. Together, our findings indicate that climate warming consistently reduces plant productivity of different types of grassland ecosystems, and emphasize the importance of soil temperature in driving the decline in grassland productivity under climate change.

Plain Language Summary Future climate may profoundly impact the functioning of terrestrial ecosystems. However, we do not know well how the functioning of different types of grassland ecosystems is associated with variation in temperature and precipitation. Here, we used long-term field measurements to examine how climatic changes between the 1980s and the 2010s (i.e., growing season temperature, precipitation, habitat moisture index, solar radiation, and sunshine duration) have affected aboveground net primary productivity (ANPP) for all major grassland types in northern China. We found that ANPP consistently declined over the 30-year period across all types of grassland, on average by about 6.1%. Warming, associated with increased solar radiation and, hence, soil temperature, was the primary factor driving the decrease of ANPP. We further show that ANPP was more sensitive to climate change in alpine and lowland grasslands than in temperate grasslands. Together, our findings indicate that climate warming consistently reduces plant productivity of different types of grassland ecosystems, and emphasize the importance of soil temperature in driving the decline in grassland productivity under climate change.

1. Introduction

Global changes in climate, nitrogen deposition, and land use are expected to modify processes and functions in terrestrial ecosystems (Sala et al., 2000), particularly in grassland ecosystems. Climate changes will affect carbon and water cycles, mineral cycles, solar energy flow, and plant community composition, thereby directly and indirectly influencing primary productivity of grasslands (Brookshire & Weaver, 2015; Craine et al., 2012; Liu et al., 2018; Vicente-Serrano et al, 2013; Zhu et al., 2016). In terrestrial ecosystems, primary productivity of grasslands is particularly responsive to climatic variability (Knapp & Smith, 2001). However, predicting grassland productivity responses to climate change is challenging, due to the multiple drivers of climatic factors and the possibility of interactive effects on ecological, physiological, and biogeochemical aspects of grassland ecosystems (Hu et al., 2018; Paruelo et al., 1998). A large number of manipulative experiments have tested grassland primary productivity responses to controlled variation in temperature and/or precipitation (Craine et al., 2012; Liu et al., 2018; Song et al., 2019; Zhu et al., 2016), but few studies have explored the long-term effects of multifactor climate change on aboveground net primary productivity (ANPP) in natural grassland ecosystems.

Climate warming strongly governs major biotic process (García-palacios et al., 2018; Pugnaire et al., 2019) and can reduce soil moisture via stimulating evapotranspiration (Bell et al., 2010; Niu et al., 2008), while drought will in turn limit the ability of ecosystems to withstand climate warming (Hoeppner & Dukes, 2012). Additionally, a synthesized ecosystem carbon-cycling to global change from 1,119 experiments showed that the magnitude of warming was consistent with the ranges of future projections, whereas those of precipitation changes exceeded the projected ranges (Song et al., 2019). The challenge with exploring the effects of climate change on ecosystem productivity is that the different mechanisms of climate change are complex (for example, warming and altered precipitation regime), they may be interactive or additive, and often significantly modify plant community productivity (Buitenwerf, 2016; Kardol et al., 2010). For example, Hoeppner and Dukes (2012) found that the interactive responses of warming and reduced precipitation treatments were negative to aboveground productivity. Nevertheless, another experimental study demonstrated that warming and decreased precipitation had a direct effect on aboveground biomass production and the effects were additive rather than interactive (Kardol et al., 2010). Such interactions between temperature and precipitation changes with grassland community productivity are often difficult to interpret (Shaw et al., 2002), although numerous manipulative experiments have provided invaluable insights, they are restricted to specific combinations of environmental conditions and plant communities (Buitenwerf, 2016; Hoeppner & Dukes, 2012; Kardol et al., 2010; Song et al., 2019; Wang et al., 2012b). Consequently, there is still a dearth of more information on multifactor climate change impacts on natural grassland ANPP.

The sensitivity of grassland ecosystem to climate fluctuations may depend on soil fertility, community types, dominant functional group types and soil water availability, etc., (Song et al., 2019). Alpine grasslands occur at high altitudes, where plant growth is primarily limited by temperature (Ma et al., 2010). For example, a recent study in alpine grasslands demonstrated that climate warming advanced plant phenology, promoted plant growth rate and increased spring biomass production (Wang et al., 2020). On the other hand, located in arid and semiarid regions, most grasslands are restricted by water availability (Niu et al., 2008). Hence, most studies conducted in temperate grasslands have shown positive correlations between ANPP and precipitation (Guo et al., 2012; Mowll et al., 2015). Most previous studies on grassland productivity responses to climate change have mostly focused on a single type of grassland (e.g., alpine grassland or temperate grassland) (Brookshire & Weaver, 2015; Durante et al., 2017; Knapp et al., 2018; Liu et al., 2018; Song et al., 2016). However, it is important to predict ANPP responses to climate change across a broad range of differ grassland ecosystems. Walker et al., (2020) reported that >50 years of warming drove the subarctic grassland ecosystem to a new steady state possessing a distinct biotic composition and reduced biomass, and this steady state was dependent on warming intensity.

How the grassland ecosystems have responded to long-term climate changes is, however, largely unknown. Especially, climate warming is accelerating (Christensen et al., 2013; Liu et al., 2018), it is still uncertain whether climate change has consistent effects on ANPP in different grassland ecosystem types. Here, we used grassland ANPP data from a total of 254 sites across three grassland ecosystems (i.e., low-land, alpine, and temperate grassland ecosystems) which were monitored in the 1980s and again in the 2010s. Specifically, we used the changes of aboveground productivity, the main climate variables over the past 30 years, including mean annual growing season air temperature, soil temperature, precipitation, solar radiation, sunshine duration, and habitat moisture index to (a) examine effects of climate change on aboveground net primary productivity (ANPP) across three grassland ecosystems; (b) determine the main climate variables and quantify their contributions in driving the changes in ANPP for each of these three grassland ecosystems. The findings will better predict the sensitivity of different grassland ecosystems to future climate change scenarios.

2. Materials and Methods

2.1. Study Sites

Our study region (32°11′–42°57′N, 92°13′–108°46′E) is located at the intersection of the Qinghai Tibetan grassland, the Loess Plateau, and the Inner Mongolian Plateau (Figure 1). The climate is mostly dry, with

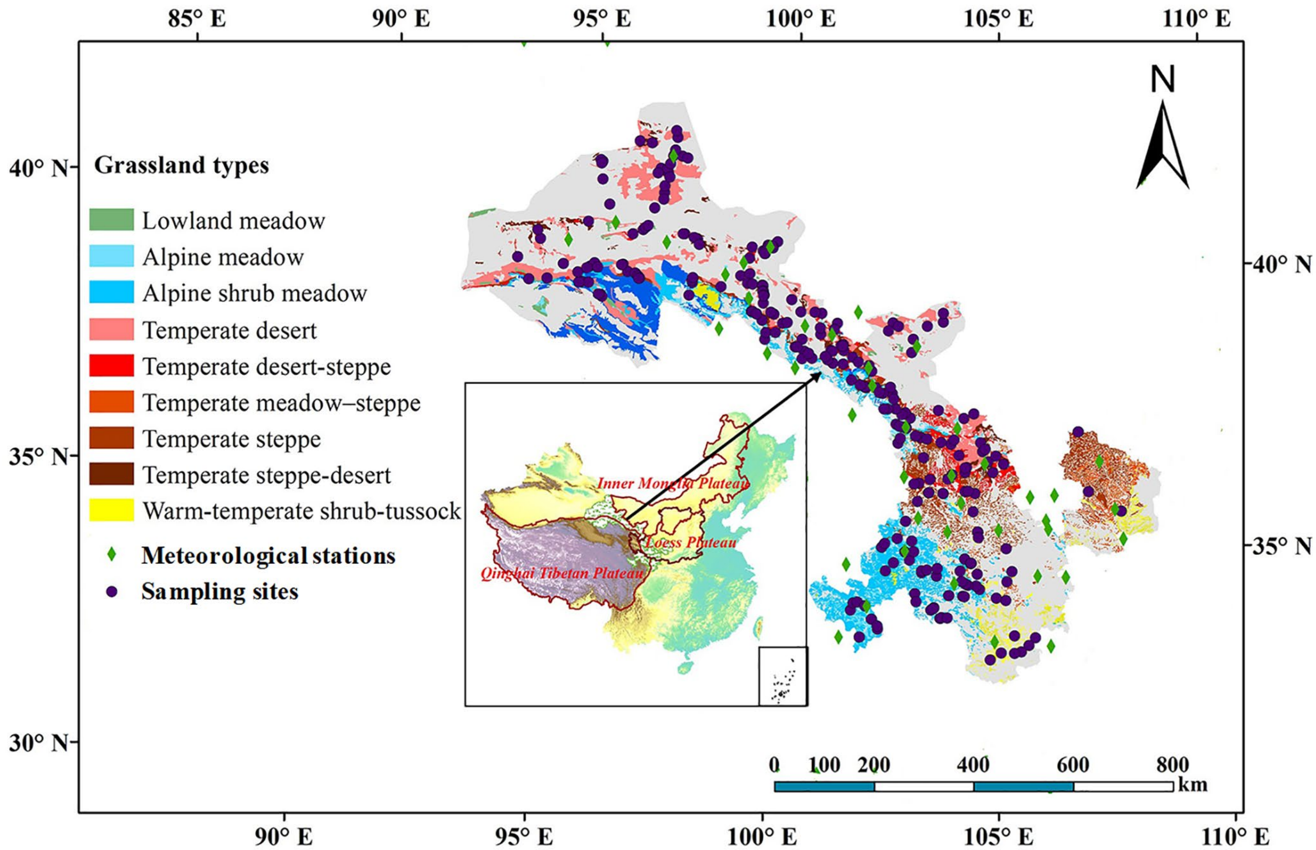

Figure 1. Locations of sampling sites and grassland types in the study region. Spatial distribution of nine grassland types in study area (based on data of the Department of Animal Husbandry Veterinary [1996]). Sampling sites were selected in different grassland types distributed throughout the region.

mean annual precipitation of 37–735 mm and mean annual temperature of 0°C–16°C. The annual distribution of rainfall is uneven, with most rainfall occurring from June to September. The study region includes nine different arid and semi-arid grassland types (Table S1; Figure 1). These nine grassland types were grouped into three larger grassland ecosystem types: Alpine grasslands, lowland grasslands, and temperate grasslands (Table S1), based on similarity in structural and functional attributes in climatically similar regions, such as ANPP and the composition of plant functional types. Since the 1990s, China have successively carried out the program of restoring grazing to grasslands to ensure the sustainable development of grasslands. Therefore, all grassland sampling sites were natural grasslands, not grazed or mowed.

2.2. Grassland Productivity

Aboveground net primary productivity (ANPP) was determined by harvesting peak aboveground biomass, a method widely used to estimate grassland ANPP (Scurlock et al., 2002). Based on the distribution of the nine types of grasslands in the study region (Figure 1), a total of 254 sites were selected and surveyed in the 1980s and again in the 2010s. In 1980s, China conducted a comprehensive survey of grassland resources in key pastoral areas across the country. All information about grassland sites in 1980s in this study came from the " Gansu Grassland Resources " data in 1980s. The landmark method was also used to ensure that the sampling sites in the 2010s were the same as those in the 1980s. At each site, aboveground biomass of all plants was sampled in late July and August 1980 within ten 1 m × 1 m quadrats distributed randomly within a 100 m × 100 m area. For each quadrat, fresh aboveground biomass was weighed, oven-dried at 65°C for 48 h, and weighed again. Mean dry mass for each site in 1980 was calculated. The elevation and dominant species at each site were also recorded in 1980 and used in the investigation 30 years later, when grassland ANPP at the sites was determined once again. On that occasion, a 100 m × 100 m plot was established at each field site at the same location, and ten 1 m × 1 m quadrats were placed at intervals of 10 m along a 100-m diagonal transect. As before, for each quadrat fresh aboveground biomass was weighed, oven-dried at 65°C for 48 h, and weighed again. The mean value of all quadrats was calculated for each site. This procedure resulted in ANPP data for the 1980 and the 2010 for 254 sites distributed across nine grassland types (Tables S1 and S2).

2.3. Climate Data

Climate data were acquired for 65 meteorological stations distributed across the study region (Figure 1) from the database of China's meteorological science data-sharing service (http://data.cma.cn/). Considering the lagging response of grassland productivity to climate change (Zhang et al., 2019), we selected mean climate data of 1974–1983 (represent for the 1980) and 2004–2013 (represent for the 2010), including mean annual growing season precipitation, sunshine duration, air temperature, soil temperature at a depth of 0–20 cm, solar radiation, and cumulative daily mean temperature exceeding 5°C (AccT) (Wang et al., 2012a). The climate variables were first compiled from daily climate raster surfaces interpolated using ANUSPLIN 4.37 (Hutchinson, 2004) and then extracted for each site in ArcGIS 10.2 (ESRI, Redlands, CA, USA). The ratio "growing season precipitation/cumulative daily mean temperature exceeding 5°C″ was used as the habitat moisture index.

2.4. Satellite Observation Data

The MOD13A1 V6 Vegetation Indices product and MOD17A2H V6 Gross Primary Productivity product were clipped and calculated by boundary of study area, getting average of EVI and GPP data during the growing season. This process was implemented in Google Earth Engine (https://earthengine.google.com/). According to the annual spatial distribution maps, the growing season EVI and GPP of each sampling site from 2000 to 2010 were obtained. The spatial trends of the growing season EVI and GPP were calculated by grid subtraction over 2000–2010. Those processes were conducted in ArcGIS 10.2.

2.5. Statistical Analysis

All data sources used in the study are provided in the Data sources section (Wu et al., 2021). One-way ANOVA was performed to explore the difference of climate variables between the 1980s and the 2010s across all grassland sites. Then, we tested the ANPP data between the 1980s and the 2010s were not normally distributed in each grassland type, even though the data met the assumption of homogeneity of variances. Thus, a Mann-Whitney test (Hutchinson, 2004) was performed to test the ANPP differences between the 1980s and the 2010s separately for the three grassland ecosystems: Low-land, alpine, and temperate grassland ecosystems.

To explore the main climate variables driving grassland ANPP change, we first performed Pearson correlation analysis for all sites in the region (Figure S1). We then created a structural equation model (SEM) using the *lavaan* package (Rosseel, 2012) in R studio (R Core Team, 2014) to determine the main climate variables and quantify their contributions in driving the ANPP changes across all studied grassland sites. Moreover, the latent variables temperature, moisture index, and radiation energy were also used. Further, we used step-wise regressions (Whittingham et al., 2006) to determine the main climate variables in driving changes in ANPP for three main grassland ecosystems. One-way ANOVA was performed to further examine differences in main climate variables between the 1980s and the 2010s for three grassland ecosystems. Based on the main climate variables from step-wise regression, we constructed structural equation models for each of the three grassland types to explore the climate drivers of ANPP. The adequacy of SEMs was determined using Akaike information criterion (*AIC*), root mean square error of approximation (*RMSEA*), standardized root mean square residual (*SRMA*), and comparative fit index (*CFI*), where low *AIC*, low *SRMR*, and $CFI > 0.8$ indicate adequate model fit (Grace, 2006) (Table S3). Finally, to further investigate whether our observation results were consistent with the productivity changes predicted through remote sensing, trends in growing season EVI and GPP over 2000–2010 were analyzed.

10.1029/2020EF001837

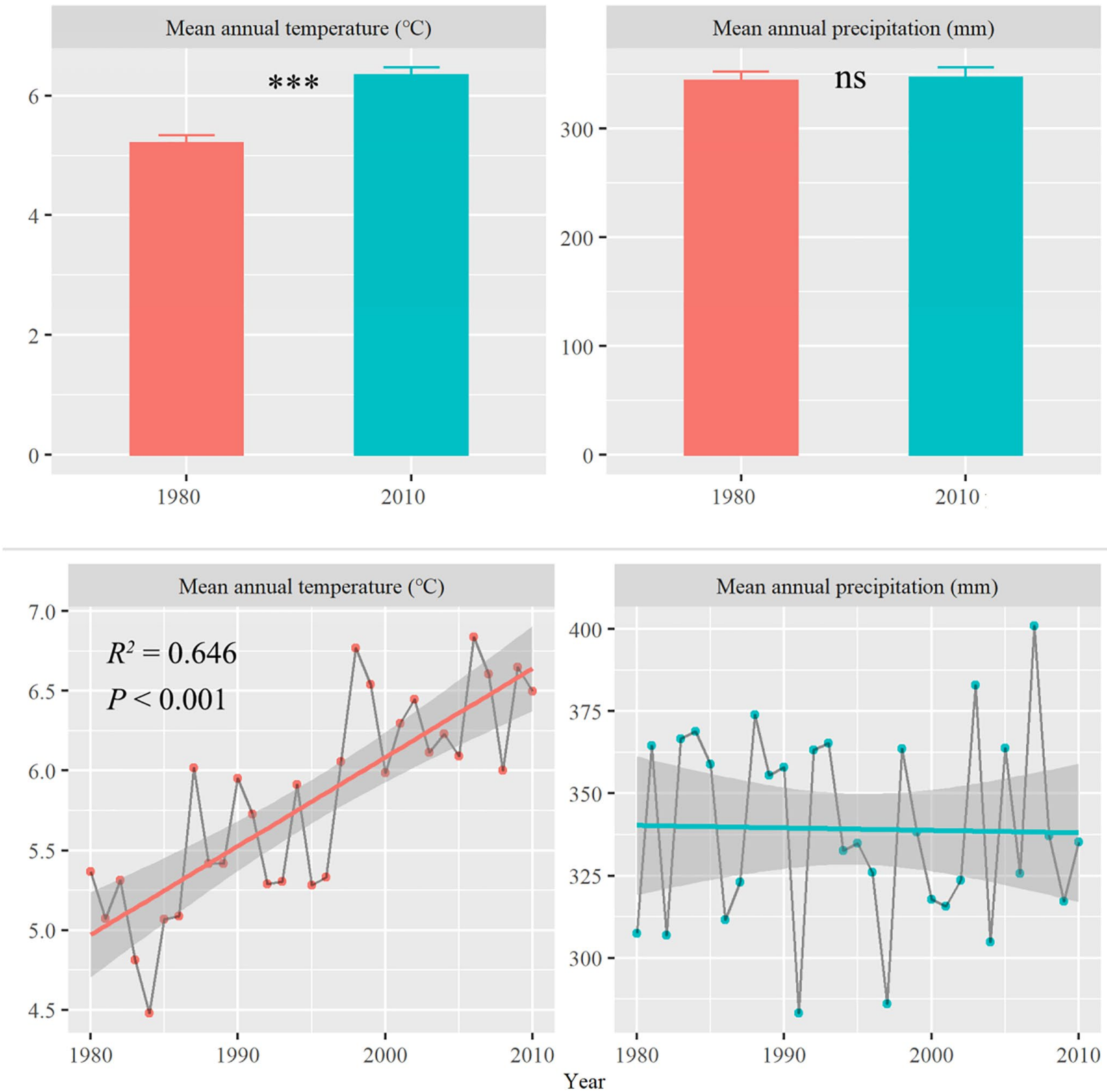

Figure 2. Mean annual precipitation (mm) and temperature (°C) over a 30-year period (from 1980 (1974–1983 represent for the 1980) to 2010 (2004–2013 represent for the 2010) and changes in mean annual temperature and mean annual precipitation. The error bars in the top two panels indicate the standard errors of the means. Dark gray areas in the bottom two panels indicate 95% confidence intervals. ***$P < 0.001$; ns, $P > 0.05$. The potential changes in regional climate by analyzing the records from 35 weather stations were used.

3. Results

3.1. Long-Term Decline in Grassland ANPP and Effects of Climate Change

Over the 30-year period, the study region has undergone a significant increased temperatures and non-significant changes in precipitation during the past 30 years (Figure 2). Meanwhile, the growing season air temperature, soil temperature, and solar radiation showed a significant increasing trend, but there was no significant variation in moisture index, growing season precipitation and habitat moisture index (Figure 3). Moreover, over the 30-year period, the ANPP of a total of 230 sampling sites decreased, with an average

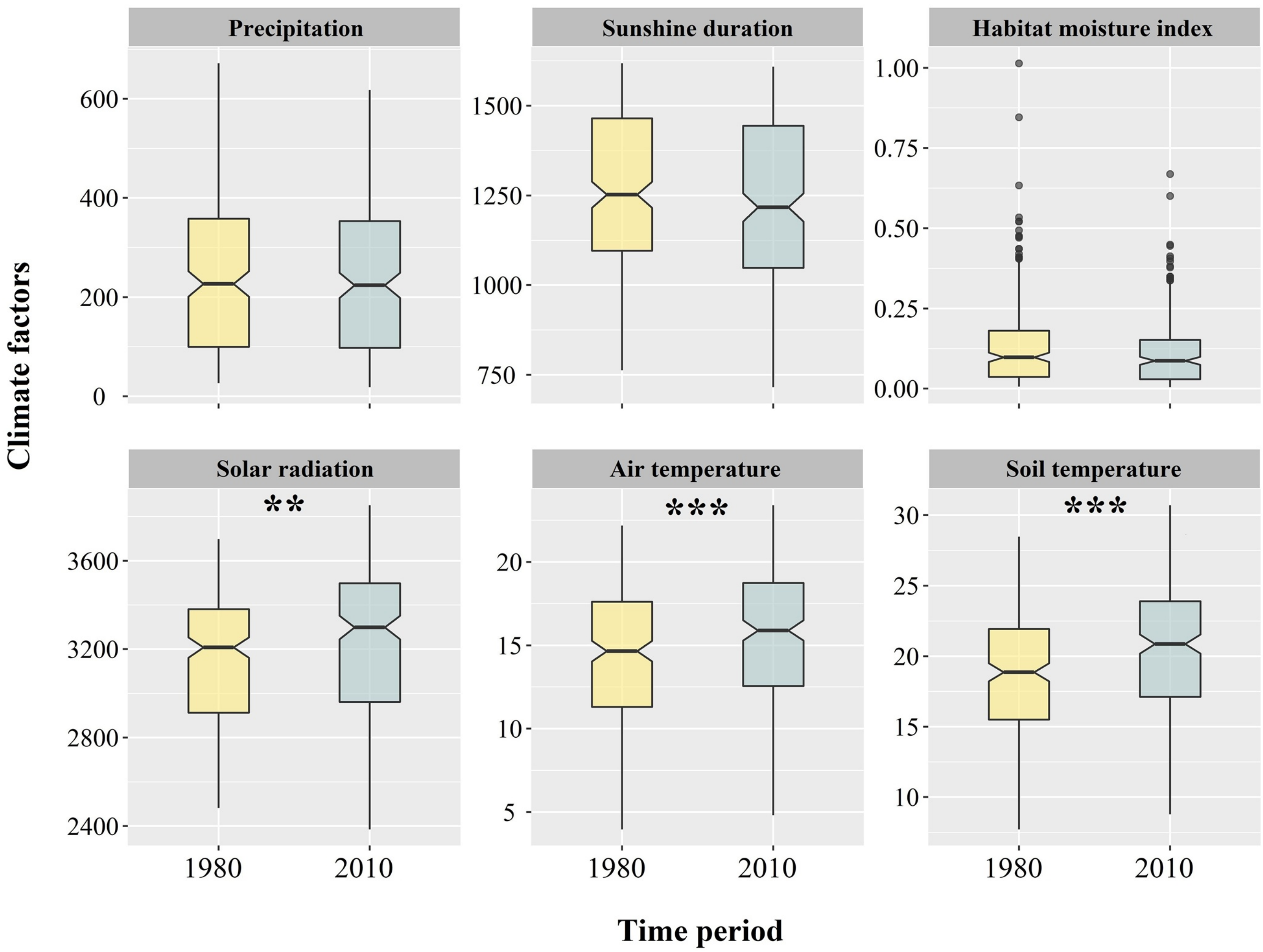

Figure 3. Comparison of climate factors in the 1980 (1974–1983 represent for the 1980) and the 2010 (2004–2013 represent for the 2010) across all grassland types studied. Climate factors were growing season mean precipitation (mm), air temperature (°C), soil temperature of the topsoil at the depth of 0–20 cm (°C), habitat moisture index, solar radiation (MJ m^{-2}), and sunshine duration (hour). ***$P < 0.001$; **$P < 0.01$.

decrease rate of ∼7.0 g m^{-2} yr^{-1} per site, while the ANPP of other 24 sampling sites increased, with an average increase rate of ANPP of ∼1.4 g m^{-2} yr^{-1} per site. Across all types of grassland, ANPP declined by more than 50% (Figure S2) and the average rate of decline was ∼6.1 g m^{-2} yr^{-1} over the 30-year period (Table S2), but the rates of decline strongly varied among the main grassland types. Specially, grassland ANPP in lowland (−78%) and alpine (−77%) grassland ecosystems significantly declined much more rapidly than in temperate (−60%) grassland ecosystems (Figure 4)

Structural equation modeling showed that moisture index and radiation energy had direct positive effects on grassland ANPP, while temperature had a direct negative effect across all sites combined. Moreover, moisture index had a stronger direct effect on ANPP than temperature and radiation energy. The contribution of growing season precipitation to moisture index was stronger than the contribution of habitat moisture index (Figure 5). Thus, precipitation is the main climate driver of ANPP across all grassland sites. However, the growing season precipitation in our grassland sites did not significantly change over the 30-year period. So, increased temperature was the primary reason for the decline in grassland ANPP. Importantly, there was a negative indirect effect of radiation energy on ANPP via shift in temperature, thus offsetting the direct positive effect of radiation energy on ANPP (Figure 5). Further, increased growing season solar radiation indirectly reduced grassland ANPP by elevating temperature.

10.1029/2020EF001837

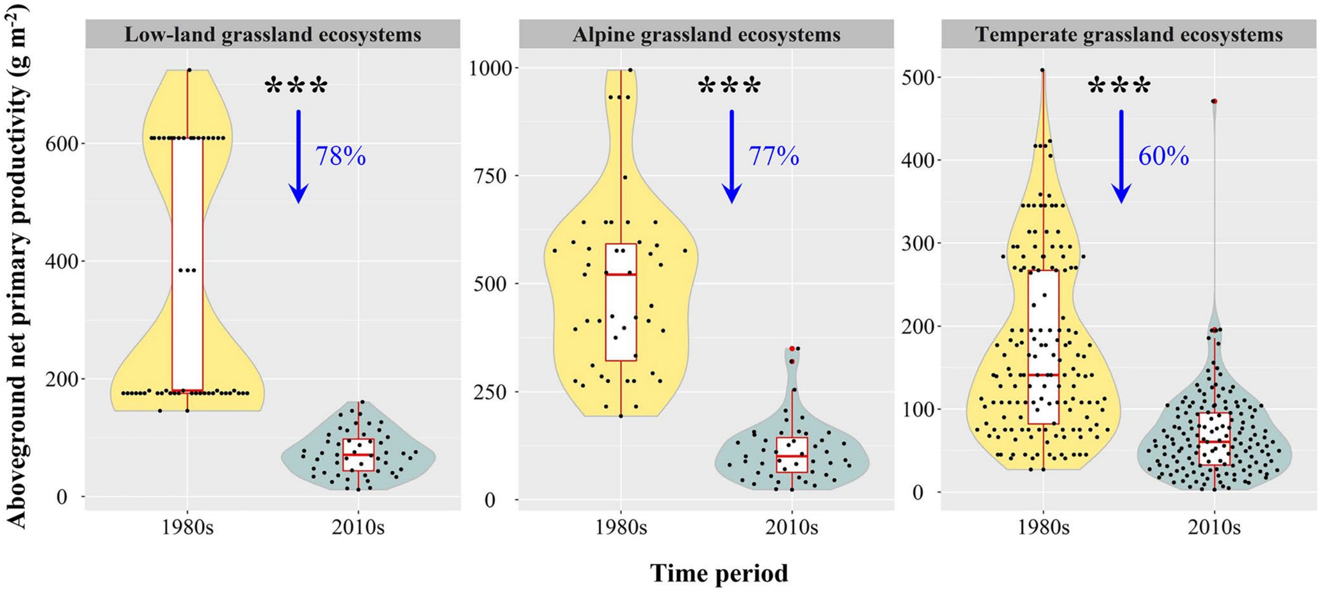

Figure 4. Violin plots comparing aboveground net primary productivity (ANPP) in the 1980 and the 2010 for three different grassland ecosystems. White box plots present the distribution of ANPP (median, inner-quartile range). The height of the violin represents the distribution range of the data, and the width represents the number of values. Black dots represent site-level ANPP measurements. ****P* < 0.001.

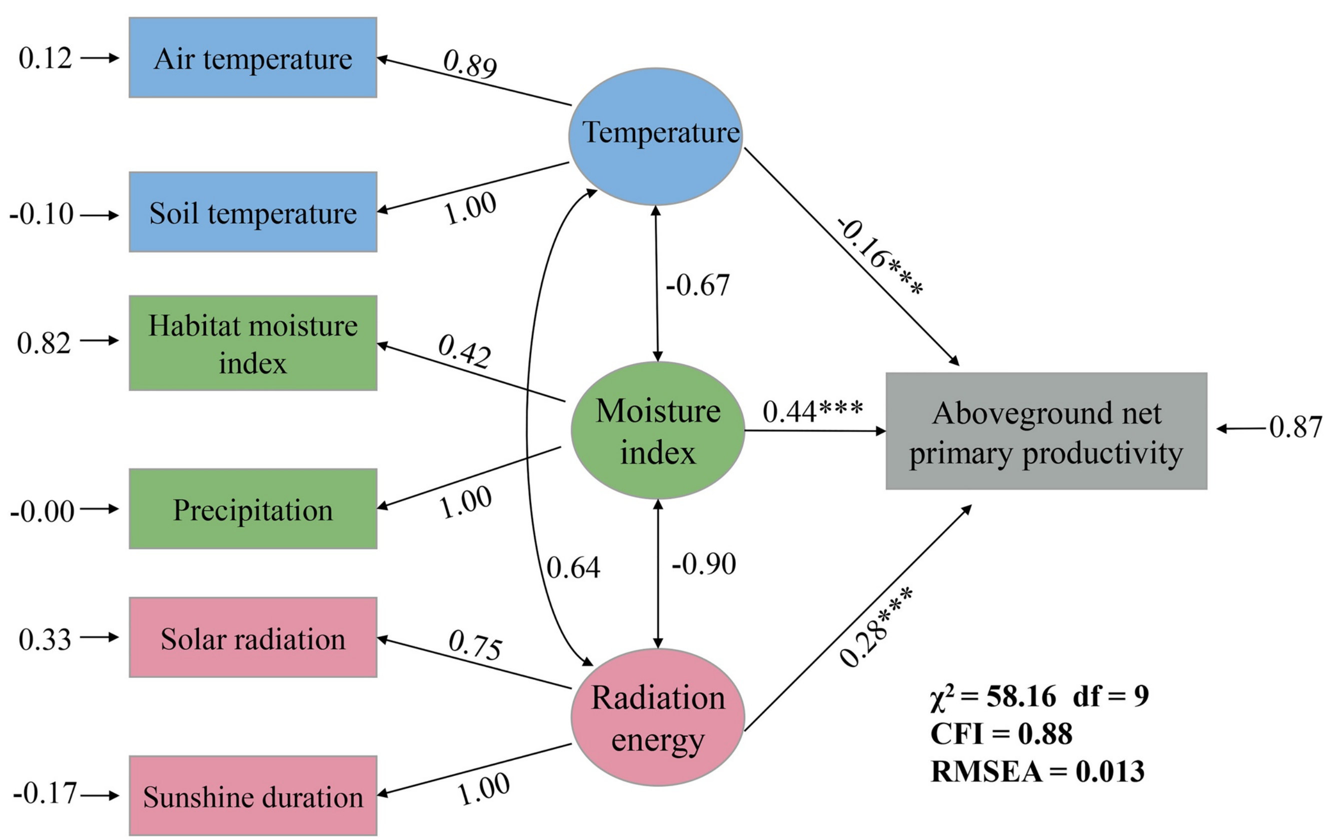

Figure 5. Structural equation model (SEMs) testing connections between aboveground net primary productivity (ANPP) and climate factors across grassland types. Climate factors were growing season precipitation, air temperature, soil temperature of the topsoil at the depth of 0–20 cm, habitat moisture index, solar radiation, and sunshine duration. The rectangles represent measured variables, while the circles represent the latent variables temperature, moisture index, and radiation energy. Values associated with path arrows represent the standardized path coefficient. Values near the rectangles show the residuals. ****P* < 0.001.

10.1029/2020EF001837

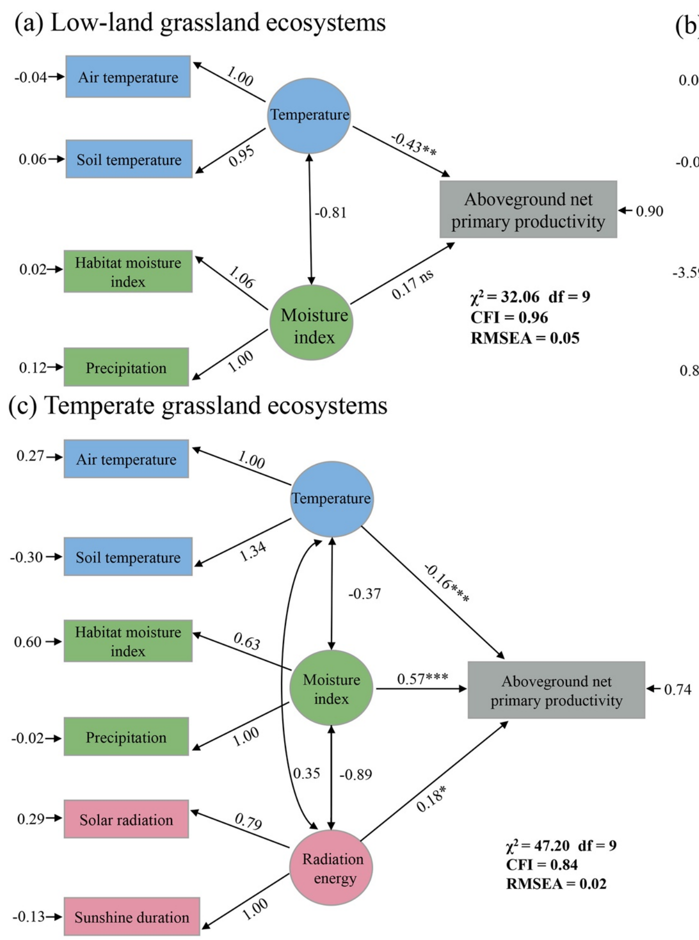

Figure 6. Structural equation models (SEMs) testing connections between aboveground net primary productivity (ANPP) and climate factors for low-land (a), alpine (b), and temperate (c) grassland ecosystems. Climate factors were growing season precipitation, air temperature, soil temperature of the topsoil at the depth of 0–20 cm, habitat moisture index, solar radiation, and sunshine duration. The rectangles represent manifest variables, while the circles represent latent variables. Values associated with path arrows represent the standardized path coefficient. Values near to the rectangles show the residuals. $^{***}P < 0.001$; $^{**}P < 0.01$; $^{*}P < 0.05$.

3.2. Key Climate Factors Determining ANPP in Different Grassland Type Groups

The climate change effects on grassland ANPP varied between grassland types and appeared to be driven by different climate factors in different grassland ecosystem types. Specifically, structural equation models indicated that high temperature exhibited a negative direct effect on grassland ANPP in all three-grassland ecosystems (Figure 6). Notably, moisture index had a positive but non-significant association with ANPP for low-land grassland ecosystems, and a significant positive association for temperate grassland ecosystems (Figures 6a and 6c). And, radiation energy had direct effects on ANPP, with the direct effects being negative in alpine and positive in temperate grassland ecosystems (Figures 6b and 6c).

Stepwise regression further revealed that growing season air temperature was the main climatic factor affecting ANPP of low-land grassland ecosystems, and growing season soil temperature was the main climatic factor affecting ANPP of alpine and temperate grassland ecosystems (Table 1). In low-land grassland ecosystems, growing season air temperature had a significant positive effect on grassland ANPP, while soil temperature had a significant negative effect. In alpine and temperate grassland ecosystems, growing season soil temperature and solar radiation significantly and negatively affected ANPP change. Besides, growing season precipitation positively affected ANPP only in temperate grassland ecosystems (Table 1). We also found that growing season soil temperature and solar radiation showed a significant increase, of 1.84°C and 71.54 MJ m^{-2}, respectively, over the 30-year period, whereas air temperature and precipitation did not vary

Table 1
Results of Step-Wise Multiple Regressions Testing the Relationships Between Aboveground Net Primary Production (ANPP) and Climate Variables in Different Grassland Ecosystems

Grassland ecosystem type	Equations	R^2	Sig.
Low-land grassland	ANPP = 186.20GST−160.90ST + 658.54	0.29	***
Alpine grassland	ANPP = −56.95ST + 2.74GSS−1.83GSR + 3871.60	0.53	***
Temperate grassland	ANPP = −12.76ST + 0.62GSS + 0.47GSP−0.34GSR + 576.34	0.39	***

Note. Significance levels: ****P* < 0.001. Climate factors included growing season precipitation (GSP, mm), air temperature (GST, °C), soil temperature of the topsoil at a depth of 0–20 cm (ST, °C), solar radiation (GSR, MJ m^{-2}), and sunshine duration (GSS, hour).

(Figure S3). Collectively, increased soil temperature was the primary drivers of ANPP decline in all three grassland ecosystems, and increased solar radiation also caused ANPP decline in alpine and temperate grassland ecosystems.

3.3. Spatial Patterns of EVI and GPP

The areas of growing season EVI and GPP in the north of study area were basically unchanged during the period 2000–2010 (Figure S4a and S4b). The areas of increase and decreased in both growing season EVI and GPP were mainly concentrated in the eastern and southern parts of study area, respectively (Figure S4a and S4b). However, the extracted growing season EVI and GPP of each site showed no significant trend over 2000–2011 (Figure S4a and S4b).

4. Discussion

A critical challenge in studies of global change is understanding different ecosystems sensitivity to long-term climate changes at spatial scales. Our results showed that climate change consistently reduces grassland ANPP over 30 years for different grassland ecosystems. Furthermore, our results showed that the increased soil temperature and air temperature from increased total solar radiation were the main drivers for ANPP decline. We also determined the main climate variables driving the ANPP changes for different grassland ecosystems, which quantify their contributions in driving the ANPP decline. These results both complement and reinforce claims regarding the importance of scale-dependent analysis when examining the relationship between ANPP and climate variables in different grassland ecosystems.

In all grassland ecosystems in the study region, there was a common trend for an ANPP decline over the 30-year period. Although changes in moisture index (precipitation and habitat moisture) are more likely to govern biomass and vegetation structure, rather than temperature changes (Ahlström et al, 2017), significant changes in climate variables in the different grasslands did not occur for moisture index, but were evident for temperature. Therefore, increasing growing season air and soil temperature were the primary drivers of the ANPP decline. Because drought caused by warmer temperatures will accelerate the decline of grassland ANPP (Breshears et al., 2005; Brookshire & Weaver, 2015). Thus, projected increases in global mean temperature of at least 2°C by the end of the 21st century (IPCC, 2013) can be expected to have profound adverse impacts on vegetation growth and primary productivity in terrestrial ecosystems. The potential mechanisms of grassland ANPP decline may be drought-induced vegetation die-off and a warming-induced soil water deficit (Breshears et al., 2005). The effects of drought-induced by a warmer temperature increase evapotranspiration (partitioning into vegetation transpiration and soil evaporation) and concomitantly decrease water availability, resulting in a decrease in the photosynthesis rate of the plant (Han et al., 2018), thus reducing grassland ANPP.

Although ANPP showed a similar declining trend in all grasslands, the ANPP decline rate was different in different grassland ecosystems. Specifically, the decreasing trend over the 30-year period was more rapid in lowland and alpine grassland ecosystems than in temperate grassland ecosystems. This result showed that more attention should be paid to the protection of alpine and low-land grassland ecosystems that were more sensitive to temperature under future climate scenarios. Alpine ecosystems are considered highly sensitive to climate change because of the harsher conditions and more fragile ecological environment compared with other ecosystems, for example, temperate ecosystems (Guo et al., 2018; Hu et al., 2018; Liu et al., 2018). Our observational finding of the more rapid grassland ANPP decline in alpine grassland ecosystem further supports the notion that alpine grassland ecosystems are highly sensitivity to climate warming. In contrast, temperate ecosystems showed slower grassland ANPP decline, which reveals its less sensitive to warming temperature. Furthermore, climate change effects on grassland ecosystem types dominated by different plant functional groups may be different (Harrison et al., 2015). A grassland with different functional groups has different effects on climate regulation because of the differences in the adaptation of different functional groups to habitat conditions and resource utilization efficiency (Eviner & Chapin, 2003). For example, the vertical root distribution among functional groups was different. The deeper-rooting species could absorb more subsoil moisture than shallow-rooted species, so grassland types composed of functional groups dominated by deep roots had stronger resistance to climate warming than grassland types dominated by shallow roots (Liu et al., 2018; Fischer et al., 2019). The response of productivity to climate change also depends on the stabilizing effect of compensatory interactions among major functional groups (Bai et al., 2004; Connell & Ghedini, 2015). So, further studies should be focused on plant functional group levels on ecosystem response to global change.

The above results reveal that the magnitude of effects of long-term climate change on different grassland ecosystem types. Furthermore, our results showed that warming temperature, especially soil warming, was a climate change factor driving the ANPP decline in low-land, alpine, and temperate grassland ecosystems. In low-land grassland ecosystems, we found that the positive effect of growing season air temperature was greater than the negative effect of soil temperature, but these effects were not found in alpine and temperate grassland ecosystems. This suggested that the wetter low-land grassland ecosystems are more responsive to the growing season air temperature than the alpine and temperate grassland ecosystems. This result may be due to increased air temperature could promote plant leaf growth and photosynthesis, thereby increasing productivity, while increased soil temperature could reduce soil moisture and impede root growth, thereby decreasing productivity (Zhou et al., 2012). Since the growing season air temperature in low-and grassland ecosystems did not change, the soil temperature increased significantly, so the negative effect of soil temperature was the main climate factor leading to the decline of ANPP in low-land grassland ecosystems.

Conversely, in alpine and temperate grassland ecosystems, we found the effect of soil temperature was greater than the effect of growing season air temperature on ANPP. This finding is important when predicting the importance of soil temperature for the productivity of terrestrial ecosystems (Guo et al., 2018). The potential mechanism behind the ANPP decline in response to increasing soil temperature could decrease soil moisture and inhibit seed germination (Adams et al., 2009), and suppress plant growth through increased evapotranspiration (Jacobs et al., 2011; Vicente-Serrano et al, 2013). This may explain why the soil temperature increasing is the main driving factor for ANPP decline in all grassland types. And the variation in grassland aboveground productivity is dominated by increasing soil temperature in our study. Compared with 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). Therefore, our findings suggest that further studies should pay great attention to soil temperature when exploring the climate change effects on terrestrial ecosystems.

Our results also showed that solar radiation can play an essential role in the ANPP decline in grassland ecosystems at a regional scale in a warming climate, apart from growing season soil temperature. Increasing growing season solar radiation also contributed to the grassland ANPP decline (direct and indirect). And the increased solar radiation presented the larger effect of soil temperature on alpine grasslands ANPP decline more than in temperate grasslands. Grassland ANPP is affected by the availability and interception of photosynthetically active radiation (Feltrin et al., 2016), with a positive relationship between grassland ANPP and solar radiation. However, water limitations must be considered (Nouvellon et al., 2000), with low water availability limiting plant growth and productivity in grassland ecosystems (Huxman et al., 2004). In all three grasslands, increased soil temperature reduces water availability and hinders the utilization of solar radiation by plants (Han et al., 2018; Huxman et al., 2004; Nouvellon et al., 2000). In those conditions, an increase in solar radiation will accelerate the increase in soil temperature, possibly leading to a severe drought that in turn accelerates the grassland ANPP decline (Breshears et al., 2005; Brookshire &

10.1029/2020EF001837

Weaver, 2015). Therefore, we concluded that increased soil temperature accompanied by increased solar radiation is the main climate factor driving the productivity decline response to climate change in grassland ecosystems at regional scale. In addition, when exploring ecosystem responses to climate change in temperate grassland ecosystems, growing season precipitation should be taken into consideration, as precipitation decrease will slightly exacerbate the ANPP decline for temperate grassland ecosystems, especially in arid and semi-arid areas (Ahlström et al., 2017; Hufkens et al., 2016).

Although our study just sampled the data at two single time periods and without getting the full-time series. Through the analysis of meteorological data for three years before and after 2010s (Figure S5), we found that the annual temperature and precipitation in 2010s were close to the multi-year (2006–2013) average temperature and precipitation, which indicated that 2010s was not a dry year. So, the decline in ANPP was not caused by the low precipitation in the 2010s. Meanwhile, by analyzing the satellite-measured growing season EVI and GPP of each site over 2000–2010, we found that EVI and GPP did not show a decreasing trend and remained basically unchanged. We further analyzed the relationships between observed ANPP and remote sensing GPP data in 2010, and found that ANPP and GPP are logarithmic (Figure S6). The slope of the ANPP-GPP relationships showed a decreasing trend with increasing GPP, and it was almost flat under high GPP. Therefore, the increased GPP did not necessarily cause a significant increase in ANPP, indicating that the observed ANPP and remote sensing GPP data showed different trends. This result might be attributed to the inherent deficiencies in the quality of satellite remote sensing data (Zhang et al., 2013). Remote sensing is difficult to distinguish the differences between different grassland types. Furthermore, satellite-derived vegetation data are easily contaminated by adverse atmospheric conditions and other background factors (Shen et al., 2013). For example, aerosols will reduce the vegetation data sensed by satellite sensors, and are also subject to the limitations of phenological inversion methods (Yi & Zhou, 2011). Importantly, GPP is the sum of above- and below-ground net primary productivity (BNPP) and the organic C consumed by plant respiration (Wang et al., 2019). The increased temperature would accelerate the amount of organic C consumed by plant respiration, and cause a shift from ANPP to BNPP (Liu et al., 2018). So, the organic C consumed by respiration and the increased in BNPP might offset the increase in GPP, resulting in an opposite trend in observed ANPP and remote sensing GPP data. Therefore, field observation is more accurate and truer for studying different grassland types and will help to better predict trends in the productivity of different grassland ecosystems under future climate.

5. Conclusions

Our findings showed a universal decrease in ANPP over 30 years across different grassland types, and highlight the magnitude of ANPP decline differed between grassland types. Our results suggest that the increased growing season air temperature and soil temperature, rather than precipitation, were the primary drivers of the ANPP decline response by grasslands to climate change. The solar radiation is being critical climate variable, given the important contributions of the increased air temperature and soil temperature from increased total solar radiation were the main drivers for ANPP decline. These findings are important when predicting the potential mechanisms behind the grassland ecosystem productivity decline driven by climate warming. Our results also showed that the decline rate of ANPP was more rapid in alpine and lowland grasslands than in temperate grasslands. This indicates that the alpine and lowland grasslands may be more sensitive to climate warming than temperate grasslands. Our results emphasize that climate warming has caused irreversible adverse consequences on the productivity functions of different grassland ecosystems, and the different responses for different grassland types may be focused on further studies which predict the response of different terrestrial ecosystems to climate change. Our results reveal new opportunities and challenges for grassland ecosystem types in response to the long-term climate change.

Conflict of Interest

The authors declare that they have no conflict of interest.

Data Availability Statement

All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. All data sources used in the study are provided in the Data sources section in Dryad Digital Repository, https://doi.org/10.5061/dryad.2fqz612nx.

Acknowledgments
The authors thank the editors and three anonymous reviewers for their constructive comments and suggestions, and thank Prof. Johannes M.H. Knops and Paul Kardol for their suggestions and improvement on this manuscript draft, and thank our workteam members for the field works. This study was funded by the Strategic Priority Research Program of Chinese Academy of Sciences (XDB40000000), the National Natural Science Foundation of China (NSFC 41722107), the Natural Science Foundation of Qinghai Province (2020-ZJ-726), and the Open Project of the Qinghai Provincial Key Laboratory of Restoration Ecology in Cold Area (2020-KF-07).

References

Adams, H. D., Guardiola, C. M., Barron, G. G. A., Villegas, J. C., Breshears, D. D., Zou, C. B., et al. (2009). Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 7063–7066.

Ahlström, A., Canadell, J. G., Schurgers, G., Wu, M., Berry, J. A., Guan, K., & Jackson, R. B. (2017). Hydrologic resilience and Amazon productivity. *Nature Communications*, *8*, 387. https://doi.org/10.1038/s41467-017-00306-z

Bai, Y. F., Han, X. G., Wu, J. G., Chen, Z. Z., & Li, L. H. (2004). Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature*, *431*, 181–184. https://doi.org/10.1038/nature02850

Bell, J. E., Sherry, R., & Luo, Y. Q. (2010). Changes in soil water dynamics due to variation in precipitation and temperature: An ecohydrological analysis in a tallgrass prairie. *Water Resources Research*, *46*, W03523. https://doi.org/10.1029/2009WR007908

Breshears, D. D., Cobb, N. S., Rich, P. M., Price, K. P., Allen, C. D., Balice, R. G., et al. (2005). Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences*, *102*, 15144–15148. https://doi.org/10.1073/pnas.0505734102

Brookshire, E. N. J., & Weaver, T. (2015). Long-term decline in grassland productivity driven by increasing dryness. *Nature Communications*, *6*, 7148. https://doi.org/10.1038/ncomms8148

Buitenwerf, R. (2016). Vegetation productivity: Humans did it. *Nature Climate Change*, *6*, 898–899. https://doi.org/10.1038/nclimate30810.1038/nclimate3081

Christensen, J. H., Krishna, K. K., Aldrian, E. H., An, S. I., Cavalcanti, I. F. A., de Castro, M., et al. (2013). Climate phenomena and their relevance for future regional climate change, (Eds.). In Climate change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change (pp. 1217–1308). Cambridge University Press.

Connell, S. D., & Ghedini, G. (2015). Resisting regime-shifts: The stabilizing effect of compensatory processes. *Trends in Ecology & Evolution*, *30*, 513–515. https://doi.org/10.1016/j.tree.2015.06.014

Craine, J. M., Nippert, J. B., Elmore, A. J., Skibbe, A. M., Hutchinson, S. L., & Brunsell, N. A. (2012). Timing of climate variability and grassland productivity. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 3401–3405. https://doi.org/10.1073/pnas.1118438109

De Boeck, H. J., Dreesen, F. E., Janssens, I. A., & Nijs, I. (2011). Whole-system responses of experimental plant communities to climate extremes imposed in different seasons. *New Phytologist*, *189*, 806–817. https://doi.org/10.1111/j.1469-8137.2010.03515.x

Del Grosso, S., Parton, W., Stohlgren, T., Zheng, D., Bachelet, D., Prince, S., et al. (2008). Global potential net primary production predicted from vegetation class, precipitation, and temperature. *Ecology*, *89*, 2117–2126. https://doi.org/10.2307/2765073710.1890/07-0850.1

Department of Animal Husbandry and Veterinary (1996). *The General Station of Animal Husbandry and Veterinary of the Ministry of Agriculture of China*. Rangeland Resources of China. Science and Technology Press of China.

Durante, M., Piñeiro, G., Irisarri, J. G. N., & Oesterheld, M. (2017). Primary production of lowland natural grasslands and upland sown pastures across a narrow climatic gradient. *Ecosystems*, *20*, 543–552. https://doi.org/10.1007/s10021-016-0039-2

Eviner, V. T., & Chapin, F. S. (2003). Functional matrix: A conceptual framework for predicting multiple plant effects on ecosystem processes. *Annual Review of Ecology Evolution and Systematics*, *34*, 455–485. https://doi.org/10.1146/annurev.ecolsys.34.011802.132342

Feltrin, R. P., Will, R. E., Meek, C. R., Masters, R. E., Waymire, J., & Wilson, D. S. (2016). Relationship between photosynthetically active radiation and understory productivity across a forest-savanna continuum. *Forest Ecology and Management*, *374*, 51–60. https://doi.org/10.1016/j.foreco.2016.04.049

Fischer, C., Leimer, S., Roscher, C., Hildebrandt, A., de Kroon, H., Kreutziger, Y., et al. (2019). Plant species richness and functional groups have different effects on soil water content in a decade-long grassland experiment. *Journal of Ecology*, *107*, 127–141. https://doi.org/10.1111/1365-2745.13046

García-palacios, P., Gross, N., Gaitán, J., & Maestre, F. T. (2018). Climate mediates the biodiversity-ecosystem stability relationship globally. *Proceedings of the National Academy of Sciences of the United States of America*. *115*, 8400–8405. https://doi.org/10.1073/pnas.1800425115

Grace, J. (2006). *Structural equation modeling and natural systems*. Cambridge University Press.

Guo, L., Chen, J., Luedeling, E., He, J. S., Cheng, J. M., Wen, Z. M., & Peng, C. H. (2018). Early-spring soil warming partially offsets the enhancement of alpine grassland aboveground productivity induced by warmer growing seasons on the Qinghai-Tibetan Plateau. *Plant and Soil*, *425*, 1–188. https://doi.org/10.1007/s11104-018-3582-0

Guo, Q., Hu, Z. M., Li, S. G., Li, X. R., Sun, X. M., & Yu, G. R. (2012). Spatial variations in aboveground net primary productivity along a climate gradient in Eurasian temperate grassland: Effects of mean annual precipitation and its seasonal distribution. *Global Change Biology*, *18*, 3624–3631. https://doi.org/10.1111/gcb.12010

Han, D., Wang, G., Liu, T., Xue, B., Kuczera, G., & Xu, X. (2018). Hydroclimatic response of evapotranspiration partitioning to prolonged droughts in semiarid grassland. *Journal of Hydrology*, *563*, 766–777. https://doi.org/10.1016/j.jhydrol.2018.06.048

Harrison, S. P., Gornish, E. S., & Copeland, S. (2015). Climate-driven diversity loss in a grassland community. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, 8672–8677. https://doi.org/10.1073/pnas.1502074112

Helama, S., Tuomenvirta, H., & Venäläinen, A. (2011). Boreal and subarctic soils under climatic change. *Global and Planetary Change*, *79*, 37–47. https://doi.org/10.1016/j.gloplacha.2011.08.001

Hoeppner, S. S., & Dukes, J. S. (2012). Interactive responses of old-field plant growth and composition to warming and precipitation. *Global Change Biology*, *18*, 1754–1768. https://doi.org/10.1111/j.1365-2486.2011.02626.x

Hu, Z. M., Shi, H., Cheng, K. L., Wang, Y. P., Piao, S. L., Li, Y., et al. (2018). Joint structural and physiological control on the interannual variation in productivity in a temperate grassland: A data-model comparison. *Global Change Biology*, *24*, 2965–2979. https://doi.org/10.1111/gcb.14274

Hufkens, K., Keenan, T. F., Flanagan, L. B., Scott, R. L., Bernacchi, C. J., Joo, E., et al. (2016). Productivity of North American grasslands is increased under future climate scenarios despite rising aridity. *Nature Climate Change*, *6*, 710–714. https://doi.org/10.1038/nclimate2942

Hutchinson, M. (2004). *Anusplin Version 4.37. Centre for resource and environmental studies*. The Austrian National University.

Huxman, T. E., Smith, M. D., Fay, P. A., Knapp, A. K., Shaw, M. R., Loik, M. E., et al. (2004). Convergence across biomes to a common rain-use efficiency. *Nature*, *429*, 651–654. https://doi.org/10.1038/nature02561

IPCC (2013). *Climate change 2013*. In The physical science basis. Working group I contribution to the fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press.

Jacobs, A. F. G., Heusinkveld, B. G., & Holtslag, A. A. M. (2011). Long-term record and analysis of soil temperatures and soil heat fluxes in a grassland area, The Netherlands. *Agricultural and Forest Meteorology*, *151*, 774–780. https://doi.org/10.1016/j.agrformet.2011.01.002

Kardol, P., Campany, C. E., Souza, L., Norby, R. J., Weltzin, J. F., & Classen, A. T. (2010). Climate change effects on plant biomass alter dominance patterns and community evenness in an experimental old-field ecosystem. *Global Change Biology*, *16*(10), 2676–2687. https://doi.org/10.1111/j.1365-2486.2010.02162.x

Knapp, A. K., Carroll, C. J. W., Robert, J., Griffin-Nolan, I. J., Chaves, F. A., et al. (2018). A reality check for climate change experiments: Do they reflect the real world? *Ecology*, *99*, 2145–2151. https://doi.org/10.1002/ecy.2474

Knapp, A. K., & Smith, M. D. (2001). Variation among biomes in temporal dynamics of aboveground primary production. *Science*, *291*, 481–484. https://doi.org/10.1126/science.291.5503.481

Liu, H., Mi, Z., Lin, L., Wang, Y., Zhang, Z., Zhang, F., et al. (2018). Shifting plant species composition in response to climate change stabilizes grassland primary production. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, 4051–4056. https://doi.org/10.1073/pnas.1700299114

Ma, W. H., He, J. S., Yang, Y. H., Wang, X. P., Liang, C. Z., Anwar, M., et al. (2010). Environmental factors covary with plant diversity-productivity relationships among Chinese grassland sites. *Global Ecology and Biogeography*, *19*, 233–243. https://doi.org/10.1111/j.1466-8238.2009.00508.x

Mowll, W., BlumenthalCherwinSmith, D. M. K. L. A., Symstad, A. J., Vermeire, L. T., Knapp, A. K., Vermeire, L. T., et al. (2015). Climatic controls of aboveground net primary production in semi-arid grasslands along a latitudinal gradient portend low sensitivity to warming. *Oecologia*, *177*, 959–969. https://doi.org/10.1007/s00442-015-3232-7

Niu, S. L., Wu, M. Y., Han, Y., Xia, J. Y., Li, L. H., & Wan, S. Q. (2008). Water-mediated responses of ecosystem carbon fluxes to climatic change in a temperate steppe. *New Phytologist*, *177*, 209–219. https://doi.org/10.1111/j.1469-8137.2007.02237.x

Nouvellon, Y., Seen, D. L., Rambal, S., Bégué, A., Moran, M. S., Kerr, Y., & Qi, J. (2000). Time course of radiation use efficiency in a shortgrass ecosystem: Consequences for remotely Sensed estimation of primary production. *Remote Sensing of Environment*, *71*, 43–55. https://doi.org/10.1016/S0034-4257(99)00063-2

Paruelo, J. M., Jobbagy, E. G., Sala, O. E., Lauenroth, W. K., & Burke, I. C. (1998). Functional and structural convergence of temperate grassland and shrubland ecosystems. *Ecological Applications*, *8*, 194–206. https://doi.org/10.2307/264132110.1890/1051-0761(1998)008[0194:fascot]2.0.co;2

Pugnaire, F. I., Morillo, J. A., Penuelas, J., Reich, P. B., Putten, W. H. V. D., Gaxiola, A., et al. (2019). Climate change effects on plant-soil feedbacks and consequences for biodiversity and functioning of terrestrial ecosystems. *Science Advances*, *5*, eaaz1834. https://doi.org/10.1126/sciadv.aaz1834

Qian, B., Gregorich, E. G., GamedaHopkins, S. B. D. W., Wang, X. L., & Wang, X. L. (2011). Observed soil temperature trends associated with climate change in Canada. *Journal of Geophysical Research*, *116*, D02106. https://doi.org/10.1029/2010JD015012

R Core Team (2014). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rosseel, Y. (2012). lavaan: An R package for structural equation modeling. *Journal of Statistical Software*, *48*, 1–36. https://doi.org/10.18637/jss.v048.i02

Sala, O. E. F. S., III, Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., & Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. *Science*, *287*, 1770–1774. https://doi.org/10.1126/science.287.5459.1770

Scurlock, J. M. O., Johnson, K., & Olson, R. J. (2002). Estimating net primary productivity from grassland biomass dynamics measurements. *Global Change Biology*, *8*, 736–753. https://doi.org/10.1007/s11136-006-9005-310.1046/j.1365-2486.2002.00512.x

Shaw, M. R., Zavaleta, E. S., Chiariello, N. R., Cleland, E. E., Mooney, H. A., & Field, C. B. (2002). Grassland responses to global environmental changes suppressed by elevated CO_2. *Science*, *298*, 1987–1990. https://doi.org/10.1126/science.1075312

Shen, M. G., Sun, Z. Z., Wang, S. P., Zhang, G. X., Kong, W. D., Chen, A. P., & Piao, S. L. (2013). No evidence of continuously advanced green-up dates in the Tibetan Plateau over the last decade. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, E2329. https://doi.org/10.1073/pnas.1304625110

Song, B., Niu, S. L., & Wan, S. Q. (2016). Precipitation regulates plant gas exchange and its long-term response to climate change in a temperate grassland. *Journal of Plant Ecology*, *9*, 531–541. https://doi.org/10.1093/jpe/rtw010

Song, J., Wan, S. Q., Piao, S. L., Knapp, A. K., Classen, A. T., Vicca, S., et al. (2019). A meta-analysis of 1,119 manipulative experiments on terrestrial carbon-cycling responses to global change. *Nature Ecology & Evolution*, *3*, 1309–1320. https://doi.org/10.1038/s41559-019-0958-3

Vicente-Serrano, S. M., Gouveia, C., Camarero, J. J., Beguería, S., Trigo, R., López-Moreno, J. I., et al. (2013). Response of vegetation to drought time-scales across global land biomes. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, 52–57. https://doi.org/10.1073/pnas.1207068110

Walker, T. W., Janssens, I. A., Weedon, J. T., Sigurdsson, B. D., Richter, A., Peñuelas, J., et al. (2020). A systemic overreaction to years versus decades of warming in a subarctic grassland ecosystem. *Nature Ecology and Evolution*, *4*, 101–108. https://doi.org/10.1038/s41559-019-1055-3

Wang, H., Liu, H. Y., Cao, G. M., Ma, Z. Y., Li, Y. K., Zhang, F. W., et al. (2020). Alpine grassland plants grow earlier and faster but biomass remains unchanged over 35 years of climate change. *Ecology Letters*, *23*, 701–710. https://doi.org/10.1111/ele.13474

Wang, N., Quesada, B., Xia, L. L., Butterbach-Bahl, K., Goodale, C. L., & Kiese, R. (2019). Effects of climate warming on carbon fluxes in grasslands- A global meta-analysis. *Global Change Biology*, *25*, 1839–1851. https://doi.org/10.1111/gcb.14603

Wang, S. P., Duan, J. C., Xu, G. P., Wang, Y. F., Zhang, Z. H., Rui, Y. C., et al. (2012a). Effects of warming and grazing on soil N availability, species composition, and ANPP in an alpine meadow. *Ecology*, *93*, 2365–2376. https://doi.org/10.1890/11-1408.1

Wang, Z., Luo, T., Li, R., Tang, Y., & Du, M. (2012b). Causes for the unimodal pattern of biomass and productivity in alpine grasslands along a large altitudinal gradient in semi-arid regions. *Journal of Vegetation Science*, *24*, 189–201. https://doi.org/10.1111/j.1654-1103.2012.01442.x

Whittingham, M. J., Stephens, P. A., Bradbury, R. B., & Freckleton, R. P. (2006). Why do we still use stepwise modeling in ecology and behavior? *Journal of Animal Ecology*, *75*, 1182–1189. https://doi.org/10.2307/383841110.1111/j.1365-2656.2006.01141.x

Wilcox, K. R., Blair, J. M., Smith, M. D., & Knapp, A. K. (2015). Does ecosystem sensitivity to precipitation at the site-level conform to regional-scale predictions? *Ecology*, *97*, 561–568. https://doi.org/10.1890/15-1437.1

Wu, G. L., Cheng, Z., Alatalo, J. M., Zhao, J. X., & Liu, Y. (2021). Data from: Climate warming consistently reduces grassland ecosystem productivity. *Dryad Digital Repository*. *6*, 26958. https://doi.org/10.5061/dryad.2fqz612nx

Yi, S. H., & Zhou, Z. Y. (2011). Increasing contamination might have delayed spring phenology on the Tibetan Plateau. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, E94. https://doi.org/10.1073/pnas.1100394108

Zhang, C., Zhang, Y., & Li, J. (2019). Grassland productivity response to climate change in the Hulunbuir steppes of China. *Sustainability*, *11*, 6760. https://doi.org/10.3390/su11236760

Zhang, G. L., Zhang, Y. J., Dong, J. W., & Xiao, X. M. (2013). Green-up dates in the Tibetan Plateau have continuously advanced from 1982 to 2011. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, 4309–4314. https://doi.org/10.1073/pnas.1210423110

Zhou, X. H., Fei, S. F., Sherry, R., & Luo, Y. Q. (2012). Root biomass dynamics under experimental warming and doubled precipitation in a tallgrass prairie. *Ecosystems*, *15*, 542–554. https://doi.org/10.1007/s10021-012-9525-3

Zhu, K., Chiariello, N. R., Tobeck, T., Fukami, T., & Field, C. B. (2016). Nonlinear, interacting responses to climate limit grassland production under global change. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 10589–10594. https://doi.org/10.1073/pnas.1606734113