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Critical climate periods for grassland productivity on China's Loess Plateau

Liang Guo[a], Jimin Cheng[a,*], Eike Luedeling[b,c], Sally E. Koerner[d], Jin-Sheng He[e], Jianchu Xu[f,g], Chengcheng Gang[a], Wei Li[a], Ruimin Luo[h], Changhui Peng[a,i,**]

[a] State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Northwest A&F University, Yangling 712100, China
[b] World Agroforestry Centre, Nairobi 00100, Kenya
[c] Centre for Development Research (ZEF), University of Bonn, Bonn 53113, Germany
[d] Department of Integrative Biology, University of South Florida, Tampa, FL 33620, USA
[e] Department of Ecology, College of Urban and Environmental Sciences, Peking University, Beijing 100871, China
[f] Centre for Mountain Ecosystem Studies, Kunming Institute of Botany, Chinese Academy of Science, Kunming 650201, China
[g] World Agroforestry Centre, East and Central Asia, Kunming 650201, China
[h] College of Animal Science and Technology, Northwest A&F University, Yangling 712100, China
[i] Department of Biology Science, Institute of Environment Sciences, University of Quebec at Montreal, Montreal H3C 3P8, Canada

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ABSTRACT

Strong correlations between aboveground net primary productivity (ANPP) of grasslands and mean annual temperature or precipitation have been widely reported across regional or continental scales; however, inter-annual variation in these climate factors correlates poorly with site-specific ANPP. We hypothesize that the reason for these weak correlations is that the impacts of climatic variation on grassland productivity depend on the timing and intensity of variation in temperature and precipitation. In this study, long-term records of grassland productivity on the Loess Plateau in China were related with daily temperature and precipitation during 1992–2011 using Partial Least Squares (PLS) regression to test the above-mentioned hypothesis. Our results suggested that temperature increases during the early stage of the growing season (April–May) were positively correlated with ANPP. However, these effects were canceled out when this phase was followed by a hot and dry summer (June–July). Impacts of drought and heat in August on productivity were negligible. Increased temperature and precipitation during the senescence period (September–October) and a warmer dormancy phase (November–March) were negatively correlated with productivity in the following year, while precipitation during the dormancy period had no detectable effects. Climatic variability in summer has thus far been the dominant driver of temporal variation in grassland productivity. Warming during winter and spring currently play minor roles, but it seems likely that the importance of these secondary impacts may increase as warming trends continue. This evaluation of climate variability impacts on ecosystem function (e.g. grassland productivity) implies that not only the magnitude but also the timing of changes in temperature and precipitation determines how the impacts of climate changes on ecosystems will unfold.

1. Introduction

Grasslands, one of the most important and largest terrestrial ecosystems in the world covering 30% of the land surface, are mainly distributed in arid and semi-arid regions (Shi et al., 2014), and they are considered very sensitive to climate changes (Craine et al., 2012; Grime et al., 2000; Hsu et al., 2012; Knapp et al., 2002). Aboveground net primary productivity (ANPP) of grasslands is highly temporally variable, as compared to other ecosystems, such as forest and cropland (Fang et al., 2001; Knapp and Smith, 2001). Climate-driven variability in grassland productivity impacts the global carbon balance, ecosystem service delivery, profitability of pastoral livelihoods and the sustainability of grassland resources as a whole (Grime et al., 2000; Guo et al., 2012; Sala et al., 2012). Temporal variation in ANPP and its interactions with global climate change have therefore long been of interest to ecologists.

* Corresponding author.
** Corresponding author at: State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Northwest A&F University, Yangling 712100, China.
E-mail addresses: gyzcjm@ms.iswc.ac.cn (J. Cheng), peng.changhui@uqam.ca (C. Peng).

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Much of the previous work considering the impacts of climate variability on ANPP has focused on annual precipitation and temperature (Bai et al., 2004; Hu et al., 2007; Knapp and Smith, 2001; Lauenroth and Sala, 1992; Rosenzweig, 1968). While the importance of these annual-scale metrics has often been confirmed in studies at regional and continental scales, numerous site-specific reports have indicated that inter-annual variability in ANPP is poorly or even not at all correlated with annual climate conditions (Hsu and Adler, 2014; Sala et al., 2012), with much of the temporal variation in ANPP left unexplained (Fabricante et al., 2009; Jobbágy and Sala, 2000; Oesterheld et al., 2001). Changes in precipitation or temperature during certain parts of the year are more relevant drivers of ANPP than annual changes (Chou et al., 2008; La Pierre et al., 2011; Milchunas et al., 1994; Robinson et al., 2013), since vegetation production responds differently to climatic variation during different seasons (Craine et al., 2012; Hovenden et al., 2014; La Pierre et al., 2011; Ma et al., 2010). For example, warming in early spring eases cold temperature constraints on plant growth in northern mid and high latitudes (Chen and Weber, 2014; Chollet et al., 2014) and also appears to advance spring greening phenology (Menzel et al., 2001; Piao et al., 2006; Reyes-Fox et al., 2014), which leads to a longer growing season and higher productivity for grasslands. Rising temperatures in summer, however, can depress productivity by reducing soil moisture and intensifying physiological stress (Craine et al., 2012). Future climates are likely to include more frequent extreme weather events and more pronounced seasonal variation in temperature and precipitation (Knapp et al., 2008; Piao et al., 2010; Yang et al., 2008).

Here, we examine the impacts of climate variability at different times of the year on grassland productivity of the Loess Plateau in China, which is well known for its fragile ecological environment, frequent severe droughts, and problems with water runoff and soil erosion (Xin et al., 2008). In contrast to numerous studies in the temperate grasslands of Inner Mongolia and the alpine grasslands of the Tibetan Plateau, very few reports are available on responses of grassland productivity to climate variability on the more arid Loess Plateau in China (Zhang et al., 2006), especially with respect to responses to seasonal climatic variation. Dramatic warming and drought since the 1980s in this region (Yao et al., 2005) have further threatened the already vulnerable ecosystems and may have negative effects on the progress of the Returning Land from Farming to Forestry and Grassland Project, currently the largest ecological restoration plan in China. In the present study, long-term productivity and weather records have been collected since 1982 at Yunwushan National Nature Reserve, a typical steppe grassland on the Loess Plateau and Partial Least Squares (PLS) regression was used to correlate grass productivity to variation in temperature and precipitation at daily resolution.

We hypothesize that the timing of climate variability is just as important – if not more important – than its intensity for explaining temporal variation in grassland productivity, so that variation in temperature and precipitation during different periods should have different effects on grassland productivity (Fig. A.1). Specifically, (i) increased temperature during the early stage of the growing season (April-May) will enhance ANPP due to increased or advanced spring vegetation growth. (ii) Hotter and drier conditions in summer will have negative effects on ANPP by causing plant physiological stress during the middle of the growing season (June-July). (iii) Additionally, we expect that temperature increases during the dormancy period (November-March) will negatively correlate with productivity in the following year since winter warming has been reported to delay spring phenology which is partly attributed to a reduced vernalization effect (Fu et al., 2015; Guo et al., 2015; Luedeling et al., 2013; Yu et al., 2010). (iv) As for the other climate periods, we have no clear expectations of how productivity will respond to variation in temperature and precipitation. Here we address each of these questions with the goal of clarifying the relationship between grassland productivity and timing of climatic variability across the whole year.

2. Materials and methods

2.1. Site description

Located on the steppe grassland of the Loess Plateau in China, Yunwushan National Nature Reserve (36°10′–36°17′N, 106°21′–106°27′E, 1800–2100 m a.s.l.; Fig. A.2) was established as a long-term ecological monitoring station in 1982. A semi-arid temperate climate prevails there. Mean annual temperature (MAT) during 1982–2011 was 7 °C with mean monthly temperature extremes of −22 °C in January and 25 °C in July. Annual precipitation (AP) averaged 425 mm and mainly fell in summer from June to August (57% of total AP), with less precipitation in autumn (September–October, 21%) and spring (April–May, 16%). Annual evaporation is 1017–1739 mm and the frost-free season averages 137 days. Snow begins accumulating in early November, with snow depth peaking around late February or early March and then rapid declining until early April. Winters with little precipitation, however, have an average snow cover depth of 1.2 cm during the dormancy period.

Since 1982 grazing and agricultural activities have been excluded to protect and restore these grasslands, which had previously been degraded by over-grazing and possibly by climate change. After 10 years of natural restoration, species productivity and diversity had increased significantly (Fig. A.3). The vegetation consists of 313 species, which are dominated by *Stipa bungeana*, *Stipa grandis*, *Thymus mongolicus*, *Artemisia sacrorum* and *Potentilla acaulis* (Cheng et al., 2014).

2.2. Data collection

Peak aboveground biomass, including live biomass as well as standing dead biomass produced in the current year, has been widely used to estimate ANPP for grasslands (Scurlock et al., 2002). A field harvest was conducted in mid or late August each year from 1982 to 2011, when the standing biomass reached its maximum. For each harvest in each year, 15 quadrats (1 m × 1 m) were selected (avoiding sample plots from previous years) along a transect (300 m × 100 m), which was located on relatively flat terrain and represented the entire ecosystem in this nature reserve. Aboveground biomass was clipped and dried at 65 °C to constant weight. Between 1982 and 1992, the degraded grassland recovered rapidly and biomass production increased almost linearly (Fig. A.3). This phenomenon was mainly caused by the exclusion of human disturbance, particularly over-grazing. After 1992, grasslands assumed a relatively balanced state with lower variation in productivity and diversity (Cheng et al., 2014; Fig. A.3). Further variation in productivity was likely caused primarily by climatic variation. We therefore used the peak aboveground biomass during 1992–2011 to evaluate the impacts of climate variability on grassland productivity.

Mean daily temperature and precipitation during 1992–2011 were obtained from a weather station established in 1982, located only 0.9 km from the surveyed transect. Daily temperature and precipitation data were then subjected to a 15-day running mean (Guo et al., 2015; Luedeling and Gassner, 2012; Luedeling et al., 2013) to ensure emergence of recognizable response patterns between climate variables and grassland productivity in subsequent statistical analyses. Apart from precipitation, snow cover is also a vital water resource and has some interplay with temperatures in winter; unfortunately, no daily information was recorded in the weather station. Thus, impacts of snow cover on grassland productivity were not analyzed in detail in this study and we only focused on effects of daily temperature and precipitation during the past 20 years.

2.3. Statistical analysis

Partial Least Squares (PLS) regression was used to analyze the responses of grassland productivity to variation in daily temperature and precipitation during all 365 days of the year based on data for 1992–2011. Unlike many other regression approaches, PLS analysis works effectively in situations where the number of independent variables substantially exceeds the number of observations and the independent variables are highly auto-correlated. Such situations are encountered in relating productivity data to climate records at daily resolution and recent work has shown that PLS regression can effectively be used in this context (Guo et al., 2015; Luedeling and Gassner, 2012; Yu et al., 2010).

The two major outputs of PLS analysis are the variable importance in the projection (VIP) and standardized model coefficients. The VIP values reflect the importance of all independent variables for explaining variation in dependent variables. The VIP scores are based on a weighted sum of squares of the PLS loadings and calculated for each variable. The VIP threshold for considering variables as important is often set to 0.8 (Wold, 1995). The standardized model coefficients indicate the strength and direction of the impacts of each variable in the PLS model. Centering and scaling of dependent and independent variables is necessary to allow comparison between different variables.

In the present study, dependent variables were productivity between 1992 and 2011, while independent variables were daily temperature and precipitation for 365 days preceding the peak biomass harvest (i.e. running from the 1 st of the previous September to the end of August of each year since the average harvest date of peak aboveground biomass at our study region was mid-August; in leap years, the last day of this interval was excluded). The root mean squared errors (RMSE) of the regression analyses were calculated to determine 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 productivity. Positive model coefficients indicate that increasing temperature or precipitation during the respective period should increase ANPP, while negative model coefficients imply negative impacts on productivity.

Based on the PLS analysis results, the relevant phases influencing grassland productivity were identified. Of particular interest was that climate variation during April-May and June-July had distinctly opposite impacts on ANPP. To clarify which period was more important, we constructed three-dimensional productivity response surfaces. These surfaces were drawn using the Kriging interpolation technique to describe productivity as a function of temperature or precipitation during both periods. Default settings of the Kriging procedure in the R package ‘fields’ (Furrer et al., 2013) were used in the interpolation. We further explored relationships between ANPP and mean temperature and precipitation during each relevant period by using linear regression. Results were assessed for significance using analysis of variance (i.e. ANOVA). All temporal trends in temperature and precipitation in the present study were also analyzed using linear regression, with trends tested for statistical significance using the Mann-Kendall test (Tao et al., 2006), which is appropriate for time series data.

All analyses were implemented in the R 3.2.0 programming language (R Core Team, 2015). PLS analysis was mainly based on the ‘pls’ package (Mevik et al., 2011) and used within procedures implemented in the ‘chillR’ package (Luedeling, 2015). Codes for reproducing the PLS analyses in the present study, the grassland productivity dataset, as well as mean climate conditions during each relevant period are provided as Supplementary materials to this paper.

3. Results

3.1. Temperature and precipitation trends

Between 1992 and 2011, mean annual temperature (MAT) increased significantly ($P < 0.01$), while annual precipitation (AP) appeared to be variable, but did not show a statistically significant trend (Fig. A.4). Mean temperature increased for all months except September (Fig. A.5a). Compared to high increases of temperature in winter and early spring, warming during the summer months was weak. Mean precipitation decreased for the summer, but these decreases were only statistically significant for July (Fig. A.5b). In contrast, rainfall in September showed a strong and significant increasing trend over the past 20 years.

3.2. Response of grassland productivity to variation in daily temperature and precipitation

Weak correlations between ANPP and AP (Fig. A.6a) and MAT (Fig. A.6b) in our study region during 1992–2011 indicated that much temporal variation in ANPP could not be explained by annual climate variables. Thus, we turned to examine the impacts of variation in daily temperature and precipitation on grassland productivity in the present study.

Between 1992 and 2011, the average harvest date of peak aboveground biomass for grassland at Yunwushan National Nature Reserve was the 15th of August. The 365 daily temperature values between the previous September and August of the year of harvest were used as independent variables in the PLS regression. A low root mean squared error (RMSE) of 8.13 g m^{-2} for the resulting PLS model indicated that the model was a good fit for the data. Based on the VIP and standardized model coefficients of the PLS analysis, we found that warming during different periods had varied impacts on grassland productivity (Fig. 1a).

Between 30 March and 30 May, model coefficients for temperature analysis (Fig. 1a) were always positive and VIP values mostly exceeded 0.8 (the threshold for variable importance), indicating that warming in April and May increased grassland productivity. During 31 May–1 August, model coefficients were consistently negative and VIP values were mostly important, implying that temperature increases in summer (June–July) depressed productivity, forming a striking contrast with the impacts of spring warming. It was of interest that the relevant periods influencing productivity, as identified by PLS regression, were almost the same as the phases of plant growth (i.e. the early and middle stages of the growing season) at our study area and the impacts of temperature variability during both periods were identical with expectations illustrated in Fig. A.1. No obvious impacts of temperature variation in August on grassland productivity were apparent. Compared with the consistent and important impacts of weather conditions during April–May and June–July, weaker effects of temperature variability during other periods were detected (Fig. 1a). During September–October (the senescence period for vegetation), most model coefficients were negative, indicating that high temperature at that time was unfavorable for productivity of the following year. During 1 November–29 March, the dormancy period, model coefficients were mostly negative, although this phase also included some short intervals with positive coefficients. This variation might indicate that dormancy for grassland is a complex physiological and ecological process. Moreover, it seems possible that the strength of temperature impacts varies throughout the dormancy period. Taking a broader view at model coefficients and aiming at con-

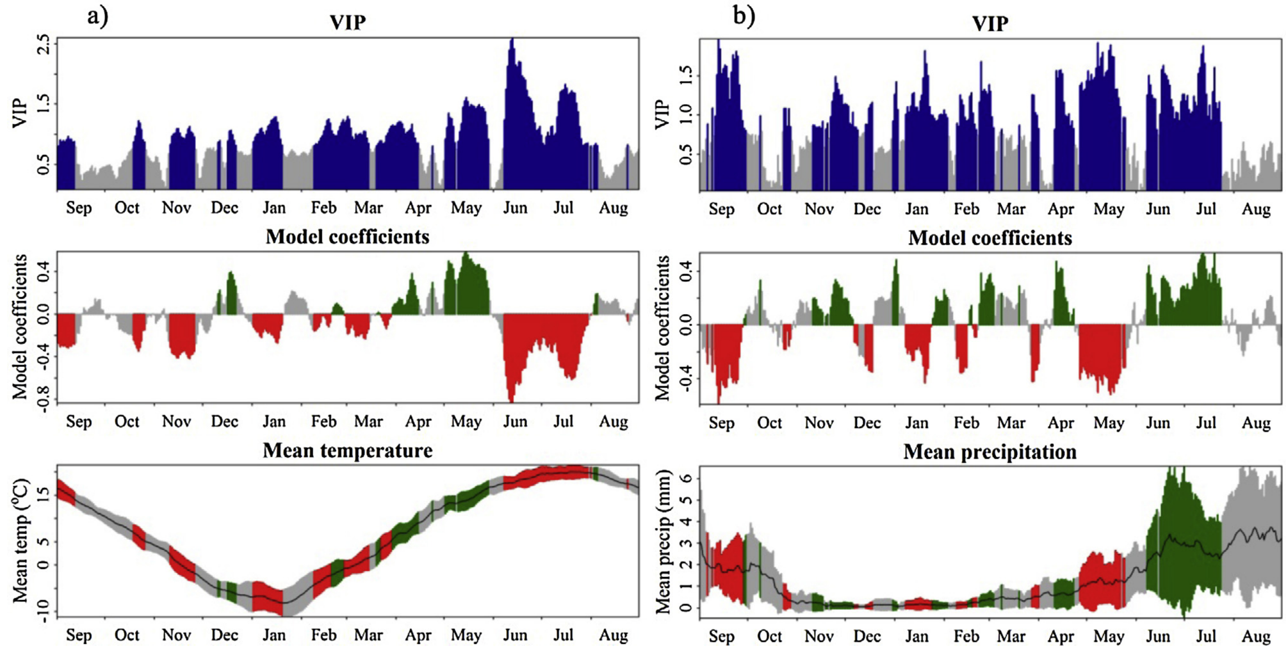

Fig. 1. Results of Partial Least Squares (PLS) regression correlating grassland productivity at Yunwushan during 1992–2011 with 15-day running means of (a) daily mean temperature and (b) daily precipitation from previous September to August. Blue bars in the top row indicate that VIP values are greater than 0.8, the threshold for variable importance. In the middle row, red color means model coefficients are negative and important, while green color indicates important positive relationships between grassland productivity and climate variables. The black lines in the bottom panel stand for daily mean temperature and precipitation, while grey, green and red areas represent the standard deviation of daily climate variables. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sistency with established phenological phases, we interpreted the entire period (November–March) as another relevant period during which temperature increases appeared to reduce grassland productivity.

The 365 daily precipitation values between the previous September and August were also used as independent variables in the PLS analysis. The resulting model still proved to be a good fit for the data, with an RMSE of 6.53 g m^{-2}. Unlike the clear-cut response pattern of ANPP to variability in temperature, more complex impacts of precipitation on grassland productivity were identified (Fig. 1b). In contrast to the positive effects of higher precipitation in June and July, increasing rainfall during the senescence period (September–October) and the early growing season (April–May) was correlated with low productivity. However, during the latter period consistently negative impacts of precipitation occurred after 24 April until the end of May. Similar to temperature effects in August, no significant relationship was found between grassland ANPP and precipitation in August. During the dormancy period, there was no consistent correlation between precipitation and productivity. Positive impacts were almost offset by negative ones. It should be noted, however, that very little precipitation falls between November and March. Thus, precipitation during the dormancy phase seemed to be of little importance for determining grassland productivity.

3.3. Critical climate periods for grassland productivity on the Loess Plateau

Impacts of climate variability on grassland productivity varied according to the plant growth phases that these changes coincided with, as was clearly delineated in Fig. 1. It seemed that variations in temperature and precipitation during the early and middle stages of the growing season had more important impacts on productivity, as indicated by greater model coefficients (Fig. 1). Additionally, warm spring (April–May) with little precipitation appeared to increase ANPP, while dry summer (June–July) with high temperature seemed to have a negative effect.

Solely based on the PLS results shown in Fig. 1, it was unclear whether temperature increases in spring could compensate for productivity decline induced by hotter summer and whether precipitation in summer had greater impacts on ANPP than precipitation in spring. Thus, we plotted grassland productivity as a function of climate variables during both spring and summer (Fig. 2). The contour lines drawn in Fig. 2a clearly indicated that variation in productivity was mainly correlated with temperature variation during June–July. With temperature increases in summer, productivity decreased. The growth-enhancing effect of warm spring was also visible in Fig. 2a, but it was less pronounced than the negative impacts of warm summer. As for impacts of precipitation during both periods, the almost horizontal contour lines in Fig. 2b implied that variability of summer rainfall has dominated impacts on productivity compared with variation in spring precipitation.

Relationships between productivity and mean temperature and precipitation during each period were further explored using linear regression (Fig. 3). Climatic variation during June-July explained the variability of grassland productivity well (52% for temperature and 30% for precipitation). Increasing temperature and decreasing precipitation during June–July reduced productivity significantly in the study area. Temperature increases during the senescence period (previous November–March) further lowered grassland productivity, explaining 16% of the variation in ANPP. No significant impacts of climate variation on productivity were found for other periods of plant growth.

4. Discussion

4.1. Seasonal, not annual precipitation and temperature drive community productivity

While numerous studies considering impacts of climate variability on grass productivity have focused on yearly or growing

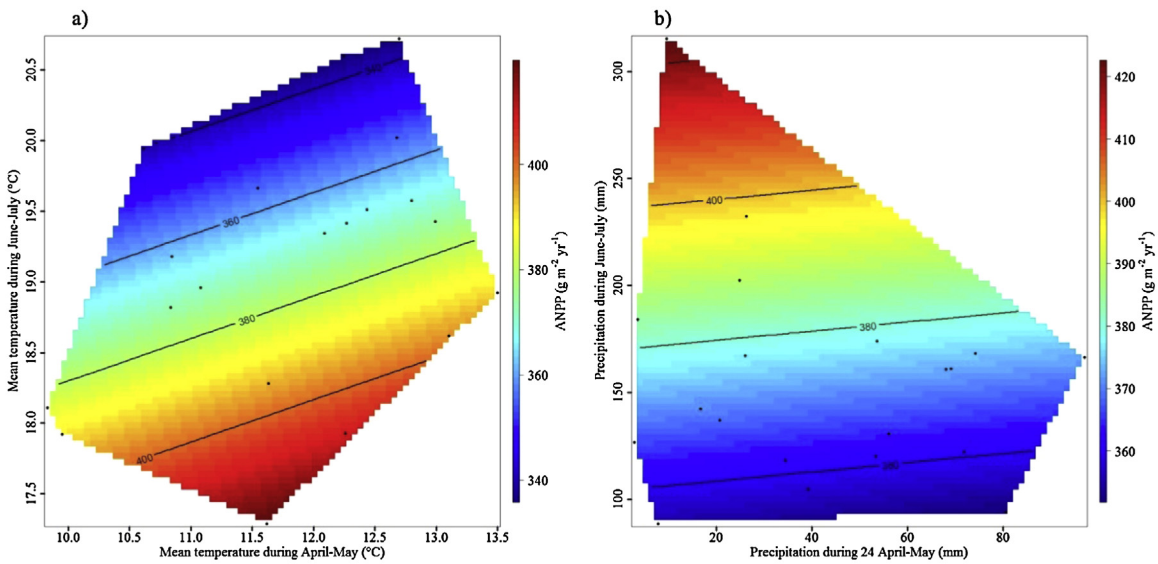

Fig. 2. Grassland productivity at Yunwushan as a function of (a) temperature and (b) precipitation during both spring (April–May for temperature analysis and 24 April–May for precipitation analysis since consistently negative impacts of precipitation occurred after 24 April until the end of May in Fig. 1; x-axis) and summer (June–July, y-axis). Variation in color reflects variation in ANPP, while the black dots indicate the annual productivity records between 1992 and 2011.

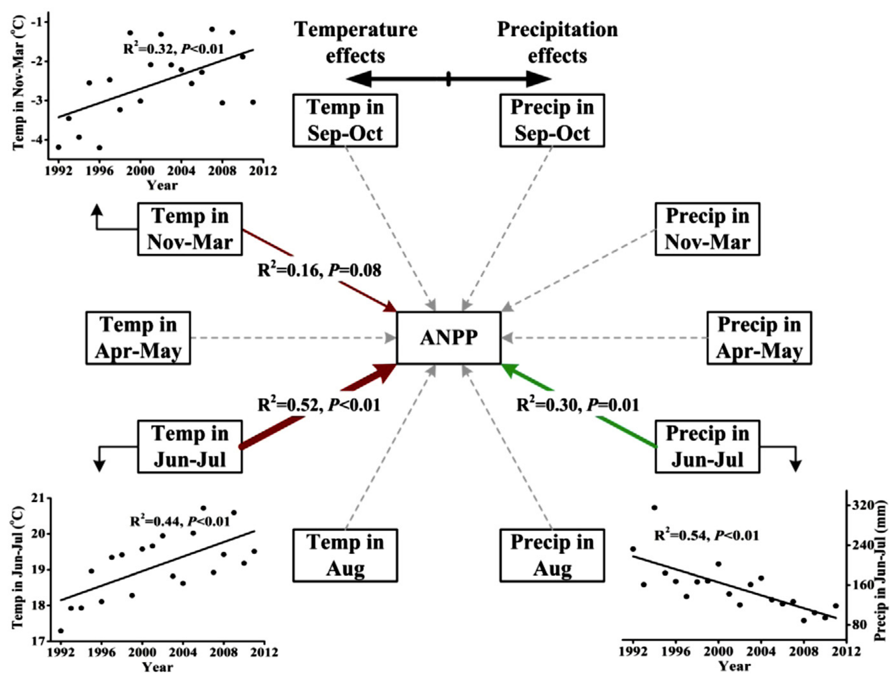

Fig. 3. Relationships between grassland productivity and mean temperature and precipitation for different periods during 1992–2011 at Yunwushan. Trends of temperature during November–March and June–July, as well as precipitation during June–July are shown in the inset plots. Red arrows indicate significant negative correlations between grassland productivity and climate variables, while green arrows mean significant positive relationships. The dashed lines imply that no significant correlations were detected between ANPP and climate variation during these periods. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

season precipitation and mean annual temperature (Bai et al., 2004; Gherardi and Sala, 2015; Hu et al., 2007; Knapp and Smith, 2001; Lauenroth and Sala, 1992; Rosenzweig, 1968), our results clearly indicate that variability in temperature and precipitation during different periods had different impacts on grassland productivity and that annual trends may be too coarse of a time scale to study the impacts of climate variability on ANPP. We found that temperature increases during the early stage of the growing season (April–May) appeared to promote grassland ANPP, but warming during other periods strongly reduced it, especially in summer. In arid and semi-arid regions, precipitation is normally regarded as the most important determinant of grassland productivity (Lauenroth and Sala, 1992; Oesterheld et al., 2001; Sala et al., 2012). In the present study, more heterogeneous impacts of precipitation on productivity were delineated by the PLS regression. Our results thus added more weight to studies attributing impacts of climate variation on grassland productivity to seasonal or even daily variation in climatic variables, rather than to annual variation (Chou et al., 2008; Hovenden et al., 2014; La Pierre et al., 2011; Milchunas et al., 1994; Robinson et al., 2013).

Simple correlation analysis between grassland productivity and climatic factors during certain months or seasons has commonly been used to clarify impacts of seasonal climate variability (Chen and Weber, 2014; Ma et al., 2010). Recently, a forward stepwise regression has successfully explained the response of ANPP to climate variability at daily scale based on long-term ecological research (LTER) on temperate grassland in Kansas, United States (Craine et al., 2012). This study greatly advanced knowledge on productivity responses to climate variation at higher temporal resolution. However, impacts of temperature and precipitation variability were only considered for the growing season, with no attention paid to other seasons, especially the dormancy period. To fill this gap, we used PLS regression analysis to relate grassland productivity to variation in mean daily temperature and precipitation during all 365 days of the year. Results indicated that relevant periods identified by the PLS analysis happened to match different phases of vegetation growth cycles in the study region. PLS regression therefore proved an effective approach to analyze impacts of daily climate variation on grass productivity across the whole year. Our results also gave support to studies arguing that climate variables should be divided into seasonal components pertinent to the life history or phenology of the vegetation (La Pierre et al., 2011; Robinson et al., 2013). All these findings will further improve our ability to explain the variation in ANPP that has been left unexplained by previous studies.

4.2. *Productivity response to climate variability during the growing season*

Our analysis indicated that increased temperature with reduced precipitation in spring (April–May) could improve grassland productivity. Biomass produced in spring is often believed to be limited by cold temperatures at mid or high latitude (Chen and Weber, 2014; Chollet et al., 2014). Temperature increases early in the growing season may stimulate plant growth directly by raising leaf temperatures or indirectly by increasing water absorption and N mineralization (Craine et al., 2012; Sierra, 1997; Fig. 4a). Additionally, warmer springs also likely accelerate snowmelt and advance spring greening (Cleland et al., 2006; Menzel et al., 2001; Piao et al., 2006; Yu et al., 2010, 2012), which might lengthen the growing season and result in increased photosynthesis and carbon acquisition (Bradford et al., 2006; Nemani et al., 2003). In contrast to some studies reporting that more precipitation during April–May promoted grassland productivity (Ma et al., 2010; Robinson et al., 2013), we found a negative relationship between these variables. To some extent, this discrepancy can be explained by the site hydrology. Frequent winter snow (lasting from November to March) in our study area provides sufficient soil water for plant growth in early spring. The sporadic precipitation during April–May (with an average of 59.5 mm during these two months between 1992 and 2011) may not have important direct impacts on productivity. In contrast, low air and soil temperature, as well as limited solar radiation caused by frequent rain events in May might partially explain the negative correlations between spring rainfall and grassland productivity. Increases in spring biomass therefore appear to be mainly triggered by rising spring temperatures (Chen and Weber, 2014; Fay et al., 2011; Jobbágy and Sala, 2000; Ma et al., 2010), while impacts of variation in precipitation are less important. Future warming in spring may further stimulate grassland productivity.

Hotter and drier summers (June–July) appeared to cancel out the productivity increment induced by warmer springs and dominated the temporal variation in ANPP. Warming in summer coinciding with drought can generate physiological stress for plant growth (De Boeck et al., 2016; Fig. 4b), which can explain the reduced productivity in our study area. Moreover, increases in summer temperature can also lower ANPP, perhaps by reducing soil moisture through increased evapotranspiration (Epstein et al., 1996). Decrease in precipitation amounts and lengthening of intervals between precipitation events (Fig. A.7) during the past 20 years further reduced soil water availability in our study region. This is in line with the hypothesis that impacts of climate variation and change on plant productivity might occur via variability in soil moisture (Hsu and Adler, 2014; Knapp et al., 2006, 2002; Koerner and Collins, 2014). While not as commonly available as long-term time series, soil moisture data may relate more directly to plant growth than rainfall and temperature. They also allow a reasonable mechanistic explanation of how warming, drought and precipitation pattern affect grass productivity (Nippert et al., 2006). Continuous warming and drought in summer could also affect N mineralization negatively (Dessureault-Rompré et al., 2010) and limit soil resource availability (de Valpine and Harte, 2001), thereby reducing productivity. All these potential developments may threaten the already vulnerable grassland ecosystems on the Loess Plateau in China.

PLS regression did not detect a response of grassland productivity to climatic variation in August. Similar results have also been reported for grasslands in Kansas, USA (Craine et al., 2012). The

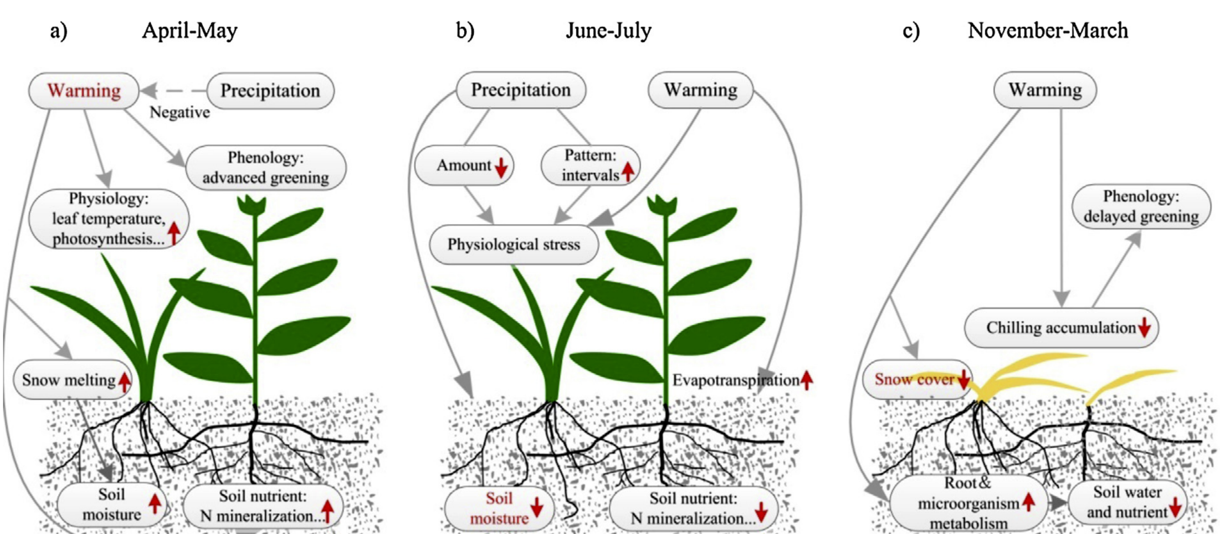

Fig. 4. Potential relationships between grassland productivity and climate variability during (a) April–May, (b) June–July and (c) November–March at Yunwushan.

authors saw a likely reason for the lack of responsiveness to late summer conditions in the greater chance of reproductive success it conveyed to species that showed this behavior. This may initially have been a decisive evolutionary advantage, which eventually led to most, if not all, species displaying this trait. Compared to climate variation during June-July, August shows more variable temperature and precipitation in our study region, although August is cooler on average than July. For instance, the coefficient of variation (CV) of precipitation in August between 1992 and 2011 was 53.3%, while it was only 33.5% for June-July. It is also worth noting, however, that in our study biomass was mostly harvested around the 15th of August, so that the vegetation was only exposed to half a month of August conditions.

4.3. Productivity response to climate variability during the senescence and dormancy periods

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 winter climate on temperate ecosystems (Bokhorst et al., 2009; Cook et al., 2012; Fu et al., 2015; Ladwig et al., 2016; Yu et al., 2010). Even so relatively few reports are available on the response of grassland productivity to climate variation during the senescence and dormancy periods. Use of PLS regression helped fill this gap. Increases in temperature and precipitation during September-October in the previous year were negatively correlated with productivity in the current year, which can be partially explained by the widely reported delays of senescence caused by warming and wetting later in the year (Bradford et al., 2006; Qian et al., 2012; Reyes-Fox et al., 2014). Delay in the senescence period may be related to some extent to increased soil nutrient and water depletion. This would imply that fewer resources may have been available for biomass production in the following year.

While some studies reported that weather during the dormancy period had limited impacts on grassland productivity (La Pierre et al., 2011), such effects may become more important, as temperature in winter further increases. Our results indicated that high temperatures during the dormancy period were negatively correlated with productivity. This is consistent with warming experiments in two limestone grasslands in the UK, which showed that winter heating combined with drought reduced the biomass of both communities (Grime et al., 2000). Warmer winter can lead to some unanticipated consequences (Fig. 4c). The most direct impacts have been a shortening of the snow season and a reduction in snow cover, which have been observed in our study area (Fig. A.8). Declines in the area and depth of snow cover may expose the land surface to more frequent freezing events (Grimm et al., 2013), exerting negative effects on plant growth. This is supported by observations in northern Scandinavia where extensive areas of vegetation died due to loss of snow cover after extreme winter warming in December 2007 (Bokhorst et al., 2009). Increased demands of soil nutrients and water due to accelerated root and microorganism metabolism caused by winter warming might also contribute to the productivity reduction. Finally, variation in spring phenology can also help explain this phenomenon. The timing of spring phenology in most temperate plants results from the interplay of winter cold and spring heat (Yu et al., 2010). Plants that evolved in temperate climates fall dormant in autumn to protect themselves from winter freezes and will only resume growth in spring when they have been exposed sufficiently to cold conditions (Luedeling et al., 2013). This is known as the plants' chilling or vernalization requirement. Temperature increases in spring can advance spring phenology (e.g. greening for grassland), but warming in winter may delay the fulfillment of chilling requirements and thus lead to a slowdown in the advance of spring events or even later onset of spring phenology (Cook et al., 2012; Fu et al., 2015; Guo et al., 2013, 2015; Luedeling et al., 2013; Yu et al., 2010). The advancing trend in spring greening still dominates climate change responses of plants in our study region so far, since chilling requirements for vegetation are easily satisfied in all winters under the present cold climate with a mean temperature of $-2.6\,^{\circ}C$ for the dormancy period. As global warming progresses, especially when rates and effects of warming in winter exceed those in spring, advances in greening might be slowed or even turn into delays (Yu et al., 2010). This may occur in our study area in the future, since most climate scenarios of the CMIP5 (Coupled Model Intercomparison Project) ensemble, spanning the four major Representative Concentration Pathways (RCP) agree that winter warming will increase more strongly than spring warming by 2040–2060 (Table A.1). We therefore recommend increased scientific attention to impacts of winter warming on grassland productivity and the timing of spring phenology events.

5. Conclusions

PLS regression between ANPP and daily climate variables during the past 20 years successfully delineated how timing of temperature and precipitation variability affected grassland productivity on the Loess Plateau in China. Results indicated that analysis of productivity responses should account not only for the magnitude of climate variation but also for its timing. At present, heat waves coinciding with drought in summer dominate the temporal variation in productivity and explain 82% of the reduced ANPP. Warmer winter further decreases ANPP, perhaps due to shrinking snow cover and exposure of vegetation to frequent warm and cold temperatures. Impacts of warming in early spring – although less important currently – should also be considered in evaluating ANPP variability, because a productivity-enhancing effect is only observed for warming during this period. Finally, we call for more scientific attention to trends in spring phenology (i.e. advanced or delayed onset) and their impacts on productivity, since the implications of simultaneous warming in both winter and spring remain uncertain.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agrformet.2016.11.006.

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