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Climate change alters interannual variation of grassland aboveground productivity: evidence from a 22-year measurement series in the Inner Mongolian grassland

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Abstract Climate change is known to influence interannual variation in grassland aboveground net primary productivity (ANPP), or seasonal biomass, but direct, long-term ground observations are rare. We present a 22-year (1982–2003) measurement series from the Inner Mongolia grassland, China, to examine the effect of climate change on interannual variations in ANPP and monthly aboveground biomass (MAB). ANPP exhibited no increase over 1982–2003 but there was an association with previous-year precipitation. MAB in May increased by 21.8% from 47.8 g m^{-2} (averaged for 1982–1984) to 58.2 g m^{-2} (2001–2003), whereas there was no significant variation in June, July and August, and a decrease of 29.7% in September. The MAB increase in May was correlated with increases in precipitation and temperature in the preceding months. These findings suggest that the effects of climate change on grassland production vary throughout the growing season, with warmer and wetter springs resulting in increased biomass early in the growing season, and drier falls causing a decrease in biomass late in the growing season.

Keywords Aboveground net primary productivity · Interannual variation · Monthly aboveground biomass · Precipitation · Temperate grassland · Temperature

Introduction

In the past several decades, the Earth has experienced profound climate changes, such as increased temperature and changed patterns of precipitation (IPCC 2007; Hansen et al. 2006). These changes are significantly altering temporal variation of aboveground net primary productivity (ANPP) of terrestrial ecosystems (Fang et al. 2001; Huxman et al. 2004). Long-term ecological records provide an alternative approach to reveal the temporal dynamics of terrestrial ecosystems with which to predict the potential responses to climatic change. Considerable evidence of the change of ANPP induced by climate change has been identified by atmospheric CO_2 measurements (Keeling et al. 1996; Randerson et al. 1999; Ciais et al. 2000), remote sensing analysis (Myneni et al. 1997; Zhou et al. 2001; Hicke et al. 2002; Fang et al. 2003; Slayback et al. 2003; Piao et al. 2006; Fabricante et al. 2009) and manipulative experiments (Knapp et al. 2002; Shaw et al. 2002; Epstein et al. 2004). However, direct, long-term ground-based observations on the production of natural ecosystems are very limited (Jobbágy and Sala 2000; Bai et al. 2004).

The grassland ecosystem, one of the largest terrestrial biomes in the world, commonly exhibits higher interannual variation in ANPP compared to forest ecosystems, and has been considered very sensitive to climatic changes (Grime et al. 2000; Knapp et al. 2002), especially to changes in precipitation (Oesterheld et al. 2001; Nippert et al. 2006; Yang et al. 2008). Several long-term records have shown

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that the inter-annual variation in grassland productivity is correlated with the annual variation in precipitation (Lauenroth and Sala 1992; Xiao et al. 1995; Bai et al. 2004; Fabricante et al. 2009). However, Knapp and Smith (2001), analyzing data from 11 long term ecological research sites across North America, found that grassland ANPP was poorly explained by interannual variability in precipitation. These opposite responses of ANPP to precipitation variability may be related to inherent community attributes (i.e., dominant species or community composition) among grassland ecosystems (Piao et al. 2006; Nippert et al. 2006) or the complex responses to precipitation patterns within a growing season (Swemmer et al. 2007). For example, interannual ANPP in the short steppe of North America was observed to be affected by current- or previous-year precipitation (Lauenroth and Sala 1992; Oesterheld et al. 2001), while tallgrass prairies were demonstrated to be more sensitive to the seasonal variation in precipitation (Knapp and Smith 2001).

Another key issue in understanding of the temporal dynamics of productivity in grassland biomes and its responses to climate change is to investigate the interannual variation in vegetation production for individual seasons or months (Fabricante et al. 2009). However, most previous studies have focused on interannual variability of ANPP, rather than the interannual variability of seasonal production (Peñuelas et al. 2004; Fabricante et al. 2009). For grassland ecosystems, variation in production at the seasonal scale (month) may be more sensitive and complex than response to climatic change at the annual scale. For example, Piao et al. (2006) found that the influence of climate on the vegetation activity of temperate grasslands in China varied between growing seasons, and increased vegetation productivity was closely coupled with climate warming, with the maximum increase occurring in April and May. Therefore, the lack of long-term direct measurements, especially seasonal observations, may limit our understanding of how grassland ecosystems responds to climate change, particularly to climate warming and changing precipitation patterns.

In order to investigate temporal variations in annual and seasonal production of grassland ecosystems and their responses to climatic change, long-term biomass monitoring has been conducted each month since the early 1980s in the Inner Mongolia Grassland Ecosystem Research Station (IMGERS), which is dominated by *Leymus chinensis* grassland. In this study, using these biomass measurements combined with local meteorological data, we investigated long-term seasonal variations in monthly aboveground biomass (MAB) and ANPP over the period 1982–2003, and explored the possible effects of temperature and precipitation on grassland productivity.

Materials and methods

Study site

Biomass measurements were conducted at IMGERS, which is located in typical temperate grassland in the Xilin River Basin, Inner Mongolia Autonomous Region, China (116.7°E, 43.6°N, 1187 m a.s.l.). The climate is continental with cold, dry winters and warm, rainy summers. Mean annual temperature (MAT) and annual precipitation (AP) during 1982–2003 averaged 0.6°C and 342 mm, respectively. Precipitation occurs mainly in summer from June to August (67% of total AP), less in spring from April to May (12%) and fall from September to October (15%).

IMGERS is covered by a typical native C3 steppe dominated by perennial grasses, such as *Leymus chinensis* (Frin.) Tzvel and *Stipa grandis* P. Smirn., which are representatives of the most widely distributed grassland communities in the middle Inner Mongolia steppe region. The study site, 25 ha (500 m × 500 m) in area, is flat with a slope less than 5°, and has been fenced to prevent grazing since 1979.

Data collection

Aboveground biomass was measured twice a month (mostly at 15-day intervals) over the growing season from May to September during the study period. For each harvest, 20 quadrats (1 × 1 m^2) were located along a transect 50 m long and 1 m wide. Green plants were clipped and oven-dried at 65°C to constant weight. In this study, aboveground biomass at the end of each month was used as MAB. Considering that plant growth peaked at different periods, we used annual peak biomass (usually in August or early September) as the measure of ANPP for each year. MAB data for 1995 and 1996 were missing, and thus only 20 years of the data were used for the analysis. In addition, MAB in September was available only for 15 years because the grass were brown by the end of August when frost damage occurred in five of the years monitored and no further measurements could be conducted.

The climate data used in this study included MAT, AP, and the preceding cumulative mean temperature and precipitation before the monthly biomass were investigated. These data were compiled from the records of the weather station of IMGERS during 1982–2003.

Statistical analysis

We calculated the annual rate of change in monthly mean temperature and precipitation (trend) using the slopes of linear regression equations for the relationships between temperature or precipitation and year.

We conducted correlation analysis and stepwise regression to examine interannual variability of monthly MAB and its relationship with climate variables in the preceding (1–12) and current months. All statistical analyses were performed using SPSS software (version 11.0, 2001; SPSS, Chicago, IL). In order to investigate interannual variations in monthly mean temperature and precipitation over the period, we used the linear regression slope of these two variables against years as an indicator of their trends over time.

Results

Climate change

Over the period 1982–2003, MAT showed a significant increase, increasing at a rate of 0.07°C year^{-1} ($r^2 = 0.26$, $P = 0.016$), while AP fluctuated between 260 and 507 mm with an average of 344 mm (Fig. 1). The trends of mean temperature were positive for most months (January–September, and December), indicating that the mean temperature increased for these months over the 22 years, with the largest increases in February (0.21°C year^{-1}, $r^2 = 0.18$, $P = 0.06$) and March (0.20°C year^{-1}, $r^2 = 0.24$, $P = 0.03$, Fig. 2a). The mean temperatures in October and November showed a decreasing trend (negative value), albeit statistically insignificant. In contrast, monthly precipitation did not exhibit any significantly increasing or decreasing trend (Fig. 2b).

Trends of ANPP and MAB

The average ANPP was 208 g m^{-2} with a fluctuation from 129.2 to 265.8 g m^{-2}. The lowest ANPP (129.2 g m^{-2}) occurred in 1983 after severe drought in 1982. The MAB was low in May (with an average of 45.6 g m^{-2}) when the growing season starts, reached a peak in August (195.7 g m^{-2}), and then decreased in September (182.1 g m^{-2}; Table 1).

ANPP did not show a significant trend during the period 1982–2003 ($P = 0.77$, Fig. 3). In contrast, the interannual variation of MAB within the growing season exhibited various trends in 1982–2003 (Fig. 4). Specifically, MAB in May increased from 47.8 g m^{-2} in the early 1980s (averaged for the period 1982–1984) to 58.2 g m^{-2} year^{-1} by the end of the experiment (averaged for 2001–2003), with an overall increase of 21.8% (an annual increasing rate of 1.2 g m^{-2}, $r^2 = 0.15$, $P = 0.09$). In contrast, no significant changes were detected in MAB in the middle of the growing season from June to August ($P = 0.60$–0.99). Furthermore, MAB in September declined ($r^2 = 0.21$, $P = 0.08$, $n = 15$), from 225.9 g m^{-2} year^{-1} in the early 1980s (averaged for 1982–1984) to 158.8 g m^{-2} year^{-1} by the end of the measurement period (averaged for 2001–2003), with an annual decreasing rate of 2.16 g m^{-2}, i.e., a total decrease of 29.7%.

Relationships between ANPP and MAB and climatic variables

Aboveground net primary productivity did not show significant correlations with MAT or AP ($P > 0.05$), or with any previous temperature variables (Fig. 5a), but was significantly correlated with precipitation of the previous September through current August ($r^2 = 0.19$, $P = 0.05$; Fig. 5g).

Within the growing season, MAB showed different responses to temperature and precipitation. The MAB in May was correlated positively with the mean temperature for the previous 3 (March–May; $r^2 = 0.23$, $P = 0.033$) and 4 (February–May; $r^2 = 0.23$, $P = 0.034$) months of the current year. The correlations between MAB in May and temperature were weaker when earlier months were

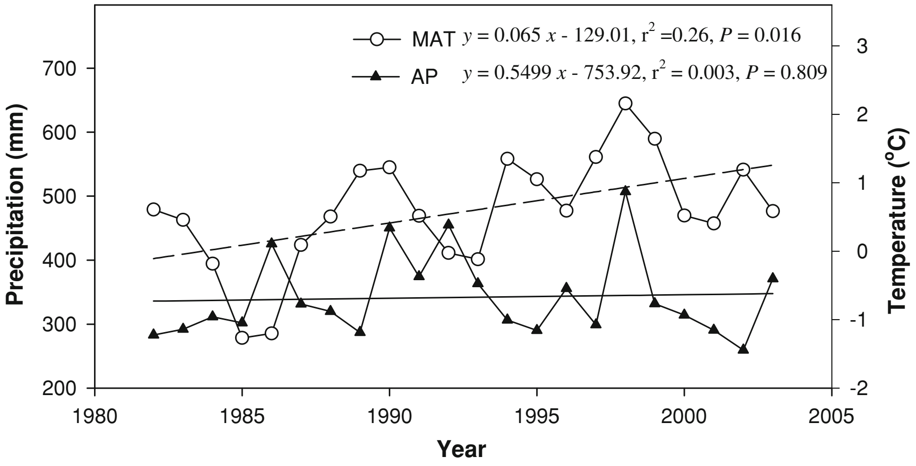

Fig. 1 Interannual variations in temperature and precipitation at Inner Mongolia Grassland Ecosystem Research Station (IMGERS) over 1982–2003. *MAT* Mean annual temperature, *AP* annual precipitation

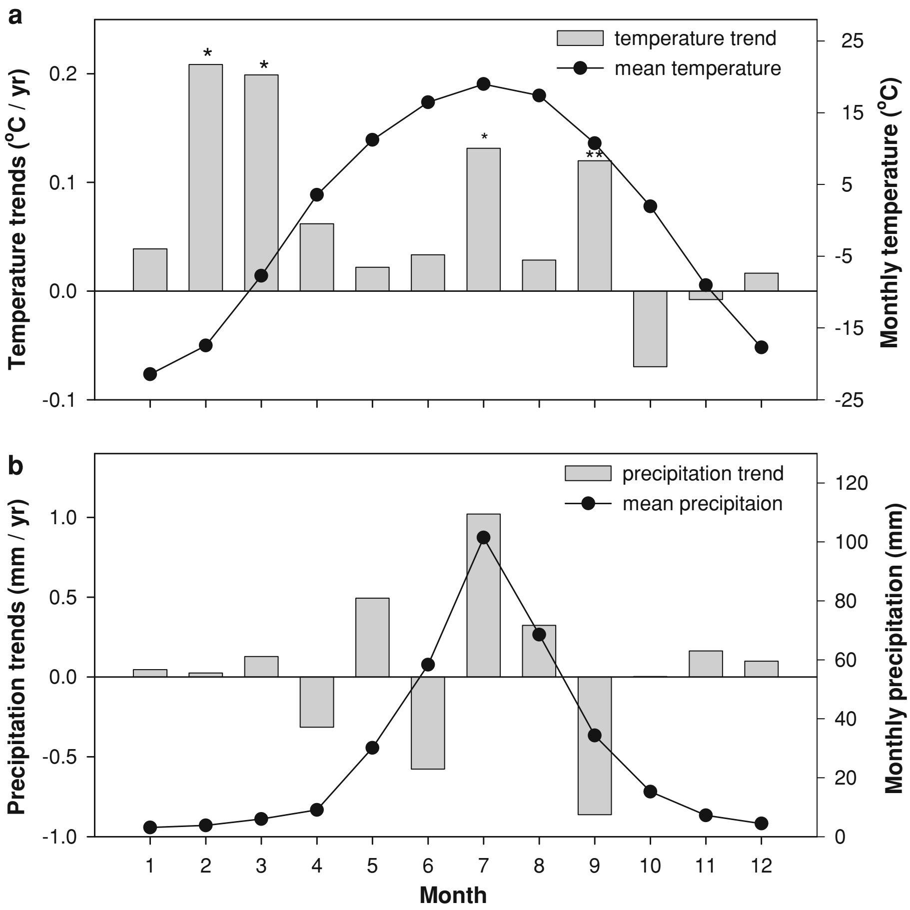

Fig. 2 Seasonal changes in temperature and precipitation in the Inner Mongolia grassland during the years 1982–2003. The annual changing rate was expressed as the slopes of linear regression equations for the relationships between temperature or precipitation and year. *Grey bars* Changing rates, *lines* average temperature or precipitation. Significant (*$P < 0.05$, **$P < 0.01$) slopes are shown above the columns. **a** Changes in monthly mean temperature and its trend (annual changing rate). **b** Changes in monthly precipitation and its trend

included (Fig. 5b). In contrast, MAB in June and August was negatively related to the temperatures for the preceding 2 ($r^2 = 0.26$, $P = 0.023$) and 4–5 ($r^2 = 0.26$, $P = 0.023$) months, respectively (Fig. 5c, e), while MAB in July and September did not show significant correlations with temperature (Fig. 5d, f).

When the relationships between MAB and precipitation were analyzed, MAB in May and June showed strong responses to precipitation input (Fig. 5h, i). For example, the maximum correlation coefficient for mean MAB in May against precipitation was observed in the previous 2 months (i.e., April–May) of the current year ($r^2 = 0.46$, $n = 20$, $P < 0.001$; Fig. 5h). MAB in June could be well explained by cumulative precipitation from the previous August to current June ($r^2 = 0.76$, $P < 0.001$). In contrast, the responses to precipitation of biomass during the late growing season (July–September) were less sensitive than in early months ($P > 0.05$; Fig. 5j, k, l).

Furthermore, the stepwise regression models showed different influences of precipitation and temperature on MAB (Table 2). For example, MAB in May was strongly coupled with total precipitation for April–May, February–March, and mean temperature for March–May. Precipitation accounted for 59.6% of the variation and the temperature explained an additional 9.7% of the variation in biomass (Table 2). In this regression model, temperature positively influenced plant growth. MAB in June could be best explained by cumulative precipitation from the previous August to current June ($r^2 = 0.76$, $P < 0.001$). The stepwise regression suggested that August biomass was related primarily to the previous May–August temperature ($r^2 = 0.26$, $P = 0.023$).

Discussion

Analysis of time series of ANPP and climate variables is an important approach to reveal the temporal patterns of natural ecosystem production and to predict the potential responses of terrestrial ecosystems to future climatic changes (Lauenroth and Sala 1992; Nippert et al. 2006). Most grassland areas in North China have experienced significant warming (Piao et al. 2006); however, the increasing temperature, as illustrated in this study, has had no significant effect on grassland ANPP. Therefore, although there are a considerable number of studies documenting global warming as the probable cause of the increase in terrestrial net primary production (Myneni et al.

Table 1 Aboveground net primary productivity (ANPP), monthly aboveground biomass (MAB) over the growing season from May (MAB-05) to September (MAB-09), and mean annual temperature (MAT) and annual precipitation (AP) data for a research site located in temperate grassland of Inner Mongolia, China for 1982–2003

Year	ANPP ($g\ m^{-2}\ year^{-1}$)	MAB-05 ($g\ m^{-2}$)	MAB-06 ($g\ m^{-2}$)	MAB-07 ($g\ m^{-2}$)	MAB-08 ($g\ m^{-2}$)	MAB-09 ($g\ m^{-2}$)	MAT (°C)	AP (mm)
1982	265.8	66.7	208.1	259.7	260.7	237.1	0.6	283.2
1983	129.2	30.9	74.6	120.9	129.2	NA	0.5	291.9
1984	214.7	45.7	138.6	186.4	208.6	214.7	−0.2	311.3
1985	196.6	41.9	109.9	186.1	196.6	181.6	−1.3	302.1
1986	198.6	33.2	75.8	142.6	185.4	154.2	−1.2	425.4
1987	221.4	47.6	123.7	203.0	214.7	221.4	0.1	331.4
1988	246.9	26.8	121.5	187.5	246.9	NA	0.5	319.8
1989	149.2	25.9	108.4	149.2	141.6	134.2	1.2	287.1
1990	202.7	32.2	76.2	148.2	194.0	175.7	1.2	450.3
1991	196.1	9.3	105.4	196.1	173.2	NA[a]	0.5	374.2
1992	230.6	43.9	156.2	175.2	230.6	200.6	0.0	455.0
1993	245.3	37.7	108.0	177.1	239.8	209.7	−0.1	363.3
1994	193.7	22.7	54.3	147.2	177.7	162.2	1.4	306.6
1997	194.2	83.2	153.7	172.1	180.5	165.8	1.4	298.9
1998	238.1	88.0	141.2	221.1	221.8	211.6	2.2	507.0
1999	228.6	70.6	152.0	221.2	200.9	NA	1.6	332.0
2000	173.7	30.7	100.4	161.3	129.0	145.1	0.5	314.1
2001	168.9	60.3	97.0	116.2	149.6	NA	0.4	290.6
2002	261.0	50.2	75.8	211.3	248.2	153.4	1.2	259.6
2003	204.7	64.0	136.0	202.2	184.5	164.2	0.6	371.0
Mean	208.0	45.6	115.8	179.2	195.7	182.1	0.6	343.7

[a] No data available

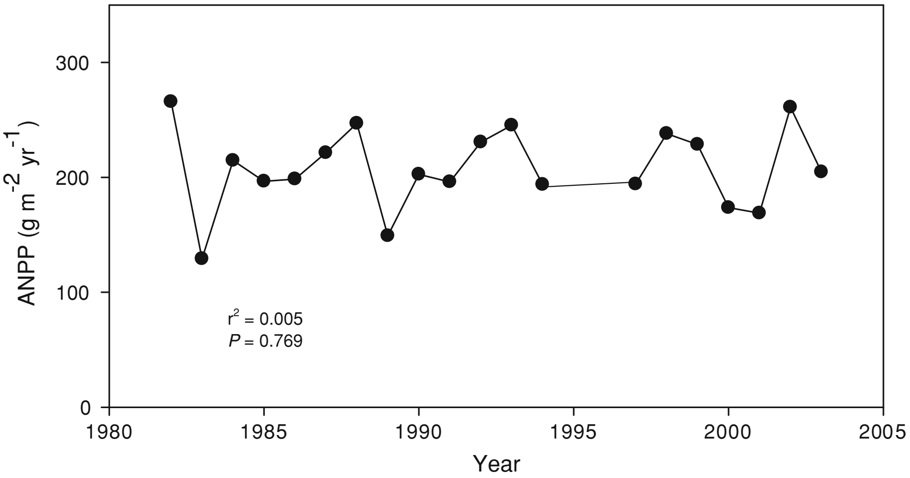

Fig. 3 Long-term record of aboveground net primary production (ANPP) in IMGERS

1997; Nemani et al. 2003), we should be cautious in extending such deductions to grassland ecosystems.

For most of the grasslands of the world, precipitation is the primary control on spatial or temporal patterns in ANPP. Several studies have confirmed precipitation to be the primary determinant of the interannual variation in ANPP (Lauenroth and Sala 1992; Oesterheld et al. 2001; Bai et al. 2004; Nippert et al. 2006). In this case, although ANPP did not show any significant correlation with current year precipitation or any preceding seasonal precipitation, previous AP was positively correlated with ANPP, which explained nearly 20% of the interannual variation in ANPP. Several studies compared spatial and temporal models relating ANPP and precipitation and revealed much lower regression coefficients in temporal models than in spatial models (Lauenroth and Sala 1992; Huxman et al. 2004).

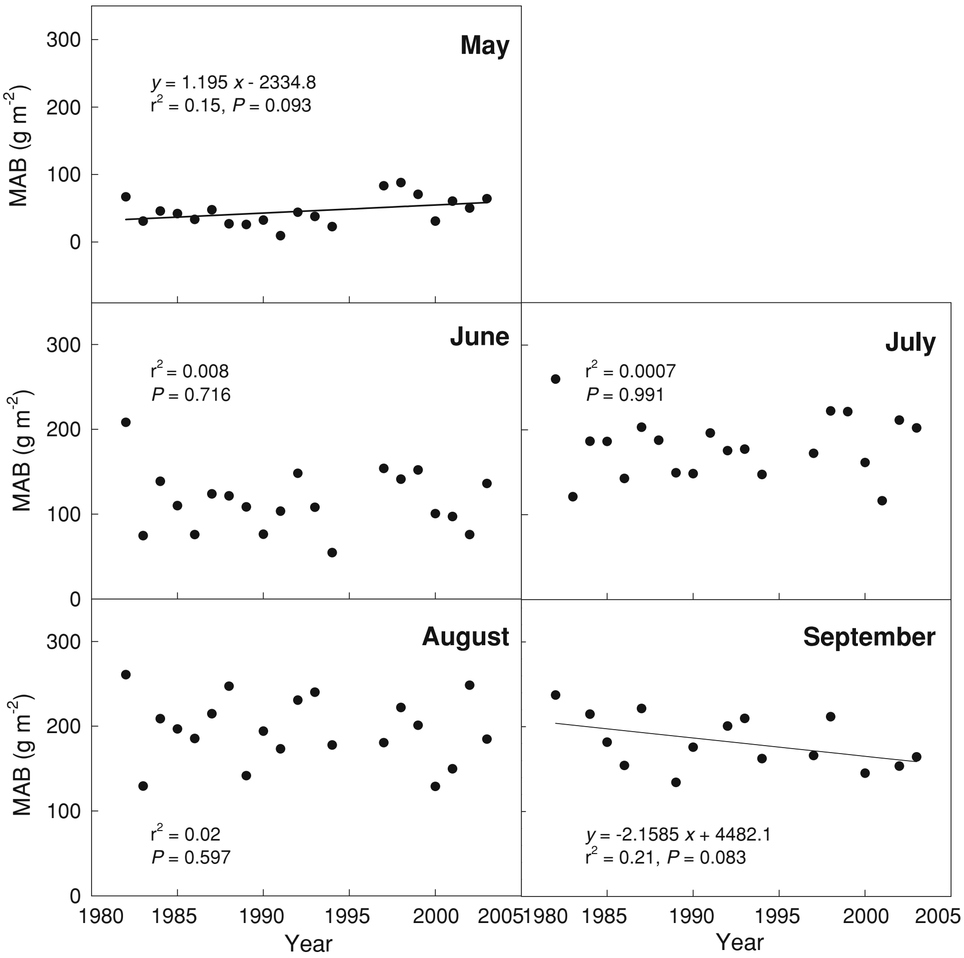

Fig. 4 Monthly aboveground biomass (MAB) within growing season (May–September) over 1982–2003

It has been reported that the effects of climate factors on grassland biomass varied among various seasons (Jobbágy and Sala 2000; Fabricante et al. 2009). For example, Jobbágy and Sala (2000) found that winter productivity in the Patagonian steppe was determined by fall temperature, and spring productivity was controlled by July–December precipitation. Our time series analysis of the seasonal aboveground biomass also indicated various patterns and different controls by climatic factors among growing seasons. Aboveground biomass in early growing season (May) showed an increasing trend over the past two decades. It is probably caused by advanced spring phenology, which has been supported by results from satellite remote sensing studies (Menzel et al. 2001; Lee et al. 2002; Piao et al. 2006). Therefore, warmer springs are probably a major driver for the increase in aboveground biomass in May. In North China, spring temperature is relative low and often limits plant growth (Alward et al. 1999). Increasing temperatures in early spring may stimulate plant growth directly by promoting plant metabolism or indirectly by enhancing water absorption and nutrient supply (Mckenna and Houle 2000). Insignificant changes in MAB were detected during the middle of the growing season (June–August) over the 22 years. This might be explained by fluctuating temperature and precipitation during this period. Additionally, water availability was sufficient for plant growth, thus the sensitivity of the whole community to climate change may be eliminated or dampened by complex species interactions (i.e., complementary effect; Cleland et al. 2006).

Conclusion

We examined interannual variations in ANPP and MAB and their relationships with climate in the Inner Mongolian temperate grassland over the period 1982–2003. Over the 22 years, ANPP did not exhibit any significant change, although the interannual variation of ANPP was positively correlated with previous-year precipitation. MAB in the early growing season (May) increased by 21.8%, while that in September has decreased significantly by 29.7%. Increased spring temperatures and preceding cumulative precipitation may have contributed to the increase in May

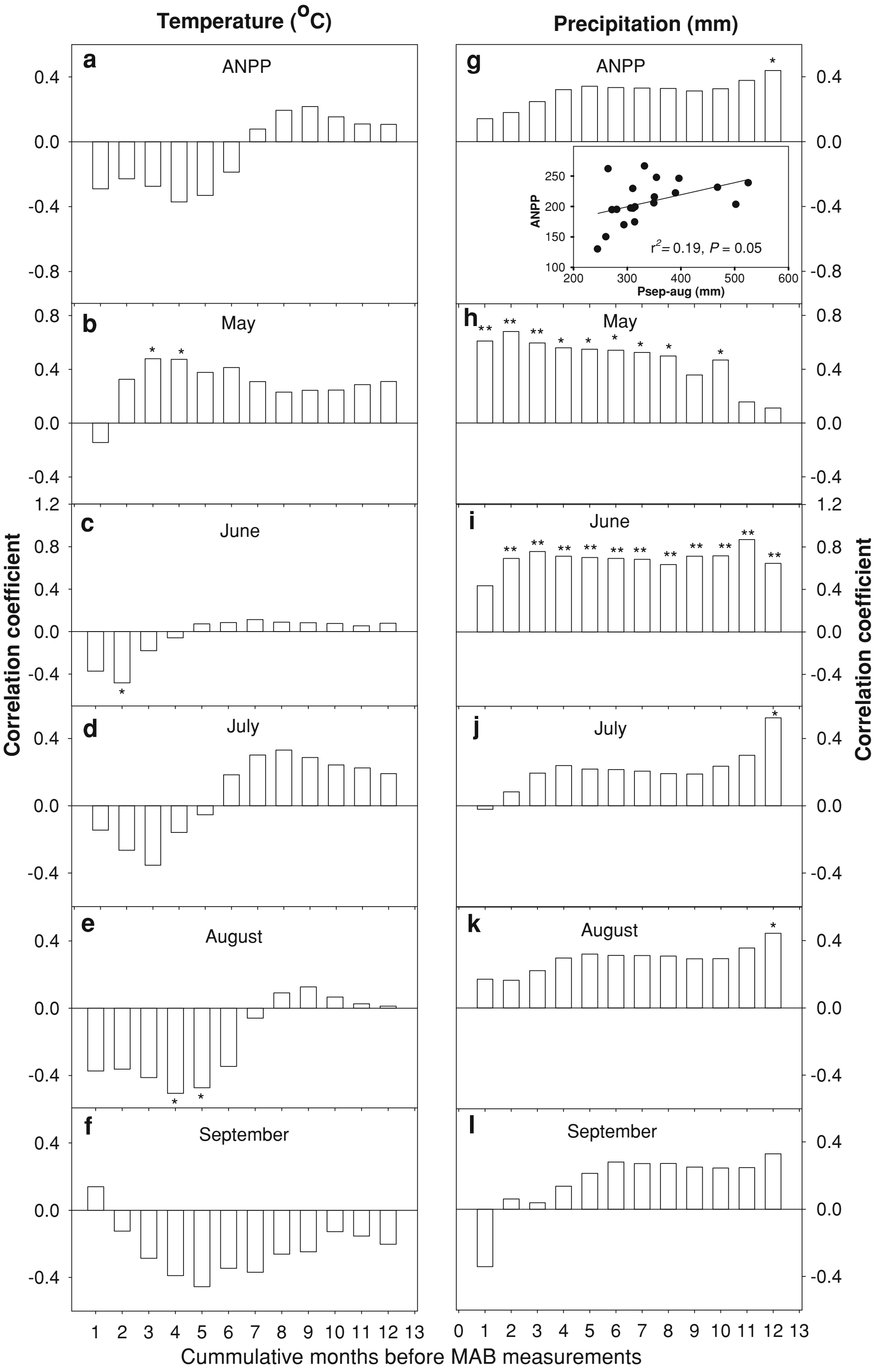

Fig. 5 Correlation coefficients between ANPP and MAB and temperature (**a–f**) and precipitation (**g–l**) in different periods. The period included 1–12 months preceding the data of each MAB measurement (May–September). *Inset* Relationship between ANPP and previous year precipitation since last September to current August (ANPP = 0.1986 × precipitation + 139.87; $r^2 = 0.19$, $P = 0.05$); *asterisks* significant effect of temperature or precipitation on MAB ($^*P < 0.05$; $^{**}P < 0.01$)

Table 2 Climate variables retained in the regression model, and their contributions in explaining MAB in May, June and August

Biomass (g m^{-2})	Stepwise regression			
	Limiting factors	r^2	P	Model
MAB-May	$P_{04\text{–}05}$	0.46	<0.001	MAB = 18.73 + 0.662$P_{04\text{–}05}$ − 1.388$P_{02\text{–}03}$ + 5.615$T_{03\text{–}05}$
	$P_{02\text{–}03}$	0.60	0.019	
	$T_{03\text{–}05}$	0.69	0.039	
MAB-June	$P_{08\text{–}06}$	0.76	<0.001	MAB = −22.38 + 0.568$P_{08\text{–}06}$
MAB-August	$T_{05\text{–}08}$	0.26	0.023	MAB = 564.365 − 22.948$T_{05\text{–}08}$

$P_{04\text{–}05}$ Cumulative precipitation from April to May in current year, $P_{02\text{–}03}$ cumulative precipitation from February to March, $T_{03\text{–}05}$ mean temperature from March to May, $P_{08\text{–}06}$ cumulative precipitation from last August to current June, $T_{05\text{–}08}$ mean temperature from May to August

For each variable, accumulated r^2 are reported

MAB, while increased temperature may cause decreased biomass in the late growing season. These results indicate that the responses of plant growth to climate change vary among the growing seasons for grassland biomes. The interannual variations in ANPP and seasonal biomass revealed by these long time series datasets are thus an important theme in predicting the feedbacks of grassland ecosystems to future climate change.

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