

# Spatial and temporal relationships between precipitation and ANPP of four types of grasslands in northern China

GUO Ran<sup>1</sup>, WANG Xiao-ke<sup>1\*</sup>, OUYANG Zhi-yun<sup>1</sup>, LI Ying-nian<sup>2</sup>

(1. Key Lab of Systems Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing 100085, China. E-mail: wangxk@rcees.ac.cn; 2. Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining 810001, China)

**Abstract:** Precipitation is considered to be the primary resource limiting terrestrial biological activity in water-limited regions. Its overriding effect on the production of grassland is complex. In this paper, field data of 48 sites (including temperate meadow steppe, temperate steppe, temperate desert steppe and alpine meadow) were gathered from 31 published papers and monographs to analyze the relationship between above-ground net primary productivity (ANPP) and precipitation by the method of regression analysis. The results indicated that there was a great difference between spatial pattern and temporal pattern by which precipitation influenced grassland ANPP. Mean annual precipitation (MAP) was the main factor determining spatial distribution of grassland ANPP ( $r^2 = 0.61$ ,  $P < 0.01$ ); while temporally, no significant relationship was found between the variance of ANPP and inter-annual precipitation for the four types of grassland. However, after dividing annual precipitation into monthly value and taking time lag effect into account, the study found significant relationships between ANPP and precipitation. For the temperate meadow steppe, the key variable determining inter-annual change of ANPP was last August—May precipitation ( $r^2 = 0.47$ ,  $P = 0.01$ ); for the temperate steppe, the key variable was July precipitation ( $r^2 = 0.36$ ,  $P = 0.02$ ); for the temperate desert steppe, the key variable was April—June precipitation ( $r^2 = 0.51$ ,  $P < 0.01$ ); for the alpine meadow, the key variable was last September—May precipitation ( $r^2 = 0.29$ ,  $P < 0.05$ ). In comparison with analogous research, the study demonstrated that the key factor determining inter-annual changes of grassland ANPP was the cumulative precipitation in certain periods of that year or the previous year.

**Keywords:** above-ground net primary productivity; mean annual precipitation; spatial sensitivity; inter-annual changes

## Introduction

The net primary productivity (NPP) is a key variable of terrestrial ecosystems and an important component of the global carbon cycle; its variability with environmental factors (especially hydrothermal factors) makes it possible to predict local vegetation productivity through building mathematic model with climate factors. It was suggested that precipitation is one of the key elements limiting above-ground net primary productivity (ANPP) of grasslands in arid and semiarid areas (Boutton et al., 1988; Deshmukh, 1984). Fang et al. (2001) found a significant correlation between inter-annual variability in NPP and precipitation across China, which is opposite to the trends observed by Knapp and Smith (2001). The positive relationship between ANPP and mean annual precipitation (MAP) has been documented for many areas around the world (Rosenzweig, 1968; Lauenroth, 1979; Rutherford, 1980; Le Houerou et al., 1988; Sala et al., 1988; McNaughton et al., 1993).

The variability of ANPP with precipitation was usually analyzed in spatial and temporal scale. Spatially, annual precipitation was positively correlated with grassland vegetation productivity (Frank and Inouye, 1994; Knapp and Smith, 2001; Bai et al., 2000). Temporally, however, the relationship between ANPP and precipitation is site specific. For example, the productivity declines with precipitation from east to west in North American pampas; and the productivity correlated significantly with annual

precipitation in the drier western short-grass steppe (Lauenroth and Sala, 1992), but not in the eastern tallgrass prairie (Knapp and Smith, 2001; Briggs and Knapp, 1995).

Much research on grassland productivity concluded that precipitation was the key determinant of the fluctuation of grassland production in China (Bai, 1999; Bai et al., 2001; Chen et al., 1998; Liu, 1993). But little comparison between spatial and temporal pattern by which precipitation influences ANPP has been analyzed, though much field data of site-specific research exists. Here we collected some ANPP and precipitation data from previous studies to analyze their spatial and temporal relations. Our objective was to compare the difference between spatial and temporal responses of ANPP to the variance of precipitation across the precipitation gradient.

## 1 Methods and materials

We gathered field data of 48 grassland sites in northern China from 31 published papers or monographs. Each site belonged to one of the grassland types grouped by the classification system of a specialized statistical book "Data on Grassland Resources of China" (DAHV et al., 1994), whose classification scheme is believed to have enough information to characterize Chinese grasslands and match the grassland areas and other characteristics in the national grassland survey (DAHV et al., 1994). The criteria of selecting the research sites were the

following: definite quantification of the ANPP averaged by at least three years (see "sampling time" in Appendix 1) with uniform method, maximum above-ground biomass, which was one of the acknowledged methods summarized by Scurlock et al. (2002); data of MAP; introduction of the main site background such as mean annual temperature, site position, vegetation, relatively light artificial disturbance, and so on.

The 48 selected sites contain four types of grassland (Table 1) which cover about half of the grassland area in northern China according to the survey (DAHV et al., 1994).

We fit straight lines to determine the relationship between ANPP and MAP. The slope of the linear model fit to the data was the spatial sensitivity (sensitivity here means change in ANPP divided by change in precipitation, e.g. Huxman et al., 2004). Then we separated each type and fit its temporal sensitivity.

To analyze the relationship between ANPP and inter-annual precipitation, we selected four sites from the 48 sites where relatively long-term ANPP and precipitation had been documented (see details in Appendix 2). Similarly, we fit straight-lines using ANPP and precipitation (both yearly and monthly value) for the four sites. For the temperate meadow steppe and alpine meadow where perennial grasses

usually dominate the region, we took time effect into account because the vegetation could survive cold winter and the precipitation of precious year could influence its growth. While for the temperate meadow and temperate desert steppe the precipitation during growth period was vital for its productivity. The slope of the line fit to the data was the temporal sensitivity. We also fit lines using the data of precipitation and rain-use efficiency (RUE; ANPP/precipitation) of the four sites, with a view of finding some underlying links between ANPP and precipitation.

## 2 Results and discussion

The ANPP of the four types of grassland varied greatly, ranging from 20.7 to 350.2 g/ (m<sup>2</sup>·a) (Table 1). The alpine meadow had the highest average ANPP (246.1—350.2 g/(m<sup>2</sup>·a)) and lowest coefficient of variance (CV; 17.1%). The temperate meadow steppe had median ANPP (117.6—279.6 g/(m<sup>2</sup>·a)), with the CV of 24.2%. The ANPP of the temperate steppe ranged from 42.2 to 215.7 g/ (m<sup>2</sup>·a), with the CV of 40.9%. The most variable and lowest ANPP occurred in the temperate desert steppe (20.7—127.5 g/ (m<sup>2</sup>·a)), with the CV of 63.1%.

### 2.1 Spatial analysis

For the 48 sites, the overall spatial sensitivity was 0.59, and the proportion of ANPP accounted for by MAP was very high ( $r^2=0.61$ ; Fig.1).

Table 1 Summary of characteristics and ANPP of 48 sites used in this analysis

Grassland type	Latitude and longitude, °	Mean annual temp.,	Precipitation min-max (mean ± SE), mm/a	ANPP min-max (mean ± SE), g/(m <sup>2</sup> ·a)	CV of ANPP, %	Number of sites
Temperate meadow steppe	43.54—49.82N, 116.84—124.18E	-2.9—5.5	294.9—470.0 (365.6 ± 50.9)	117.6—279.6 (198.3 ± 48.0)	24.2	20
Temperate steppe	42.30—44.74N, 115.79—117.63E	-1.3—7.1	273.0—472.0 (363.9 ± 55.6)	42.2—215.7 (130.9 ± 53.6)	40.9	12
Temperate desert steppe	37.80—42.15N, 107.50—110.97E	3.2—7.8	91.6—344 (240.8 ± 71.6)	20.7—127.5 (53.4 ± 33.7)	63.1	9
Alpine meadow	37.48—37.76N, 101.20—101.57E	-3.0—0.3	414.5—600.0 (522.8 ± 73.4)	246.1—350.2 (306.0 ± 39.3)	12.9	7

Notes: \* CV of ANPP means coefficient of variation of ANPP, it equals standard error of ANPP divided by mean value, CV = SE/Mean. It is an index of the stability of ANPP

By selecting each type from the 48 sites, we fit lines for the four types of grassland and got each type's sensitivity (Fig. 2).

For the temperate meadow steppe, the ANPP was not sensitive to MAP. This type of grassland is distributed in the transitional zones from grassland to forest where water availability is not limited and does not become the primary determinant for grassland production. We found significant negative correlation between RUE and MAP in this type ( $r^2=0.21$ ,  $P<0.05$ , Fig. 3). The trend indicates that the excessive water supply resulted in low RUE and low water supply incurred high RUE, or extra water supply was not used efficiently, which was consistent with previous research (Knapp and Smith, 2001; Huxman et al.,

2004), and that might be the main reason why we found no significant spatial relationship between ANPP and MAP in the temperate meadow steppe. In this region temperature might be vital for the grassland production when water supply is not limited.

The distribution area of the alpine meadow was more humid than that of the temperate meadow steppe. But unlike the latter, the alpine meadow had high spatial sensitivity (0.43), with the highest linear accountability of 64%. The difference was probably related to local climatic and vegetational characteristics. The dominant species in the alpine meadow were frost resisting and deep-rooted, geared to the cold and wet weather; May—September precipitation occupied about 80% of the annual

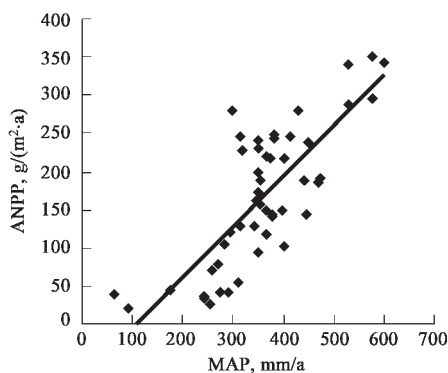


Fig.1 Relationship between above-ground net primary productivity (ANPP) and mean annual precipitation (MAP) for the field data; each dot corresponds to the average ANPP and MAP for a particular site; the line corresponds to the regression model fit to spatial data (spatial model);  $ANPP = 0.66MAP - 69.24$ ,  $r^2 = 0.61$ ,  $n = 48$ ,  $P < 0.01$

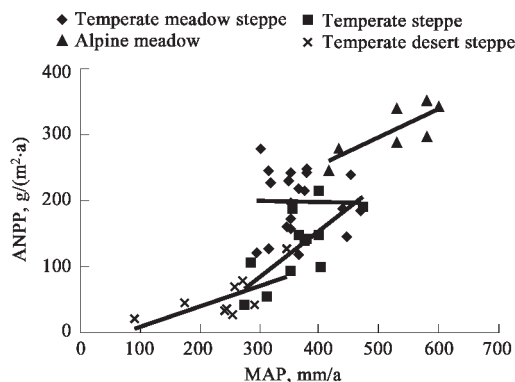


Fig.2 Relationships between ANPP and mean annual precipitation (MAP) for the four types of grassland (spatial model); the four lines were fit for: temperate meadow steppe:  $ANPP = -0.03MAP + 207.79$ ,  $r^2 = 0.00$ ,  $n = 20$ ,  $P = 0.91$ ; temperate steppe:  $ANPP = 0.69MAP - 121.65$ ,  $r^2 = 0.52$ ,  $n = 12$ ,  $P < 0.01$ ; alpine meadow:  $ANPP = 0.43MAP + 81.36$ ,  $r^2 = 0.64$ ,  $n = 7$ ,  $P = 0.03$ ; temperate desert steppe:  $ANPP = 0.32MAP - 22.91$ ,  $r^2 = 0.45$ ,  $n = 9$ ,  $P < 0.05$

precipitation with favorable heat conditions, which provide favorable conditions for the growth of local vegetation and improved RUE in the alpine meadow (Zhou, 2001). Long-term adaptation to the environment made local vegetation with high relatively growth rates (RGRs) require stable water supply for growth.

The sensitivity of the temperate steppe (0.69) was even higher than that of the alpine meadow, and the linear accountability was 52%. That type of grassland was distributed in semiarid region and its dominant species also had high RGRs. Such water-limited regions with relatively high production potential should be very sensitive to variation in water availability (Huxman et al., 2004).

For the temperate desert steppe, the spatial sensitivity was 0.32, with linear accountability of 45%. As a transitional type from grassland to desert, the temperate desert steppe was located in arid zones where water supply was extremely limited. July—

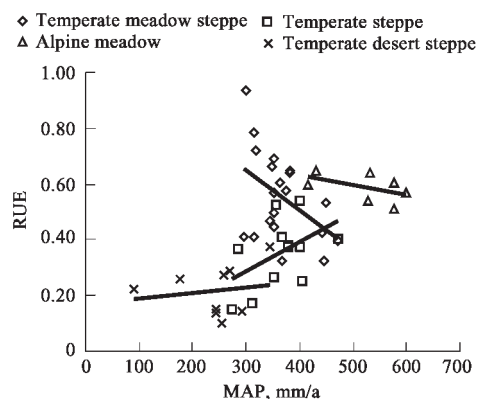


Fig.3 Relationships between RUE and mean annual precipitation (MAP) for the four types of grassland

The four lines were fit for: temperate meadow steppe:  $RUE = -0.0074MAP + 1.08$ ,  $r^2 = 0.21$ ,  $n = 20$ ,  $P < 0.05$ ; temperate steppe:  $RUE = 0.001MAP + 0.0286$ ,  $r^2 = 0.23$ ,  $n = 12$ ,  $P = 0.12$ ; alpine meadow:  $ANPP = -0.0003MAP + 0.7558$ ,  $r^2 = 0.23$ ,  $n = 7$ ,  $P = 0.28$ ; temperate desert steppe:  $ANPP = -0.0002MAP + 0.1641$ ,  $r^2 = 0.03$ ,  $n = 9$ ,  $P = 0.65$

September precipitation accounted for 60%—70% of the annual precipitation in the region (DAHV and GSAHV, 1996), which was favorable for the growth of vegetation; the windy weather and high solar radiation intensity in the temperate desert steppe resulted in high evaporation from land and vegetation, which was constraint of the growth of local vegetation. The vegetation with low RGRs and coverage could only respond mildly to MAP.

## 2.2 Temporal analysis

Inter-annual change of ANPP was not significantly related with annual precipitation for the four types of grassland. But after dividing annual precipitation into monthly value and taking time lag effect into account, we found significant relationships. The temporal relationships between ANPP and precipitation were (Fig.4): for the temperate meadow steppe, August—May (August—May of every sequential year, i.e. for the ANPP of 1984, the precipitation period was the data from August 1983 to May 1984) precipitation was the key determinant for inter-annual change of ANPP, with the temporal sensitivity of 0.75 and the linear accountability of 47%; for the temperate steppe, July precipitation was the key determinant, with the temporal sensitivity of 0.65 and the linear accountability of 36%; for the temperate desert steppe, April—June precipitation was the key determinant, with the temporal sensitivity of 0.32 and the linear accountability of 51%; for the alpine meadow, September—May (September—May of every sequential year, i.e. for the ANPP of 1980, the corresponding precipitation period was the data from September 1979 to May 1980) precipitation was the key determinant, with the temporal sensitivity of 0.36 and the linear accountability of 29%.

The results indicated that precipitation seasonality was vital to inter-annual change of grassland production. In the temperate meadow steppe

and the alpine meadow, precipitation showed its time lag effect on ANPP. While in drier regions, where the temperate steppe and the temperate desert steppe were distributed, ANPP was controlled by the precipitation of growth period.

The results were basically consistent with some other previous research. For the alpine meadow, Zhou (1995a,b) found that seasonal distribution of precipitation was the main factor causing inter-annual changes of the primary productivity. Bai et al. (2004) found January—July precipitation was the primary factor determining inter-annual changes of ANPP for

the temperate meadow steppe and temperate steppe. For the temperate desert steppe, Han (1999) found that the April—August precipitation was the key determinant of inter-annual variance of ANPP; yet Xin and Sai (1990) found that April—June precipitation was the key determinant. All the research on the relationship between ANPP and precipitation was based on previous field study data, so the results were both representative and site specific. But all the research show that the precipitation in certain period (usually growth period) was the main determinant for the inter-annual changes of grassland ANPP.

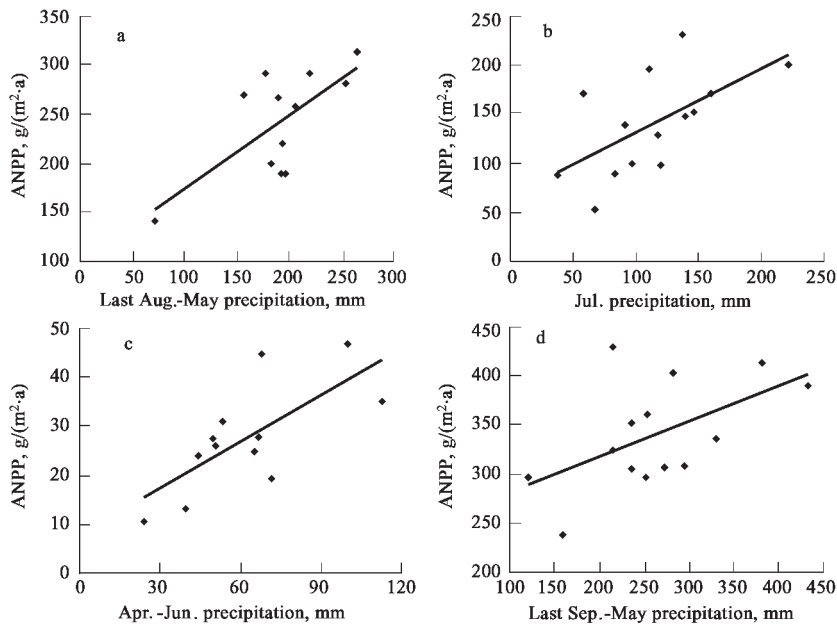


Fig.4 Relationship between above-ground net primary productivity (ANPP) and precipitation

a. for the temperate meadow steppe:  $ANPP = 0.75 \text{ precipitation} + 98.93$ ,  $r^2 = 0.47$ ,  $n = 12$ ,  $P = 0.01$ ; b. for the temperate steppe:  $ANPP = 0.65 \text{ precipitation} + 66.75$ ,  $r^2 = 0.36$ ,  $n = 14$ ,  $P = 0.02$ ; c. for the temperate desert steppe:  $ANPP = 0.32 \text{ precipitation} + 7.88$ ,  $r^2 = 0.51$ ,  $n = 14$ ,  $P < 0.01$ ; d. for the alpine meadow:  $ANPP = 0.36 \text{ precipitation} + 224.95$ ,  $r^2 = 0.29$ ,  $n = 14$ ,  $P < 0.05$

### 2.3 Possible causes

The pattern of ANPP sensitivity to precipitation across the precipitation gradient could be interpreted as the result of changes in the relative magnitude of vegetational and biogeochemical constraints (Parelo et al., 1999; Huxman et al., 2004). In the temperate desert steppe, the low vegetation coverage and low RGRs of the dominant species constrain the response of ANPP to inter-annual changes in precipitation. In the alpine meadow (the wettest extreme of the gradient), the dominance of species with high RGRs combined with relatively low inter-annual variability in precipitation reduces the magnitude of the vegetational constraint; these species (e.g. *Kobresia humilis*) can adjust total cover or LAI faster than can those (e.g. *Stipa klyrovii*) at the temperate steppe. However, an increase in biomass or LAI may result in nutrient limitations. The increase in nitrogen-use efficiency with increased water availability (Vinton and Burke 1995) indicates a potential for N limitation (Vitousek, 1982) and, consequently, for an increase in

biogeochemical constraints (Parelo et al., 1999).

Possible underlying cause of transition between vegetational and biogeochemical constraint might be the precipitation pulse events. The amount of water received in the form of small events varies very little, whereas the amount of water in large events varies markedly among years; and the occurrence of large rainfall events could be a major source of among year variability in ecosystem functioning (Schwinning and Sala, 2004). Even in dry years, short periods of high resource abundance triggered by rainfall events can saturate the resource demand of some biological processes for some time (Schwinning and Sala, 2004). So in some years when water shortage happens, the ANPP could still keep high, rather than change proportionately with annual precipitation. The mechanism of how precipitation pulse events influence grassland productivity remains vaguely understood. Is there a threshold value of precipitation under which little significant biogeochemical change would happen (so the precipitation can not contribute

Appendix 1 Characteristics of 48 grassland study sites used in the present analysis and principal reference for each study

Province	Grassland type	Precipitation, mm	Temperature, °C	Elevation, m	Sampling time	ANPP, g/(m <sup>2</sup> ·a)	Sources
Inner Mongolia	TMS	348.1	-1.9	743	1984—1995	229.5	Bai et al., 2001
Inner Mongolia	TMS	315.4	-2.3	833	1980—1985	128.5	Yang, 1992
Inner Mongolia	TMS	380	4.12	200	1987—1992	243.1	Liu et al., 1996
Inner Mongolia	TMS	350	-2.66	750	1982—1992	173.4	Yang et al., 1994
Inner Mongolia	TMS	350	1.2	1100	1982—1984	197.7	Wang et al., 1987
Inner Mongolia	TMS	380	4.12	N/A	1987—1991	247.1	Seyin and Bao, 1992
Inner Mongolia	TMS	315.4	-2.4	770	1982—1988	246.6	Yang, 1989
Inner Mongolia	TMS	353	-2.93	770	1982—1992	157.8	Yang et al., 1994
Inner Mongolia	TMS	345	-2.17	650	1982—1992	161.8	Yang et al., 1994
Inner Mongolia	TMS	317	-1.78	733	1982—1992	228.6	Yang et al., 1994
Inner Mongolia	TMS	440	1.82	350	1987—1992	187.2	Liu et al., 1996
Inner Mongolia	TMS	375	-0.4	1200	1981—1986	216	Liu and Li, 1987
Inner Mongolia	TMS	365.6	-0.5	1200	1985—1988	117.6	Li and Li, 1991
Inner Mongolia	TMS	364.7	1.7	1420	1983—1995	219.3	Bai and Xu, 1997
Inner Mongolia	TMS	294.9	1.7	N/A	1986—1996	120.2	Zhao and Zhang, 2002
Heilongjiang	TMS	451.0	4.0	N/A	1986—1988	238.6	Zhao et al., 1993
Jiling	TMS	470.0	4.9	N/A	1978—1990	186.0	Guo and Zhu, 1994
Jiling	TMS	447.0	5.5	N/A	1992—1994	145.0	Chen et al., 1998
Inner Mongolia	TMS	300.0	-2.4	609	1981—1985	279.6	Lu, 1994
Inner Mongolia	TMS	350.0	1.2	1100	1982—1984	241.8	Wang et al., 1987
Inner Mongolia	TS	354.1	1.1	1150	1984—1995	187.2	Bai et al., 2001
Inner Mongolia	TS	379.1	1.7	1284	1984—1995	143.6	Bai et al., 2001
Inner Mongolia	TS	350.4	0.6	1100—1300	1990—1997	93.7	Wang et al., 1998
Inner Mongolia	TS	376.5	1.7	1284	1982—1995	140.4	Bai, 1999
Inner Mongolia	TS	400	7.1	468—514	1984—1989	215.7	Wang and Wang, 1997
Inner Mongolia	TS	403	3.63	621	1983—1992	101.1	Liu et al., 1996
Inner Mongolia	TS	472	-0.19	621	1983—1989	190.7	Liu et al., 1996
Inner Mongolia	TS	284	-1.29	705	1984—1990	104.8	Xing et al., 1994
Inner Mongolia	TS	399	-0.46	1150	1984—1990	148.2	Xing et al., 1994
Inner Mongolia	TS	273	-0.21	1200	1984—1990	42.2	Xing et al., 1994
Inner Mongolia	TS	310.2	4.4	1430	1982—1991	53.6	Zhang et al., 1992
Inner Mongolia	TS	365.1	1.5	1420	1983—1990	149.2	Bai et al., 1992
Qinghai	AM	578.1	-2.0	3200	1996—1999	350.2	Yi and Ben, 2000
Qinghai	AM	528	-2.95	3200—3400	1980—1985	286.6	Yang et al., 1988
Qinghai	AM	430.9	N/A	N/A	1980—1982	279.1	Zhou et al., 2001
Gansu	AM	414.5	0.3	29.30	1980—1983	246.1	Hu et al., 1988
Qinghai	AM	600	-1.7	3250	1983—1993	343.0	Zhou et al., 1995a
Qinghai	AM	530.0	-2.0	3250	1983—1993	340.4	Zhou et al., 1995a
Qinghai	AM	578.1	-1.7	N/A	1980—1985	296.7	Yang et al., 1987
Inner Mongolia	TDS	254.8	4.7	1050	1984—1995	26.0	Bai et al., 2001
Inner Mongolia	TDS	242.5	4.1	1200	1983—1994	33.5	Han, 2002
Inner Mongolia	TDS	243	3.23	N/A	1984—1987	36.8	Laobusheng et al., 1990
Ningxia	TDS	290.2	7.8	1300—1500	1987—1993	41.8	Liu et al., 1998
Inner Mongolia	TDS	344	5.8	490	1984—1992	127.5	Liu et al., 1996
Inner Mongolia	TDS	256.6	N/A	N/A	1983—1988	70.8	Xin and Sai, 1990
Inner Mongolia	TDS	174.8	N/A	N/A	1983—1988	45.7	Xin and Sai, 1990
Inner Mongolia	TDS	270.0	N/A	1375	1983—1990	77.9	Liu, 1993
Inner Mongolia	TDS	91.6	N/A	1538	1983—1990	20.7	Liu, 1993

Notes: Precipitation, temperature are mean annual precipitation and temperature for nearest weather station, as reported in the original literature; grassland type is classification after DAHV and GSAHV (1996); TMS, temperate meadow, TS, temperate steppe, TDS, temperate desert steppe, AM, alpine meadow; N/A, not available

Appendix 2 Inter-annual variation in ANPP and precipitation of the four selected sites

Year	TMS <sup>a</sup>		TS <sup>b</sup>		TDS <sup>a</sup>		AM <sup>c</sup>	
	Precipitation, mm/a	ANPP, g/(m <sup>2</sup> ·a)	Precipitation, mm/a	ANPP, g/(m <sup>2</sup> ·a)	Precipitation, mm/a	ANPP, g/(m <sup>2</sup> ·a)	Precipitation, mm/a	ANPP, g/(m <sup>2</sup> ·a)
1980	N/A	N/A	N/A	N/A	N/A	N/A	529.3	296.7
1981	N/A	N/A	N/A	N/A	N/A	N/A	500.0	296.8
1982	N/A	N/A	354.3	89.5	N/A	N/A	455.7	237.3
1983	N/A	N/A	351.2	53.3	N/A	N/A	529.8	430.0
1984	425.6	188.8	401.0	138.2	299.6	35.2	486.3	403.2
1985	346.9	220.3	433.9	170.7	241.5	46.7	824.5	307.8
1986	180.0	200.0	347.4	152.4	218.2	13.2	674.2	390.1
1987	247.0	141.5	293.6	171.0	206.3	27.5	619.3	306.4
1988	405.1	257.4	351.8	195.2	297.3	44.7	773.1	360.3
1989	391.4	189.7	243.5	88.2	266.0	10.6	840.4	414.1
1990	494.2	270.0	332.8	231.0	257.5	26.0	520.2	336.4
1991	367.3	281.3	351.4	99.5	177.1	24.7	425.3	305.0
1992	332.3	292.0	562.8	200.0	296.1	19.3	562.7	325.0
1993	356.5	314.0	343.9	147.6	265.1	23.9	506.4	352.0
1994	349.9	291.6	423.5	128.7	298.3	31.0	N/A	N/A
1995	281.3	266.4	459.7	97.7	234.8	27.7	N/A	N/A

Notes: N/A. not available; <sup>a</sup>Bai et al., 2001; <sup>b</sup>Bai, 1999; <sup>c</sup>Wang et al., 1998

to the increment of grassland ANPP)? What is the value for each specific type of grassland? The weakness of the data source in our study was that only one site for each type of grassland was selected in the temporal analysis, and the observation time was relatively short. Further research could be based on more detailed data of precipitation (including precipitation amount and pulse events) and ANPP from more sites with long-term observation data.

### 3 Summary and conclusions

There is a great difference exhibited between spatial and temporal patterns in which precipitation influences ANPP. One important reason for the results may be that the data of ANPP and precipitation used in spatial scale were averages for many years, which offset fluctuations of between year changes. Overall, MAP was the key factor of spatial distribution of grassland ANPP. Among the three types whose ANPP significantly correlated with MAP, median precipitation (temperate steppe) incurred the highest sensitivity.

Temporally, precipitation was the key element influencing inter-annual changes of ANPP. For the temperate meadow steppe, last August—May precipitation was the main variable for inter-annual changes of ANPP. For the temperate steppe, July precipitation was the main variable. For the temperate desert steppe, April—June precipitation was the main variable. For the alpine meadow, last September—May precipitation was the main variable for inter-annual variance of the ANPP. In the temporal scale, the research was based on single-site data, the results would be site specific. Yet from the results of many analogous researches we could always find that precipitation in certain period of a year or previous

year was the main factor influencing inter-annual changes of grassland ANPP. Changes in the relative magnitude of vegetational and biogeochemical constraints might explain the pattern of precipitation sensitivity to ANPP across the precipitation gradient. Research on how precipitation pulses to trigger biogeochemical changes could be helpful to better understand the functioning of the water-limited grasslands.

### References:

- Bai Y, Wang W, Zhang Z et al., 1992. Study on fluctuations of *Stipa grandis* steppe community in southeastern Inner Mongolia [J]. *Grassland of China*, 12(4): 1—5.
- Bai Y, Xu Y, 1997. A model of aboveground biomass of *Leymus chinense* community in response to seasonal precipitation [J]. *Acta Prataculturae Sinica*, 6(2): 1—6.
- Bai Y, 1999. Influence of seasonal distribution of precipitation on primary productivity of *Stipa krylovii* community [J]. *Acta Phytocologica Sinica*, 23(2): 155—160.
- Bai Y, Li L, Wang Q et al., 2000. Changes in plant species diversity and productivity along gradients of precipitation and elevation in the Xilin river basin, Inner Mongolia [J]. *Acta Phytocologica Sinica*, 6: 667—673.
- Bai Y, Li L, Huang J et al., 2001. The influence of plant diversity and functional composition on ecosystem stability of four *Stipa* communities in the Inner Mongolia Plateau [J]. *Acta Botanica Sinica*, 43(3): 280—287.
- Bai Y, Han X, Wu J et al., 2004. Ecosystem stability and compensatory effects in the Inner Mongolia grassland [J]. *Nature*, 431: 181—184.
- Boutton T W, Tieszen L L, Imbamba S K, 1988. Biomass dynamics of grassland vegetation in Kenya [J]. *African Journal of Ecology*, 26: 89—101.
- Briggs J M, Knapp A K, 1995. Interannual variability in primary production in tallgrass prairie [J]. *Journal of Range Management*, 29: 19—23.
- Chang B, Jiang Y, 1989. Research on productivity dynamics of the community in upland grassland [J]. *Inner Mongolia Prataculture*, 2: 31—35.
- Chen J, Zu Y, Ni H et al., 1998. The growing law of above-ground biomass of main plant communities in grazing field of the Songnen grasslands [J]. *Journal of Northeast Forestry University*, 26(5): 49—52.
- DAHV (Department of Animal Husbandry and Veterinary), GRICAAS (Grassland Research Institute of Chinese Academy of Agricultural Sciences), CINSR (Commission for Integrated Survey of Natural Resources, Chinese Academy of Sciences) (ed.), 1994. Data on grassland resources of Beijing, China [M].

- Beijing: Chinese Agricultural Science and Technology Press.
- DAHV (Department of Animal Husbandry and Veterinary, Institute of Grassland, Chinese Academy of Agricultural Sciences), GSAHV (General Station of Animal Husbandry and Veterinary, China Ministry of Agriculture) (ed.), 1996. Rangeland resources of China[M]. Beijing: Chinese Science and Technology Press.
- Deshmukh I K, 1984. A common relationship between precipitation and grassland peak biomass for east and southern Africa [J]. *African Journal of Ecology*, 22: 181—186.
- Duo L, Tian D, Li J et al., 1994. Study on production dynamics of the *Leymus chinensis* + *Herbarum variarum* community [J]. *Heilongjiang Journal of Animal Science and Veterinary Medicine*, 8: 4—6.
- Fang J Y, Piao S L, Tang Z Y et al., 2001. Interannual variability in net primary production and precipitation[J]. *Science*, 293: 479—480.
- Frank D A, Inouye R S, 1994. Temporal variation in actual evapotranspiration of terrestrial ecosystems: patterns and ecological implications [J]. *Journal of Biogeography*, 21: 401—411.
- Guo J, Zhu T, 1994. Effect of climatic factors on the yield of *Aneurolepidium chinense* community [J]. *Acta Botanica Sinica*, 36(10): 790—796.
- Han L, Lv X, 1992. Yield estimation and revision of no synchronous to the above ground biomass of *Leymus chinensis* with remote sensing method (in Chinese)[J]. *Journal of Northeast Normal University*, 2: 99—106.
- Han G, 2002. Influence of precipitation and air temperature on primary productivity of *Stipa klemenzii* plant community, NeiMongol[J]. *Acta Scientiarum Naturalium Universitatis NeiMongol*, 33(1): 83—88.
- Hu Z, Sun J, Zhang Y et al., 1988. Studies on matter production and efficiency of energy in Tianzhu alpine *Kobresia Capillifolia* grassland: I. structure characteristics of community and dynamics of phytomass[J]. *Pratacultural Science of China*, 5(5): 7—13.
- Huxman T E, Smith M D, Fay P A et al., 2004. Convergence across biomes to a common rain-use efficiency [J]. *Nature*, 429: 651—654.
- Paruelo J M, Lauenroth W K, Burke I C et al., 1999. Grassland precipitation-use efficiency varies across a resource gradient[J]. *Ecosystems*, 2: 64—68.
- Knapp A K, Smith M D, 2001. Variation among biomes in temporal dynamics of above-ground primary production [J]. *Science*, 291: 481—484.
- Laobusheng D, Sun C, Chen Z et al., 1990. The dynamics of biomass and relationship between biomass and precipitation of desert steppe in Inner Mongolia[J]. *Arid Land Geography*, 13(1): 10—17.
- Lauenroth W K, 1979. Grasslands primary production [M]. *North American grasslands in perspective*. New York: Springer-Verlag, 3—24.
- Lauenroth W K, Sala O E, 1992. Long-term forage production of a North American shortgrass steppe[J]. *Ecological Applications*, 2: 397—403.
- Le Houerou H N, Bingham R L, Skerbek W, 1988. Relationship between the variability of primary production and the variability of annual precipitation in world arid lands [J]. *Journal of Arid Environments*, 15: 1—18.
- Li Y, Li B, 1991. Study on the biomass of *Leymus chinense* grassland in Xilin River Basin of Inner Mongolia [J]. *Grassland of China*, 11(1): 5—8.
- Liu Z, Li Z, 1987. Primary productivity of *Leymus chinense* and *Stipa grandis* steppe in Inner Mongolia [J]. *Journal of Arid Land Resources and Environments*, 1(3/4): 13—33.
- Liu D, 1993. Research on above-ground biomass dynamics of desert steppe in Inner Mongolia[M]. *Research on dynamics monitoring of grazing ecosystem in the north of China* (Li B et al., ed.). Beijing: China Agricultural Science and Technology Press, 167—177.
- Liu Y, Xing Q, Zhang Z et al., 1996. Dynamics of aboveground biomass in Horqin grassland [J]. *Pratacuture of Inner Mongolia*, (3/4): 36—45.
- Liu J, Qiu B, Zhang Z et al., 1998. Dynamics of primary productivity in *Artemisia ordorsica* community [J]. *Acta Prataculturæ Sinica*, 5(4): 23—29.
- Lu X, 1994. Dynamics of primary productivity on the meadow steppe in Hulunbeir Region[J]. *Grassland of China*, 4: 9—11.
- McNaughton S J, Sala O E, Oesterheld M, 1993. Comparative ecology of African and South American arid to subhumid ecosystems[M]. *Biological relationships between Africa and South America*. New Haven: Yale University Press, 548—567.
- Rosenzweig M L, 1968. Net primary productivity of terrestrial communities: prediction from climatological data [J]. *The American Naturalist*, 102(923): 67—74.
- Rutherford M C, 1980. Annual plant production-precipitation relations in arid and semiarid regions [J]. *South African Journal Science*, 76: 53—56.
- Sala O E, Parton W J, Joyce L A et al., 1988. Primary production of the central grassland region of the United States [J]. *Ecology*, 69: 40—45.
- Schwinnig S, Sala O E, 2004. Hierarchy of response to resource pulses in arid and semi-arid ecosystems[J]. *Oecologia*, 141: 211—220.
- Scurlock J M O, Johnson K, Olson R J, 2002. Estimating net primary productivity from grassland biomass dynamics measurements[J]. *Global Change Biology*, 8: 736—753.
- Seyin B, Bao M, 1992. Dynamics of primary productivity in plain lowland meadow grassland [J]. *Pratacuture of Inner Mongolia*, 4: 50—56.
- Vinton M A, Burke I C, 1995. Interactions between individual plant species and soil nutrient status in shortgrass steppe [J]. *Ecology*, 76: 1116—1133.
- Vitousek P, 1982. Nutrient cycling and nutrient use efficiency [J]. *The American Naturalist*, 119: 553—572.
- Wang G, Yu G, Su H, 1987. Research on biomass and nutrient dynamics of different natural grasslands [J]. *Grassland of China*, 7: 18—24.
- Wang Q, Wang S, 1997. Biomass and grazing of sheep in sand grassland, Aohan pasture [J]. *Pratacuture of Inner Mongolia*, 2: 1—5.
- Wang Q, Wang W, Deng Z, 1998. The dynamics of biomass and the allocation of energy in alpine *Kobresia* meadow communities, Haibei region of Qinghai Province [J]. *Acta Phytocologica Sinica*, 22(3): 222—230.
- Wu Y, Zhang Y, 1998. The characteristic of species diversity along water gradients in Xilinguole steppe [J]. *Acta Scientiarum Naturalium Universitatis Nemongol*, 29(3): 407—413.
- Xin L, Sai S, 1990. Study on the dynamics of primary productivity of desert steppe in Inner Mongolia [J]. *Grassland of China*, 1: 40—46.
- Xing Q, Liu Y, Han Z et al., 1994. Dynamics of aboveground biomass and nutrition of typical steppe in Inner Mongolia [J]. *Pratacuture of Inner Mongolia*, (1/2): 34—38.
- Yang F, Wang Q, Shi S, 1987. The allocation of biomass and energy in *Kobresia humilis* meadow in Haibei District (in Chinese)[J]. *Acta Phytocologica Et Geobotanica Sinica*, 11(2): 106—111.
- Yang F, Wang Q, Shi S et al., 1988. Seasonal and annual biomass dynamics of *Kobresia humilis* meadow [M]. In: *The proceedings of the international symposium of alpine meadow ecosystem* (Editorial Committee ed.). Beijing, China: Science Press, 61—71.
- Yang D, 1989. Dynamics of primary productivity in *Leymus chinense* and *Carex pediformis* pasture[J]. *Pratacuture of Inner Mongolia*, 4: 22—26.
- Yang D, 1992. Dynamics of biomass of *Carex pediformis* meadow in Great Xingan Mountains[J]. *Grasslands of China*, 12(5): 27—31.
- Yang D, Zhang M, Hu Q et al., 1994. Biomass dynamics of the four rangelands in Hulun Buir [J]. *Pratacultural Science of China*, 11(3): 12—16.
- Yi X, Ben G, 2000. Seasonal variation in photosynthesis of *Kobresia humilis* population and community growth at Haibei alpine meadow[J]. *Grassland of China*, 1: 12—15.
- Zhang M, Sun C, Laobusheng D et al., 1992. Dynamics of aboveground biomass in *Stipa krylowii* grassland [J]. *Pratacuture of Inner Mongolia*, 2: 48—50.
- Zhang H, 1999. Study on dynamics of above-ground biomass and conversion efficiency to the total solar radiation of grass + forbs steppe in southern fringe of Mu Us sandland [J]. *Pratacultural Science*, 16(5): 9—14.
- Zhao X, Li J, Liu H et al., 1993. Climatic influence on the productivity of *Leymus chinensis* meadow [J]. *Grassland of China*, 6: 26—29.
- Zhao H, Zhang W, 2002. Study on the effects of herbage growth period and output at the natural grassland under arid climate [J]. *Environmental Protection of Inner Mongolia*, 14(2): 22—25.
- Zhou L, Wang Q, Zhou Q, 1995a. Research on periodicity of the nonlinear vibration of Alpine meadow ecosystem: I. analysis on the power spectrum and its wave period of precipitation and primary productivity [M]. In: *Alpine meadow ecosystem*. No. 4 (the Haibei Research Station of Alpine Meadow Ecosystem, the Chinese Academy of Sciences ed.). Beijing: Science Press, 219—240.
- Zhou L, Wang Q, Zhou Q, 1995b. Research on periodicity of the nonlinear vibration of Alpine meadow ecosystem: II. analysis on the power spectrum of temperature fluctuation and the relation between its wave period and the oscillation period of primary productivity [M]. In: *Alpine meadow ecosystem*. No. 4 (the Haibei Research Station of Alpine Meadow Ecosystem, the Chinese Academy of Sciences ed.). Beijing: Science Press, 241—252.
- Zhou X, 2001. *Kobresia* meadow ecosystem in China [M]. Beijing: Science Press.

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