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Spatiotemporal dynamics of aboveground primary productivity along a precipitation gradient in Chinese temperate grassland

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Investigating the spatial and temporal variance in productivity along natural precipitation gradients is one of the most efficient approaches to improve understanding of how ecosystems respond to climate change. In this paper, by using the natural precipitation gradient of the Inner Mongolian Plateau from east to west determined by relatively long-term observations, we analyzed the temporal and spatial dynamics of aboveground net primary productivity (ANPP) of the temperate grasslands covering this region. Across this grassland transect, ANPP increased exponentially with the increase of mean annual precipitation (MAP) (ANPP=24.47e^{0.005MAP}, R²=0.48). Values for the three vegetation types desert steppe, typical steppe, and meadow steppe were: 60.86 gm⁻²a⁻¹, 167.14 gm⁻²a⁻¹ and 288.73 gm⁻²a⁻¹ respectively. By contrast, temperature had negative effects on ANPP. The moisture index (K), which takes into account both precipitation and temperature could explain the spatial variance of ANPP better than MAP alone (ANPP=2020.34 $K^{1.24}$, R^2 =0.57). Temporally, we found that the inter-annual variation in ANPP (calculated as the coefficient of variation, CV) got greater with the increase of aridity. However, this trend was not correlated with the inter-annual variation of precipitation. For all of the three vegetation types, ANPP had greater inter-annual variation than annual precipitation (PPT). Their difference (ANPP CV/PPT CV) was greatest in desert steppe and least in meadow steppe. Our results suggest that in more arid regions, grasslands not only have lower productivity, but also higher inter-annual variation of production. Climate change may have significant effects on the productivity through changes in precipitation pattern, vegetation growth potential, and species diversity.

grassland transect, spatial variance, temporal variance, temperature, precipitation gradient, Inner Mongolia

To effectively predict the impact of global change on terrestrial ecosystems, it is particularly necessary to understand the mechanism of how ecosystems respond to environmental factors^[1,2]. As the basic process in ecosystems, aboveground net primary productivity (ANPP) strongly influences most ecosystem functions. It is of great importance in controlling nutrient flow, energy flow and carbon/water flux^[3–5]. Therefore, detecting how environmental change affects ANPP is one of the most important subjects in the field of global climate change research^[1,2].

For most ecosystems, especially those in arid and semiarid environment, precipitation is the predominant climate factor controlling ecosystem processes. Precise understanding of the influence of precipitation on ANPP is very important in predicting climate change effects on ecosystems^[6,7]. Moreover, investigating how ANPP varies temporally and spatially across a precipitation gradi-

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ent provides insights of the mechanisms involved in ecosystem responses to precipitation change^[2,8,9]. There have been several reports on this topic^[2,7-13].

Through long-term researches, scientists have acquired some general knowledge of the relationship between precipitation and ANPP. However, there are still some uncertainties. Spatially, it is well known that ANPP increases with the increase of mean annual precipitation (MAP)^[2,7–11]. But different studies have found different patterns in the trend of this increase. Mostly, it has been found that ANPP increases linearly with the increase of MAP^[7-9,11]. But some have suggested that ANPP increases exponentially with MAP^[10], which means that the trend becomes progressively greater with increase MAP. Others have found that the relationship is better described by a logarithm function, i.e. the trend for increase becomes weaker with the increase of MAP^[2]. Temporally, because of the lack of long-term observations, there are only a few reports on inter-annual variation of ANPP across precipitation gradients. Furthermore, results of these few studies have not been consistent with each other. For example, studies of Knapp and Smith in North America suggested that both desert and forest have relatively low inter-annual variation of ANPP^[9]. Grassland, which has an intermediate precipitation level, had the most variable ANPP. On the other hand, Fang et al.^[14] and Huxman et al.^[2] found that variability in ANPP decreased with the increase of MAP. i.e. desert was the most variable, and then grassland and forest. Understanding the reason why there is such uncertainty about the spatiotemporal variance of ANPP may be helpful to understanding the mechanisms of how ecosystems adapt to climate change.

Temperate grassland is the main grassland type in China. It has great significance for global climate change research and grassland livestock production^[15]. There have been many studies of ANPP of Chinese temperate grasslands^[16–18]. However, because of the lack of long-term observations sites of corresponding data at particular sites, there is a shortage of studies on the spatiotemporal variation of ANPP in in relation to precipitation change. Zhou et al. ^[16] analyzed the relation-ship between precipitation and ANPP on the North East China Transect (NECT) and Ni^[18] established an elementary database of ANPP in northern China grassland. But their measurements of ANPP were mostly for single years, and long-term continuous data were lack-

ing. Because of the high variability of ANPP in grassland, their results may not reflect the real relationship between MAP and ANPP^[6,9]. Bai et al.^[19] also investigated the relationship between MAP and ANPP in Chinese temperate grassland by observations along transect. However their transect was short, extending over tens of kilometers, and as their data were also of short duration their results may not be applicable at regional scales. At present, to our knowledge there has been no report on the inter-annual variation in ANPP along a long regional precipitation gradient in China.

In this work, using the natural precipitation gradient of Inner Mongolian grassland and relatively long-term *in situ* measurement of ANPP, we investigated how ANPP varied spatially and temporally along this gradient. As well we explored the biotic and abiotic factors involved in the dynamics of the variation of ANPP. By doing this we aimed to improve understanding of how grasslands respond to changes of precipitation and to predict the influence of climate change on Chinese temperate grassland.

1 Methods

1.1 Study area

The transect used this study was mainly located in Inner Mongolian and extended for shorter distances into Gansu and Ningxia. It extended from Hailar in east Inner Mongolia (E122°23', N46°38') to Alxa in west Inner Mongolia (E104°46', N39°38'), for 2100 km in length and 500 km in width (Figure 1). Precipitation is the main limiting climatic factor in this region. From east to west, MAP decreases from 600 mm to about 100 mm. Because latitude decreases from east to west, mean annual temperature (MAT) is higher at more arid sites, ranging from -3° C to 9° C. The Pearson correlation coefficient between MAP and MAT was -0.44 (P=0.001) (Figure 2). The eastern zone is mostly hilly with an area of plain at the foot of Da Hinggan Mountains and has an average altitude of about 1000 m. The middle zone is the broad and level Mongolian Plateau where the altitude is about 1000-1600 m. The western zone is a transition area between the Ordos Plateau, Loess Plateau and Hexi Corridor and is mainly composed of Mu Us Desert and loess hills. The altitude in this zone is 1500-2500 m.

The study area is the main region of temperate grassland in China. Vegetation changes progressively from

Figure 1 Range of the grassland transect and distribution of selected sites. Triangles are sites of long-term observation stations, i.e. data source (1) (n=23). solid circles are sites used by Ni (2004), i.e. data source (2) (n=33) (see Subsection 1.2).



Figure 2 Mean annual precipitation (MAP) and mean annual temperature (MAT) in relation to longitude on the transect (data plotted are from selected sites, see Figure 1).

meadow steppe in the east to typical steppe in the middle and desert steppe in the west. Meadow steppe is distributed in the east of Hulun Buir Plateau, the east Xilin Gol Plateau and the southeast of Songnen Plain. The main species of this vegetation type are Stipa baicalensis, Leymus chinensis, Filifolium sibiricum, and Stipa grandis. Typical steppe is distributed in the midwest of Xilin Gol Plateau, for most of the area of the Ordos Plateau, and in the west of Loess Plateau. The main species are Stipa grandis, Leymus chinensis, Stipa krylovii, Cleistogenes squarrosa, Agropyron cristatum, Artemisia frigida, and Caragana microphylla. Desert steppe is distributed in the west of the Mongolian Plateau, the west of the Ordos Plateau and west of the Loess Plateau. The main species are Stipa klemenzii, Stipa klemenzii, Agropyron desertorum, Stipa gobica, Cleistogenes songorica, Artemisia frigida, and Salsola collina. In the east zone of the grassland transect the main soils are chernozem,

dark chestnut soil, and meadow soil. In the middle zone most is chestnut soilwith scattered sandy soil. In the west zone the main soil is brown soil, and with some scattered salt meadow soil and sandy soil ^[15]. Apparently the patterns of vegetation, soil and climate are interrelated on this transect.

1.2 Data sources and ANPP algorithm

Two data sources were used: (1) Data of long-term observation stations (acquired from the Grassland Resource Survey Database of Grassland Research Institute of Chinese Academy of Agricultural Sciences). These stations were established for forage yield measurement (No-zonal sites were excluded in this work). Aboveground biomass (including standing dead biomass) was measured monthly to monitor the dynamics of grass forage yield. We took the maximum aboveground biomass as the ANPP in each year. For shrubs, ANPP was calculated by the leaves and new twigs produced in the current year (It is known that the production of old stems of shrub could be negligible^[13]). At each site, there were at least four year's ANPP data (seven on average). Sampling quadrates were set in enclosures without disturbance. (2) Data from Ni^[18]. Ni collected productivity data in north China from published literature, books and reports (All ANPP was estimated through biomass dynamics). From this paper, we selected those sites located within and next to our grassland transect. Before analysis, we carried out three steps to eliminate unsuitable data: first, excluding no-zonal ecosystem data; second, excluding the ANPP derived from less-thanthree year's measurement; third, excluding data measured at the same locations (including those overlapped with data source (1)) and kept those with longer periods of measurement. In order to standardize the data as much as possible for data source (1) we took the maximum aboveground biomass (some did not include standing dead biomass) as ANPP if it was estimated by other algorithms. Eventually, 56 sites were used for analysis (23 from data source (1) and 33 from data source (2), for more details see Appendix) (Figure 1). The algorithm used to estimate ANPP in this study is that mostly used in other recent studies $\frac{5,18,20,211}{2}$. Because all data have more than three-year observations we assumed that they could generally represent the long-term average ANPP. Furthermore, in order to verify their accuracy, we conducted analyses separately for the two data sources to derive functions between ANPP and climatic factors, and made comparisons between the functions arrived from each data source.

Sites of data source (1) had no records of precipitation and temperature in the observation years. We extracted theses meteorological data from the Meteorological Database of the Chinese Ecological Research Network (CERN) Synthesis Research Center. MAP and MAT were the average values of 1970-2000 (resolution: $1 \times 1 \text{ km}^2$ ^[22]. In addition, we extracted annual precipitation data (resolution: 10×10 km²) to analyze the relationship between the inter-annual variation of precipitation and that of ANPP. Every site in data source (2) had records of MAP and MAT and we used these directly (comparison between the two meteorological data sources showed the difference of 2% and 10% for MAP and MAT respectively). Because data source (2) did not have records of yearly ANPP, we did not analyze the relationship between the variation of ANPP and precipitation for this data set.

2 Results

2.1 Spatial pattern of ANPP across precipitation gradient

ANPP in this region exhibited an obvious spatial pattern. ANPP gradually decreased from the east to the west on the transect (Figure 3). The maximum was 669.20 $gm^{-2}a^{-1}$ in eastern meadow steppe, and the minimum was 28.53 $gm^{-2}a^{-1}$ in the western desert steppe. Mean ANPP (±1 SE) of each vegetation type were, meadow steppe 288.73 (± 34.83) $gm^{-2}a^{-1}$ > typical steppe 167.14 (±13.47) $gm^{-2}a^{-1}$ > desert steppe 60.86 (± 7.24) $gm^{-2}a^{-1}$. (One-Way ANOVA, LSD P<0.01). (the two data sources provided the information about the vegetation type of each site following the classification system of the China Grassland Resources^[15]).

2.2 Relationship between ANPP and climate factors

Spatially, the relationship between ANPP and MAP could be described by an exponential function:

ANPP=24.47 $e^{0.005MAP}$ (n=56, $R^2=0.48$, p<0.001). (1) Similar functions were derived from each data source. For data source (1):

ANPP=24.21 $e^{0.005MAP}$ (*n*=23, *R*²=0.46, *p*<0.001). (2) And for data source (2):

ANPP=24.50e^{0.005MAP} (
$$n$$
=33, R^2 =0.51, p <0.001). (3)

The two functions for ANPP were not significantly dif-



Figure 3 ANPP spatial pattern along the grassland transect.

ferent from each other (T test, P=0.99) (Figure 4(a)). This result could to a large extent indicate that the ANPP values selected represent long-term average levels of ANPP. Slopes of the functions increased with the increase of MAP, implying that ecosystem in wetter area may use precipitation more efficiently. The intercept with *Y* axis was positive (24.47), suggesting that plants may not mainly use current year rainfall, but water stored in soil^[23].

In addition to precipitation, we also investigated the effect of temperature across the transect. Because of the correlated relationship between MAP and MAT, partial correlation analysis between MAT and ANPP was conducted. The partial correlation coefficient was -0.43 (p=0.001), indicating that temperature had a negative effect on ANPP in our transect. This effect may be due to higher temperatures making the climate even more arid in arid or semiarid environments^[24,25]. Furthermore, we analyzed the relationship between ANPP and a moisture index *K* (*K*=MAP/(Cumulative temperature above 0°C×0.1)) developed by Ren et al.^[26] especially for Chinese grasslands, and acquired the function:

ANPP=2020.34 $K^{1.24}$ (n=56, $R^2=0.57$, p<0.001). (4) Meanwhile, for the two data sources respectively:

ANPP=1662.1 $K^{1.16}$ (n=23, R^2 =0.52, p<0.001). (5)

ANPP=2687.33 $K^{1.38}$ (n=33, R^2 =0.66, p<0.001). (6)

These functions were not significantly different (T test, P=0.98) (Figure 4(b)). The fit between the moister index (*K*) and ANPP spatial variation ($R^2=0.57$) was better than that with MAP ($R^2=0.48$).



Figure 4 Relationships between ANPP (aboveground net primary productivity) and (a) MAP (mean annual precipitation), (b) moister index (K). Solid dots and continuous line were drawn from data source (1); open circles and dashed lines were drawn from data source (2).

2.3 Inter-annual variation of ANPP across precipitation gradient

Studying ANPP spatial variation along a precipitation gradient is useful for predicting the effect of precipitation on ecosystems. As well research on ANPP temporal variation along precipitation gradients is a valuable approach to clarify the mechanism of how ecosystems respond to the climate change [8.9]. Using the coefficient of variation index (CV, standard deviation divided by mean), we investigated the inter-annual variation in ANPP of sites along the transect. Because data source (2) had only the mean values, the 23 sites in data source (1) were used to conduct this analysis. Along the transect, inter-annual variation in ANPP increased with the decrease of MAP (CV=220.4-32.6LnMAP, R^2 =0.30, p <0.001. The most variable site was in desert steppe, with a CV of 80.9%. The least variable site was in the humid meadow steppe, with a CV of 13.2%. On average, desert steppe was the most variable for ANPP (CV=36.7%, n=7), typical steppe was intermediate (CV=33.3%, n=10) and meadow steppe was the least variable (CV=23.5%, n=6) (Figure 5). However, the trend of temporal variation in ANPP across the precipitation gradient was not correlated with the inter-annual variation in precipitation (PPT) (P=0.71). (Figure 6). On this transect the variation of PPT did not increase with aridity. Generally, variability of ANPP was greater than that of PPT. The ratios of the two CV (CV of ANPP and CV of PPT) in each vegetation type were: desert steppe 3.01, typical steppe 1.89, and meadow steppe 1.28. These changing CV ratios imply that, with the improvement of vegetation

condition for the increased water availability, ecosystems are buffered against inter-annual variation of precipitation.



Figure 5 Pattern of ANPP coefficient of variation (CV) along precipitation gradient. Inset illustrates the CV of each vegetation type. D, Desert steppe; T, typical steppe; M, meadow steppe.

3 Discussion

3.1 Spatial variation of ANPP and the controlling factors

Aridity increased from the northeast to the southwest along the transect, vegetation changed from meadow steppe to desert steppe, and correspondingly, ANPP decreased. This is consistent with previous studies^[16,18,19]. Specifically, ANPP in desert steppe and typical steppe was close to the results of Ni^[18]. But ANPP in meadow steppe was a little higher. Possibly this was because some of the ANPP estimated by Ni^[18] did not take into



Figure 6 Relationship between coefficient of variation (CV) of ANPP and CV of annual precipitation (PPT).

account the standing dead matter. In desert steppe and typical steppe the proportion of standing dead matter is small. But in humid meadow steppe standing dead matter should not be neglected (unpublished data). Compared with other grasslands with similar climatic conditions, ANPP in desert steppe and typical steppe was equivalent to that in Argentina Patagonian grassland^[13] and North American shortgrass steppe^[111].

In arid environments, precipitation is considered to be the most important factor controlling ecosystem processes. Both temporally and spatially, precipitation determines the magnitude of ecosystem productivity and its variability^[6]. We found ANPP increased with the increase of precipitation and this is consistent with previous studies $\frac{[2,7-12]}{1}$. Most previous studies have found ANPP to be linearly correlated with MAP^[7,8,11,12]. In our work, however, we found that ANPP increased exponentially with the increase of MAP, suggesting increasing efficiency of the use of precipitation for primary productivity, i.e.the slope increased^[10]. This might be caused by vegetation condition. Some researchers assume that in humid environments vegetation has high growth potential and most precipitation is used for growth and water loss from soil evaporation or runoff only is proportionally small. Consequently, higher precipitation use efficiency is achieved^[2,27]. Although Ni and Bai et al. found linear relationships between ANPP and MAP in this re $gion^{[18,19]}$, most of the ANPP they used for analysis were those measured in a single year. For the high and variable ANPP of temperate grasslands their results may be too general to describe the real situation $\frac{[6,9]}{}$.

Although precipitation is the most important climatic factor for grassland ecosystem in arid environment, in most studies the predictive function of MAP on ANPP spatial variation was not very high^[9–12,16]. In addition,

only a few studies have considered the effect of other factors, and especially temperature on ANPP. Through partial analysis, we found temperature had negative effect on ANPP, and this is consistent with the studies of Epstein et al.^[24] and Burke et al.^[25]. This may be connected with the special environmental conditions. In arid environments obviously water is the dominant factor controlling ecosystem processes. Increased temperature may enhance soil evaporation, increase aridity, and consequently reduce ANPP^[24,25]. That the moisture index (K) explained ANPP spatial variance better than MAP supports this point of view (Figure 4). Further- more, some studies in the same region are consistent with this result. At different spatial scale, Ni^[18] and Bai et al.^[19] also found the negative relationship between ANPP and MAT. Through experiment, Xu and Zhou^[28] observed the growth dynamics of Leymus chinensis at different soil moisture and nighttime temperature levels. Their result showed that in conditions of water deficit increased nighttime temperatures could make plant photosynthetic rate and biomass decrease substantially. Thus, because of the combined effects of precipitation and temperature in arid areas, using MAP alone to estimate ANPP at regional scale may involve considerable error.

3.2 Temporal variation of ANPP and the affecting factors

In this work, we found the inter-annual variation in ANPP increased with aridity (Figure 5), which was consistent with the results of Fang et al.^[14] and Huxman et al.^[2]. But differently, Fang et al. suggested that the ANPP temporal variation could be explained by the inter-annual variation of precipitation. In our study, we did not found a positive relationship between them, a result coincident with Knapp and Smith^[9]. Generally, it is considered that the variation of precipitation plays a determinant role in the variability of ANPP^[6,8,11,14]. In addition, vegetation growth potential e.g. Leaf Area Index, LAI) is also of great importance. High growth potential can make ANPP sensitive to variation of precipitation^[9]. Along this grassland transect with increased aridity, on one hand, inter-annual variation of precipitation did not show a well defined trend (mostly, the variation of precipitation increased with aridity). On the other hand vegetation growth potential decreased. Obviously, the two mechanisms mentioned above (effect of inter-annual variation of PPT and effect of vegetation growth potential) cannot explain the temporal variability in ANPP across the gradient. Factors controlling variance of ANPP at a regional scale are most likely complex. We suggest that there might be two other important mechanisms that make ANPP temporal variation increase with aridity in this region:

(1) Growing season rainfall pattern. Effects of precipitation on productivity have two main components. One is the total amount, and the other is the distribution pattern. With the same amount of total rainfall, the timing and quality of rainfall could also have a great impact on productivity $^{[29-32]}$. The experiment of Knapp et al. showed that when the interval between two rainfall events was lengthened by 50%, ANPP declined substantially^[30]. In this transect, although variation in inter-annual precipitation did not exhibit a clear trend, gradients in variation of rainfall pattern may exist. In more arid areas, the rainfall pattern in the growing season may be more variable.

(2) Biodiversity. In communities that are species-rich, different plant species may have different water use strategies. Whether in years with abundant or low precipitation, there always be some species with relatively high productivity. This compensatory effect among species could make ANPP of the whole community steady. For example, with 20 years observations, Bai et al.^[17] investigated aboveground biomass dynamics in a Levmus chinensis grassland. They found, in humid years Levnus chinensis had the most biomass. In droughty years, another species, Stipa grandis, took its place. Because of their compensatory effect, the community aboveground biomass was not as variable as a single species or functional group. At the transect scale, species richness exhibits an apparent gradient along the precipitation gradient. In the driest area there are few species in the ecosystems. Consequently productivity could be influenced more by precipitation variation^[27].

4 Summary and research needs

Along natural precipitation gradients, detecting the spatiotemporal variance in ANPP is very helpful in understanding how ecosystem respond to climate changes and in exploring the mechanism by which ecosystems adapt to such changes. In this study, with long-term field measurement data, we analyzed ANPP across a grassland transect, and made the following conclusions: (1) from east to west on the transect, aridity increased, and ANPP declined. The order of ANPP for the three vegetation types was meadow steppe>typical steppe>desert steppe; (2) precipitation was most likely the dominant climatic factor controlling ANPP at the transect scale. The relationship between MAP and ANPP could be described by an exponential function; and (3) temperature was another important factor affecting ANPP spatial variance. It had negative impact on ANPP. The moister index (K), which took into account both precipitation and temperature, could improve the predictive explanation of spatial variation of ANPP; and (4) with the increase of aridity, ANPP was more variable but this variation was not significantly correlated with inter-annual variation in precipitation.

Some models have predicted that, it might be more humid in north China in future^[33]. Through changes in vegetation composition, the predicted increase of ANPP may be higher than expected, and inter-annual variability in ANPP could decrease. This would be advantageous for the sustainability of livestock production. However, most models predict that in the coming decades variation of rainfall pattern in the growing season will increase and severe drought events will be more fre $quent^{[34]}$. The outcome of such climatic conditions may be contrary to the previous scenario, with great negative impacts on livestock production. Consequently, effective management of grasslands would be of critical importance in order to maintain species diversity and ANPP stability^[17]. Therefore, accurate prediction of the variance of ANPP in Chinese temperate grasslands is very important in the development of a regional climate model.

The use of natural gradients is an invaluable tool for understanding mechanisms of abiotic controls on ecosystem processes^[35], but it also has some limits. Along a transect there will usually be several environmental factors varying simultaneously. It is hard to quantify the contribution of each factor^[25]. In addition, only investigation ANPP along transects cannot let us completely understand the effects of biotic and abiotic factors (e.g. rainfall pattern, vegetation growth potential and biodiversity on ecosystem productivity. Combination of transect method, controlled experiments, and long-term continuous observations (e.g. eddy covariance technology) is considered as the most effective and promising way to address these questions^[36, 37].

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Appendix Site information: site No., site name (NA means not available), observation year, vegetation type, longitude, latitude, mean annual precipitation (MAP, mm), mean annual temperature (MAT, $^{\circ}$ C), moisture index (*K*), above net primary productivity (ANPP, gm⁻²a⁻¹), coefficient of variance (CV) of ANPP. Site Nos. 1–23 are the long-term observation stations, 24–56 are those selected from Ni (2004). Details of these sites can be looked up in the original paper: Ni J. Estimating grassland net primary productivity from field biomass measurements in temperate northern China. Plant Ecology, 2004, 174: 217–234

Site No.	Site name	Observation year	Vegetation type	Longitude (E)	Latitude (N)	MAP	MAT	K	ANPP	CV of ANPP
1	NA	1984-1992	meadow steppe	118°30′	44°30′	511	-0.3	0.23	216.38	0.13
2	NA	1981-1992	meadow steppe	118°45′	48°46′	350	-0.8	0.14	164.85	0.31
3	NA	1984-1989	typical steppe	116°6′	42°18′	375	2.2	0.15	148.68	0.26
4	NA	1984-1989	typical stepp	116°27′	42°53′	374	1.2	0.16	77.18	0.16
5	NA	1984-1987	desert steppe	110°58′	41°37′	294	3.7	0.11	77.79	0.38
6	Hailar	1983-1995	meadow steppe	120°08′	49°49′	443	-1.15	0.21	669.2	0.18
7	Ewenki	1987-1995	meadow steppe	119°41′	48°27′	402	-3.2	0.17	510.44	0.27
8	Chen Barag	1986-1994	typical stepp	118°46′	48°17′	346	-0.5	0.14	329.17	0.40
9	Xilinhot	1987-1990,1992-1994	typical stepp	115°50′	43°54′	313	1.7	0.12	187.99	0.35
10	Xi Ujimqin	1984-1995	typical stepp	117°43′	44°36′	395	0.8	0.16	202.72	0.20
11	Sonid Zuoqi	1988-1995	typical stepp	113°59′	43°36′	210	3.5	0.07	105.61	0.73
12	Zhenlan	1986-1990,1992-1995	typical stepp	113°57′	42°39′	274	4.4	0.09	171.77	0.24
13	Dongsheng	1984-1989,1991-1995	typical stepp	110°08′	39°46′	384	5.3	0.12	44.93	0.38
14	Hanggin	1984-1986,1988-1992	desert steppe	108°17′	39°52′	230	7	0.07	134.71	0.38
15	Damao	1983-1992	desert steppe	110°36′	42°05′	230	5.2	0.07	37.88	0.25
16	Urad Houqi	1987-1992	desert steppe	107°03′	41°27′	166	4.6	0.06	49.19	0.34
17	Yanbei	1992-1995	typical stepp	112°6′	42°06′	289	3	0.11	148.4	0.47
18	Yanchi	1992-1995	desert steppe	106°52′	37°20′	307	7.7	0.09	28.53	0.29
29	Kailu	1991-1994	meadow steppe	121°18′	48°27′	605	-2.76	0.33	474.5	0.22
20	Dorbod	1983-1985,1992-1995	desert steppe	111°57′	42°12′	274	3.7	0.10	88.64	0.31
21	Alxa Youqi	1988-1990,1992-1994	desert steppe	101°43′	38°56′	145	8.2	0.04	61.65	0.81
22	Durbod	1992-1994	meadow steppe	124°30′	46°35′	470	4.6	0.14	226.28	0.30
23	Jingbian	1992-1995	typical stepp	108°49′	37°37′	338	8.2	0.09	157.78	0.13
24	Aohan	1984-1989	typical stepp	119°52′	42°17′	493	3.6	0.16	216.8	
25	Bairin Youqi	1983-1992	typical stepp	118°39′	43°32′	403	3.63	0.13	117.2	
26	Bairin Zuoqi	1983-1989	typical stepp	118°09′	44°03′	472	-0.19	0.20	218.5	
27	Balagener river	1982-1984	meadow steppe	117°32′	44°35′	346	0.08	0.14	241.8	
28	Bayan Xil	1979-1982	typical stepp	116°38′	43°43′	356	-1.04	0.15	282.7	
29	Bayan Xil	1981-1986	typical stepp	116°04′	43°26′	323	-1.24	0.15	217.6	
30	Bultai sum	1984-1987	desert steppe	111°51′	42°13′	243	3.23	0.08	65.9	
31	Chen Barag	1981-1983	meadow steppe	120°08′	49°41′	358	-3.43	0.16	257.8	
32	Darhan	1983-1987	desert steppe	111°25′	42°41′	202	3.21	0.06	49.1	
33	Darhan	1983-1987	desert steppe	110°55′	42°20′	209	3.75	0.06	63.2	
34	Darhan	1983-1987	typical stepp	110°25′	41°41′	271	2.78	0.09	93.5	
35	Darhan	1983-1985	desert steppe	110°37′	42°06′	205	4.07	0.06	33.8	
36	Da Hinggan	1982-1988	meadow steppe	119°58′	48°36′	350	-2.66	0.16	181.2	
37	Haijinshan	1984-1986	typical stepp	118°58′	42°17′	405	4.68	0.13	144.4	

(To be continued on the next page)

										(Continued)
Site No.	Site name	Observation year	Vegetation type	Longitude (E)	Latitude (N)	MAP	MAT	K	ANPP	CV of ANPP
38	Haniwulashan	1981-1984	typical stepp	114°58′	44°02′	273	-0.21	0.10	123.4	
39	Horqin Youyi	1987-1992	meadow steppe	121°27′	45°03′	380	4.12	0.12	276.2	
40	Hulun Buir	1982-1992	meadow steppe	120°18′	49°04′	353	-2.93	0.15	221.6	
41	Hulun Buir	1982-1992	meadow steppe	119°58′	48°36′	350	-2.66	0.16	181.2	
42	Hulun Buir	1982-1992	meadow steppe	119°41′	48°28′	317	-1.78	0.13	237.7	
43	Hulun Buir	1982-1992	typical stepp	119°40′	48°13′	345	-2.17	0.15	170.9	
44	Inner Mongolia	1983-1992	typical stepp	117°44′	44°24′	399	-0.46	0.18	141.9	
45	Inner Mongolia	1983-1991	typical stepp	115°03′	43°57′	273	-0.21	0.10	105.8	
46	Jalaid	1987-1992	meadow steppe	122°23′	46°38′	440	1.82	0.14	242.8	
47	Kailu	1991-1993	typical stepp	121°38′	43°36′	383	5.29	0.12	290.6	
48	Ongniud Qi	1984-1992	typical stepp	119°27′	43°13′	344	5.77	0.11	147.5	
49	Shabianzi	1987-1993	typical stepp	107°30′	37°54′	381	7.02	0.10	58.3	
50	Dorbod	1982-1991	typical stepp	111°41′	41°31′	341	2.62	0.12	81.9	
51	Urad Zhongqi	1983-1985	desert steppe	108°28′	41°50′	164	4.68	0.06	40.9	
52	Urad Zhongqi	1983-1985	desert steppe	108°17′	41°49′	158	4.71	0.05	88.8	
53	Xil Tal	1981-1985	meadow steppe	120°08′	49°49′	367	-3.61	0.18	279.6	
54	Zhao Zhou	1986-1988	meadow steppe	125°14′	45°43′	448	3.72	0.13	238.2	
55	Zhenglan	1983-1995	typical stepp	116°03′	42°27′	374	-0.92	0.16	219.3	
56	Zhenglan	1983-1990	typical stepp	116°00′	42°13′	360	0.91	0.14	199.4	

- Schimel D S, House J I, Hibbard K A, et al. Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. Nature, 2001, 414: 169-172[DOI]
- 2 Huxman T E, Smith M D, Fay P A, et al. Convergence across biomes to a common rain-use efficiency. Nature, 2004, 429: 651-654[DOI]
- 3 McNaughton S J, Osterheld M, Frank D A, et al. Ecosystem-level pattens of primary productivity and herbivory in terrestrial habitats. Nature, 1989, 341: 142-144[DOI]
- 4 Chase J M, Leibold M A, Downing A L, et al. The effects of productivity, herbivory, and species turnover in grassland food webs. Ecology, 2000, 81(9): 2485-2497[DOI]
- 5 Sala O E, Austin A T. Methods of estimating aboveground net primary productivity. In: Sala O E, Jackson R B, Mooney H A, et al. Methods in Ecosystem Science, New York: Springer, 2000. 31-43
- 6 Le Houérou H N, Bingham R L, Skerbek W. Relationship between the variability of production and the variability of annual precipitation in world arid lands. J Arid Environ, 1988, 15: 1–18
- 7 Sala O E, Parton W J, Joyce L A et al. Primary production of the central grassland region of the United States. Ecology, 1988, 69: 40-45[DOI]
- 8 Paruelo J M, Lauenroth W K, Burke I C, et al. Grassland precipitation-use efficiency varies across a resource gradient. Ecosystems, 1999, 2: 64-68[DOI]
- 9 Knapp A K, Smith M D. Variation among biomass in temporal dynamics of aboveground primary production. Science, 2001, 291: 481-484[DOI]
- 10 Le Houérou H N. Rain use efficiency: A unifying concept in arid land ecology. J Arid Environ, 1984, 7: 213-247
- 11 Lauenroth W K, Sala O E. Long-term forage production of North American shortgrass steppe. Ecol Appl, 1992, 2:397-403
- 12 Briggs J M, Knapp A K. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position and fire as determinants of aboveground biomass. Am J Bot, 1995, 82: 1024-1030[DOI]
- Jobbagy E G, Sala O E. Controls of grassland and shrub aboveground production in the Patagonian Steppe. Ecol Appl, 2000, 10(2): 541-549
- Fang J Y, Piao S L, Tang Z Y, et al. Interannual variability in net primary production and precipitation. Science, 2001, 293(5536):
 1723[DOI]
- 15 National Station of Psturage of China Agriculture Department. Chinese Gassland resources (in Chinese). Beijing: China Agricultural Sciences Press, 1996. 5-20

- 16 Zhou G, Wang Y, Jiang Y, et al. Carbon balance along the Northeast China Transect (NECT-IGBP). Sci China Ser C-Life Sci, 2002, 45(supp.): 18-29
- Bai Y, Han X, Wu J, et al. Ecosystem stability and compensatory effects in the Inner Mongolia grassland. Nature, 2004, 431(9): 181-184[DOI]
- 18 Ni J. Estimating grassland net primary productivity from field biomass measurements in temperate northern China. Plant Ecol, 2004, 174: 217-234[DOI]
- 19 Bai Y F, Li L H, Wang Q B, et al. Changes in plant species diversity and productivity along gradients of precipitation and elevation in the Xilin River basin, Inner Mongolia. Acta Phytoecol Sin (in Chinese), 2000, 24(6): 667-673
- 20 Scurlock J M O, Johnson K, Olson R J. Estimating net primary productivity from grassland biomass dynamics measurements. Global Change Biol, 2002,8: 736-753[DOI]
- 21 Singh J S, Lauenroth W K, Sernhorst R K. Review and assessment of various techniques for estimating net aerial primary production in grasslands from harvest data. Bot Rev, 1975, 41: 181-232
- 22 Yu G R, He H L, Liu X A. Atlas of Spatial Imformation in Chinese Terrestrial ecosystems: Climate Volume (in Chinese). Beijing: Meterological Press, 2004
- 23 Lauenroth W K, Burke I C, Paruelo J M. Patterns of production and precipitation-use efficiency of winter wheat and native grasslands in the central Great Plains of the United States. Ecosystems, 2000, 3: 344-351[DOI]
- 24 Epstein H E, Lauenroth W K, Burke I C, et al. Ecological responses of dominant grasses along two climatic gradients in the Great Plains of the United States. J Veget Sci, 1996, 7: 777-788[DOI]
- 25 Burke IC, Lauenroth W K, Parton W J. Regional and temporal variation in net primary production and nitrogen mineralization in grasslands. Ecology, 1997, 78: 1330-1340[DOI]
- 26 Ren J Z, Hu Z Z. Bio-climate index for the first class of Chinese grassland. J Gansu Agr Univ (in Chinese), 1965, (2): 33-40
- 27 Connor T G, Haines L M, Snyman H A. Influence of precipitation and species composition on biomass of a semi-arid, African grassland. J Ecol, 2001, 89: 850-860[DOI]
- 28 Xu Z Z, Zhou G S. Effects of water stress and high nocturnal temperature on photosynthesis and nitrogen level of a perennial grass *Leymus chinensis*. Plant Soil, 2005, 269: 131–139[DOI]
- 29 Fay P A, Carlisle J D, Knapp A K et al. Productivity responses to altered rainfall patterns in a C4-dominated grassland. Oecologia, 2003, 137: 245-251[DOI]

- 30 Knapp A K, Fay P A, Blair J M, et al. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. Science, 2002, 298: 2202-2205[DOI]
- Seagle S W, McNaughton S J. Simulated effects of precipitation and nitrogen on Serengeti grassland productivity. Biogeochemistry, 1993, 22: 157-178
- Weltzin J F, McPherson G R. Implications of precipitation redistribution for shifts in temperate savanna ecotones. Ecology, 2000, 81: 1902-1913[DOI]
- Pan Y D, Mellillo J M, Kicklighter D W, et al. Effects of elevated CO₂ on the structure and function of Chinese terrestrial ecosystems. Acta Phytoecol Sin, 2001: 25(2): 175-189
- 34 IPCC. Climate Change 2001: Synthesis Report. A Contribution of

Working Groups I, II, and III to the Third Assessment Report of the Integovernmental Panel on Climate Change. eds.Watson R T and the Core Writing Team. Cambridge: Cambridge University Press, 2001

- 35 Austin A T, Sala O E. Carbon and nitrogen dynamics across a natural precipitation gradient in Patagonia, Argentina. J Veg Sci, 2002, 13: 351-60[DOI]
- 36 Weltzin J F, Loik M E, Schwinning S, et al. Assessing the response of terrestrial ecosystems to potential changes in precipitation. BioScience, 2003, 53: 941-952[DOI]
- 37 Dunne J A, Saleska S R, Fischer M L, et al. Integrating experimental and gradient method in ecological climate change research. Ecology, 2004, 85(4): 904-916