

PRIMARY PRODUCTION AND RAIN USE EFFICIENCY ACROSS A PRECIPITATION GRADIENT ON THE MONGOLIA PLATEAU

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Abstract. Understanding how the aboveground net primary production (ANPP) of arid and semiarid ecosystems of the world responds to variations in precipitation is crucial for assessing the impacts of climate change on terrestrial ecosystems. Rain-use efficiency (RUE) is an important measure for acquiring this understanding. However, little is known about the response pattern of RUE for the largest contiguous natural grassland region of the world, the Eurasian Steppe. Here we investigated the spatial and temporal patterns of ANPP and RUE and their key driving factors based on a long-term data set from 21 natural arid and semiarid ecosystem sites across the Inner Mongolia steppe region in northern China. Our results showed that, with increasing mean annual precipitation (MAP), (1) ANPP increased while the interannual variability of ANPP declined, (2) plant species richness increased and the relative abundance of key functional groups shifted predictably, and (3) RUE increased in space across different ecosystems but decreased with increasing annual precipitation within a given ecosystem. These results clearly indicate that the patterns of both ANPP and RUE are scale dependent, and the seemingly conflicting patterns of RUE in space vs. time suggest distinctive underlying mechanisms, involving interactions among precipitation, soil N, and biotic factors. Also, while our results supported the existence of a common maximum RUE, they also indicated that its value could be substantially increased by altering resource availability, such as adding nitrogen. Our findings have important implications for understanding and predicting ecological impacts of global climate change and for management practices in arid and semiarid ecosystems in the Inner Mongolia steppe region and beyond.

Key words: ANPP; arid and semiarid land; ecosystem management; Eurasian Steppe; Inner Mongolia grassland; mean annual precipitation; nitrogen addition; plant functional group composition; rain-use efficiency.

INTRODUCTION

Precipitation is an essential factor in controlling biodiversity and ecosystem functioning of terrestrial biomes, especially arid and semiarid ecosystems which account for ~45% of the earth's land surface and accommodate about 20% of the world's human population (Reynolds and Stafford Smith 2002). Global climate change is likely to produce more frequent extreme precipitation and drought events (Easterling et al. 2000), which may have greater impacts on ecosystem processes than effects of elevated CO₂ and temperature alone or in combination (Melillo et al. 1993, Weltzin et al. 2003). It has been well documented that aboveground net primary production (ANPP), a key integrative measure of ecosystem functioning, increases across ecosystem types with increasing mean annual precipitation (MAP) in space (Rosenzweig 1968, Leith and

Whittaker 1975, Le Houérou et al. 1988, Sala et al. 1988, McNaughton et al. 1989, Paruelo et al. 1999, Knapp and Smith 2001, Huxman et al. 2004). The response of ANPP to precipitation variation in time, however, varies among different ecosystems (Le Houérou 1984, Lauenroth and Sala 1992, Epstein et al. 1999, Paruelo et al. 1999, Knapp and Smith 2001, Austin 2002, Bai et al. 2004, Huxman et al. 2004). Most of the existing studies have focused mainly on North and South America, and a comprehensive understanding of the spatiotemporal pattern of ANPP in relation to precipitation in world's arid and semiarid lands is yet to be achieved.

Rain-use efficiency (RUE), the ratio of ANPP to precipitation, has been suggested as an effective integral measure for evaluating the response of primary productivity to spatial and temporal changes in precipitation in arid and semi-arid ecosystems (Le Houérou 1984, Le Houérou et al. 1988, Sala et al. 1988). In general, RUE tends to decrease spatially with increasing aridity and potential evapotranspiration, both of which are closely related to ecosystem-level water balance (Le Houérou 1984). However, this widely accepted view recently has

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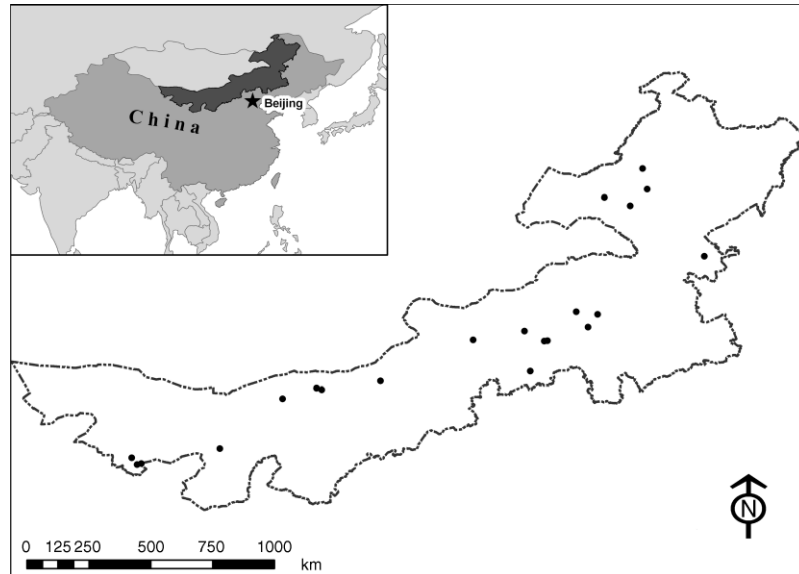


FIG. 1. Location map of the 21 study sites across the Inner Mongolia steppe region of northern China.

been challenged on several grounds (Paruelo et al. 1999, Huxman et al. 2004). For example, considering nine different terrestrial biomes in North and South America, Huxman et al. (2004) found that mean RUE declined from deserts, grasslands, to forests with increasing MAP, and that during the driest years all biomes converged to a common maximum RUE ($RUE_{max} = ANPP/\text{minimum precipitation}$) that was typical of deserts. In contrast, focusing on 11 temperate grassland sites worldwide, Paruelo et al. (1999) showed that RUE increased first, peaked at ~ 475 mm/yr, and then declined along a precipitation gradient (200–1200 mm/yr). For a given ecosystem, a number of studies have shown that RUE decreases over time with increasing annual precipitation (Lauenroth and Sala 1992, Briggs and Knapp 1995, Paruelo et al. 1999, Lauenroth et al. 2000). These seemingly conflicting patterns of RUE at different organizational levels and in space vs. time may be attributable to the controlling processes of RUE that vary with the scale of analysis: a general phenomenon commonly encountered with a variety of ecological patterns and processes (Wu and Loucks 1995, Wu et al. 2006).

Previous studies have suggested that RUE may be affected by several factors, including vegetation composition, edaphic condition, and biogeochemical constraints (Le Houérou 1984, Lauenroth and Sala 1992, Paruelo et al. 1999, Huxman et al. 2004). First, communities with higher diversity of plant species and functional groups may have greater RUE through increased ANPP (Hooper and Vitousek 1997, Tilman et al. 1997, Hector et al. 1999) and lower temporal variability through a combination of selection effects (more diverse communities tend to have a higher probability of including highly productive species),

complementarity effects (more diverse communities tend to be more productive because of fuller resource utilization and synergistic interactions among species), and statistical averaging effects (variability tends to be dampened at higher organizational levels; Loreau and Hector 2001, Loreau et al. 2001, Tilman et al. 2006). Second, traits of dominant plant species and functional groups may affect both ANPP and RUE significantly (Hooper and Vitousek 1997, Paruelo et al. 1999, Eviner and Chapin 2003). For example, grasslands dominated by mesophytic grasses are more productive and less variable than those dominated by xerophytic grasses or shrubs (Bai et al. 2000, 2002, Chen et al. 2003, 2007). Third, ANPP in arid and semiarid ecosystems is usually limited or co-limited by N availability, which is tightly coupled with water availability through biogeochemical feedbacks (Lauenroth et al. 1978, Chapin et al. 1986, Vitousek and Howarth 1991, Schimel et al. 1997, Burke et al. 1998, Hooper and Johnson 1999, Xiao et al. 2007). Furthermore, soil characteristics, such as water-holding capacity, texture, permeability, and depth are major determinants of soil water availability and have important effects on the site-level RUE (Noy-Meir 1973, Le Houérou 1984, Sala et al. 1988).

However, the relative importance of these abiotic and biotic factors and their interactions in relation to the spatiotemporal patterns of ANPP and RUE are yet to be fully understood. Therefore, this study was designed to investigate the spatial and temporal patterns of ecosystem responses to variations in precipitation and their underlying mechanisms based on a long-term data set composed of 21 natural arid and semiarid ecosystem sites across the Inner Mongolia region of China (Fig. 1). These ecosystems are representative of the Eurasian steppe region that stretches over 8000 kilometers from

TABLE 1. Abiotic and biotic characteristics of the 21 study sites in the Inner Mongolia steppe region.

Site ID no.	Site	Community type	Vegetation type	Longitude
1	Xieertala	<i>Filifolium sibiricum</i> + <i>Stipa baicalensis</i>	meadow steppe	120°7'29" E
2	Ewenke Qi	<i>Leymus chinensis</i> + <i>Carex pediformis</i>	meadow steppe	120°18'7" E
3	Modamuji	<i>L. chinensis</i> + <i>Stipa grandis</i>	typical steppe	118°45'0" E
4	Ewenke Qi	<i>S. baicalensis</i> + <i>L. chinensis</i>	meadow steppe	119°41'17" E
5	Zalaite Qi	<i>F. sibiricum</i> + <i>S. baicalensis</i>	meadow steppe	122°22'59" E
6	Xiwu Qi	<i>S. grandis</i> + <i>L. chinensis</i>	typical steppe	117°43'19" E
7	Xiwu Qi	<i>S. baicalensis</i> + <i>L. chinensis</i>	meadow steppe	118°30'0" E
8	Balinzuo Qi	<i>S. grandis</i> + <i>Artemisia sacrorum</i>	typical steppe	118°9'0" E
9	Xilinhaote	<i>S. grandis</i> + <i>L. chinensis</i>	typical steppe	115°50'20" E
10	Sunitezuo Qi	<i>S. krylovii</i> + <i>Cleistogenes squarrosa</i>	typical steppe	113°58'1" E
11	IMGERS†	<i>L. chinensis</i> + <i>S. grandis</i>	typical steppe	116°40'30" E
12	IMGERS	<i>S. grandis</i> + <i>L. chinensis</i>	typical steppe	116°33'32" E
13	Zhenglan Qi	<i>L. chinensis</i> + <i>S. grandis</i>	typical steppe	116°2'53" E
14	Damao Qi	<i>S. klemenzii</i> + <i>Cleistogenes songorica</i>	desert steppe	110°36'32" E
15	Wulatezhong Qi	<i>Caragana tibetica</i> + <i>S. gobica</i>	desert steppe	108°16'59" E
16	Wulatezhong Qi	<i>S. klemenzii</i> + <i>Agropyron desertorum</i>	desert steppe	108°28'12" E
17	Wulatehou Qi	<i>Reaumuria soongorica</i> + <i>Salsola passerina</i> + <i>S. gobica</i>	desert	107°3'0" E
18	Alashanzuo Qi	<i>Potania mongolica</i> + <i>R. soongorica</i> + <i>S. passerina</i>	desert	104°46'1" E
19	Alashanyou Qi	<i>Sympegma regelii</i> + <i>Nitraria sphaerocarpa</i>	desert	101°33'25" E
20	Alashanyou Qi	<i>Brachanthemum gobicum</i> + <i>Ceratoides latens</i> + <i>N. sphaerocarpa</i>	desert	101°54'29" E
21	Alashanyou Qi	<i>C. latens</i> + <i>N. sphaerocarpa</i> + <i>Zygophyllum xanthoxylon</i>	desert	101°45'0" E

Notes: Mean annual precipitation (MAP), mean annual temperature (MAT), and mean annual net primary production (ANPP_{mean}) are shown with standard error in parentheses. For each site, MAP and MAT were calculated for the same time period when ANPP measurements were made.

† IMGERS is the abbreviation for the Inner Mongolia Grassland Ecosystem Research Station, Chinese Academy of Sciences.

northern China and Mongolia in the east to Hungary in the west (Chinese Academy of Sciences: Integrative Expedition Team to Inner Mongolia and Ningxia 1985, Coupland 1993). This region is quite different from North American prairies and African savannas in terms of climate, soils, and dominant plant functional types, despite of some taxonomical similarities at the levels of genera and families (Coupland 1992, 1993, Sankaran et al. 2005, Bai et al. 2007, Qian et al. 2007). Specifically, we address the following four research questions: First, how does ANPP and its variability change along a precipitation gradient across the arid and semiarid region of the Eurasian Continent? Second, how do plant species richness and functional group composition change along the precipitation gradient? Third, what is the spatial and temporal pattern of RUE along the precipitation gradient? Fourth, how does N availability affect the observed pattern of RUE?

MATERIALS AND METHODS

Study area

This study was conducted in the Inner Mongolia Autonomous Region (IMAR) in northern China (Fig. 1), covering an area of 1.18 million km². IMAR has 78.8 million hectares of natural grasslands which account for 66% of the region's total land area. The Inner Mongolia Grassland biogeographically belongs to the Eurasia Steppe region (Chinese Academy of Sciences: Integrative Expedition Team to Inner Mongolia and Ningxia 1985). In this study, 21 natural arid and semiarid ecosystem sites on the Inner Mongolia Plateau were selected along

an east–west transect, which runs from 39°6'–49°48' N latitude and 101°36'–122°24' E longitude. This transect includes several vegetation types: meadow steppe, typical steppe, desert steppe, and desert from east to west with decreasing annual precipitation. The topography of the study area consists of gently rolling hills and tablelands, with elevation ranging from 700 m in the east to 1500 m in the west. Based on long-term meteorological data (1961–2000), the mean annual temperature (MAT) ranges from –1.7° to 8.6°C, with minimum mean monthly temperatures in January (–26.5° to –8.5°C) and maximum temperatures in July (19.9° to 24.0°C). The mean annual precipitation ranges from 113.9 to 425.5 mm, 70–80% of which occurs during the growing season (May–August) in synchrony with the peak temperature. The soils of the study sites are Mollisols, including chernozems, chestnut, calcic brown, and desert soils.

Several plant community types are found corresponding to zonal changes in climate and soils. At the eastern end of the gradient, the meadow steppe, dominated by *Stipa baicalensis*, *Filifolium sibiricum*, *Leymus chinensis*, and *Carex pediformis*, is the highest in both ANPP and species richness among grassland types. The typical steppe, dominated by *S. grandis*, *L. chinensis*, *S. krylovii*, *Cleistogenes squarrosa*, and *Artemisia sacrorum*, is found in the vast chestnut-soil zone of the plateau and has an intermediate level of productivity and plant richness. The desert steppe on calcic brown soils is low in ANPP and species richness, and is dominated by *S. klemenzii*, *C. songorica*, *Agropyron desertorum*, *Caragana tibetica*,

TABLE 1. Extended.

Latitude	Soil type	MAP (mm)	MAT (°C)	Number of species	Record length (yr)	ANPP _{mean} (g/m ²)
49°49'1" N	chernozem soil	365.4 (28.6)	-0.7 (0.3)	74	15	266.92 (16.15)
49°3'50" N	chernozem soil	353.4 (35.6)	-1.5 (0.3)	70	8	261.00 (16.84)
48°46'1" N	chernozem soil	288.6 (28.3)	0.2 (0.3)	42	11	161.93 (15.32)
48°27'40" N	dark chestnut soil	348.5 (18.2)	-1.1 (0.2)	58	16	229.61 (12.59)
46°37'59" N	dark chestnut soil	526.7 (71.7)	4.7 (0.3)	53	6	242.80 (11.63)
44°36'47" N	dark chestnut soil	303.0 (27.4)	1.6 (0.2)	43	13	194.30 (11.47)
44°30'47" N	dark chestnut soil	308.9 (26.9)	1.5 (0.3)	46	9	216.38 (9.62)
44°3'0" N	dark chestnut soil	410.4 (39.3)	5.2 (0.3)	26	7	218.50 (22.74)
43°54'11" N	typical chestnut soil	303.4 (27.2)	3.0 (0.2)	40	8	119.29 (17.10)
43°34'59" N	light chestnut soil	189.9 (20.9)	3.4 (0.2)	38	7	68.19 (11.65)
43°33'11" N	dark chestnut soil	340.9 (15.1)	0.6 (0.2)	86	24	192.51 (8.87)
43°32'31" N	typical chestnut soil	340.9 (15.1)	0.6 (0.2)	61	24	127.04 (7.08)
42°27'4" N	dark chestnut soil	374.8 (20.6)	2.1 (0.2)	42	14	215.67 (18.94)
42°5'38" N	dark brown soil	244.5 (10.8)	4.0 (0.2)	28	20	32.87 (2.15)
41°49'44" N	typical brown soil	173.5 (12.3)	5.1 (0.2)	28	8	59.68 (7.82)
41°46'26" N	typical brown soil	181.5 (15.0)	5.2 (0.2)	26	8	41.34 (5.76)
41°27'0" N	light brown soil	98.9 (6.3)	4.7 (0.2)	19	5	40.11 (5.83)
39°37'59" N	grey desert soil	197.7 (11.8)	8.6 (0.2)	12	8	36.29 (4.56)
39°18'0" N	light brown soil	111.5 (11.6)	8.7 (0.2)	11	7	44.36 (5.89)
39°5'31" N	light brown soil	111.5 (11.6)	8.7 (0.2)	8	7	42.16 (6.45)
39°3'22" N	light brown soil	111.5 (11.6)	8.7 (0.2)	7	7	37.96 (5.00)

and *S. gobica*. At the western edge of the gradient is desert, which is dominated by xerophytic shrubs, including *Reaumuria soongorica*, *Salsola passerine*, *Potaninia mongolica*, *Sympegma regelii*, *Nitraria sphaerocarpha*, *Brachanthemum gobicum*, *Ceratoides latens*, and *Zygophyllum xanthoxylon* (Chinese Academy of Sciences: Integrative Expedition Team to Inner Mongolia and Ningxia 1985, U.S. National Research Council 1992, Coupland 1993, Inner Mongolia Soil Census Office and Inner Mongolia Soil and Fertilizer Service 1994).

Data collection and sampling methods

Most of our data was acquired from the Long-Term Monitoring of Primary Productivity of Inner Mongolia Grassland Ecosystems Project under the auspices of the government of the Inner Mongolia Autonomous Region (Li 1993, CAAS Grassland Research Institute 1996). This data set contains information on the geographic coordinates, elevation, soil type, concentrations of soil organic carbon and total nitrogen, vegetation type, plant species composition, and aboveground biomass production of 21 ecosystem sites across the Inner Mongolia Autonomous Region (Table 1). Long-term meteorological data were obtained from the nearest weather station to each site.

For 19 of the 21 sites, permanent study plots of 250 × 40 m were fenced from grazing from large animals one year before the beginning of the field sampling. At the time of enclosure, all the sites were considered in excellent conditions, representative of undisturbed, mature communities of the four vegetation types on the Mongolia plateau (i.e., meadow steppe, typical steppe, desert steppe, and desert). Five equal-sized blocks (50 × 40 m) for meadow steppe and typical

steppe and 10 equal-sized blocks (40 × 25 m) for desert steppe and desert were established. ANPP for herbaceous plants was sampled on 15 August each year with a 1 × 1 m quadrat randomly located within each block. The only exception was the Damao Qi site where ANPP was measured on 1 September each year using the same method. All living vascular plants in each quadrat were clipped at the ground level and sorted to species. ANPP for shrubs was sampled with a 10 × 10 m quadrat at the same time. The leaves and current-year twigs of shrubs in each quadrat were collected and separated to species. Aboveground biomass was dried at 65°C for 48 h and weighed. Because the standing crop of these steppe and desert communities reached the annual peak at the middle to end of August, the estimated community biomass approximated ANPP of these ecosystems (Li 1993, Bai et al. 2004).

For the remaining two sites, data were obtained from 500 × 500 m enclosures from the Inner Mongolia Grassland Ecosystem Research Station (IMGERS) of Chinese Academy of Sciences, which is located in the Xilin River Basin, Inner Mongolia Autonomous Region (Bai et al. 2004). For the two sites, i.e., *L. chinensis* and *S. grandis* communities, ANPP of 24 continuous years was used for analysis (Table 1). Sampling methods and time were comparable with those for the 19 sites (Bai et al. 2004).

N-addition experiment

To help elucidate possible mechanisms of RUE patterns involving N availability, we also conducted an N-addition experiment in an *L. chinensis* typical steppe community located in IMGERS, a widely distributed ecosystem type in the Eurasia steppe region (Chinese

Academy of Sciences: Integrative Expedition Team to Inner Mongolia and Ningxia 1985, Wu and Loucks 1992, Bai et al. 2004). Mean annual temperature (years 1980–2003) in the study area is 0.6°C, and mean annual precipitation is 340.9 mm (Table 1). The experiment site was established in 2000 and had never received any fertilizers before this study. Fifty-four 5 × 5 m plots were laid out following a randomized block design. Plots were separated by 1-m walkways. We had six treatments that included five levels of N enrichment (0, 5.25, 10.5, 17.5, and 28.0 g N·m⁻²·yr⁻¹ of commercial NH₄NO₃) and control (i.e., no nutrient addition). Except for the control, all treatments also received the same amount of P (10 g·m⁻²·yr⁻¹ P₂O₅), S (0.2 mg·m⁻²·yr⁻¹), and trace elements (190 μg·m⁻²·yr⁻¹ Zn, 160 μg·m⁻²·yr⁻¹ Mn, 31 μg·m⁻²·yr⁻¹ B). This was done to make sure that N was the only limiting nutrient (Tilman 1987). We did not add K, Mg, Ca, or Fe in our experiment because dark chestnut soil is rich in these elements, based on the soil census data (Inner Mongolia Soil Census Office and Inner Mongolia Soil and Fertilizer Service 1994). Nutrients were added twice a year in the growing season, half in the early growing period (1–3 May) and the other half in the start of the fastest growing period (1–5 July), when high temperature and precipitation coincide. Aboveground vegetation within each of the 54 plots was sampled each year by clipping all plants at the soil surface within a strip of 0.5 × 1 m. Samples were taken at least 50 cm apart from the edge of the plots to avoid potential edge effects. All living vascular plants were sorted to species, dried, and weighed. Sampling occurred during 25 August to 2 September each year, which corresponded to the peak biomass (Bai et al. 2004).

Data analysis

Statistical analyses were performed using SAS Version 9.1 (SAS Institute, Cary, North Carolina, USA). We used simple linear regressions to evaluate effects of MAP on mean ANPP (ANPP_{mean}), interannual variation of ANPP (measured as the coefficient of variation; CV_{ANPP}), and RUE across 21 sites. RUE has been computed in two ways in the literature. First, according to its definition, RUE can be calculated directly as the ratio of ANPP to the corresponding precipitation (PPT), i.e.,

$$\text{RUE} = \frac{\text{ANPP}}{\text{PPT}}.$$

We used this formula to obtain all site-level mean RUEs in our study. The second common way of estimating RUE is to equate it to the slope of the ANPP–precipitation relationship (ANPP = $a + b(\text{PPT})$, e.g., Paruelo et al. [1999], Lauenroth et al. [2000], Huxman et al. [2004]). We obtained the regional-scale overall RUEs (overall mean RUE, RUE_{max}, and RUE_{min}) using this linear regression method. However, Veron et al. (2005) pointed out that the slope of the ANPP–precipitation

relationship is not equal to RUE unless the intercept in the regression equation is 0 (i.e., RUE = b only if $a = 0$). In most practical cases, the intercept is not zero, thus the values of RUE obtained from this regression method should be adjusted using the formula RUE_{adj} = ANPP/PPT = $(b + a)/\text{PPT}$ (Veron et al. 2005). To facilitate the comparison between our results with others in the literature, we provide both the unadjusted and adjusted values of RUE when obtained from the regression method.

We also analyzed the effects of MAP on the sensitivity of ANPP (slope of ANPP to interannual variation in precipitation at each site) as proposed by Huxman et al. (2004). Based on the long temporal records of ANPP and corresponding precipitation in each site, we also examined how ANPP was related to annual precipitation, January–July precipitation, and ANPP of the previous year across all sites. To assess how ecosystems respond to wet vs. dry years, we further analyzed the relationships between relative precipitation maxima [RP_{maxa} = (maximum – mean)/mean] and relative ANPP pulses [ANPP_{pul} = (maximum – mean)/mean] for the wettest year and between relative precipitation minima [RP_{mina} = (mean – minimum)/mean] and relative ANPP decline [ANPP_{dec} = (mean – minimum)/mean] for the driest year, as per Knapp and Smith (2001).

To identify possible factors responsible for both the ANPP_{mean} and CV_{ANPP} along the environmental gradients, we regressed the ANPP_{mean} and CV_{ANPP} by multiple regressions with stepwise backward elimination against several abiotic and biotic variables: topsoil total N concentration (TN), species richness (SR), MAP, mean annual temperature (MAT), variability of annual precipitation (CV_{MAP}), RP_{maxa}, RP_{mina}, and mean January–July precipitation (MJJ). To explore how differences in local plant functional group (PFG) composition would affect the regional patterns of variation in ANPP (CV_{ANPP}), we classified all plant species into four functional groups based on life forms: perennial grasses (PG), perennial forbs (PF), shrubs and semi-shrubs (SS), and annuals (AS). Then, we used the ordinary least squares (OLS) regression to examine the relationships between the mean relative aboveground biomass of PFGs and MAP across the 21 ecosystem sites.

For temporal patterns of RUE, we focused on two of the most widely distributed steppe communities, the *L. chinensis* community and *S. grandis* community, for which a 24-year data set from IMGERS was available. For the N-addition experiment, one-way ANOVA, followed by Duncan's multiple-range test, was performed to compare the N-addition effects on RUE for each year.

RESULTS

In this section, we present our results in the order of the four research questions outlined in the *Introduction* section: aboveground net primary productivity (ANPP)

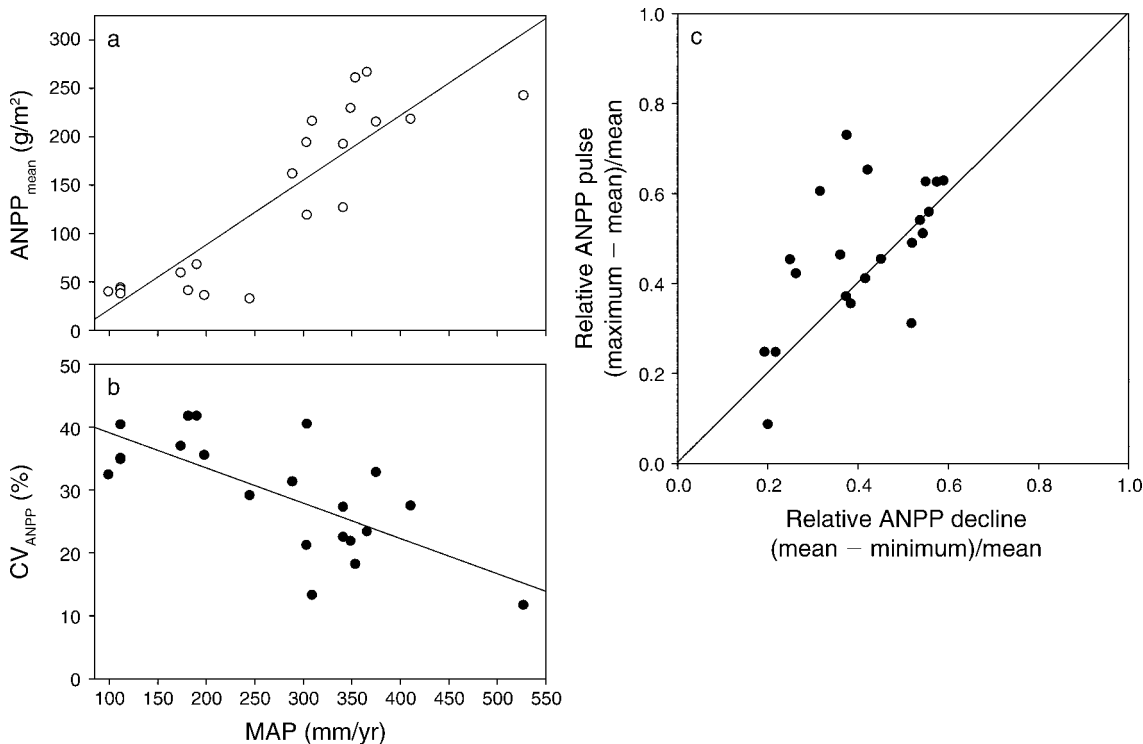


FIG. 2. Annual net primary production (ANPP) and its variability along a precipitation gradient for 21 arid and semiarid ecosystems in the Inner Mongolia steppe region. (a) $ANPP_{\text{mean}}$ is positively related to mean annual precipitation (MAP; $r^2 = 0.76$, $P < 0.0001$). The slope of the regression line represents the overall rain-use efficiency (RUE) at the regional scale. (b) The interannual variation of ANPP (measured as the coefficient of variation; CV_{ANPP}) is negatively correlated with MAP ($r^2 = 0.51$, $P = 0.0003$). (c) Relative ANPP pulses ($ANPP_{\text{pul}}$) and declines ($ANPP_{\text{dec}}$) are positively correlated ($r^2 = 0.37$, $P < 0.01$). The 1:1 line was used to denote the asymmetric relationship between $ANPP_{\text{pul}}$ and $ANPP_{\text{dec}}$.

and its variability, plant species richness and plant functional group composition, the spatial and temporal patterns of rain use efficiency (RUE), and the effects of N addition.

ANPP and its variability along a precipitation gradient

Our analysis of the 21 sites showed that the $ANPP_{\text{mean}}$ of ecosystems increased significantly with increasing mean annual precipitation (mean annual precipitation [MAP]; $ANPP_{\text{mean}} = -45.13 + 0.67(\text{MAP})$; $r^2 = 0.76$, $P < 0.0001$; Fig. 2a). Precipitation accounted for 76% of the variation in ANPP across the region. The linear relationship between $ANPP_{\text{mean}}$ and MAP can be rewritten in the form of Noy-Meir's (1973) model: $ANPP_{\text{mean}} = 0.67(\text{MAP} - 67.3)$. This indicates that the overall mean RUE of our study region is $0.67 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$ ($\text{RUE}_{\text{adj}} = 0.50 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$). Our results also showed that ANPP was significantly correlated with January–July precipitation, but not with May–August precipitation. When the time-series data were combined into the analysis, ANPP was still positively correlated with annual precipitation ($r^2 = 0.43$, $P < 0.0001$) as well as with January–July precipitation ($r^2 = 0.40$, $P < 0.0001$) across all sites. A further analysis with multiple regressions showed that, among all the abiotic and biotic

variables examined, only topsoil nitrogen concentration (TN), mean January–July precipitation (MJJ), variability of MAP (measured as the coefficient of variation; CV_{MAP}), and species richness (SR) were significant factors, together explaining 96% of the variation in ANPP ($ANPP_{\text{mean}} = 717.6\text{TN} + 0.38\text{SR} + 0.17\text{MJJ} + 1.38\text{CV}_{\text{MAP}} - 39.96$; $r^2 = 0.96$, $F_{4,20} = 104.49$, $P < 0.0001$). Also, ANPP for all sites were temporally autocorrelated, i.e., ANPP of a given year was significantly correlated with ANPP of the previous year across the regional gradient.

In contrast with ANPP itself, the variability of ANPP, CV_{ANPP} , decreased from desert, desert steppe, typical steppe, to meadow steppe ($r^2 = 0.51$, $P = 0.0003$; Fig. 2b). Following the method by Knapp and Smith (2001), we further explored the relationship between precipitation maxima (RP_{maxa}) and ANPP pulses ($ANPP_{\text{pul}}$) for the wettest year and the relationship between precipitation minima (RP_{mina}) and ANPP declines ($ANPP_{\text{dec}}$) for the driest year for all sites. Although neither of the above two relationships was found to be significant ($P > 0.05$), ANPP pulses were positively correlated with ANPP declines ($r^2 = 0.37$, $P < 0.01$; Fig. 2c). In general, ANPP pulses in wet years were much stronger than the declines in dry years (Fig. 2c). For example, $ANPP_{\text{pul}}$ for typical

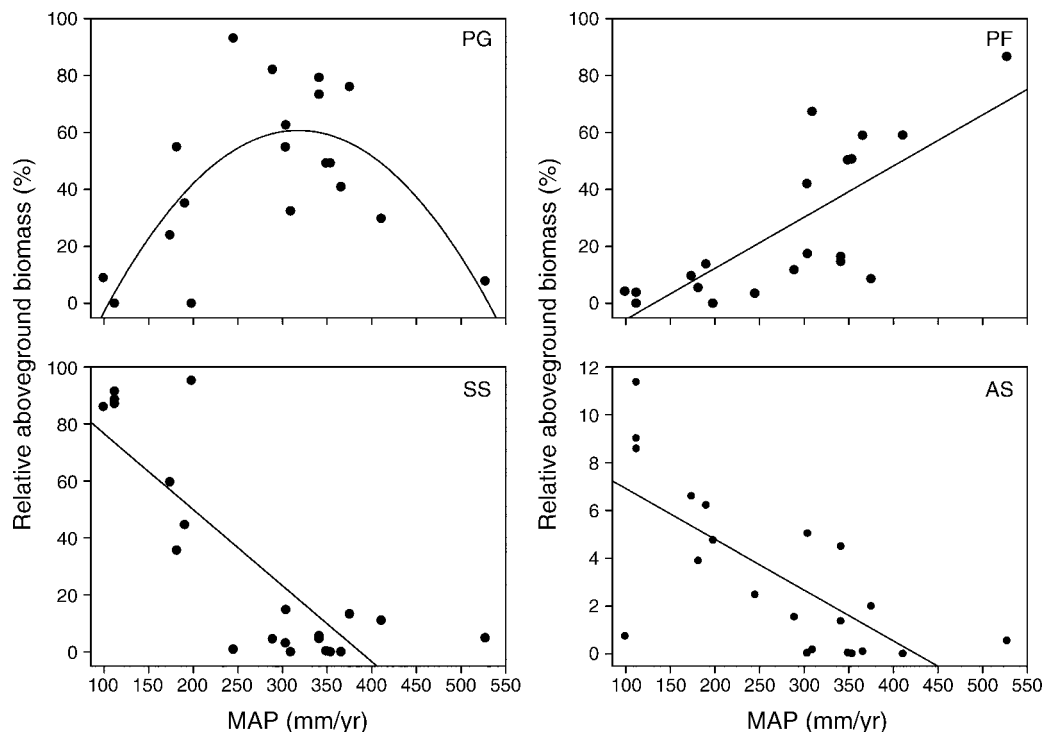


FIG. 3. Changes in plant functional group composition along a precipitation gradient in the Inner Mongolia steppe region. A unimodal relationship was found between the mean relative biomass (MRB) of perennial grasses (PG) and MAP across all sites ($\text{MRB}_{\text{PG}} = -0.001(\text{MAP})^2 + 0.852(\text{MAP}) - 74.76$; $r^2 = 0.62$, $P = 0.0002$). The MRB of perennial forbs (PF) was positively correlated with MAP ($\text{MRB}_{\text{PF}} = 0.179(\text{MAP}) - 23.58$; $r^2 = 0.61$, $P < 0.0001$), but both MRB of shrubs and semi-shrubs (SS) and MRB of annuals (AS) were negatively correlated with MAP ($\text{MRB}_{\text{SS}} = -0.267(\text{MAP}) - 103.28$; $r^2 = 0.69$, $P < 0.0001$; $\text{MRB}_{\text{AS}} = -0.021(\text{MAP}) - 9.04$; $r^2 = 0.50$, $P = 0.0003$).

steppe dominated by *L. chinensis* and *S. grandis* was 0.61, whereas ANPP_{dec} for the same community was 0.32. Our multiple regression analysis with stepwise backward elimination showed that SR, RP_{maxa} , RP_{mina} , and MJJ were significant factors affecting the interannual variation of ANPP ($\text{CV}_{\text{ANPP}} = -0.18\text{SR} + 58.41\text{RP}_{\text{maxa}} - 28.84\text{RP}_{\text{mina}} - 0.06\text{MJJ} + 35.07$; $r^2 = 0.80$, $F_{4,20} = 16.25$, $P < 0.0001$). This means that ANPP becomes less variable with increasing species richness, January–July precipitation, and relative precipitation minima, but with decreasing relative precipitation maxima.

Species richness and plant functional group (PFG) composition along the precipitation gradient

Plant species richness also increased linearly with MAP ($r^2 = 0.52$, $P = 0.0002$) and $\text{ANPP}_{\text{mean}}$ ($r^2 = 0.60$, $P < 0.0001$). The composition of PFGs in terms of relative aboveground biomass differed among ecosystems with increasing MAP. The mean relative biomass of perennial grass (PG), the most dominant functional group in both typical and desert steppe, increased at low levels of MAP and decreased at high levels of MAP, producing a unimodal relationship ($r^2 = 0.62$, $P = 0.0002$; Fig. 3a). On average, the relative biomass of PG was 36% for meadow steppe, 62% for typical steppe, 57% for desert

steppe, and 2% for desert. The mean relative aboveground biomass of PF increased monotonically with MAP ($r^2 = 0.61$, $P < 0.0001$; Fig. 3b). That is, perennial forbs (PF) were more abundant in the wetter sites. For example, the mean relative biomass of PF was 63% for meadow steppe, 23% for typical steppe, 6% for desert steppe, and <2% for desert. On the other hand, the relative biomass of shrubs and semi-shrubs (SS) declined linearly with increasing MAP ($r^2 = 0.69$, $P < 0.0001$; Fig. 3c). In desert communities, SS was the most predominant among the four PFGs in terms of relative biomass, whereas PG and PF were least abundant. The mean relative biomass of SS was 90% for desert, 32% for desert steppe, 13% for typical steppe, and only 1% for meadow steppe. Moreover, the relative biomass of annuals (AS) also decreased linearly with increasing MAP ($r^2 = 0.50$, $P = 0.0003$; Fig. 3d).

Spatial and temporal patterns of RUE

Along the regional-scale precipitation gradient, RUE_{mean} , RUE_{max} , and RUE_{min} all tended to increase with MAP from desert in the west to the meadow steppe in the east (Fig. 4a). Regressing ANPP for all 21 sites against historic minimum annual precipitation resulted in an overall RUE_{max} of $1.08 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$ ($r^2 = 0.43$, $P = 0.0012$; adjusted $\text{RUE}_{\text{max}} = 0.78 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$;

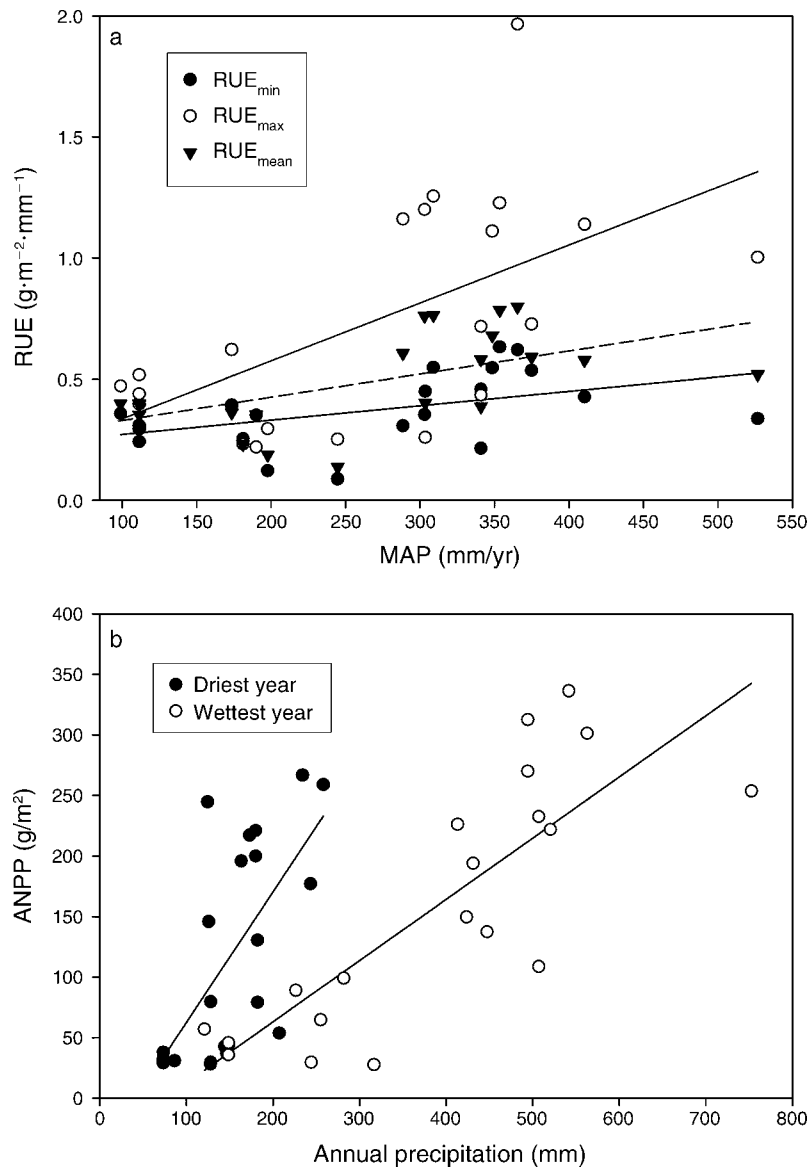


FIG. 4. Variation in mean, maximum, and minimum RUE of the 21 ecosystems along a precipitation gradient in the Inner Mongolia steppe region. (a) RUE_{mean} , RUE_{max} , and RUE_{min} are all positively correlated to MAP (for RUE_{mean} , $r^2 = 0.35$, $P = 0.005$; for RUE_{max} , $r^2 = 0.33$, $P = 0.0069$; for RUE_{min} , $r^2 = 0.21$, $P = 0.0349$). All data points but one (RUE_{max}) fall within the 95% confidence intervals for each regression line. (b) The relationship between ANPP and annual precipitation (AP) in driest years (solid circles, $ANPP = -1.08(AP) + 44.95$; $r^2 = 0.43$, $P = 0.0012$) and wettest years (open circles, $ANPP = 0.51(AP) - 38.15$; $r^2 = 0.69$, $P < 0.0001$). The slopes of the two regression lines represent the overall RUE_{max} (driest years) and RUE_{min} (wettest years) for the 21 ecosystems.

Fig. 4b). This indicates that, during the driest years, all ecosystems in the Inner Mongolia steppe region converged to a common maximum RUE ($cRUE_{max}$). Similarly, we obtained an overall minimum RUE_{min} of $0.51 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$ as the slope of the regression line between ANPP and maximum annual precipitation ($r^2 = 0.69$, $P < 0.0001$; adjusted $RUE_{min} = 0.29 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$; Fig. 4b), suggesting that during the wettest years all ecosystems converged to a common minimum RUE ($cRUE_{min}$).

The general increasing trend for the three RUE measures still held true when site-level data were aggregated by vegetation types (figure not shown). The mean value of RUE_{mean} was $0.71 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$ for meadow steppe, $0.53 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$ for typical steppe, $0.24 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$ for desert steppe, and $0.35 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$ for desert. The mean value of RUE_{max} was $1.31 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$ for meadow steppe, $0.73 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$ for typical steppe, $0.37 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$ for desert steppe, and $0.42 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$ for desert. The mean value of RUE_{min}

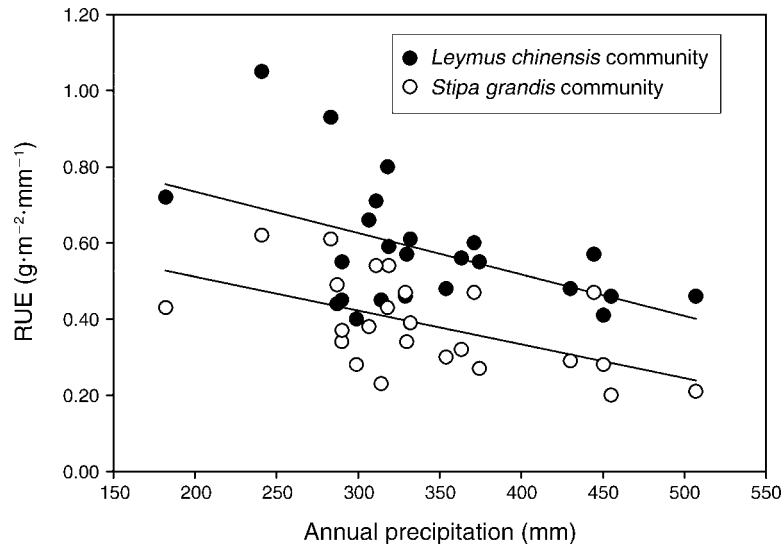


FIG. 5. Responses of RUE to variation in annual precipitation in two Inner Mongolia steppe communities. RUE of the two steppe communities decreased with increasing annual precipitation over a 24-yr period (for the *L. chinensis* community, $RUE = -0.001(AP) + 0.95$; $r^2 = 0.24$, $P = 0.0144$; for the *S. grandis* community, $RUE = -0.001(AP) + 0.69$; $r^2 = 0.29$, $P = 0.0062$). The values of RUE for each community were means of five replicates.

for meadow steppe, typical steppe, desert steppe, and desert, were 0.54, 0.39, 0.24, and 0.26 $\text{g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$, respectively. For all the RUE measures, values between desert and desert steppe were not statistically significant.

We also examined the temporal pattern of RUE on the site level based on a 24-year data set for two typical steppe communities, one dominated by a rhizomatous grass (*L. chinensis*) and the other by a bunchgrass (*S. grandis*). The results showed that RUE for both sites decreased with increasing annual precipitation with a similar slope, while the *L. chinensis* community had consistently higher RUE for all years than the *S. grandis* community (Fig. 5). Due to the short and uneven time series for the other 19 sites, the temporal pattern of RUE was only analyzed for the two sites at IMGERS.

Effects of N addition on ANPP and RUE

Nitrogen addition significantly increased the ANPP of the *L. chinensis* community over three consecutive years (Fig. 6a). No significant difference was found between the control and zero-N treatment ($P > 0.05$). Plots receiving 5.25–28.00 $\text{g}\cdot\text{N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ had significantly higher ANPP than those without N addition, except for the treatment with 5.25 $\text{g}\cdot\text{N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in the first year (Fig. 6a). For example, at high N-addition rates (17.5 and 28.0 $\text{g}\cdot\text{N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), ANPP increased by 55% in 2001, 107% in 2002, and 212% in 2003, as compared to the zero-N treatment.

Similarly, RUE was enhanced by N addition in all three years (Fig. 6b), with a 55% increase in the first year at high N-addition rates of 17.5 and 28.0 $\text{g}\cdot\text{N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$. A greater increase of RUE following N addition, however, was found in the dry year (2002, with growing season precipitation of 183 mm) than the wet year (2003,

with growing season precipitation of 273 mm; Fig. 6b). For example, the mean value of RUE at the high N-addition rates was 2.4 $\text{g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$ in 2002, but only 1.6 $\text{g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$ in 2003. Compared to cRUE_{max} , the mean RUE was 110% higher in 2002 and 40% higher in 2003, but 28% lower in 2001. Without N addition, the RUE was comparable with the cRUE_{min} in both 2001 and 2003 (Fig. 6b).

We further examined whether changes in plant species composition were responsible for the observed patterns of ANPP and RUE. Results showed that the relative biomass of perennial grasses remained constant in the first two years, but declined with increasing N-addition rate in the third year ($P < 0.0001$). The relative biomass of perennial forbs decreased significantly with increasing N-addition rates in the second and third year ($P < 0.01$). In contrast, the nitrophilous annuals that are rare in undisturbed mature steppe communities increased dramatically with N-addition rate in the second and third year ($P < 0.0001$). However, we found little response of shrubs and semi-shrubs to N-addition rates over the three years ($P > 0.05$).

DISCUSSION

Patterns of ANPP and their controlling factors

This study represents the first comprehensive examination of the spatial and temporal variation in ANPP among ecosystems based on long-term data from the Inner Mongolia steppe region, part of the largest contiguous grassland in the world. Our results have shown that, at the regional scale, ANPP increased significantly across ecosystems with increasing MAP, which accounted for 76% of the variation in ANPP. The

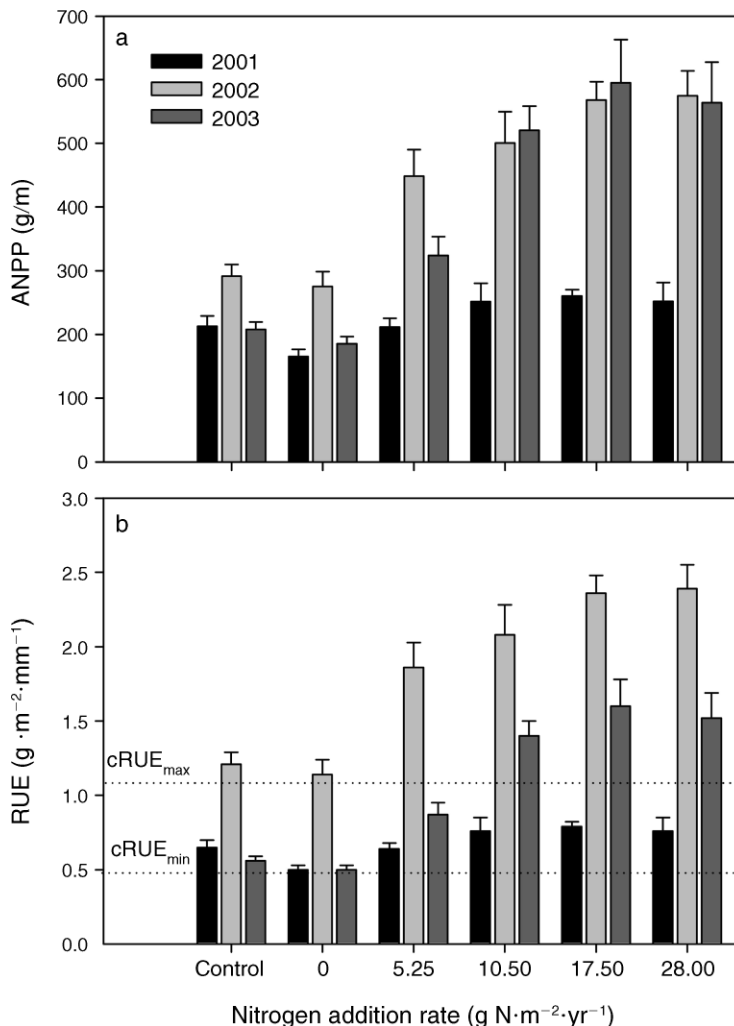


FIG. 6. Effects of N addition on ANPP and RUE of the *L. chinensis* community in the Inner Mongolia steppe region. The precipitation was 329.8 mm in 2001, 240.9 mm in 2002, and 371.0 mm in 2003. (a) ANPP increased significantly with N-addition levels in three consecutive years (ANOVA for 2001, $F_{5,53} = 3.32$, $P = 0.0118$; for 2002, $F_{5,53} = 14.22$, $P < 0.0001$; for 2003, $F_{5,53} = 17.91$, $P < 0.0001$). (b) RUE increased significantly with N-addition rates. Results from the ANOVA analysis were qualitatively similar to those for ANPP over the three years. The values of ANPP and RUE were the means of nine replicates, and error bars indicate the standard error. The horizontal dotted lines denote the common RUE maximum and minimum (cRUE_{max} and cRUE_{min}) computed for all 21 sites.

controlling effect of precipitation on grassland productivity was corroborated by previous studies (Bai 1999, Bai et al. 2000, 2001, Guo et al. 2006). The overall mean RUE ($0.67 \text{ g} \cdot \text{m}^{-2} \cdot \text{mm}^{-1}$ or $\text{RUE}_{\text{adj}} = 0.50 \text{ g} \cdot \text{m}^{-2} \cdot \text{mm}^{-1}$) for the Inner Mongolia steppe region is within the broad range of RUE ($0.05\text{--}1.81 \text{ g} \cdot \text{m}^{-2} \cdot \text{mm}^{-1}$) reported for the rest of the world's arid and semiarid ecosystems (Le Houérou et al. 1988), and comparable with the mean RUE ($0.73\text{--}0.82 \text{ g} \cdot \text{m}^{-2} \cdot \text{mm}^{-1}$ or $\text{RUE}_{\text{adj}} = 0.49\text{--}0.54 \text{ g} \cdot \text{m}^{-2} \cdot \text{mm}^{-1}$) for the North America grassland (Epstein et al. 1996, Burke et al. 1997, Lauenroth et al. 2000). The response pattern of ANPP to precipitation in the Inner Mongolia steppe was generally congruent with previous studies in grasslands elsewhere (Le Houérou et al. 1988, Sala et al. 1988, Burke et al. 1997, Hooper and Johnson

1999, Lauenroth et al. 2000). However, the "ineffective precipitation," i.e., water loss through evaporation and runoff (Noy-Meir 1973), in Inner Mongolia was ~65% lower than that of the North America grassland (Epstein et al. 1996, Burke et al. 1997, Lauenroth et al. 2000). This may be explained in part by the lower MAT and lower MAP in Inner Mongolia. The relatively low ineffective precipitation may also be attributable to the sandy loam and sandy soils with 80–98% sand ($0.02\text{--}2.0 \text{ mm}$) found at most sites along the precipitation gradient in Inner Mongolia (Inner Mongolia Soil Census Office and Inner Mongolia Soil and Fertilizer Service 1994).

ANPP is affected by an array of biotic and abiotic factors, including precipitation, nutrient availability, physical properties of soil, and intertwining biotic

interactions (Lauenroth et al. 1978, Sala et al. 1988, Lauenroth and Sala 1992, Paruelo et al. 1999, Knapp and Smith 2001, Bai et al. 2004). In arid and semiarid ecosystems, water is often considered the most important factor (Noy-Meir 1973), and the effect of N on ANPP has been overlooked (Vitousek and Howarth 1991). Our results indicate that both factors significantly affect ANPP because N and water availability are tightly coupled in these arid and semiarid ecosystems. This was corroborated by our result that ANPP responded to N addition more strongly in wet than dry years, although it is almost impossible to separate the relative importance of water and N availability on ANPP as stated by Burke et al. (1997). Available soil N (rather than total N) directly affects the ANPP in most terrestrial as well as aquatic ecosystems (Vitousek and Howarth 1991). Nevertheless, both total N and soil organic matter (SOM) are closely related to N availability in grassland ecosystems, so they can serve as proxies for N availability. For example, in North American grasslands net N mineralization rates are positively related to SOM (Burke et al. 1997). In several sites of the Inner Mongolia grassland, net N mineralization rates are positively correlated with total soil N and MAP (H. Zhao, Y. Bai, Q. Wang, and X. Han, *unpublished data*). In our study of the *L. chinensis* typical steppe, when N was added ANPP increased in all three years, implying an apparent N limitation. Therefore, our results support the hypothesis of co-limitation by water and nitrogen (Hooper and Johnson 1999, Chapin et al. 2002).

Ecosystem stability and its controlling factors

The interannual variability of ANPP (CV_{ANPP}), which is conversely related to ecosystem stability (Bai et al. 2004, Tilman et al. 2006), decreased progressively across sites with increasing MAP. Our analyses suggest that increased stability is associated with increased species richness, January–July precipitation, and relative precipitation minima, but with decreased relative precipitation maxima. This indicates that greater ecosystem stability was associated simultaneously with the high species richness and January–July precipitation. For meadow steppe and typical steppe ecosystems, the complementary interactions between PG and PF may have contributed to the high ANPP and low CV_{ANPP} in the face of environmental fluctuations. In contrast, the low species diversity, low growth potential and increased dominance of SS may have been responsible for the low ANPP and high CV_{ANPP} in desert steppe and desert ecosystems. These results lend further support to the findings on ecosystem stability in our previous study (Bai et al. 2004).

Across sites, the relative precipitation minima (RP_{\min}) and relative precipitation maxima (RP_{\max}) also contributed to the interannual variability of ANPP. However, RP_{\min} and RP_{\max} showed clearly opposite effects on CV_{ANPP} . RP_{\max} had a positive effect on CV_{ANPP} , reflecting a sharply pulsed increase of ANPP in extremely

wet years, whereas RP_{\min} was negatively correlated with CV_{ANPP} . This suggests that extremely high precipitation events had greater impacts on drier sites, whereas extreme droughts had greater impacts on wetter sites. As a result, the correlation coefficients for RP_{\min} and RP_{\max} had the opposite signs. For a given site, total soil N exhibited the least variation and was eliminated from the multiple-regression model, suggesting that N may not be an important factor determining ecosystem stability. Moreover, we found an asymmetric relationship between ANPP pulse and decline: greater ANPP pulses were found in wet years than ANPP declines in dry years, a result also found in the North American grassland (Knapp and Smith 2001). This was likely caused in part by increased water-use efficiency through stomatal control mechanisms in dry years (Chen et al. 2005). In addition, a positive linear relationship between the current-year ANPP and previous-year ANPP across the 21 sites indicates a carry-over effect (O'Connor et al. 2001), which is caused primarily by the lagged effects of previous-year precipitation induced transfer of soil water, nonstructural carbohydrate reserves in plant belowground tissues, and bud density on current-year plants (Cable 1975, Hanson et al. 1982, O'Connor et al. 2001).

Spatial vs. temporal patterns of RUE

The increasing trend of RUE_{mean} , RUE_{max} , and RUE_{min} with MAP in the Inner Mongolia steppe region is in contrast with the continental-scale pattern found in the Americas that the mean RUE declines from deserts, grasslands, to forests with increasing MAP (Huxman et al. 2004). This difference may be due, at least in part, to the scale of analysis. However, whether the spatial pattern of RUE differs on the regional vs. continental scale in such a diametrical way still needs further confirmation. Alternatively, these different patterns may reflect the different relationships between ANPP and MAP on the two continents. One useful study would be to analyze the RUE pattern for all major biomes on the Eurasian Continent, including deserts, grasslands, and forests, and then compare the results with those of Huxman et al. (2004).

However, previous studies also showed that drier sites tend to have lower and less variable RUE because of low plant density, low production potential, high evaporation potential, and high tolerance to water stress (Noy-Meir 1973, Grime 1977, Paruelo et al. 1999). In the Serengeti grassland of East Africa, McNaughton (1985) found that RUE increased from 0.17 to 0.94 $\text{g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$ along a precipitation gradient (480–1150 mm/yr). Based on 11 temperate grassland sites (seven from the USA and four from Eurasia) with annual precipitation ranging from 200 to 1200 mm, Paruelo et al. (1999) found that RUE_{mean} first increased and then decreased with increasing MAP, peaking around 475 mm. Our results are congruent with this pattern up to 500 mm in MAP, close to the upper limit of annual

precipitation for the Eurasian steppe region. All these studies together seem to suggest that regional and continental patterns of RUE are significantly different. Because RUE is simply the ratio of ANPP to precipitation, the increase in RUE along the precipitation gradient in the Inner Mongolia steppe region may be attributable to several factors that affect ANPP, as discussed earlier.

Huxman et al. (2004) showed that during the driest years, all biomes in North and South America converge to a common RUE_{max} that is typical of deserts. Our results support the existence of a common RUE, but the value of RUE_{max} we obtained for the Inner Mongolia steppe region ($1.08 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$ or adjusted $RUE_{max} = 0.78 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$) is much higher than that for North and South America ($0.42 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$) reported in Huxman et al. (2004). The difference may be attributed to several factors. First, the scale of analysis may directly affect the absolute value of RUE. For example, at the continental scale, the mean RUE for different biomes of North and South America is $0.51 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$ (Huxman et al. 2004). Within North America, the mean RUE is $0.65 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$ for semiarid ecosystems and drops to $0.44 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$ for subhumid and humid ecosystems (Knapp and Smith 2001). At a finer scale, the mean RUE for the Great Plains grassland of the United States is $0.73\text{--}0.82 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$ or $RUE_{adj} = 0.49\text{--}0.54 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$ (Epstein et al. 1996, Burke et al. 1997, Lauenroth et al. 2000). Second, the higher RUE in the Inner Mongolia steppe region may result partly from the synchronized rainfall and temperature, both peaking in July. Third, the regression method for estimating RUE without adjustments used in Huxman et al. (2004) may have introduced errors into their analysis (Veron et al. 2005).

In addition, our result of RUE for the two widely distributed steppe communities, based on a 24-year data set, suggests that RUE of different ecosystems within the same biome may respond similarly to temporal variation in precipitation even though the absolute value of RUE varies. Also, the ecosystem-level temporal pattern of RUE which decreases with increasing annual precipitation is the opposite of the regional-scale cross-ecosystem spatial pattern. We hypothesize that the differences between spatial and temporal patterns of RUE in the Inner Mongolia steppe region reflect different underlying mechanisms on regional and local ecosystem scales. That is, the regional pattern of RUE is determined primarily by precipitation and N gradients as well as the greater range of biological responses provided by distinctive plant communities, whereas the temporal pattern of RUE for a given ecosystem is influenced mainly by the interaction between water and N availability as well as the limited response capacity of the single ecosystem. Our analysis indicated that the overall mean RUE declined by 25% when the long-term temporal data were incorporated into the regression analysis across arid and semiarid ecosystems in the Inner

Mongolia steppe region. This hypothesis is also consistent with the previous finding from the North American shortgrass steppe that the ANPP–annual-precipitation relationship at the regional scale had a much steeper slope than that at the ecosystem scale, meaning that the regional model will generally overestimate ecosystem productivity in wet years and underestimate it in dry years (Lauenroth and Sala 1992).

Effects of N addition

Our field manipulative experiment with the *L. chinensis* community showed that N addition significantly increased both ANPP and RUE. The claim by Huxman et al. (2004) that $cRUE_{max}$ could not be increased by altering resource availability was only supported by our first year finding. The dramatic increase in RUE in the second and third years was caused by N addition and concurrent changes in species composition and precipitation. In particular, the explosive increase in annuals, with higher relative growth rate and greater growth response to added N, was a main cause for the increase in ANPP and RUE. This indicates that the $cRUE_{max}$ could be substantially increased by chronically altering resource availability, such as N addition.

Implications for global change and ecosystem management

Our findings have several implications for understanding ecological impacts of global climate change and better managing arid and semiarid ecosystems in the Inner Mongolia region and beyond. Global climate change is projected to increase MAP by 30–100 mm and MAT by $\sim 3^\circ\text{C}$ in the next 100 years in the Inner Mongolia steppe, with slightly less precipitation during growing season because almost all the increase in MAP occurs in winter (Ni and Zhang 2000). We expect that ANPP will consequently increase on a regional scale and that the magnitude of change will increase from desert to meadow steppe because of increased RUE, resource availability, and biodiversity along this gradient. However, the regional-scale increase in ANPP will be limited by several ecosystem-level factors, including elevated N limitation and enhanced evapotranspiration associated with increased MAT.

Our results also suggest that the spatial relationship between ANPP and MAP is not appropriate for predicting the response of ANPP to temporal variation in precipitation for a given ecosystem because the specific patterns of both ANPP and RUE differ with scale. Finally, a key to increasing the primary production of arid and semiarid ecosystems is to improve RUE, and our study indicates that this can be achieved by improving N availability as well as other measures of conserving biodiversity and ecosystem functioning through management practices that control overgrazing and soil erosion.

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LITERATURE CITED

- Austin, A. T. 2002. Differential effects of precipitation on production and decomposition along a rainfall gradient in Hawaii. *Ecology* 83:328–338.
- Bai, Y. F. 1999. Influence of seasonal distribution of precipitation on primary productivity of *Stipa krylovii* community. *Acta Phytocologica Sinica* 23:155–160.
- Bai, Y. F., X. G. Han, J. G. Wu, Z. Z. Chen, and L. H. Li. 2004. Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature* 431:181–184.
- Bai, Y. F., L. H. Li, J. H. Huang, and Z. Z. Chen. 2001. The influence of plant diversity and functional composition on ecosystem stability of four *Stipa* communities in the Inner Mongolia Plateau. *Acta Botanica Sinica* 43:280–287.
- Bai, Y. F., L. H. Li, Q. B. Wang, L. X. Zhang, Y. Zhang, and Z. Z. Chen. 2000. Changes in plant species diversity and productivity along gradients of precipitation and elevation in the Xilin River Basin, Inner Mongolia. *Acta Phytocologica Sinica* 24:667–673.
- Bai, Y. F., J. G. Wu, Q. M. Pan, J. H. Huang, Q. B. Wang, F. S. Li, A. Buyantuyev, and X. G. Han. 2007. Positive linear relationship between productivity and diversity: evidence from the Eurasian steppe. *Journal of Applied Ecology* 44: 1023–1034.
- Bai, Y. F., L. X. Zhang, Y. Zhang, and Z. Z. Chen. 2002. Changes in plant functional composition along gradients of precipitation and temperature in the Xilin river basin, Inner Mongolia. *Acta Phytocologica Sinica* 26:308–316.
- Briggs, J. M., and A. K. Knapp. 1995. Interannual variability in primary production in tallgrass prairie: climate, soil-moisture, topographic position, and fire as determinants of aboveground biomass. *American Journal of Botany* 82: 1024–1030.
- Burke, I. C., W. K. Lauenroth, and W. J. Parton. 1997. Regional and temporal variation in net primary production and nitrogen mineralization in grasslands. *Ecology* 78:1330–1340.
- Burke, I. C., W. K. Lauenroth, M. A. Vinton, P. B. Hook, R. H. Kelly, H. E. Epstein, M. R. Aguiar, M. D. Robles, M. O. Aguilera, K. L. Murphy, and R. A. Gill. 1998. Plant-soil interactions in temperate grasslands. *Biogeochemistry* 42: 121–143.
- CAAS Grassland Research Institute. 1996. Dynamic monitoring of grassland ecosystems in northern China: the dataset. Inner Mongolia University Press, Hohhot, China.
- Cable, D. R. 1975. Influence of precipitation on perennial grass production in the semidesert southwest. *Ecology* 56:981–986.
- Chapin, F. S., III, P. A. Matson, and H. A. Mooney. 2002. Principles of terrestrial ecosystem ecology. Springer-Verlag, New York, New York, USA.
- Chapin, F. S., III, P. M. Vitousek, and K. Vanclve. 1986. The nature of nutrient limitation in plant communities. *American Naturalist* 127:48–58.
- Chen, S. P., Y. F. Bai, and X. G. Han. 2003. Variations in composition and water use efficiency of plant functional groups based on their water ecological groups in the Xilin River Basin. *Acta Botanica Sinica* 45:1251–1260.
- Chen, S. P., Y. F. Bai, G. H. Lin, J. H. Huang, and X. G. Han. 2007. Variations in $\delta^{13}\text{C}$ values among major plant community types in the Xilin River Basin, Inner Mongolia, China. *Australian Journal of Botany* 55:48–54.
- Chen, S. P., Y. F. Bai, L. X. Zhang, and X. G. Han. 2005. Comparing physiological responses of two dominant grass species to nitrogen addition in Xilin River Basin of China. *Environmental and Experimental Botany* 53:65–75.
- Chinese Academy of Sciences: Integrative Expedition Team to Inner Mongolia and Ningxia. 1985. The vegetation of Inner Mongolia. Science Press, Beijing, China.
- Coupland, R. T. 1992. Ecosystems of the world 8A. Natural grasslands: introduction and Western Hemisphere. Elsevier, Amsterdam, The Netherlands.
- Coupland, R. T. 1993. Ecosystems of the world 8B. Natural grasslands: Eastern Hemisphere and résumé. Elsevier, Amsterdam, The Netherlands.
- Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate extremes: observations, modeling, and impacts. *Science* 289:2068–2074.
- Epstein, H. E., I. C. Burke, and W. K. Lauenroth. 1999. Response of the shortgrass steppe to changes in rainfall seasonality. *Ecosystems* 2:139–150.
- Epstein, H. E., W. K. Lauenroth, I. C. Burke, and D. P. Coffin. 1996. Ecological responses of dominant grasses along two climatic gradients in the Great Plains of the United States. *Journal of Vegetation Science* 7:777–788.
- Eviner, V. T., and F. S. Chapin, III. 2003. Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. *Annual Review of Ecology, Evolution, and Systematics* 34:455–485.
- Grime, J. P. 1977. Evidence for existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111:1169–1194.
- Guo, R., X. K. Wang, Z. Y. Ouyang, and Y. N. Li. 2006. Spatial and temporal relationships between precipitation and ANPP of four types of grasslands in northern China. *Journal of Environmental Sciences* 18:1024–1030.
- Hanson, C. L., J. R. Wight, J. P. Smith, and S. Smoliak. 1982. Use of historical yield data to forecast range herbage production. *Journal of Range Management* 35:614–616.
- Hector, A., et al. 1999. Plant diversity and productivity experiments in European grasslands. *Science* 286:1123–1127.
- Hooper, D. U., and L. Johnson. 1999. Nitrogen limitation in dryland ecosystems: responses to geographical and temporal variation in precipitation. *Biogeochemistry* 46:247–293.
- Hooper, D. U., and P. M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. *Science* 277:1302–1305.
- Huxman, T. E., et al. 2004. Convergence across biomes to a common rain-use efficiency. *Nature* 429:651–654.
- Inner Mongolia Soil Census Office and Inner Mongolia Soil and Fertilizer Service. 1994. The soils of Inner Mongolia. Science Press, Beijing, China.
- Knapp, A. K., and M. D. Smith. 2001. Variation among biomes in temporal dynamics of aboveground primary production. *Science* 291:481–484.
- Lauenroth, W. K., I. C. Burke, and J. M. Paruelo. 2000. Patterns of production and precipitation-use efficiency of winter wheat and native grasslands in the Central Great Plains of the United States. *Ecosystems* 3:344–351.
- Lauenroth, W. K., J. L. Dodd, and P. L. Sims. 1978. The effects of water-induced and nitrogen-induced stresses on plant community structure in a semi-arid grassland. *Oecologia* 36: 211–222.
- Lauenroth, W. K., and O. E. Sala. 1992. Long-term forage production of North American shortgrass steppe. *Ecological Applications* 2:397–403.

- Le Houérou, H. N. 1984. Rain use efficiency: a unifying concept in arid-land ecology. *Journal of Arid Environments* 7:213–247.
- Le Houérou, H. N., R. L. Bingham, and W. Skerbek. 1988. Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. *Journal of Arid Environments* 15:1–18.
- Leith, H., and R. H. Whittaker. 1975. *Primary productivity of the biosphere*. Springer, New York, New York, USA.
- Li, B. 1993. *Dynamic monitoring of grassland ecosystems in northern China: the design on technical implementation*. Agricultural Science and Technology Press of China, Beijing, China.
- Loreau, M., and A. Hector. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72–76.
- Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294:804–808.
- McNaughton, S. J. 1985. Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs* 55:259–294.
- McNaughton, S. J., M. Oesterheld, D. A. Frank, and K. J. Williams. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature* 341:142–144.
- Melillo, J. M., A. D. McGuire, D. W. Kicklighter, B. Moore III, C. J. Vorosmarty, and A. L. Schloss. 1993. Global climate change and terrestrial net primary production. *Nature* 363:234–240.
- Ni, J., and X. S. Zhang. 2000. Climate variability, ecological gradient and the Northeast China Transect (NECT). *Journal of Arid Environments* 46:313–325.
- Noy-Meir, I. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4: 25–51.
- O'Connor, T. G., L. M. Haines, and H. A. Snyman. 2001. Influence of precipitation and species composition on phytomass of a semi-arid African grassland. *Journal of Ecology* 89:850–860.
- Paruelo, J. M., W. K. Lauenroth, I. C. Burke, and O. E. Sala. 1999. Grassland precipitation-use efficiency varies across a resource gradient. *Ecosystems* 2:64–68.
- Qian, H., P. S. White, and J.-S. Song. 2007. Effects of regional vs. ecological factors on plant species richness: an intercontinental analysis. *Ecology* 88:1440–1453.
- Reynolds, J. F., and D. M. Stafford Smith. 2002. Do humans cause deserts? Pages 1–21 in J. F. Reynolds and D. M. Stafford Smith, editors. *Global desertification: do humans cause deserts?* Dahlem University Press, Berlin, Germany.
- Rosenzweig, M. L. 1968. Net primary productivity of terrestrial communities: prediction from climatological data. *American Naturalist* 102:67–74.
- Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1988. Primary production of the central grassland region of the United States. *Ecology* 69:40–45.
- Sankaran, M., et al. 2005. Determinants of woody cover in African savannas. *Nature* 438:846–849.
- Schimel, D. S., et al. 1997. Continental scale variability in ecosystem processes: models, data, and the role of disturbance. *Ecological Monographs* 67:251–271.
- Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs* 57:189–214.
- Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277:1300–1302.
- Tilman, D., P. B. Reich, and J. M. H. Knops. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* 441:629–632.
- U.S. National Research Council. 1992. *Grasslands and grassland sciences in northern China*. National Academy Press, Washington, D.C., USA.
- Veron, S. R., M. Oesterheld, and J. M. Paruelo. 2005. Production as a function of resource availability: slopes and efficiencies are different. *Journal of Vegetation Science* 16:351–354.
- Vitousek, P. M., and R. W. Howarth. 1991. Nitrogen limitation on land and in the sea: how can it occur? *Biogeochemistry* 13: 87–115.
- Weltzin, J. F., et al. 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. *BioScience* 53:941–952.
- Wu, J., and O. L. Loucks. 1992. Xilinge. Pages 67–84 in *The U.S. National Research Council, editor. Grasslands and grassland sciences in northern China*. National Academy Press, Washington, D.C., USA.
- Wu, J., and O. L. Loucks. 1995. From balance-of-nature to hierarchical patch dynamics: a paradigm shift in ecology. *Quarterly Review of Biology* 70:439–466.
- Wu, J. G., K. B. Jones, H. B. Li, and O. L. Loucks. 2006. Scaling and uncertainty analysis in ecology: methods and applications. Springer, Dordrecht, The Netherlands.
- Xiao, C., I. A. Janssens, P. Liu, Z. Zhou, and O. J. Sun. 2007. Irrigation and enhanced soil carbon input effects on below-ground carbon cycling in semiarid temperate grasslands. *New Phytologist* 174:835–846.