

Observation and modeling of plant biomass of meadow steppe in Tumugi, Xingan League, Inner Mongolia, China

Xiangming Xiao^{1,2,*}, Du Chen², Yumei Peng³, Xianyi Cui³ & Dennis S. Ojima^{1,2}

¹Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523, USA; ²Department of Rangeland Ecosystem Science, Colorado State University, Fort Collins, CO 805523, USA; ³Tumugi Institute of Grasslands, Xingan League, Inner Mongolia Autonomous Region, China; (*present address: The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA 02543, USA)

Received 21 August 1994; accepted in revised form 26 July 1996

Key words: Ecosystem model, Grasslands, Primary production, Rain use efficiency, Temporal variability

Abstract

We examined the long-term dynamics of plant biomass of *Filifolium sibiricum* steppe, *Stipa baicalensis* steppe and *Leymus chinense* (syn. *Aneurolepidium chinense*) steppe relative to interannual variation of precipitation and temperature during 1981–1990 in the Tumugi, Xingan League, eastern Inner Mongolia of China. On the average, annual precipitation was 41.1 cm. Peak live aboveground biomass (PLAB) was 152 g m⁻² for *F. sibiricum* steppe and *S. baicalensis* steppe and 162 g m⁻² for *L. chinense* steppe. Peak live belowground biomass (PLBB) varied between 968 g m⁻² for *F. sibiricum* steppe and 1022 g m⁻² for *L. chinense* steppe. The coefficient of variation (CV) in annual precipitation (25%) was lower than the CV in PLAB (35% to 37%) but larger than the CV in PLBB (10%) of the three meadow steppe sites. Rain use efficiency was 3.6 gDM m⁻² cm⁻¹ yr⁻¹ for *F. sibiricum* steppe and *S. baicalensis* steppe, and 3.9 gDM m⁻² cm⁻¹ yr⁻¹ for *L. chinense* steppe, respectively.

Using the CENTURY ecosystem model, simulation results agreed reasonably well with the observed soil organic matter, seasonal dynamics and interannual variation of plant biomass of these three steppe sites during 1981–1990. The CENTURY model is slightly more successful than the empirical regression models that use annual precipitation to estimate PLAB of these meadow steppe over time. Both seasonal distribution and interannual variation in precipitation and temperature are the important controls of temporal dynamics of plant biomass, rain use efficiency, carbon flux and storage of these meadow steppe ecosystems over time.

Introduction

Abundant literature indicates that climate, soil texture, livestock grazing, and cultivation are important controls of spatial patterns of net primary production (NPP) and soil organic matter of grasslands. At regional and global scales, spatial patterns of net primary production of grasslands are strongly correlated to annual precipitation (Sims and Singh 1978; Lauenroth 1979; Le Houérou 1984; Sala et al. 1988; Wang et al. 1991; Parton et al. 1993). However, few field ecological studies have focused on the long-term dynamics of net primary production of grasslands (Towne and Owensby 1984; Smoliak 1986; Le Houérou 1988; Lauenroth and Sala 1992), particularly

grasslands in Inner Mongolia of China (Xing and Lin 1993; Xiao et al. 1995a, 1996). Information on interannual variation in net primary production of grasslands is essential to determine the stocking rate of livestock for rangeland ecosystem management and to project the response of grassland ecosystems to CO₂-induced global climate change.

Dominant meadow steppes in the eastern Inner Mongolia of China are *Filifolium sibiricum* steppe, *Stipa baicalensis* steppe and *Leymus chinense* (syn. *Aneurolepidium chinense*) steppe, and their total area in Inner Mongolia is about 5 million ha (Zhang 1990). These meadow steppe ecosystems are widely distributed in the Euro-asian steppe zone (Wang 1985; Wu 1980). Meadow steppe provides good-quality forage

to livestock and are used mainly as natural grazing lands for livestock. Net primary production of these grasslands varies considerably over space (Wang et al. 1991) and is also very sensitive to interannual variation of precipitation and temperature (Xing and Liu 1993) and land use change (Zhang 1990).

In this study, we examined a 10-year data set of climate and plant biomass of *F. sibiricum* steppe, *S. baicalensis* steppe and *L. chinense* steppe over the period of 1981–1990 in the Tumugi, Xingan League, Inner Mongolia. First, we calculated the temporal variations in precipitation, temperature, net primary production and rain use efficiency for these meadow steppes. Second, we used regression models to establish the quantitative relationships between key climatic variables and net primary production in the domain of time. However, the empirical NPP-climate regression models have limited potential to be used to project responses of grasslands to climate change and land use change. Therefore, we applied a process-based ecosystem model (CENTURY, Parton et al. 1987, 1988, 1993) to simulate dynamics of plant biomass and soil organic matter in the three meadow steppe ecosystems. The CENTURY model has been tested, using observed data from 11 temperate and tropical grassland sites in the world (Parton et al. 1993) and from typical steppe of Inner Mongolia (Xiao et al. 1996). We used the field data to validate the CENTURY plant-soil ecosystem model (Parton et al. 1987, 1993) for meadow steppe ecosystems in the eastern Inner Mongolia, China. This study is part of a larger project that studies climate and soil texture controls of spatial-temporal variations of grassland ecosystems in Inner Mongolia of China from patch to regional scales.

Study sites and methods

Study sites

The field study sites are located at Tumugi, Xingan League, eastern Inner Mongolia, within 122°46'–123°07' E longitude and 46°04'–46°13' N latitude. Elevation in Tumugi area ranges from 136 to 246 m. Climate is continental sub-humid and is dominated by monsoon rains. Winter is usually cold and dry, whereas summer is warm and wet. Averaged over the period of 1960–1993, annual mean temperature and annual precipitation were 4.3 °C and 39.5 cm, respectively. Precipitation is concentrated in April–September. Non-frost period lasts about 132 days. Plants initiate growth

in early April and become senescent in mid-October. The natural *F. sibiricum* steppe, *S. baicalensis* steppe and *L. chinense* steppe are dominated by C₃ plants and are representative of meadow steppes in eastern Inner Mongolia. In Tumugi area, natural grasslands are grazed by sheep and cattle at moderate grazing intensity.

The three study sites (250 m × 40 m each) for natural *F. sibiricum* steppe, *S. baicalensis* steppe and *L. chinense* steppe were established in 1976 for long-term monitoring of net primary production. Each of three sites is divided up into five 50 m × 40 m subplots for field observations. The sites are representative of meadow steppe in Tumugi area and have been fenced to protect from livestock grazing since 1976. The sites are rich in species composition. The *S. baicalensis* steppe site includes *L. chinense* and *F. sibiricum*. The *F. sibiricum* site includes *L. chinense* and *S. baicalensis*. The *L. chinense* site includes *S. baicalensis*.

Soils in Tumugi area are mostly chernozem and dark chestnut (Mollisols). There are slight differences in soil depth and texture at the top 20 cm among the *F. sibiricum* steppe site, *S. baicalensis* steppe site, and *L. chinense* steppe site. In soil texture analysis, soil particle size was measured at such scales as <0.001 mm, 0.001–0.005 mm, 0.005–0.01 mm, 0.01–0.05 mm, 0.05–1.0 mm and >1.0 mm. Clay was defined as having particle size of <0.005 mm and sand as >0.05 mm. In the *F. sibiricum* site, the B horizon is usually less than 70 cm deep, and soil texture is about 33% of clay, 35% of sand and 32% of silt. In the *S. baicalensis* site, the B horizon is about 100 cm deep, and soil texture is about 37% of clay, 42% of sand and 21% of silt. In the *L. chinense* site, the B horizon is usually about 120 cm deep, soil texture is about 35% of clay, 43% of sand and 22% of silt. Soil of the *L. chinense* steppe site is relatively deeper and has coarser texture, compared to soils of the *F. sibiricum* steppe site and *S. baicalensis* steppe site.

Vegetation sampling

In the fenced sites of *F. sibiricum* steppe, *S. baicalensis* steppe and *L. chinense* steppe, field sampling has been conducted at the 15th day of each month from April to November since 1981. One 1-m² quadrat was randomly placed within each of the five subplots at each sampling date. Plant species, density, cover, height and phenological phase were recorded. Aboveground biomass was measured by the harvest technique. Plant materials were clipped to the ground surface and litter

on the harvested quadrats was collected by hand. At the laboratory, the clipped aboveground plant material was separated for live biomass and standing dead.

Belowground standing biomass was sampled from $1 \times 1 \times 1 \text{ m}^3$ of soil cores. At the laboratory, root materials were sorted by hand from soil and washed using 0.5 mm sieve. Live root and dead root were visually separated out, using the criteria of attachment to individual plants, color (green) and flexibility. Most of roots are distributed within surface to 40 or 50 cm depth. A Calcium layer exists usually under 60 cm deep.

Both the clipped aboveground plant materials and root materials were oven-dried at 65°C at the laboratory and weighed as dry weight (g m^{-2}). In this paper, we used data of live aboveground biomass and belowground biomass of plant community during 1981–1990.

Data analysis

There are many methods of estimating annual aboveground net primary production (ANPP) of grasslands, which use data of plant biomass (Singh et al. 1975). In this paper, we used peak live aboveground biomass (PLAB) as a crude estimate of ANPP, because it is relatively simple and practical. Linear regression analysis was applied to establish the quantitative relationship between climatic variables and PLAB of *F. sibiricum* steppe, *S. baicalensis* steppe and *L. chinense* steppe over time. The climate data from the local weather station include monthly precipitation and monthly minimum/maximum/mean temperature in the period of 1981–1990. Climatic variables used in regression analysis are annual precipitation, total precipitation in April–September, monthly precipitation, monthly maximum and minimum temperature, and average maximum and minimum temperature in April–September. A forward model selection algorithm was applied to select climatic variables that are statistically significant in relation to PLAB at $\alpha = 0.05$ level (SAS Institute Inc. 1985).

Rain use efficiency is defined as the ratio of ANPP to annual precipitation (Le Houérou 1984), in the unit of $\text{gDM m}^{-2} \text{ cm}^{-1} \text{ yr}^{-1}$. We used the coefficient of variation (CV) as an index of variability for climate and plant biomass. We also used the Production to Rain Variability Ratio, which is defined as the ratio of the coefficient of variation in ANPP over the coefficient of variation in annual precipitation (Le Houérou et al. 1988), to evaluate the significance of the relationship

between the variability of primary production and the variability of annual precipitation.

The description of the CENTURY model

The CENTURY model (Parton et al. 1987, 1988, 1993), a general computer model of plant-soil ecosystems, simulates dynamics of carbon (C), nitrogen (N) of different types of terrestrial ecosystems at monthly time step (Figure 1). The model consists of plant production submodels, soil organic matter (SOM) submodel and water budget submodel. There are three plant production submodels: grasslands, forests and crops. These plant production submodels are linked to the common SOM submodel. The SOM submodel simulates the dynamics of C and N in the organic and inorganic parts of the soil system. The soil organic carbon is divided up into three major components which include active (microbe), slow and passive soil carbon. The simplified water budget submodel calculates monthly evaporation and transpiration water loss, water content of soil layers, snow water content and saturated flow of water between soil layers.

The parameters for the CENTURY model was mostly derived from the information of shortgrass steppe in the Central Plain grasslands of United States (Parton et al. 1987, 1988). Major site-specific input variables include monthly climate (monthly minimum and maximum temperature, monthly precipitation), plant chemistry characteristics (e.g., lignin content, plant N content) and soil properties (e.g., soil texture, soil depth, soil pH, bulk density, C and N levels). The CENTURY model was already calibrated to two types of typical steppe (*S. grandis* steppe and *L. chinense* steppe) in the Xilin river basin of the central Inner Mongolia (Xiao et al. 1996). In addition to the site-specific parameters, the most significant difference in model parameters between typical steppe in the Xilin river basin of Inner Mongolia and short grass steppe in the Central Plain grasslands of Northern America is that higher nitrogen input was assumed for typical steppe of Inner Mongolia (Xiao et al. 1996), as was done in Russian and Mongolian grasslands (Parton et al. 1993).

We used PC version 3.0 of CENTURY in this study (see Parton et al. 1992, 1993 for detailed description of the version 3.0). We used the same climate data set in the CENTURY simulation for the three sites. The information on soil properties (e.g. soil texture, soil depth) among the three sites were implemented. First, we ran the model for 5000 years, using long-term average climate data, so that soil organic matter

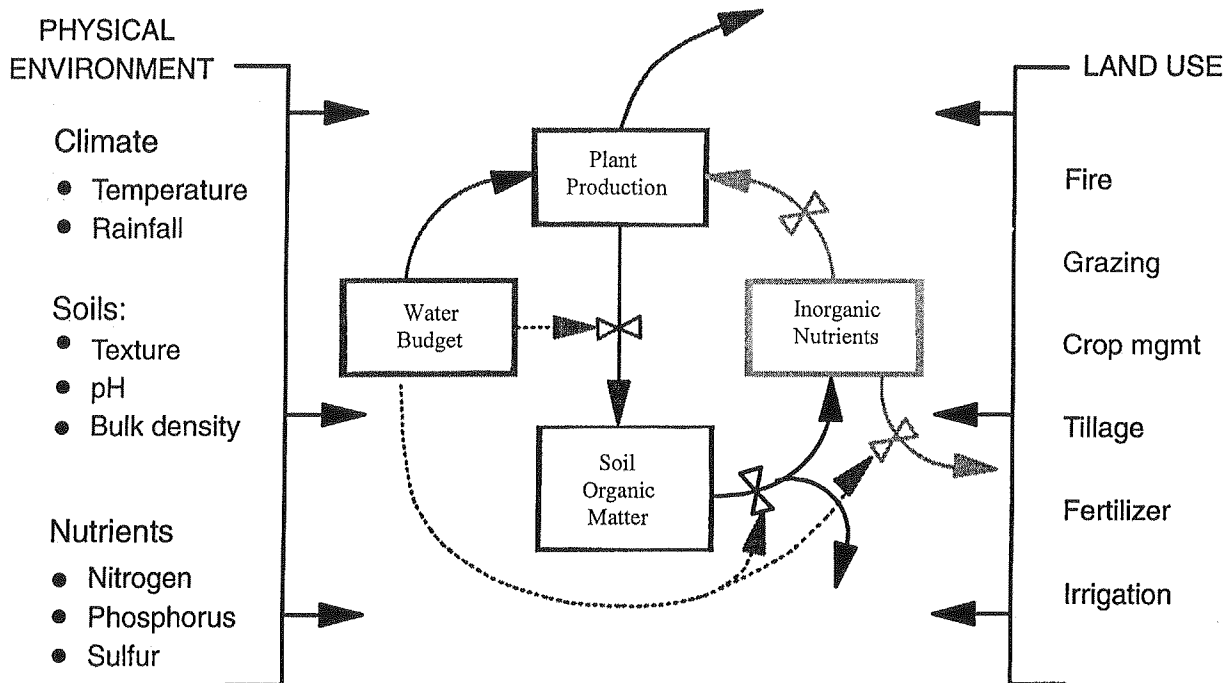


Figure 1. The schematic diagram of the CENTURY ecosystem model.

reached equilibrium levels. The equilibrium levels of soil organic matter were then taken as initial conditions for the validation run. Next, using actual weather data during 1981–1990, the CENTURY model was run again under no grazing conditions. Such model output variables as soil organic carbon level at the top 20 cm soil, aboveground live biomass and belowground live biomass were selected to compare with the observed data. We used three techniques for testing the CENTURY model: (1) linear regression of the observed data versus simulation results, (2) comparison of CENTURY model predictions with empirical regression model based on climate variables, and (3) graph comparison of CENTURY model predictions with observed data.

Results

Interannual variation in climate, plant biomass and rain use efficiency

Annual mean temperature varied slightly during the period of 1981–1990, ranging from 3.4 °C in 1984 to 5.4 °C in 1982 (Figure 2). On the average, annual mean temperature during 1981–1990 was 4.5 °C. There was

a slight interannual variation in seasonal distribution of temperature (Figure 2). Seasonal distribution of temperature determines the beginning and length of plant growing season. Plants usually turn green in April. In the field, we observed that plants initiated growth in March 1989, which is likely to be related to high monthly maximum temperature in March (5.2 °C).

Over the period of 1981–1990, there was a large interannual variation in precipitation (Figure 2). The mean and the coefficient of variation (CV) in annual precipitation were 41.1 cm and 25%, respectively. Precipitation was concentrated in plant growing season. Total precipitation in April–September varied from 16.6 cm in 1982 to 49.3 cm in 1988, with a mean of 38.7 cm and a CV of 24%. Monthly precipitation in July varied from 6.1 cm in 1982 to 24.8 cm in 1986. Monthly precipitation in August ranged between 5.2 cm in 1989 and 16.2 cm in 1987. On the average, monthly precipitation is the largest in July (15.3 cm) and second largest in August (9.0 cm). The coefficient of variation in monthly precipitation is also large in July (39%) and August (51%). This large variation in seasonal distribution of precipitation may have significant effects on plant growth and biomass production.

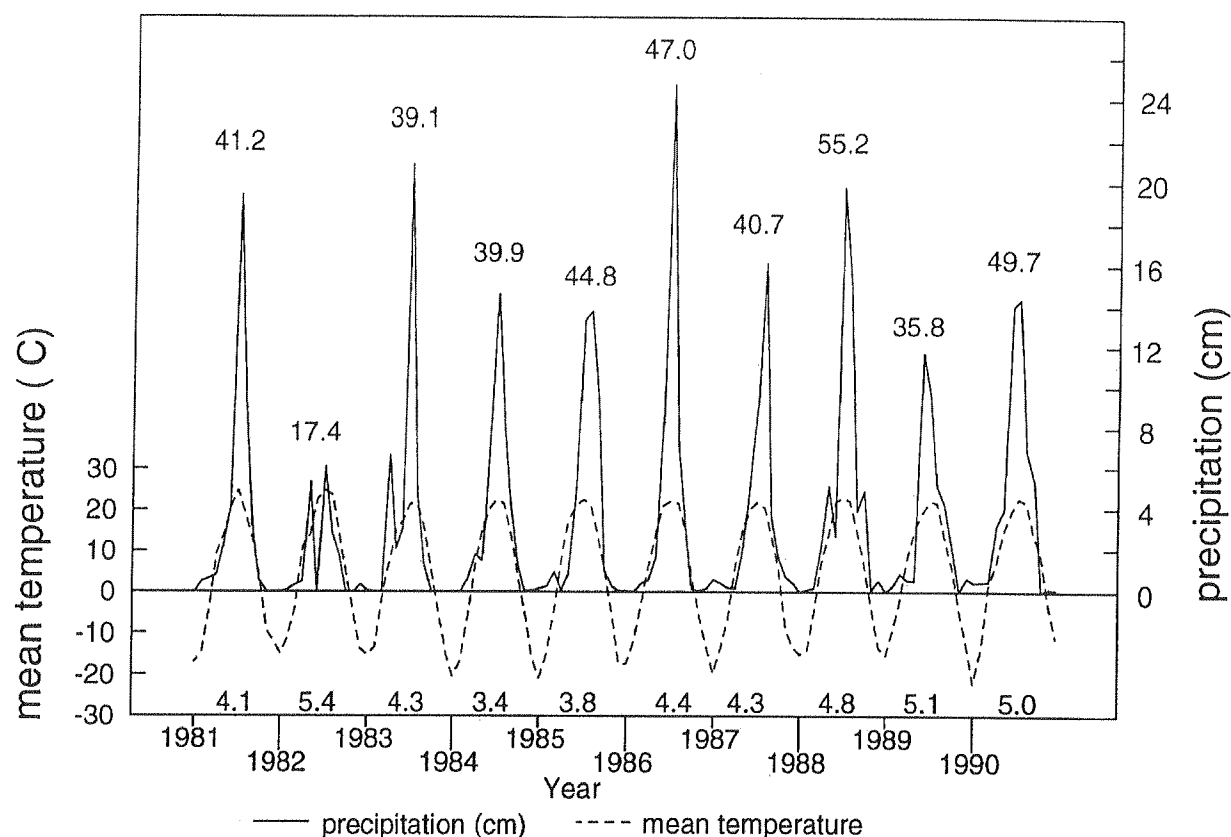


Figure 2. Interannual variation in precipitation and temperature during 1981–1990 in Turnugi, Xingan League, Inner Mongolia, China. The number on the top are annual precipitation (cm) and the numbers on the bottom are annual mean temperature ($^{\circ}\text{C}$).

Table 1. The mean and coefficient of variation (CV, %) in peak live aboveground biomass (PLAB, g m^{-2}), peak live belowground biomass (PLBB, g m^{-2}) and rain use efficiency (RUE, $\text{gDM m}^{-2} \text{ cm}^{-1} \text{ yr}^{-1}$) for *Filifolium sibiricum* steppe, *Stipa baicalensis* steppe and *Leymus chinense* steppe over the period of 1981–1990.

Variable	<i>Filifolium sibiricum</i> steppe	<i>Stipa baicalensis</i> steppe	<i>Leymus chinense</i> steppe
mean in PLAB	152	152	162
CV in PLAB	37%	36%	35%
mean in PLBB	968	983	1022
CV in PLBB	9.7%	9.9%	10.3%
mean in RUE	3.6	3.6	3.9
CV in RUE	20%	20%	18%

Peak live aboveground biomass (PLAB) of the three sites varied considerably over the period of 1981–1990 (Figure 3). PLAB of the *S. baicalensis* steppe site was similar to PLAB of the *F. sibiricum* steppe site. On the average, PLAB of the *L. chinense* steppe site was approximately 7% higher than PLAB of the *S. baicalensis* site and the *F. sibiricum* site (Table 1).

Similarly, peak live belowground biomass (PLBB) of the *L. chinense* site was slightly higher than PLBB of the other two sites (Figure 3, Table 1). The PLBB of these three meadow steppe sites has much smaller interannual variation than PLAB of the sites (Figure 3). The coefficient of variation (CV) in PLBB for the three sites during 1981–1990 were approximately 10% (Table 1).

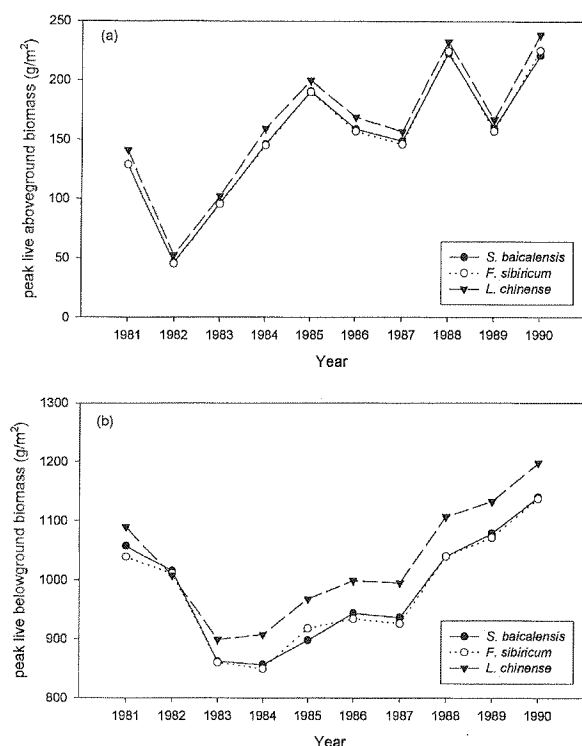


Figure 3. Interannual variation in plant biomass of *Filifolium sibiricum* steppe, *Stipa baicalensis* steppe and *Leymus chinense* steppe during 1981–1990. (a) peak live aboveground biomass and (b) peak live belowground biomass.

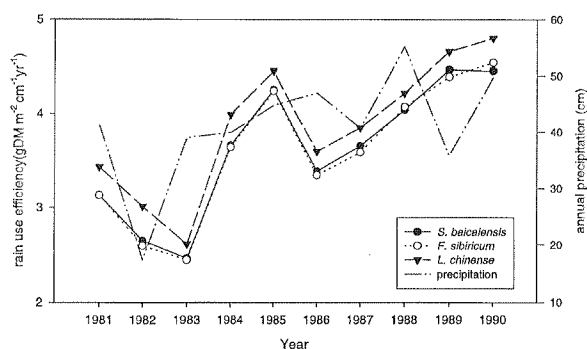


Figure 4. Interannual variation in rain use efficiency of *Filifolium sibiricum* steppe, *Stipa baicalensis* steppe and *Leymus chinense* steppe during 1981–1990.

Over the period of 1981–1990, rain use efficiencies (RUE) of both the *F. sibiricum* steppe site and the *S. baicalensis* steppe site ranged from 2.4 gDM m⁻² cm⁻¹ yr⁻¹ in 1983 to 4.5 gDM m⁻² cm⁻¹ yr⁻¹ in 1990 (Figure 4). Rain use efficiency of *L. chinense* steppe site varied between 2.6 gDM m⁻² cm⁻¹ yr⁻¹ in 1983 and 4.8 gDM m⁻² cm⁻¹ yr⁻¹ in 1990. Rain use

efficiency was the lowest in 1983 but not in the most drought year 1982. It may be attributed to previous-year vegetation condition and seasonal distribution of precipitation (Figure 4). The RUE in 1986 is also lower than the RUE in 1985 and 1987, although annual precipitation was higher in 1986 than in 1985 and 1987.

In the severe drought year 1982, aboveground biomass and belowground biomass reduced significantly (Figure 3, 5, 6, 7). Aboveground biomass responded positively to the increase in annual precipitation in the following years, but belowground biomass continued to drop considerably in 1983 (Figures 3, 5, 6, 7). Belowground biomass increased in 1985 and reached the similar biomass level of year 1981 in 1988. The field observations show clearly that severe drought has more significant impact on belowground biomass than on aboveground biomass of meadow steppe.

The quantitative relationship between PLAB and climate over time

Linear regression analysis show that peak live aboveground biomass of *F. sibiricum* steppe, *S. baicalensis* steppe and *L. chinense* steppe are significantly correlated to annual precipitation (P_{ann} , cm) at $p \leq 0.05$ level (see model 1, 5 and 9 in Table 2). Increase of 1 cm in annual precipitation may result in an increase of PLAB by 4.9 g m⁻² for *F. sibiricum* steppe, 4.8 g m⁻² for *S. baicalensis* steppe and 5.0 g m⁻² for *L. chinense* steppe. PLAB of the three sites is also significantly related to total precipitation in April–September (P_{49} , cm) at $p \leq 0.05$ level (see model 2, 6, and 10 in Table 2). Annual precipitation has slightly higher r^2 values with PLAB of these three meadow steppes than total precipitation in April–September (Table 2). Precipitation in July (R_7 , cm) is significantly but negatively correlated to PLAB of *F. sibiricum* steppe ($\text{PLAB}_F = -49.5 - 4.6 \times R_7 + 6.6 \times P_{\text{ann}}$, $r^2 = 0.93$, $p = 0.0001$), *S. baicalensis* steppe ($\text{PLAB}_S = -45.0 - 4.6 \times R_7 + 6.5 \times P_{\text{ann}}$, $r^2 = 0.94$, $p = 0.0001$) and *L. chinense* steppe ($\text{PLAB}_L = -42.7 - 4.7 \times R_7 + 6.7 \times P_{\text{ann}}$, $r^2 = 0.93$, $p = 0.0001$) at $p \leq 0.05$ level. While holding annual precipitation constant, a decrease of 1 cm in precipitation in July may result in an increase of PLAB by about 4.6 g m⁻² for *F. sibiricum* steppe, 4.6 g m⁻² for *S. baicalensis* steppe and 4.7 g m⁻² for *L. chinense* steppe, respectively. This negative correlation between PLAB and precipitation in July indicates that PLAB could be higher if the weather system allowed this 1 cm precipitation to be distributed to the other months rather than in July, while holding annu-

Table 2. Relationships between climatic variables and peak live aboveground biomass (PLAB, g m^{-2}) of *Filifolium sibiricum* steppe, *Stipa baicalensis* steppe and *Leymus chinense* steppe over the period of 1981–1990.

Vegetation	Regression model	r^2	P	N	#
<i>Filifolium sibiricum</i> steppe	$\text{PLAB}_F = -48.3 + 4.9 \times P_{\text{ann}}$	0.79	0.0006	10	1
	$\text{PLAB}_F = -36.9 + 4.9 \times P_{49}$	0.70	0.0026	10	2
	$\text{PLAB}_F = -96.7 + 17.5 \times \text{MIT}_8$	0.65	0.0049	10	3
	$\text{PLAB}_F = 1541.0 - 58.6 \times \text{MIT}_{49}$	0.68	0.0034	10	4
<i>Stipa baicalensis</i> steppe	$\text{PLAB}_S = -43.9 + 4.8 \times P_{\text{ann}}$	0.79	0.0006	10	5
	$\text{PLAB}_S = -32.3 + 4.8 \times P_{49}$	0.69	0.0027	10	6
	$\text{PLAB}_S = -94.7 + 17.4 \times \text{MIT}_8$	0.67	0.0039	10	7
	$\text{PLAB}_L = 1528.0 - 58.0 \times \text{MXT}_{49}$	0.69	0.0028	10	8
<i>Leymus chinense</i> steppe	$\text{PLAB}_L = -41.5 + 5.0 \times P_{\text{ann}}$	0.79	0.0006	10	9
	$\text{PLAB}_L = -30.4 + 5.0 \times P_{49}$	0.70	0.0025	10	10
	$\text{PLAB}_L = -94.0 + 18.1 \times \text{MIT}_8$	0.66	0.0040	10	11
	$\text{PLAB} = 1606.1 - 60.9 \times \text{MXT}_{49}$	0.71	0.0023	10	12

P_{ann} – annual precipitation (cm); P_{49} – total precipitation in April–September (cm); MIT_8 – monthly minimum temperature in August ($^{\circ}\text{C}$); MXT_{49} – average maximum temperature in April–September ($^{\circ}\text{C}$); N – sample size; # – model number used in the text.

al precipitation constant. In other words, monthly and seasonal distribution of precipitation is important control of PLAB of these three meadow steppes in Tumugui area over time.

PLAB of these three meadow steppes is positively correlated to monthly minimum temperature in August (see model 3, 7 and 11 in Table 2) but negatively correlated to average maximum temperature during April–September at $p \leq 0.05$ level (see model 4, 8 and 12 in Table 2). Average maximum temperature during April–September has a larger impact on PLAB than monthly minimum temperature in August (Table 2). PLAB may decrease 58.6 g m^{-2} for *F. sibiricum* steppe, 58.0 g m^{-2} *S. baicalensis* steppe and 60.9 g m^{-2} for *L. chinense* steppe, due to 1°C increase of average maximum temperature in April–September, while PLAB may increase only 17.5 g m^{-2} for *F. sibiricum* steppe, 17.4 g m^{-2} for *S. baicalensis* steppe and 18.1 g m^{-2} for *L. chinense* steppe, due to 1°C increase of minimum temperature in August (Table 2).

CENTURY simulations of plant biomass and soil organic matter

Soil organic matter integrates changes in plant production and decomposition over time. It is central to the cycling of plant nutrients and influences water

relation, erosion potential and soil structure (Parton et al. 1993). For the CENTURY simulations, steady-state soil organic carbon level at the top 20 cm soil is 6039 gC m^{-2} for *S. baicalensis* steppe site, 6077 gC m^{-2} for the *F. sibiricum* steppe site, and 6142 gC m^{-2} for the *L. chinense* steppe site, respectively. The observed soil organic carbon for the top 20 cm soil is 5654 gC m^{-2} for the *F. sibiricum* steppe site, 6486 gC m^{-2} for the *L. chinense* steppe site and 6812 gC m^{-2} for the *S. baicalensis* steppe site, respectively. The simulated soil organic carbon levels of these three steppe sites are within $\pm 25\%$ of the observed soil organic carbon levels.

Simulated seasonal and interannual dynamics of both aboveground live biomass and belowground live biomass of *F. sibiricum* steppe (Figure 5), *S. baicalensis* steppe (Figure 6) and *L. chinense* steppe (Figure 7) are in good agreement with the observed data during 1981–1990. Simulated data were all within $\pm 25\%$ of the observed data. On the average, simulated PLAB is 152 g m^{-2} for *F. sibiricum* steppe, 161 g m^{-2} for *S. baicalensis* steppe and 167 g m^{-2} for *L. chinense* steppe. The comparison between the observed PLAB (Y) and the simulated PLAB (X) over the period of 1981–1990 resulted in r^2 values greater than 0.9 for all three steppe ecosystems: for *S. baicalensis* steppe, $Y = 29.24 + 0.76 \times X$, $r^2 = 0.92$, $p = 0.0001$;

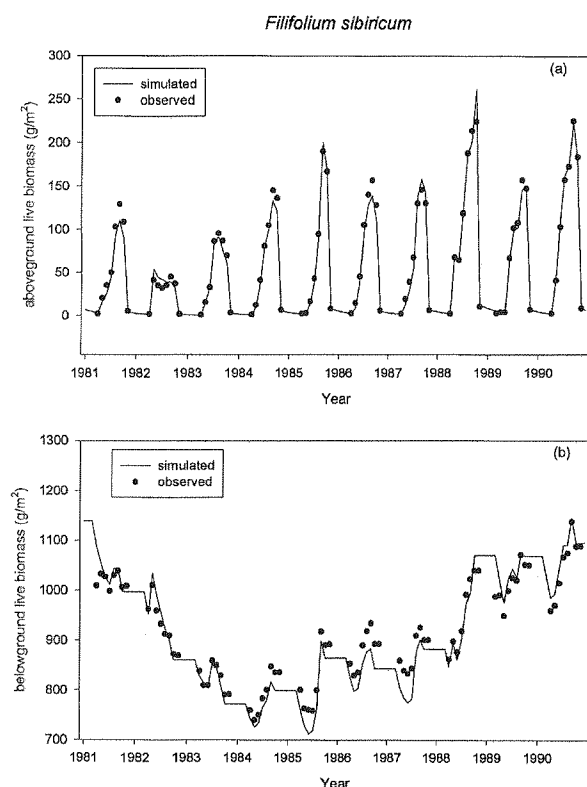


Figure 5. The comparison between the observed and simulated seasonal dynamics of aboveground and belowground live biomass of *Filifolium sibiricum* steppe during 1981–1990. (a) live aboveground biomass and (b) live belowground biomass.

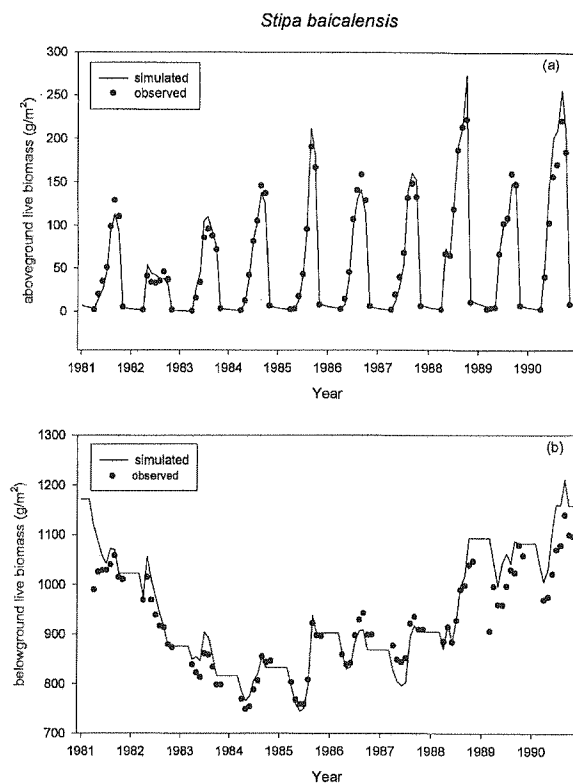


Figure 6. The comparison between the observed and simulated seasonal dynamics of aboveground and belowground live biomass of *Stipa baicalensis* steppe during 1981–1990. (a) live aboveground biomass and (b) live belowground biomass.

for *F. sibiricum* steppe, $Y = 21.65 + 0.85 \times X$, $r^2 = 0.93$, $p = 0.0001$; and for *L. chinense* steppe, $Y = 34.20 + 0.76 \times X$, $r^2 = 0.90$, $p = 0.0001$, respectively. The CENTURY simulations for these meadow steppe ecosystems over this 10-year period predict the interannual variability of PLAB better than the regression models that use annual precipitation to predict PLAB in Tumugi area. In CENTURY, plant production in grasslands is a function of soil temperature and available water, limited by nutrient availability (e.g. N) and a self-shading factor (Parton et al. 1993). Nutrients, especially N, are an important control of primary production of grasslands (Parton et al. 1987, 1988; Wang et al. 1991).

Net annual CO_2 flux ($\text{gC m}^{-2} \text{yr}^{-1}$) of the plant-soil systems is calculated by taking annual net primary production (aboveground plus belowground) minus annual respiration from decomposition. CENTURY simulations show that there is a large interannual variation in net annual CO_2 flux in the three meadow steppe

sites (Figure 8). As shown in Figure 8, the positive flux implies net carbon sink (a net flux of CO_2 from the atmosphere to grasslands), while the negative flux is net carbon source (a net flux of CO_2 from grasslands to the atmosphere). These steppe ecosystems are a net carbon source in 1981, 1983 and 1986 but a net carbon sink in 1982, 1985, 1987, 1988, 1989 and 1990. Net carbon gain of plant-soil systems over the period of 1981–1990 is 66 gC m^{-2} at *F. sibiricum* steppe site, 115 gC m^{-2} at *S. baicalensis* steppe site and 131 gC m^{-2} at *L. chinense* steppe site, respectively. Simulated net carbon gains of plant-soil systems in the three fenced sites are relatively small. Grazing by livestock may have significant impact on carbon storage and flux of these plant-soil systems, as livestock may consume large portion of annual primary production and consequently there is a small amount of litter that remains on the soil surface. Moreover, aboveground and belowground net primary productions, biomass allocation and species composition in grasslands of

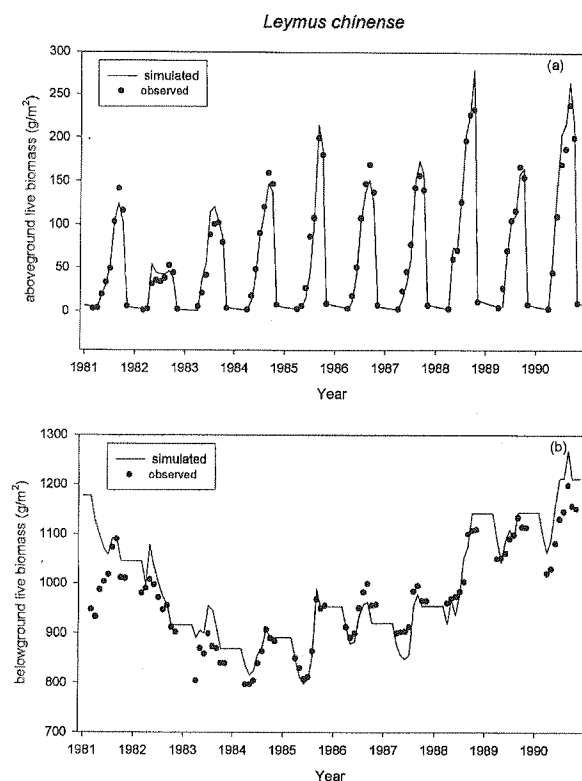


Figure 7. The comparison between the observed and simulated seasonal dynamics of aboveground and belowground live biomass of and *Leymus chinense* steppe during 1981–1990. (a) live aboveground biomass and (b) live belowground biomass.

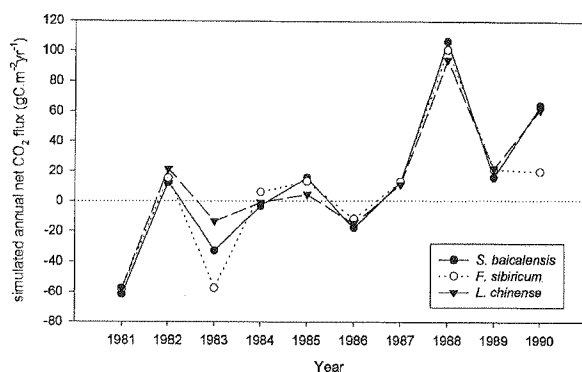


Figure 8. Interannual variation in simulated net annual CO_2 flux of the *Filifolium sibiricum* steppe, *Stipa baicalensis* steppe and *Leymus chinense* steppe sites during 1981–1990.

Inner Mongolia are also greatly affected by livestock grazing (Dong 1992; Li 1989).

Discussion

There are large interannual variations in annual precipitation and seasonal distribution of precipitation over the period of 1981–1990 in Tumugi, Xingan League, Inner Mongolia. Correspondingly, the interannual variations in plant biomass, net primary production and rain use efficiency for *F. sibiricum* steppe, *S. baicalensis* steppe and *L. chinense* steppe is considerable. The coefficient of variation in annual precipitation (25%) is lower than the coefficient of variation in peak live aboveground biomass of *F. sibiricum* steppe (37%), *S. baicalensis* steppe (36%) and *L. chinense* steppe (35%). The belowground biomass has much smaller interannual variation in the three meadow steppe sites. The Production to Rain Variability Ratio (PRVR) is similar for the three steppe communities (1.48 for *F. sibiricum* steppe, 1.44 for *S. baicalensis* steppe and 1.40 for *L. chinense* steppe) and indicates the greater interannual variability of plant production to annual rainfall. These three meadow steppe sites have higher ANPP but slightly lower RUE and PRVR than the average values ($\text{ANPP}=136.9 \text{ g m}^{-2} \text{ yr}^{-1}$, $\text{RUE}=4.0 \text{ gDM m}^{-2} \text{ cm}^{-1} \text{ yr}^{-1}$ and $\text{PRVR}=1.5$) of 77 series data from the world arid lands (Le Houérou et al. 1988).

The empirical regression models indicate that both annual precipitation and seasonal distribution of precipitation and temperature are important controls of plant biomass and net primary production of these meadow steppes over the period of 1981–1990. PLAB of *L. chinense* steppe, *S. baicalensis* steppe and *L. chinense* steppe in the Tumugi area are positively and significantly correlated to annual precipitation at $p \leq 0.05$ levels. In a study that examined a 52-year data set of forage production and climate, Lauenroth and Sala (1992) found that forage production of short grass steppe at the Central Plain Experimental Range, Colorado, USA, is significantly related to annual precipitation at $p \leq 0.05$ level. PLAB of these meadow steppes are negatively correlated to average maximum temperature in April–September at $p \leq 0.05$ level (see model 4, 8 and 12 in Table 1). Among the three meadow steppes, *L. chinense* steppe was relatively more sensitive to change of temperature and precipitation over time than *S. baicalensis* steppe and *F. filifolium* steppe. *L. chinense* species has an extensive distribution in Euro-asian grasslands (Wu 1980) and plant biomass of *L. chinense* steppe varies considerably at regional scale. For instance, PLAB of *L. chinense* steppe in the Tumugi area is lower than PLAB of *L. chinense* steppe (183 gm^{-2}) in the Xilin river basin, Inner Mongolia,

where average annual precipitation and annual mean temperature during 1980–1989 is 31.3 cm and 0.02 °C, respectively (Xiao et al. 1995a). In an earlier study using spatial data of plant biomass, climate and soil organic matter, Wang et al. (1991) found that aboveground annual net primary production of *S. baicalensis* steppe is significantly related to cumulative temperature (≥ 5 °C), rainfall in plant growing season (April–September) and soil organic matter content.

Peak live aboveground biomass, peak live belowground biomass and rain use efficiency of the *L. chinense* steppe site are slightly higher than those of the *S. baicalensis* steppe and *F. sibiricum* steppe sites, probably due to slight difference in soil depth and soil texture. The CENTURY simulation results also show that the *L. chinense* steppe site has higher plant biomass and net primary production than the *S. baicalensis* steppe and *F. sibiricum* steppe sites. These results suggest that soil properties (soil depth and soil texture) are important controls of plant biomass and primary production of meadow steppe at local scale. In CENTURY, soil depth is related to plant root depth, which determines how deep can plants take up water from soils. The deeper the plant root depth, the greater the water availability. In CENTURY, soil texture also influences a number of processes, e.g., actual evapotranspiration, soil moisture, turnover and accumulation of organic matter in soils (Parton et al. 1987, 1988). Noy-Meir (1973) proposed the inverse soil texture hypothesis: primary production in arid and semi-arid regions is higher in coarse texture soils than in fine texture soils. In grasslands of the Central Plain of United States, aboveground net primary production increases with coarser soil texture when annual precipitation is less than 370 mm, but decreases when annual precipitation is larger than 370 mm (Sala et al. 1988). In arid and semi-arid regions, coarse soils, which allow deeper infiltration, may have lower evaporation but higher transpiration rate than fine soils (Noy Meir 1973; Sala et al. 1988). In a study that used three alternative data sets of soil texture, Pan et al. (1996) found that the estimates of annual net primary production for the conterminous United States differ among soil texture data sets, and the differences are scale-dependent, ranging from large difference at the scale of grid cells (0.5° latitude \times 0.5° longitude resolution) to small difference at the continental scale.

The estimates of the CENTURY simulations agree well with the observed aboveground live biomass, belowground live biomass of *F. sibiricum* steppe, *S. baicalensis* steppe and *L. chinense* steppe over the

period of 1981–1990. The CENTURY model is more successful than the empirical regression models in estimating peak live aboveground biomass of *F. sibiricum* steppe, *S. baicalensis* steppe and *L. chinense* steppe, because of the greater process level controls of plant production in CENTURY. The application of regression models for future predictions is limited, as regression models are constrained by the range of data used to generate the coefficients and often are not expected to hold beyond this range. Climate is expected to change in the next century as the results of increasing anthropogenic emissions of greenhouse gases (e.g. CO₂, N₂O, CH₄). Climate change has significant impacts on net primary production and soil carbon storage of grasslands in the world (Parton et al. 1995). The projected changes in annual mean temperature and annual precipitation between current CO₂ and doubled CO₂ simulations in the Tumugi area are 5.9 °C and 0.6 cm by the Canadian Climate Center atmospheric general circulation model (GCM), and 5.3 °C and –4.4 cm by the Geophysical Fluid Dynamics Laboratory GCM. Potential CO₂-induced global warming may have significant negative impacts on plant biomass and net primary production of these three meadow steppes in the Tumugi area (Xiao et al. 1995b).

Field data and model simulations indicate the strong linkage between climate variability and plant production in this meadow steppe region. Changes in the dynamics of grassland ecosystems may result in changes in land surface-atmosphere interactions (Parton et al. 1993; Schimel et al. 1991; Pielke and Avissar 1990). Land use such as livestock grazing, fire, fertilization and irrigation have also been incorporated into the CENTURY model (Parton et al. 1992, 1993). Net primary production of grasslands in Inner Mongolia is substantially affected by livestock grazing (Li 1989), fire (Jiang et al. 1985), fertilization (Chen et al. 1985). Therefore, the CENTURY model would be a useful tool for us to investigate sensitivity of meadow steppe in Inner Mongolia to global climate change and land use change at various spatial and temporal scales.

Acknowledgements

The field work was supported by the National Science Foundation of China. The field data have been collected by Du Chen, Yumei Peng and Xianyi Cui at the Tumugi Institute of Grasslands, Xingan League, Inner Mongolia, China. D.S. Ojima and X. Xiao were supported by the NASA Earth Observing System inter-

disciplinary project NACW-2662 'Using multi-sensor data to model factors limiting carbon balance in global grasslands'. We thank W.J. Parton, Z. Chen, J. Wu and anonymous reviewers for their comments and discussions.

References

- Chen, Z., Shen, X., Yang, Z. & Huang, D. 1985. Ecological effects of fertilization during rainy season on various types of steppe on the Xilin river basin, Inner Mongolia. In: Inner Mongolia Grassland Ecosystem Research Station (ed.) Research on Grassland Ecosystems 1: 225–232. Science Press, Beijing (in Chinese with English abstract).
- Dong, Y. 1992. Effect of livestock grazing on grasslands. Grasslands of Inner Mongolia 2: 8–21 (in Chinese).
- Jiang, S., Wang, Y. & Qi, Q. 1985. The influence of burning on community structure and biomass of *Stipa grandis* grassland in Inner Mongolia region. In: Inner Mongolia Grassland Ecosystems Research Station (ed.) Research on Grassland Ecosystems 1: 75–82. Science Press, Beijing (in Chinese with English abstract).
- Lauenroth W. K. 1979. Grassland primary production: North American grassland in perspective. In: French N. R. (ed.) Perspectives in Grassland Ecology. Ecological Studies 32. Pp. 3–24. Springer-Verlag, New York.
- Lauenroth, W. K. & Sala, O. E. 1992. Long-term forage production of North American shortgrass steppe. Ecological Applications 2 (4): 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., Bingham, R. L. & Skerbek, W. 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.
- Li, Y. 1989. Impact of grazing on *Aneurolepidium chinense* steppe and *Stipa grandis* steppe. Acta Oecologica Application 10 (1): 31–46.
- Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4: 25–51.
- Pan, Y., McGuire, A. D., Kicklighter D. W. & Melillo, J. M. 1996. The import soils for estimates of net primary production: a sensitivity analysis with the terrestrial ecosystem model. Global Change Biology 2: 5–23.
- Parton, W. J., Schimel, D. S., Cole, C. V. & Ojima, D. S. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Science Society of America Journal 51 (5): 1137–1179.
- Parton, W. J., Stewart, J. W. B. & Cole, C. V. 1988. Dynamics of C, N, P and S in grassland soils: a model. Biogeochemistry 5: 109–131.
- Parton, W. J., McKeown, B., Kirchner, V & Ojima, D. S. 1992. CENTURY Users' Manual. Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523, USA.
- Parton, W. J., Scurlock, J. M. O., Ojima, D. S. 1992. CENTURY Users' Manual. Natural Kirchner, T., Menaut, J. C., Seastedt, T., Garcia Moya, T., Apinan Kamnalrut & Kinyamario, J. I. 1993. Observation and modelling of biomass and soil organic matter dynamics for the grassland biome worldwide. Global Biogeochemical Cycle 7 (4): 785–809.
- Parton, W. J., Scurlock, J. M. O., Ojima, D. S., Schimel, D. S., Hall, D. O., and SCOPE GRAM group members. 1995. Impact of climate change on grassland production and soil carbon worldwide. Global Change Biology 1: 13–22.
- Pielke, R. A. and Avissar, R. 1990. Influence of landscape structure on local and regional climate. Landscape Ecology 4: 133–135.
- Sala, O. S., Parton, W. J., Joyce, L. A. & Lauenroth, W. K. 1988. Primary production of the central grassland region of the United States. Ecology 69 (1): 40–45.
- SAS Institute Inc. 1985. SAS/STAT User's Guide. SAS Institute Inc. Cary, North Carolina.
- Schimel, D. S., Kittel, T. G. F. and Parton, W. J. 1991. Terrestrial biogeochemical cycles: global interactions with the atmosphere and hydrosphere. Tellus 43AB: 188–203.
- Sims, P. L. & Singh, J. S. 1978. The structure and function of ten western North American grasslands III: net primary production, turnover and efficiencies of energy and water use. Journal of Ecology 66: 573–597.
- Singh, J. S., Lauenroth, W. K. & Steinhorst, R. K. 1975. Review and assessment of various techniques for estimating net aerial primary production in grassland from harvest data. The Botanical Review 41: 181–232.
- Smoliak, S. 1986. Influence of climatic conditions on production of *Stipa-Bouteloua* over a 50-year period. Journal of Range Management 39: 100–103.
- Towne, G. & Owensby, C. E. 1984. Long-term effects of annual burning at different dates in ungrazed Kansas tallgrass prairie. Journal of Range Management 37: 392–397.
- Wang, Y. 1985. The Vegetation of Inner Mongolia. Science Press, Beijing (in Chinese).
- Wang, Y., Zhao, N. & Xu, Z. 1991. The relationship between primary production and the major ecological factors and its prediction models in *Stipa baicalensis* steppe in Northeastern China. Vegetatio 96: 15–23.
- Wu, Z. 1980. Vegetation of China. Pp. 519–533. Science Press, Beijing (in Chinese).
- Xiao, X., Ojima, D. S., Parton, W. J. & Bonham, C. 1996. Modelling of plant biomass and soil organic matter of *Leymus chinense* steppe and *Stipa grandis* steppe in the Xilin river basin, Inner Mongolia, China. In: Inner Mongolia Grassland Ecosystem Research Station (ed.) Research on Grassland Ecosystems (in press).
- Xiao, X., Wang, Y., Jiang, S., Ojima, D. S. & Bonham, C. D. 1995a. Interannual variation in climate and aboveground biomass of *Leymus chinense* steppe and *Stipa grandis* steppe in the Xilin river basin, Inner Mongolia, China. Journal of Arid Environments 31: 283–299.
- Xiao, X., Ojima, D. S., Parton, W. J., Chen, Z. & Chen, D. 1995b. Sensitivity of Inner Mongolia grasslands to climate change. Journal of Biogeography 22: 643–648.
- Xing, Q. & Liu, D. 1993. Dynamics of aboveground biomass of natural grasslands in Inner Mongolia. In: Li, B. (ed.) Research on Dynamic Monitoring of Grazing Ecosystem in the Northern China. Press of Agricultural Science and Technology, Beijing. Pp. 143–154 (in Chinese).
- Zhang, Z. 1990. Grassland Resources of Inner Mongolia. People's Press, Huhhot. Pp. 119–149 (in Chinese).

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65
66
67
68
69
70
71
72
73
74
75
76
77
78
79
80
81
82
83
84
85
86
87
88
89
90
91
92
93
94
95
96
97
98
99
100

101
102
103
104
105
106
107
108
109
110
111
112
113
114
115
116
117
118
119
120
121
122
123
124
125
126
127
128
129
130
131
132
133
134
135
136
137
138
139
140
141
142
143
144
145
146
147
148
149
150
151
152
153
154
155
156
157
158
159
160
161
162
163
164
165
166
167
168
169
170
171
172
173
174
175
176
177
178
179
180
181
182
183
184
185
186
187
188
189
190
191
192
193
194
195
196
197
198
199
200