

Temporal variation in aboveground biomass of *Leymus chinense* steppe from species to community levels in the Xilin River Basin, Inner Mongolia, China

Xiao Xiangming^{1,2}, Jiang Shu³, Wang Yifeng³, D.S. Ojima^{1,2} & C.D. Bonham²

¹Natural Resource Ecology Laboratory, Colorado State University; ²Department of Rangeland Ecosystem Science, Colorado State University, Fort Collins, CO 80523, USA; ³Inner Mongolia Grassland Ecosystem Research Station, Institute of Botany, Chinese Academy of Sciences, Beijing 100044, China

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Abstract

We analyzed the long-term dynamics of aboveground biomass of *Leymus chinense* steppe in relation to interannual variation of precipitation and temperature during 1980–1989 at levels of community, growth form and species in the Xilin river basin, Inner Mongolia Autonomous Region, China. Annual aboveground net primary production (ANPP) varied from 154.00 g m⁻² yr⁻¹ in 1980 to 318.59 g m⁻² yr⁻¹ in 1988, with a mean of 248.63 g m⁻² yr⁻¹ and the coefficient of variation of 25%. ANPP was not significantly correlated to annual precipitation and total precipitation during April–September at $p \leq 0.05$ level, but precipitation in May and August accounted for 69% of interannual variation of ANPP. The means of rain use efficiency and water use efficiency of *L. chinense* steppe were 8.1 kg DM ha⁻¹ mm⁻¹ yr⁻¹ and 0.89 mg DM g⁻¹ H₂O respectively. Aboveground biomass of various growth forms and species had different response patterns to interannual variation of precipitation and temperature. Monthly and seasonal distribution of precipitation and temperature were the key controls of aboveground biomass of species.

Introduction

The relationship between net primary production of natural vegetation and abiotic factors, especially climatic variables, has been an important theme of plant ecology. Considerable work has been done on primary production (Lauenroth 1979; Li Bo *et al.* 1988; Sala *et al.* 1988; Webb *et al.* 1983, 1978), water use efficiency (WUE) and rain use efficiency (RUE) of temperate grasslands (Fischer & Turner 1978; Le Houérou 1984; Sims & Singh 1978; Webb *et al.* 1978). Few field works emphasized temporal variability of primary productivity, WUE and RUE (Lauenroth & Sala 1992; Le Houérou *et al.* 1988; Li Bo *et al.* 1988; Sims & Singh 1978). Information on year-to-year variation of grassland ecosystems is necessary for us to estimate net primary productivity accurately and to evaluate effects of global climate change on terrestrial ecosystems (Hall & Scurlock 1991; Long & Hutchin 1991).

In this study, we report long-term dynamics of aboveground biomass, net primary production and efficiencies of water use of *Leymus chinense* (syn. *Aneurolepidium chinense*) steppe during 1980–1989 in the Xilin river basin within the Unesco/MAB Xilinqol Steppe Biosphere Reserve, Inner Mongolia; and examine response of aboveground biomass of *L. chinense* steppe to interannual fluctuation of precipitation and temperature over time at levels of community, growth form and species. *L. chinense* steppe is widely distributed in the eastern Eurasian steppe zone. The total area of *L. chinense* steppe was estimated at 420,000 km², half of which is within China (Wu Zenyi 1980). Within China, *L. chinense* steppe is distributed in Northeastern Plain and eastern Inner Mongolia under the temperate sub-humid and semi-arid climate (Fig. 1). There were considerable variations in species compositions and productivity of *L. chinense* steppe in China (Jiang Shu *et al.* 1985; Li Bo *et al.* 1988; Qi Qihui *et al.* 1985; Wang Yifeng *et al.* 1979; Wu Zenyi

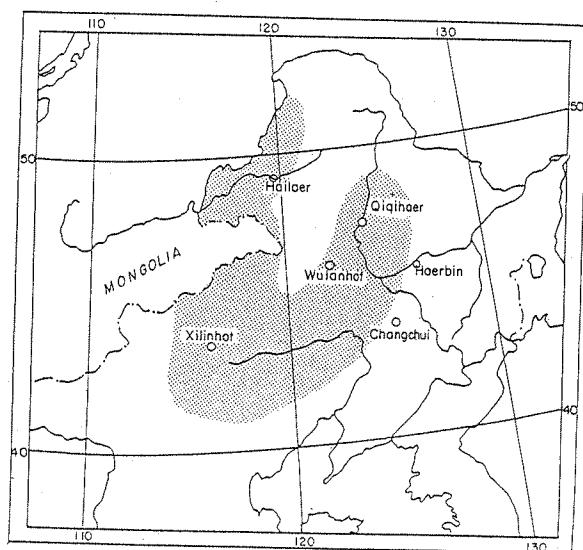


Fig. 1. Distribution of *Leymus chinense* steppe in China (after Wu Zenyi 1980).

1980). The objectives of this study were twofold: (1) to quantify temporal variability of aboveground biomass, aboveground net primary production, water use efficiency and rain use efficiency of *L. chinense* steppe; and (2) to establish quantitative relationships between climatic variables and aboveground biomass and net primary production of *L. chinense* steppe in the domain of time. The analysis at species level will help us to understand the temporal variation of *L. chinense* steppe at community level.

Study site and methods

Study site

Climate in the Xilin river basin is the continental middle temperate semi-arid. Winter is generally cold and dry, while summer is warm and wet (Chen Zuozhong 1988). Stable snow cover occurs at the end of November and melts at the end of March. Non-frost period lasts about 102–136 days. There were large interannual variations in precipitation and mean temperature during 1980–1989 (Fig. 2). On the average, annual mean temperature and annual precipitation during 1980–1989 were 0.02 °C and 313.3 mm, respectively, and 89% of annual precipitation was concentrated in April–September. The growing season of grass plants

is from the end of April to the end of September, lasting about 150 days (Jiang Shu 1985).

L. chinense steppe, *Stipa grandis* steppe and *S. krylovii* steppe are dominant vegetation in the Xilin river basin and are representative of typical steppe in Inner Mongolia. Grasslands in Xilin river basin are clearly dominated by C₃ species and only one C₄ species (*Cleistogenes squarrosa*) was found in a stable isotopic study (Tieszen & Song 1990). Aboveground net primary production of *L. chinense* steppe in the Xilin river basin ranges from 150 g m⁻² yr⁻¹ to 250 g m⁻² yr⁻¹ (Li Bo *et al.* 1988) and has a normal distribution (Hayashi *et al.* 1988). Rich species composition, diverse vegetation and ecosystems in the Xilin river basin are the most well preserved in Inner Mongolia and the first nation-level steppe natural reserve was established in the Xilin river basin in 1985 (Li Bo *et al.* 1988).

The study site (25 ha) of pristine *L. chinense* steppe was set up in 1979 and is located at about 60 km southeast of Xilinhot at 43° 43' N and 116° 38' E and 1200 m in elevation (Fig. 1). It is representative of natural *L. chinense* steppe in the Xilin river basin (Jiang Shu 1985, 1988). *L. chinense* (Trin.) Tzvelev (syn. *Aneurolepidium chinense* (Trin.) Kitagawa), a xeric rhizomous grass, is the most dominant species. The soil is dark chestnut with coarse texture (Wang Jiuwen & Cai Weichi 1988). The *L. chinense* steppe site was very lightly grazed by sheep and cattle before the enclosure was established in 1979, as it is far away from drinking water spots and residential villages. There was little difference in species composition and plant biomass between the inside and outside enclosure areas, due to very light degree of livestock grazing, according to the field survey in July–August 1987 (Hayashi *et al.* 1988).

Vegetation sampling

In the fenced site of *L. chinense* steppe, field sampling has been conducted from the beginning of May to early October at the interval of two weeks since 1980. Five 1 m² quadrats were randomly placed at each sampling date. Aboveground biomass of individual species were measured by harvesting the plant material onto the ground surface. Litter was collected by hand from the harvested quadrats. At the laboratory, the clipped plant material was separated into live and standing dead parts. The plant material was put into oven at 65 °C and weighed as dry weight of live biomass and standing dead. Data of peak live aboveground biomass

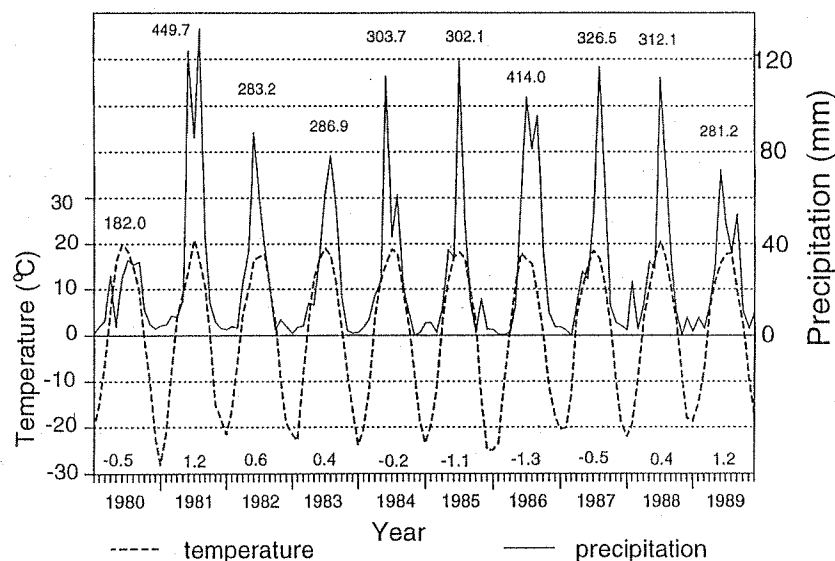


Fig. 2. Interannual variation in monthly precipitation and monthly mean temperature during 1980–1989. Numbers on the top are annual precipitation (mm) and numbers on the bottom are annual mean temperature (°C).

of 66 species recorded during 1980–1989 were used in this analysis and reported in dry weight (g m^{-2}). These 66 species were grouped into 5 growth forms (Liu Shurun & Liu Zongling 1988): annual forbs (5 species), biennial forbs (3 species), perennial forbs (47 species, including one *Carex* species), grass (7 species of *Gramineae* and small shrubs (4 species).

Data analysis

Annual aboveground net primary productivity (ANPP) of *L. chinense* steppe was estimated by summation of peak live aboveground biomass (PLAB) of individual species during plant growing season. Although this method gives a conservative estimate as it doesn't account for materials produced, senesced and detached in the form of standing dead before the peak live aboveground biomass of a given species occurs, it is still a reasonable and accurate method for estimating primary productivity (Singh *et al.* 1975). PLAB of growth form was estimated by summation of peak live aboveground biomass of its individual species.

Rain use efficiency (RUE) was defined as the ratio of ANPP to annual precipitation in $\text{kg DM ha}^{-1} \text{ mm}^{-1} \text{ yr}^{-1}$ (Le Houérou 1984). Water use efficiency (WUE) was defined as the ratio of ANPP to actual evapotranspiration (AET) during the growing season (April–September) in $\text{mg DM g}^{-1} \text{ H}_2\text{O}$ (Sims & Singh 1978).

Data from the local weather stations show that measured monthly evaporation during April–September was always larger than monthly precipitation, thus it is reasonable to assume that AET is equal to precipitation during the growing season. As AET was a crude estimate, WUE was a relative measure. The production to rain variability ratio (PRVR) was defined as the ratio of the coefficient of variation in ANPP over the coefficient of variation in annual precipitation (Le Houérou *et al.* 1988) and used to characterize the relationship between variability of primary production and variability of annual precipitation.

The following climatic variables were used in linear regression analysis to determine their effect on aboveground biomass of *L. chinense* steppe at levels of community, growth forms and species: annual precipitation, total precipitation during April–September, monthly precipitation, average annual minimum and maximum temperature, average minimum and maximum temperature during April–September, monthly minimum and maximum temperature. Forward and stepwise model selection algorithms were used to select those climatic variables that are statistically significant in relation to ANPP and aboveground biomass of various growth forms and species at $\alpha = 0.05$ level (SAS Institute Inc. 1985).

Principal component analysis was also applied to a 30 (species) \times 10 (year) biomass matrix in which no missing data of peak live aboveground biomass of

Table 1. The mean and the coefficient of variation (CV) in peak aboveground live biomass (g m^{-2}), rain use efficiency ($\text{kg DM ha}^{-1} \text{mm}^{-1} \text{yr}^{-1}$) and water use efficiency ($\text{mg DM g}^{-1} \text{H}_2\text{O}$) of the five growth forms of *L. chinense* steppe during 1980–1989

Growth forms	Biomass		RUE		WUE	
	Mean	CV (%)	Mean	CV (%)	Mean	CV (%)
Annual forb	9.55	71	0.30	76	0.033	76
Biennial forb	1.73	59	0.05	58	0.009	48
Perennial forb	56.23	31	1.85	33	0.207	35
Shrub	24.75	40	0.78	38	0.085	36
Grass	156.38	33	5.08	32	0.562	30

species occurred. Principal components were derived from the covariance matrix. It aimed to illustrate response patterns of various species over time domain and to identify those species that have similar interannual variation during 1980–1989.

Results

Magnitude and variation of aboveground biomass and ANPP

Field data show that there were large interannual variations in seasonal dynamics and magnitude of aboveground biomass of *L. chinense* steppe during 1980–1989. Community peak live aboveground biomass ranged from 90.31 g m^{-2} in 1980 to 242.01 g m^{-2} in 1988. The date on which community peak live aboveground biomass occurred, shifted every year, although seasonal community live aboveground biomass followed a unimodal growth pattern. ANPP of *L. chinense* steppe varied from $154.00 \text{ g m}^{-2} \text{yr}^{-1}$ in 1980 to $318.59 \text{ g m}^{-2} \text{yr}^{-1}$ in 1988 (Fig. 3). The mean of ANPP and the coefficient of variation in ANPP during 1980–1989 were $248.63 \text{ g m}^{-2} \text{yr}^{-1}$ and 25%, respectively.

Figure 3 shows the interannual variation of aboveground biomass of five growth forms of *L. chinense* steppe. Grass had the largest amount of aboveground biomass and the second lowest coefficient of variation in aboveground biomass (Table 1). These 7 grass species accounted for 45% to 80% of ANPP of *L. chinense* steppe. On the average, grass accounted for 62% of ANPP, perennial forbs for 23%, shrubs for 10%, biennial forbs for 1% and annual forbs for 4% (Fig. 3). Large interannual variation in grass contributes most

to interannual variation of ANPP of *L. chinense* steppe during 1980–1989. Aboveground biomass of annual forbs did not increase in dry years but increased in the year following a dry year, as shown in year 1981, 1983, 1984 (Fig. 3). Drought had the most significant effect on grass species as aboveground biomass of grass decreased considerably in dry year 1980, 1983 and 1984 (Fig. 3).

The sum of peak live aboveground biomass of such 10 species as *L. chinense*, *S. grandis*, *Serratula centauroides*, *Poa argunensis*, *Caragana microphylla*, *Artemisia commutata*, *Carex korshinski*, *Salsola collina*, *Achnatherum sibiricum* and *Agropyron cristatum* accounted for 82.4% of ANPP of *L. chinense* steppe in 1980, 81.8% in 1981, 83.7% in 1982, 78.9% in 1983, 79.0% in 1984, 81.8% in 1985, 91.3% in 1986, 82.2% in 1987, 83.9% in 1988 and 86.2% in 1989, i.e., 83% on the average. The growth curves of these 10 species were quite different from each other and had large interannual variation. For instance, peak live aboveground biomass of *L. chinense* occurred on September 1, 1981 (wet year) and on August 4, 1982 (dry year), but *S. grandis* on August 2, 1981 and August 15, 1982. The different growth curves implied that each species had its own response pattern to monthly and seasonal distribution of precipitation and temperature over time. The magnitude and temporal variation of peak live aboveground biomass of these 10 species are listed in Table 2.

Magnitude and temporal variation in efficiencies of water use

Rain use efficiency (RUE, $\text{kg DM ha}^{-1} \text{mm}^{-1} \text{yr}^{-1}$) of *L. chinense* steppe ranged from 5.5 in 1983 to 11.2 in 1982 (Fig. 4a). The mean of RUE and the coefficient of variation (CV) in RUE were $8.1 \text{ kg DM ha}^{-1} \text{mm}^{-1} \text{yr}^{-1}$ and 23%, respectively. Water use efficiency (WUE, $\text{mg DM g}^{-1} \text{H}_2\text{O}$) of *L. chinense* steppe varied from 0.61 in 1983 to 1.17 in 1982 (Fig. 4b). The mean and CV in WUE were $0.89 \text{ mg DM g}^{-1} \text{H}_2\text{O}$ and 22%, respectively.

The five growth forms had large interannual variation in WUE and RUE (Fig. 4). Grass had the largest WUE and RUE but the lowest coefficient of variation in RUE and WUE (Table 1).

At species level, there were large interannual variations in WUE and RUE (Table 2). *L. chinense* had the highest RUE and WUE but the second lowest coefficient of variation in WUE and RUE. *S. grandis* had the second largest RUE and WUE (Table 2).

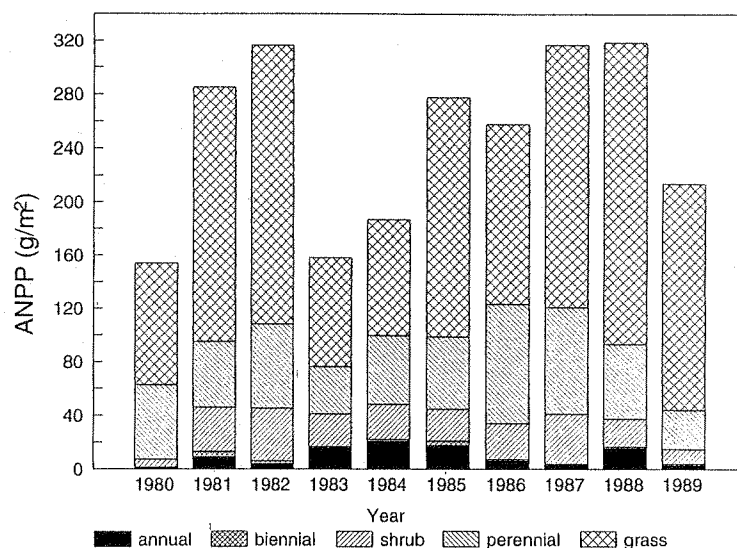


Fig. 3. Temporal variation of ANPP and aboveground biomass of five growth forms of *Leymus chinense* steppe in 1980–1989.

Table 2. The mean and the coefficient of variation (CV) in peak aboveground live biomass (g m^{-2}), rain use efficiency ($\text{kg DM ha}^{-1} \text{mm}^{-1} \text{yr}^{-1}$) and water use efficiency ($\text{mg DM g}^{-1} \text{H}_2\text{O}$) of 10 species of *L. chinense* steppe during 1980–1989

Species	Biomass		RUE		WUE	
	Mean	CV (%)	Mean	CV (%)	Mean	CV (%)
<i>Leymus chinense</i>	95.1	38	3.09	37	0.341	35
<i>Stipa grandis</i>	30.3	49	0.98	49	0.108	47
<i>Agropyron cristatum</i>	7.3	54	0.25	58	0.027	58
<i>Caragana microphylla</i>	15.7	47	0.49	46	0.054	44
<i>Artemisia commutata</i>	12.8	73	0.46	92	0.052	96
<i>Achnatherum sibiricum</i>	10.3	43	0.33	33	0.036	32
<i>Poa argunensis</i>	8.0	160	0.25	131	0.028	133
<i>Carex korshinski</i>	9.0	34	0.30	41	0.033	41
<i>Salsola collina</i>	6.6	82	0.22	86	0.023	86
<i>Serratula centauroides</i>	12.2	132	0.35	110	0.039	114

The relationship between climate and aboveground biomass and ANPP

ANPP was not significantly related to annual precipitation and total precipitation during April–September at $p \leq 0.05$ (Fig. 5a,b), neither with average annual minimum and maximum temperature and average minimum and maximum temperature during April–September at $p \leq 0.05$ level. However, forward model selection algorithm showed that ANPP had significant linear relation with precipitation in May ($R5$, cm) and

August ($R8$, cm) at $p \leq 0.05$ level (Fig. 5c,d):

$$\text{ANPP} = 163.22 + 36.38 \times R5 \quad (1)$$

$$r^2 = 0.41; F = 5.574; p = 0.0459$$

$$\text{ANPP} = 77.96 + 41.99 \times R5 + 10.25 \times R8 \quad (2)$$

$$r^2 = 0.69; F = 7.622; p = 0.0175.$$

Model (1) implied that ANPP was more sensitive to precipitation in early wet season than to annual precipitation, as May could be considered as the beginning of wet season. Model (1) and (2) indicated that seasonal distribution of precipitation accounted for large proportion of interannual variation of ANPP.

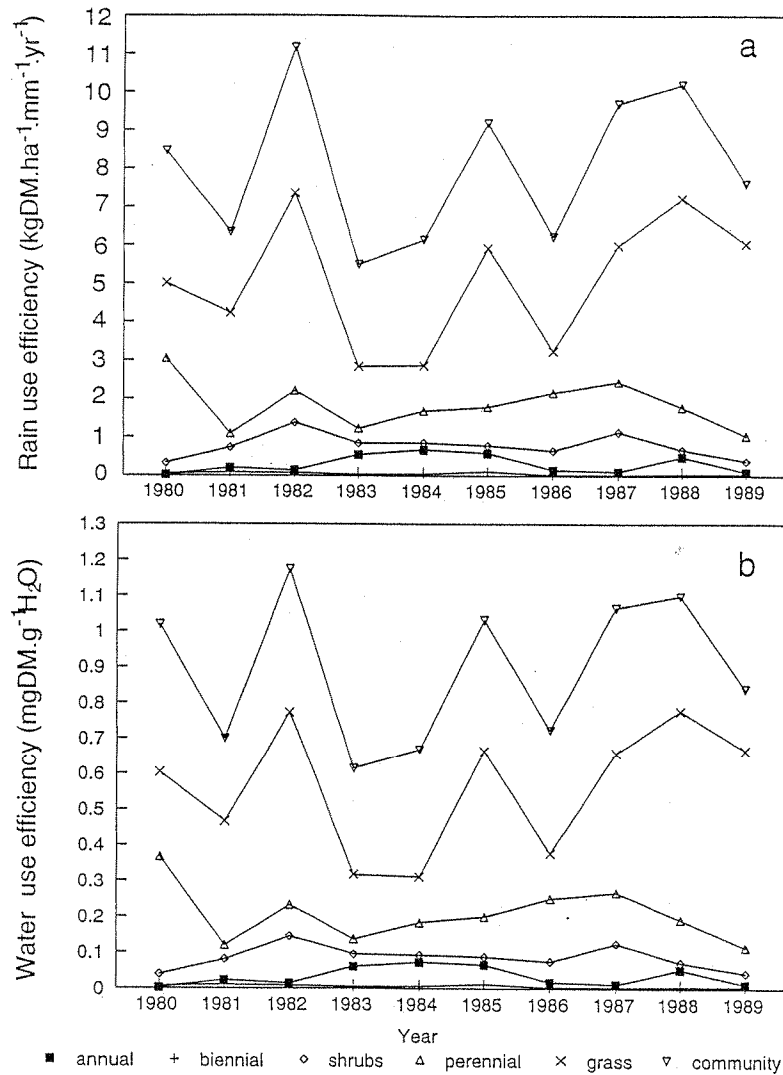


Fig. 4. Temporal variation in RUE and WUE of community and five growth forms of *Leymus chinense* steppe in 1980–1989.

Table 3 lists those climatic variables that have significant effect on PLAB of growth forms at $p \leq 0.05$ level. PLAB of annual forbs, perennial forbs, shrubs and grass was not significantly related with annual precipitation and precipitation during April–September, while PLAB of biennial forbs had significant linear relation with annual precipitation and precipitation during April–September at $p \leq 0.05$ level (see model 4 on Table 3). Annual mean minimum temperature, average minimum temperature during April–September and minimum temperature in April accounted together for 91% of the interannual variation of annual forbs (see model 3 on Table 3). Increase of 1 °C in the average minimum temperature during April–September may

result in an increase of 13.52 g m⁻² PLAB of annual forbs. Precipitation in July and maximum temperature in August accounted for 82% of the interannual variation of PLAB of biennial forbs and were much better predictors than annual precipitation (see model 8 on Table 3). Average maximum temperature during April–September accounted for 62% of interannual variation of PLAB of perennial forbs (see model 9 on Table 3). Precipitation in May accounted for 49% of the interannual variation of grass (see model 10 on Table 3). Increase of 1 cm precipitation in May would result in an increase of PLAB of grass by 32.49 g m⁻². PLAB of shrubs was not significantly related to any of climatic variables. These regression models demon-

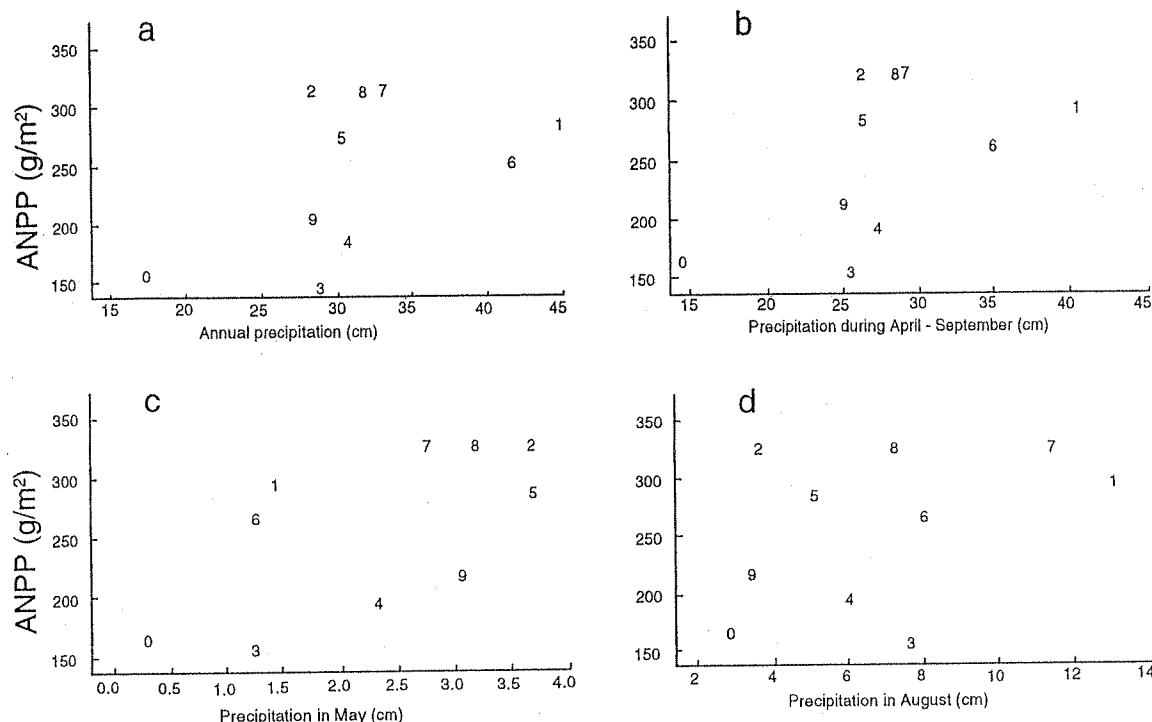


Fig. 5. The relationships between precipitation and ANPP of *Leymus chinense* steppe. The numbers are from the last digit of each year, i.e., 0 = 1980, 1 = 1981, ..., 9 = 1989.

strated that aboveground biomass of various growth forms had different response patterns to climate variation over time.

The linear regression analysis between PLAB of species and climatic variables indicated that PLAB of *L. chinense*, *S. grandis*, *Serratula centauroides*, *Poa argunensis*, *Caragana microphylla*, *Artemisia commutata*, *Carex korshinski*, *Salsola collina*, *Achnatherum sibiricum* and *Agropyron cristatum* was not significantly related to annual precipitation and total precipitation during April–September at $p \leq 0.05$ level. However, PLAB of *L. chinense*, *S. grandis*, *Serratula centauroides*, *Poa argunensis*, *Achnatherum sibiricum* and *Salsola collina* had significant linear relation with monthly precipitation and temperature at $p \leq 0.05$ level, except for *Carex korshinski* and *Artemisia commutata* (Table 4). For instance, the lower the maximum temperature in May and the higher precipitation in May, the higher PLAB of *L. chinense* is (see model 13 in Table 4). Increase of 1 °C in the maximum temperature in May would result in a decrease of PLAB of *L. chinense* by 11.84 g m⁻², when holding precipitation in May constant. Increase of 1 cm in precipitation in May would result in an increase in PLAB of *L. chi-*

nense by 18.15 g m⁻², when holding maximum temperature in May constant. This indicated that PLAB of *L. chinense* was more sensitive to change in precipitation in May than to change in maximum temperature in May. Precipitation in May accounted for 54% of interannual variation of PLAB of *S. grandis* (see model 14 in Table 4). Increase of 1 cm in precipitation in May would increase 9.92 g m⁻² PLAB of *S. grandis*. PLAB of *Serratula centauroides* and *Poa argunensis* was mostly affected by average maximum temperature during April–September (see model 16 and 19 in Table 4).

Principal component analysis of 30 species showed that dominant species (*L. chinense*, *Stipa grandis*, *Serratula centauroides*, *Poa argunensis*, *Caragana microphylla*, *Artemisia commutata*, *Carex korshinski*) had large but different responses, while the other species had similar response patterns over these 10 years (Fig. 6). The first principal component (PC1) accounted for 92.7% of the total variance, PC2 for 4.2% of the total variance. PC1 implied response of plant species to precipitation, as monthly precipitation in May has larger impact to *L. chinense* than to *S. grandis* (see model 11 & 14 in Table 4). PC2 implied

Table 3. The relationships between peak live aboveground biomass (g m^{-2}) of various growth forms of *L. chinense* steppe and climatic variables

Growth form	Regression model	r^2	p	N	#
Annual form	Biomass = $-109.12 - 5.29 \times \text{TMa} + 13.52 \times \text{TMs} - 1.56 \times \text{TM4}$	0.91	0.001	10	3
Biennial forb	Biomass = $-1.66 + 0.13 \times \text{PPTa}$	0.40	0.049	10	4
	Biomass = $-1.75 + 0.13 \times \text{PPTs}$	0.41	0.048		5
	Biomass = $-0.70 + 0.46 \times \text{R7}$	0.76	0.001		6
	Biomass = $23.13 - 0.87 \times \text{TX8}$	0.45	0.035		7
	Biomass = $8.36 + 0.38 \times \text{R7} - 0.36 \times \text{TX8}$	0.82	0.003		8
Perennial forb	Biomass = $849.51 - 39.27 \times \text{TXs}$	0.62	0.008	10	9
Grass	Biomass = $80.08 + 32.49 \times \text{R5}$	0.49	0.025	10	10
Shrub				10	

TMa – average annual minimum temperature ($^{\circ}\text{C}$); TM4 – minimum temperature in April ($^{\circ}\text{C}$); TMs – average minimum temperature during April–September ($^{\circ}\text{C}$); PPTa – annual precipitation (cm); PPTs – total precipitation during April–September (cm); TX8 – average maximum temperature in August ($^{\circ}\text{C}$); TXs – average maximum temperature during April–September ($^{\circ}\text{C}$); R5 – precipitation in May (cm); R7 – precipitation in July (cm); N – sample size; # – model number.

response of plant species to temperature, as illustrated by significantly linear correlation between maximum temperature and *Serratula centauroides*, *Poa argunensis*, *Caragana microphylla* (see Table 4). As shown in Figure 6, the shorter distance between two species is, the more similar these two species are in terms of response to interannual variation of precipitation and temperature.

Discussion

On the average, ANPP of *L. chinense* steppe ($248.63 \text{ g m}^{-2} \text{ yr}^{-1}$) at the study site is much higher than ANPP of shortgrass steppe ($97 \text{ g m}^{-2} \text{ yr}^{-1}$) in the Central Plain Experiment Range in Colorado, USA, where annual precipitation was 321 mm (Lauenroth & Sala 1992), and slightly higher than or close to ANPP of northern mixed prairie of northern American grasslands where annual precipitation ranged from 400 mm to 600 mm (Sims & Singh 1978), although annual precipitation during 1980–1989 in the Xilin river basin was 313 mm. Relatively high ANPP of *L. chinense* steppe may be attributed partially to (1) optimum monthly and seasonal distribution of precipitation and temperature (Xiao *et al.* 1995a) and (2) more coarse soil texture in Inner Mongolia grasslands. We suggest

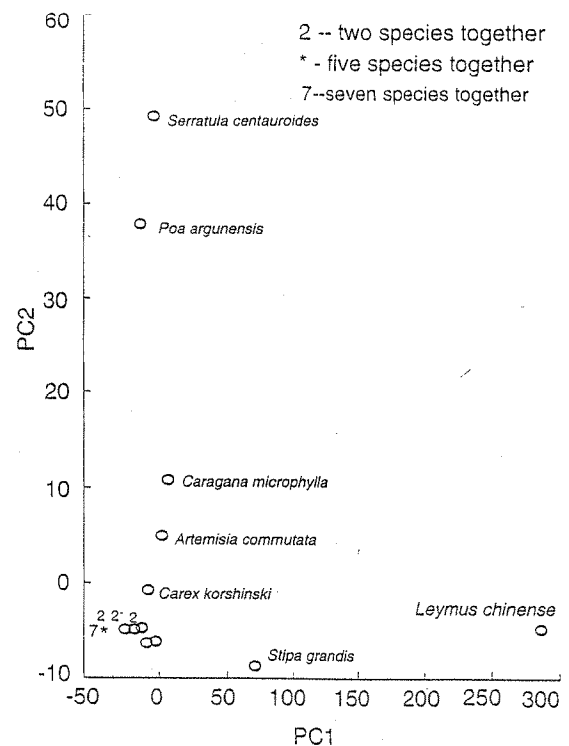


Fig. 6. Scattered diagram of 30 species of *Leymus chinense* steppe in the first principal component (PC1) and the second principal component (PC2).

Table 4. The relationships between peak live aboveground biomass (PLAB, g m⁻²) of species and climatic variables

Species	Regression model	r ²	p	N	#
<i>Leymus chinense</i>	PLAB = 38.23 + 24.21 × R5	0.54	0.015	10	11
	PLAB = 467.00 - 19.33 × TX5	0.43	0.040		12
	PLAB = 280.37 - 11.84 × TX5 + 18.15 × R5	0.67	0.021		13
<i>Stipa grandis</i>	PLAB = 7.02 + 9.92 × R5	0.54	0.015	10	14
<i>Poa argunensis</i>	PLAB = -9.23 + 4.01 × R9	0.52	0.019	10	15
	PLAB = 564.68 - 27.56 × TXs	0.54	0.016		16
	PLAB = 414.24 - 20.74 × TXs + 2.96 × R9	0.79	0.005		17
<i>Serratula centauroides</i>	PLAB = -8.16 + 4.73 × R9	0.46	0.031	10	18
	PLAB = 790.69 - 38.54 × TXs	0.67	0.004		19
	PLAB = 630.48 - 31.28 × TXs + 3.15 × R9	0.85	0.001		20
<i>Achnatherum sibiricum</i>	PLAB = 4.84 + 0.89 × R6	0.52	0.019	10	21
	PLAB = -37.52 + 1.45 × TX4 + 1.23 × TX7	0.74	0.024		22
	PLAB = -22.01 + 2.67 × TM7	0.46	0.031		23
	PLAB = -36.24 + 1.03 × TX4 + 1.22 × TX7 + 0.62 × R6	0.92	0.001		24
<i>Salsola collina</i>	PLAB = -0.87 + 0.36 × R6	0.45	0.034	10	25
	PLAB = 3.20 - 0.87 × TM5	0.44	0.038		26
	PLAB = 1.08 - 0.63 × TM5 + 0.26 × R6	0.65	0.026		27
<i>Agropyron cristatum</i>	PLAB = 46.69 - 2.05 × TX5	0.41	0.048	10	28
<i>Caragana microphylla</i>	PLAB = 297.29 - 19.28 × TXs + 6.04 × TX9	0.71	0.034	10	29

R5 - precipitation in May (cm); R6 - precipitation in June (cm); R9 - precipitation in September (cm); TX4 - monthly maximum temperature in April (°C); TX5 - monthly maximum temperature in May (°C); TX7 - monthly maximum temperature in July (°C); TX9 - monthly maximum temperature in September (°C); TXs - average maximum temperature during April-September (°C); TM5 - monthly minimum temperature in May (°C); TM7 - monthly minimum temperature in July (°C); N - sample size; # - model number.

that the relative higher N input to the *L. chinense* steppe ecosystem from biological N-fixation could be another important factor. In addition to a few species of N-fixed Legume forbs (e.g., *Melissitus runthenica*) in *L. chinense* steppe, the most unique species may be a small shrub Legume species *Caragana microphylla*, which is widely distributed in Inner Mongolia grasslands but does not exist in the Central Plain grasslands of Northern America. Although there has been no experiment to determine its N-fixation capacity, a lot of nodules has been observed in *Caragana microphylla* roots. In an

element chemistry analysis of 122 species in the Xilin river basin (Chen *et al.* 1985), N content of *Caragana microphylla* plant is 4.221%, being higher than average N content of 122 species (2.389%), particularly N content of *L. chinense* (1.811%) and *Melissitus ruthenica* (3.984%). Our simulation study using CENTURY plant-soil ecosystem model (Parton *et al.* 1987) supported our hypothesis on high N input and the simulation results were reported in another paper (Xiao *et al.* 1995b). Field and laboratory experiments for quantifying relative contribution of biological N-

fixation and atmospheric N deposition to *L. chinense* steppe ecosystem in the Xilin river basin are critically needed.

There were considerable interannual variations in aboveground biomass, ANPP, rain use efficiency and water use efficiency of *L. chinense* steppe at levels of community, growth form and species in the period of 1980–1989, primarily due to climate variability. The coefficient of variation (CV) in annual precipitation was 22%, while the CV in ANPP of *L. chinense* steppe was 25%. The Production to Rain Variability Ratio (PRVR) of *L. chinense* steppe was 1.14, that is to say, ANPP of *L. chinense* steppe had greater interannual variability than annual precipitation. This phenomenon should be attributed to the high variability of intraseasonal patterns of precipitation over time. *L. chinense* steppe had higher ANPP and RUE but lower PRVR values in comparison with the average values of 77 series data (ANPP = $136.9 \text{ g m}^{-2} \text{ yr}^{-1}$, RUE = $4.0 \text{ kg DM ha}^{-1} \text{ mm}^{-1} \text{ yr}^{-1}$ and PRVR = 1.5) from the world arid lands (Le Houérou *et al.* 1988).

ANPP of *L. chinense* steppe in the Xilin river basin was not significantly correlated to annual precipitation over time $p \leq 0.05$ level. Annual precipitation (PPTa, cm) accounted for only 24% of variance of ANPP of *L. chinense* steppe during 1980–1989 (ANPP = $116.12 + 4.23 \times \text{PPTa}$, $r^2 = 0.24$, $p = 0.1531$) and total precipitation during April–September (PPTs, cm) for 30% of variance of ANPP (ANPP = $97.16 + 5.34 \times \text{PPTs}$, $r^2 = 0.30$, $p = 0.1017$). By analyzing 52-year data of forage production and climate at the Central Plain Experimental Range, Colorado, USA, Lauenroth & Sala (1992) found that forage production of shortgrass steppe was significantly related to annual precipitation at $p \leq 0.05$ level, but annual precipitation accounted for only 39% of interannual variation in forage production of shortgrass steppe. The difference between these two case studies should be attributed to the difference in species composition, climate and response of species to climate. The carry-over of previous-year precipitation contributed significantly to ANPP of shortgrass prairie and cold desert of western USA at $p \leq 0.05$ level (Webb *et al.* 1978) and may account to some degree for interannual variation of ANPP of *L. chinense* steppe. However, linear regression analysis showed that the previous-year precipitation had no significant linear relation with the current-year ANPP of *L. chinense* steppe at $p \leq 0.05$ level. While in spatial analysis of climate and primary production, annual precipitation and/or annual mean temperature are good independent variables for predicting annual primary

production on the regional and global scales in a few regional models (Lauenroth 1979; Lieth 1975; Sala *et al.* 1988; Sims & Singh 1978; Webb *et al.* 1978). Sims & Singh (1978) found that annual rainfall accounted for 67% of the variation in primary production among 10 grassland sites in central and western United States. Whittaker (1970) also noted that there is nearly a linear increase in net primary production with increase in annual precipitation in arid lands. The regional model (Sala *et al.* 1988) underestimated ANPP under dry condition and overestimated ANPP under wet conditions, when it was applied to a set of time-series data (Lauenroth & Sala 1992). The poor temporal correlation between ANPP of *L. chinense* steppe and annual precipitation should be attributed to (1) the high interannual variability of monthly and seasonal distribution of precipitation and temperature in the Xilin river basin (Xiao *et al.* 1995a) and (2) various responses of individual species to interannual variation of precipitation and temperature. Community, growth forms and species of *L. chinense* steppe had different response patterns to precipitation and temperature over time. Both annual precipitation and year-to-year variation in intraseasonal patterns of precipitation were important in determining the magnitude and variation of primary production of *L. chinense* steppe in the Xilin river basin over time.

Principal component analysis and regression analysis highlighted the important role of temperature in determining interannual variation of aboveground biomass of *L. chinense* steppe at species level. Aboveground biomass of a few species is to some degree sensitive to change in temperature within plant growing season. Therefore, potential CO₂-induced global warming may have significant impact on relative contribution of various species to ANPP of *L. chinense* steppe and furthermore on species composition. Change in species composition would affect primary production of *L. chinense* steppe. The projected differences in annual mean temperature and annual precipitation between $2 \times \text{CO}_2$ and $1 \times \text{CO}_2$ simulations in the Xilin river basin are $+6.3^\circ \text{C}$ and $+1.5 \text{ cm}$ by high-resolution general circulation model of the Canadian Climate Center but $+4.9^\circ \text{C}$ and -0.8 cm by the Geophysical Fluid Dynamics Laboratory. Increase of monthly maximum temperature in May would result in decrease of aboveground biomass of *L. chinense* (see model 13 in Table 4). The difference in response of aboveground biomass to maximum temperature between *L. chinense* and *S. grandis* may be important in their geographical distribution (see model 13

and 14 in Table 4). *S. grandis* dominates to the west of *L. chinense* steppe (Fig. 1), where temperature is higher. *L. chinense* is a better forage plant to livestock than *S. grandis*. Decrease of aboveground biomass of *L. chinense* would result in lower forage quality of *L. chinense* steppe. Low-quality forage will have negative impact to livestock. Livestock grazing has significant impact on primary production and species composition of *L. chinense* steppe (Li Yonghong 1989, 1992). Studies on the effects of the interactions between climate and livestock grazing on grasslands are critically needed in order to achieve sustainable use of Inner Mongolia grasslands.

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