

Y. Z. Gao · M. Giese · X. G. Han · D. L. Wang
Z. Y. Zhou · H. Brueck · S. Lin · F. Taube

Land use and drought interactively affect interspecific competition and species diversity at the local scale in a semiarid steppe ecosystem

Received: 25 November 2007 / Accepted: 19 June 2008 / Published online: 23 July 2008
© The Ecological Society of Japan 2008

Abstract Few studies have considered interactive effects of grazing and drought on species composition and the relative contribution of species to total biomass, although it is important to understand the short-term dynamics and community succession in grazed ecosystems. We monitored species diversity and relative biomass contribution at one site protected from grazing since 1979 (UG79), and at winter grazing (WG) and heavily grazed (HG) sites. Continuous heavy grazing resulted in lower plant height and more but small individuals (tillers or stolons). Drought significantly reduced

total plant density on all sites. Grazing affected species diversity more than drought. Species richness at site UG79 was significantly higher than at sites WG and HG, while drought only tended to reduce species diversity. Drought stress and grazing disturbance interactively controlled species competition and functional groups. Both perennial grasses and forbs had greater contribution to total biomass at site UG79, and perennial grasses contributed more than 97% of total biomass at site WG. The contribution to total biomass of annual forbs and semi-shrubs significantly increased at site HG after two dry years. The significant decrease in *Potentilla acaulis* and a substantial increase in annual species at this site indicate that the perennial vegetation of this ecosystem is in great danger of extinction under conditions of prolonged drought.

Y. Z. Gao · D. L. Wang
Key Laboratory of Vegetation Ecology,
Northeast Normal University,
Changchun 130024, China

Y. Z. Gao · M. Giese · H. Brueck · F. Taube (✉)
Institute of Crop Science and Plant Breeding,
Section Grass and Forage Science/Organic Farming,
Christian-Albrechts University of Kiel,
24118 Kiel, Germany
E-mail: ftaube@email.uni-kiel.de
Tel.: +49-431-8802134

X. G. Han
Laboratory of Quantitative Vegetation Ecology,
Institute of Botany, Chinese Academy of Sciences,
100093 Beijing, China

Z. Y. Zhou
Key Laboratory for Silviculture and Conservation of Ministry
of Education, College of Forest Science,
Beijing Forestry University, Beijing 100083, China

M. Giese · H. Brueck
Institute for Plant Production and Agroecology in the Tropics
and Subtropics, Section Crop Water Stress Management,
Garbenstr. 13, 70599 Stuttgart, Germany

S. Lin
Department of Plant Nutrition,
China Agricultural University,
Yuanmingyuan West Road 2,
Beijing 100094, China

Keywords Heavy grazing · Functional group · Inner Mongolian steppe · Relative biomass

Introduction

Native grasses of the Chinese semi-arid steppe, defined as a rhizome and bunchgrass steppe with many or few forbs, are well adapted to herbivory and have supported grazing as the dominant land use for thousands of years (Zhu 1993). However, in the past four decades, overgrazing has resulted in substantial degradation of the Inner Mongolian steppe (Xie and Wittig 2004; Zhong et al. 2005) and drastically reduced community productivity (Liu et al. 1998; Katoh et al. 1998), litter accumulation (Snyman 2005), and site fertility, because of loss of fertile topsoil (Zhong et al. 2005). These losses, in combination with altered soil physical properties and water availability have a strong impact on species composition and long-term succession direction in this ecosystem (Banyikwa 1988; Liu et al. 1998; Li and Li 2002). It has been demonstrated that, when heavy grazing persists on degraded grasslands, ruderals,

typically unpalatable herbaceous and woody perennials, become dominant (Milton et al. 1994). In the study area, the abundance of *Leymus chinensis* and *Stipa grandis* is substantially reduced under high grazing pressure (Li 1989; Liu et al. 1998; Xie and Wittig 2003) whereas dicotyledonous species, for example *Artemisia frigida*, *Potentilla acaulis*, the C₄ grass *Cleistogenes squarrosa*, and the sedge *Carex duriuscula* are typical grazing increasers (Liu et al. 1998; Li and Li 2002; Gao et al. 2007).

In addition to grazing disturbance, drought can significantly affect species composition and functional components, because of species differences in drought resistance or tolerance (Biondini et al. 1998; Thurow and Taylor 1999; Bai et al. 2001; Briggs and Knapp 2001; O'Connor et al. 2001; Nippert et al. 2006). Generally, drought-tolerant species or functional groups become more abundant and/or make a greater contribution to total community productivity in relatively dry years (Bai et al. 2001, 2004; O'Connor et al. 2001). Briggs and Knapp (2001) found peak biomass of grasses correlated strongly with soil water availability whereas biomass of forbs did not. However, drought and grazing always interactively affect ecosystem processes in grazed grasslands (Milchunas et al. 1989; Hartvigsen 2000). Drought stress on heavily grazed sites is likely to be manifested more frequently and more severely than on ungrazed sites because of a higher portion of unproductive water loss by evaporation from bare soil. Consequently, plants from heavily grazed sites may have less water available for growth compared with ungrazed sites (Fahnestock and Detling 2000). Therefore, our hypothesis is that drought combined with heavy grazing can drastically accelerate the shift speed of species or functional groups because of species differences in drought resistance and grazing tolerance.

The relationship between species richness and grassland productivity is fundamental to the management and preservation of biodiversity, but remains controversial when different scales (spatial and temporal), disturbances, stressors (abiotic and biotic), and ecosystems are considered (Mittelbach et al. 2001). The relationship between biodiversity and productivity is strongly affected by the mode and severity of disturbance in semiarid steppe ecosystems, and it has been shown that heavy grazing can lead to both lower productivity and lower species diversity (Zhou et al. 2006; Bai et al. 2007). However, few studies have investigated potential interactions of grazing disturbance and drought on species diversity and productivity (Cingolani et al. 2005).

In the work reported here, we investigated:

- 1 whether different species or functional groups responded differently to grazing over three years with variable amounts of rainfall; and
- 2 whether the relationship between species richness, diversity, and productivity was similar on differently managed sites facing extreme weather conditions.

Materials and methods

Experimental sites

The principal study area is the Xilin River watershed (3,800 km²) in Inner Mongolia. A short vegetation period of approximately 150 days (Xiao et al. 1995) and precipitation, mainly of convective nature in combination with high evapo-transpiration, are the factors most limiting plant growth of the typical steppe which covers more than 60% of the Xilin river catchment. Main soil types in the low hills and plains are chestnut soils and chernozems with high soil organic carbon and total N contents. Main vegetation types are *L. chinensis* and *S. grandis* communities with ground cover of 30–70%, depending on precipitation between the years and a vegetation height of 0.3 m in the long-term enclosures. This steppe is mainly used for pastoralism, with only a few fertile sites of artificial grassland used for hay production. Compared with the local long-term average precipitation from May to September (294 mm), rainfall was 288, 131, and 212 mm in 2004, 2005, and 2006, respectively, indicating that 2005 and 2006 were relatively dry years.

The grazing experiment was conducted at three sites within this area. One site of 24 ha, established and maintained by the Inner Mongolia Grassland Ecosystem Research Station (IMGERS), Institute of Botany, the Chinese Academy of Sciences, has been protected from grazing since 1979. Within this site (ungrazed since 1979, hereafter denoted UG79), a representative plot of 150 m × 150 m was used for sampling. The second site of 40 ha has been used for winter grazing since 2000 (winter grazing, hereafter denoted WG). Before 2000, this area was continually grazed at a low to moderate intensity (two sheep per hectare). Within this site, a representative plot of 200 m × 200 m was used for sampling. The sampling plots of UG79 and WG were 600 m apart. The third site of approximate 100 ha has been heavily grazed in the past 30 years during the vegetation period. The average grazing intensity during the last 10 years has been four sheep per hectare. Within this heavily grazed site (hereafter denoted HG), a representative area of 200 m × 200 m was selected for sampling. Site HG is 3.3 km from sites UG79 and WG. Soil types of these three sites are similar, although site HG has a slightly higher coarse sand fraction in the very topsoil. For further soil characterization, see Krümmelbein et al. (2006).

Biomass harvest

The aboveground net primary production (ANPP) was determined by measuring the peak biomass, because our study sites contained mostly herbaceous plants with above ground tissues that die back annually. The aboveground biomass of individual species was harvested by clipping biomass within ten 1 m × 1 m

quadrats at the three sites down to the soil surface in the middle of August of 2004–2006. The tillers or stolons of each species were counted in each quadrat and the height was measured with a meter rule. Shrubs and semishrubs (for example *Caragana microphylla* and *A. frigida*) were clip-harvested in late April and mid-August and biomass differences were considered to represent ANPP. Dry mass weight was measured after oven-drying at 75°C to constant weight. Species were grouped into categories of total community and plant functional group according to Bai et al. (2004) on the basis of life form: annuals and biennials (AB), perennial rhizome grass (PR), perennial bunchgrass (PB), perennial forbs (PF), perennial grass (PG), and shrubs and semishrubs (SS).

Data calculation

The position and/or competitive ability of each species in the community is partially reflected by its relative biomass (Connolly and Wayne 2005). Therefore, the relative biomass was expressed as the ratio of the contribution of single-species biomass to total biomass. Average height of the plant community was calculated from those species for which relative biomass was more than 1%. The Simpson diversity index (D) was used to describe species diversity

$$D = 1 / \sum_{i=1}^S (N_i/N)^2$$

where S is the number of species per quadrat, N_i is the biomass of species i , and N is the total biomass per quadrat.

Statistical analyses

Because of the field-history of the long-term established grassland sites, treatment comparison was unavoidably based on pseudo-replicated data collection. Statistical analyses were performed using SAS version 8.0. Normality distribution of residuals was tested with Proc Univariate. Transformation of variables was not required in any case. ANPP, community height, plant density, species diversity, and different functional

components were subjected to analysis of variances by Proc Mixed including grazing treatments (fixed effect) and years (random effect). In the case of non-significant interaction between grazing treatments and years, comparison of main factor means was based on Tukey's HSD test with an experimental wise error of 0.05. Because of the significant interaction between grazing treatments and years, multiple comparisons of ANPP, plant density, and different functional components least square means were based on the Bonferoni–Holm procedure with nine comparisons. The significance of species differences between years was analysed with one-way analysis of variance, and comparison of means was based on Tukey's HSD test with an experimental wise error of 0.05.

Results

ANPP, community height, and total plant density

ANPP was significantly higher in the year with average rainfall (2004) compared with the dry years 2005 and 2006 (Tables 1, 2). In all years ANPP at site UG79 was significantly higher than that at site HG. ANPP at site UG79 was significantly higher than that at site WG in 2004, and ANPP at both sites was similar in 2005 and 2006. ANPP of site WG was not significantly different from that of site HG in 2004; it was higher in 2005 and 2006. Average community height was significantly higher at sites UG79 and WG than at site HG; it was similar at sites UG79 and WG. The community height was significantly higher in 2004 than in the dry years 2005 and 2006 (Tables 1, 2). In all three years, total plant density was highest at site HG and lowest at site UG79 and was higher in 2004 than in 2005 and 2006 (Tables 1, 2). Total plant density decreased from 2005 to 2006 (in the second dry year) at sites WG and HG, but not at site UG79.

Relative biomass of single species

Leymus chinensis, *S. grandis*, *Carex* spp., *Agropyron michnoi*, and *C. squarrosa* were found at all three sites (Table 3). *Caragana microphylla* was only found at site

Table 1 The probability ($\text{Pr} > F$) of two-factors ANOVA on aboveground net primary productivity, community height, plant density, different functional groups, and species diversity

Sources	df	ANPP	CH	PD	AB	SS	PR	PB	PF	PG	SD
S	2	***	***	***	***	***	***	***	***	***	***
Y	2	***	***	***	***	***	***	**	***	***	NS
S × Y	4	*	NS	***	***	***	***	***	***	***	NS

S, site; Y, year; NS, no significant difference; df , degrees of freedom; ANPP, aboveground net primary productivity; CH, community height; PD, plant density; AB, annual and biennial; SS, shrubs and semishrubs; PR, perennial rhizome grass; PB, perennial bunchgrass; PF, perennial forbs; SD, species diversity

* $P < 0.05$, ** $P < 0.001$, *** $P < 0.0001$

Table 2 Aboveground net primary productivity (ANPP), average height of community, and total plant densities at differently managed sites in 2004, 2005, and 2006 ($X \pm SE$)

Sites	2004	2005	2006	Site ME
Aboveground net primary productivity (g m^{-2})				
UG79	175.5 \pm 6.2 ax	111.7 \pm 11.3 bx	106.5 \pm 4.8 bx	
WG	126.3 \pm 1.9 ay	99.1 \pm 3.0 bx	95.7 \pm 2.9 bx	
HG	121.6 \pm 7.9 ay	76.6 \pm 3.8 by	75.3 \pm 2.6 by	
Community average height (cm)				
UG79	31.0 \pm 1.3	25.0 \pm 1.2	22.7 \pm 1.2	26.2 \pm 1.7 x
WG	29.3 \pm 1.3	20.6 \pm 1.1	23.1 \pm 1.3	24.3 \pm 1.7 x
xHG	11.0 \pm 0.6	7.0 \pm 0.5	6.8 \pm 0.5	9.0 \pm 0.8 y
Year ME	23.8 \pm 1.8 a	17.5 \pm 1.5 b	17.6 \pm 1.5 b	
Total plant density (ind. m^{-2})				
UG79	466 \pm 12 az	361 \pm 9 bz	334 \pm 11 by	
WG	553 \pm 12 ay	492 \pm 10 by	386 \pm 6 cx	
HG	623 \pm 9 ax	536 \pm 9 bx	401 \pm 11 cx	

Site UG79 has been protected from grazing since 1979, site WG is used for winter-grazing, and site HG is heavily grazed. A significant interaction occurred between sites and years for ANPP and total plant density at $P < 0.05$; differences among years within a site are indicated by letters (a–c) and differences among sites within a year indicated by letters (x–z). Significant main effects of sites (site ME) and years (year ME) for community average height are indicated by bold

UG79 and its relative biomass ranged from 4 to 7%. *Anemarrhena asphodeloides* was absent at site HG, and quite rare at site WG, while its relative biomass varied between 5 and 7% at site UG79. *Achnatherum sibiricum* had high relative biomass at sites UG79 and WG, while it was completely absent at site HG, and relative biomass of *C. squarrosa* (C_4 , bunchgrass) at site HG was substantially higher than at sites UG79 and WG.

Sites and precipitation had strong interactive effects on some species (Table 3). *Chenopodium aristatum* and *Chenopodium glaucum* usually are opportunity species at all three sites, but heavy grazing in combination with drought significantly increased the relative biomass of these two species. The relative biomass of *L. chinensis* was reduced under drought, and heavy grazing with prolonged drought made this species almost absent at site HG. *Carex* spp. did not respond consistently at the three grassland sites in the dry years 2005 and 2006. Relative biomass was reduced at site UG79 and increased at site WG; there was no clear trend at site HG. However, this species made a large contribution to total biomass at all three sites after the two dry years. Relative biomass of *S. grandis* increased in dry years and this trend was most evident at site WG in the extremely dry year 2005. Similarly, *Achnatherum sibiricum* did not respond to drought at site UG79 whereas its relative biomass decreased significantly after drought at site WG. *P. acaulis*, which is regarded as an important indicator of heavy grazing, was a rare species at sites UG79 and WG, and was dominant at site HG in 2004 and 2005. However, it was almost absent in the second dry year. *A. frigida*, a semi-dwarf shrub, which was not found at site WG and was a rare species at site UG79, became the dominant species at site HG after the two dry years. Total numbers of species involved in the contribution to total biomass are quite different among

these sites (Table 3). Approximately 80% of total biomass came from more than 15 species at site UG79 whereas more than 90% of total biomass was from only five species at site WG and six or seven species at site HG.

Functional groups

Variation of precipitation and grazing interactively affected plant functional group composition (Table 1; Fig. 1). Usually, AB only made very small contribution to total biomass at all sites, however, it became important at site HG after two continuous dry years and contributed 22% to total biomass (Fig. 1a). SS exhibited a more or less stable contribution to total biomass over time at site UG79 (Fig. 1b) and was not found at site WG, while SS significantly increased its contribution to total biomass with drought at site HG (Fig. 1b). PR, PB, and PF were the most important components of this perennial grassland. At site UG79, PG accounted for 60 and 69% of total biomass in 2004 and 2005, whereas its contribution to total biomass significantly decreased in 2006 (Fig. 1f), when PF made a greater contribution to total biomass (Fig. 1e). The reduction of PG was due to a decrease of PR (Fig. 1c), while the relative biomass of PB remained more or less stable (Fig. 1d). At site WG, PG was, irrespective of years, by far the most dominant plant functional group and accounted for more than 97% of total biomass (Fig. 1f). The relative biomass of PR and PB compensated each other from year to year (Fig. 1c, d). PF made very small contribution to total biomass at this site (Fig. 1e). PF and PG varied greatly from year to year at site HG, contribution of PF and PG to total biomass ranging from 5 to 44 and 49 to 75%, respectively (Fig. 1e, f).

Table 3 The relative biomass contribution of single species (%) to total biomass at three differently managed sites (see footnote of Table 2) in 2004, 2005, and 2006

Species	UG79			WG			HG		
	2004	2005	2006	2004	2005	2006	2004	2005	2006
Annual and biennial									
<i>Chenopodium glaucum</i>	— ^a	— ^a	1	— ^a	— ^b	— ^a	— ^a	— ^b	7
<i>Salsola collina</i>	— ^a	— ^a	1	— ^a	— ^b	— ^a	— ^a	— ^b	— ^a
<i>Chenopodium aristatum</i>	— ^a	— ^b	— ^a	1	— ^b	— ^a	— ^a	— ^b	15
Perennial rhizome grass									
<i>Carex korshiskyi</i>	14 a	13 a	9 b	5 b	11 a	12 a	— ^a	— ^a	— ^a
<i>Carex duriuscula</i>	— ^a	— ^a	— ^a	— ^a	— ^a	— ^a	29 a	12 c	25 b
<i>Leymus chinensis</i>	10 a	6 b	7 b	30 a	27 ab	26 b	9 a	1 b	— ^a
<i>Agropyron michnoi</i>	4 b	18 a	4 b	14 a	6 c	10 b	5 b	9 a	5 b
Perennial bunchgrass									
<i>Stipa grandis</i>	14 b	17 a	13 b	23 c	36 b	39 a	8 ab	10 a	7 b
<i>Achnatherum sibiricum</i>	12	12	12	20 a	11 b	6 c	— ^b	— ^b	— ^b
<i>Cleistogenes squarrosa</i>	4 a	1 b	2 ab	5 a	3 ab	2 b	24 a	15 c	19 b
<i>Koeleria cristata</i>	1	— ^a	2	— ^a	2	1	1	— ^a	— ^a
<i>Festuca dahurica</i>	— ^a	— ^a	— ^b	— ^a	2	1	— ^b	— ^b	— ^b
Perennial forbs									
<i>Anemarrhena asphodeloides</i>	7	5	7	— ^b	— ^a	— ^b	— ^b	— ^b	— ^b
<i>Allium senescens</i>	5 a	— ^a	2 b	— ^a	— ^a	— ^a	— ^b	— ^a	— ^b
<i>Serratula centauroides</i>	3	2	1	— ^b	— ^b	— ^b	— ^b	— ^b	— ^b
<i>Potentilla tanacetifolia</i>	4 a	— ^a	1 b	— ^b	— ^b	— ^b	— ^a	— ^a	1
<i>Potentilla bifurca</i>	2 b	5 a	1 b	— ^b	— ^b	— ^b	— ^a	— ^a	— ^a
<i>Potentilla acaulis</i>	— ^a	— ^a	— ^a	— ^a	— ^a	— ^a	19 b	43 a	3 c
<i>Allium tenuissimum</i>	2	— ^a	1	1	1	1	— ^a	— ^a	— ^a
<i>Allium anisopodium</i>	2	— ^a	— ^a	— ^a	— ^b	— ^b	— ^a	— ^a	— ^b
<i>Allium bidentatum</i>	1	1	2	— ^a	— ^a	1	— ^b	— ^b	— ^b
<i>Allium condensatum</i>	— ^a	— ^a	— ^a	— ^a	— ^a	— ^a	— ^b	— ^a	— ^b
<i>Cymbaria dahurica</i>	— ^a	5	3	— ^b	— ^b	— ^b	— ^b	— ^b	— ^b
<i>Pulsatilla tenuiloba</i>	— ^a	1 b	4 a	— ^b	— ^b	— ^b	— ^b	— ^b	— ^b
<i>Filifolium sibiricum</i>	1 b	1 b	8 a	— ^b	— ^b	— ^b	— ^b	— ^b	— ^b
<i>Silene jenissensis</i>	1 b	1 b	3 a	— ^b	— ^b	— ^b	— ^b	— ^b	— ^b
<i>Galium verum</i>	— ^a	— ^a	1	— ^b	— ^b	— ^b	— ^b	— ^b	— ^b
<i>Heteropappus altaicus</i>	— ^a	— ^a	2	— ^b	— ^b	— ^b	— ^a	— ^a	— ^a
Shrubs and semishrubs									
<i>Caragana microphylla</i>	7 a	4 b	5 ab	— ^b	— ^b	— ^b	— ^b	— ^b	— ^b
<i>Artemisia frigida</i>	1	2	— ^a	— ^b	— ^b	— ^b	3 c	7 b	16 a
<i>Kochia prostrata</i>	1	— ^b	— ^a	— ^b	— ^b	— ^b	— ^a	— ^a	— ^a

Significant differences between years within one site are indicated by different small letters ($P < 0.05$, $n = 10$). Site descriptions are as for Table 2

^aRelative biomass less than 1%

^bAbsent

Species richness and species diversity

In total, 55 species were found at site UG79, and 25 and 26 species at sites WG and HG, respectively, in 2004, a relatively wet year (Table 4). The total number of species decreased at all three sites after two drought years, and variation of species richness between years was mainly from functional groups AB and PF, whereas perennial grasses (PR + PB) and SS remained more stable during extreme drought events (Tables 3, 4). The Simpson diversity index was not significantly ($P = 0.126$) different between years but tended to decrease with drought (Tables 1, 5). Grazing had a strong effect on species diversity index ($P < 0.0001$), and the index was significantly higher at site UG79 than at sites WG and HG, while no significant difference between the other two sites was found during the study period.

Discussion

ANPP, community height, and total plant density

From our data it is obvious that community height was reduced more by heavy grazing than by drought (Table 2), and that drought and heavy grazing had opposite effects on total plant density. Drought tended to reduce it and heavy grazing significantly increased total plant density (Table 2). Therefore, drought and grazing had interactive effects on plant height and density, which resulted in different ANPP under fluctuating levels of rainfall (Table 1). It must be mentioned that although plants produced more small and thin tillers or stolons, this increase could not compensate for the sharp decrease of the height, which led to lower ANPP at site HG.

Fig. 1 The relative biomasses of different plant functional groups in 2004, 2005, and 2006 at three grassland sites of Inner Mongolia. Site UG79 has been protected from grazing since 1979, site WG is used for winter-grazing, and site HG is heavily grazed. *AB*, annuals and biennials; *SS*, shrubs and semishrubs; *PR*, perennial rhizome grass; *PB*, perennial bunchgrass; *PF*, perennial forbs; *PG*, perennial grass. A significant interaction occurred between sites and years for all different functional groups; differences among years within a site are indicated by letters (*a–c*) and differences among sites within a year by letters (*x–z*)

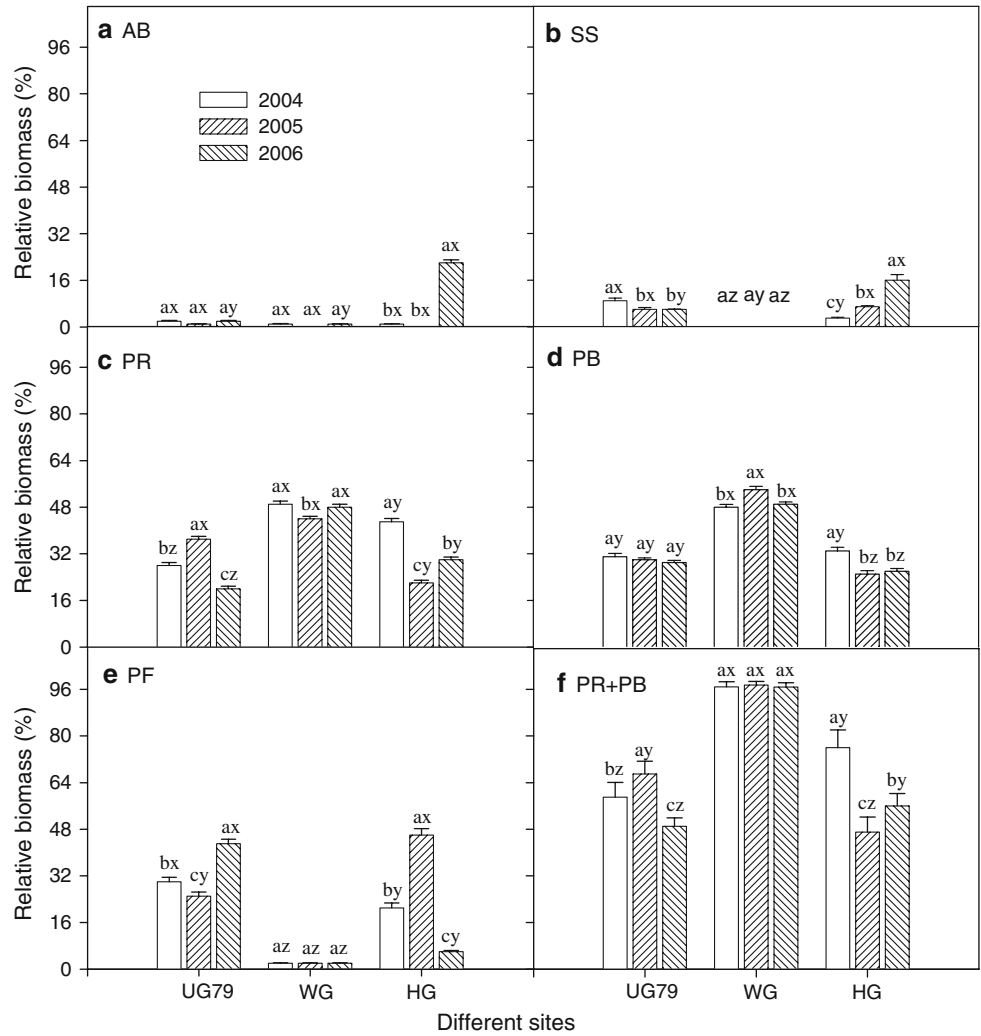


Table 4 Species richness of different functional groups on the differently managed sites in 2004, 2005, and 2006

Species	UG79			WG			HG		
	2004	2005	2006	2004	2005	2006	2004	2005	2006
Annual and biennial	7	2	4	5	0	3	4	0	4
Perennial forbs	34	31	29	11	12	7	12	14	8
Perennial grass	9	9	8	9	9	9	7	7	6
Shrubs and semishrubs	5	4	5	0	0	0	3	3	3
Total	55	46	46	25	21	19	26	24	20

Site descriptions as for Table 2

Table 5 Simpson diversity index at differently managed sites in 2004, 2005, and 2006

Sites	2004	2005	2006	Site ME
UG79	7.49 ± 0.41	6.64 ± 0.43	6.03 ± 0.83	6.79 ± 0.34 a
WG	4.05 ± 0.27	3.82 ± 0.24	3.08 ± 0.21	3.67 ± 0.16 b
HG	3.55 ± 0.35	3.87 ± 0.35	4.00 ± 0.17	3.78 ± 0.18 b
Year effects	5.03 ± 0.38	4.78 ± 0.35	4.37 ± 0.38	

Significant main effects of sites (site ME) are indicated by different small letters in the last column. Significant main effects of sites (site ME) and year effects are indicated by bold. Site descriptions as for Table 2.

Relative biomass of species

Grazing-sensitive species, for example *Achnatherum sibiricum* and *Anemarrhena asphodeloides*, disappeared at the heavily grazed site whereas *P. acculis*, *A. frigida*, and *C. duriuscula* became dominant under heavy grazing conditions. These species are adapted to grazing because of their strong gap colonization ability and prostrate growth habit, which are effective grazing avoidance mechanisms (Milchunas and Noy-Meir 2002; Bullock et al. 2001). Grazing tolerance is another important adaptation mechanism to grazing. *C. squarrosa*, despite being preferentially eaten by sheep, has a high over-compensatory ability because of strong tillering and high photosynthetic capacity (Liang et al. 2002; Wang and Wang 2001; Gao et al. 2007), which makes it an important species on the heavily grazed site. The relative biomass of *L. chinensis* was significantly reduced after drought at sites UG79 and WG. Because of sheep preference for this species much more in drought years than in years of normal rainfall (Wang 2000), it was almost completely absent at site HG after two dry years (Table 3).

Carex spp. characterised by strong colonization ability and drought tolerance (Liu et al. 1998) can produce many thin and small tillers or stoloniferous branches, so it occupies huge horizontal space. This strategy can partially explain why *Carex* spp. became an important species at all three sites after drought (Table 3). It should be noted that *Carex* has two main species in this area, more than 98% of *Carex* spp. is *Carex korshinskyi* at sites UG79 and WG, and more than 98% of *Carex* spp. is *C. duriuscula* at site HG (personal communication with Bai). *C. duriuscula* has stronger colonization ability and drought tolerance than *Carex korshinskyi*.

Annual and biennial usually make a very small contribution to total community productivity in terms of relative biomass and species richness in this perennial steppe grassland (Fig. 1a; Table 4). The increases in these species were only temporary and highly affected by rainfall distribution and abundance. In the first dry year, 2005, almost no annual species, for example *Chenopodium glaucum*, *Chenopodium aristatum* L., and *Salsola collina*, were found. However, these opportunity species have the ability to quickly occupy space during periods of water availability, resulting in a biomass contribution of 22% in 2006 at site HG where the amount of bare soil was large after the first dry year, 2005.

Carry-over effects of drought on species were reflected by the substantial increase of biomass contribution of *Agropyron michnoi* and *P. acculis* in 2005 compared to 2004. Because of the favourable growth conditions in 2004, these two rhizome species probably accumulated enough root carbohydrates for the second year's growth, but failed to do so in 2005, resulting in a substantial decrease of relative biomass in 2006.

Competition and facilitation for resources are two of the most decisive factors determining vegetation pattern

(Michalet 2007) and the relative importance of facilitation and competition varies inversely across gradients of abiotic stress, with facilitation dominant under highly stressful conditions (Brooker and Callaghan 1998). However, it seems that interspecific competition, instead of facilitation, plays a vital role in determining community structure and species composition under harsh environmental conditions (Zhou et al. 2006). Despite its strong colonization ability and low palatability (Wang 2000), the abundance of drought-susceptible *P. acculis* was substantially reduced on site HG after two dry years, and drought-tolerant *A. frigida* (Gao et al. 2007) and opportunity species of AB significantly increased because of release from competition by *P. acculis*. It has been argued that high abundance of *P. acculis* is indicative of severe degradation of the grassland (Liu et al. 1998; Li and Li 2002) and it is regarded as the last perennial species in this native grassland, which in cases of disappearance indicates a high danger of extinction (Li and Li 2002). However, as suggested by our data, prolonged drought periods may reduce the predictability of degradation by means of this typical indicator species, because the decrease of *P. acculis* is partially compensated by *A. frigida*.

Species compensatory effects

A growing number of experiments have demonstrated that species compensatory effects can ensure greater and more stable production (Tilman and Downing 1994; Bai et al. 2001, 2004). Types of compensatory effect are very different in different land-use types. PR and PF compensated each other, while PB and SS remained more or less stable in the long-term enclosure (Fig. 1); the sharp decrease of PF was mainly compensated by functional groups AB and SS after two dry years on the heavily grazed site; compensatory effects between species were more evident on the winter grazing area, where the perennial grasses were overridingly dominant (Fig. 1f). The relative decrease of *L. chinensis* was partially compensated by the relative increase of *Carex* spp. and *Achnatherum sibiricum* was mainly compensated by *S. grandis* in the dry year (Table 4). However, species and/or functional groups compensatory effects did not prevent low total productivity in 2005 and 2006 at all three sites (Table 1).

Species diversity

A review (Mittelbach et al. 2001) of 171 published studies revealed the relationship between species richness and productivity is hump-shaped and positive. To stress this relationship in specific grazing ecosystems, Cingolani et al. (2005) argued that grazing can substantially change species composition, instead of species richness or diversity, based on the assumption that the numbers of less grazing-resistant species are similar to the

numbers of grazing-resistant species. In contrast with argument, our data illustrated that heavy grazing significantly reduced species richness and biodiversity. In addition, the positive relationship between productivity and species diversity was only found in the relatively normal year 2004, and no relationship was observed between species diversity and productivity in the dry years 2005 and 2006. This discrepancy indicates that regulatory processes at the community level in response to varying soil nutrient and water availability are quite complex in grassland ecosystems in general, and in this semi-arid grassland in particular (Baer et al. 2003; Cingolani et al. 2005). When one resource, for example soil water availability, becomes limiting, all ecosystem processes are slowed down. In addition, the responses of productivity to drought are quicker than species richness, which leads to the divergence between productivity and species diversity. It should be noted that this ecosystem seems to have greater resilience, as indicated by the fact that none of the important perennial species disappeared after extreme drought, despite high fluctuation of species contributions to community production in different years.

In conclusion, drought stress and grazing disturbance interactively control species composition and community structure in this ecosystem. Nonetheless, we emphasized that severe drought combined with heavy grazing has greatly changed species composition and functional components, which led to unstable production and degradation of this perennial grassland.

Acknowledgments This work was supported by the Deutsche Forschungsgemeinschaft (DFG, SA 359/30-1) embedded in joint-research project FG 536, Matter fluxes in grasslands of Inner Mongolia as influenced by stocking rate (MAGIM), and the State Key Basic Research Program and Development Plan (2007CB106801). We would like to thank the Inner Mongolia Grassland Ecosystem Research Station for providing meteorological data.

References

- Baer SG, Blair JM, Collins SL, Knapp AK (2003) Soil resources regulate productivity and diversity in newly established tallgrass prairie. *Ecology* 84:724–735
- Bai YF, Li LH, Huang JH, Chen ZZ (2001) The influence of plant diversity and functional composition on ecosystem stability of four *Stipa* communities in the Inner Mongolia plateau. *Acta Bot Sin* 43:280–287
- Bai YF, Han XG, Wu JG, Chen ZZ, Li LH (2004) Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature* 431:181–184
- Bai YF, Wu JG, Pan QM, Huang JH, Wang QB, Li FS, Buyantuyev A, Han XG (2007) Positive linear relationship between productivity and diversity: evidence from the Eurasian steppe. *J Appl Ecol* 44:1023–1034
- Banyikwa FF (1988) The growth response to two East Africa perennial grasses to defoliation, nitrogen fertilizer and competition. *Oikos* 51:25–30
- Biondini ME, Patton BD, Nyren PE (1998) Grazing intensity and ecosystem processes in a northern mixed-grass prairie, USA. *Ecol Appl* 8:469–479
- Briggs JM, Knapp AK (2001) Determinants of C₃ forb growth and production in a C₄ dominated grassland. *Plant Ecol* 52:93–100
- Brooker RW, Callaghan TV (1998) The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. *Oikos* 81:196–207
- Bullock JM, Franklin J, Stevenson MJ, Silvertown J, Coulson SJ, Gregory SJ, Tofts R (2001) A plant trait analysis of responses to grazing in a long-term experiment. *J Appl Ecol* 38:253–267
- Cingolani AM, Noy-Meir I, Diaz S (2005) Grazing effects on rangeland diversity: a synthesis of contemporary models. *Ecol Appl* 15:757–773
- Connolly J, Wayne PM (2005) Assessing determinants of community biomass composition in two-species plant competition studies. *Oecologia* 142:450–457
- Fahnestock JT, Detling JK (2000) Morphological and physiological responses of perennial grasses to long-term grazing in the Pryor Mountains, Montana. *Am Midl Nat* 143:312–320
- Gao YZ, Wang SP, Han XG, Chen QS, Zhou ZY, Patton BD (2007) Defoliation, nitrogen and competition: effects on plant growth and biomass allocation of *Cleistogenes squarrosa* and *Artemisia frigida*. *J Plant Nutr Soil Sci* 170:115–122
- Hartvigsen G (2000) Competition between co-dominant plants of the Serengeti plains depends on competitor identity, water, and urine. *Plant Ecol* 148:31–41
- Katoh K, Takeuchi K, Jiang DM, Nan YH, Kou ZW (1998) Vegetation restoration by seasonal enclosure in the Kerqin sandy land, Inner Mongolia. *Plant Ecol* 139:133–144
- Krümmelbein J, Wang ZH, Zhao Y, Peth S, Horn R (2006) Influence of various grazing intensities on soil stability, soil structure and water balance of grassland soils in Inner Mongolia, P. R. China. *Adv Geo Ecol* 38:93–101
- Li YH (1989) Impact of grazing on *Leymus chinensis* steppe and *Stipa grandis* steppe. *Acta Oecol* 10:31–46
- Li JH, Li ZQ (2002) Clonal morphological plasticity and biomass allocation pattern of *Artemisia frigida* and *Potentilla acaulis* under different grazing intensities. *Acta Phytoecol Sin* 26:35–44
- Liang C, Michalk DL, Millar GD (2002) The ecology and growth patterns of *Cleistogenes* species in degraded grasslands of eastern Inner Mongolia, China. *J Appl Ecol* 39:584–594
- Liu ZL, Wang W, Liang CZ, Hao DY (1998) The regressive succession pattern and its diagnostic of Inner Mongolia steppe in sustained and super-strong grazing. *Acta Agrest Sin* 6:244–251
- Michalet R (2007) Highlighting the multiple drivers of change in interactions along stress gradients. *New Phytol* 173:3–6
- Milchunas DG, Noy-Meir I (2002) Grazing refuges, external avoidance of herbivory and plant diversity. *Oikos* 99:113–130
- Milchunas DG, Lauenroth WK, Chapman PL, Kazempour MK (1989) Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. *Vegetation* 80:11–23
- Milton SJ, Dean WR, du Plessis MA, Siegfried WR (1994) A conceptual model of arid rangeland degradation. *Bioscience* 44:70–76
- Mittelbach GG, Steiner CF, Scheiner SM, Gross KL, Reynolds HL, Waide RB, Willig MR, Dodson SI, Gough L (2001) What is the observed relationship between species richness and productivity? *Ecology* 82:2381–2396
- Nippert JB, Knapp AK, Briggs JM (2006) Intra-annual rainfall variability and grassland productivity: can the past predict the future? *Plant Ecol* 184:65–74
- O'Connor TG, Haines LM, Snyman HA (2001) Influence of precipitation and species composition on phytomass of a semi-arid African grassland. *J Ecol* 89:850–860
- Snyman HA (2005) Rangeland degradation in a semi-arid South Africa—I: influence on seasonal root distribution, root/shoot ratios and water-use efficiency. *J Arid Environ* 60:457–481
- Thurow TL, Taylor CA Jr (1999) Viewpoint: the role of drought in range management. *J Range Manage* 52:413–419
- Tilman D, Downing JA (1994) Biodiversity and stability in grasslands. *Nature* 367:363–365
- Wang SP (2000) The dietary composition of fine wool sheep and plant diversity in Inner Mongolia steppe. *Acta Ecol Sin* 20:951–957

- Wang SP, Wang YF (2001) Study on over-compensation growth of *Cleistogenes squarrosa* population in Inner Mongolia steppe. *Acta Bot Sin* 43:413–418
- Xiao XM, Wang YF, Jiang S, Ojima DS, Bonham CD (1995) Interannual variation in the climate and above-ground biomass of *Leymus chinense* steppe and *Stipa grandis* steppe in the Xilin river basin, Inner Mongolia, China. *J Arid Environ* 31:283–299
- Xie Y, Wittig R (2003) Growth parameters of characteristic species of *Stipa* steppes in northern China as indicators of the grazing intensity. *J Appl Bot* 77:68–74
- Xie Y, Wittig R (2004) The impact of grazing intensity on soil characteristics of *Stipa grandis* and *Stipa bungeana* steppe in northern China (autonomous region of Ningxia). *Acta Oecol* 25:197–204
- Zhong SY, Li YL, Cui JY, Zhao WZ (2005) Influence of continuous grazing and livestock exclusion on soil properties in a degraded sandy grassland, Inner Mongolia, northern China. *Catena* 59:267–278
- Zhou Z, Sun OJ, Huang J, Gao Y, Han X (2006) Land use affects the relationship between species diversity and productivity at the local scale in a semi-arid steppe ecosystem. *Funct Ecol* 20:753–762
- Zhu TC (1993) Grasslands of China. In: Coupland RT (ed) *Ecosystems of the World. Natural grasslands: Eastern Hemisphere and resume*. Elsevier, NY, pp 61–82