

**Impacts of grazing intensity, precipitation and temperature
on productivity, forage quality, species composition and
diversity in typical steppe of Inner Mongolia**

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To my mother

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List of abbreviations

GI Grazing intensity

P Precipitation

T Temperature

ANPP Aboveground net primary production

AB Aboveground biomass

FNV Forage nutritive value

FNY Forage nutritive yield

FQ Forage quality

SC Species composition

SD Species diversity

R Richness

E Evenness

Y Year

B Block

ADF Acid detergent fibre

ADL Acid detergent lignin

CDOM Cellulase digestible organic matter

CP Crude protein

ME Metabolizable energy

NDF Neutral detergent fibre

CDOMY Cellulase digestible organic matter yield

CPY Crude protein yield

MEY Metabolizable energy yield

NDFY Neutral detergent fibre yield

OM Organic matter

DM Dry matter

EULOS Non-soluble enzymatic substance

HM Herbage mass

MAGIM Matter Fluxes of Grasslands in Inner Mongolia

SD Standard deviation

SE Standard error

SR Stocking rate

TS Traditional System

MSL Milchunas-Lauenroth-Sala model

Chapter 1

General Introduction

1 General introduction

1.1 The grassland in Inner Mongolia, P.R. China

The Eurasian grassland is one of the largest ecosystems and contiguous biome in the world (Bai *et al.* 2010). In China, approximate 400 million ha of the total land area are grasslands, which account for 42% of the nation' total land area and are equivalent to 12% of the world's grassland area (Hong 2006). They play very important roles in conserving biodiversity and supporting the livelihoods of farmers (Suttie *et al.* 2005). During recent decades, with the pressure of increased human and livestock populations, Chinese grasslands are facing dramatic degradation and desertification as a result of significant overgrazing, overpopulation and worse effects of drought induced by climate change (Li *et al.* 2008), especially in arid and semi-arid environments (Suttie *et al.* 2005).

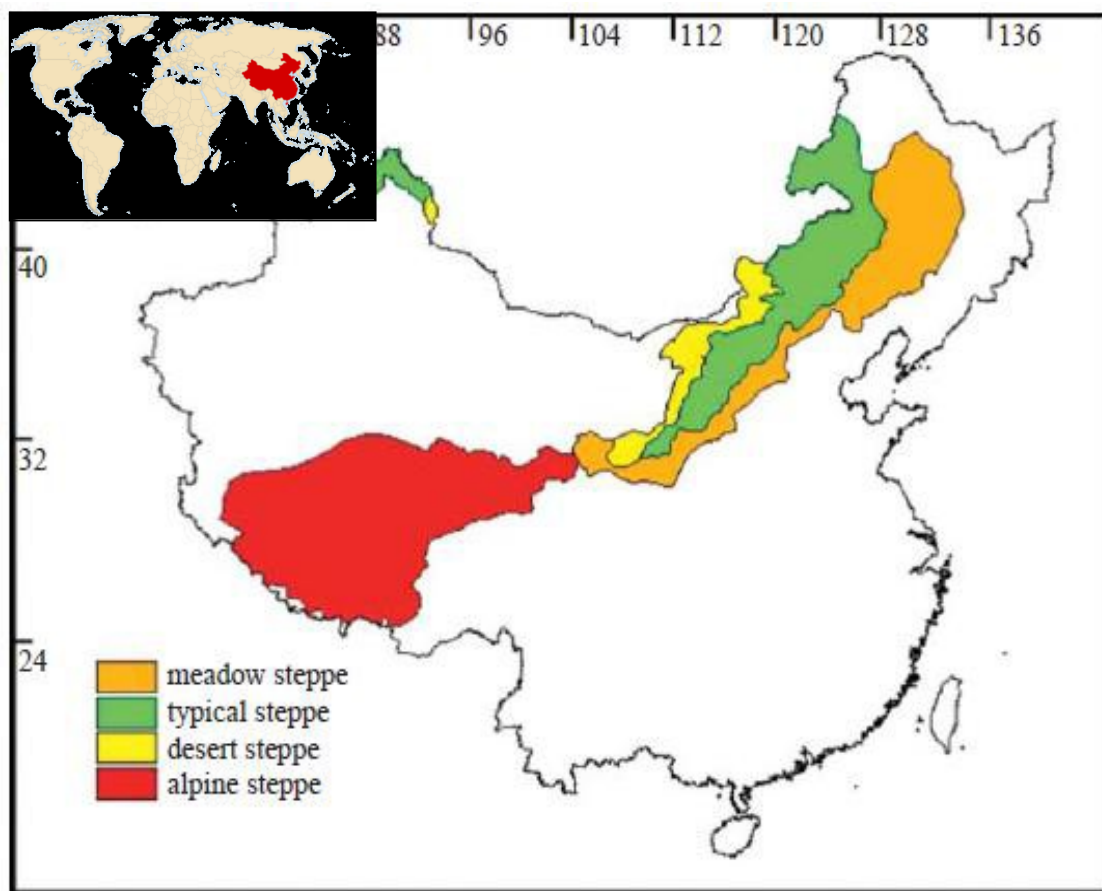


Figure 1 Distribution of steppe ecosystems in China (Kang *et al.* 2007)

Most of the temperate grasslands in China are semi-arid and arid grasslands and are distributed throughout the northern plain. The grasslands of Inner Mongolia are classified as four major steppe types: meadow, typical, desert and alpine (Sun, 2005; Kang *et al.* 2007) (Figure 1). Typical steppes dominate the grassland in Inner Mongolia and are developed under a semi-arid and arid continental climate. Based on the long-term meteorological data (1982-2004), the mean annual precipitation in this area is 343 mm and the mean annual temperature is 0.7°C. Long-term overgrazing in this typical steppe has led to severe ecological and economic problems (Wang and Ripley, 1997; Tong *et al.*, 2004). Grazing-induced pressures on these steppe ecosystems exceed their carrying potential (Yu *et al.*, 2004) and therefore reduce productivity, lose biodiversity and bring dust storms (Kemp and Michalk, 2011). The plant growth in typical steppe starts from late March and lasts until the end of September. There are seven dominant species distributed in current vegetation communities: *Stipa grandis*, *Stipa krylovii*, *Cleistogenes squarrosa*, *Agropyron cristatum*, *Leymus chinensis*, *Artemisia frigida*, and *Salsola collina*. The most common two species are *Stipa grandis* and *Leymus chinensis* (Sun 2005), which comprise 60-80% biomass of whole vegetation communities (Figure 2).

Due to the major drivers of global climate change and grazing disturbance (Yu *et al.* 2004; Wang *et al.* 2008), sand and dust storms occurred frequently in the past two decades. It indicates that the grassland ecosystems in China are facing severe degradation and desertification. Local farmers sharply increased the grazing intensities so that they can maximize their short-term economic profit rather than considering long-term perspectives (Glindemann *et al.*, 2009). Intensive grazing has deleterious impacts on climate, soil, hydrology, vegetation and biodiversity, for example, decreases productivity and changes species composition (Wang and Ripley, 1997; Wang, 2004).

Together with dramatic drought events, the adverse impacts of long-term heavy grazing on arid and semi-arid steppe ecosystem are undeniable.

However, the current grazing management strategies in Inner Mongolia definitely cannot meet the needs of maintaining sustainable grasslands. The problems resulting from the current state of grassland and related issues across the landscape in China require strong effective management ways to conserve and restore the grasslands. Therefore, understanding the causal relationship and degradation process of grasslands and study on their degradation mechanisms will be very helpful for providing conservation strategies and guiding grassland managements.



Figure 2 Typical steppe (short grass communities, dominated by *Leymus chinensis* and *Stipa grandis*)

1.2 Study area

1.2.1 Location

The grazing experiment was carried out closed to the Inner Mongolia Grassland Ecosystem Research Station (IMGERS, 43°38' N, 116°42' E, 1200 m a.s.l) in the Xilin River Basin (Figure 3), classified as central Asian typical steppe ecosystem. Our study site covered around 150 ha area. The soil is classified as Calcic Chestnuts and Calcic Chernozems (IUSS Working Group WRB 2006), with a texture of sandy loam or loamy sand. The lab analysis was performed at the IMGERS of the Chinese Academy of Sciences.

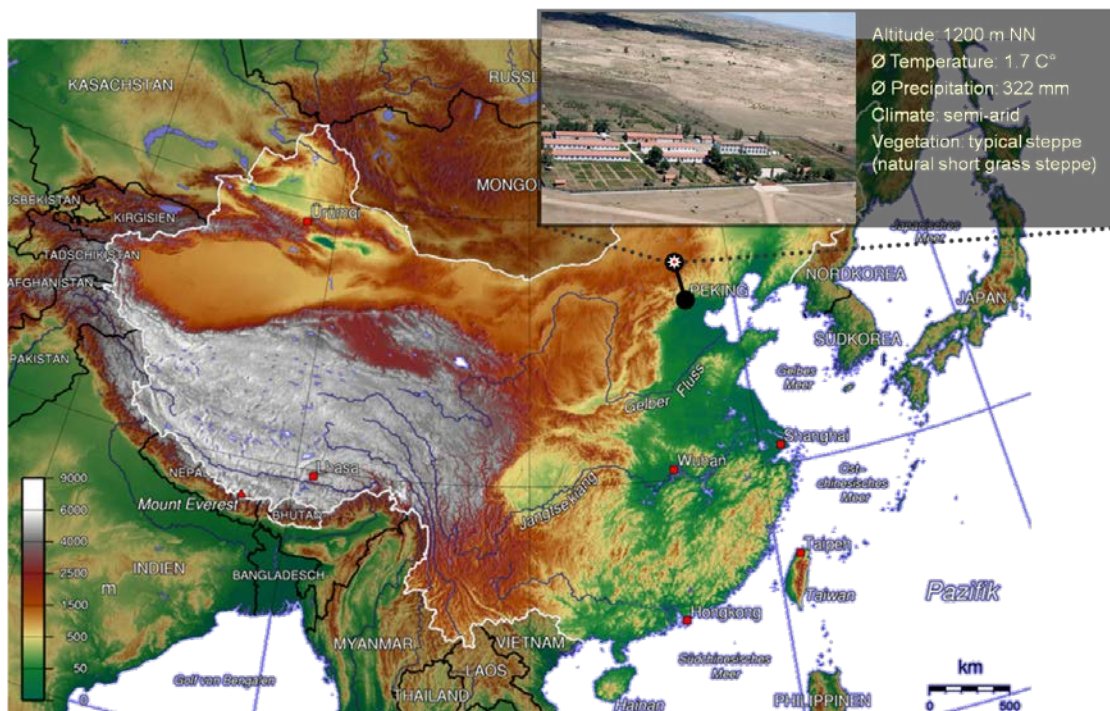


Figure 3 The location of Inner Mongolia grassland research station

The field experimental sites characterized by a continental, semi-arid climate with mean annual precipitation in this region of 335mm (1982-2006), with about 80% occurring during the growing season (May-September) and mean annual temperature of

0.7°C. Figure 4 shows the monthly dynamic of precipitation and temperature in our research region.

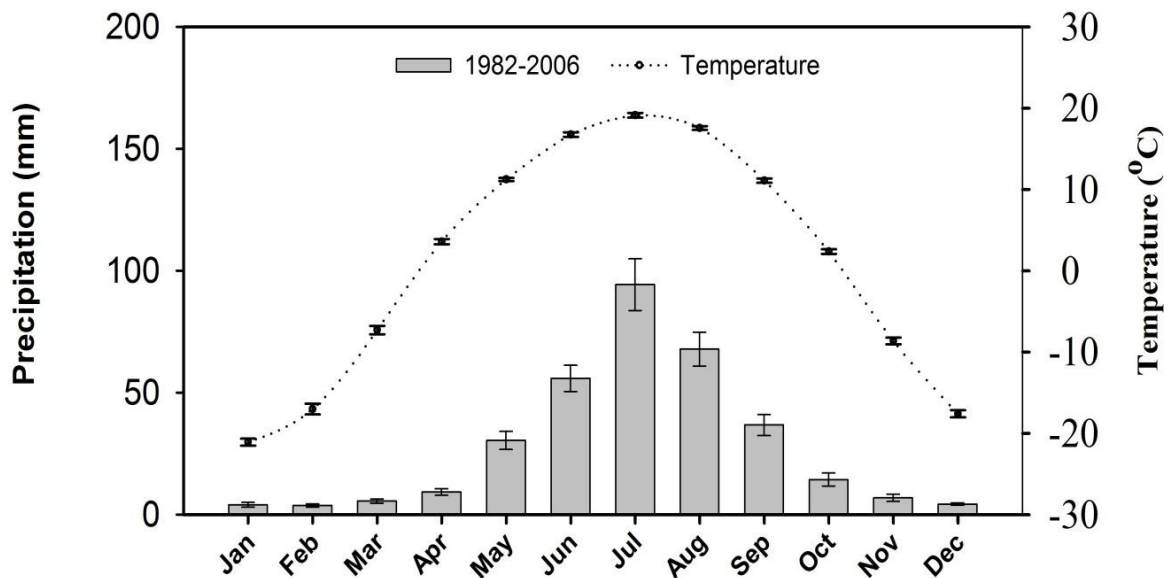


Figure 4 Long-term mean monthly precipitation and temperature (1982-2006).

1.2.2 Vegetation

The most common species in this study area are listed as follows: *S. grandis* (perennial C3 bunchgrass), *L. chinensis* (perennial C3 rhizomatous grass), *A. cristatum* (perennial C3 bunchgrass with short rhizome), *C. squarrosa* (perennial C4 bunchgrass), *A. frigida* (perennial forb or hemi-shrub) and *Caragana microphylla* (shrub). The potential climax vegetation of this typical steppe community is dominated by the fast-growing grass *L. chinensis* adapting to wet and resources rich conditions and the drought tolerant slow-growing needle grass *S. grandis* (Bai *et al.*, 2004, Wan *et al.* 2008). Altogether these two species account for 60-80% of total aboveground biomass. On degraded plant community, *C. squarrosa* and *A. frigida* are indicators for overgrazing (Tong *et al.*, 2004). All these grasses are widely used for sheep, goat and

cattle grazing. Thus, as the previous studies showed that, the grassland in Inner Mongolia dredged from *L. chinensis* steppe and *S. grandis* steppe to more mature *A. frigida* and *C. squarrosa* dominated steppe (Li 1988, Li 1989). The growing season lasts from April to September for perennial plant species, whereas typically starts from July for annual plants following the period of highest rainfall (Bai *et al.*, 2004).

1.3 MAGIM-Project

Sino-German cooperation was set up to investigate the multiple effects of grazing on the typical steppe of Inner Mongolia within the Xilin River catchment (Figure 1b). The research group (FG 536) MAGIM (Matter fluxes of Grasslands in Inner Mongolia as influenced by stocking rate), funded by the Deutsche Forschungsgemeinschaft (DFG). In this project, German and Chinese scientists coming from different institutes were working together to investigate the multiple effects of grazing on the typical steppe; to understand ecosystem functioning and clarify the interactions between grazing of steppe ecosystems and matter fluxes for developing improved grassland management concepts in Inner Mongolia. The inter-disciplinary project analyzed steppe degradation processes on plot as well as on regional scale. In total 11 participating groups were set up to contribute to the overall aim of MAGIM. The sub-projects include diverse topics:

1. Amount, composition, and turnover of organic matter pools in grassland soils with different grazing management
2. Nitrogen supply of grassland and its belowground productivity as influenced by stocking rate, management, and water availability
3. Grazing intensity and grazing management effects on typical steppe ecosystem (comprising primary and secondary productivity)

4. Grazing intensity effects on animal performance, feed intake, and herbage quality in typical steppe ecosystems
5. Modeling of carbon and nitrogen turnover processes and biosphere-atmosphere exchange
6. Water and carbon fluxes of managed grasslands (surface and airborne observations)
7. Regional water balance and matter flow
8. Impact of grazing on hydraulic, thermal, and mechanical soil properties of grassland soils
9. Regional identification of sensitive areas for wind-driven matter fluxes
10. Influence of grazing pressure on the carbon isotope composition of the grasslands of China
11. Surface and satellite based remote sensing to infer rain rates within the Xilin River Basin

The present study was based on the joint research interests of sub-project 3 (P3), cooperating with the Institute of plant nutrition at University of Kiel, Germany and Crop Science and Plant Breeding, section Grass and Forage Science/ Organic Agriculture at University of Kiel, Germany and the Institute of Botany, Chinese Academy of Sciences, Beijing (P.R. China). A long-term grazing experiment has been established from 2005 in the typical steppe of Inner Mongolia. The field experiment was performed under close cooperation between P3 and P4, which is administered by the Institute of Animal Nutrition and Physiology, University of Kiel. The aim of this sub-project is to evaluate the impact of grazing management on yield performance, herbage quality and persistence of grassland ecosystems of Inner Mongolia.

1.4 Objectives and outlines of the thesis

1.4.1 Scientific background

The overall goal of this study is to analyze and evaluate the long-term effects of sheep grazing intensity on yield performance, herbage quality, species diversity and species composition in grassland ecosystems in Inner Mongolia, and then to provide efficient practices preventing grassland degradation. Data was collected through a field grazing trial that was lasted for six years (from 2005 to 2010). Grazing induced community structural changes and affects ecosystems by removing tissue and returning nutrient through dung and urine deposition (Archer 1989, Bosch 1989, Noy-Meir *et al.* 1989, Westoby *et al.* 1989). In addition, ungulate trampling reduces the aboveground biomass, increases in bulk density and decreases in soil water storage, and then finally affects microbial growth of plant and soil (Zhao *et al.* 2007). As a result, the grassland which suffered high grazing density distributes less palatable and valuable species (e.g. *L. chinensis* and *S. grandis*) and turns into more unpalatable species (*A. frigida*) dominated community (Li, 1999; Wang *et al.*, 2002; Barger *et al.*, 2004; Zhao *et al.*, 2005).

Then the degradation status of the grassland formed. In the meanwhile, climate factors such as precipitation and temperature act on the responses of vegetation to grazing. As previous studies suggested that the amount and seasonal distribution of precipitation triggers and maintains biological processes like productivity and nutrient cycling in arid and semi-arid ecosystems (Noy-Meir 1973; Bai *et al.* 2004; Yu *et al.* 2004). In this context, information was needed to investigate the grassland growth dynamics and grazing responses under variable climate conditions. It is the key property to maintain an intact ecosystem. This is of high priority for efficient management and recovery of this widely degraded grassland. In accordance to the overall aim of the sub-project of MAGIM, different aspects and assumptions were addressed in the three

scientific studies of chapter 2, 3, and 4. The investigations on climate pattern, grazing intensity, nutrient flow and plant response will help to provide fundamental knowledge to understand the complex interaction of grazing – vegetation – climate (just as the Figure 5 shown). In the following, the chapters of the thesis are briefly introduced:

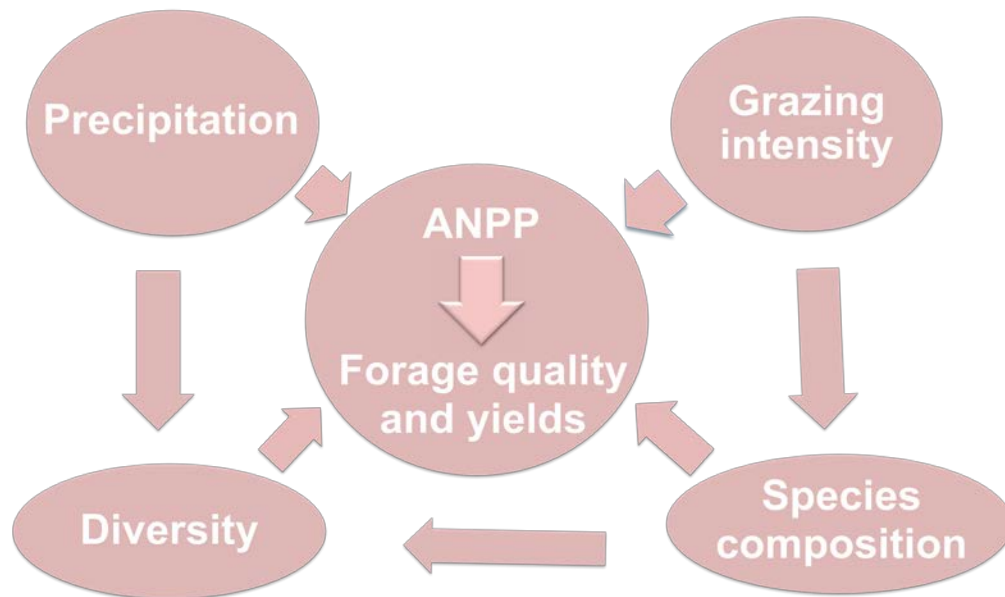


Figure 5 The interactions between biotic and abiotic factors effects and grassland vegetation

In the first study - **Chapter 2**, six years data from 2005-2010 were used to analyze the effect of grazing, precipitation and temperature on species shifts and species diversity in the typical steppe. Parameter analysis included diversity index, evenness, richness and species composition. For understanding potential shifts in vegetation and underlying processes, three research aspects were conducted: (1) What's the response of plant species (species composition and diversity) to grazing intensity, varying precipitation and temperature, (2) What's the effect of temporal within-year variation (annual, seasonal, monthly) in

precipitation and temperature on species composition and diversity, and (3) How's the homeostasis between C3 and C4 species as a function of temporal precipitation and temperature patterns.

In the second study - **Chapter 3**, the six years effects of grazing intensity, different years, and forage species on aboveground net primary productivity (ANPP) and on nutritional forage characteristics were tested by using the same grazing experiment. Nutritional forage characteristics analysis included nutritional value and nutritional yield. The forage nutritional value is characterized by the concentration of crude protein (CP), cellulase digestible organic matter (CDOM), metabolizable energy (ME) and neutral detergent fibre (NDF). The forage nutritional yield is a function of ANPP and the forage nutritional value. The primary questions we addressed relate to four aspects: (1) What is the relationship between forage nutritional value, ANPP and forage nutritional yield?; (2) How do grazing intensity, precipitation and temperature affect forage nutritional value, ANPP and forage nutritional yield?; (3) How do species composition and species diversity affect forage nutritional value, ANPP and forage nutritional yield?; and 4) how much contributions ANPP and dominant species can make to affect FNY?

In the last study - **Chapter 4**, we rather focus on the responses of five specific dominant species (three C3 species and two C4 species) in Inner Mongolia grassland community. Again, we used the same grazing experiment but collected the data in wet year 2008 and drought year 2010. We tested the effects of grazing, year, growing period, year \times grazing intensity and year \times growing period on five plant species' nutritive value. In order to figure out the causal linkage between shifts in species composition and changes in plant nutritive value under different influence factors, we assess the following three questions: (1) How does nutritive value dynamic of the five species vary with grazing intensity, growing period and precipitation? (2) Are there any shifts in the nutritive value of forage linked to changes

in species composition in response to grazing intensity, growing period or variation in precipitation? (3) What are the trade-offs between C3 and C4 species in their nutritive value with grazing effect over the growing season?

1.4.2 Grazing experiment

A large sheep grazing experiment was established on a typical steppe in June 2005 to investigate the processes of steppe degradation along a gradient of seven grazing. Before the experiment started, the steppe was recovered for 2 years by excluding grazing. It covers an area around 150 ha. All treatments were replicated on a level area as well as on slopes, two out of several typical areas with different environmental conditions, and then considered as block level and block slope. The experiment was carried out in the form of split-plot on a random complete block design. The ‘management system’ was the main plot factor (traditional versus mixed systems), while the sub-plots was the ‘grazing intensity’ (classified by stocking rate from 0 to 9 sheep ha⁻¹, by an increment of 1.5). Detailed experimental design information please refers to Chapter 3. In the mixed system, the two sub-plots which are used for haymaking and grazing under each intensity of grazing will alternate year by year. In the traditional system, these two sub-plots will be used for haymaking or grazing consistently. The overview and the experiment layout of the field grazing experiment were shown in Figure 6. Mixed systems were expected to exhibit more positive effects on vegetation, since plant could release from grazing stress and have more time to recovery (Wang, 2004). In our three studies, we only focused on traditional systems since it is a more representative grazing mode in Inner Mongolia. The seven grazing intensities comprise of ungrazed, very light, light, light-moderate, moderate, heavy, and very heavy grazing. Figure 7 illustrates the overview of different grazing treatment that was indicated by herbage mass and soil coverage. Due to

spatial heterogeneity of site productivities, herbage allowance was applying to moderate the intensity of grazing according to the herbage offered per kg of sheep live weight for a certain

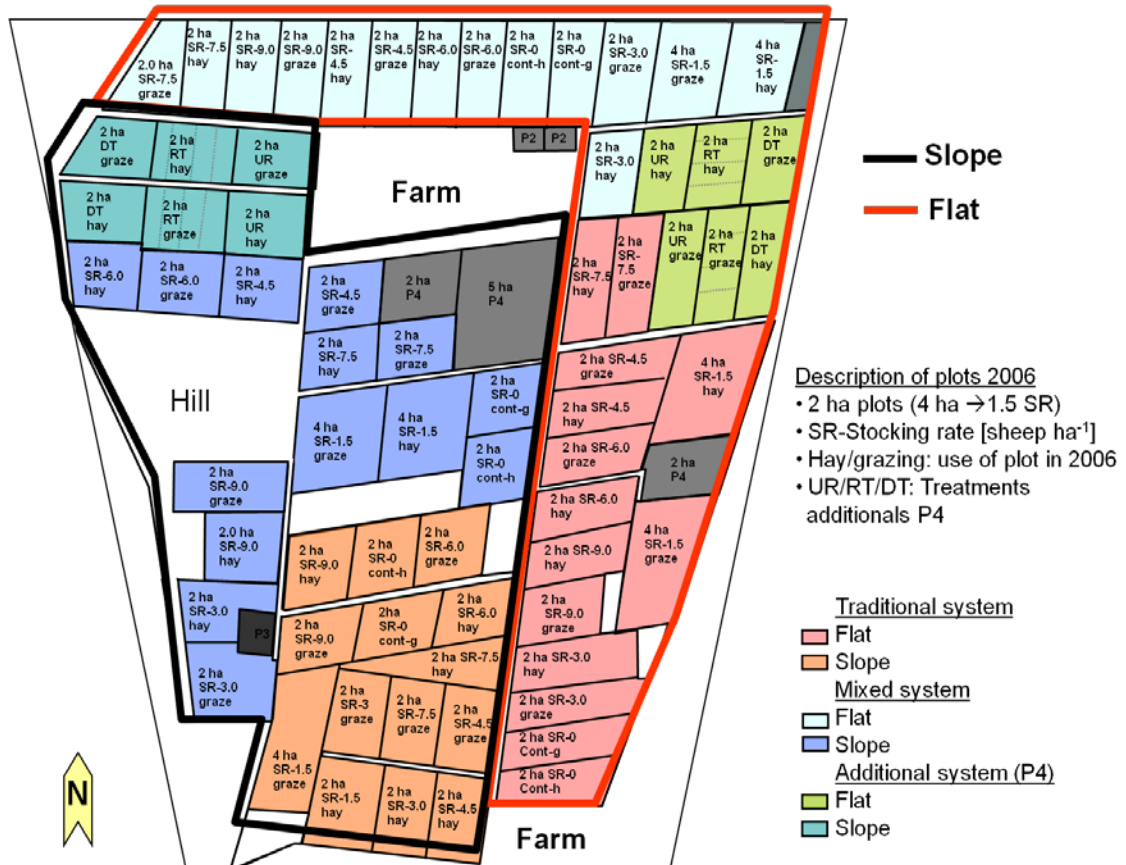


Figure 6 The layout of the field grazing experiment

Notes for the experimental layout: The top side together with right side is the flat block, the rest is the slope block; 0-9 by an increment of 1.5 represents the stocking rate; H, G stands for hay-making and grazing respectively; plots with shallow blue (top) and the blue green (left middle) background are mixed system, plots with the pink (left down) and shallow red (right down) background are traditional system; the differences regarding the management systems please refer to the text.

time period (Sollenberger *et al.*, 2005). Grazing intensities of very light, light, light-moderate, moderate, heavy, and very heavy were defined by standing biomass allowance target ranges

of <1.5, 1.5-3.0, 3.0-4.5, 4.5-6.0, 6.0-12.0, >12.0 kg dry matter kg⁻¹ live weight. Further details about herbage allowance target range were shown in Chapter 3.

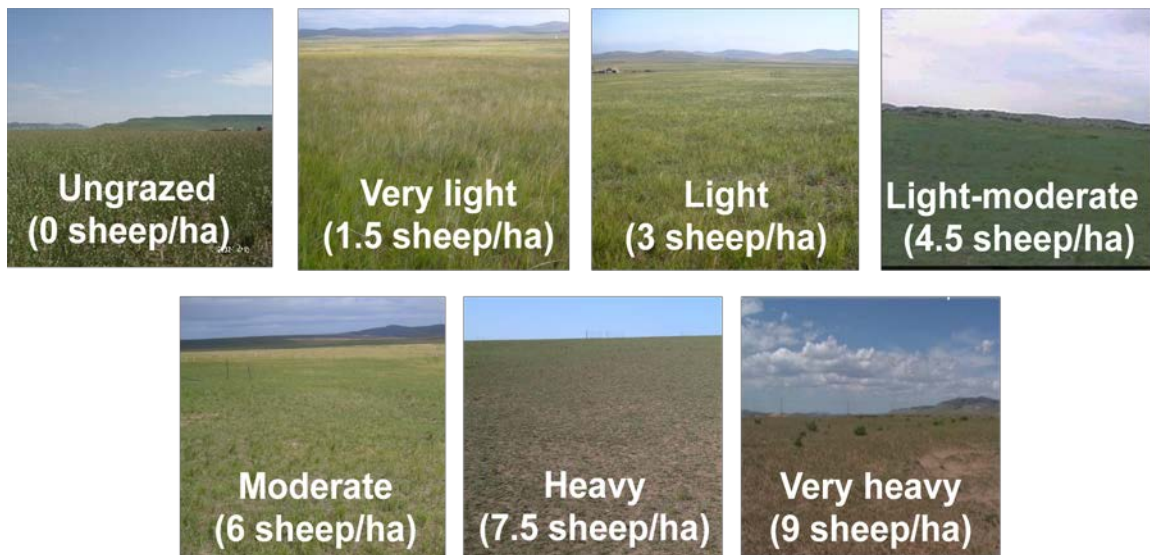


Figure 7 The layout of the field grazing experiment

1.5 Terminology

The definitions and terms used for grassland and rangeland activities vary largely because of the different professional background. Terminology in the present thesis adopts recommendations of Hodgson (1979) and the IRC (2008).

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Chapter 2

**Effects of Grazing Intensity and
Environmental Factors on Species Composition and
Diversity in Typical Steppe of Inner Mongolia, China**

Effects of Grazing Intensity and Environmental Factors on Species Composition and Diversity in Typical Steppe of Inner Mongolia, China

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Abstract

In the present study, we aim to analyze the effect of grazing, precipitation and temperature on plant species dynamics in the typical steppe of Inner Mongolia, P.R. China. By uncoupling biotic and abiotic factors, we provide essential information on the main drivers determining species composition and species diversity. This is of high priority for efficient management and recovery of this widely degraded grassland. Effects of grazing by sheep were studied in a controlled experiment along a gradient of seven grazing intensities (from ungrazed to very heavily grazed) during six consecutive years (2005-2010). The results show that plant species composition and diversity varied among years but were little affected by grazing intensity, since the experimental years were much dryer than the long term average, the abiotic constraints may have overridden any grazing effect. Among-year differences were predominantly determined by the abiotic factors of precipitation and temperature. Most of the variation in species dynamics and coexistence between C3 and C4 species was explained by seasonal weather conditions, i.e. precipitation and temperature regime during the early-season (March-June) were most important in determining vegetation dynamics. The dominant C3 species *Stipa grandis* was highly competitive in March-June, when the temperature levels were low and rainfall level was high. In contrast, the most common C4 species *Cleistogenes squarrosa* benefited from high early-season temperature levels and low early-season rainfall. However, biomass of *Stipa grandis* was positively correlated with temperature in March, when effective mean temperature ranges from 0 to 5°C and thus promotes vernalization and vegetative sprouting. Our results suggest that, over a six-year term, it is temporal variability in precipitation and temperature rather than grazing that determines vegetation dynamics and species co-existence of grazed steppe ecosystems. Furthermore, our data support that the variability in the biomass of dominant species, rather than diversity, determine ecosystem functioning. The present study provides fundamental knowledge on the complex interaction of grazing – vegetation – climate.

Keywords Species composition, diversity, grazing intensity, precipitation and temperature, C3-C4 competitive balance, typical steppe

Introduction

Sustainable grazing management of semi-arid grassland ecosystems requires holistic knowledge about vegetation dynamics and their responses to varying climatic conditions and grazing intensity in order to understand the causes of change in species composition of plant communities. Grazing by livestock is the main anthropogenic disturbance of native grasslands [1] and it plays an important role in determining species composition and plant species diversity [2,3]. Previous studies have indicated that long-term grazing can affect species diversity of plant communities in grasslands either positively or negatively [4-6] but grazing at moderate intensity could promote increased species diversity [7-9]. However, in some previous studies the effect of grazing on species diversity may have been overestimated and limited either by the duration of the study or lack of information on grazing intensity and the effects of climatic variability [9-11]. Recent studies have shown that environmental moisture, the evolutionary history of grazing, and community productivity also need to be considered when determining the relationships between grazing intensity and species diversity [3, 5].

In semi-arid grassland ecosystems climatic factors are the main drivers that determine plant growth and species dynamics [13-15]. Inter-annual variations in precipitation and temperature are reported to be closely correlated to aboveground net primary production and vegetation dynamics (e.g. botanical composition, species diversity) [10,16-18]. However, the vegetation dynamics in semi-arid grasslands have predominantly been analyzed in terms of mean annual precipitation rates and the effect of intra-annual variability in precipitation or temperature remains largely unknown. Little is known about the linkage between temporal variability in precipitation and temperature and the shift in species composition, in particular with regard to the interdependencies between C3 and C4 species. In semi-arid grasslands, initial growth of C4 grasses typically lags behind that

of C3 species owing to their requirement for higher temperature in metabolic processes [19]. Thus, C4 species are presumably disadvantaged relative to C3 species in their ability to utilize early spring water resources [20]. In this context, the effects of within-year variation in precipitation and temperature, as well as the interaction between these two abiotic factors, are still not fully understood.

The present study aims to analyze the effect of abiotic (i.e. precipitation and temperature) and biotic factors (i.e. grazing intensity) on the vegetation dynamics in semi-arid grassland of Inner Mongolia, P.R. China. The semi-arid grassland was considered unproductive owing to the relatively low annual precipitation (340mm) and low aboveground net primary production (under 200 DM g/m²) in the context of the MSL (Milchunas, Sala, and Lauenroth [1988]) model [5,12]. An important aspect was the effect of temporal intra-annual variability of precipitation and temperature and their interactions with the effect of different grazing intensities. The vegetation dynamics were analyzed by the parameters of species diversity and species composition. The relationship between species diversity and ecosystem functioning has been studied for several decades and results have suggested that species diversity may increase, decrease or have no significant effect on primary production [6,21-24]. Furthermore, individual species may respond in different ways to varying environmental factors [25-27]. Thus, not only diversity, but also species composition plays an important role in determining ecosystem functioning [28-31]. According to the intermediate disturbance hypothesis [7], we assume a positive and negative effect of moderate and heavy grazing, respectively, on species diversity. Furthermore, based on the study of Milchunas and Lauenroth [33], we assume that precipitation has positive effect on species diversity. This may counteract, at least partly, the effect of grazing, due to the current low productivity grassland that has a long evolutionary history. We also hypothesize that increasing temperatures change the

proportions of C3 to C4 species according to the different metabolism preferences [19]. In order to comprehensively understand potential shifts in vegetation and underlying processes, it is necessary to uncouple biotic and abiotic determinants of species dynamics in the investigated grazed grassland system. Therefore, a six-year (2005-2010) grazing experiment was conducted to determine: (1) the response of plant species (species composition and diversity) to grazing intensity, varying precipitation and temperature, (2) the effect of temporal within-year variation (annual, seasonal, monthly) in precipitation and temperature on species composition and diversity, and (3) the homeostasis between C3 and C4 species as a function of temporal precipitation and temperature patterns.

Materials and methods

Study area

The present grazing experiment was conducted during 2005-2010 in a semi-arid grassland of Inner Mongolia, P.R. China, situated near the Inner Mongolia Grassland Research Station of the Chinese Academy of Sciences (IMGERS: 43° 38'N; 116° 42'E, 1200 m a.s.l.). This grassland is classified as typical steppe ecosystem [34]. Based on the long-term meteorological data (1982-2004), the mean annual precipitation of 343 mm and mean annual temperature of 0.7°C characterize a semi-arid, continental climate. This region is characterized by high inter-annual variations in precipitation, which is described by a coefficient of variation (CV) of 22%. Plant growth typically starts between late March and May and lasts until September/October. The typical steppe is dominated by C3 grasses, i.e. *Stipa grandis* P. Smirn. (perennial bunchgrass) and *Leymus chinensis* Trin. Tzvel. (a perennial rhizomatous grass) which together account for approximately 60-80% of the total community aboveground biomass in the experimental area. The most common

C4 species is *Cleistogenes squarrosa* (Trin.) Keng, which accounts for 3-9% of the community aboveground biomass (Table 3).

Experimental design

An area of 150 ha of natural grassland was fenced and split into 2-ha sized paddocks. Seven grazing intensities (GI) (no grazing (GI0), very light (GI1), light (GI2), light-moderate (GI3), moderate (GI4), heavy (GI5) and very heavy (GI6) grazing) were randomly distributed to 2-ha sized paddocks. A gradient of herbage allowances was used to modulate the grazing intensities. The seven GI corresponded to different herbage allowance classes ranges from <1.5, 1.5–3, 3–4.5, 4.5–6, 6–12 to >12 kg dry matter (DM) kg⁻¹ live weight (LW) of sheep. Due to the spatial heterogeneities and the varied available herbage on offer between the plots, the numbers of sheep were adjusted monthly to achieve herbage allowance target ranges [12,17] and thus to keep the grazing pressure of each grazing intensity constant by using the put-and-take stocking method [36]. Further details on herbage allowances, stocking rates and the grazing intensity classification are given in Schönbach *et al.* [12]. GI treatments were replicated on two blocks according to the topographic positions: one was on a level area and the other on slopes. The area has a long history of being managed at moderate to heavy grazing intensity levels, but livestock had been excluded from this area two years prior to the start of the experiment in 2005. Sheep grazing lasted from June to September for 98, 90, 93, 94, 94 and 95 days in 2005, 2006, 2007, 2008, 2009 and 2010, respectively. The duration of grazing was in accordance with the common local grazing season,

Sampling

On each treatment plot, three representative sampling areas were chosen before the

grazing period started in June. In each sampling area, enclosure cages (2 × 3 m) were set up and moved at monthly intervals, subsequent to each sampling, to locations that had been grazed previously. The aboveground community biomass was sampled monthly (June, July, August and September) inside and outside of the enclosures, with sampling taken inside a 0.25 m × 2 m rectangular frame (=3 × 0.5 m² frames). Aboveground biomass sampling of each species was done once a year at peak biomass in July inside the enclosures for determination of botanical composition (i.e., species biomass sampled was not subjected to current-year grazing). Plant species were recorded as present / absent for the purpose of assessing species richness (R) inside the rectangular frames, then clipped to 1 cm stubble-height, separated by species, and taken to the laboratory for quantitative dry matter determination after drying at 60°C for 48h.

‘Species composition’ comprises aboveground biomass of the six most common grass species sampled (*L. chinensis*, *S. grandis*, *C. squarrosa*, *Carex korshinskyi*, *Agropyron cristatum*, and *Achnatherum sibiricum*). Other plant species that comprised less than 1% of the biomass were allocated to the fraction termed “remaining species”. Species diversity was characterized by three different parameters. The number of plant species and plant biomass density of each species in each plot was counted to calculate (i) the ‘species richness’ (R), (ii) the ‘Shannon–Wiener diversity index’ (D) (see equation 1), (iii) and the ‘species evenness’ (E) (see equation 2).

$$D = -\sum P_i \ln P_i; \text{ (equation 1)}$$

$$E = D / \ln R; \text{ (equation 2)}$$

Where P_i is the weighted average proportional biomass density of the i species.

Meteorological data

In order to determine the relationship of vegetation dynamics with precipitation and

temperature, three different scales of temporal variation were investigated: annual, seasonal, and monthly. Seasonal partitioning comprises three periods: early-season (March-June), late-season (July-October) and out-of-season (November-February) (Table 1). In order to increase the level of detail, early-season precipitation and temperature were further divided into four sub-periods, i.e. March, April, May and June (Table 2). Thus, precipitation sums and temperature means during certain periods were used to analyze their relationship with vegetation dynamics.

The annual effect of precipitation was determined by using the effective annual precipitation (previous-year September to current-year September) instead of using calendar annual (January to December) sums (Figure 1). This was because the previous-year precipitation during winter was likely to have affected species composition in the current growing season [37]. On a monthly basis, the mean daily temperatures above 0°C were used to calculate effective mean temperature for March, April, May and June; whereas for seasonal and annual periods all temperature values were included.

Apart from the above-mentioned mean temperature, further temperature indices (e.g. active accumulated temperature) were tested by multiple stepwise regression analysis (see statistics section) regarding their effect on vegetation dynamics. However, in this study we focus only on the indices that explained most of the variances in vegetation dynamics, i.e. precipitation sums during specified periods, effective annual precipitation (previous-year September to current-year September), mean temperature during specified periods and effective mean temperature in individual months.

The decision to use effective mean temperature rather than actual mean temperature on a monthly basis was made, because mean temperatures in March and April in this region are below 0°C, and plant species will not grow under this temperature.

Precipitation and temperature

During the six experimental years (2005-2010), effective annual precipitation varied from a minimum of 219 mm (2009) to a maximum of 345 mm (2008) and annual mean temperature ranged from a minimum of 0.5°C (2010) to a maximum of 2.2°C (2007) (Figure 1). In comparison with the long-term average (1982-2004) of 343 mm, the effective annual precipitation rates during the experimental period (2005-2010) were relatively low (Figure 1). The opposite is true for annual mean temperature during the experimental period, which was above the long-term average of 0.7°C for most years (Figure 1). During the 6 experimental years, the mean annual precipitation and temperature are 264mm and 1.4°C, respectively, and the CV is 19%. Temporal patterns of precipitation and temperature were observed from 2005 to 2010 (Table 1 and 2). During the early-season, monthly precipitation and effective mean temperature (above 0 °C mean daily temperature) varied strongly within and among years (Table 2).

Statistics

The experimental design was a randomized complete block design with two replicates, i.e. one on a level area and one on a sloping area. All statistical analyses were carried out in SAS, Version 9.1 (SAS Institute Inc., Cary, NC, USA). Simple linear regression was used to test the correlation between the biomass of the target species and diversity parameters. The effects of grazing intensity, year and their interactions on species composition and species diversity were analyzed by using the residuals of diversity-species biomass linear regression in the Repeated Measures ANOVA - mixed model. The statistical model included grazing intensity, block, year and their interactions as fixed effects. The factor year was used as repeated effect and grazing intensity × block as

random effect. ‘Block’ was a fixed effect because treatments were replicated on a level area as well as on slopes, and then considered as block level and block slope. Thus block was not randomly chosen but explicitly assigned to two out of several typical areas with different environmental conditions. The level of significance was $P < 0.05$. Owing to the limitation of the ANOVA mixed model to deal with quantitative determining variables, the effects of seasonal variations in precipitation and temperature were tested by Pearson

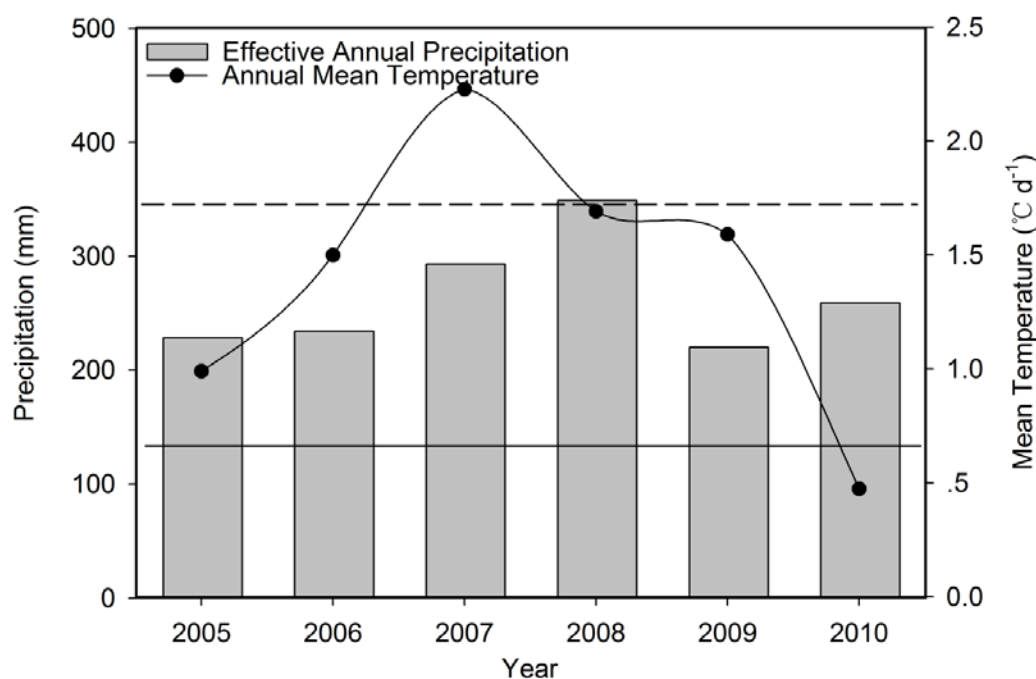


Figure 1 Effective annual precipitation rates (left y-axis) and annual mean temperature (right y-axis) from 2005-2010. The horizontal dashed line denotes the 20-year (1983-2004) mean effective annual precipitation of 343mm, and the horizontal solid line denotes the mean annual temperature of 0.7 °C over the same 20-year period.

correlation and multiple regressions. The Pearson correlation analysis was used to examine the associations of species composition and diversity parameters (richness, diversity index and evenness) with the variation of both the precipitation rates and mean temperature at annual and seasonal level. The multiple regression model with stepwise selection was additionally applied to in order to provide quantitative information on the correlations and importance of precipitation and temperature on species biomass and diversity parameters. Variables of precipitation and temperature during certain periods of time were selected, and the variable that improved the model the most (determined by higher R-square and significance at the 0.05 level) was maintained by using stepwise selection model comparison criterion. The stepwise-building used forward selection and the variables already built in could not be thrown out at a later stage. The coefficient of determination R-square was tested with a two-sided test for significance of the stepwise regression model ($P < 0.05$). By comparing the model coefficients of determination, the optimum model accounting for maximum variation was chosen.

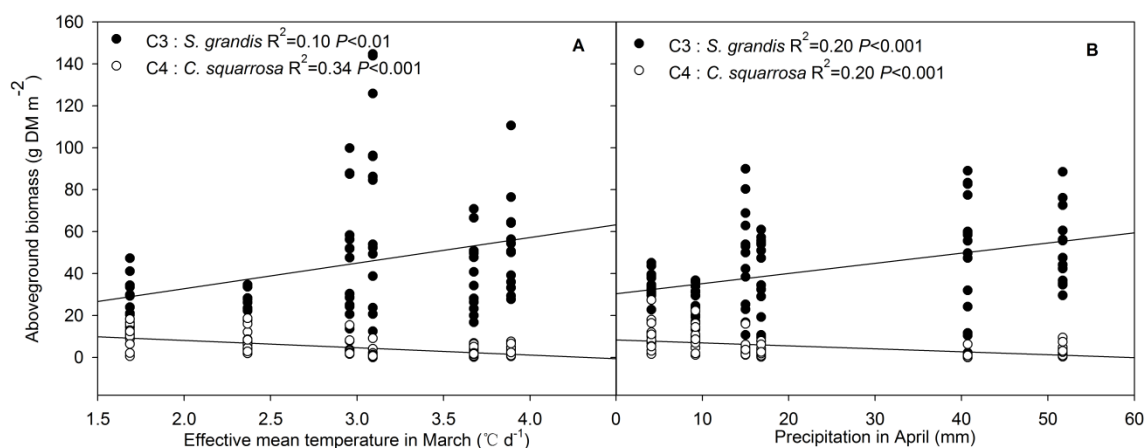


Figure 2 Relationship between aboveground biomass (g DM m⁻²) of the C3 species *S. grandis* and C4 species *C. squarrosa* and effective mean temperature (°C d⁻¹) in March (A) and precipitation rates (mm) in April (B) ($n = 84$, i.e. 14 observations per year).

Table 1 Precipitation (PPT in mm) and mean temperature (MT in °C d⁻¹) in early season (March-June), late season (June-October) and out of season (October-March) in six experimental years

Year	Early-season		Late-season		Out-of-season	
	MT	PPT	MT	PPT	MT	PPT
2005	8.8	68.7	1.9	230	-15.9	13.6
2006	8.4	130	0.6	79.0	-16.9	18.7
2007	9.8	131	1.3	154	-15.4	31.5
2008	9.6	146	0.7	86.8	-16.6	17.5
2009	8.6	111	1.6	196	-14.5	16.7
2010	6.9	116	1.1	131	-16.9	2.1
Mean	8.7	117	1.2	146	8.7	16.7

Early season: March to June; Late season: July to October; Out of season: November to February

Table 2 Monthly precipitation (PPT in mm) and effective mean temperature (EMT in °C d⁻¹) during the early season (i.e. March, April, May, June) in six experimental years

Year	March		April		May		June	
	EMT	PPT	EMT	PPT	EMT	PPT	EMT	PPT
2005	1.7	1.7	6.5	9.2	10.4	3.8	17.8	54.0
2006	2.4	2.5	5.8	4.1	11.7	62.7	16.4	60.5
2007	3.7	16.4	4.3	16.8	11.4	32.3	20.4	65.4
2008	3.0	15	7.2	25.2	9.7	32.3	17.2	73.1
2009	3.9	1.3	5.5	51.7	12.8	10.6	14.9	47.2
2010	3.1	3.4	3.3	40.7	10.7	50.4	17.8	21.5
Mean	2.9	6.7	5.4	24.6	11.1	32.0	17.4	53.6

Effective mean temperature: above 0 °C mean daily temperature in the respective period of time

Results

The effects of grazing intensity and years

The aboveground biomass of dominant species *L. chinensis* significantly decreased with increased grazing intensity, while other investigated species and species diversity parameters (richness, Shannon-Wiener diversity index and evenness) were not significantly affected by grazing intensity (Table 3). However, species composition and diversity varied significantly among experimental years over all grazing intensities. The biomass of the dominant C3 grass *S. grandis* was two-fold higher in the final year 2010 compared with the first experimental year of 2005, whereas the biomass of the C4 species *C. squarrosa* and C3 species *A. sibiricum* decreased by 83% and 60% respectively. The species grouped as ‘remaining species’ contributed the highest amount of biomass in the initial year 2005 and reached the lowest value in 2009. In comparison to 2005, species richness, diversity and evenness in 2010 decreased by 34, 31 and 16%, respectively. No significant interactions between year and grazing intensity on species composition and diversity were detected.

The effects of precipitation and temperature

Pearson correlation analysis showed that calendar year-based annual precipitation and mean temperature had no significant effect on almost all measures of species biomass. The exception was *C. squarrosa* which was negatively correlated with annual precipitation. There was also no significant relationship between the variations of both effective annual precipitation and mean temperature and diversity (except richness) (Table 4). On a seasonal scale, most of species biomass and all diversity parameters were correlated with early-season (March to June) precipitation and mean temperature, whereas precipitation and temperature conditions during late-season (July to October)

and out-of-season (November to February) had only little effect on species dynamics (Table 4).

Table 3 Effect of grazing intensity (GI) and year on aboveground biomass (g DM m⁻²) of species and diversity indices (richness, diversity and evenness)

GI	<i>L.ch</i>	<i>S.gr</i>	<i>C.sq</i>	Richness	Diversity	Evenness
0	33.5	55.0	6.1	11.5	1.4	0.6
1	71.0	33.2	3.1	13.1	1.3	0.5
2	42.5	56.7	6.1	10.8	1.3	0.5
3	21.5	62.6	5.7	9.5	1.2	0.5
4	36.4	38.3	4.5	12.4	1.4	0.6
5	19.8	47.2	5.6	9.9	1.3	0.6
6	20.8	37.5	3.0	11.3	1.3	0.6
YEAR						
2005	45.4	26.4	9.8	14.1	1.6	0.6
2006	30.2	26.2	7.8	13.0	1.5	0.6
2007	40.4	38.1	2.4	10.4	1.2	0.5
2008	42.0	48.8	4.3	12.4	1.2	0.5
2009	29.7	53.1	3.1	8.1	1.2	0.6
2010	40.0	73.5	1.7	9.3	1.1	0.5
<i>F</i> -values statistics for the test of particular analysis						
GI	3.6*	1.9ns	0.7ns	0.9ns	1.1ns	0.4ns
YEAR	1.9ns	8.3***	12.4***	14.7***	12.3***	3.9**
BLOCK	15.4**	1.0ns	0.2ns	2.1ns	0.8ns	0.0ns
GI×YEAR	0.6ns	1.7ns	1.5ns	1.1ns	2.0ns	1.7ns

The abbreviations are: *L.ch* (*Leymus chinensis*), *S.gr* (*Stipa grandis*), *C.sq* (*Cleistogenes squarrosa*).

(*: 0.01 < *P* < 0.05, **: 0.001 < *P* < 0.01, ***: *P* < 0.001, and ns means not significant, *P* > 0.05)

Multiple regression analysis indicated that early-season precipitation and early-season mean temperature strongly correlated with *S. grandis*, *C. squarrosa* and *A. sibiricum* biomass, 'remaining species' biomass and diversity parameters (Table 5). The coefficients of determination from the multiple stepwise regression analysis showed that early-season precipitation and early-season mean temperature accounted for most of the variations in species composition and diversity. Precipitation and mean temperature during the early-season together explained 12- 42% of the variation in species biomass and 11- 40% of the variation in diversity (Table 5). The dominant C3 species *S. grandis* responded positively to increasing early-season precipitation and negatively to early-season mean temperature, whereas the opposite was true for all other species and for all diversity parameters (Table 5).

In order to increase the level of detail, early-season precipitation and temperature were further subdivided into monthly periods of March, April, May and June. Multiple stepwise regression analysis revealed a strong linkage of monthly precipitation and effective mean daily temperature with *S. grandis* biomass, *C. squarrosa* biomass and diversity (Table 6). In March, the variability in the biomass of the C3 species *S. grandis*, the C4 species *C. squarrosa* and in diversity were correlated only with effective mean daily temperature but not with precipitation. Meanwhile, inverse responses were found as the biomass of the C3 species *S. grandis* increased while that of the C4 species *C. squarrosa* and any of the diversity parameters decreased with increasing effective mean daily temperature in March (Fig. 2A, Table 6). In April, it was precipitation rather than temperature that determined vegetation dynamics, i.e. C3 species *S. grandis* biomass increased while C4 species *C. squarrosa* biomass and any of the diversity parameters decreased with increasing precipitation (Fig. 2B, Table 6). By combining precipitation and effective mean daily temperature of March and April, 30% of the variance in the

biomass of the C3 species *S. grandis*, 59% of that of the C4 species *C. squarrosa*, and 60 and 54% of the variance of richness and diversity, respectively, can be explained. In May, no significant correlation relationship was found for any parameter. In June, only the aboveground biomass of the C3 species *S. grandis*, richness and diversity were correlated with precipitation, and the coefficients of determination were low (Table 6).

Table 4 Correlation coefficients ($n = 84$) for relationship between aboveground biomass of each species and diversity indices (richness, diversity and evenness) with precipitation (PPT in mm) and mean temperature (MT in $^{\circ}\text{C d}^{-1}$)

Parameters	Early season (Spring)		Late season (Summer)		Out of season (Winter)		Annual	
	PPT	MT	PPT	MT	PPT	MT	PPT	MT
<i>L.ch</i>	-0.1ns	0.0ns	0.1ns	-0.1ns	-0.0ns	-0.1ns	0.1ns	0.1ns
<i>S.gr</i>	0.3*	-0.3**	-0.1ns	-0.2ns	-0.2*	-0.0ns	0.2ns	0.1ns
<i>C.sq</i>	-0.3**	0.2*	0.1ns	0.0ns	0.0ns	-0.1ns	-0.2*	-0.1ns
Richness	-0.3**	0.2*	-0.1ns	0.1ns	0.1ns	-0.1ns	-0.1ns	0.2*
Diversity	-0.3**	0.2*	0.1ns	0.1ns	0.1ns	-0.1ns	-0.1ns	-0.2ns
Evenness	-0.3*	-0.0ns	0.2ns	-0.0ns	0.0ns	0.1ns	-0.1ns	-0.2ns

Early-season: March to June; Late-season: July to October; Out-of-season: November to February.

(*: $0.01 < P < 0.05$, **: $0.001 < P < 0.01$, ***: $P < 0.001$, and ns means not significant, $P > 0.05$)

For abbreviations of species names see Table 3.

Table 5 Partial R-square coefficients of determination ($n = 84$) associated species diversity and species composition with precipitation (PPT in mm) and mean temperature (MT in $^{\circ}\text{C d}^{-1}$) in the early-season (March - June) for stepwise variance regression analysis

Parameters	<i>L.ch</i>	<i>S.gr</i>	<i>C.sq</i>	Richness	Diversity	Evenness
Partial R ² coefficients of determination						
Precipitation (mm)	0.0ns	0.1**	0.3***	0.2***	0.3***	0.1**
Temperature ($^{\circ}\text{C d}^{-1}$)	0.0ns	0.2***	0.1**	0.1**	0.1**	0.0ns
	Model Equation			Adjusted R ²	<i>P</i>	
<i>S. grandis</i>	$Y_{S.gr} = 0.186\text{PPT} - 0.234\text{MT} + 103.686$			R ² =0.3	<i>P</i> <0.0001	
<i>C. squarrosa</i>	$Y_{C.sq} = -0.036\text{PPT} + 0.024\text{MT} + 15.726$			R ² =0.4	<i>P</i> <0.0001	
Richness	$Y_{\text{Richness}} = -0.017\text{PPT} + 0.017\text{MT} + 9.755$			R ² =0.3	<i>P</i> <0.0001	
Diversity	$Y_{\text{Diversity}} = -0.002\text{PPT} + 0.001\text{MT} + 1.763$			R ² =0.4	<i>P</i> <0.0001	
Evenness	$Y_{\text{Evenness}} = -0.001\text{PPT} + 0.714$			R ² =0.1	<i>P</i> <0.01	

For abbreviations of species names see Table 3.

(*: $0.01 < P < 0.05$, **: $0.001 < P < 0.01$, ***: $P < 0.001$, and ns means not significant, $P > 0.05$)

Table 6 Adjusted R-Square coefficients of determination ($n = 84$) associated C3 vs. C4 species (*S. grandis* vs. *C. squarrosa*) and diversity with precipitation (PPT in mm) and effective mean temperature (EMT in $^{\circ}\text{C d}^{-1}$) for multiple stepwise variance regression analysis

Parameters	March		April		June		R ²	P	
	Equation	R ²	P	Equation	R ²	P			
<i>S. grandis</i>	Y= 12.174EMT+8.501	0.1	0.0038	Y= 0.76PPT+26.917	0.2	<0.0001	Y= 0.678PPT+80.653	0.2	0.0003
<i>C. squarrosa</i>	Y= -3.513EMT+15.190	0.3	<0.0001	Y=-0.085PPT+0.914EMT+1.829	0.3	<0.0001	NS	NS	>0.05
Richness	Y= -2.487EMT+18.536	0.3	<0.0001	Y= -0.112PPT+13.778	0.3	<0.0001	Y= 0.066PPT+7.679	0.1	0.0036
Diversity	Y= -0.217EMT+1.936	0.3	<0.0001	Y= -0.008PPT+1.488	0.2	<0.0001	Y= 0.004PPT+1.067	0.1	0.0287
Evenness	Y= -0.035EMT+0.670	0.1	0.0088	NS	NS	>0.05	NS	NS	>0.05

“NS” means no variable met the 0.05 significance level for entry into the model

Effective mean temperature: above 0 $^{\circ}\text{C}$ mean daily temperature in the respective period of time

Discussion

The effects of grazing intensity and years

An aim of this study was to investigate whether grazing intensity has a strong effect on species composition and diversity in the Mongolian steppe. Our results demonstrate that grazing intensity has relatively little effect on species composition; only the aboveground biomass of *L. chinensis* differed among grazing intensities, and no diminishing effect on species diversity was observed. Also, grazing intensity had no effect on cumulative biomass of species and diversity over six consecutive years of grazing. The results obtained, therefore, do not support the intermediate disturbance hypothesis, which assumes that moderate grazing intensity increases species diversity and that high grazing intensity leads to a shift in the proportion of dominant and opportunistic species [7, 8, 34]. It has been suggested that long-term grazing induces a significant shift in the aboveground biomass composition of Inner Mongolian grasslands, from perennial C3 grasses, such as *S. grandis* or *L. chinensis*, to C4 grass species such as *C. squarrosa* (e.g. [19,38]). Thus, the time scale over which the grazing effects are analyzed plays an important role in determining whether or not grazing affects vegetation dynamics. According to the findings of many previous studies, and as suggested by the above-cited references [7, 8, 19, 34, 38], shifts in the botanical composition and species diversity are likely to occur under long-term grazing, i.e., during periods of at least ten years duration. Long-term experiments are indeed very valuable but also very rare. Transect studies provide an alternative to highlight grazing effects. Although these studies have to consider the unfairly heterogeneous areas, such as different vegetation unit, steppe type, species richness and soil parameters, they allow assessments covering historical old gradients of grazing activity, as some work already done in the same region, e.g. [9,39,40]. However, our findings suggest that vegetation dynamics are much less

influenced by grazing in the medium-term, as most of the investigated species and all of the analyzed diversity indices remained unaffected by the factor of grazing intensity. The long history of grazing in the study region may have led to the development of a steppe vegetation community that was adapted to and tolerant of grazing [3]. It has also been considered likely that selective grazing by sheep and the competitive balance among species (e.g. various grazing resilience abilities and regrowth rates of species) counteract the effects of grazing in the medium-term. Furthermore, during the experimental period, annual precipitation patterns in the study region were much lower than the long-term average. Most of the species present, and their composition, may have been well adapted to more average conditions. Therefore, the current grazing system was perhaps untypical for the conditions with abiotic constraints, including droughts. Conversely, the biotic constraints of grazing may become more effective under more average conditions. The long evolutionary history of grazing and low habitat productivity as a result of low environmental moisture on this study site have contributed to the grazing intensity-diversity relationship fitting the MSL (Milchunas, Sala, and Lauenroth [1988]) original equilibrium curves. According to our results, the aboveground biomass of the plant species investigated here respond differently to the effects of grazing. The pronounced decrease in the aboveground biomass of *L. chinensis* with increased grazing intensity was presumably a result, at least in part, of its relatively high forage quality [41-43]. In consequence, sheep preferentially graze *L. chinensis* so that the aboveground standing biomass of this species was significantly reduced with increased grazing intensity. In contrast, *S. grandis* is characterized by a relatively low nutritive forage value owing to high concentrations of fibre and lignin and thus has low digestibility [41]. Therefore, *S. grandis* is less-preferentially grazed by sheep compared with *L. chinensis* [44,45]. However, it should be taken into account that current-year species sampling was done in

July inside exclosures, and therefore any grazing-related effects on species would have been determined by the previous year's grazing, rather than grazing in the current year. Furthermore, not only grazing preference will have determined the grazing effect on the aboveground biomass of plant species, but also the different strategies of plants to compensate for herbage removal under grazing. For example, *C. squarrosa* is characterized by a relatively high nutritive forage value [41], but nevertheless grazing intensity had no effect on aboveground biomass of this major C4 species. We therefore assume that the strong regrowth ability (grazing tolerance) of *C. squarrosa* [41] compensated for the removal of its biomass under grazing.

In the present study, vegetation dynamics were predominantly determined by inter-annual differences and to a lesser extent by grazing intensity. Owing to the weak correlation between the investigated vegetation parameters and annual precipitation (data not shown), the decrease of species diversity over time may not be attributed to the cumulative effects of persistent droughts. Even though the precipitation increased from 2005 to an average level in 2008, species diversity did not show increase with higher precipitation. This result did not support our assumption that precipitation leads to species diversity increasing. Thus, precipitation and temperature factors and their inter-annual variability have to be taken into account when analyzing the complex competition and colonization processes of grazed steppe vegetation [10, 33, 46]. In our study, the vegetation was subjected to six years of grazing at different intensity levels. Therefore it should be considered as a starting point during the long-term dynamic process of vegetation formation in grazed grasslands. The pronounced variability in species composition and diversity among years supports the hypothesis that inter-annual variability in precipitation and temperature predominantly determines vegetation responses to grazing [10]. Therefore, the effect of year is discussed in the following sub-

section in the context of precipitation and temperature.

The effects of precipitation and temperature

Our results highlight the importance of temporal distribution patterns of precipitation and temperature on vegetation dynamics. Most of the variation in species composition and diversity was determined by precipitation rates and temperatures in the early season (March to June), whereas only a small proportion of the variance in the investigated vegetation parameters could be explained by precipitation rates and mean temperature on an annualized scale or in late-season (July to October) or out-of-season (November to February) period. In terms of the responses of species composition (slowly and long-term) and plant productivity (fast and short-term) to environmental influences, previous studies also reported that the temporal distribution, rather than the annual sum of precipitation, determines aboveground net primary productivity of semi-arid grasslands [47,48]. Thus, seasonal distribution of precipitation and temperature presented in the following paragraphs are considered when analyzing vegetation dynamics in steppe ecosystems. Stepwise regression analysis confirmed that vegetation dynamics are strongly affected by precipitation and mean temperature in the early season (March to June). In this period, most species initiate their growth processes and thus they are highly sensitive to variations in precipitation and temperature. According to our results, a combination of those two factors (precipitation and temperature) explains most of the variation in species diversity ($R^2 = 0.32 - 0.40$) and species composition ($R^2 = 0.12 - 0.42$). However, species varied in their response to precipitation and temperature. For example, the early-season mean temperature ($R^2 = 0.18$) was the main factor determining the aboveground biomass of the dominant C3 species *S. grandis*, with a slightly greater effect than early-season precipitation ($R^2 = 0.13$) (Table 4). In contrast, aboveground biomass of *C. squarrosa*

was predominantly determined by early-season precipitation ($R^2 = 0.34$) and to a lesser extent by early season-temperature ($R^2 = 0.09$) (Table 4). The inverse impact of temperature and precipitation on plant species in the Inner Mongolian steppe is presumably a result of their different sensitivity to temporal fluctuations of precipitation or temperature variability and thereby diverse behavior and strategies to adapt to the habitats (e.g. high photosynthetic capacity and high resource-use efficiency of C4 species in the dry environment and high freezing-resistance of C3 species in the frozen environment). In order to predict and explain shifts in plant species composition, both precipitation rates and temperature sums during the early season need to be taken into account.

The inverse responses of the C3 species *S. grandis* and C4 species *C. squarrosa* to early-season precipitation and temperature support the temporal niche differentiation theory, which claims that the competitive balances of C3 and C4 species are related to temporal variances of climatic factors [49]. Considering that C3 and C4 species have different phenological (reproductive) development as well as different competitive strategies (e.g. trade-off between fast growth and nutrient storage) within a given growing stage, this would change their final survival [19,50], the effects of monthly distribution of precipitation and effective mean daily temperature were tested further. The results show that March and April were two very important months for C3 and C4 species and for species diversity for the upcoming growing period. In March, the main driver was the effective mean temperature. In April, the main driver was precipitation. The shift from temperature to precipitation between March and April may be attributed to the main determining factor changing in response to the different growth stage of plant species, as reported by Lundholm and Larson [51]. Taking the effects in these two months together, 59% of the aboveground biomass variance of C4 species *C. squarrosa* and 54 - 60% of

the variance in diversity can be explained.

From March to June, the responses of species to precipitation and effective mean temperature vary. In the early spring phenophases during March, the stimulating of propagation in *S. grandis* occurred. This included seeds germinating and vegetative sprouting [52,53]. The seeds of *S. grandis* were presumably stimulated by low temperature for vernalization and breaking dormancy [52,54-56]. The vegetative sprouting of *S. grandis* was also presumably stimulated by effective mean temperature for a period of warm stratification after the cooler winter temperatures [52], which resulted in the spring phenophases moved earlier and promoted lengthening of its growing season. Thus the competitor C3 species *S. grandis* started its growth in March one month earlier than C4 species *C. squarrosa*, when the effective mean daily temperatures in March (< 4.0 °C) are suboptimal for growth of C4 plants but are optimal for C3 species vernalization and sprouting. The C4 species *C. squarrosa* required higher temperature to activate tillers and initiate new-season growth, and higher temperature for metabolism than C3 species like *S. grandis*. For this reason *S. grandis* is able to exhibit a superior metabolic performance at low temperatures [19,57]. In April, the precipitation amount increased and the C3 species *S. grandis* could make full use of rainfall for aboveground biomass growth, while the C4 species *C. squarrosa* was unable to grow, owing to its delayed spring initial growth and shallow rooting depth of only 20cm [58]. In May, in order to provide enough energy for later flowering and fruiting, species gradually started to accumulate carbohydrate in their root system, so that they need less precipitation and temperature for aboveground biomass growth [37]. This may explain why no significant correlation was found between precipitation and temperature factors in May and species aboveground biomass. In June, the C3 species *S. grandis* turns moves into its flowering and fruiting period and thus needs water to continue growing, but the C4 species *C.*

squarrosa remains in the root carbohydrates accumulating period. This may explain the positive response of C3 species and the lack of response of C4 species to precipitation in June. Information on the temporal dynamics of species composition regarding C3 and C4 species is required in order to formulate carrying capacities and predict future change of C3 and C4 species with specific temporal distribution of precipitation and temperature variation, as well as to develop appropriate management practices.

Species diversity parameters were observed to have the same trends as the C4 species *C. squarrosa* to either early-season or monthly distributions of temperature and precipitation. The results suggest that not just C4 species, but other subdominant species and rare species are contributing to the species diversity, have similar mechanisms to stay competitive against the trade-off with dominant species, according to temporal distribution of environmental factors. The dominant species *S. grandis* is generally known for its root biomass being several times larger than the above-ground biomass [19]. It may prove to be highly competitive to maintain its population in the community because it occupies resource space for long periods, and therefore captures the chance of other species for contributing to early season production. Under persistent limited resource availability, the semi-arid grassland may be evenly distributed by dominant species in the long term, as species richness and evenness decreased over time. The similar responses of C4 species' biomass and diversity parameters and inverse responses of C3 species *S. grandis*' biomass to environmental factor effects are consistent with the result confirmed by our data that there is no significant correlation between diversity parameters and community biomass ($R^2_{\text{richness}}=0.06$; $R^2_{\text{diversity}}=0.03$; $R^2_{\text{evenness}}=0.10$) (detailed data not shown). From another point of view, since controversial arguments about the relationship between species diversity and community productivity or ecosystem stability are presented, the mass ratio hypothesis, which holds that ecosystem

functioning and stability is largely controlled by dominant species rather than diversity in the medium-term, supports our results [32]. Since dominant species could also control the effect of diversity on community stability, our finding that the variances of the most productive species *S. grandis* influenced species dynamic more than species diversity is considered to be evidence for this.

Conclusion

We find that temporal distribution of precipitation and temperature, in particular during the early-season (from March to June), determined the variation in vegetation dynamics much more strongly than annual rates of precipitation or temperature. In the medium term (6 years), the effects of early-season precipitation and temperature on the trade-off among species were more important than the effect of grazing. However, grazing decreased the aboveground biomass of those species that are more preferentially grazed by sheep, such as *L. chinensis*. Therefore, based on these findings, the effect of grazing in a grassland system cannot be analyzed without considering the characteristic traits of species and also the precipitation and temperature variation, especially in the medium term. Our findings demonstrate that the temporal fluctuation of precipitation and temperature, especially in early season, seems to provide more robust and comprehensive predictions on vegetation dynamics in semi-arid typical steppe, and helps to understand species coexistence and grassland management in response future extreme precipitation and drought events.

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Chapter 3

**Forage Nutritional Characteristics and Yield
Dynamics in A Grazed Typical Steppe Ecosystem of
Inner Mongolia, China**

**Forage Nutritional Characteristics and Yield Dynamics in A Grazed Typical
Steppe Ecosystem of Inner Mongolia, China**

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Abstract

Background and Aims: In the steppe of Inner Mongolia, forage is the only source of feed for sheep. Evaluation of forage quality and quantity is therefore of critical importance. The efficiency of forage nutrients used by livestock is determined by environmental and anthropogenic factors.

Methods: The effects of grazing intensity, year effects, and forage species on aboveground net primary productivity (ANPP) and nutritional forage characteristics were investigated in a controlled grazing experiment over six years (2005-2010) on typical Mongolia steppe. Nutritional forage characteristics were defined by the nutritional value (concentrations of crude protein (CP), cellulase digestible organic matter (CDOM), metabolizable energy (ME) and neutral detergent fibre (NDF)) and the nutritional yield. The forage nutritional yield is a function of ANPP and the forage nutritional value. Grazing effects were investigated along a gradient of seven grazing intensities (from ungrazed to very-heavily grazed).

Key Results: Both grazing intensity and year significantly affected ANPP as well as forage nutritional value. Forage nutritional value increased but ANPP and nutritional yields decreased with increasing grazing intensity. The inter-annual variation of ANPP, forage nutritional value and yield were closely linked to the inter-annual variability of precipitation. However, nutritional value also varied during the growing season, i.e. seasonal distribution of precipitation and temperature influence forage digestibility (CDOM) and metabolizable energy (ME) as they were higher at high seasonal precipitation and low seasonal mean temperature. Furthermore, forage nutritional value and yield, as well as ANPP, were predominantly determined by the dominant species rather than by species diversity.

Conclusions: The results suggest that forage nutritional yield in the Inner Mongolia steppe is predominantly determined by the ANPP and only to a minor extent by forage nutritional value. Therefore, herbage productivity seems to be the most limiting factor in managing this steppe ecosystem as a feeding resource for livestock.

Keywords: forage nutritional characteristic, forage nutritional yield, diversity, grazing intensity, precipitation, Inner Mongolian steppe

Introduction

The semi-arid grassland in Inner Mongolia is one of the most important grazing ecosystems in the whole Eurasia steppe region (Chen and Wang, 2000, Kang *et al.*, 2007). The ability of grassland to provide forage as the single source of nutrients to support livestock productivity depends on both its aboveground net primary productivity (ANPP) and its nutritional value (Snyman, 2002). Both ANPP and forage nutritional value (FNV) determine the forage nutritional yields (FNY) i.e. the quantities of crude protein (CP), neutral detergent fibre (NDF), cellulase digestible organic matter (CDOM) or metabolizable energy (ME) per unit of area on a seasonal or annual basis, although the former study did not quantify their respective contributions to FNY (Schonbach *et al.*, 2012). Grazing is known to affect ANPP and forage nutritional characteristics and thus animal performance (Li *et al.*, 2008, Schonbach *et al.*, 2009). For example, increasing the stocking density and the grazing intensity can improve FNV and animal live weight gain per area while also decreasing forage productivity (Schonbach *et al.*, 2009, Schonbach *et al.*, 2011). Understanding the dynamics of FNY in semi-arid grassland is therefore very important, as the combined evaluation of grazing effects on ANPP and FNV is the crucial parameter that can determine livestock performance. The FNY determines the quality and also the total amount of forage available to livestock. Thus the value of grassland as a feed resource is closely linked to the FNY. Previous observations have emphasized the effect of grazing intensity on FNV and animal intake of nutrients on grasslands (e.g. McKown *et al.* (1991) and Wang *et al.* (2009)) though there has been relatively less emphasis on FNY. Although the Inner Mongolia steppe is a major feed resource for livestock farming, relatively little is known about the effect that grazing has on FNY.

However, ANPP and FNV are affected not only by grazing but also by other factors, including environmental factors such as topography and botanical composition and diversity (Buxton, 1996, Hooper *et al.*, 2005, Schonbach *et al.*, 2009). In arid and semiarid grassland ecosystems, the mean annual precipitation has been considered to be a highly reliable measure of water availability for community productivity (Bai *et al.*, 2008). Temperature has also been shown to directly affect community productivity and FNV (Knapp *et al.*, 2002, Auerswald *et al.*, 2012). Inter-annual variations in precipitation and temperature have been reported to be closely correlated to ANPP (Bai *et al.*, 2007, Wittmer *et al.*, 2010, Schonbach *et al.*, 2011, Auerswald *et al.*, 2012). However, little is known about the linkage between temporal variability in precipitation and temperature and the shift in forage nutritional characteristics. Furthermore, species composition and diversity are likely influence plant productivity and plant nutrient value in most habitats (Loreau *et al.*, 2001, Hooper *et al.*, 2005). Each individual species plays a different role in influencing community productivity (Hooper *et al.*, 2005) and the positive linear, negative linear or non-significant correlation between species diversity and productivity has long been a disputed topic (Tilman *et al.*, 1996, Bakker *et al.*, 2002, Tilman *et al.*, 2006). However, as regards species diversity and species composition within a grassland ecosystem, it remains uncertain which of these contributes the greatest effect on productivity and forage nutrient use, and on the overall FNY.

Based on the results reported in the above-mentioned studies, we hypothesize that the variation in FNV, ANPP and FNY in steppe are determined largely by grazing and environmental factors, such as precipitation and temperature; furthermore, we presume that species diversity will improve FNY. In order to test the effects of grazing intensity and of different years, species composition and species diversity on FNV, ANPP and FNY, we collected data from a large-scale controlled grazing experiment in the Inner

Mongolian steppe of China during six consecutive years (2005-2010). Instead of the results presented by Schönbach covering a 4year dataset, we used an extend dataset covering six years allowing us to combine effects of grazing and environmental conditions on ecosystem functioning on the one hand and diversity effects on the other hand. So this dataset included much broader data and could give more convincible results than the previous study. The primary questions we addressed were: 1) What is the relationship between FNV, ANPP and FNY?; 2) How do grazing intensity, precipitation and temperature affect FNV, ANPP and FNY?; 3) How do species composition and species diversity affect FNV, ANPP and FNY?; and 4) how much contributions that ANPP and the dominant species can make to affect FNY?

Materials and methods

Experimental site

The grazing experiment was established in 2005 in a typical steppe ecosystem of Inner Mongolia, P.R. China, close to the Inner Mongolia Grassland Research Station of the Chinese Academy of Sciences (IMGERS, 43° 38'N, 116° 42'E), approximately 1,200 m a.s.l. As the precipitation during the winter of the previous year could affect the growth of vegetation in the subsequent year (Yuan and Zhou, 2005), effective annual precipitation (previous-year September to current-year September) rather than calendar annual sums (January to December) was applied in this study. This was considered to be a more appropriate period for relating precipitation to grassland vegetation (Figure 1). According to the long-term meteorological data (1970-2011), the effective mean annual precipitation and mean annual temperature in the region is 335 mm and 0.7°C. Typically, about 80% of the annual precipitation occurs during the growing season (May-August),

thus supporting productivity of the steppe vegetation (Yu *et al.*, 2004).

Stipa grandis P. Smirn. (perennial bunchgrass) and *Leymus chinensis* Trin. Tzvel. (perennial rhizomatous grass) are the two dominant species in area of the experimental site and are widely distributed in the Eurasia steppe. Together these two grasses account for approximately 60-80% of the total community aboveground biomass (AB) (Wan *et al.*, 2011). The major soil types of this region are dark chestnut soils (Calcic Chernozem according to ISSS Working Group RB, 1998), with fine-sand loess texture (Bai *et al.*, 2010).

Experimental design

The grazing experiment was conducted over six years (from 2005 to 2010) as a continuous stocking system (terminology of Allen *et al.*, 2011). A randomized complete block design with two replicates (one level block and one sloping block) was applied to analyze the effects of grazing intensity on productivity, forage nutritional value and nutritional yields. The grazed area covers 150 ha of natural grassland in total and was divided into 2-ha paddocks by randomly allocating along seven grazing intensities. The gradients of grazing intensity were: no grazing (GI0), very-light (GI1), light (GI2), light-moderate (GI3), moderate (GI4), heavy (GI5) and very heavy (GI6) grazing. In each experimental year sheep were kept on the plots continuously throughout the vegetation period (June-September) for approximately 95 days. In order to maintain equal levels of grazing intensity during the six experimental years, the numbers of sheep were regulated by balancing the herbage on offer and stocking rates in each plot (Schonbach *et al.*, 2011, Schonbach *et al.*, 2012). The classifications of herbage allowance target ranges and the stocking rate are shown in Table 1.

Forage sampling

On each 2 ha paddock, three representative sampling areas were chosen prior to the start of grazing in June. Within each sampling area, grazing exclosures (3 × 2 m) were randomly allocated. The aboveground community biomass was sampled monthly (in June, July, August and September) inside 0.25 m × 2 m rectangular frames positioned inside and outside the exclosures. The collected plant material was clipped to 1 cm stubble-height, mixed by species and taken to the laboratory for dry matter (DM)

Table 1 Average herbage allowance in kg dry matter (DM) kg⁻¹ liveweight (LW) and stocking rates in sheep ha⁻¹ grazing season⁻¹ assigned to herbage allowance target ranges (TR) and grazing intensity classification. Data represent seasonal means ± s.e.

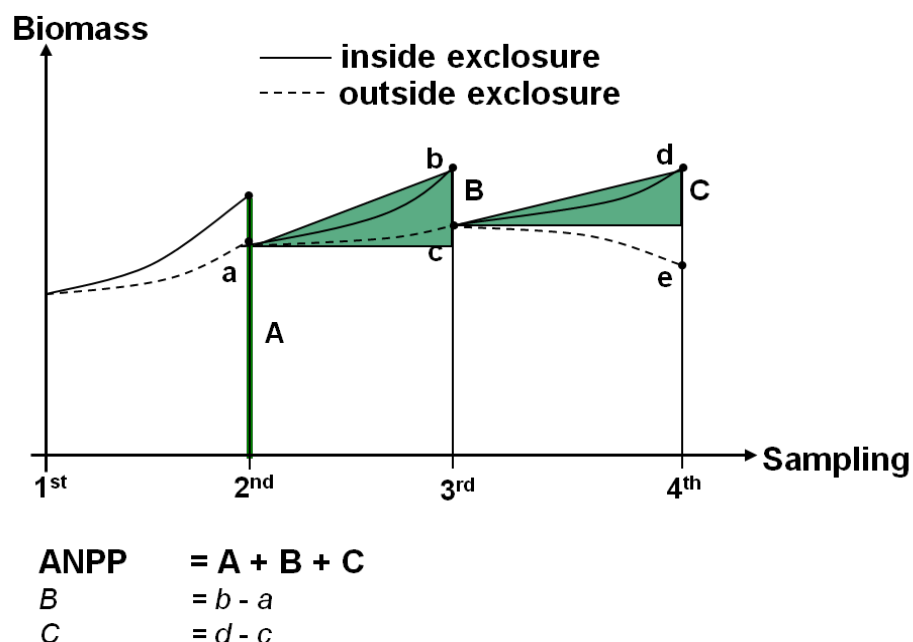
Grazing intensity classification ^a	Grazing intensity						
	0	1	2	3	4	5	6
Herbage allowance TR (kg DM kg ⁻¹ LW)	-	>12	6-12	4.5-6	3-4.5	1.5-3	<1.5
2005							
Stocking rate (sheep ha ⁻¹ grazing season ⁻¹)	0±0	1.5	3	4.5	6	7.5	9
Herbage allowance (kg DM kg ⁻¹ LW)	-	23.7±7.2	9.0±3.4	5.4±1.6	4.9±1.8	2.4±0.3	1.6±0.5
2006							
Stocking rate (sheep ha ⁻¹ grazing season ⁻¹)	0±0	1.5	3	4.5	6	7.5	9
Herbage allowance (kg DM kg ⁻¹ LW)	-	20.6±5.4	8.0±1.8	3.2±0.6	2.7±0.1	1.1±0.4	0.8±0.5
2007							
Stocking rate (sheep ha ⁻¹ grazing season ⁻¹)	0±0	2.8±0.8	4.2±0.7	4.8±0.7	6.1±0.8	7.9±0.6	9.0±1.3
Herbage allowance (kg DM kg ⁻¹ LW)	-	15.3±4.6	4.8±0.2	4.1±0.6	4.3±1.4	1.8±0.1	1.2±0.0
2008							
Stocking rate (sheep ha ⁻¹ grazing season ⁻¹)	0±0	2.8±0.8	4.1±0.3	4.8±1.1	6.9±0.9	8.4±0.6	10.1±1.1
Herbage allowance (kg DM kg ⁻¹ LW)	-	20.5±2.6	11.8±3.4	5.5±1.1	4.0±1.6	1.8±0.5	0.7±0.2
2009							
Stocking rate (sheep ha ⁻¹ grazing season ⁻¹)	0±0	2.6±0.7	4.4±0.1	5.3±0.8	7.2±0.3	8.8±0.8	10.6±1.1
Herbage allowance (kg DM kg ⁻¹ LW)	-	16.6±0.2	10.7±3.6	5.2±0.9	3.6±0.5	2.6±0.2	1.0±0.1
2010							
Stocking rate (sheep ha ⁻¹ grazing season ⁻¹)	0±0	2.3±0.0	4.7±0.0	6.5±0.0	7.5±0.2	9.0±0.2	10.3±0.0
Herbage allowance (kg DM kg ⁻¹ LW)	-	25±5.4	11.1±2.0	7.1±0.0	2.8±0.7	2.4±0.4	1.3±0.1

^aGrazing intensity classification: 0, ungrazed; 1, very-light; 2, light; 3, light-moderate; 4, moderate; 5, heavy; 6, very heavy

determination at 60°C for 48h. We used bulk samples that included green material and standing dead material. In order to calculate ANPP, litter was considered to be a result of the previous year's productivity and was thus removed before clipping the green and standing dead material. The green, dead and litter part of samples could be clearly differentiated. After each sampling time, exclosures were removed to new, previously grazed locations to measure the growth of aboveground biomass (AB) for each month and thereby enable calculation of the annual aboveground net primary productivity (ANPP); here AB is the live biomass (green) plus standing dead (we assume standing dead is current year material):

$$ANPP = July AB_{in} + (August AB_{in} - July AB_{out}) + (September AB_{in} - August AB_{out}) \quad (1)$$

(1) Subscripts of AB out (outside the exclosure) and in (inside the exclosure) represent access of sheep to the biomass that was inside (no access) and outside (access) the exclosure.



Calculation of the annual aboveground net primary productivity (ANPP) (McNaughton et al. 1996)

Species composition was measured once each year at the July sampling. Aboveground biomass was clipped to 1 cm stubble-height inside 0.25 m × 2 m rectangular frames that were positioned inside the exclosures. The collected plant material was separated by species, and taken back to the laboratory for dry matter determination at 60°C for 48h. Species composition was summarized by the aboveground biomass of each species. These comprised: *L. chinensis*, *S. grandis*, *Cleistogenes squarrosa*, *Carex korshinskyi* (Kom.) Malyshev., *Agropyron cristatum* (L.) Gaertn, *Achnatherum sibiricum* (Linn.) Keng, and other remaining and infrequently occurring species were combined as a single category. Species diversity included three different parameters: richness, Shannon-wiener index and evenness. Species richness (R) was represented by the number of species per unit area:

$$R = S; \quad (2)$$

where S means the number of species;

Shannon–Wiener’s species diversity index (D) was calculated by:

$$D = -\sum_{i=1}^R P_i \ln P_i; \quad (3)$$

P_i means the proportion of species i in total species numbers;

and the species evenness (E) was calculated by:

$$E = D / \ln R; \quad (4)$$

For quality analysis, the collected plant materials were mixed, dried at 60°C for 48 hours until constant weight, then weighed and ground to pass a 1 mm sieve using a Cyclotec 1093 Sample Mill (Tecator, Sweden) and scanned using the Near-Infrared-Spectroscopy (NIRS) technique for forage nutritional quality determination. The forage nutritional value (FNV) is characterized by the concentrations in the mixed herbage of organic matter (OM), crude protein (CP), neutral detergent fibre (NDF), acid detergent fibre (ADF), acid detergent lignin (ADL), cellulase digestible organic matter (CDOM)

and metabolizable energy (ME). For measuring the pepsin cellulase solubility of OM, CDOM value in % of OM and ME value in MJ kg⁻¹ DM were calculated by using crude ash (CA) and non-soluble enzymatic substance (EULOS) (Weissbach *et al.*, 1999; Schönbach *et al.*, 2009, 2012):

$$CDOM = 100 (940 - CA - 0.62 EULOS - 0.000221EULOS^2) / (1000 - CA); \quad (5)$$

$$ME = 13.98 - 0.0147 CA - 0.0102 EULOS - 0.00000254 EULOS^2 + 0.00234 CP; \quad (6)$$

The forage nutritional yield (FNY) is a function of ANPP and the FNV, including CP yield (CPY), CDOM yield (CDOMY), NDF yield (NDFY) and ME yield (MEY). The annual weighted means of FNY were calculated by multiplying ANPP with the weighted average FNV sampled from outside the enclosure cages:

$$FNY = ANPP \times FNV \quad (7)$$

Statistical analyses

The statistical analysis was performed using SAS Version 9.1 (SAS Institute Inc., Cary, NC, USA). The experimental design was based on randomized complete block design. Analysis of variance (ANOVA) processed with mixed model was applied by using ‘grazing intensity’ as fixed effect, ‘year’ as repeated effect and ‘block’, ‘year’ and their interactions as random effects, and grazing intensity × block as experimental error. Simple linear regression analysis was used to analyze the correlations of ANPP, FNV and FNY on grazing intensity or precipitation. The level of significance was $P < 0.05$. The multiple stepwise regression model with stepwise selection was used to analyze the correlations and importance of FNV on seasonal temperature and seasonal precipitation; the correlations and importance of FNY on ANPP and FNV; the correlations and importance of species diversity parameters (richness, diversity and evenness) on FNY and plant species composition. The variable that improves the model the most

(determined by higher R-square and significance at the 0.05 level) was kept by using stepwise bidirectional selection model comparison criterion. The stepwise-building used forward selection. The significance of the coefficient of determination R-square for the multiple regression analysis was tested by using a two-sided test ($P < 0.05$). By comparing the model coefficients of determination, the optimum model accounting for maximum variation was chosen.

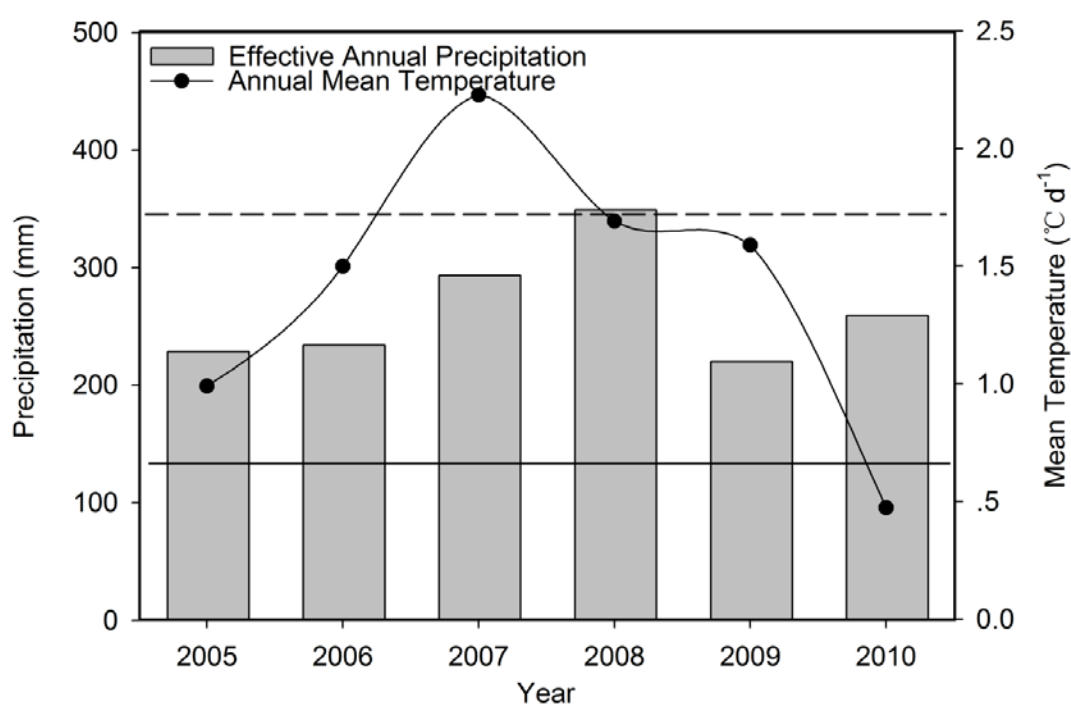


Fig. 1 Effective annual precipitation rates (previous-year September to current-year September) (left y-axis) and annual mean temperature (right y-axis) from 2005-2010. Dashed line means mean effective annual precipitation for 20 years (1983-2004), it is 343mm; bold line means mean annual mean temperature for 20 years (1983-2004), it is 0.7 °C

Results

Annual precipitation and annual mean temperature

During the six experimental years (2005-2010), effective annual precipitation (previous-year September to current-year September) ranged from 219-345mm and annual mean temperature ranged from 0.5-2.2°C (Figure 1). The effective annual precipitation during the experiment period (2005-2010) was lower than long-term mean annual precipitation of 343mm (from 1982-2004), but annual mean temperature during the six years was above the 20-years annual mean temperature of 0.7°C (Figure 1).

Table 2 The F-statistics by repeated measurement ANOVA test for the nutritional value and yields of forage with grazing intensities from 2005 to 2010

Values	Year	B	GI	GI*Year
CP (g kg ⁻¹ DM)	16.3***	17.5***	16.5***	1.3ns
NDF (g kg ⁻¹ DM)	14.6***	39.0***	11.4**	1.0ns
CDOM (g kg ⁻¹ OM)	25.0***	27.3***	10.9***	1.3ns
ME (MJ kg ⁻¹ DM)	27.9***	28.9***	11.1***	1.3ns
Yields	Year	B	GI	GI*Year
ANPP (g DM m ⁻²)	6.5***	14.5**	5.3**	1.4ns
CP (g m ⁻²)	20.8***	11.0**	2.6ns	0.9ns
NDF (g m ⁻²)	5.4***	14.9**	5.3*	1.4ns
CDOM (g m ⁻²)	7.4***	13.4**	5.3**	1.4ns
ME (MJ m ⁻²)	7.1***	13.6**	5.5**	1.4ns

Abbreviations: block (B); grazing intensity (GI); crude protein (CP); neutral detergent fibre (NDF); cellulase digestible organic matter (CDOM); metabolizable energy (ME)
ns, *, ** and *** denote $P > 0.05$, $0.01 < P < 0.05$, $0.001 < P < 0.01$ and $P < 0.001$, respectively

Aboveground net primary productivity (ANPP)

ANPP was significantly affected by grazing intensity and year (Table 2 and Figure 2). The effect of grazing intensity accounted for most of the variation in ANPP. With increased grazing intensity ANPP decreased from 200 to 104 g DM m⁻². The relationship between ANPP and grazing intensity was described well by the negative linear regression ($P < 0.01$) (Figure 2a). ANPP significantly increased in years of higher precipitation (Figure 2b). In the wettest year 2008, ANPP reached the highest value of 170 g DM m⁻², whereas in the driest year 2005, ANPP was only 134 g DM m⁻². The regression model analysis revealed that ANPP was positively correlated with annual rainfall ($P < 0.01$) (Figure 2b).

Forage nutritional value (FNV)

FNV was significantly affected by grazing intensity (Table 2). The relationships between grazing intensity and FNV were further described by regression analysis (Figure 3). Increasing the grazing intensity resulted in increased CP concentration from 99 to 149 g kg⁻¹ DM (dry matter), a 51% increment; the cellulase digestible organic matter (CDOM) increased from 612 to 659 g kg⁻¹ DM, and metabolizable energy (ME) from 8.45 to 9.25 MJ kg⁻¹ DM, whilst neutral detergent fibre (NDF) concentration decreased from 694 to 676 g kg⁻¹ DM (Figure 3 a). In grazing intensity 0-4 there were no significant changes for NDF value, but in intensity 5 and 6 NDF decreased significantly.

FNV was significantly affected by year (Table 2), but the linear regression relationships between annual precipitation and FNV was weak. Only CP and NDF value were positively correlated with annual precipitation (Figure 3b). We further analyzed the FNV using the seasonal precipitation and mean temperature variations (Table 3). The dataset showed that FNV fluctuations with years were determined by both precipitation

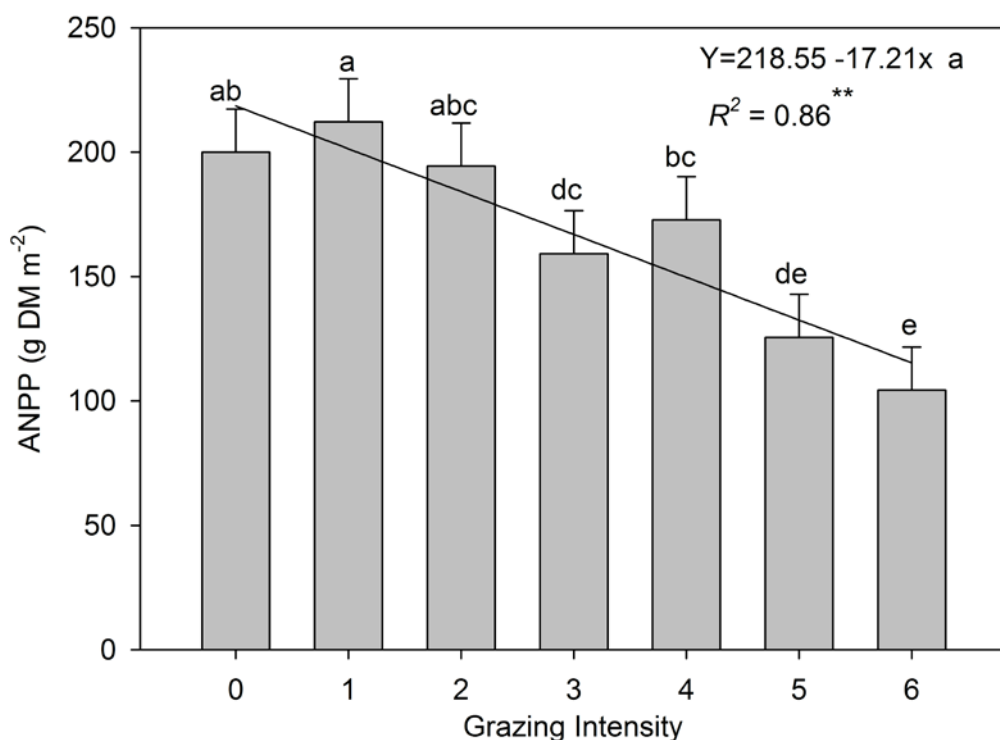


Fig. 2a Effect of grazing intensity on aboveground net primary productivity (ANPP). Bars show the means of six experimental years (2005-2010)

Grazing intensity: 0, ungrazed; 1, very-light; 2, light; 3, light-moderate; 4, moderate; 5, heavy; 6, very-heavy (Details on grazing intensity classification are given in Table 1).

Error bars show the standard error of the means; Different letters (a, b, c, d, e) on bars represent significant differences among treatments (LSD test, $P < 0.05$); Adjusted R-square and significant levels (** means $P < 0.01$) of the linear regression are shown in the figure

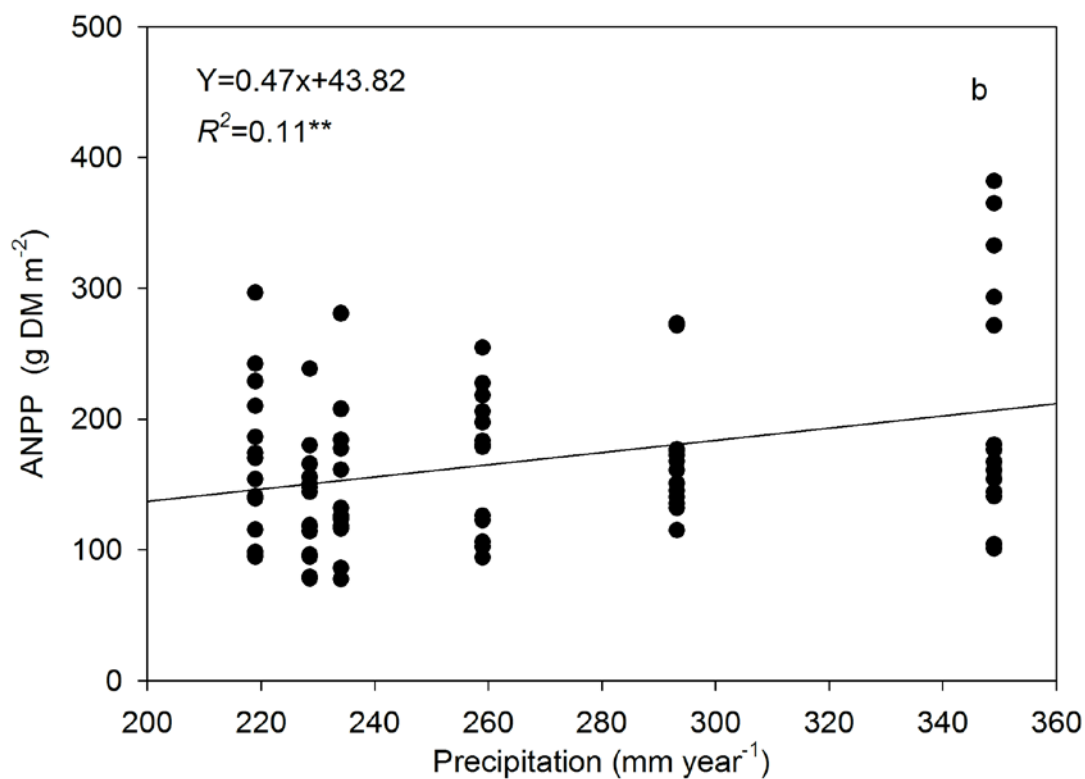


Fig. 2b Effect of effective annual precipitation (previous-year September to current-year September) on aboveground net primary productivity (ANPP) during six experimental years (2005-2010)

Adjusted R-square and significant levels (** means $P < 0.01$) of the linear regression are shown in the figure

(P: mm) and mean temperature (T: °C d⁻¹) from early spring season to summer season, which started from March and ended until the beginning of September (Table 3). Stepwise multiple regression analysis revealed a positive effect on the CP, NDF, CDOM and ME values against precipitation in the growing periods, and a negative effect on the CDOM and ME against mean temperature in the growing periods.

Table 3 Partial and total model adjusted R-Square coefficients of determination ($N=84$) associated with forage nutritional value parameters for stepwise multiple regression analysis, effective precipitation (mm) and mean temperature (°C d⁻¹) in growing period (March-September) as independent variables

Values	Model equations	Precipitation		Mean Temperature		Sum	
		Partial R^2	P	Partial R^2	P	Sum R^2	P
CP (g kg ⁻¹ DM)	Y=+0.023P+12.566	$R^2=0.15$	$P<0.0001$				
NDF (g kg ⁻¹ DM)	Y= -0.020P+69.044	$R^2=0.26$	$P<0.0001$				
CDOM (g kg ⁻¹ OM)	Y=+0.015P-0.076T+67.656	$R^2=0.08$	$P=0.0008$	$R^2=0.17$	$P<0.0001$	$R^2=0.25$	$P<0.0001$
ME (MJ kg ⁻¹ DM)	Y=+0.003P-0.012T+9.460	$R^2=0.04$	$P=0.0177$	$R^2=0.18$	$P<0.0001$	$R^2=0.22$	$P<0.0001$

Abbreviations: crude protein (CP); neutral detergent fibre (NDF); cellulase digestible organic matter (CDOM); metabolizable energy (ME)

Forage nutritional yields (FNY)

The FNY was significantly affected by grazing intensity and mean annual precipitation (Table 2). The FNV-grazing intensity relationship described by regression analysis is coincident with the ANOVA results (Figure 4a, b). The FNY was characterized by CPY, CDOMY, MEY and NDFY. Increasing grazing intensity resulted in decreased CPY from 19.44 to 15.37 g m⁻², CDOMY from 122 to 68 g m⁻², MEY from 1.68 to 0.96 g m⁻², and NDFY from 139 to 71 g m⁻² (Figure 4 a). The quadratic regression model explains more than 90% of FNY variability, which was induced by

grazing ($P < 0.01$). Furthermore, mean annual precipitation amount had a significant effect on FNY. Regression model analysis displayed a positive linear relationship between FNY and rainfall ($P < 0.01$). The responses of FNY to grazing intensity and mean annual precipitation showed a similar trend to the responses of ANPP to these variables.

Table 4 Adjusted R-Square coefficients of determination ($N=84$) associated with forage nutritional value and aboveground net primary productivity for stepwise multiple regression analysis; forage nutritional yields parameters are dependent variables

Yields	ANPP (g DM m ⁻²)	CP (g kg ⁻¹ DM)	NDF (g kg ⁻¹ DM)	CDOM(g kg ⁻¹ OM)	ME (MJ kg ⁻¹ DM)
CP (g m ⁻²)	0.68***	0.26***	----	----	----
NDF (g m ⁻²)	1.00***	----	0.00***	----	----
CDOM (g m ⁻²)	0.99***	----	0.00***	0.01***	----
ME (MJ m ⁻²)	0.98***	----	0.00***	----	0.01***

Abbreviations: crude protein (CP); neutral detergent fibre (NDF); cellulase digestible organic matter (CDOM); metabolizable energy (ME)

Partial R^2 coefficients are given only when there are significant correlations; *, ** and *** denote $P > 0.05$, $0.01 < P < 0.05$, $0.001 < P < 0.01$ and $P < 0.001$, respectively

The relationship between FNV, ANPP and FNY

Stepwise multiple regression analysis quantified the relationships between each FNY (i.e., CPY, NDFY, CDOMY and MEY) and FNV parameter (i.e., CP, NDF, CDOM and ME) and ANPP by using FNY as independent variable (Table 4). FNY was strongly associated with ANPP, but was less associated with FNV. Adjusted R^2 coefficient of determination indicated that multiple regression models could finally interpret from 68% to nearly 100% of the variations of FNY parameters that were produced by ANPP variations. Except for the CP value, variation of which could explain

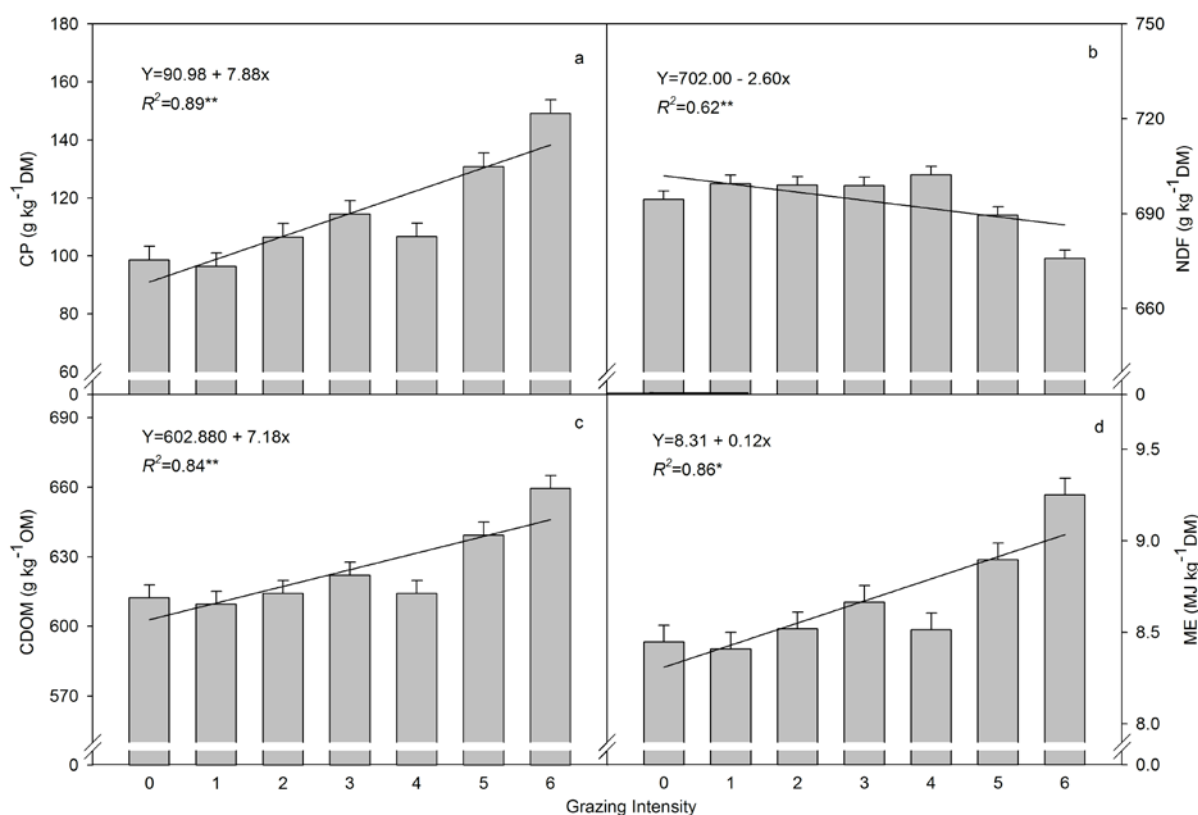


Fig. 3a Relationship between forage nutritional values (FNV) and grazing intensity during six years from 2005-2010. The abbreviations means: crude protein (CP); neutral detergent fibre (NDF); cellulase digestible organic matter (CDOM); metabolizable energy (ME)

Adjusted R-square and significant levels of the linear regression are shown in the figure; *, **, and *** denote significant difference at $0.01 < P < 0.05$, $0.001 < P < 0.01$ and $P < 0.001$, respectively

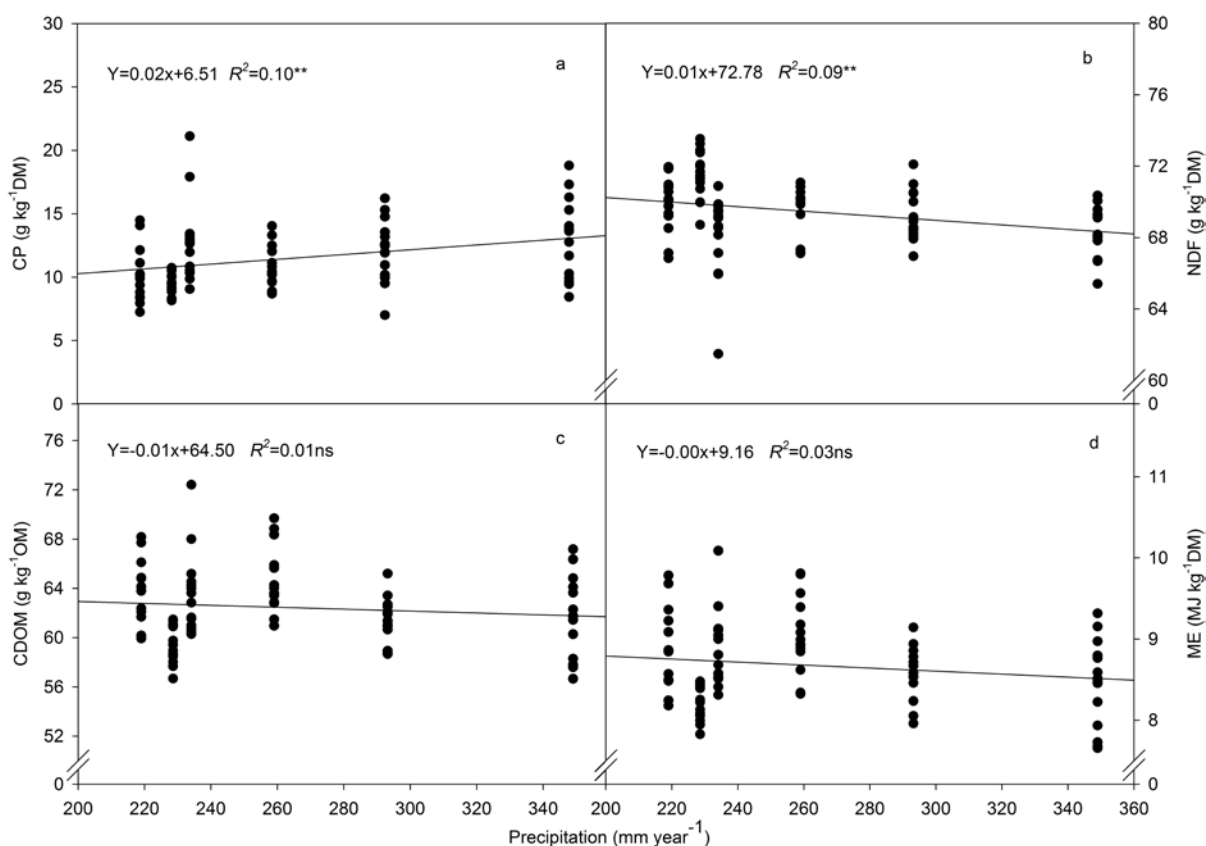


Fig. 3b Relationship between forage nutritional values (FNV) and effective annual precipitation (previous-year September to current-year September) during six years from 2005-2010. The abbreviations means: crude protein (CP); neutral detergent fibre (NDF); cellulase digestible organic matter (CDOM); metabolizable energy (ME)

Adjusted R-square and significant levels of the linear regression are shown in the figure; *, **, and *** denote significant difference at $0.01 < P < 0.05$, $0.001 < P < 0.01$ and $P < 0.001$, respectively; ns means no significant difference

up to 26% of CPY variations, variations of CDOM value, ME value and NDF value could explain less than 1% of CDOMY, MEY and NDFY variations correspondingly. Altogether, an increase of 1g DM m⁻² in ANPP on average over the experimental years resulted in the CPY increase of 0.07g m⁻², NDFY decrease of 0.71g m⁻², CDOMY increase of 0.56g m⁻² and ME increase of 0.08MJ m⁻² (Table 4).

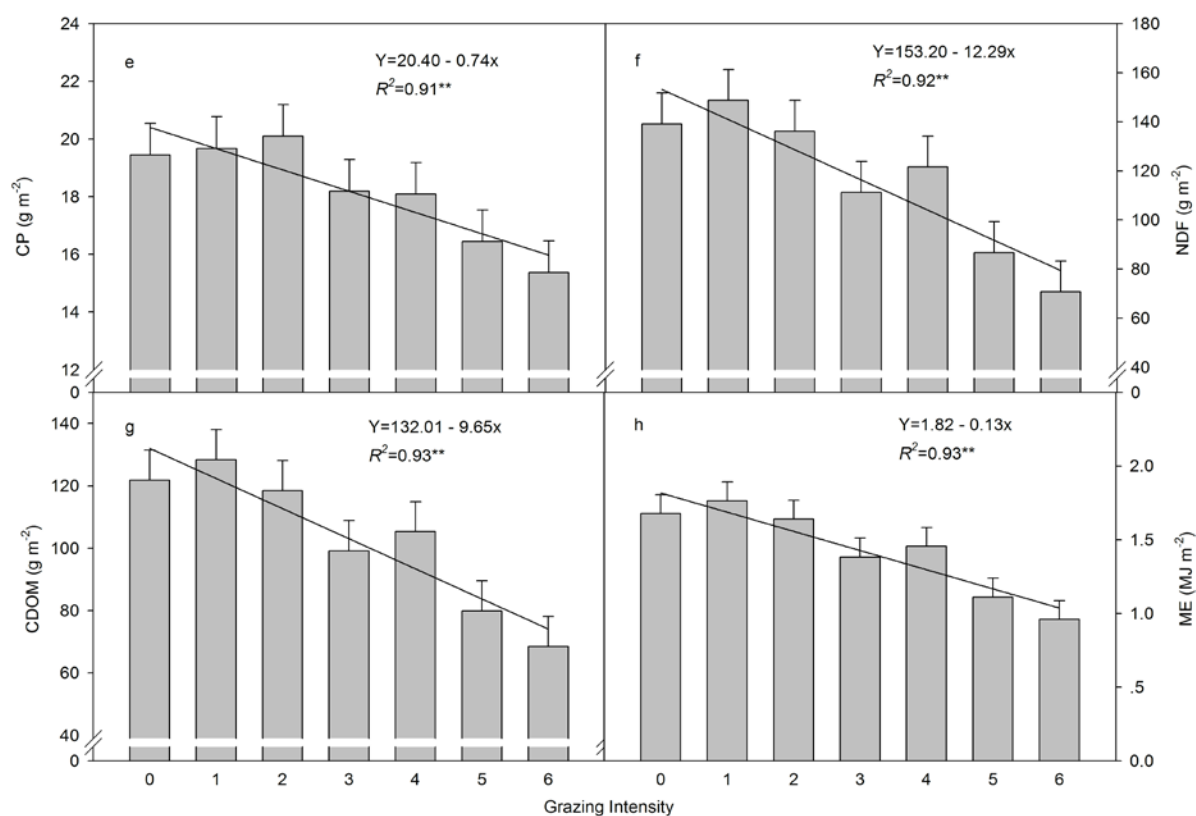


Fig. 4a Relationship between forage nutritional yields (FNY) and grazing intensity during six years from 2005-2010. The abbreviations means: crude protein (CP); neutral detergent fibre (NDF); cellulase digestible organic matter (CDOM); metabolizable energy (ME)

Adjusted R-square and significant levels of the linear regression are shown in the figure; *, **, and *** denote significant difference at $0.01 < P < 0.05$, $0.001 < P < 0.01$ and $P < 0.001$, respectively

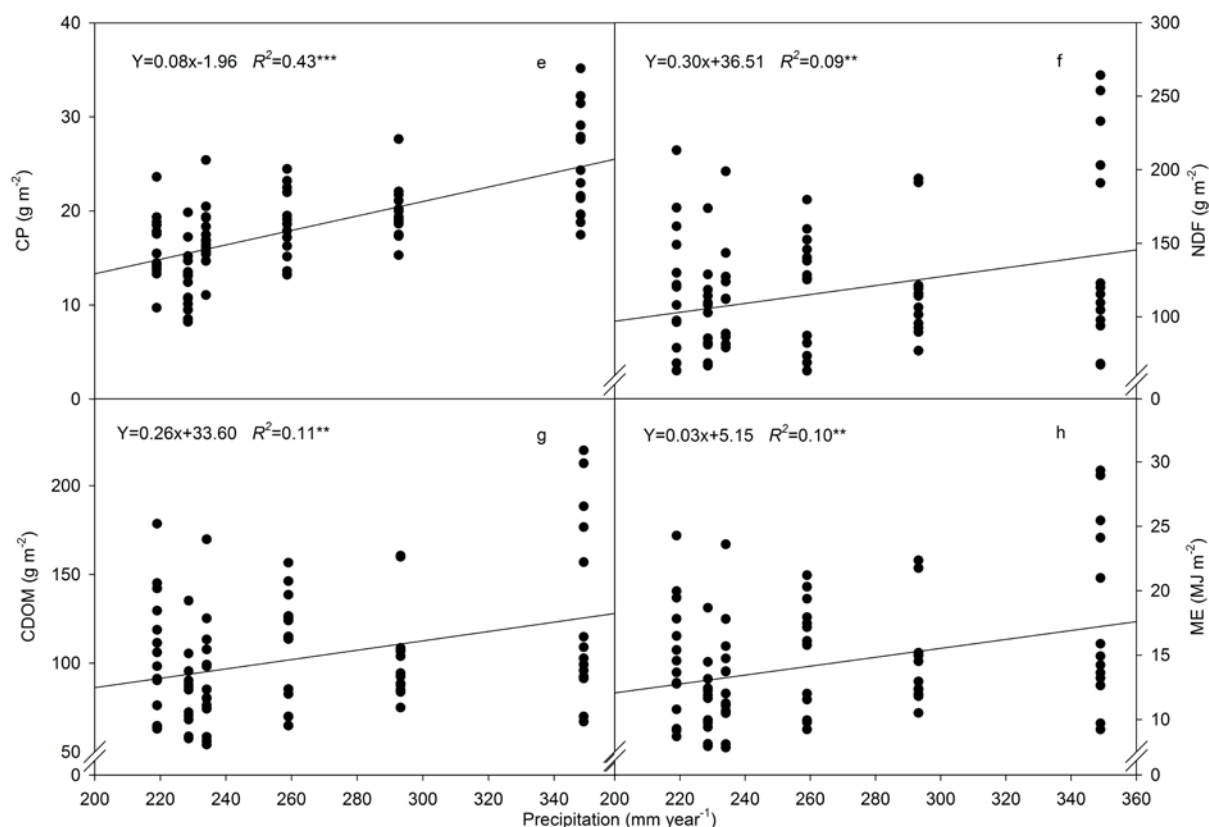


Fig. 4b Relationship between forage nutritional yields (FNY) and effective annual precipitation (previous-year September to current-year September) during six years from 2005-2010. The abbreviations means: crude protein (CP); neutral detergent fibre (NDF); cellulase digestible organic matter (CDOM); metabolizable energy (ME). Adjusted R-square and significant levels of the linear regression are shown in the figure; *, **, and *** denote significant difference at $0.01 < P < 0.05$, $0.001 < P < 0.01$ and $P < 0.001$, respectively

The relationship between species diversity and species composition with FNY

The average species composition for the seven levels of grazing intensity, determined at the July sampling in each of the six years, is summarized in Table 5. The biomass proportions of each species are based on herbage dry matter yield. The biomass of two dominant species *L. chinensis* and *S. grandis* accounted for more than 80% of total community biomass. Stepwise regression analyses showed the correlations and importance of species composition and species diversity indices (Richness, Shannon-Wiener diversity index and Evenness) on ANPP and each parameter of FNV and FNY (Table 6). The FNV, ANPP and FNY were less correlated with species diversity parameters and other subdominant or rare species, but were predominantly correlated with two dominant species: *L. chinensis* and *S. grandis*. By combining these two dominant species, 21-29%, 58%, 30-59% of the FNV, ANPP and FNY variation, respectively, could be explained. Species diversity parameters could only explain 3-4% of the variation.

Discussion*Aboveground net primary productivity (ANPP)*

In our six-year grazing experiment, the ANPP decreased with increasing intensity of grazing. This indicates that plant regrowth cannot compensate for the biomass reduction that occurs as a result of defoliation and sward damage induced by grazing and trampling (Schonbach *et al.*, 2009, Schonbach *et al.*, 2011, Schonbach *et al.*, 2012). The negative ANPP-grazing intensity relationship is not simply consistent with the hump-shaped intermediate disturbance hypothesis, which proposes that moderate grazing intensity maintains high levels community productivity (Noy-Meir, 1993;

Patton *et al.*, 2007).

The inconsistent results observed by others are therefore not necessarily comparable, since many factors could affect the complex relationship between grazing intensity and ANPP. Firstly, the variation between the non-experimental approaches in previous work and the experimental approaches used in our work, as well as the different grazing histories and grazing intensities applied. The herbage composition of grazed natural grassland is partly determined by its recent history of grazing management and by the actual grazing management at different temporal and spatial scales. Our controlled experiment has seven grazing intensities, and anyone of them could fit to the effect of long grazing history for previous long-term studies. And therefore, we could quantify the intensity of moderate grazing or heavy grazing. But we cannot know the exact grazing intensity from the non-experimental study. Secondly, the different starting conditions of the studied sites together with an assessment of grazing intensities could lead to different conclusions being reached. For example, the different grassland ecosystems and environmental conditions may define different standards for grazing intensities (Patton *et al.*, 2007). A non-experimental study cannot provide reliable measures of actual grazing intensity. However, our study included a gradient of seven different levels of grazing intensity. Thirdly, the complex effects of variability in weather, species composition, biodiversity and grazing confound the results and cannot be easily disentangled, for all these factors could affect ANPP directly or indirectly. For instance, in the case of non-experimental approaches, sampling of a long-term study may include the effects of grazing on vegetation (e.g. botanical composition of a steppe community after 50 years of moderate grazing), but without providing information on the processes (e.g. changes in the botanical composition, diversity, nutritive value, yield formation over time). However, the controlled

experimental approaches provide additional knowledge about the grazing-induced change in vegetation.

Evidence presented by Noy-Meir (1993) suggests that the effect of grazing on plant growth could be zero, negative or positive, depending on several factors including plant species' functional traits, soil properties, and grazing intensity. Therefore the negative ANPP-grazing intensity relationship in our study accords with just one of these situations. Furthermore, our findings demonstrate that the variation of ANPP among years could be attributed predominantly to the variability of effective annual precipitation. ANPP increased linearly with increased effective annual precipitation. Since water availability is a key factor limiting plant growth and ANPP in semiarid grassland (Bai *et al.*, 2008), the vegetation could make full use of the precipitation

Table 5 Species composition determined at the July sampling with grazing intensity (% of dry matter)

GI classification	Grazing intensity (GI)						
	0	1	2	3	4	5	6
<i>L.ch</i>	28.63±0.40	54.15±0.68	34.11±0.57	20.54±0.33	46.01±0.52	22.06±0.34	40.34±0.34
<i>S.gr</i>	46.98±0.50	25.29±0.49	45.43±0.62	59.76±0.64	28.06±0.36	52.43±0.53	36.06±0.40
<i>A.cr.</i>	7.84±0.27	3.55±0.22	5.19±0.20	6.12±0.22	8.80±0.24	9.24±0.26	6.11±0.24
<i>C.sq</i>	5.19±0.20	2.40±0.19	4.86±0.24	5.42±0.26	4.44±0.22	6.17±0.21	3.86±0.16
<i>C.ko</i>	5.79±0.22	8.88±0.28	5.76±0.29	5.70±0.20	8.90±0.28	6.60±0.21	9.63±0.17
<i>K.ma</i>	2.24±0.18	0.55±0.11	0.55±0.12	0.16±0.05	0.31±0.06	0.19±0.06	0.16±0.04
<i>A.si</i>	1.67±0.12	3.14±0.17	2.29±0.14	0.53±0.10	0.81±0.12	1.34±0.15	2.42±0.16
<i>Res^a</i>	2.37±0.08	2.98±0.08	3.04±0.04	2.13±0.06	3.46±0.06	2.21±0.06	1.52±0.06

Abbreviations: *L.ch* (*Leymus chinensis*), *S.gr* (*Stipa grandis*), *A.cr* (*Agropyron cristatum* (L.) Gaertn), *C.sq* (*Cleistogenes squarrosa* (Trin.) Keng), *C.ko* (*Carex korshinskyi* (Kom.) Malyshev.), *K.ma* (*Koeleria macrantha* (Ledeb.) Schult), *A.si* (*Achnatherum sibiricum* (Linn.) Keng), *Res* (Remaining species).

^a Includes all species with biomass proportions of > 0% and < 1% in dry matter.

availability to enable its maximum potential productivity. This result is consistent with several studies, which have reported that, in the case of both dry and wet grassland, the highest levels of productivity are attained in the wettest years and the lowest productivity in the driest years (Knapp *et al.*, 2002, Bai *et al.*, 2008).

Table 6 Adjusted R-Square coefficients of determination ($N=84$) associated with species diversity parameters: richness (Ric), diversity index (Div) and evenness (Eve) and species level biomass for stepwise multiple regression analysis; forage nutritional value, aboveground net primary productivity and forage nutritional yields parameters are dependent variables

Parameters	<i>L.ch</i>	<i>S.gr</i>	<i>C.sq</i>	Div
ANPP (g DM m ⁻²)	0.34***	0.24***	0.02*	0.04*
Forage nutritional value				
CP (g kg ⁻¹ DM)	0.20***	0.09***	0.02*	0.10***
NDF (g kg ⁻¹ DM)	0.12**	0.09***	0.00ns	0.04*
CDOM (g kg ⁻¹ OM)	0.25***	0.03**	0.01*	0.04*
ME (MJ kg ⁻¹ DM)	0.28***	0.00ns	0.01*	0.00ns
Forage nutritional yields				
CP (g m ⁻²)	0.20**	0.10**	0.02*	0.00ns
NDF (g m ⁻²)	0.35***	0.24***	0.00ns	0.04*
CDOM (g m ⁻²)	0.30***	0.29***	0.01*	0.03*
ME (MJ m ⁻²)	0.29***	0.30***	0.00ns	0.03*

Abbreviations: *L.ch* (*Leymus chinensis*), *S.gr* (*Stipa grandis*), *C.sq* (*Cleistogenes squarrosa* (Trin.) Keng), Div (species diversity), crude protein (CP); neutral detergent fibre (NDF); cellulase digestible organic matter (CDOM); metabolizable energy (ME)

Forage nutritional value (FNV)

Grazing resulted in a significant increase of the FNV indicated by a significant decrease in NDF and a significant increase in CP, CDOM and ME, which have also been reported by Noy-Meir (1993) and Schönbach *et al.*, (2009; 2012). Grazing disturbance accelerates regrowth of new tissues and thereby reduces the mean age of plant tissue in the sward. Therefore younger plant material remains, which has less fibre in the regrowth after grazing. In addition, animal excretion of nitrogen through urine and faeces increases the mineral nitrogen assimilated by plant species (Kurz *et al.*, 2006, Schönbach *et al.*, 2012). Efficient utilization of forage ensures that forage is supplied that is of sufficient quality to match the protein and energy requirements of ruminants. Some previous studies have concluded that the optimal CP concentration was around 132 g/kg OM, a level that could be digested by growing sheep (40 kg live weight) (Yang, 1999, Wang *et al.*, 2011), and the optimal ME concentration should be 5.3 MJ/day for sheep (of 35 kg live weight) using published standards (National Research Council, 2007, Wang *et al.*, 2009). Therefore, for feeding sheep at maintenance level, the grazing intensity should be modified by farmers according to the FNV variations.

FNV was strongly improved in years with increased effective annual precipitation. The increased CP concentration relative to effective annual precipitation corresponds to the effects of high water availability in improving herbage-nitrogen concentration and plant nitrogen uptake. The decreased NDF value in relation to effective annual precipitation corresponds to the higher proportion of younger plant tissue, resulting in low fibrous concentration and less-digestible composition. This is consistent with the conclusions confirmed by several recent studies (Biondini *et al.*, 1998, Gebauer and Ehleringer, 2000, Giese *et al.*, 2009). Many factors could lead to the positive

relationship between availability of nitrogen and nitrogen assimilation rates of plant with precipitation, i.e. mineralization rate or net photosynthetic rate (Xu and Zhou, 2006). In addition, the severe water stress could accelerate maturation by enhancing the accumulation of fibrous and less-digestible material (Buxton, 1996).

Seasonal precipitation and mean temperature together could explain most of the variation of CDOM and ME value among years. For CP and NDF, they were much more strongly correlated with seasonal precipitation than annual precipitation rates. These results suggest that not only the amount but also the seasonal distributions of precipitation and temperature determine the nutritional value of forages. Growing season lasts from early spring season (March) to late summer season (September). During this time, forage species run through their growth stages from budding, flowering, seeding and senescence, and thus they possess high sensitivity to variations in precipitation and temperature during this growing period. There were no interactions between year and grazing intensity and the variations of FNV over time were not influenced by grazing intensity. Therefore, the variation of FNV between years may be responsible for the inter-annual temporal variations in precipitation and temperature, which affect the maturity stage of harvested forage. As reported by Buxton (1996), even if forages were harvested at the same maturity stages, the year-to-year and seasonal variation in environment can alter their optimal maturation stage for a given quality. The increased precipitation during the growing period may promote the generation of new tissues and retard the process of lignifications, and thus increase the digestibility and dietary energy content, as indicated by increased CDOM and ME values, respectively. Meanwhile, the decreased temperature affects forage quality in the same way. This is consistent with the results of Anderson (1985) and Bertrand *et al.* (2008), who found a decrease in forage fibre concentrations and an increase in forage

digestibility in response to lower temperatures. Our results provided clear evidence to show the dominant effects of precipitation and temperature on the community forage nutritional quality dynamic. They widely extended the previous conclusion from Schönbach *et al.*, (2012)

Forage nutritional yields (FNY)

According to our findings, the FNY was affected by both grazing and precipitation, and this was also reported by Schönbach *et al.* (2009; 2012). With the effect of FNV as a driver for FNY related to ANPP, FNY is the key parameter for potential livestock performance in steppe ecosystems. However, the response of FNY to grazing or to precipitation just follows the response of ANPP. For most FNY parameters, nearly 99% of the contribution came from ANPP; the exception being CPY, which had a 26% contribution from CP concentration (Table 4). The 51% increment of CP concentration with increased grazing intensity resulted in its higher contribution to CPY variations than other FNV (Figure 3 a). This result could be indirectly supported by the findings of a cutting-frequency experiment of Schiborra *et al.* (2010), who found a significant increase in the CP concentration in the vertical quality of structure of species, but only minor differences in other quality parameters (e.g. NDF). The increment in the FNV with increased grazing intensity could not compensate for decreased ANPP, which led to the obvious reduction in FNY. Buxton and Casler (1993) and Buxton (1996) also concluded that the effects of grazing on forage nutritional quality are usually smaller in magnitude than the effect that grazing has on forage yields. This provides important information for future farm management: forage on offer for livestock should be based on ANPP dynamic rather than FNV, since ANPP could determine the most community FNY. Our study quantified the respective contribution of ANPP and FNV to FNY, so

our conclusions may be more comprehensive than the similar study concluded by Schönbach *et al.*, (2012). Because of the reduction in DM yield with increased grazing intensity, long-term intensive grazing will reduce the sustainable development of the agricultural industry in the Inner Mongolian typical steppe. Nowadays, more frequent extreme precipitation and drought events are predicted to occur in response to increased climatic change (Easterling *et al.*, 2000). The increased severity of drought together with overgrazing may accelerate a shift of forage from high to poor quality and from high to low yields, and consequently slow down the cycle of the ecosystem processes (Zheng *et al.*, 2011). Our findings provide meaningful guidance for improving the management of arid and semiarid grassland ecosystems and their conservation in response to the effects of abiotic and biotic disturbance.

Species diversity and species composition effects on ANPP, FNV and FNY

ANPP, FNV and FNY were predominantly determined by the dominant species *L. chinensis* and *S. grandis* rather than by the species diversity. In order to maintain community stability, the species composition in grassland ecosystems is likely to be at least as important as the species diversity, which is in line with the results reported by previous studies (Chapin, 1980, Wedin and Tilman, 1990, Hobbie, 1992, Hooper and Vitousek, 1997). Species composition brings into play all the different functional traits (e.g. leaf area, stem-leaf ratio, meristems, stored nutrients, phenology) from dominant species to opportunistic species (Zheng *et al.*, 2011). This may explain the contribution of species composition on community ANPP exceeding those of plant species number (Richness) present. Huston (1997) reported that the most productive species determine the specific trophic level because they are well adapted to the environment. Thus, the perennial rhizomatous grass *L. chinensis* and the perennial bunchgrass *S. grandis*, the

two most dominant species in our study region, affected the ANPP, FNV and FNY more than diversity and other plant species in the community. In future studies, grassland ecosystems reflecting a similar range of species diversity compared to our experiment, species composition, especially in terms of dominant species rather than species diversity, could be used as an effective parameter to predict the fluctuation of forage nutritional quality and yields in response to different grazing intensities and over successive years, to predict vegetation dynamic and grassland stability.

Conclusion

Grazing intensity was one of the main drivers that determined ANPP and forage nutritional value and yields in Mongolian steppe. Since forage nutritional yields were predominantly determined by ANPP, the grazing-induced increase in forage nutritional value could not offset the decrease in forage ANPP, and thereby could not affect the variation of forage nutritional yields with grazing. In terms of management options (e.g. grazing intensity), it is recommended that farmers should focus primarily on forage productivity to manage their grassland. Precipitation was another important driver. However, the seasonal distributions of precipitation and temperature contributed more in terms of affecting forage nutritional value than the annualized sum, especially for forage digestibility (CDOM) and metabolizable energy (ME). It was the dominant species, rather than species diversity as indicated by the number of species present in the vegetation community, that affected forage ANPP, FNV and FNY.

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Chapter 4

**Effects of Grazing Intensity on Nutritive Value of
Five Dominant Species in Typical Steppe of Inner
Mongolia, China**

**Effects of Grazing Intensity on nutritive value of Five Dominant Species in
Typical Steppe of Inner Mongolia, China**

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Abstract

Understanding the effects of grazing disturbance, abiotic drivers and temporal variations on plant nutritive value is important for grassland management and conservation. Here, the nutritive value of five dominant species (three C3 species and two C4 species) in the Inner Mongolia grassland of China were studied, within a large-scale grazing experiment including seven grazing intensities (from ungrazed to very heavily grazed) in a wet year (2008) and a dry year (2010). Our results showed that for the five species, the effects of grazing, year, growing period, year×grazing intensity, and year×growing period on plant nutritive value were highly significant in most parameters. Grazing increased crude protein (CP) and cellulase digestible organic matter (CDOM) concentration and decreased neutral detergent fibre (NDF) concentration in all species. All five species had higher CP and CDOM concentration in the wet year (2008) than in the dry year (2010). C4 species *C. squarrosa* showed increased trend in CP and CDOM concentration over growing season (from June to August), which was inverse to C3 species. Our results suggest that grazing, precipitation and growing period were three main factors in driving species nutritive value dynamics. Droughts and heavy grazing may accelerate the degenerating of forage nutritive value in the long run. The nutritive value trade-offs between C4 and C3 species over growing season provided an approach to understand the balance of forage quality at the community level. When using grazing to manage grassland ecosystems and modulate livestock productivity, the effects of abiotic environment and temporal variation on forage nutritive dynamic should be taken into consideration.

Keywords nutritive value, C3 and C4 species, grazing, precipitation, growing period, temperate steppe

Introduction

Forage nutritive value is a function of the nutrient concentration, the amount of forage intake and digestibility (Bertrand et al. 2008; Buxton 1996; Corona et al. 1998). As forage is the single feed source of grassland to support livestock production, the nutritive value of forage impact both herbivore behavior, e.g. migration (Albon and Langvatn 1992; Hebblewhite et al. 2008) and performance, e.g. the variation in their body weights (Mysterud et al. 2011; Mysterud et al. 2001).

In recent years, with increasing demand for income and food, grazing intensities increased sharply and have led to serious negative effects on grassland vegetation (Liang et al. 2009). The negative impact of grazing on forage is indicated by damage in plant biomass accumulation (Milchunas and Lauenroth 1993; Schonbach et al. 2009) and by changes in species composition (Belesky et al. 2002a; Cao et al. 2011). First of all, grazing –induced forage removal and damage by grazers reduce the species' aboveground biomass. Furthermore, the shifts of grazing-induced species composition over time may affect forage nutritive value (Roukos et al. 2011; Sleugh et al. 2000). For example, after long-term overgrazing, the species composition of grassland changed from high- to poor-quality species (Christensen et al. 2003; Zhang et al. 2004). Because the selectivity of herbivore on available forage and the different regrowth rate of species after grazing, the species could create variable nutrient patterns of grassland vegetation (Bakker et al. 2006; Fanselow et al. 2011; Olofsson et al. 2008; Schonbach et al. 2009). In addition, precipitation is a crucial factor in modulating grazing intensity by influencing productivity of semi-arid grasslands (Bai et al. 2004; Milchunas and Lauenroth 1993; Schonbach et al. 2009), and further affects forage quality (Adler et al. 2004; Pakeman 2004; Vesik et al. 2004). Precipitation obliges forage quality for plant nutrient uptake based on the positive correlation between soil nutrient and water

availability, especially in arid and semi-arid regions (Biondini et al. 1998; Gebauer and Ehleringer 2000; Schonbach et al. 2009). As a result, the competition among species for water as well as soil nutrients determines species composition and forage quality (Wang et al. 2008; Warren et al. 2002). Besides, plant species' on-going development stage over growing season corresponds to decreased crude protein (CP) and digestibility and increased neutral detergent fiber (NDF) concentrations (Wang et al. 2007; Wang et al. 2011). The nutritive value of forage varied with the stage of plant maturity and thus impacted herbage palatability and production of livestock (Bruinenberg et al. 2002; Karn et al. 2006; Roukos et al. 2011; Vazquez-de-Aldana et al. 2000). In all, all the above mentioned factors have effects on the nutritive value of forage (Schonbach et al. 2012; Schonbach et al. 2011; Wang et al. 2011).

Many studies have evaluated the nutritive value of forage in natural rangelands (Fanselow et al. 2011; Kalmbacher 1983; Schonbach et al. 2012) and analyzed either the effect of grazing (Liang et al. 2002; Liang et al. 2009) or precipitation (van Staaldunen and Anten 2005; Zhao et al. 2008) on different steppe grass species, but fewer simultaneously consider both effects within a given locality. Little is known about the effects of precipitation, grazing, growing period and their interaction on species nutritive value. Nor is information available on the nutritive value dynamic of grass species in semi-arid typical steppe since most of the previous studies focused on community level. Species differ in their potential contribution to ecosystem functioning. Hence, the identities of such or certain species in term of nutritive dynamic play an important role in dominating ecosystem processes. Until now, there are still large uncertainties about the causal linkage between shifts in species composition and changes in plant nutritive value under different influence factors. The present study investigates the responses of five dominant steppe species to grazing along a gradient of seven grazing intensities in both

wet year and dry year, which conducted under a long-term controlled grazing experiment in semi-arid typical steppe. We assess the following three questions: First, how does nutritive value of the five species vary with grazing intensity, growing period and inter-annual precipitation variation? Second, are there any changes in the nutritive value of forage linked to shifts in species composition? Third, what are the trade-offs between C3 and C4 species in their nutritive value with grazing effect over the growing season? As the climatic conditions of grazing systems in typical semi-arid steppe for plant growth was limited (Zheng et al. 2011), our findings would be important to understand the species specific nutritive dynamic in response to biotic (grazing intensity) and abiotic (precipitation and plant growing period) factors for improving livestock productivity.

Materials and methods

Experimental site

The research was conducted in the typical steppe region of Inner Mongolia, P.R. China, adjacent to the Inner Mongolia Grassland Research Station of the Chinese Academy of Sciences (IMGERS, 43° 38'N, 116° 42'E) at an altitude of around 1,200 m a. s. l.. The mean annual precipitation is 335mm (1982-2011), with about 80% occurring during the growing season (May-September). The mean annual temperature is 0.7°C (1982-2011). The temporal seasonal distribution of precipitation and temperature in 2008 and 2010 is shown in Figure 1. The typical steppe is dominated by perennial C3 grasses. About 60-80% of the total plant community aboveground biomass is composed by *Stipa grandis* P. Smirn. (perennial bunchgrass), *Leymus chinensis* Trin. Tzvel. (perennial rhizomatous grass), and *Agropyron michnoi* Roshev. (perennial bunchgrass) (Table 1). The most important C4 species are the perennial bunchgrass *Cleistogenes squarrosa* Trin.Keng and the annual forb *Salsola collina* Pall. Given their relative importance in this area, the five

most dominant species were chosen for nutritional/chemical analysis (Table 1). The soil in this area is classified as dark chestnut soil (Calcic Chernozem according to ISSS Working Group RB, 1998).

Experimental design

The present study was carried out within an on-going grazing experiment that was initiated in 2005 (Schönbach et al. 2012), and covers an area of 150 ha. The grazed area was divided into 2 ha paddocks by randomly allocating along seven grazing intensities, which were: no grazing (GI0), very-light (GI1), light (GI2), light-moderate (GI3), moderate (GI4), heavy (GI5) and very heavy (GI6) grazing. Stocking rates gradient and herbage allowances are used to define grazing intensities. The seven grazing intensities classified by stocking rates from 0, 1.5, 3, 4.5, 6, 7.5, to 9 sheep/ha, respectively. Herbage allowances were used to modify the numbers of sheep per area by maintaining the grazing pressure of each of intensity. Further details on grazing intensity classification are given in Schönbach *et al.* (2012). From 2005 to 2010, sheep were kept on the plots for approximate 95 days per year, throughout the vegetation period (June-September). In this study, samples were taken in 2008 and 2010. A randomized complete block design with four replicates was applied to analyze the effects of grazing intensity in two different years and four different growing periods on the forage nutritive value of the top-three C3 and the top-two C4 plant species.

Sampling

In order to provide the information about the phenological development of the plant species at different growing periods, about 20 g of the aboveground biomass of chosen five species (the top-three C3 species and the top-two C4 species, refer to Table 1) was

sampled monthly (in June, July, August and September) in the grazed (representing herbage on offer for livestock) and ungrazed plot. The collected plant material was clipped to 1 cm stubble-height and taken back to laboratory for dry matter determination at 60°C for 48h.

Species composition was measured once each season to record species number and relative proportion in the beginning of July (Table 1). The aboveground biomass was clipped to 1 cm stubble-height inside 0.25 m×2 m rectangular transects in the ungrazed control plot. The collected plant material was separated by species, and taken back to laboratory for dry matter determination at 60°C for 48h. Prior to the drying of samples, sub-samples of 5 g were taken and fractionated into stem (including petiole and leaf sheath) and leaf (only leaf blade) to provide additional information on the nutritive value of the different plant parts of four selected grazing intensities (no grazing (GI0), light (GI2), moderate (GI4) and very heavy (GI6) grazing). After fractionation, samples were also dried at 60°C for 48 hours.

For analyzing the forage nutritive value, samples were ground to pass a 1 mm sieve using a Cyclotec 1093 Sample Mill (Tecator, Sweden) and scanned twice by using the Near-Infrared-Spectroscopy (NIRS) technique for forage quality value determination. For chemical laboratory analysis calibration (n = 228) and validation (n = 113), a 5-year dataset (2004-2008) was used to develop NIRS prediction equations. Statistics of NIRS calibration for the chosen parameters were listed in Table 2. The forage quality parameters included crude protein (CP), neutral detergent fibre (NDF) and cellulase digestible organic matter (CDOM). CDOM value in % of OM was calculated by using crude ash (CA) and non-soluble enzymatic substance (EULOS) (Schonbach et al. 2009):

$$CDOM = \frac{100 \cdot (940 - CA - 0.62EULOS - 0.000221EULOS^2)}{1000 - CA} \quad (1)$$

Statistics

By applying analysis of variance (ANOVA) processed with mixed model, ‘grazing intensity’, ‘period’ and their interactions was used as fixed effects, ‘year’ as repeated effect, ‘block’, ‘year’ ‘period’ and their interactions as random effects and ‘grazing intensity × block’ was used as experimental error (SAS Version 9.1 (SAS Institute Inc., Cary, NC, USA). Multiple comparisons of means were done by applying Tukey’s test. The level of significance was $P < 0.05$.

Table 1 Species composition determined at the July sampling in 2008 and 2010 gDM/m²)

	2008		2010	
	Mean	s.d.	Mean	s.d.
<i>Leymus chinensis</i> Trin. Tzvel. ^b	41.97	11.10	40.03	9.15
<i>Stipa grandis</i> P. Smirn. ^b	48.84	7.31	73.47	11.87
<i>Carex korshinskyi</i> (Kom.) Malyshev.	10.14	2.60	6.75	1.80
<i>Agropyron michnoi</i> Roshev. ^b	7.62	1.74	9.71	1.36
<i>Cleistogenes squarrosa</i> Trin.Keng ^b	4.26	1.02	1.67	0.64
<i>Achnatherum sibiricum</i> (Linn.) Keng	1.86	0.71	1.42	0.46
<i>Salsola collina</i> Pall. ^b	0.90	0.44	1.21	0.75
Remaining species ^a	2.60	0.68	2.93	0.98

^a Includes all species with proportions of >0% and < 1% in biomass dry matter.

^b Species chosen for chemical analysis.

Table 2 Statistics of NIRS calibration for the chosen parameters

	N	Mean	S.D	SEC
CP	290	10.987	3.671	0.268
CDOM	290	61.840	6.140	1.290
NDF	295	68.958	5.493	1.410

N: number of samples; SEC: standard error of calibration

Results

The effect of grazing intensity

Grazing intensity generally decreased the NDF value and increased the CP and CDOM value on species individual level (Table 2 and Table 3). The effect of grazing on species nutritive value was weakened in drought year 2010. Except *S. collina* and *S. grandis*, the interactive effects of grazing intensity \times year on species nutritive value were all highly significant for other three species ($P < 0.01$). Annual C4 species *S. collina* had highest nutrient value than other four species in seven grazing intensities. From GI0 to GI6, the CP value of C4 species *C. squarrosa* was always lower than C3 species *L. chinensis* and *A. michnoi*, but tended to be higher than *S. grandis* in higher grazing intensity (from G3 to G6) in the year 2008. In the year 2010, C4 species *C. squarrosa* had higher CP value than all other three C3 species through all seven grazing intensities.

The annual average nutritive value of both leaf and stem fraction of all five species consistently responded to grazing in a similar way along with four selected intensities (no grazing (GI0), light (GI2), moderate (GI4) and very heavy (GI6) grazing) (Figure 3), e. g. CP and CDOM value of leaf and stem for all species increased with increasing grazing intensity. NDF of leaf and stem for C4 species *C. squarrosa* and *S. collina* decreased significantly with grazing intensity. For other three C3 species, their NDF value of leaf and stem had no response to grazing intensity (Figure 3). No matter which grazing intensity, the nutritive value of species' leaf was always higher than species' stem.

Table 3 Source of variation (ANOVA) on the effects of year, block, grazing intensity (GI), sampling period and their interactions on five species crude protein (CP), cellulase digestible organic matter (CDOM) and neutral detergent fibre (NDF) value

		Crude Protein (CP)						
		<i>L.ch</i>	<i>S.gr</i>	<i>A.mi</i>	<i>C.sq</i>	<i>S.co</i>		
Effect	DF	N	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	
Year	1	63	<.0001	<.0001	<.0001	<.0001	0.3011	
Block	1	63	0.6845	0.9046	0.9130	<.5701	0.5079	
GI	6	63	<.0001	<.0001	<.0001	<.0001	<.0001	
Period	3	63	<.0001	<.0001	<.0001	<.0001	<.0001	
Year*GI	6	63	<.0001	0.1019	0.0001	<.0001	0.8029	
Year*Period	3	63	<.0001	<.0001	<.0001	<.0001	0.6403	
GI*Period	18	63	0.1201	0.5994	0.1617	0.4679	0.1134	
GI*Period*Year	18	63	0.7419	0.7494	0.9128	0.1058	0.1228	
		Cellulase Digestible Organic Matter (CDOM)						
		<i>L.ch</i>	<i>S.gr</i>	<i>A.mi</i>	<i>C.sq</i>	<i>S.co</i>		
Effect	DF	N	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	
Year	1	63	<.0001	0.0117	<.0001	0.6994	0.0022	
Block	1	63	0.1735	0.8244	0.2802	<.1121	0.2068	
GI	6	63	0.0003	0.0011	0.0945	<.0001	<.0001	
Period	3	63	<.0001	<.0001	<.0001	<.0001	<.0001	
Year*GI	6	63	<.0001	0.2101	0.0006	<.0001	0.0198	
Year*Period	3	63	<.0001	<.0001	<.0001	<.0001	0.0018	
GI*Period	18	63	0.0053	0.5522	0.6319	0.4512	0.0031	
GI*Period*Year	18	63	0.3328	0.3280	0.2878	0.3903	0.1712	
		Neutral Detergent Fibre (NDF)						
		<i>L.ch</i>	<i>S.gr</i>	<i>A.mi</i>	<i>C.sq</i>	<i>S.co</i>		
Effect	DF	N	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	
Year	1	63	<.0001	0.0004	<.0001	<.0001	<.0001	
Block	1	63	0.0348	0.5920	0.1314	0.0613	0.1386	
GI	6	63	0.0007	0.1464	0.2958	<.0001	0.8316	
Period	3	63	<.0001	<.0001	<.0001	<.0001	<.0001	
Year*GI	6	63	<.0001	0.9157	0.0286	<.0001	0.2752	
Year*Period	3	63	<.0001	<.0001	<.0001	0.0107	<.0001	
GI*Period	18	63	0.0001	0.1900	0.8054	0.1545	0.4600	
GI*Period*Year	18	63	0.0504	0.1357	0.3942	0.2345	0.2701	

Abbreviation: *L.ch*: *Leymus chinensis*; *S.gr*: *Stipa grandis*; *A.mi*: *Agropyron michnoi*; *C.sq*:

Carex korshinskyi; *S.co*: *Salsola collina*

Table 4 Effect of grazing intensity on five individual species crude protein (CP), cellulase digestible organic matter (CDOM) and neutral detergent fibre (NDF) value in year 2008 and 2010

Unit: (% DM)	Grazing intensity →						S.E.	
	G0	G1	G2	G3	G4	G5		G6
<i>L.ch</i> CP 2008	11.93e	13.8de	13.07e	15.16cd	16.22bc	17.14b	19.14aA	0.33
<i>L.ch</i> CP 2010	10.63a	11.82a	11.23a	11.59a	11.57a	11.79a	12.24aB	0.36
<i>L.ch</i> CDOM 2008	62.33b	63.87ab	61.98b	64.97ab	65.17ab	65.80a	66.91aA	0.42
<i>L.ch</i> CDOM 2010	62.15a	63.48a	62.38a	62.06a	61.65a	61.77a	62.88aB	0.71
<i>L.ch</i> NDF 2008	68.23a	67.02ab	67.02ab	66.14ab	66.38ab	66.48ab	64.73bA	0.35
<i>L.ch</i> NDF 2010	69.45a	68.27a	69.41a	69.96a	70.07a	70.14a	68.95aB	0.31
<i>S.gr</i> CP 2008	11.36e	12.86d	13.45cd	14.09bcd	14.5abc	15.21ab	15.53aA	0.21
<i>S.gr</i> CP 2010	9.86b	10.88ab	11.29ab	11.73ab	11.35ab	11.42ab	12.29aB	0.28
<i>S.gr</i> CDOM 2008	60.87a	62.44a	62.61a	62.27a	62.06a	62.32a	62.39aA	0.38
<i>S.gr</i> CDOM 2010	57.78a	58.37a	60.47a	60.52a	60.59a	60.49a	60.56aA	0.52
<i>S.gr</i> NDF 2008	71.36a	71.25a	69.99a	70.27a	70.36a	70.80a	71.00aA	0.20
<i>S.gr</i> NDF 2010	71.54a	71.08a	70.91a	70.91a	71.17a	71.24a	70.88aA	0.19
<i>A.mi</i> CP 2008	11.51d	13.77cd	13.44cd	15.89bc	17.12b	18.33ab	20.09aA	0.44
<i>A.mi</i> CP 2010	9.74a	10.20a	10.90a	11.16a	10.97a	10.77a	11.98aB	0.35
<i>A.mi</i> CDOM 2008	65.90bc	67.47abc	65.81c	68.32abc	69.21abc	69.93ab	71.37aA	0.49
<i>A.mi</i> CDOM 2010	66.56a	66.30a	65.68a	64.75a	64.60a	63.58a	65.76aB	0.58
<i>A.mi</i> NDF 2008	66.79a	66.56a	66.29a	66.41a	65.14a	65.16a	64.64aA	0.30
<i>A.mi</i> NDF 2010	68.11a	68.17a	68.48a	69.37a	69.33a	69.53a	68.45aB	0.22
<i>C.sq</i> CP 2008	10.88e	12.65de	13.28cde	14.57bcd	15.54abc	16.73ab	17.59aA	0.38
<i>C.sq</i> CP 2010	10.82c	12.03bc	12.33abc	13.18ab	13.74ab	14.03a	14.01aA	0.24
<i>C.sq</i> CDOM 2008	67.29a	68.49a	68.83a	69.01a	70.69a	70.88a	71.35aA	0.64
<i>C.sq</i> CDOM 2010	61.54c	62.64bc	63.49bc	66.51ab	68.42a	70.54a	70.53aA	0.52
<i>C.sq</i> NDF 2008	73.23a	72.39ab	70.92bc	69.83c	68.36d	67.06de	66.33eA	0.33
<i>C.sq</i> NDF 2010	72.05a	71.19ab	70.74ab	70.57abc	69.60bc	69.75bc	68.88cA	0.23
<i>S.co</i> CP 2008	14.38c	14.55bc	16.55abc	16.12abc	18.11ab	17.5abc	18.53aA	0.48
<i>S.co</i> CP 2010	13.57b	17.33ab	17.06a	20.30a	19.18a	19.43a	19.69aA	0.56
<i>S.co</i> CDOM 2008	74.36b	72.84b	75.74b	83.59a	80.20a	80.36a	75.68aA	1.03
<i>S.co</i> CDOM 2010	73.34a	76.65a	74.65a	73.23a	75.69a	74.72a	83.00aA	1.39
<i>S.co</i> NDF 2008	38.55a	38.53a	37.31a	41.13a	40.28a	39.33a	37.70aA	1.19
<i>S.co</i> NDF 2010	42.71a	47.06a	44.09a	38.68a	42.50a	40.62a	37.87aA	0.94

a, b, c, d within rows, means followed by different small letters are significant different

($P < 0.05$). Herbage quality parameters are annual means expressed as weighted averages

Inter-annual variation of nutritional quality of dominant species

The nutritive value of each of the five species differed significantly between the wet (2008) and the dry (2010) year (Table 2 and Table 3). CP and CDOM were higher in the wet year than that in the dry year, while the opposite was true for NDF (Table 2 and 3).

The differences between means of nutritive value of these two years were much greater

under higher grazing intensity conditions (GI4 to GI6; Table 3). Compared with C3 species, the CDOM value of perennial C4 species *C. squarrosa* was not significantly influenced by year. For C4 species *C. squarrosa* and *S. collina*, the inter-annual variation of their nutritive value in each of grazing intensity were lower than other C3 species. The annual average nutritive value of all species was always higher in leaf than in stem. The nutritive value of leaf and stem for all species was higher in the wet year than in the dry year (Figure 2).

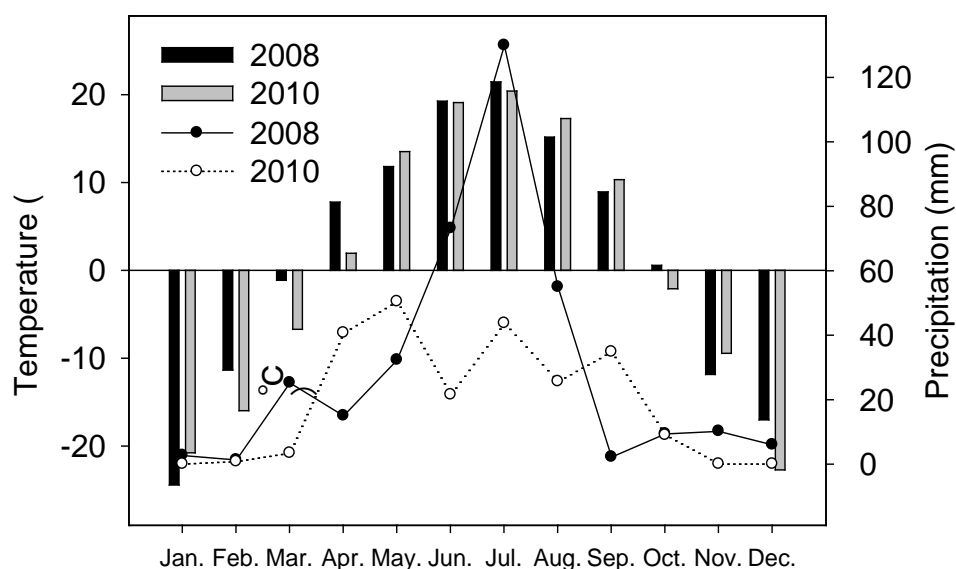


Figure 1 Monthly mean temperature and monthly precipitation in Inner Mongolia steppe in 2008 and 2010. Grey and black bars represent mean temperatures in 2008 and 2010, and lines with white circles and black circles represent precipitation in 2008 and 2010

The effect of growing period

During growing seasons of 2008 and 2010, CP and CDOM of annual C4 species *S. collina* decreased while NDF increased from June to September (Figure 4). C3 species had

higher nutritive value in the beginning of growing period (June), and C4 species reached higher nutritive value in later growing period (July and August). As a whole, C4 species had higher nutritive value than C3 species. The trade-off between C3 and C4 species in nutritive value was more obvious in wet year than the dry year. Among the five species, annual C4 species *S. collina* had the highest nutritive value from June to August, and C3 species *S. grandis* had the lowest nutritive value.

Discussion

The effects of grazing intensity on species nutritive value

Our study showed that species nutritive value was enhanced by intensive grazing characterized by increased CP and CDOM concentration and decreased NDF concentration along the grazing intensity gradient (Table 3). This result is consistent with those from previous observations in the same region on community level (Fanselow et al. 2011; Schonbach et al. 2009). For the five coexisting species, no matter the differentiation in their regrowth capacities or competition strategies (Zheng et al. 2010), or the roles they played in grassland community, their nutritive value showed similar positive response to grazing. However, compared with other C3 species, the highest relative growth rate of C4 grass *C. squarrosa* during its regrowth period favored its ability to compensate grazing (Fanselow et al. 2011; Wang and Wang 2001). The increasing nutritive value and high relative growth rate of *C. squarrosa* with grazing intensity could maintain the vegetation quality of grassland in the short term. Due to long-term grazing, the maturation and lignifications processes of species retarded and the CP concentration increased because of the regrowth of new tissue (Garcia et al. 2003; Milchunas et al. 1995). Grazing could affect plant

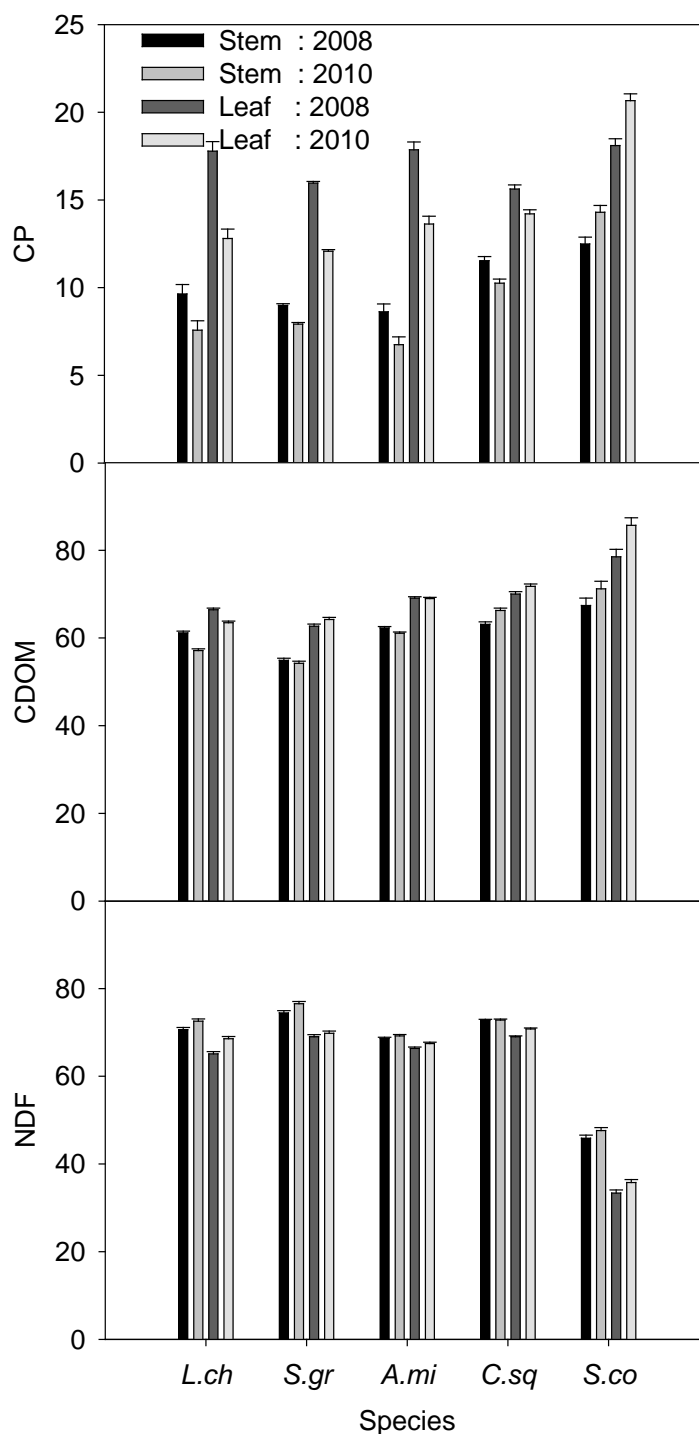


Figure 2 Species nutritive value parameters of stem and leaf (% DM) in 2008 and 2010: (a) crude protein (CP), (b) cellulase digestible organic matter (CDOM), (c) neutral detergent fibre (NDF)

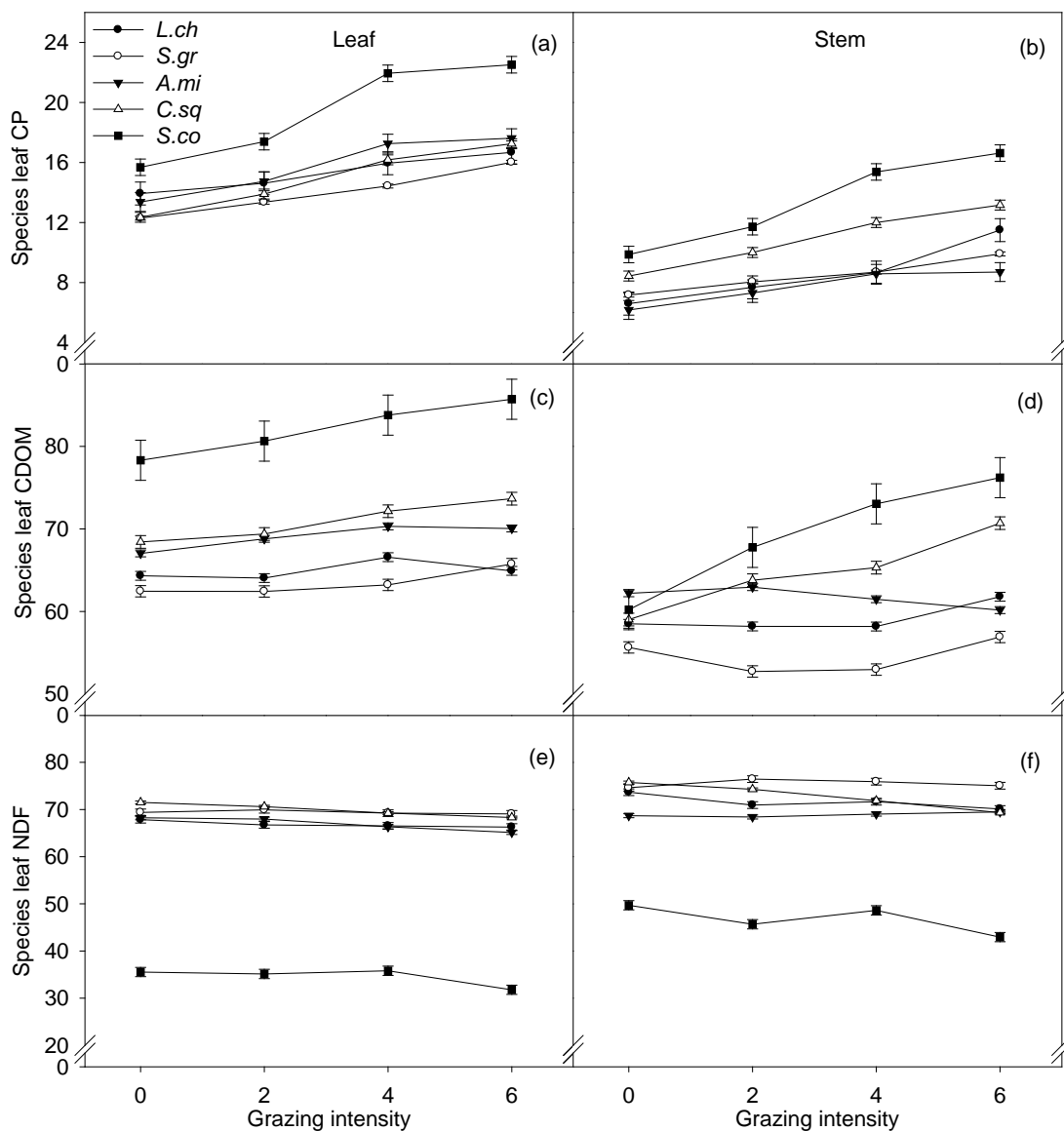


Figure 3 Effect of grazing intensity on species nutritive value parameters of leaf and stem (% DM): (a) (b) crude protein (CP), (c) (d) cellulase digestible organic matter (CDOM), (e) (f) neutral detergent fibre (NDF)

nutritive value during growing season by using young and protein-rich re-growth to replace the older senescent parts of plants, as being frequently suggested (Albon and Langvatn 1992; Hebblewhite et al. 2008; Mysterud et al. 2011; Schonbach et al. 2009). There was, however, clear evidence that the grazing effects on nutritive value of species were most evident in CP and digestibility (CDOM), and to a somewhat lesser degree on fiber fractions (NDF) (Milchunas et al. 2005; Schiborra et al. 2010). In our study, grazing could lead to maximum 75% increasing of species' CP value and 15% increasing of species' CDOM value, but less than 9% decreasing of species' NDF. That may attribute to the better nitrogen availability in intensive grazing treatments in terms of faster nutrient cycling of feces and urine and the higher proportion of roots in the topsoil based on the adapted root system to higher grazing intensities (Shan et al. 2011).

Although for young stems, the CDOM (which is negatively correlated with NDF) value of grasses is comparable to leaves until the stage of ear emergence in term of high amount of water soil content under the temperate climate (Schiborra et al. 2010). It is generally accepted that leaves have higher nutritive value than stems. Thus, it is quite understandable to argue that the changes of biomass allocation under grazing conditions can mix the variation of forage nutritive value in response to grazing. However, our results confirm that the effects of grazing intensity on nutritive value of all five species in terms of stems and leaves were similar. Although the mobilization of CP from stems to leaves may affect plant regrowth (Schonbach et al. 2011; Volenec et al. 1996), the responses of plant species to grazing intensity in terms of nutritive value of stems and leaves were not changed. Therefore, the confirmed positive response of forage nutritive value in community level (Ren. et al. 2012) resulted from the increased nutritive value of the whole plant species with heavy grazing, according to their equal positive

responses of stems and leaves to grazing, but not because of the shift in species composition.

Although the similar responses of plant's nutritive value to grazing are observed, the variations of nutrient quality between plant species are obvious (e.g. the CP value of plant leaves in our study varied from 10.88 (*S. grandis*) to 14.38 % DM (*S. collina*) in ungrazed plot). As is known, the changes of plant growth in species level result in their variations in community level and the widely acceptable conclusion is that grazing led to changes of community composition. Our study indicates that the effect of grazing on the forage quality of community not just rely on the changes of species composition, the response of each species' nutrient quality to grazing is also a key factor. For example, the range of CP concentration between species could vary from 37% DM to 75% DM in response to heavy grazing (Table 4).

The effects of precipitation on species nutritive value

Besides biotic factors, abiotic factors had strong effect on forage nutritive value. Precipitation is the most important driver in influencing forage nutritive concentration in semi-arid grassland. All five species had higher CP and CDOM concentration in the wet year than in the dry year, as the plant nitrogen availability in grassland community generally was positively correlated with water availability (Jamieson et al. 1999; Kleinebecker et al. 2011). The effect of precipitation on nutritive value in different species was significant (except *S. collina*), especially at higher grazing intensity (G4 to G6) (Table 3). Compared with light grazing, the analyzed species showed higher variation of nutritive value in moister condition after heavily grazed, suggesting that precipitation could accelerate the regrowth of young tissue and the nitrogen use

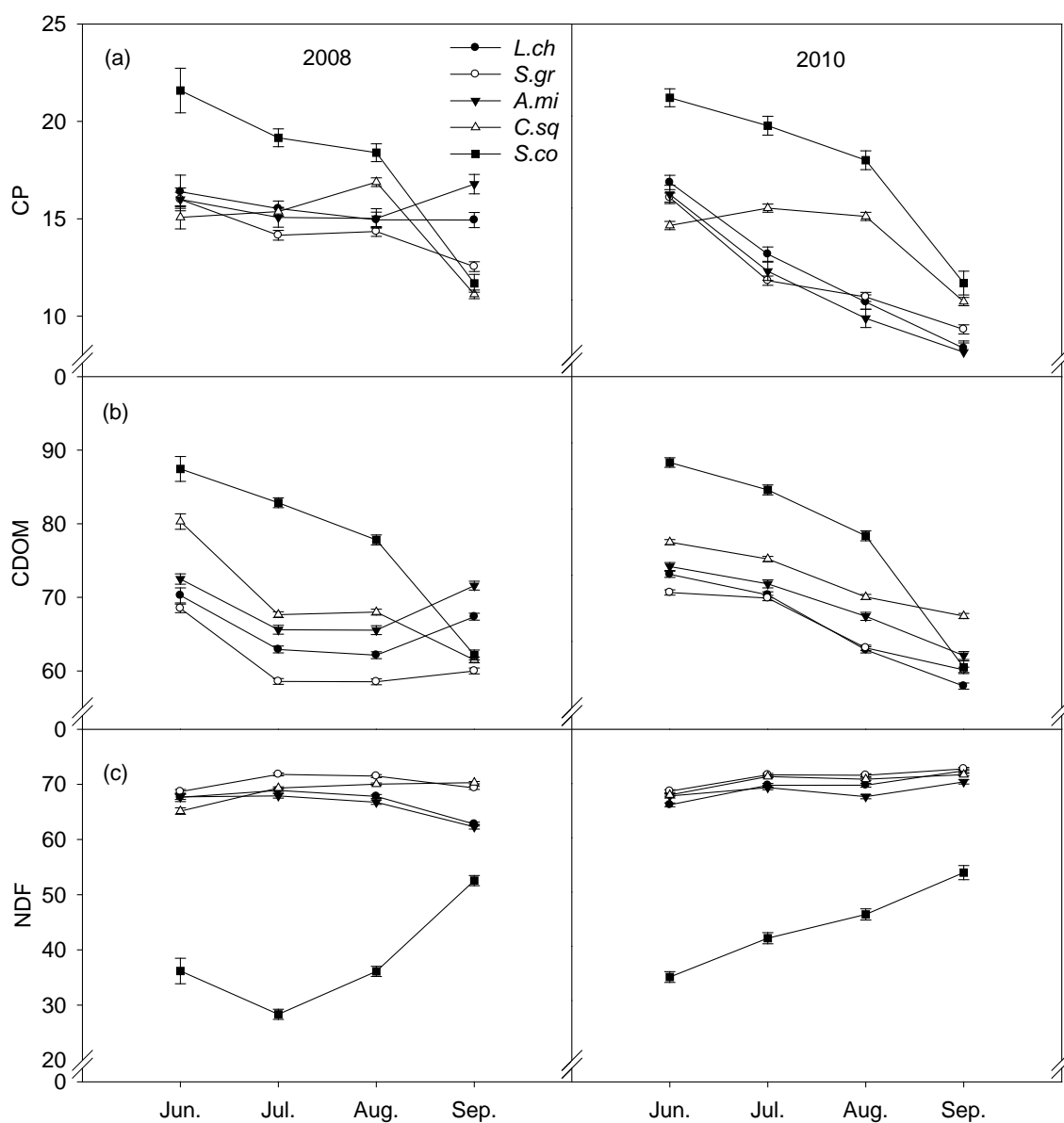


Figure 4 Effect of growing period on species nutritive value parameters (% DM): (a) crude protein (CP), (b) cellulase digestible organic matter (CDOM), (c) neutral detergent fibre (NDF). Figures on the left side represent data for the year 2008 and on the right side data for the year 2010

efficiency of additional nitrogen availability from feces and urine in intensively grazed plots (e.g. fecal CP concentration was from 76 to 282 g/kg OM as reported by Wang et al.(2009)), and thus buffer the effect of grazing on grassland. However, C4 species were not as sensitive as C3 species in response to drought under heavy grazing plots. It indicates that C4 species may be able to keep relative even nutritive quality of forage for livestock in short term. In further detail, when separated species into leaves and stems, the variation of their nutritive value in moist and dry condition suggested that species could benefit from higher precipitation availability in their whole aboveground composing (Figure 3).The only exception is annual forb *S. collina*. Because of its drought enduring trait, *S. collina* showed inverse response to high precipitation. However, the observed modification of the effect of grazing induced by precipitation variability does not necessarily mean that high grazing intensity could keep higher forage nutritive value in semi-arid grassland ecosystem in the long term. It has been shown that long-term overgrazing could lead to a sharp decrease in aboveground biomass and changes of community composition (from high to low nutritive value forage), both of which could overwhelm the increase of community forage nutritive value with grazing (Schonbach et al. 2012; Schonbach et al. 2011; Zheng et al. 2011). In future, drastic drought events could occurs more often (Zheng et al. 2011). Although species *S. collina* has high drought tolerance, it contributed very less to community nutritive quality because of its quite low biomass proportion. Therefore, the interactions between grazing, climate and the nutritive dynamics of forage should be considered to ensure high productivity and nutritive quality of herbage offer for livestock.

The effects of growing period on species nutritive value

Growing stage was another main factor affecting species nutritive value, with

decreasing concentrations of CP and CDOM and increasing NDF over the growing season. The strong decline of plants nutritive value from the beginning toward late of growing season was reported in other studies, and the major driver is the nutrient availability and its redistribution (Andrighetto et al. 1993; Fierro and Bryant 1990; Pinchak et al. 1990). Decreasing nutritive value of plant species during the growing season could be attributed to nutrient re-translocation to roots and litters (Bobbink et al. 1989; Hejcman et al. 2010; Kleinebecker et al. 2011). The different nutrient distributions of different species in growing season may change the pattern of species composition in typical steppe. Younger, newly emergent plants synthesize higher protein and fats contents in early growth stages for later use at flowering and fruiting. Consequently, young tissue generally has higher quality than older senescent plant parts (Hussain and Durrani 2009; Mysterud et al. 2011).

The C4 species *C. squarrosa*, showed increasing CP concentration from June to August, even with higher value than C3 species. As a drought resistant species and a perennial bunchgrass, *C. squarrosa* is more resistant to grazing than C3 species (Fair et al. 1999; Redmann et al. 1995; Wang et al. 2008). Together with *L. chinensis* and *S. grandis*, these three species are co-dominant in the Inner Mongolia steppe (Li 1989; Liang et al. 2002). Strong nutritive variations among species may make the relationship between species composition and ecosystem functioning very variable, as adding certain species may enhance or reduce the ecosystem functioning or may leave it unchanged (Peterson et al. 1998; Snyder et al. 2005). The mechanism that C4 species *C. squarrosa* showed increased trend in CP and CDOM concentration over growing season rather than the decreased trend showed by C3 species could be owing to its younger phenological status induced by later growth initiation than C3 grasses (Fanselow et al. 2011; Liang et al. 2002). The increase of *C. squarrosa* in nutritive value over growing

season was much more significant in the dry year because of its high drought resistance. The competitive strategy for resources between C3 and C4 species and their reverse trends of nutritive value over time may provide further evidence for shifting of species composition in grassland community. As suggested by Zheng et al. (2010), the original dominant C3 species, *L. chinensis* and *S. grandis*, would be replaced by C4 species *C. squarrosa* with the degenerating of grassland. However, the species may complement each other and better occupy temporal and spatial niches to maintain ecological resilience (Bengtsson et al. 2002; Loreau et al. 2003). Besides, the result that annual grass *S. collina* showed greater decrease in nutritive value than the other four perennial grasses is consistent with previous studies (Hussain and Durrani 2009). This might result from its short life cycle and ending up with high fiber fractions, e.g. NDF. Based on our results, abundance of C4 species *C. squarrosa* to a certain extent could ensure CP nutrient availability for livestock in the later growing season. It was found that for growing sheep's (40 kg live weight) maintenance and performance during the grazing season, optimal herbage offer for their growth occurred at around 13.4 g CP/100 g DM (Wang et al. 2011). So when C3 species' CP value tends to decrease to this threshold value from July to September, the C4 species could consecutively meet the nutrient requirement for livestock (e.g. the CP value of species in 2010 year was 15.0 g/100g DM in July and 14.5 g/10g DM in August). As the increasing nutritive quality of C4 species with grazing intensity and growing season, and as the decline of individual animal performance over season have been observed (Glindemann et al. 2009; Schonbach et al. 2009), allowing the growth of high quality forage for feeding in different growing period like C4 grasses, may moderate the herbage availability and the nutrient balance of vegetation and therefore the productivity of grazing livestock. Our findings have implications for understanding species nutritive dynamic and their

coexistence over growing season, and will be helpful for grassland management. Combined our results with the mass ratio hypothesis that dominant species play more important roles in influencing ecosystem functioning and stability than species diversity (Grime 1998; Ren et al. 2012), we conclude that dominant species are not only driving botanical composition but also benefitting available nutrient for ruminants. Although high proportion of *C. squarrosa* in the sward is considered to be an indicator for grassland degradation (Liang et al. 2002), but as the most dominant C4 species in semi-arid steppe (Ren et al. 2012), it could bring into positive effect on economic outputs and ecosystem functioning when it accounts for the proper percentage in the community vegetation.

Conclusion

In this study, we found that the quality of plant species consistently varied with grazing intensity, precipitation, and growing period. The potentially increased occurrence of drought events together with heavy grazing may lead to poor forage nutritive value in the long-term. In the typical steppe, the inverse trends of nutritive value between C3 and C4 species over growing season may play an important role in keeping the nutrient balance of vegetation. Rather than as an adverse species for degradation, C4 species could also benefit nutrient for livestock in later growing season. Disturbances are inevitable in grassland ecosystems, and its capacity to reorganize and adapt to changes may rely on the traits of diverse species, so it can keep its ecological resilience in the long run. Our results indicated that comprehensive understanding of the effects of grazing on forage nutritive dynamic in conjunction to the abiotic environment and temporal variation is needed.

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Chapter 5

General discussion

5 General Discussion

Interactions between climatic conditions and grazing effects still are an intensively debated issue in rangeland ecology and thus of crucial importance for management of >30% of the terrestrial surface. Over utilization of natural resources by human activities has resulted in a lot serious environmental problems on the grasslands of Inner Mongolian steppe ecosystem, China, such as forage and livestock productivity decline, frequent dust storms and the loss of biodiversity. It is widely agreed that high grazing intensities are one of the major factors (Hodgson and Illius 1996; Verburg and Van Keulen, 1999), since it removes biomass and tramples plant species, as well as alters the soil physical and chemical properties (Bullock 1996). In addition, as the primary limiting resource in semi-arid grassland ecosystems (Huxman *et al.*, 2004; Bai *et al.*, 2008), precipitation plays a key role in semi-arid ecosystem functioning (Knapp *et al.*, 2002). In fact, in the semi-arid regions, both the precipitation pattern and grazing affect ecosystem functions (Anderson *et al.*, 2007; Austin *et al.*, 2004; Heisler-White *et al.*, 2008; Schonbach *et al.*, 2010). However, the widely debated theories of equilibrium and non-equilibrium rangeland ecology emphasize on the different main drivers in grassland: grazing pressure or environmental fluctuations. They aimed to address how and to what extent grazing and climate factors contribute to the degradation of Inner Mongolia steppe grasslands. The non-equilibrium theory states that under highly variable conditions forage often becomes limited, triggering breakdowns in herbivore populations and therefore relatively low animal numbers that have limited impact on the vegetation. This theory also commonly described as the coefficient of variation (CV) for the interannual variability of precipitation. Non-equilibrium conditions are thought to become increasingly important above >30% CV. The CV in our study site suggested a long-year variability of 22% and

grazing pressure was kept constant by monthly adjusting the number of sheep according to the forage on offer in the respective grazing intensity treatment. We used constant grazing intensity by varying the number of animals rather than using constant livestock numbers as in other studies (the put and take method to balance stocking density to feed on offer is a well established method). We thus realized that the non-equilibrium theory doesn't fit well to the present study. As a matter of fact, steppe ecosystems are highly variable and complex systems and, therefore, equilibrium and non-equilibrium systems can hardly be distinguished only on the basis of unique processes or functions, but rather by the evaluation of system dynamics at various temporal and spatial scales (Briske *et al.*, 2003). The number of studies on grazing and precipitation effects is huge, but fewer studies simultaneously consider climatic variability and different intensities of grazing within a given locality. In present study, a long-term and large scale grazing experiment was conducted in 2005 to provide reliable information about the effect of grazing on grassland sward. The design included experimental manipulation of grazing intensity at 7 levels; measurements were conducted over a relatively long period of 6 years. This allowed us to assess the relative importance of both intra- and interannual variability of temperature and precipitation versus the impact of grazing intensity.

Summary of the studies

Effects of grazing intensity, precipitation and temperature on species composition and diversity (Chapter 2)

The first study focused on the effect of grazing, precipitation and temperature on plant species dynamics. Our results showed that in the long term (6 years), the effects of

early-season precipitation and temperature on the trade-off among species were more important than the effect of grazing. Grazing only decreased the aboveground biomass of those species that are more preferentially grazed by sheep, such as *L. chinensis*. However, temporal distribution of precipitation and temperature, in particular during the early-season (from March to June), determined the variation in vegetation dynamics much more strongly than annual rates of precipitation or annual mean temperature. Thus, the effect of grazing in a grassland system cannot be analyzed without considering the characteristic traits of species and also the precipitation and temperature variation, especially in the long-term. Our findings demonstrate that the temporal fluctuation of precipitation and temperature, especially in early season, seems to provide more robust and comprehensive predictions on vegetation dynamics in semi-arid typical steppe, and helps to understand species coexistence and grassland management in response future extreme precipitation and drought events.

Forage nutritional characteristics and yield dynamics in a grazed typical steppe ecosystem of Inner Mongolia, China (Chapter 3)

The second study analyzed the effects of grazing intensity, environmental factors, species composition and species diversity on the aboveground net primary production (ANPP), forage nutritional value (FNV) and forage nutritional yields (FNY). The results confirmed that grazing intensity was one of the main drivers that determined ANPP and forage nutritional value and yields. Since forage nutritional yields were predominantly determined by ANPP, the grazing-induced increase in forage nutritional value could not offset the decrease in forage ANPP, and thereby could not affect the variances of

forage nutritional yields with grazing. In terms of management options (e.g. grazing intensity), it is recommended that farmers should focus primarily on forage productivity to manage their grassland. Precipitation was another important driver. However, the seasonal distributions of precipitation and temperature contributed more in terms of affecting forage nutritional value than the annualized sum, especially for forage digestibility (CDOM) and metabolizable energy (ME). Dominant species, rather than species diversity as indicated by the number of species present in the vegetation community, affected forage ANPP, FNV and even FNY. Thus, the modulating of species composition on the grazing system may bring more benefits than diversity in terms of ensuring effective vegetation recovery and sustainable grassland management in the Inner Mongolian steppe.

Effects of Grazing Intensity on nutritive value of Five Dominant Species in Typical Steppe of Inner Mongolia, China (Chapter 4)

The third study focused on nutritive quality responses of five dominant species to grazing intensity, growing period and precipitation. We found that the quality of all five plant species varied with grazing, precipitation and season. The potentially increased occurrence of drought events together with heavy grazing may lead to poor forage nutritive value in the long-term. In the typical steppe, the shift between C3 and C4 species in terms of nutritive quality over time may help to manage herbivore performance and productivity. The inverse trends of nutritive value between C3 and C4 species over growing season may play an important role in keep the nutrient balance of vegetation. Rather than as an adverse species for degradation, C4 species could also benefit nutrient

for livestock in later growing season. Our results indicated that comprehensive understanding of the effects of grazing on forage nutritive dynamic in conjunction to the abiotic environment and temporal variation is needed.

5.1 Grazing effect

Grazing by livestock is identified to be the most important disturbance factors in the native grasslands (Wang and Ripley 1997; Verburg and Van Keulen 1999) and the major reason for steppe degradation process in Inner Mongolia (Sneath 1998; Tong *et al.*, 2004). It plays an important role in determining grassland productivity, forage quality, species composition and plant species diversity (Lane *et al.*, 1998; Sala *et al.*, 1988; Wondzell *et al.*, 1996; Schonbach *et al.*, 2012). Previous studies have indicated that long-term grazing can affect species diversity of plant communities in grasslands either positively or negatively (Bullock *et al.*, 2001; Cingolani *et al.*, 2005; Grace *et al.*, 2007) but grazing at moderate intensity could promote increased species diversity (Connell, 1978; Huston, 1979; Sasaki *et al.*, 2009). Beside, environmental moisture, the evolutionary history of grazing, and community productivity should be considered when determining the relationships between grazing intensity and species diversity (Bullock *et al.*, 2001; Cingolani *et al.*, 2005; Milchunas *et al.*, 1988).

The Milchunas-Lauenroth-Sala (MSL) model explicitly addresses differences among grassland with short vs. evolutionarily long history of grazing, and of grassland with low and high productivity. This semi-arid grassland was considered unproductive owing to the relatively low annual precipitation (340mm) and low aboveground net primary production (under 200 DM g/m²) (Schonbach *et al.*, 2012 and Cingolani *et al.*,

2005). The relationship between grazing intensity and species diversity in the semiarid sites was categorized into low productivity and long history of grazing equilibrium curves model.

Herbivores on grassland are highly selective, i.e. they would preferentially feed on highly digestible and palatable species while avoiding unpalatable, highly lignified plants. Grazing disturbance accelerates regrowth of new tissues and thereby reduces the mean age of plant tissue in the sward. Therefore younger plant material remains, and this contains amounts of nitrogen but it has less fibre in the regrowth after grazing. The differential responses of *S. grandis* and *L. chinensis* to grazing indicate that slow-growing *S. grandis* is more avoidant and fast growing *L. chinensis* are more tolerant. In grazed conditions, sheep selectively intake the tolerant species (*L. chinensis*) and avoid the avoidant species (*S. grandis*), therefore grazing negative affects *L. chinensis* but has little influence on *S. grandis*. This conclusions is supported by (Wang 2002, 2004), they reported that sheep preferentially intake *L. chinensis* in compared with *S. grandis*.

The forage nutritive quality value, i.e. crude protein (CP) and cellulase digestible organic matter (CDOM) are significantly influenced by plant maturity (Buxton 1996). In the process of growing period, increased grazing intensity led to high proportion of regrown plants, i.e. younger plant species with retardation in maturation and lignifications processes phonologically (Buxton 1996; Garcia *et al*, 2003; Milchunas *et al*, 1995). Therefore, forage nutritive quality increased with grazing. However, the increased forage nutritive value could not compensate for the decreased forage productivity. The grassland will be destroyed finally because of the long-term heavy grazing.

5.2 Precipitation and temperature effect

In all chapters, the unifying conclusion was suggested: climatic dynamic, especially in seasonal distribution of precipitation, had a fundamental influence on the grassland sward either in community level or in the species level. The relationship between precipitation and plant productivity as well as ecosystem functioning in Inner Mongolia grasslands has been discussed by several authors (Bai *et al.*, 2004; Ni 2004). Inter-annual variations in precipitation and temperature are reported to be closely correlated to aboveground net primary production and vegetation dynamics (e.g. botanical composition, species diversity) (Bai *et al.*, 2007; Wittmer *et al.*, 2010; Schonbach *et al.*, 2011; Auerswald *et al.*, 2012). However, our results highlight the importance of temporal distribution patterns of precipitation and temperature on vegetation dynamics. Most of the variation in species composition, forage nutritive quality value, i.e. crude protein and cellulase digestible organic matter and diversity was determined by precipitation rates and temperatures in the early season (March to June), whereas only a small proportion of the variance in the investigated vegetation parameters could be explained by precipitation rates and mean temperature on an annualized scale. These findings are in agreement with the findings of Lauenroth and Sala (1992) and Knapp and Smith (2001) who reported that the temporal distribution, rather than the annual sum of precipitation, determines aboveground net primary productivity of semi-arid grasslands (Lauenroth and Sala, 1992; Knapp and Smith, 2001). In terms of forage nutritive quality, seasonal precipitation and mean temperature together could explain most of the variances of CDOM and ME value among years. For CP and NDF, they were much more strongly correlated with seasonal precipitation than annual precipitation rates. These results provided clear evidence to show the dominant

effects of precipitation and temperature on the community forage nutritional quality dynamic.

In a word, both biotic (grazing) and abiotic (precipitation and temperature) factors influence the grassland ecosystem functions. As reported, substantial loss in productivity or species diversity and changes in species composition are intensified when drought events coincide with long-term overgrazing (Christensen *et al.*, 2003). Furthermore, the increased severity of drought together with overgrazing may accelerate a shift of forage from high to poor quality and from high to low yields, and consequently slow down the ecosystem (Zheng *et al.*, 2011). Our findings provide meaningful guidance for improving the management of arid and semiarid grassland ecosystems and their conservation in response to the effects of abiotic and biotic disturbance.

5.3 The role of species diversity and species composition in natural grasslands

Each individual species plays a different role in influencing community productivity (Hooper *et al.*, 2005) and the positive linear, negative linear or non-significant correlation between species diversity and productivity has long been a disputed topic (Tilman *et al.*, 1996, Bakker *et al.*, 2002, Tilman *et al.*, 2006). Both species diversity and species composition play important role in maintaining community stability and determining ecosystem functioning (Loreau *et al.*, 2001, Hooper *et al.*, 2005; Chapin, 1980, Hobbie, 1992, Hooper and Vitousek, 1997). Controversial arguments about the relationship between species diversity and community productivity or ecosystem stability are presented. The mass ratio hypothesis holds that ecosystem

functioning and stability is largely controlled by dominant species rather than diversity in the long-term (Grime, 1998). Since dominant species could also control the effect of diversity on community stability, our finding that the variances of the most productive species *S. grandis* influenced species dynamic more than species diversity is considered to be evidence for this hypothesis. The dominant species *S. grandis* may prove to be highly competitive to maintain its population in the community because it occupies resource space for long periods, and therefore captures the chance of other species for contributing to early season production. Under persistent limited resource availability, the semi-arid grassland may be evenly distributed by dominant species in the long term, as species richness and evenness decreased over time. Furthermore, aboveground net primary production and its nutritional value were predominantly determined by the dominant species *L. chinensis* and *S. grandis* rather than by the species diversity. Species composition brings into play all the different functional traits (e.g. leaf area, stem-leaf ratio, meristems, stored nutrients, phenology) from dominant species to opportunistic species (Zheng *et al.*, 2011). This may explain the contribution of species composition on community ANPP exceeding those of plant species number (Richness) present. Huston (1997) reported that the most productive species determine the specific trophic level because they are well adapted to the environment. Thus, the perennial rhizomatous grass *L. chinensis* and the perennial bunchgrass *S. grandis*, the two most dominant species in our study region, affected the ANPP, FNV and FNY more than diversity and other plant species in the community. In future studies, species composition, especially in terms of dominant species rather than species diversity, could be used as an effective parameter to predict the fluctuation of forage nutritional quality and yields in response to different grazing intensities and over successive years, to

predict vegetation dynamic and grassland stability as well.

5.4 The role of plant productivity and its nutrient quality

Plant productivity is one of the major parameters to evaluate the quality of grassland. It is affected by precipitation, grazing, season, soil, nutrient availability and so on. There is evidence from Noy-Meir (1993) suggesting that the effect of grazing on plant growth could be zero, negative or positive, depending on several factors including plant species' functional traits, soil properties, and grazing intensity. The negative ANPP-grazing intensity relationship in our study accords with one of these situations. In our six year grazing experiment, ANPP decreased with increasing intensity of grazing. This indicates that plant regrowth cannot compensate for the biomass reduction that occurs as a result of defoliation and sward damage induced by grazing and trampling (Schonbach *et al.*, 2009, Schonbach *et al.*, 2011, Schonbach *et al.*, 2012). As forage is the single feed source of grassland to support livestock production, the nutritive value of forage therefore impact both herbivore behavior, e.g. migration (Albon and Langvatn 1992; Hebblewhite *et al.* 2008) and performance, e.g. the variation in their body weights (Mysterud *et al.* 2011; Mysterud *et al.* 2001). It is a function of nutrient concentration, amount of forage intake, nutrient digestibility and metabolized energy of livestock feeding (Buxton, 1996; Corona *et al.*, 1998; Bertrand *et al.*, 2008). Studies have indicated that the quality of forage varies with the soil, season, rainfall, grazing intensity, chemical nature, and age of the plants that affects palatability and health of grazing animals (Fierro and Bryant, 1990).

In our study, the increment in the forage nutritive value with increased grazing intensity cannot compensate for decreased ANPP, which led to the obvious reduction in

forage nutritive yield. Buxton and Casler (1993) and Buxton (1996) also concluded that the effects of grazing on forage nutritional quality usually are smaller in magnitude than the effect that grazing has on forage yields. This provides important information for future farm management: forage on offer for livestock should be based on plant productivity dynamic rather than its nutritive quality, since plant productivity could determine the most community nutritive yield. Because of the reduction in dry matter yield with increased grazing intensity, long-term intensive grazing will reduce the sustainable development of the agricultural industry in the Inner Mongolian typical steppe. Meanwhile, as the climatic conditions of grazing systems in typical semi-arid steppe for plant growth was limited (Zheng *et al.* 2011), our findings would be important to understand the dynamic of nutritive value of forage in response to biotic (grazing intensity) and abiotic (precipitation and plant growing period) factors for improving livestock productivity.

5.5 The role of C3 and C4 species in grassland

In our study, the contrasting responses of C3 and C4 plants to the precipitation and temperature temporal distribution clearly indicated a temporal niche separation of these two plant functional groups. The competitive strategy for resources between C3 and C4 species and their reverse trends of nutritive value over time may provide further evidence for shifting of species composition in grassland community. As suggested by Zheng *et al.* (2011), the original dominant C3 species, *L. chinensis* and *S. grandis*, would be replaced by C4 species *C.squarrosa* with the degenerating of grassland. As the decline of individual animal performance over season have been observed

(Schonbach et al. 2009), selecting allowing the growth of high quality forage for feeding in different growing period like C4 grasses, may moderate the herbage palatability availability and the nutrient balance of vegetation and therefore the productivity of grazing livestock.

As the mass ratio hypothesis suggest that dominant species play more important roles in influencing ecosystem functioning and stability than species diversity (Grime 1998), we conclude that dominant species are not only driving botanical composition but also benefitting available nutrient for ruminants. Although high proportion of *C. squarrosa* in the sward is considered to be an indicator for grassland degradation, but as the most dominant C4 species, it could also bring into positive effect on economic outputs and ecosystem functioning when it accounts for the proper percentage in the community vegetation. These informations are necessary to formulate carrying capacities and predict future change of C3 and C4 species to develop appropriate management practices.

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Chapter 6

Summary

Zusammenfassung

6 Summary / Zusammenfassung

6.1 Summary

Inner Mongolian semi-arid grasslands are one of the main regions for raising livestock in China. After many years' increasing land using, overgrazing and drastic drought events induced grassland degradation and desertification lead to severe ecological and environmental problems coming along with decreasing productivity and loss of soil organic matter and plant nutrients and increasing in potential of erosion. As a result, the frequently dust and sand storms occurred. Sustainable grazing management of semi-arid grassland ecosystems requires holistic knowledge about vegetation dynamics and their responses to varying climatic conditions and grazing intensity to understand specific changes in plant communities. Therefore, experimental evidences from basic scientific studies are urgently required. From the beginning of 2005, the Institute of Crop Science and Plant Breeding - Grass and Forage Science/ Organic Agriculture, Christian-Albrechts-University Kiel (Germany), the Institute of Animal Nutrition and Physiology, Christian-Albrechts-University Kiel (Germany), and the Institute of Botany, Chinese Academy of Sciences, Beijing (P.R. China) jointly conduct a controlled sheep grazing experiment in the Inner Mongolian steppe ecosystem. These research activities have been carried out within the frame of the Sino-German interdisciplinary project MAGIM (Matter fluxes of Grasslands in Inner Mongolia as influenced by stocking rate), funded by the Deutsche Forschungsgemeinschaft (DFG). The overall aim of the MAGIM research group is the investigation and analysis of interaction processes between grazing and the steppe ecosystem. Based on that, the objectives of the present thesis were to evaluate the impact of grazing management and climatic variations on yield performance,

herbage quality, vegetation dynamic and persistence of grassland ecosystems of Inner Mongolia, seeking the development of concepts for improved rangeland management. A large plot-scale field manipulation experiment with seven different grazing intensities (ungrazed, very light, light, light-moderate, moderate, heavy, and very heavy) have been carried out in the semi-arid steppe ecosystem from 2005 to 2010. The plant species responses over the growing season, the nutritive values of the main grassland in species level and in community level, the species composition and diversity dynamic were tested. Plant species responses comprised their shifts or coexistences in composition, i.e the trade-off between C3 and C4 species, their biomass productivity and quality parameters, i.e. crude protein and organic matter digestibility.

The major conclusions we have drawn from this study confirmed the important role of grazing, precipitation, temperature and their interaction on vegetation dynamic. We find that temporal distribution of precipitation and temperature, in particular during the early-season (from March to June), determined the variation in vegetation dynamics much more strongly than annual rates of precipitation or temperature. In the 6 years study, the effects of early-season precipitation and temperature on the trade-off among species were more important than the effect of grazing. However, grazing decreased the aboveground biomass of those species that are more preferentially grazed by sheep, such as *L. chinensis*. Dominant species are more important than diversity in terms of recovering vegetation and sustaining grassland development, which match to the mass ratio hypothesis. Analysis of crude protein, in vitro digestibility, metabolizable energy, and fibre fractions (neutral detergent fibre, acid detergent fibre, and acid detergent lignin) shows consistent positive effects of precipitation and grazing on herbage quality. However, forage on offer for livestock should be based on aboveground net primary

productivity (ANPP) dynamic rather than forage nutritive quality, since ANPP could determine the most community forage nutritive yield. Therefore, based on these findings, the effect of grazing in a grassland system cannot be analyzed without considering the characteristic traits of species and also the precipitation and temperature variation, especially in the long term. Our findings provide more robust and comprehensive predictions on vegetation dynamics in semi-arid typical steppe, and help to understand species coexistence and grassland management in response future extreme precipitation and drought events.

6.2 Zusammenfassung

Die semi-ariden Grünlandflächen der Inneren Mongolei sind eine der wichtigsten Regionen für Viehzucht in China. Nach vielen Jahren zunehmender Landnutzung führen die durch Überweidung und extreme Dürreereignisse verursachte Degradierung des Grünlandes und die Ausbreitung der Wüsten zu schweren ökologischen und umweltrelevanten Problemen. Diese gehen mit sinkender Produktivität sowie Verlust an organischer Masse und Pflanzennährstoffen im Boden und nicht zuletzt einer steigenden Erosionsgefahr einher. Infolgedessen kommt es regelmäßig zu Staub- und Sandstürmen. Nachhaltiges Weidemanagement erfordert im Rahmen des Ökosystems semi-ariden Grünlandes ganzheitliches Wissen über die Vegetationsdynamik und deren Reaktionen auf wechselnde klimatische Bedingungen und Beweidungsintensitäten, um die spezifischen Veränderungen in den Pflanzengesellschaften zu verstehen. Daher sind experimentelle Nachweise dieser Zusammenhänge durch grundlegende wissenschaftliche Studien dringend erforderlich. Seit Beginn des Jahres 2005 werden in Zusammenarbeit des Instituts für Pflanzenbau und Pflanzenzüchtung - Grünland und Futterbau/Ökologischer Landbau, Christian-Albrechts-Universität zu Kiel (Deutschland), des Instituts für Tierernährung und Stoffwechselphysiologie, Christian-Albrechts-Universität zu Kiel (Deutschland) und des Instituts für Botanik, Chinesische Akademie der Wissenschaften, Peking (Volksrepublik China) kontrollierte Weideexperimente mit Schafen im Steppenökosystem der Inneren Mongolei organisiert. Diese Forschungsaktivitäten wurden im Rahmen des interdisziplinären Projektes MAGIM (Matter fluxes of Grasslands in Inner Mongolia as influenced by stocking rate) als deutsch-chinesisches Gemeinschaftsprojekt durchgeführt, welches durch die Deutsche Forschungsgemeinschaft (DFG) finanziert wird. Das übergeordnete Ziel der MAGIM-Forschungsgruppe ist die Untersuchung und Analyse von Interaktionsprozessen zwischen

Beweidung und Ökosystem in der Steppe. Darauf aufbauend bestanden die Zielsetzungen der vorliegenden Doktorarbeit in der Bewertung des Einflusses von Beweidungsmanagement und klimatischen Veränderungen auf Ertragsleistung, Grünfütterqualität, Vegetationsdynamik und Persistenz von Grünland-Ökosystemen der Inneren Mongolei, um Konzepte für ein verbessertes Weideflächenmanagement zu entwickeln. Von 2005 bis 2010 wurde im semi-ariden Steppenökosystem in großem Maßstab ein Feldmanipulationsversuch mit sieben verschiedenen Beweidungsintensitäten (keine, sehr geringe, geringe, gering-moderate, moderate, starke und sehr starke Beweidung) durchgeführt. Es wurden die Reaktionen der Pflanzenarten im Verlauf der Vegetationsperiode, die Nährstoffgehalte des Grünlandes sowohl auf Artenniveau als auch auf Niveau der Pflanzengesellschaft, die Spezieszusammensetzung und die Diversitätsdynamik untersucht. Die Reaktionen der Pflanzenarten umfassten deren Verschiebung oder Koexistenz innerhalb der funktionellen Gruppen, also die Austauschbeziehung zwischen C3- und C4-Arten, ihre Biomasseproduktivität und Qualitätsparameter wie Rohprotein und Verdaulichkeit der organischen Masse.

Die wesentlichen Schlussfolgerungen aus dieser Studie bestätigten die große Bedeutung von Beweidung, Niederschlag, Temperatur und deren Interaktion für die Vegetationsdynamik. Die zeitliche Verteilung von Niederschlag und Temperatur, vor allem zu Beginn der Vegetationsperiode (von März bis Juni), hatte sehr viel größeren Einfluss auf Veränderungen in der Vegetationsdynamik als die jährliche Summe an Niederschlag oder Temperatur. Während der 6-jährigen Studie waren die Effekte von Niederschlag und Temperatur zu Beginn der Vegetationsperiode von größerer Bedeutung für die Austauschbeziehungen zwischen den Arten als der Einfluss durch Beweidung. Allerdings reduzierte eine Beweidung die oberirdische Biomasse der Arten, die von Schafen bevorzugt konsumiert werden, wie beispielsweise *L. chinensis*. Die dominanten

Arten sind im Hinblick auf die Erholung der Vegetation und eine nachhaltige Grünlandentwicklung wichtiger als die Diversität, was der Massenverhältnis-Hypothese entspricht. Die Analysen von Rohprotein, in vitro Verdaulichkeit, metabolischer Energie und Faserfraktionen (neutrale Detergenzienfaser, saure Detergenzienfaser, saures Detergenzienlignin) zeigen einheitlich die positiven Effekte von Niederschlag und Beweidung auf die Grünfutterqualität. Dennoch sollte das dem Viehbestand angebotene Grünfutter auf Basis der Dynamik der oberirdischen primären Nettoproduktivität (ANPP) bewertet werden anstatt alleinig aufgrund der Nährstoffqualität, da ANPP für den Nährstofftrag des Grünfutters maßgeblich ist. Deshalb können, basierend auf diesen Ergebnissen, die Effekte von Beweidung auf ein Grünlandsystem nicht analysiert werden, ohne die charakteristischen Eigenschaften der Arten ebenso wie Niederschlags- und Temperaturveränderungen vor allem langfristig zu berücksichtigen. Unsere Erkenntnisse ermöglichen stabilere und umfangreichere Voraussagen über die Vegetationsdynamik der typischen semi-ariden Steppe und tragen dazu bei, die Koexistenz von Arten und das Grünlandmanagement in Reaktion auf zukünftige extreme Niederschlags- und Dürreereignisse zu verstehen.

Lebenslauf

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