Institut für Pflanzenernährung und Bodenkunde

der Christian-Albrechts-Universität zu Kiel

Yingzhi Gao

Influences of Different Land Use Management on Net Primary Productivity and Belowground Carbon Allocation in a semi-arid Inner Mongolia Steppe

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M.Sc. Yingzhi Gao
Aus Jilin Changchu. V. R. China
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Influences of Different Land Use Management on Net Primary Productivity and Belowground Carbon Allocation in a semi-arid Inner Mongolia Steppe

Candidate: Yingzhi Gao

Supervisors: Prof. Burkhard Sattelmacher†
Prof. Friedhelm Taube
Dr. Holger Brueck

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Introduction

Background and problem

Compared to 137 million hectares (Mha) of arable land, grasslands account for 400 Mha in China. In Inner Mongolia Autonomous Region native grasslands cover an area of 88 Mha, which is the largest part of grassland. For centuries grazing is a major form of land use in this area. Due to the increase in population and a shift in the socio-economic system in the past four decades, these grasslands are subject to an increased grazing pressure by sheep and goats that leads to the degradation and risk of severe soil erosion and desertification (Zhong et al., 2005). At present, 80% of the natural grassland exhibits certain degradation and 42% are already badly degraded. Striking evidence for the extent of these degradations comes from the numerous sandstorms attacking for example Beijing with an increasing frequency. Yet processes and factors responsible for the phenomena of grassland decay are not fully understood, but there is no doubt that overgrazing-induced processes make a major contribution.

State of the art

Net primary productivity (NPP) is a key variable of terrestrial ecosystems and an important component of the global carbon cycle. The better understanding of NPP is essential to comprehending the terrestrial carbon cycle, biosphere-atmosphere interaction and response of ecosystem function to climate change and land use changes (Melillo et al., 1993; Scurlock et al., 2002). However, a synthesis of NPP data based on field biomass measurements is lacking for all terrestrial worldwide ecosystems (Ni, 2004), and especially for semiarid grazing ecosystems. NPP of steppe ecosystems are interlinked through complex feedback loops involving grass, soil, land management and environmental factors. In large parts of Inner Mongolia overgrazing has already led to severe losses of soil organic matter, depletion of nutrients (Liu et al., 1998), a sharp decrease in steppe primary productivity and litter input (Liu et al., 1998; Bai et al., 2004; Zhong et al., 2005), changes in species composition and decreases in species richness and diversity (Liu et al., 1998; Zhou et al., 2006). It needs to be pointed out seasonal and yearly distribution of precipitation and grazing interactively affect aboveground net primary productivity (ANPP), belowground net primary productivity (BNPP), species composition and ecosystem processes. It has been shown that grassland condition has a major impact on the severity of any drought. On the heavily grazed area, there are high evaporation due to less plant basal cover and litter coverage, which can reduce soil water availability and lead to plants reaching water stress points easier than the site where the grassland are in good condition (Snyman, 2005). Therefore, the grassland, where is heavily grazed, is more susceptible to drought, and prone to being degradation in dry years.

Inner Mongolia grassland is characterized by large nutrient and organic matter stocks in belowground (Schimel, 1995). Belowground biomass often exceeds aboveground standing biomass by factors of two to five (Wang and Wang, 1999). Thus, the contribution of root litter to the pool of soil organic matter can greatly exceed the contribution of shoot litter. However, we do not have information on how grazing affects the biomass partitioning between aboveground and belowground. Reasons for a lack of such data include difficulty in root sampling and no good methods in estimates of BNPP. In almost all previous studies root/shoot ratio was calculated either using belowground biomass or live roots biomass, which can lead to high error, because a lot of necromass is in belowground biomass pool and live roots are usually long lived in perennial grasslands. Results from such data can’t give real biomass allocation information.

In the past, grazing studies unfortunately largely concentrated on aboveground part, with an almost complete lack of data on effects of grazing on annual root production, carbon allocation and root turnover in semiarid native grassland. Biswell and Weaver (1933) showed that frequent clipping may dramatically decrease root growth, and this effect has been verified repeatedly (Allsopp, 1998), but pot experiments with artificial defoliation are difficult to transfer to field conditions, as natural grazing has multiple effects on species composition, soil compaction, generation of nutrient patches and changes in tillering habit. Consequently, results from field experiments give a much less distinct picture on the effects of grazing on BNPP and C allocation in general.

Restoration and N fertilisation

Resources limitation usually is expected to result in close and positive correlations between productivity and uptake efficiency, while utilization efficiency is more relevant under conditions of high resource availability (Willby et al., 2001). This aspect has been illustrated in terms of nutrient availability but likely is also relevant for water. Studies on effects of small amounts of N fertiliser application and irrigation and the interaction of these resources manipulations on BNPP and carbon allocation have significant implications for the management of Inner Mongolia grassland. From a practical point of view, de-stocking to low, sustainable grazing intensity is one restoration strategy (Katoh et al., 1998), however, for severely degraded sites, other measures, such as prohibition of grazing or application of small amounts of N fertiliser may accelerate the restoration processes. We suppose that small amount of N fertilizer application can enhance NPP, which in turn would speed up the restoration process.

Root function, difficulties and methods in root research

Roots, the 'hidden half' of plants, serve a multitude of functions. They are responsible for anchorage, supply the plants with water and with nutrients, and exchange various growth substances with the shoots (Waisel et al., 2002). In an efficiency context, plants should optimize carbon expenditure for uptake of nutrients that limit growth. Plasticity, as exemplified here by the proliferation response, is a fundamental characteristic of the growth of root systems and is perhaps the most important adaptive feature of roots to their environment, ensuring that they achieve their primary functions of resource acquisition and anchorage. In spite of the great importance of roots for basic and applied scientific aspects and a long history of root research, there remains much to be learned about root development and functions. Roots are buried in the soil and any attempt to investigate their activity causes them irreversible damage. In addition, because roots live in very close contact with all other soil biota, the relationships may be so consolidated that it is hard to distinguish between a root as a plant organ and a root as a symbiont.

Investigations of root growth in grassland ecosystems and especially attempts to estimate BNPP rather than just biomass is labor intensive, time consuming and boring and dirty work. In most cases the root coring method or monolith techniques were applied. These attempts however give mean or maximum belowground biomass, and BNPP has then to be calculated by the formula suggested by Dahlman and Kutschera (1965) or sum of significant positive increments of belowground biomass. However we know that biomass coring calculations for BNPP are very seriously flawed and cannot be trusted for anything (personal communication with Milchunas). Most people really into roots have abandoned these old methods – again it is worth making comparisons with ingrowth, but only very briefly. Isotope decay from pulse or bomb labeling, minirhizotron, and ingrowth – these are the 3 that are still debated as useful but with still unknown problems and differences. While minirhizotron is difficult to transfer to area-related data, and is not possible to get root mass directly, isotope decay bears specific error risks since in contrast to the basic assumption of this method, the ^{14}C allocated to the root system may be re-mobilised by some plants and hence may lead to a severe overestimation of root turnover (unpublished, Sattelmacher). The application of the modified ingrowth core technique was suggested by Steingrobe et al. (2000) and represents a feasible, straight-forward attempt. In this method, it is assumed that root decay in such a short interval is negligible. Hence root dry matter in the mesh bags may be taken as a first estimate of BNPP. However, each method has merits and shortcomings, and no single best method exists for calculating below-ground production until now (Norby and Jackson, 2000; Milchunas and Lauenroth, 2001). The preferred use of one method over another can therefore be based on practical or logistical reasons. Considering soil condition of the grassland and safety reason, the ingrowth core method was used rather than methods of isotopes or minirhizotron.

Although a handful of studies on BNPP were done using the ingrowth core method (Steen, 1984; Hansson and Andrén, 1986; Vogt et al., 1998; Makkonen and Helmisaari, 1999; Steingrobe et al., 2000), Much of the work has been done in agricultural crops, e. g. sugar beet (Van et al., 1994), oilseed rape (Steingrobe et al., 2000), fruit and economic trees (Vogt et al., 1998; Hertel and Leuschner, 2002) and forests (Persson, 1983; Jones et al., 2003). Much less work has been done in native semi-arid steppe ecosystems. So far, no any attempts were made to estimate BNPP using comparable reliable methods in Inner Mongolian steppe ecosystem. We are the first work group to estimate root production using ingrowth cores. Further, the very few numbers of papers that look at BNPP and C allocation in response to grazing in all over the world that do NOT use old biomass coring methods, and all that old literature out there that does is totally unreliable (Milchunas et al., 2001; Hendricks et al., 2006).

Our objectives

Different land management, especially overgrazing, have greatly effects on grassland productivity, species composition, species richness and species diversity. Therefore, our objectives are to: (1) show important parameters relative to productivity which can indicate grazing intensity, (2) elucidate mechanisms of varying productivity under different grazing intensity from ecological and physiological aspects.

The four main specific hypotheses will be test

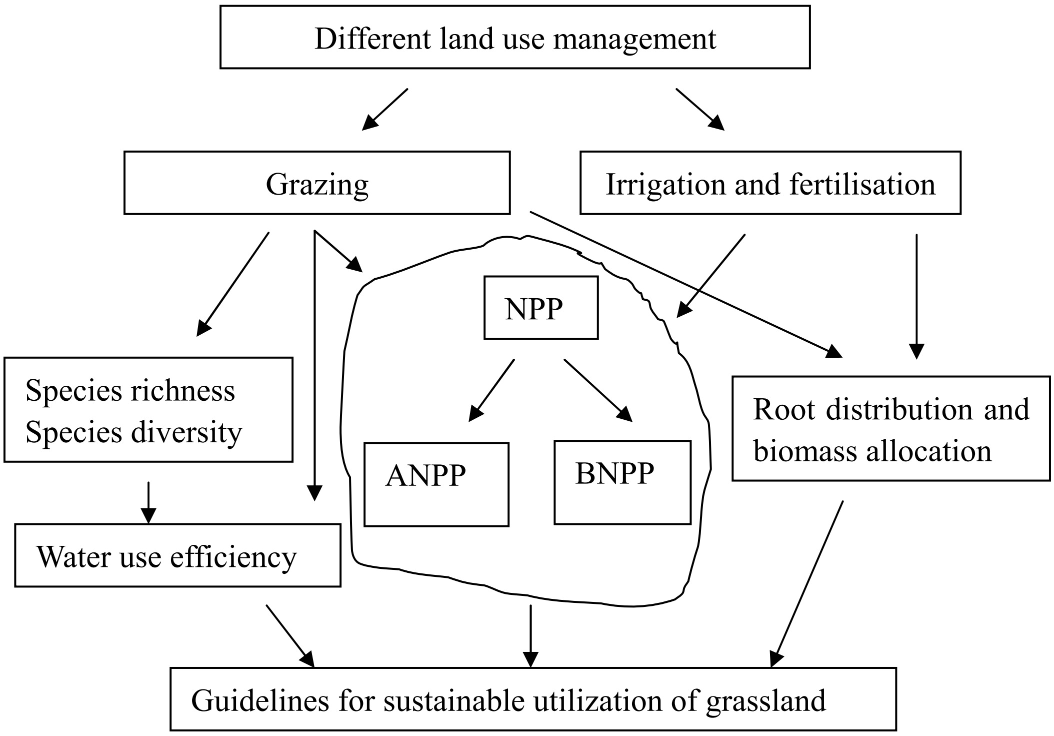
A) Species diversity, species richness and species composition are interactively affected by land use and drought due to species difference in drought resistance and grazing tolerance.

B) Crop growth rate or relative growth rate is accelerated by moderate and seriously restricted by heavy grazing, which leads to less ANPP on the heavily grazed site. This is a result of both changes in leaf area size and botanical composition as well as decreases in plant net assimilation rate.

C) Belowground biomass, BNPP and root size is stimulated by moderate- and hampered by heavy grazing. Distribution of roots over depth is affected, and the root system is shallower on heavily grazed site. BNPP is reduced stronger than ANPP resulting in a decrease of the root fraction. This makes heavily grazed site more susceptible to water deficit.

D) ANPP, BNPP and NPP were strongly increased by N supply and irrigation. NPP is not as much affected as ANPP by N fertiliser and water input due to the shift in relative allocation of carbon between shoot and root, and the reported increase of ANPP is partially due to reduced investment into BNPP.

The skeleton diagram of the thesis



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Materials and Methods

Experimental sites

General description

The typical steppe region of Inner Mongolia China, extends across 41° to 47° N and 109° to 117° E. The principal study area is the Xilin River watershed (3.800 km^2), which is located at 43°26′-44°08′ N, 116°04′-117°05′ E with most of it being more than 1,000 m above sea level. Precipitation, mainly of convective nature in combination with high evapotranspiration is the most limiting factor of plant growth in the typical steppe which covers more than 60% of the Xilin river catchment. Main soil types in the low hills and plains are chestnut soils and chernozems with high soil organic carbon and total N contents. Main vegetation types are *Leymus chinensis* and *Stipa grandis* communities with a ground cover of 30-70% and a vegetation height of 0.3 m in the long-term enclosure. 25 years average annual temperature is 1.0 °C with extremes ranging from -1.3 to 2.7 °C. 25 years average annual precipitation is 334 mm but varies between 158 mm to 507 mm. In general, 80-90% of annual precipitation occurs within the growing season. Compared to the local long-term average precipitation from May to August (249 mm), rainfall was 235 mm, 117 mm, and 164 mm in 2004, 2005, and 2006, respectively, indicating that 2005 and 2006 were comparably dry years (Appendix 1).

Grazing sites

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

Fertilisation and irrigation experiment

Site description

Additionally to the three sites described above a factorial experiment was established in 2005 at two sites. The experiment was conducted at a moderately (hereafter MG) and the above described heavily grazed site. Site MG was moderately grazed with 2 sheep per hectare until 2000 and used for winter grazing since then. At onset of the experiment, the dominating plant species at site MG were *Stipa grandis*, *Leymus chinensis* and *Cleistogenes squarrosa*, while *Carex spp.*, *Agropyron michnoi* and *Artemisia frigida* were dominant at site HG. Basic soil properties are listed in Appendix 2. Soil types at sites MG and HG were sandy loam and loamy sand, respectively and both are classified as calcic Chernozems (ISSS working group). Total N at site MG was higher than at site HG, whereas Olsen P and available K were higher at site HG than at site MG.

Fertilisation and irrigation design

Areas of 0.2 ha were fenced in May 2005 and divided into 32 plots of 5m x 8m. The experiment was designed as a two-factorial split-plot with 4 replicates and 8 treatments combining main plots of two water supply levels (rainfed, W0 and irrigated, W1) and subplots of four N fertiliser treatments (control, N0; N1, 25 kg N ha^{-1} as urea;

N2, 50 kg N ha^{-1} as urea; N3, 50 kg N ha^{-1} as NH_4NO_3). Subplots and main plots were separated by 0.8 and 3 metre pathways, respectively. The same split-plot experiment design was established at both sites.

Irrigation schedule

Rainfall data from 1982-2003 were used to decide about the additional amount of water supplied to plots during the growing season of 2006. Long-term rainfall data were divided into three groups of low (6 years), medium (11 years), and high (6 years) rainfall. The mean precipitation from May to September in dry years was 234 mm and 375 mm in wet years (Appendix 3). Plots were irrigated every 10 days with the required amount of water in order to match the average precipitation of the wet years during that period. Total precipitation from May to September 2006 was 219 mm and therefore 170 mm of water was irrigated to simulate the precipitation of an average wet year. Irrigation was realized by a calibrated pump-line injector system from water reservoirs, established at both sites in 2005. The required water amount was determined by supplying water to plots for precisely defined time-periods (Appendix 3). By automatic application at low heights and at calm times of the day (often at sunset) unintended water loss by drift and run-off was avoided.

Material and methods

Aboveground part

ANPP sampling

At the three sites of contrasting land-use management (sites UG79, WG, and HG, see above) plant samples were harvested at seven dates (2004: June 11, June 27, July 12 and 27, August 11 and 27, and September 16; 2005: May 11, June 2 and 23, July 15, August 7 and 28, and September 22) and in 2006 at five dates (May 15, June 11, July 12, August 12, and September 12) with five (2004), seven (2005) and eight (2006) replicates. Litter was collected by hand before cutting plants. Then plant material of 1 x 1 m ground area was cut with grass shears down to the soil surface. The biomass was first separated into green plant parts and dead material. The green parts were further separated into leaves and stems. Peak live biomass was considered to represent ANPP of sites UG79 and WG, both which were not grazed during the vegetation period. ANPP of site HG was estimated as the difference between biomass measured simultaneously within and outside of sheep exclosure cages of 1.5 m x 1.5 m size. The cages were randomly re-positioned between different sampling dates. ANPP was estimated from final residual live biomass plus the estimates of consumption by sheep for all time periods with five replications.

In the irrigation x fertilizer experiment, aboveground green biomass was sampled at June 15, July 15 and August 15 in 2006. Aboveground vegetation of single plots was sampled by clipping all plants of three 0.25 x 1 m areas at the soil surface. Samples were pooled, green parts separated from standing dead biomass and litter. ANPP was estimated from peak live biomass. All materials were dried at 75 °C for 48 hours.

Leaf area sampling

Leaf dry matter and leaf area (LA) were additionally measured at grazed sites by clipping five representative areas of 0.08 m^2 at August 01 and August 20 in 2005 and June 10 and July 12, August 12, and September 12 in 2006. LA was measured using a portable area meter (LI-3000A) in connection with a transparent belt conveyer (LI-3050A, LI-COR Nebraska, USA), and leaf dry matter was also determined. Pooled over all sampling dates, leaf area was related to leaf dry mass ($y = 0.016\ x^{0.84}$, $n = 126$, $R^2 = 0.93$) (Appendix 4). This equation was used to convert leaf dry matter data of the grazing experiment into values of leaf area.

Species composition, functional groups and relative biomass

At peak biomass time in 2004, 2005 and 2006, plant material of 1 m x 1 m ground area was cut with grass shears down to the soil surface with 10 replications at the grazing experimental sites. Additionally to the number of species, height, number of tillers and number of individuals were recorded before harvesting. After cutting, the biomass was separated by species and samples were dried at 75 °C to constant weight. According to life form, species were grouped into annual and biennial (AB); perennial rhizome grass (PR); perennial bunchgrass (PB), perennial forbs (PF); perennial grass (PG); shrubs and semishrubs (SS). Species resources acquisition ability may be described by species height (vertical direction) and density (horizontal direction) (Hao et al., 2002). Species biomass is the final product of net carbon gain, which could be highly correlated to the height and/or density (Ammann and Nyberg, 2005). The position and/or competitive ability of each species in the community can be partially reflected by its relative biomass (Connolly and Wayne, 2005). Therefore, relative height (RH), relative density (RD) and relative biomass (RB) of each species were calculated. Average height of plant community was calculated of those data where species RB was > 1%. The Simpson diversity index (D) were used to describe species diversity

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

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

Parameters calculations

Leaf weight ratio (LWR) is the ratio of leaf dry matter to aboveground dry matter; LAI (m^2 m^{-2}) is defined as the single-side leaf area per unit ground area; specific leaf area (SLA) (m^2 kg^{-1}) is the ratio of leaf area to leaf DM. Crop growth rate (CGR), relative growth rate (RGR), net assimilation rate (NAR) and leaf area growth rate (ΔLAI) were calculated as follows:

$$CGR = \frac{B_2 - B_1}{t_2 - t_1},$$

$$RGR = \frac{\log_e B_2 - \log_e B_1}{t_2 - t_1},$$

$$NAR = -4.88\left(\frac{B_2 - B_1}{t_2 - t_1}\right)\left(\frac{LA_2^{-0.17} - LA_1^{-0.17}}{LA_2^{0.83} - LA_1^{0.83}}\right)$$

$$\Delta LAI = \frac{LAI_2 - LAI_1}{t_2 - t_1}$$

where 1 and 2 refer to two consecutive harvest dates and B and LA are aboveground dry mass and leaf area, respectively. The equation for NAR was based on the relationship between leaf area and ANPP (y = 0.0128 $x^{0.83}$, n = 126, R^2 = 0.93) (Appendix 5). Growth analysis was based on growing degree days (GDD) as accumulated day temperatures starting when the consecutive 10-day mean daily air temperature was ≥ 0 °C. As my work started at mid of May, information about the start of the vegetation period was given by the station, where these data are routinely recorded. Rain-use efficiency (kg DM ha^{-1} mm^{-1} a^{-1}) was calculated from the ratio of ANPP to annual precipitation (Le Houérou, 1984). Water use efficiency (g DM L^{-1} H_2O) was defined as the ratio of ANPP to actual evapotranspiration (AET) during the growing season with the assumption that AET is equal to precipitation plus the net change of stored water during the growing seasons.

Leaf N content (LNC) was determined with a CN elemental analyser (EA1108, Italy).

Belowground part

Soil auger sampling

At the three differently managed grassland sites, root samples were taken at three (27 June, 11 August, and 16 September of 2004), seven (11 May, 2 June, 23 June, 15 July, 7 August, 28 August, and 22 September of 2005) and five (15 May, 12 June, 12 July, 13 August, and 12 September of 2006) sampling dates with a soil auger of 100 cm length and 85 mm diameter (Cobra TT motor-hammer, Eijkelkamp, The Netherlands). Samples were taken to a depth of 1 metre and separated into soil depths intervals of 0-10 cm, 10-20 cm, 20-40 cm, 40-60 cm, 60-80 cm, and 80-100 cm in 2004. In order to compare soil auger data with ingrowth core data, soil cores were separated into soil depths intervals of 0-10 cm, 10-20 cm, 20-50 cm, 50-70 cm, and 70-100 cm in 2005 and 2006. Root auger samples were taken with ten (2004), seven (2005) and eight (2006) replications for each sampling date.

In the irrigation x N fertiliser experiment, N and water effects on root parameters were recorded at treatments N0 and N1. Root samples were taken at both sites with the soil auger mentioned above on August 20 2006 to a depth of 0.5 metre and separated into depths intervals of 0-10 cm, 10-20 cm and 20-50 cm. Root samples were washed out at the same day, soil particles removed under a water stream and finally cleaned by decanting (at least four times). Roots were sieved over a 0.2 mm mesh, transferred into small plastic bags and stored in a refrigerator and finally separated by means of a magnifying glass and tweezers into a dead and live root part. The division into dead and live roots was done visually based on colour and flexibility of roots. Live root DW was determined at four and five sampling dates in 2005 and 2006 at grazing experimental sites, respectively. Root length was determined with the line intersection method using a ×8 magnifying glass according to Tennant (1975).

Ingrowth cores

The ingrowth-core method was used to estimate BNPP. At the end of the vegetation period in 2004 and 2005, holes of 4 cm diameter and a length of 70 cm were carefully drilled into the soil at an angle of 45° with a hand drill at the grazing experimental sites and plastic tubes were installed in order to keep the surrounding soil structure intact. The collected soil was separated into two soil layers (0-20 cm, 20-50 cm), sieved in order to remove roots, put into plastic bags (giving a specific number for each site sample), and stored below 0°C over the winter time for next year use. But at the end of the vegetation period, eight tubes for each treatment were refilled with the corresponding interim soil for the first harvest in the next year. Tubes were carefully pulled out of the holes and mantled with polyester mesh bags (mesh size 1 mm) and again inserted into the holes. For filling of tubes with soil, the tubes were pulled out of the mesh bag by a few centimeters and soil was filled in and compressed to a density comparable to the bulk soil. The tubes were pulled out step by step and the procedure was repeated until the mesh bag was completely filled with soil. When harvesting the tubes in the next year, another set of tubes was refilled with the corresponding interim stored soil for the next sampling date. Eight mesh bags at each site were harvested after three (2005) and four (2006) weeks, giving seven and five sampling dates, subdivided into depth intervals of 0-10 cm, 10-20 cm and 20-50 cm. BNPP was estimated as the sum of the root dry mass of sampling dates. For irrigation and fertilisation experiments, at the end of the vegetation period in 2005, eight tubes for each treatment were refilled with the corresponding interim soil for the first harvest at 15 May of 2006. When harvesting the tubes, another set of tubes was filled for the next sampling date. Totally five sampling dates at 15 May, 15 June, 15 July, 15 August, and 13 September of 2006 were realised. Mesh bags were harvested at each sampling date and subdivided into depth intervals of 0-10 cm, 10-20 cm and 20-50 cm. BNPP was estimated as the sum of the root dry mass of sampling dates. Samples were treated like mentioned above for the soil auger samples.

All root samples were dried at 75°C for 48 h and weighed. 30 root samples for each site were combusted for 6 h at 600 °C and weighed to determine the ash content. For fertilisation and irrigation experiments, the average ash content was 11.2 ± 1.7 % and 7.2 ± 0.7 on sites MG and HG, respectively, and the average value of ash content was 11 ± 2.5 % at grazing experimental sites. Results are given as ash-free dry mass.

BNPP estimates

BNPP, either expressed as g m^{-2} or as a fraction of the total net primary productivity, was estimated from the difference between maximum and minimum total belowground DW (ΔBGB) and live root DW (ΔLRB), and from accumulated root biomass of ingrowth cores (ARB). Further, BNPP was calculated according to the approach used by Gill et al. (2002):

$$\text{BNPP} = \text{BGB} \times \frac{Live\,BGB}{BGB} \times \text{turnover.}$$

Model 1

The calculation follows strictly the proposed empirical relationships given by Gill *et al.* (2002) with BGB = 0.79 ANPP - 33.3 (MAT+10) + 1289, a ratio of Live

BGB/BGB of 0.6, and turnover = $0.2884e^{0.046MAT}$, where MAT is mean annual temperature. The 22 year's average MAT at this location is 0.7 °C with a variation between 0.3 to 1.1 °C (95% confidence interval). MAT in 2005 was 2.2 °C.

Model 2

As Model 1, but with a ratio of Live BGB/BGB of 0.3 (see Results).

Model 3

Experimental data of BGB and Live BGB/BGB were used.

Data analysis

Statistical analyses were performed using SAS version 8.0. Three-way analysis of variances (ANOVA) included years (random), sites (fixed), and dates in a mixed model with PROC Repeated were performed of those parameters which were evaluated at several harvest dates(CGR, LAI, NAR, RGR, LWR and leaf N concentration, LNC). In order to test grazing effect, the analysis of each parameter was separated by year, and multiple comparisons among means were analyzed with Tukey's HSD test at each sampling date. Comparisons between years were based on paired-samples T tests.

Two-way ANOVA included grazing treatments (fixed effect) and years (random effect) for ANPP, BNPP, belowground biomass, live root biomass, community height, total plant density, and diversity index. In case of non-significant interaction between grazing treatments and years, comparison of main factor means was based on Tukey's HSD test, pooled over years and treatments. In the case of interaction between grazing treatments and years, significance of grazing effects was based on multiple comparison of means with an experimental wise error of 0.05 (level of significance for the three comparisons < 0.0166), significance of year effects (two years) was tested with the SLICE option for LSMEANS site*year.

For the irrigation and fertiliser experiment, three-way ANOVA included sites, nitrogen and irrigation in a fixed model with Procedure Repeated. Multiple comparisons among means were analysed with Tukey's HSD test. For root distribution data, three-way ANOVA was performed for depths separately.

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Land Use and Drought Interactively Affect Interspecific Competition and Species Diversity

Introduction

Native grasses of the Chinese semi-arid steppe, defined as a rhizome and bunchgrass steppe with many or few forbs, are well adapted to herbivory and have supported grazing as the dominant land use form for thousands of years (Zhu, 1993). However, in the past four decades, overgrazing resulted in substantial degradation of the Inner Mongolian steppe (Xie and Wittig, 2004; Zhong et al., 2005) and drastically decreased community productivity (Liu et al., 1998; Katoh et al., 1998), litter accumulation (Liang et al., 2002) and site fertility due to loss of fertile topsoil (Zhong et al., 2005). Overgrazing and N losses in combination with altered soil physical parameters and water availability further have been shown to exert strong impact on species composition and long-term succession direction (Banyikwa, 1988; Liu et al., 1998; Li and Li, 2002). It has been demonstrated that when heavy grazing persists on degraded grasslands, ruderals, typically unpalatable herbaceous and woody perennials become dominant (Milton et al., 1994). In the study area, the abundance of *Leymus chinensis* and *Stipa grandis* is substantially reduced under high grazing pressure (Li, 1989; Liu et al., 1998; Xie and Wittig, 2003), while dicotyledonous species like *Artemisia frigida* and *Potentilla acaulis* as well as the C_4 grass *Cleistogenes squarrosa* and sedge *Carex spp.* are typical grazing increasers (Liu et al., 1998; Li and Li, 2002; Gao et al., 2007).

In addition to grazing disturbance, drought can significantly affect species composition and functional components (Biondini et al., 1998; Thurow and Taylor, 1999; Bai et al., 2001; Briggs and Knapp, 2001; O'Connor, 2001; Nippert, 2006). Generally, species or functional groups tolerant to drought become more abundant in dry ecosystems and/or make a greater contribution to total community productivity in relative dry years (Bai et al., 2001 and 2004; O'Connor, 2001). After an analysis of long-term data set, Briggs and Knapp (2001) found a strong correlation between peak biomass of grasses and soil water availability, while biomass of forbs had no distinct pattern with rainfall variability. However, drought and grazing always interactively influence ecosystem processes in grazing ecosystems (Milchunas et al., 1989; Hartvigsen, 2000). Drought stress on heavily grazed areas are even more serious than on ungrazed grasslands under the same weather condition due mainly to less litter coverage and higher evaporation. Plants from heavily grazed areas may have less water available for growth compared to ungrazed sites (Fahnestock and Detling, 2000). Therefore our hypothesis is that drought combined with heavy grazing can drastically accelerate the shift of species composition or functional groups due to difference in drought resistance ability and grazing tolerance.

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

In the work reported here, we investigated (1) whether different species or functional components respond differently to grazing under the fluctuating levels of rainfall; and (2) whether the relationship between species richness, diversity and productivity is consistent on the differently managed sites under constrasting weather conditions.

Results

Years and grazing effects on ANPP, community height and total plant density

ANPP was significantly higher in the year of average rainfall (2004) compared to the dry years 2005 and 2006 (Table 1 and 2a). In all years ANPP at site UG79 was

Table 1 The probability (Pr>F) of two factors ANOWA results on aboveground net primary productivity (ANPP), community height (CH), plant density (PD) and different functional groups and species diversity (SD).

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

AB = annual and biennial, SS = shrubs and semishrubs, PR = perennial rhizome grass, PB = perennial bunchgrass, PF = perennial forbs. S = site, Y = year. *$P < 0.05$, ** $P < 0.001$ and *** $P < 0.0001$, NS: no significant difference.

significantly higher compared to that at site HG. ANPP at site UG79 was significantly higher compared to that at site WG in 2004, while ANPP at both sites was similar in 2005 and 2006. ANPP of site WG was not significantly different from that of site HG in 2004, while it was higher in 2005 and 2006. Average community height was significantly higher at sites UG79 and WG than at site HG, while it was similar at sites UG79 and WG. The community height was 26 cm at site UG79, and only 9 cm at site HG and was significantly higher in 2004 than in the dry years 2005 and 2006 (Table 1 and 2b). In all three years, total plant density was highest at site HG and lowest at site UG79 and was higher in 2004 than in 2005 and 2006 (Table 1 and 2c). Total plant density was not different between 2005 and 2006 at site UG79, while it further decreased in the second dry year at sites WG and HG.

Years and grazing effects on relative biomass of single species

Leymus chinensis, *Stipa grandis*, *Carex spp.*, *Agropyron michnoi*, and *Cleistogenes squarrosa* were found at all three sites (Table 3). *Caragana microphylla* was only found at site UG79 and its relative biomass ranged from 4% to 7%. *Anemarrhena asphodeloides* was absent at site HG, and quiet rare at site WG, while its relative biomass varied from 5%-7% at site UG79. *Achnatherum sibiricum* had high relative biomass at sites UG79 and WG, while it was completely absent at site HG, and

Table 2 (a) Aboveground net primary productivity (ANPP) (g m^{-2}), (b) average height of community (cm) and (c) total plant densities (ind. m^{-2}) at differently managed sites (1) in 2004, 2005 and 2006. (mean ± SE), n = 10.

Sites	2004	2005	2006	Average
(a) Aboveground net primary productivity				
UG	175.5 ± 6.2 a A	111.7 ± 11.3 a B	106.5 ± 4.8 a B	**125.6 ± 8.0**
WG	126.3 ± 1.9 b A	99.1 ± 3.0 a B	95.7 ± 2.9 a B	**104.5 ± 3.3**
HG	121.6 ± 7.9 b A	76.6 ± 3.8 b B	75.3 ± 2.6 b B	**87.3 ± 5.2**
Average	**141.1 ± 7.3**	**95.8 ± 5.1**	**92.5 ± 3.3**	
(b) Average community height				
UG	31.0 ± 1.3	25.0 ± 1.2	22.7 ± 1.2	**26.2 ± 1.7 a**
WG	29.3 ± 1.3	20.6 ± 1.1	23.1 ± 1.3	**24.3 ± 1.7 a**
HG	11.0 ± 0.6	7.0 ± 0.5	6.8 ± 0.5	**9.0 ± 0.8 b**
Average	**23.8 ± 1.8 A**	**17.5 ± 1.5 B**	**17.6 ± 1.5 B**	
(c) Total plant density				
UG	466 ± 12 c A	361 ± 9 c B	334 ± 11 c B	**387 ± 12**
WG	553 ± 12 b A	492 ± 10 b B	386 ± 6 a C	**477 ± 24**
HG	623 ± 9 a A	536 ± 9 a B	401 ± 11 a C	**520 ± 18**
Average	**547 ± 13**	**463 ± 15**	**373 ± 8**	

(1)Site UG79 has been protected from grazing since 1979, site WG is winter-grazed and site HG is heavily grazed. Significant differences between grazing and years are indicated by different small and capital letters, respectively.

relative biomass of *Cleistogenes squarrosa* (C_4, bunchgrass) at site HG was substantially higher than at sites UG79 and WG.

Land use type and precipitation had strong interactive effects on the following species (Table 3). *Chenopodium aristatum* and *Chenopodium glaucum* usually are opportunity species at all three sites, but heavy grazing with drought significantly increased these two species, and their RB were 15% and 7% in 2006 at site HG. The relative biomass of *Leymus chinensis* was reduced with drought, and heavy grazing with extended

Table 3 The relative biomass of single species (%) is listed at differently managed sites in 2004, 2005 and 2006, if its relative biomass is more than 1%. Comparison was done within one site. Significant differences between years are indicated by small different letters.

Species	UG79			WG			HG		
	04	05	06	04	05	06	04	05	06
Annual and biennial									
Chenopodium glaucum	--	--	1	--	-	--	--	-	7
Salsola collina	--	--	1	--	-	--	--	-	--
Chenopodium aristatum	--	-	--	1	-	--	--	-	15
Perennial rhizome grass									
Carex spp.	14a	13a	9b	5b	11a	12a	29a	12c	25b
Leymus chinensis	10a	6b	7b	30a	27ab	26b	9a	1b	--
Agropyron michnoi	4b	18a	4b	14a	6c	10b	5b	9a	5b
Perennial bunchgrass									
Stipa grandis	14b	17a	13b	23c	36b	39a	8ab	10a	7b
Achnatherum sibiricum	12	12	12	20a	11b	6c	-	-	-
Cleistogenes squarrosa	4a	1b	2ab	5a	3ab	2b	24a	15c	19b
Koeleria cristata	1	--	2	--	2	1	1	--	--
Festuca dahurica	--	--	-	--	2	1	-	-	-
Perennial forbs									
Anemarrhena asphodeloides	7	5	7	-	--	-	-	-	-
Allium senescens	5a	--	2b	--	--	--	-	--	-
Serratula centauroides	3	2	1	-	-	-	-	-	-
Potentilla tanacetifolia	4a	--	1b	-	-	-	--	--	1
Potentilla bifurca	2b	5a	1b	-	-	-	--	--	--
Potentilla acaulis	--	--	--	--	--	--	19b	43a	3c
Allium tenuissimum	2	--	1	1	1	1	--	--	--
Allium anisopodium	2	--		--	-	-	--	--	-

Table 3 continued

Allium bidentatum	1	1	2	--	--	1	-	-	-
Allium condensatum	--	--	--	--	--	--	-	--	-
Cymbaria dahurica	--	5	3	-	-	-	-	-	-
Pulsatilla tenuiloba	--	1b	4a	-	-	-	-	-	-
Filifolium sibiricum	1b	1b	8a	-	-	-	-	-	-
Silene jenissensis	1b	1b	3a	-	-	-	-	-	-
Galium verum	--	--	1	-	-	-	-	-	-
Heteropappus altaicus	--	--	2	-	-	-	--	--	--
Shrubs and semishrubs									
Caragana microphylla	7a	4b	5ab	-	-	-	-	-	-
Artemisia frigida	1	2	--	-	-	-	3c	7b	16a
Kochia prostrata	1	-	--	-	-	-	--	--	--

--, the relative biomass less than 1%; -, absent; site's description is as Table 2.

drought made this species almost absent at site HG. *Carex spp.* did not respond consistently at the three grassland sites in dry years 2005 and 2006. Relative biomass was reduced at site UG79, increased at site WG and exhibited no clear trend at site HG. However this species had high contribution to total biomass at all three sites after two dry years. Relative biomass of *Stipa grandis* increased in dry years and this trend is most evident at site WG and in the first dry year 2005. Similarly, *Achnatherum sibiricum* did not respond to drought at site UG79, whereas its relative biomass significantly decreased after drought at site WG. *Potentilla acaulis*, which is considered as an indicator of heavy grazing, was a rare species at sites UG79 and WG, and was dominant at site HG in 2004 (RB = 19%) and 2005 (RB = 43%). However, it was nearly not present in the second dry year (RB = 3%). *Artemisia frigida*, a semi-dwarf shrub, which was not found at site WG and was a rare species at site UG79, became the dominant species at site HG after two dry years. Total numbers of species contributed to total biomasses were quite different among sites (Table 3). 80%

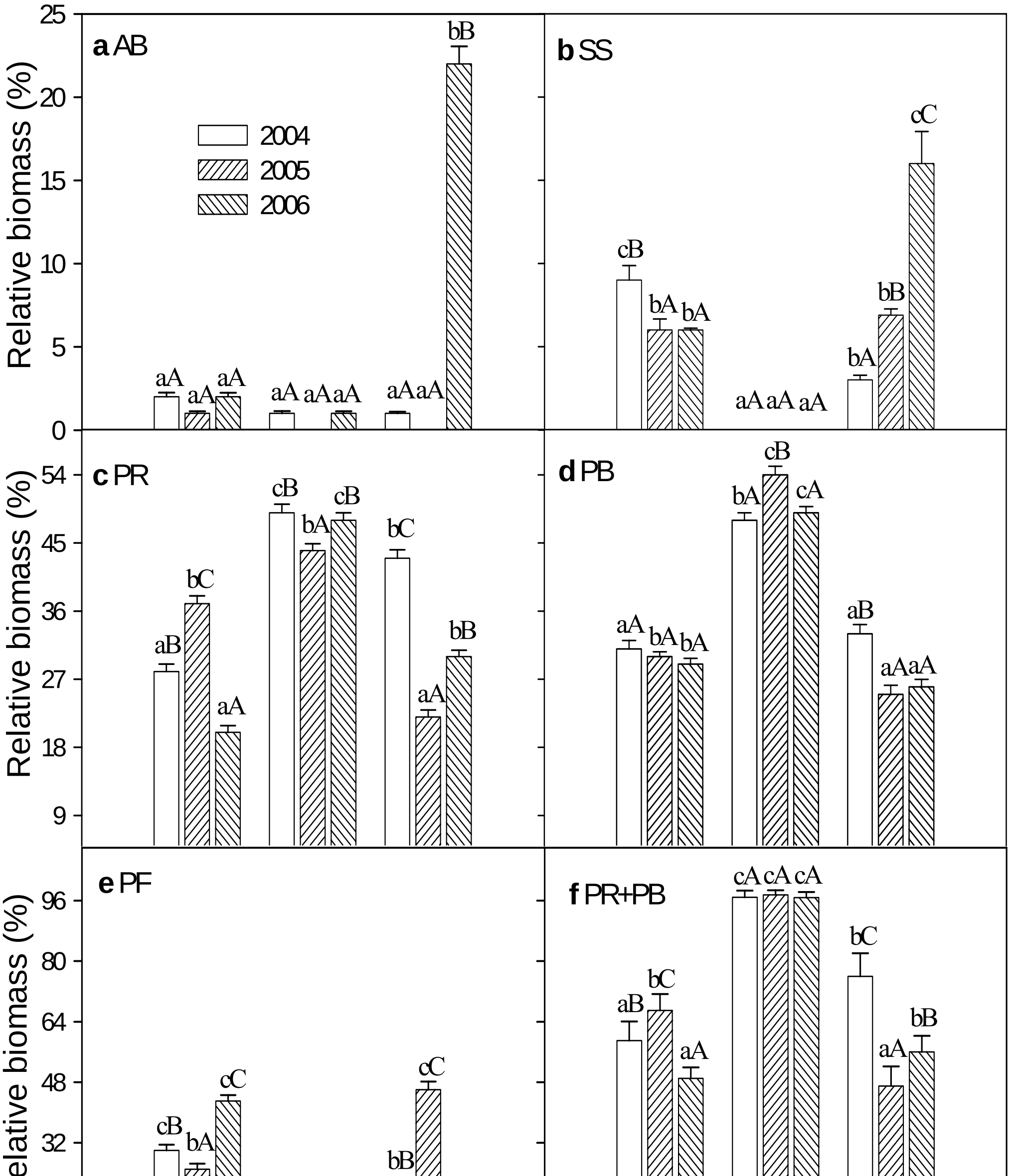

Fig. 1 The relative biomasses of different functional groups are listed from differently managed sites in 2004, 2005 and 2006. Significant differences between grazing and years are indicated by different small and capital letters, respectively. AB = annuals and biennials; SS = shrubs and semishrubs; PR = perennial rhizome grass; PB = perennial bunchgrass; PF = perennial forbs; PG = perennial grass.

of total biomass came from more than 15 species at site UG79, while more than 90% of total biomass was from only 5 species at site WG and 6-7 species at site HG.

Years and grazing effects on functional groups

Variation of precipitation and grazing interactively affected plant functional group composition (Table 1 and Fig. 1). Usually, Annuals and biennials only had very small contribution to total biomass at all sites, however, it became important at site HG after two continuous dry years and contributed with 22% to total biomass (Fig. 1a). SS exhibited a more or less stable contribution to total biomass over time at site UG79 (Fig 1b) and was not found at site WG, while they significantly increased the contribution to total biomass with drought at site HG (Fig. 1b). PR, PB and PF were the most important components in this perennial grassland (Fig. 1c, d, e and f). At site UG79, PG accounted for 60% and 69% of total biomass in 2004 and 2005, whereas their relative biomass contribution significantly decreased and accounted for only 50% of total biomass in 2006 (Fig. 1f) and PF made a greater contribution to total biomass (Fig. 1e). The reduction of PG was mainly due to the decrease of PR (Fig. 1c), while the relative biomass of PB remained more or less stable (Fig. 1d). As to site WG, PG were irrespective of years by far the most dominant plant functional group and accounted for more than 97% of total biomass (Fig. 1f). The relative biomass of PR and PB compensated each other from year to year (Fig. 1c and d), which made PG had more stable contribution to total biomass. In contrast to PG, perennial forbs had very small contribution to total biomass at this site (Fig. 1e). At site HG, PF and PG varied greatly from year to year, and the contribution of PF to total biomass ranged from 5% to 44% (Fig. 1e), and the relative biomass of PG varied from 49% to 75% (Fig. 1f).

Years and grazing effects on species richness and species diversity

In total, 55 species were found at site UG79, and 25 and 26 species at sites WG and HG in a relative wet year 2004 (Table 4, Appendix 10). The number of total species decreased at all three sites after two dry years.Variation of species richness between

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

Species	UG79			WG			HG		
	04	05	06	04	05	06	04	05	06
Annual and biennial	7	2	4	5	0	3	4	0	4
Perennial forbs	34	31	29	11	12	7	12	14	8
Perennial grass	9	9	8	9	9	9	7	7	6
Shrubs and semishrubs	5	4	5	0	0	0	3	3	3
Total	55	46	46	25	21	19	26	24	20

Site's description is as Table 2.

Table 5 Simpson diversity index at differently managed sites in 2004, 2005 and 2006. Significant differences between grazing are indicated by different small letters, respectively.

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

Site's description is as Table 2.

years was mainly from functional groups annuals and biennials and perennial forbs, while perennial grasses (PR+PB) and SS remained more stable (Table 3 and Table 4). The Simpson diversity index was not significantly ($p = 0.126$) different between years but tended to decrease with drought (Table 1 and 5). Land use management had a strong effect on species diversity index ($P < 0.0001$), with a significantly higher value at site UG79 than at sites WG and HG, while no significant difference between the other two sites was found during the study period.

Discussion

Years and grazing effects on ANPP, community height and total plant density

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

Grazing and year effects on relative biomass of species

Grazing sensitive species like *Achnatherum sibiricum* and *Anemarrhena asphodeloides* disappeared at the heavily grazed site, while *P. acculis*, *A. frigida* and *Carex spp.* became dominant under heavy grazing conditions. These species are adapted to grazing due to their strong gap colonization ability and prostrate growth habit, which is an effective grazing avoidance mechanisms (Milchunas and Noy-Meir, 2002; Bullock et al. 2001; Gao et al., 2007). Grazing tolerance is another important adaptation mechanism to grazing. *C. squarrosa*, despite preferentially eaten by sheep, has a high overcompensatory ability due to strong tillering and high photosynthetic capacity (Liang et al., 2002; Wang and Wang, 2001), which makes it become an important species on the heavily grazed site. Drought sensitivity of *Leymus chinensis* is indicated the significant reduction of relative biomass after drought at sites UG79 and WG. Due to sheep preference for eating this species much more in dry years than years of normal rainfall (Wang, 2000), it was almost completely absent at site HG in 2006 (Table 3).

Carex spp. characterised by strong colonization ability and drought tolerance (Liu et al., 1998) can produce a lot of thin and small tillers or stoloniferous branches, which makes them occupying huge horizontal space. This strategy can partially explain why *Carex spp.* became an important species at all three sites after drought

(Table 3). It should be noted that *Carex* has two main species in this area, *Carex korshinskyi* and *Carex duriuscula* C. A. Mey. Usually, *Carex korshinskyi* is more dominant at ungrazed sites and *Carex duriuscula* C. A. Mey more dominant at heavily grazed sites. Due to the difficulty of distinguishing of these two species, a separation of these species was not done in this study.

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

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

Competition and facilitation for resources are two of the most decisive factors determining vegetation pattern (Michalet, 2007) and the relative importance of facilitation and competition varies inversely across gradients of abiotic stress, with facilitation dominant under highly stressful conditions based on theoretical models (Brooker and Callaghan, 1998). However, it seems that interspecific competition, instead of facilitation, play a vital role in determining community structure and species composition under harsh environmental conditions (Zhou et al., 2006). Despite its strong colonization ability and low palatability (Wang, 2000), the abundance of drought-susceptible species *P. acculis* substantially reduced on site HG after two dry years, and drought-tolerant species *A. frigida* and opportunity species annuals and biennials significantly increased due to competitive release from *P.*

acculis. It has been argued that high abundance of *P. acaulis* indicates severe degradation of the grassland (Liu et al., 1998; Li and Li, 2002) and it is considered as the last perennial species in this native grassland, which in case of disappearance indicates high extinction danger (Li and Li, 2002). However, as suggested by our data, prolonged drought periods may reduce the predictability of degradation by means of this typical indicator species, due to the decrease of *P. acculis* partially compensated by *A. frigida*.

Years and grazing effects on species compensatory effects

A growing number of experiments have demonstrated that species compensatory effects can ensure greater and more stable production (Tilman and Downing, 1994; Bai et al., 2001 and 2004). The mode of compensatory effects exhibits great differences in different land use types. PR and PF compensated each other, while PB and SS remained more or less stable in the long term enclosure (Fig. 1); the sharp decrease of PF was mainly compensated by functional groups AB and SS after two dry years on the heavily grazed site; compensatory effects between species were more evident on the winter grazing area, where the perennial grasses were overriding dominant (Fig. 1f), and the relative decrease of *Leymus chinensis* was partially compensated by the relative increase of *Carex spp*. and *Achnatherum sibiricum* was mainly compensated by *Stipa grandis* in the dry year (Table 4). However, species and/or functional groups compensatory effects did not prevent a low total productivity in 2005 and 2006 for all three sites (Table 1). In the case of low soil water availability, water uptake per unit root mass will be decreased and nutrient uptake probably will be reduced, as the delivery of nutrients by mass flow is hampered in dry soil (Marschner, 1995). Therefore, total productivity was systematically hindered.

Years and grazing effects on species diversity

The common relationship between species richness and productivity is hump-shaped and positive after the review of 171 published studies (Mittelbach et al., 2001). To stress this relationship in specific grazing ecosystems, Cingolani et al. (2005) argued that grazing can substantially change species composition, rather than species richness or diversity, if the numbers of grazing sensitive to resistant species were similar. In opposite to this argumentation, our data illustrated that heavy grazing significantly reduced species richness and biodiversity. In addition, the positive relationship between productivity and species richness and diversity was only found in one relative normal year 2004, and no any relationship was observed between species diversity and productivity in dry years 2005 and 2006. This discrepancy indicates that regulatory processes at the community level in response to varying soil nutrient and water availability are quite complex in grassland ecosystems in general, and in this semi-arid grassland in particular (Baer et al., 2003; Cingolani et al., 2005; Gao et al., 2007). When one dominant driving force like soil water availability becomes limiting, all ecosystem processes are slowed down. In addition, the responses of productivity to drought are quicker than that on species richness, which obviously explains the divergence between productivity and species diversity. It should be noted that this ecosystem seems to have higher resilience as indicated by the fact that none of the important perennial species disappeared after extreme drought, in spite of high fluctuation of species contributions to community production in different years.

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

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Growth Parameters of Plants are Interactively Affected by Land Use and Rainfall

Introduction

Native grassland of Inner Mongolia steppe is well adapted to herbivory and has supported grazing as the dominant land use for thousands of years. In the past four decades, the replacement of nomadic and semi-nomadic grazing by stationary livestock farming and the increase of livestock (more than 8×10^8 ungulates) resulted in extensive degradation amouting for 80% (moderate) and 42% (heavily affected) of the total Inner Mongolia area (Xie and Wittig, 2004; Zhang et al., 2004; Cao and Yang, 1999).

A number of studies have shown that heavy grazing generally reduces aboveground net primary productivity (ANPP), especially in semiarid grasslands (Sims and Singh 1978 a; Milchunas and Lauenroth, 1993; Milchunas et al., 1994; Katoh et al., 1998; Zhong et al., 2005 Snyman, 2005; Zhou et al., 2006). It also has been reported that grazing can increase ANPP due to compensatory and overcompensatory growth in ecosystems with high precipitation and ample nutrient availability (McNaughton, 1979; Pandey and Singh, 1992; Frank and McNaughton, 1993; Pucheta et al., 1998; Frank et al., 2002). However, comprehensive information on the relative role of the main functional processes controlling the response of ANPP to grazing is still lacking. Plant growth is interactively affected by grazing and water regimes in this steppe ecosystem (Bai et al., 2004; Zhou et al., 2006). Monthly, seasonal and yearly pattern of precipitation, evaporation, and soil water availability are all considered as relevant for determining dynamics of ANPP under high potential evapotranspiration (Sims and Singh, 1978 a, b; Lauenroth and Sala, 1992; Briggs and Knapp, 1995; Xiao et al., 1995; Knapp et al., 2002). In addition, it has been shown that lag effects in productivity usually occurred in case of low precipitation in the previous growing season (Martín et al., 2001), and ANPP was more responsive to soil moisture variability than to mean soil water content (Knapp et al., 2002).

Overgrazing has not only drastically decreased community productivity (Katoh et al., 1998; Chen and Wang, 2000; Xie and Wittig, 2003; Zhang et al., 2004), but also changed species composition (Li, 1989; Liu et al., 1998). Inherent differences among species in leaf weight ratio (LWR), leaf area (LA), specific leaf area (SLA), net assimilation rate (NAR) and leaf N can lead to different community productivity due to different relative growth rates (RGR) (Reich et al., 1998, 2003; Galmés et al., 2005; Oikawa et al., 2005). Some experiments have illustrated that SLA is the most important component in determining species difference in RGR (Garnier, 1992, Wright and Westoby, 2000 and 2001). On the other hand, the three components (NAR, LWR and SLA) of RGR are all strongly affected by nitrogen supply, and species productivity is strongly dependent on nitrogen concentration (Gulmon and Chu, 1981; Hirose and Kitajima, 1986; Hirose, 1988). Hence, the causal interpretation of these morpho-physiological traits in the context of grassland productivity is not straightforward as traits are interrelated among each other (Warren and Adams, 2005; Glimskär and Ericsson, 1999; Hikosaka, 2003). A wealth of information about this aspect is available for agricultural crops, while no investigations were undertaken in native grasslands at the community level (Pyke and Hedley, 1983; Karimi and Siddique, 1991; Garnier, 1992; Anten and Ackerly, 2001; Warren and Adams 2005). Therefore, monitoring of these parameters in the frame of plant growth analysis may give insights how plant communities respond to climatic variables within and between years and to long-term imposed disturbance by grazing. Two specific hypotheses were tested in this work:

1) Heavy grazing substantially reduces ANPP due to the reduction of leaf area and total carbon gain, and compensatory and overcompensatory growth is not relevant in this semi arid steppe ecosystem.
2) Differences in RGR are positively related to site's difference in LWR, SLA, NAR and leaf N concentration, and ANPP differences among sites will be best explained by the difference of SLA among sites.

Results

Effects of grassland management and years on ANPP

See Chapter 3, Table 2

Effects of grassland management and years on CGR and LAI

Except of the high CGR at site UG79 at the third sampling date in 2004, CGR of these semiarid grassland sites varied from 0 to 2 g m^{-2} d^{-1} and exhibited negative growth rates towards the end of the growing season at sites UG79 and WG in all three years (Fig. 1). Sites UG79 and WG had higher CGR than site HG at the second harvest date, while the latter sustained positive CGR at the last harvest dates in 2005 and 2006. Compared to the more or less typical time course of CGR in 2005 and 2006 with peak values during the first half of the growing season (from GDD 500 to 1500), 2004 exhibited a highly dynamic pattern over time with two peak values and a growth depression at the middle of the growing season. This drought-induced growth depression was more pronounced at site UG79 compared to both other sites. Due to low precipitation in 2005 and during the first quarter of 2006, onset of growth was

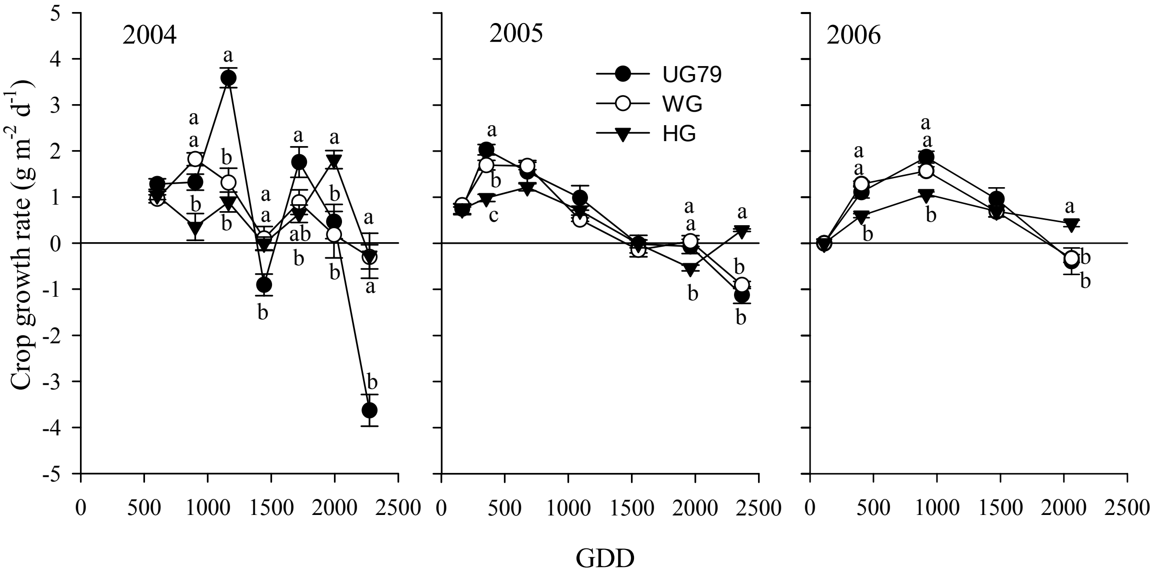

Figure 1 Crop growth rate (CGR) was affected by different land management from 2004 to 2006. Significant differences between sites are indicated by different small letters within one sampling date.

substantially delayed, no green biomass was harvested until GDD 112 and peak CGR was later (GDD 915) compared to 2005 (GDD 354). Summarizing these results, differences in ANPP were reflected in site differences in CGR. The higher ANPP of sites UG79 and WG compared to HG was due to higher CGR during the first half of the growing season. This higher productivity of sites UG79 and WG was partially offset by higher CGR at site HG towards the end of the growing season. The strong effect of rainfall on plant growth is illustrated by the lower CGR in 2005 and 2006 compared to 2004. The delayed growth and reduced peak CGR were found in 2006, the second year of below-average rainfall (Appendix 1).

LAI consistently increased during the growing seasons, except of the dry spell period in 2004 when at all sites LAI decreased transiently (Fig. 2). LAI at site HG was

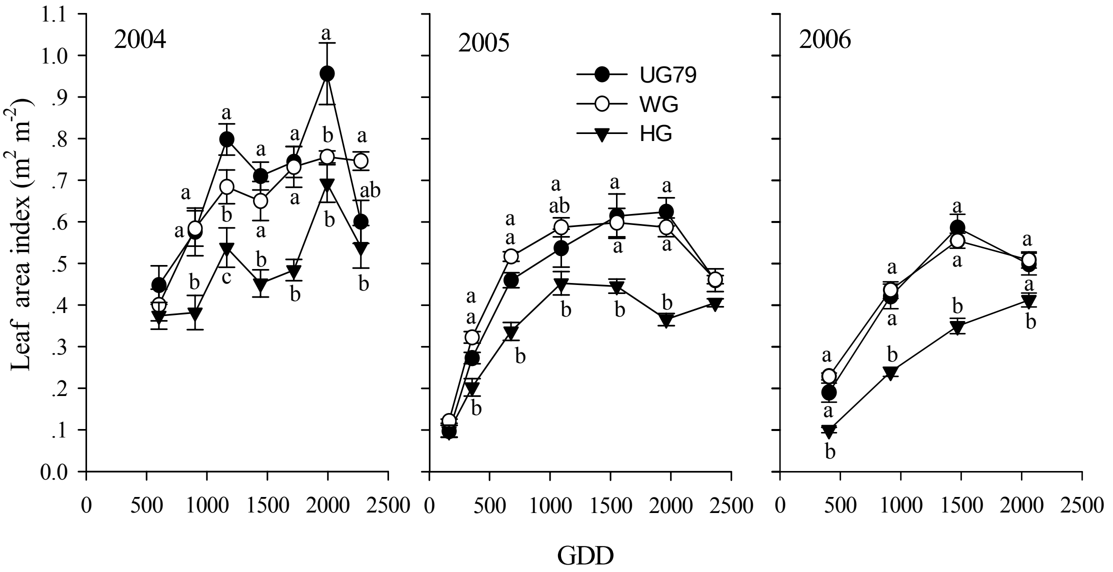

Figure 2 Leaf area index (LAI) was affected by different land management from 2004 to 2006. Significant differences between sites are indicated by different small letters within one sampling date.

significant lower than at sites UG79 and WG besides the start and end of growing seasons in 2004 and 2005. LAI differences between sites UG79 and WG were small in 2005 and 2006, while LAI at site UG79 was significantly higher than that of WG at the peak biomass time in 2004. Peak LAI values occurred at GDD 1994 for all the

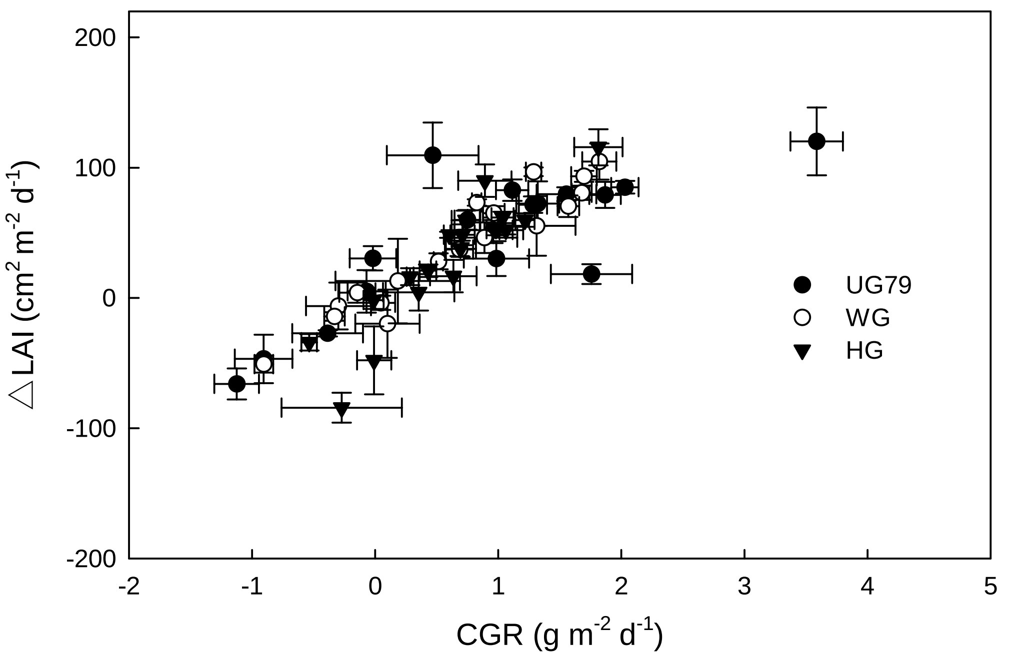

Figure 3 The relationships between crop growth rate and leaf area growth rate (ΔLAI) (ΔLAI = 47.72 CGR + 2.78, n = 53, $R^2 = 0.73$, $P < 0.001$)

treatments in 2004, while during the two dry years, sites exhibited differences. Sites UG79 and WG responded similarly with peak values at GDD 1961 in 2005 and an earlier peak at GDD 1469 in 2006. Contrarily, the peak value at site HG was early in 2005 (GDD 1092) and late (GDD 2060) in 2006. The pronounced effect of water availability on LAI is indicated by the continuous decrease of seasonal LAI from 2004 to 2006. LAI was not higher than 1 at all sites. As shown in Fig. 3, ΔLAI was positively related to CGR.

Effects of grassland management and years on NAR

As shown in Fig. 4, there was a significant interaction of years, sites, and sampling dates for NAR (Table 1). In general, there was a quite similar trend for all three treatments, and NAR tended to decline throughout the growing season, in spite of some fluctuation in 2004. The highest values of NAR, which consistently occurred at early spring time, when the plants start growing, were 41, 64 and 64 g m^{-2} d^{-1} in 2004,

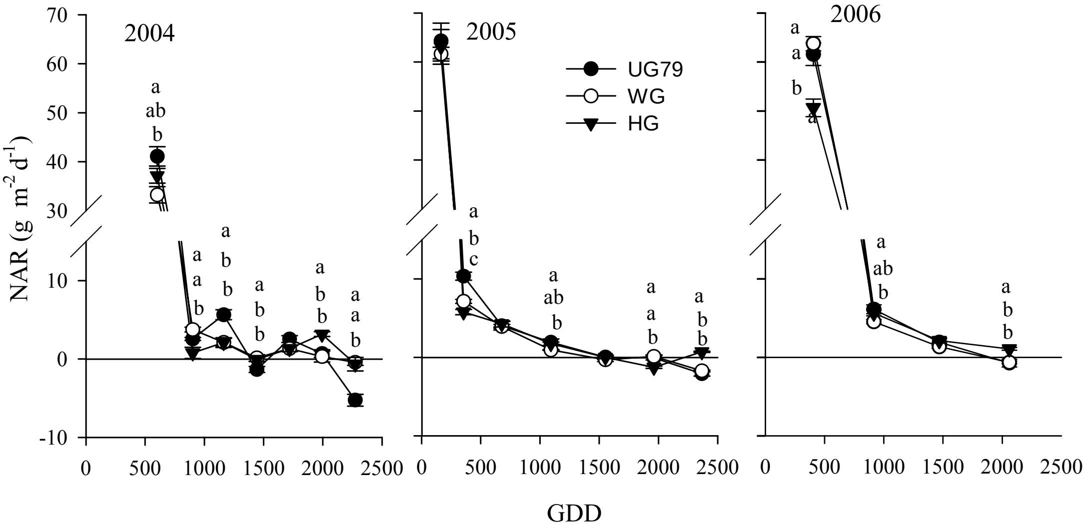

Figure 4 Net assimilation rate (NAR) was affected by different land management from 2004 to 2006. Significant difference between sites was indicated by different small letters within one sampling date.

Table 1 The probability (Pr>F) of three factors ANOWA results on crop growth rate (CGR), leaf area index (LAI), net assimilation rate (NAR), relative growth rate (RGR), leaf weight ratio (LWR) and leaf N concentration (LNC). Y = year, S = site, D = date. *P < 0.05, ** P < 0.001 and *** P < 0.0001, NS: no significant difference.

Sources	Df	CGR	LAI	NAR	RGR	LWR	LNC
Y	2	*	***	***	***	*	***
S	2	NS	***	NS	NS	***	***
D	6	***	***	***	***	***	***
Y*S	4	*	*	NS	NS	***	***
Y*D	9	***	***	***	***	***	***
S*D	12	***	***	***	***	***	***
Y*S*D	18	***	*	***	***	*	***

2005 and 2006, respectively. NAR of site UG79 had the highest value at most sampling dates in each year. The most distinct difference of NAR between site UG79 and both other sites occurred at 1163 GDD in 2004, whereas the biggest differences between sites occurred at GDD 354 and 405 in dry years 2005 and 2006. NAR at site HG was significant higher than that at site UG79 at the end of growing season in all years, and the corresponding GDD were 2274, 2367 and 2060 in 2004, 2005 and 2006, respectively.

Effects of grassland management and years on RGR

Fig. 5 summarises the time-course of RGR during the growing seasons. A significant interaction of years, sites, and sampling dates for RGR was found (Table 1). Generally, there was quite a similar trend for all three treatments, RGR declined throughout the season, in spite of some fluctuation in 2004. Like NAR, the highest RGR was found at early spring time, when the plants began to grow. RGR of site UG79 was significantly higher than that of site HG at most sampling dates, whereas RGR of site HG was significantly higher than that of site UG79 at the near end of season in all three year.

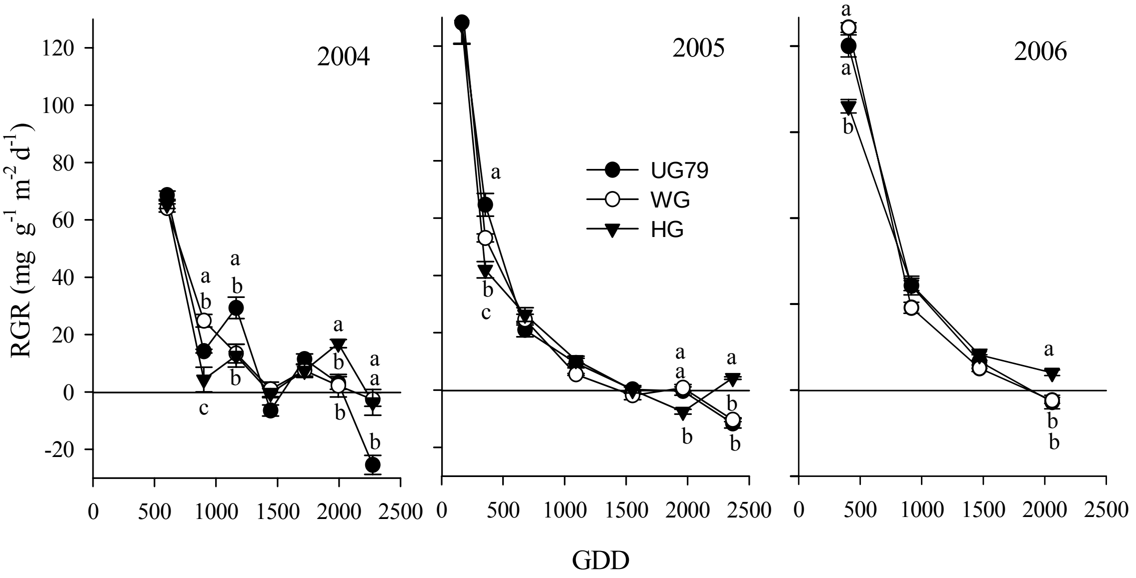

Figure 5 Relative growth rate (RGR) was affected by different land management from 2004 to 2006. Significant difference between sites was indicated by different small letters within one sampling date.

In 2004, each site had higher RGR than in 2005 and 2006 during the growing season. At GDD 902, RGR of site WG was significantly higher than at sites UG79 and HG. At GDD 1163, RGR of site UG79 was significantly higher than at sites WG and HG and at GDD 1994, RGR of site HG was significantly higher than at sites UG79 and WG. The biggest difference of RGR between sites occurred at GDD 354 and 405 in dry years 2005 and 2006.

Effects of grassland management and years on LWR

A significant interaction of years, sites, and sampling dates for LWR was found (Table 1). LWR tended to decrease over the growing season. LWR varied from a minimum of 0.69 to a maximum of 0.86 at site WG, while it varied from 0.54 to 0.77 at site UG79 and from 0.57 to 0.77 at site HG. Pooled over all data, LWR of site WG was significantly higher than that of sites UG79 (n = 116, $P < 0.0001$) and HG (n = 116, $P < 0.0001$), and LWR of site HG was significantly higher than that of site UG79 (n = 116, $P < 0.0001$).

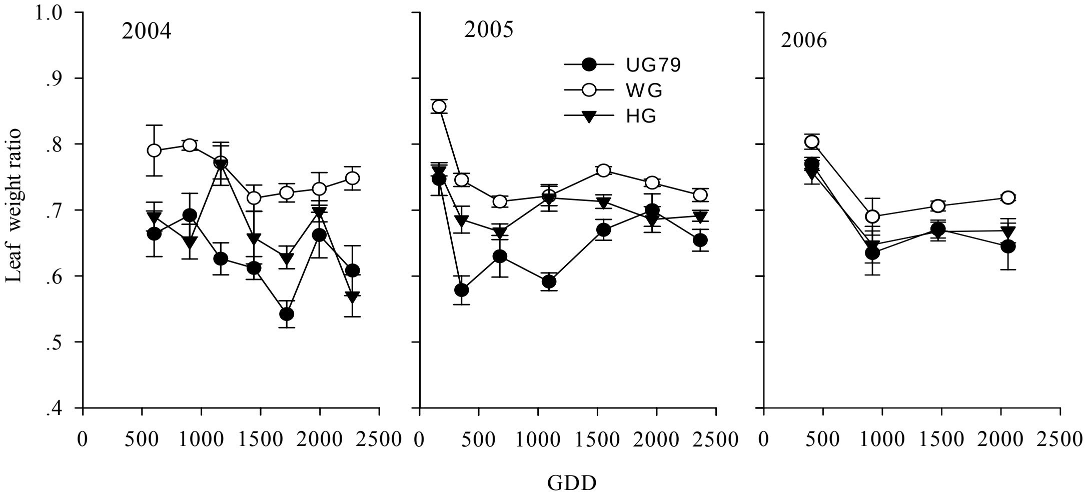

Figure 6 Leaf weight ratio (LWR) was affected by different land management from 2004 to 2006.

Effects of grassland management and years on leaf nitrogen content (LNC)

There was a significant three-factor interaction for LNC (Table 1). As shown in Fig. 7,

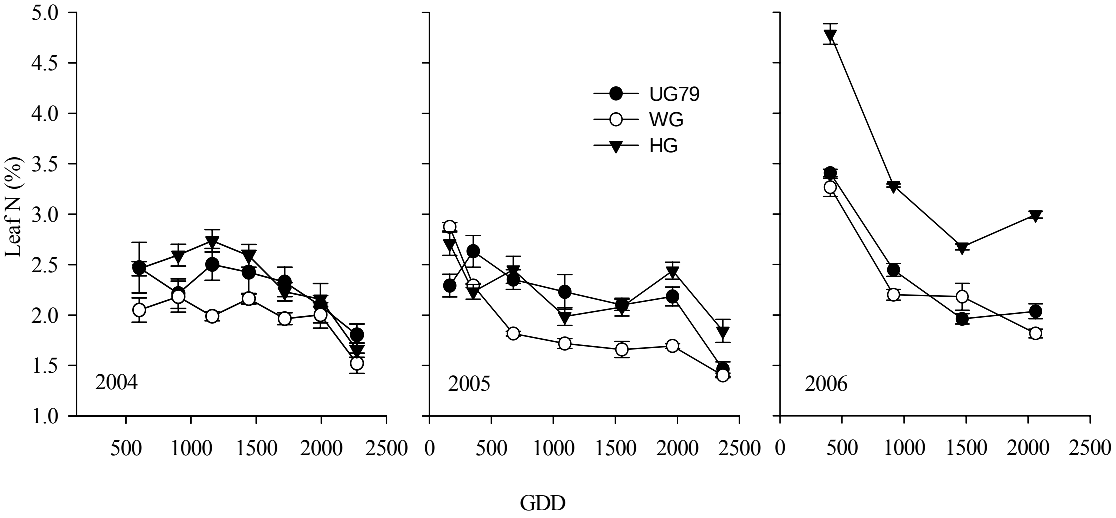

Figure 7 Leaf nitrogen content (LNC) was affected by different land management from 2004 to 2006.

LNC tended to decrease over the growing seasons in all treatments, and this trend was most evident in 2006. Pooled over different sampling dates in 2004, LNC at sites UG79 and HG was significantly higher than at site WG (n = 35, $P < 0.0001$), while there was no significant difference between sites UG79 and HG (n = 35, $P = 0.169$). The same results were found in 2005, while it was quiet different in 2006. Leaf N at site HG was still significantly higher than site WG, whereas no significant difference between sites UG79 and WG was observed. Pooled over all sampling dates in each year at each site, LNC was not significantly different among the three years at site UG79 (2004 vs 2005: n = 35, $P = 0.482$; 2004 vs 2006: n = 32, $P = 0.222$; 2005 vs 2006: n = 32, $P = 0.272$). For site WG, leaf N was no significantly different between 2004 and 2005 (n = 35, $P = 0.261$), whereas leaf N in 2006 was significantly higher than in 2004 and 2005 (2004 vs 2006: n = 32, $P = 0.002$; 2005 vs 2006: n = 32, $P = 0.001$). For site HG, no significant difference in LNC between 2004 and 2005 was found (n = 35, $P = 0.461$), while LNC in 2006 was substantially higher than in 2004 and 2005 (2004 vs 2006: n = 32, $P < 0.001$; 2005 vs 2006: n = 32, $P < 0.001$).

Relationships of RGR with NAR, SLA, LWR and LNC

Fig. 8 shows the relationship of RGR with NAR, SLA and LWR, which are the components determining RGR. Positive relationships between RGR and NAR and LWR were found, and RGR was more strongly related to NAR than LWR. The coefficient of determination between RGR and LWR differed between sites and the strongest correlation was found at site WG (P = 0.003), followed by site UG79 (P = 0.024), and the lowest at site (P = 0.06). In contrast to NAR and LWR, no relationship between RGR and SLA was observed.

A positive relationship of RGR with LNC was found (Fig. 9). Like LWR, the coefficient of determination was larger at site WG (R^2 = 0.79) than at sites UG79 (R^2 = 0.44) and HG (R^2 = 0.28).

Discussion

Aboveground net primary productivity (ANPP)

Grazing is a dominant factor which controls plant community succession dynamics and productivity in this steppe ecosystem (Liu et al., 1998). As indicated by the consistently observed negative effect of grazing on ANPP, the optimisation hypothesis (McNaughton et al., 1979, Dyer et al., 1986; Frank and McNaughton, 1993; Frank et al., 2002) obviously does not apply to the semiarid grassland investigated in this study. A similar negative response of grazing on ANPP in arid and semiarid ecosystems has been shown by e.g., Sims and Singh (1978 a), Milchunas et al. (1994), Liu et al. (1998), Katoh et al. (1998), Snyman (2005), Zhong et al. (2005), and Zhou et al. (2006). However, drought may become the dominant factor determining grassland productivity and diminish grazing effect. This is indicated the non-significant differences between sites UG79 and WG in 2005 and 2006 compared to 2004. Similarly, productivity differences between sites WG and HG were less pronounced in dry years than in the year of average rainfall (2004). Interactive effects of grazing and rainfall on ANPP are further indicated by the fact that drought reduced ANPP to a different degree at the three sites. ANPP was only 63% at sites UG79 and HG in 2005 and 2006 compared to 2004, while it was 'still' 80% at site WG. This indicates that

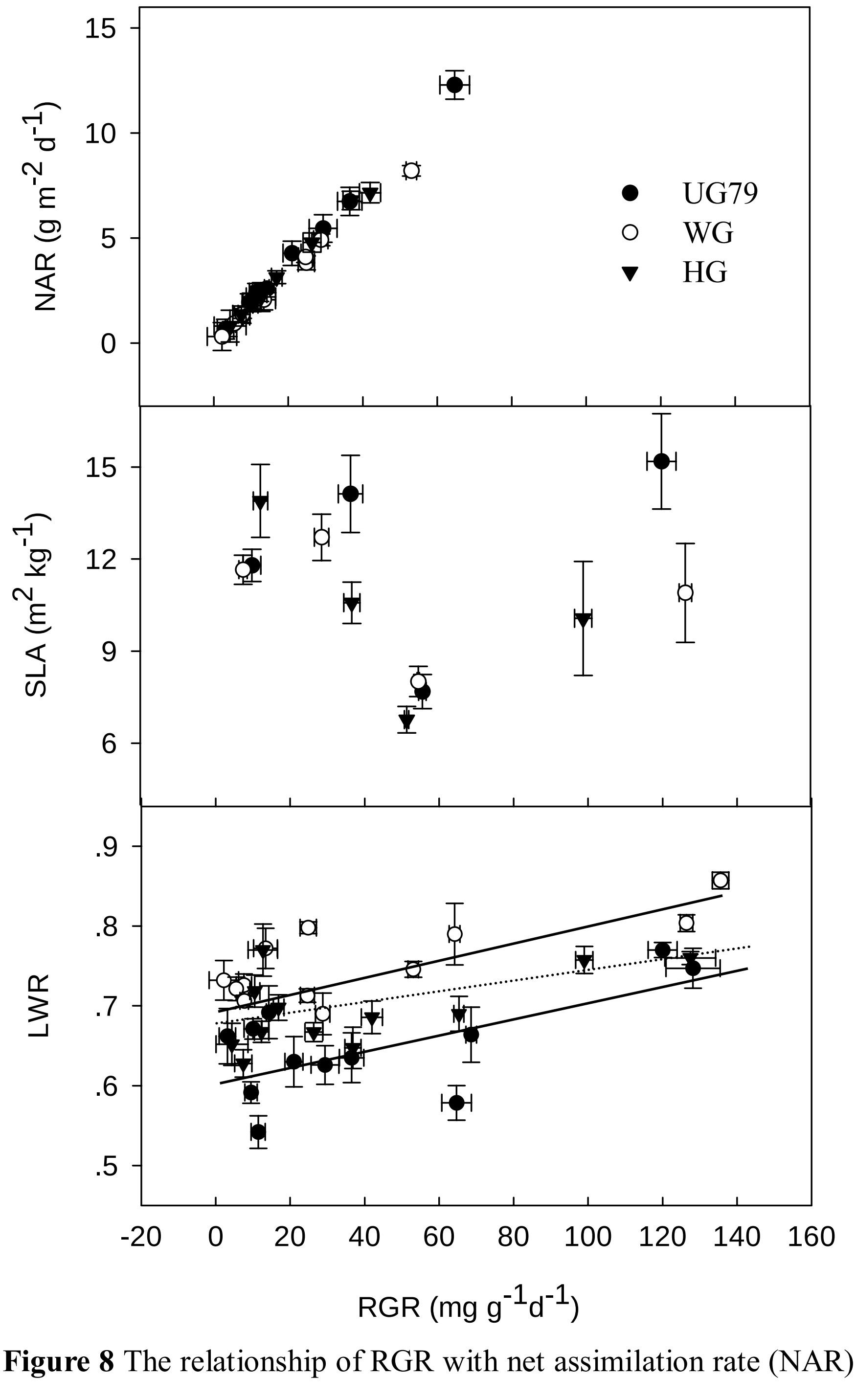

Figure 8 The relationship of RGR with net assimilation rate (NAR), specific leaf area (SLA) and leaf weight ratio (LWR). (For NAR: NAR = 6.136RGR + 0.115, n = 45, R^2 = 0.98, $P < 0.0001$; For SLA: no relationship between SLA and RGR. For LWR: UG79: LWR = 422.44 RGR – 231.88, n = 12, R^2 = 0.41, P = 0.024; WG: LWR = 719.79 RGR – 502.01, n = 12, R^2 = 0.60, P = 0.003; HG: LWR = 465.26 RGR – 285.02, n = 12, R^2 = 0.31, P = 0.060). Straight lines: UG79 and WG; dashed line: HG.

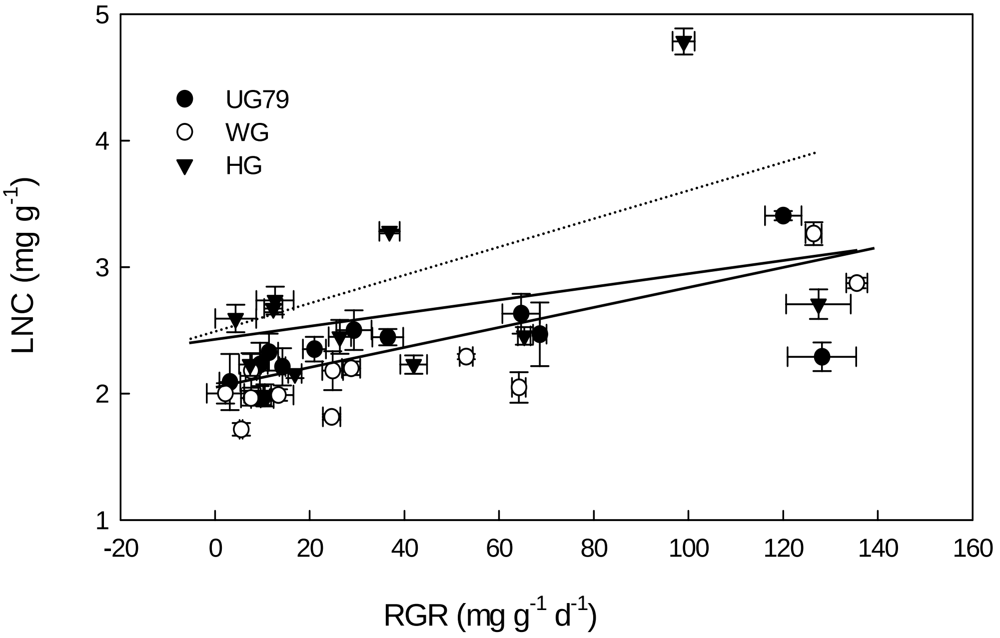

Figure 9 The relationship of RGR with leaf nitrogen content (LNC) (UG79: LNC =78.80 RGR – 146.86, n = 12, R^2 = 0.44, P = 0.019; WG: LNC = 92.61 RGR – 163.61, n = 12, R^2 = 0.79 P < 0.0001; HG: LNC = 28.09 RGR – 37.16, n = 12, R^2 = 0.28, P = 0.078). Straight lines: UG79 and WG; dashed line: HG.

grazing may alter the drought susceptibility of sites by changes of species composition. Site WG appears to be more stable under conditions of prolonged water stress, due to the high abundance of drought resistant *Stipa grandis*.

CGR and LAI

Differences in ANPP must ultimately be reflected in differences in CGR, however this parameter was highly variable over time and between years, rendering simple statements about site's differences. In 2006, no green biomass was harvested at all three treatments until 112 GDD (Fig. 1), while normal growth starts in this ecosystem usually in the middle of April (Bai et al., 2004), indicating that in 2006 soil available water was the most important factor controlling onset of growth in this ecosystem. Due to the presence of some cool season forbs, e.g., *Artemisia frigida* and *Potentilla acaulis* at site HG, CGR was higher at site HG at near end of growing season, when

GDD was larger than 2000 whereas grasses at sites UG79 and WG have already stopped growing due to phenological restriction (Bai and Xu, 1994), while higher CGR at sites UG79 and WG was observed at the middle of season, indicating that the phenology of plants is another important factor, which can determine when plants have high CGR. Development of leaf area is a major determinant of canopy photosynthesis and plant productivity (Leriche et al., 2001), as illustrated by our results that biomass increments were strongly related to leaf development (Fig. 3). LAI, controlling both primary productivity and evapotranspiration rate, is one of most frequently measured parameter in grassland systems and reflects the capacity of a plant community for carbon assimilation and water loss. LAI at site HG was significant lower than that of site UG79, suggesting that a close coupling between leaf area index and carbon assimilation. However, soil water availability, through its effect on leaf stomatal conductance, could also restrict photosynthesis (Anten and Hirose, 2003). Leaf shedding is one common strategy to reduce water losses (Sinclair, 2000). Our results are in agreement with that contention, and plants started to shed leaves for survival during a long period of drought, as evidenced by a lower LAI (Fig. 2) during the severe drought period in 2004. In addition, plants can adjust the total plant density to adapt drought, as our results showed that total plant density decreased at all three site after drought (Chapter 3, Table 2). Many perennial grasses, including some forbs, may well experience episodes of severe drought that must be survived to allow subsequent production. The avoidance of plants death by adjusting plant density and/or shedding leaves could have a substantial long-term benefit for perennial grassland productivity.

RGR, NAR, SLA, LWR and LNC

The reduction of leaf area (Fig. 2) and root system (See Chapter 5, Table 2) resulted in low total carbon gain and finally low productivity at site HG. But why was the productivity at site UG79 significantly higher than at site WG in a year of average rainfall, 2004, while no significant differences between both sites were observed in the dry years. It can be anticipated that ANPP is affected by the fraction of solar radiation intercepted, the nitrogen availability and the water supply during the growing season (Leriche et al., 2001; Anten and Hirose, 2003; Galmés et al., 2005; Warren and Adams, 2005; Oikawa et al., 2005). Due to the fact that LAI was usually less than 1 in this steppe ecosystem (Fig. 2) the usable incident solar radiation did not differ between the investigated sites.

Our results showed that LWR at site WG was consistently higher than at the other two sites. This was mainly due to different species composition between sites. *L. chinensis* and *S. grandis* which have higher leaf investment are strongly dominant at site WG. In a simple expression, RGR is factorized into NAR, LWR and SLA (Hirose, 1988; Warren and Adams, 2005). Many experiments have demonstrated that the single factor that best explained differences in RGR was SLA (Garnier, 1992, Wright and Westoby, 2000 and 2001). In opposite to this argumentation, no relationship between RGR and SLA was found in this experiment. However, we found a positive relationship of RGR with LWR and NAR (Fig. 8). Similar to our findings, Warren and Adams (2005) found no relationship of RGR with SLA. Indeed, the relative importance of SLA and NAR for the determination of RGR depends on irradiance, namely a trade-off between these components as a function of daily irradiance (Shipley, 2002). On the other hand, it has been shown that the three components of RGR are all strongly affected by the nitrogen nutrition, and the increase of NAR, LWR and SLA are strongly dependent on nitrogen concentration (Hirose, 1988). Warren and Adams (2005) defined three components of RGR based on nitrogen, and RGR is the product of leaf nitrogen productivity, LNC and LWR. In our present experiment, we found a positive relationship between RGR and LNC (Fig. 9) suggesting that plant available nitrogen was a critical factor determining ANPP (Gulmon and Chu, 1981; Hirose and Kitajima, 1986). Low LNC at site WG restricted plant growth and leaf area development in 2004, which lead to lower ANPP of site WG, compared to site UG79. However, low water availability reduces soil N mineralisation (Anten and Hirose, 2003; Martín et al., 2001) and availability to plants and the very dry weather conditions in 2005 and 2006 systematically slowed down growth in all treatments. Therefore, the N lack hypothesis is not supported by the high

LNC in 2006. Greater precipitation variability (changes in rainfall pattern, independent of seasonal amount), increased soil moisture variability and reduced mean soil water content (Appendix 6), which resulted in increased plant water stress and decreased productivity (Fay et al., 2003; Pandey and Singh, 1992).

Our conclusions for Inner Mongolia semi arid steppe ecosystem are as follows: in support of our first hypothesis that heavy grazing significantly reduced ANPP, and no compensatory and overcompensatory growth was observed, and rainfall variability and grazing intensity interactively control the formation of ANPP; in opposite to our second hypothesis that RGR are indeed positive related to LWR, NAR and LNC, however no relationship between RGR and SLA was observed, and differences of ANPP between sites UG79 and WG will be best explained by the difference of LNC. When summer grazing is involved in functional processes, the mechanism of the formation ANPP are more complex.

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Belowground Net Primary Productivity and Biomass Allocation is Affected by Land Use Management

Introduction

Non-managed and extensively managed native grassland accounts for more than half of the grassland world-wide, represents a significant contribution to global soil carbon storage (Schimel, 1995) and is of special significance for China, where grassland accounts for more than 400 M ha compared to 120 M ha of arable land.

Root biomass of grasslands often exceeds aboveground standing biomass by factors of two to thirty (Sims and Singh, 1978; van der Marrel and Titlyanova, 1989; Jackson et al., 1996; Huang et al., 1988; Scurlock et al., 2002; Chen et al., 2006) and root growth and turnover are of vital importance for the soil organic matter and nutrient pools in semi-arid steppe ecosystems (Gill et al., 1999).

Precise estimates of net primary productivity (NPP) are required for understanding patterns and controls of grasslands as affected by climate and management changes (Scurlock et al., 1999). Methods for estimating aboveground net primary productivity (ANPP) are more or less well established (Singh et al., 1975; Scurlock et al., 2002) and comprehensive ANPP estimates are available for the Inner Mongolian grassland (Xiao et al., 1995; Ni, 2004; Bai et al., 2004), while estimates of annual root production are difficult as the root system is subject to simultaneous growth and turnover (Dahlman and Kutschera, 1965; Aerts et al., 1989; Milchunas and Lauenroth, 1992, 2001; Gill and Jackson, 2000). Ni (2004), compiling data from soil pits and coring, gave BNPP estimates of 77 to 97% of total NPP for Inner Mongolia grassland. However, estimates of BNPP from ^{14}C turnover measurements or ingrowth cores indicate a lower portion from 50 to 60% of total NPP (Milchunas and Lauenroth, 1992; Neill, 1992; Milchunas et al., 2005).

Grassland of Inner Mongolia is subject to an increased grazing pressure by sheep and goats and is partially degraded (Zhou et al., 2006). About 70% of the grassland in our study area is considered as being degraded (Tong et al., 2004). Effects of grazing on BNPP are much less well understood than those on ANPP and species composition. Pot experiments showed that frequent clipping may dramatically decrease root growth (Biswell and Weaver, 1933; Allsopp, 1998; Ferraro and Oesterheld, 2002), but these findings are difficult to transfer to field conditions as natural grazing has multiple effects on species composition, soil compaction, generation of nutrient patches and changes in tillering habit. Consequently, field experiments gave a much less distinct picture on the effects of grazing on BNPP and grassland root system in general. Some studies illustrated negative effects of grazing or defoliation on belowground biomass (Milchunas and Lauenroth, 1989; Holland and Detling, 1990; Olson and Wallander, 1997; Biondini et al., 1998; Engel et al., 1998; Wang and Wang, 1999) while other studies showed non-significant (McNaughton et al., 1998; Pucheta et al., 2004) or even stimulatory effects (van der Marrel and Titlyanova, 1989; Frank et al., 2002).

Neither information about BNPP based on the ingrowth core method nor about the effect of grazing on BNPP is available for Inner Mongolia grassland. Therefore, we quantified annual root production and investigated the effects of different land-use management on BNPP and BNPP/NPP. We hypothesize that i) belowground biomass and BNPP are stimulated by moderate- and hampered by heavy grazing; and ii) BNPP is reduced stronger than ANPP resulting in a decrease of the root fraction. This makes heavily grazed site more susceptible to water deficit.

Results

Maximum BGB from 0-100 cm soil depth varied from 1632 to 2677 g m^{-2} in 2004, 1487 to 2390 g m^{-2} in 2005 and 1666 to 2465 g m^{-2} in 2006 and was not significantly different among the three years (Table 1). The interaction between years and grazing treatments was not significant and, pooled over years, BGB significantly decreased with increasing grazing intensity.

Live root DW exhibited distinct seasonal dynamics in 2005 and 2006 (Fig. 1). Noteworthy, the peak values of live root DW at the three sites were quite similar in both years occurring between 160 and 180 days of the year. The decline of live root DW was less pronounced in 2006 compared to 2005. In both years, live root DW was lower at site HG compared to that at the other two sites, while differences between treatments UG79 and WG were obvious in 2005 but not that much in 2006. Between the last sampling date of 2005 and the first of 2006, live root DW decreased slightly at site WG, increased slightly at site HG and decreased substantially at site UG79.

The effect of grassland management on ΔBGB was consistently observed in all three years. ΔBGB was significantly different between grazing treatments with the highest BNPP at site UG79 and the lowest at site HG (Table 2). ΔBGB at site WG ranked medium between both other grazing treatments. ΔBGB was significantly

Table 1 Maximum belowground biomass (BGB) at three differently managed sites in three years.

	--------- BGB (g m^{-2}) ---------			
	2004	**2005**	**2006**	**Average**
UG79	2677 ± 184	2390 ± 163	2465 ± 139	**2529 ± 97 a**
WG	2030 ± 147	1866 ± 113	2179 ± 59	**2032 ± 71 b**
HG	1632 ± 108	1487 ± 47	1666 ± 91	**1602 ± 54 c**
Average	**2113 ± 116 A**	**1914 ± 105 A**	**2103 ± 89 A**	

Factor	**df**	**Mean squares**	**P**
Year (Y)	2	286470	0.146
Site (S)	2	5132620	<0.001
Y x S	4	78699	0.703

UG79: protected from grazing since 1979; WG: winter-grazed; HG heavily grazed, further information, see Material and Methods.

Significant differences between sites and years are indicated by different small and capital letters, respectively.

Mean ± 1 s.e., n = 10 (2004), 7 (2005), and 8 (2006).

higher in 2005 compared to 2004. These differences in ΔBGB between the three sites were basically confirmed by BNPP estimates based on ΔLRB and ARB, but BNPP estimates were substantially lower compared to that by ΔBGB (Tables 2). ΔLRB at site UG79 was significantly higher than at sites HG and WG in 2005 and 2006 (Table 2). ΔLRB at site WG was similar to that at site HG in 2005 and significantly higher in 2006. As indicated by the significant interaction between years and sites (Pr>F: 0.049), the effect of year was not consistent. No differences of ΔLRB between both years were found at site HG, while ΔLRB was significantly higher in 2006 compared to 2005 at site WG and significantly lower in 2006 than in 2005 at site UG79. BNPP estimated as ARB of ingrowth cores, again, showed the same ranking between sites

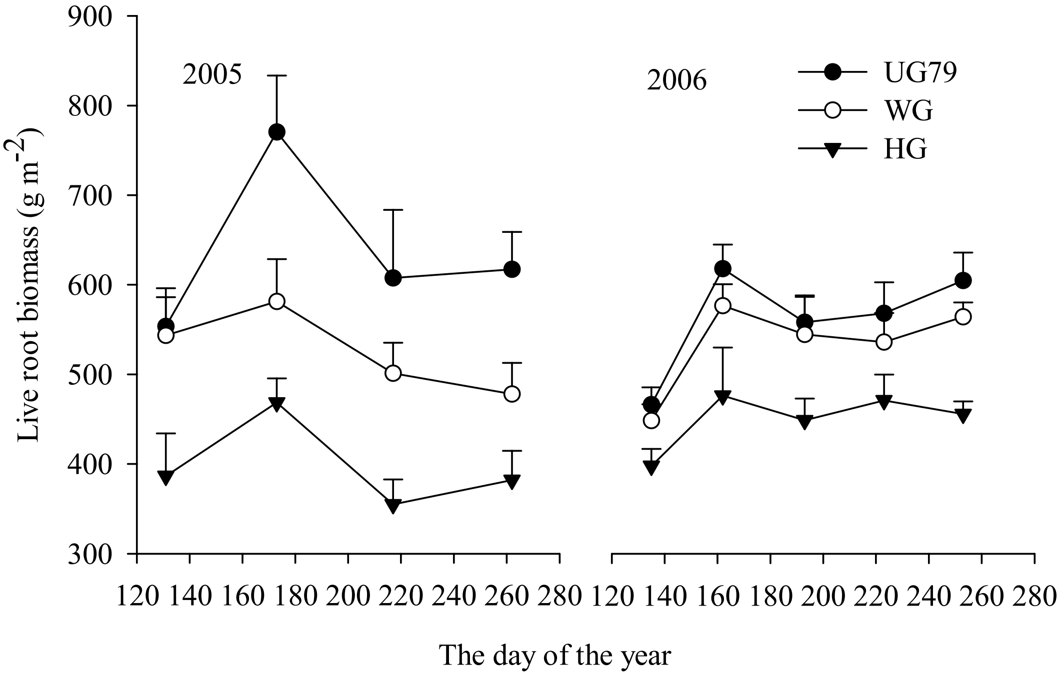

Figure 1 Seasonal dynamics of live root DW (0-100 cm) at three differently managed sites in 2005 (a) and 2006 (b). UG79: ungrazed since 1979; WG: grazing only during the winter time; HG: heavily grazed, mean ± 1 s.e., n = 7 (2005) and n = 8 (2006).

with the highest ARB at site UG79 and the lowest at site HG. ARB was higher than ΔLRB except of that at site UG79 in 2005. At all three sites ARB was higher in 2006 than in 2005. Concluding, all estimated BNPP values indicate a significant decreased of BNPP with increasing grazing intensity. Different methods give numerically different values of BNPP with the highest values of ΔBGB and the lowest of ΔLRB. Compared to the long-term ANPP data of this grassland system which ranges from 100 to 280 g m^{-2} (Bai et al. 2004), ANPP was rather low in the dry years 2005 and 2006 (Table 3). It was expected that BNPP/NPP differs between grazing treatments. With the exception of results in 2004, $f_{\Delta BGB}$ was not different between grazing treatments, while $f_{\Delta LRB}$ and f_{ARB} were lower under heavy grazing compared to the ungrazed control in 2005. Similarly in 2006, the effect of grazing on BNPP/NPP was not consistent for the different estimates. $f_{\Delta LRB}$ at site HG was lower compared to that at site UG79, whereas f_{ARB} and $f_{\Delta BGB}$ were not different between grazing treatments.

In both years, $f_{\Delta BGB}$ was substantially higher compared to f_{ARB} and $f_{\Delta LRB}$. Pooled over treatments, $f_{\Delta BGB}$ ranged from 61% (2004) to 77% (2005, 2006), whereas BNPP/NPP

Table 2 Estimated BNPP (g m^{-2}) of three differently managed sites.

	Soil auger							Ingrowth core		
	ΔBGB				**ΔLRB**			**ARB**		
	2004	**2005**	**2006**	**Average**	**2005**	**2006**	**Average**	**2005**	**2006**	**Average**
UG79	380 ± 58	464 ± 104	366 ± 82	**399 ± 44 a**	217 ± 39 a A	152 ± 13 a B	182 ± 21	180 ± 10	203 ± 14	**193 ± 9 a**
WG	191 ± 29	320 ± 35	293 ± 28	**260 ± 21 b**	80 ± 18 b B	128 ± 8 b A	106 ± 11	142 ± 5	171 ± 3	**157 ± 5 b**
HG	147 ± 42	271 ± 48	230 ± 39	**208 ± 26 b**	82 ± 20 b A	78 ± 25 c A	80 ± 16	107 ± 7	139 ± 8	**124 ± 7 c**
Average	**239 ± 31B**	**352 ± 42 A**	**296 ± 32 AB**		126 ± 95	119 ± 55		**143 ± 8 B**	**171 ± 8 A**	
Factor		**df**	**P**		**df**	**P**		**df**	**P**	
Year (Y)		2	0.049		1	0.703		1	< 0.0001	
Site (S)		2	< 0.0001		2	< 0.0001		2	< 0.0001	
Y × S		4	0.884		2	0.049		2	0.886	

Estimates are based on the difference between maximum and minimum total belowground DW (ΔBGB) and live root DW (ΔLRB) or from accumulated root biomass (ARB) of ingrowth cores. Two-way ANOVA was performed for ΔBGB, ΔLRB and ARB. Significant differences between sites and years are indicated by different small and capital letters, respectively. Mean ± 1 s.e., n = 10 (2004), 7 (2005), and 8 (2006).

Table 3 Aboveground net primary productivity (ANPP, g m^{-2}), predicted fraction of BNPP/NPP, f_{M1}, f_{M2}, f_{M3}, and empirical estimates of BNPP/NPP, based on ΔBGB ($f_{\Delta BGB}$), ΔLRB ($f_{\Delta LRB}$) and ARB of ingrowth cores (f_{ARB}) at three differently managed sites in three continuous years. One-way ANOVA and Tukey test for multiple comparisons were performed within one parameter in the same year. Significant differences between sites are indicated by different small letters. For abbreviations see Table 2.

	ANPP	f_{M1}	f_{M2}	f_{M3}	$f_{\Delta BGB}$	$f_{\Delta LRB}$	f_{ARB}
2004							
UG79	176 a	0.52 b	0.35 b	0.58 ab	0.69 a	-	-
WG	126 b	0.60 a	0.42 a	0.59 a	0.60 b	-	-
HG	122 b	0.60 a	0.43 a	0.55 b	0.55 c	-	-
2005							
UG79	112 a	0.62 b	0.45 b	0.66 a	0.80 a	0.66 a	0.62 a
WG	99 a	0.65 ab	0.48 b	0.63 a	0.76 a	0.44 c	0.58 b
HG	77 b	0.70 a	0.54 a	0.63 a	0.78 a	0.52 b	0.58 b
2006							
UG79	107 a	0.63 b	0.46 b	0.67 a	0.77 a	0.58 a	0.66 a
WG	96 a	0.65 b	0.49 b	0.67 a	0.76 a	0.57 a	0.64 a
HG	75 b	0.70 a	0.54 a	0.67 a	0.76 a	0.50 b	0.66 a

- No data available

f_{M1}, f_{M2}, f_{M3} are predicted values of BNPP/NPP by the model of Gill *et al.* (2002), see Materials and Methods.

estimated by the other two methods varied from 54-65%. $f_{\Delta BGB}$ was 21-72% (2005) and 15-52% (2006) higher compared to $f_{\Delta LRB}$ and f_{ARB}.

Model 1, in which the original parameters of Gill et al. (2002) were used (see Material and Methods) predicts BNPP/NPP for treatment UG79 which were similar to

Table 4 Average and minimum and maximum live root fraction, calculated and predicted root turnover (yr^{-1}) and turnover time (yr) and predicted BGB at three differently managed sites in 2005 and 2006. Predicted values are from the model of Gill *et al.* (2002).

		Live root fraction	Turnover (yr^{-1}) Turnover time (yr)		Predicted BGB[3]
		Average (Min.-Max.)	This study[1]	From Gill model[2]	
2005	UG79	0.31	0.23		1021
		(0.26-0.36)	(4.3)		
	WG	0.32	0.24	0.30	1011
		(0.28-0.36)	(4.1)	(3.4)	
	HG	0.31	0.23		993
		(0.26 -0.36)	(4.3)		
2006	UG79	0.24	0.33		1017
		(0.22-0.26)	(3.0)		
	WG	0.27	0.30	0.30	1009
		(0.24-0.29)	(3.4)	(3.4)	
	HG	0.29	0.29		992
		(0.28-0.30)	(3.4)		

[1] Turnover was estimated from maximum live root DW and ARB (See Table 2)

[2] Turnover was estimated from the 22 year's average MAT, which varied from 0.29 to 1.10 °C (95% confidence interval), MAT was 2.2 °C in 2005. The turnover rate is 0.32 based on MAT in 2005.

[3] BGB (g m^{-2}) was predicted from ANPP, see Material and Methods.

experimentally determined f_{ARB} in both years. Further it predicts an increase of BNPP/NPP under grazing. This finding is not supported by any of the empirical estimates of BNPP/NPP. Live root DW accounted for about 30% of BGB in 2005 irrespective of grazing intensity, was lower in 2006 and tended to be higher under heavy grazing (29%) compared to that at sites UG79 (24%) and WG (27%) (Table 4). Rather than using a Live BGB/BGB of 0.6, therefore, experimental data of Live BGB/BGB were used in Model 2. Predicted BNPP/NPP was lower compared to that of Model 1, and again increases under grazing. In Model 3, experimental data of BGB and Live BGB/BGB were used. Model 3 gave values of BNPP/NPP which were lower at site HG compared to those at the other two sites in 2004, slightly higher at site UG79 compared to that at sites WG and HG in 2005 and predicts no grazing effect on BNPP/NPP in 2006. Model 3 further predicted a lower BNPP/NPP in 2004 for all grazing treatments and an increase in 2006 compared to 2005 at sites WG and HG. Model 3 is consistent in terms of grazing effects when compared with $f_{\Delta\mathrm{BGB}}$. $f_{\Delta\mathrm{BGB}}$ was substantially reduced under grazing in 2004, slightly reduced in 2005 and not different between sites in 2006. However $f_{\Delta\mathrm{BGB}}$ was at least 10% higher compared to Model 3 estimates in 2005 and 2006 and for site UG79 in 2004, whereas Model 3 gave very similar values of BNPP/NPP for sites WG and HG in 2004. Compared to our empirical estimates of BNPP by ARB, Model 3 gave values which are numerically similar and consistent in terms of grazing effects and differences between years.

Dicussion

BGB measured in this study is comparable to published values (Liu and Li, 1987; Huang et al., 1988; Wang and Wang, 1999; Chen et al., 2006) and indicates BGB is quite large compared to yearly shoot dry mass formation which varies between 100 and 280 g m^{-2} (Bai et al., 2004).

Maximum BGB and total live root DW at site HG were significantly lower compared to that at site UG79 (Table 1, Fig. 1). The observed decrease of BGB with increasing grazing intensity is consistent with other findings (Chapin and Slack, 1979; Richards, 1984; Milchunas and Lauenroth, 1989; Holland and Detling, 1990; Olson and Wallander, 1997; Biondini et al., 1998; Wang and Wang, 1999; Chen et al., 2006) but contradictory to studies which showed non-significant (McNaughton et al., 1998; Pucheta et al., 2004) or even stimulatory effects (van der Marrel and Titlyanova, 1989;

Frank et al., 2002) of grazing on BGB. A decrease of belowground biomass under grazing is commonly explained by reduced source size of carbon assimilating organs and re-translocation of root carbohydrates to shoot meristems. The long-term impact of this decrease of BGB under heavy grazing is indicated by the low soil organic carbon concentration at site HG compared to that at sites WG and UG79 (Steffens unpublished). These results support the finding of Gill et al. (1999), who found a positive correlation between root size and SOM.

The determination of live root DW gives an estimate of the portion of BGB which is active in terms of resource acquisition and growth (Aerts et al., 1989; McNaughton et al., 1998). As separation between dead and live roots is subjective, the absolute number is difficult to compare with results from other studies, but, within one study, treatment and seasonal effects should be correctly reflected by this approach. The relatively constant fraction of live root DW/BGB of roughly 30% is contrary to results, which showed a sharp decrease of the portion of live root DW with increasing grazing intensity (van der Marrel and Titlyanova, 1989). Further, the portion of live root DW we found is much lower than the 60% found in several temperate grasslands (Jackson et al., 1997). We assume that the small portion of live root DW is due to the dry climate with low root turnover rates in this semi-arid environment.

Hui and Jackson (2006) compiled biomass partitioning data of grasslands from contrasting climates and found that BNPP/NPP varied from 0.4-0.86. Generally BNPP/NPP was smaller in savanna and humid savanna ecosystems and larger in cold and cold desert steppes. Ni (2004) compiling data from Inner Mongolia grassland gave BNPP/NPP estimates of 77 to 97%. We used three algorithms to estimate BNPP and BNPP/NPP from experimental data. The classical BNPP estimation from the difference between maximum and minimum root DW (Dahlman and Kutschera 1965) relies on an appropriate sampling schedule to determine the 'real' minimum and maximal root DW. As indicated by the dynamics of live root DW (Fig. 1), the peak root biomass time was quite early in both years (between 160-180 days of the year) and the minimum at the beginning of the vegetation period in 2006 but not on sites WG and HG in 2005. In this grassland, the identification of 'real' minimum and maximum values of live root DW from soil auger samples, therefore, seems to require very early sampling (even before start of shoot growth). Due to the late start of field work in 2004, estimates of BNPP, which were substantially lower compared to that of other years, are therefore likely less reliable. Summarizing, the maximum-minimum method is practical to detect treatment and year effects when frequent sampling during the growing season is done. BNPP and BNPP/NPP most likely are overestimated when ΔBGB is used rather than live root DW.

The ingrowth core method gives data of time-integrating root growth, is easy to handle and suitable to quantify root production on the field scale (Steingrobe et al., 2000) and fine root production in different seasons and at different sites (Hertel and Leuschner, 2002). ARB was mostly higher compared to ΔLRB (Table 2) and f_{ARB} varied between 0.58 and 0.66, values which were numerically very similar to those estimated by Model 3 (Table 3). Some methodological problems, anyhow, must be considered:

1) The grassland root system is composed of fine and thick perennial roots, which of the latter is not included in root production data when ingrowth core samples are harvested at short time intervals. Therefore, this method will tend to underestimate the 'real' BNPP and essentially gives data on fine-root production.

2) Milchunas et al. (2005) and Hendricks et al. (2006) argued that, due to architectural propensity of roots for vertical-directional growth and simultaneous root production and mortality, BNPP is likely underestimated compared to estimates gathered from ^{14}C decay or minirhizotrons. Higgins et al. (2002) emphasized that BNPP is overestimated compared to minirhizotron data, partly due to competition-free environment and low soil bulk density. In our study, we did our best to overcome some of these problems, e.g., we drilled holes before winter, such that roots could recover from damage, re-filled the same soil at a comparable soil density, installed mesh-bags at 45° rather than vertically and harvested in short interval (3-4 weeks).

It can be anticipated, that growth of roots and transpiring shoot organs is balanced and therefore, a rigorous test of the reliability of root growth data from ingrowth cores is the inspection of correlation between cumulative root growth and leaf DW. As illustrated in Fig. 2, leaf DW and cumulative RLD were highly significantly correlated in both years and differed between grassland sites. At site HG a higher RLD was required to support the same unit of leaf mass compared to sites UG79 and WG. So far, the correlation between leaf DW and cumulative RLD from ingrowth cores have not been reported before. The fairly close correlation between leaf DW and accumulated root biomass of ingrowth cores corroborates the functional equilibrium theory (Brouwer, 1983) that suggests a balance between root and shoot growth (Körner and Renhardt, 1987; Schulze et al., 1996; McNaughton et al., 1998; Farrar and Jones, 2000). Based on this correlation between RLD and leaf DW, we conclude that the ingrowth core method is a feasible and reliable method for investigating BNPP in this steppe ecosystem from a physiological aspect.

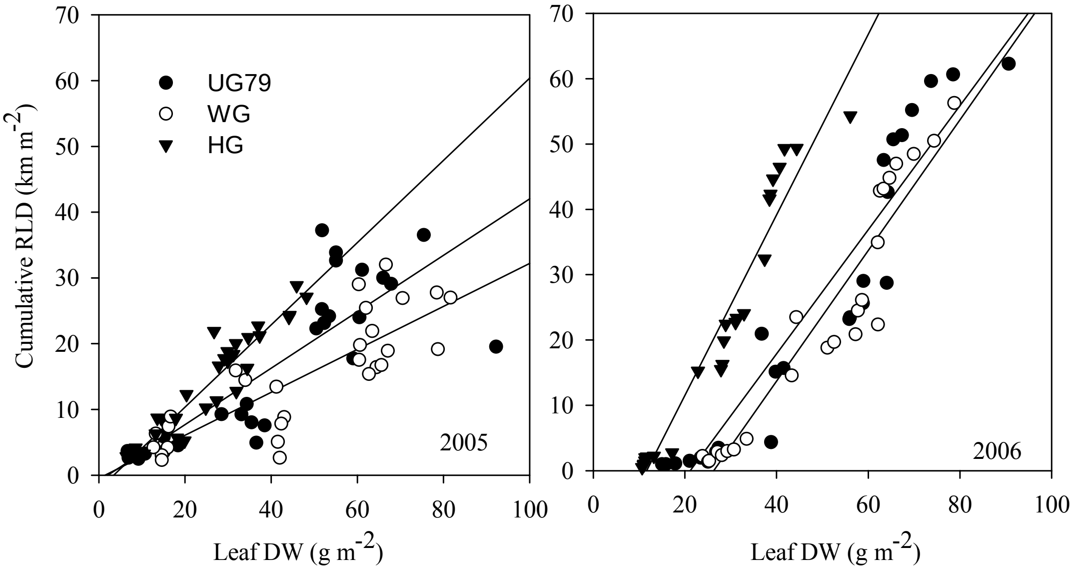

Figure 2 Correlation between leaf DW and cumulative root length density (RLD) of ingrowth core samples in 2005 and 2006. Data are from 4 (2005) and 3 (2006) subsequent sampling dates, n = 28 (2005) and 24 (2006). Symbols and abbreviations as Fig. 1.

We further propose that ARB is the most reliable estimate of BNPP and suggest that BNPP/NPP decreases with increasing grazing intensity. This effect was evident in 2005, but contrarily, in 2006, the grazing effect on BNPP/NPP could only be confirmed by ΔLRB, while estimates from ingrowth core data indicated no grazing effect. Our findings are relevant and contrary to the very few data available on the effect of grazing intensity on BNPP/NPP. Pucheta et al (1998, 2004) found a slight increase of BNPP/NPP under grazing compared to a long-term exclosure. Sims and Singh (1978) investigated the effect of grazing on BNPP/NPP in tall- and shortgrass prarie and found mostly a strong increase of BNPP/NPP under grazing.

Considering the two years with low ANPP and severe drought during the growth period, BNPP/NPP was apparently more or less similar and likely varied between 0.50 and 0.70. Our estimates are higher than estimates of 50% in a native semi-arid short-grass steppe in North America (Milchunas and Lauenroth, 1992) and the Konza prarie research natural area (Hayes and Seastedt, 1987).

Additionally to comparing our results with the few empirical data sets available from semi-arid grasslands, the model of Gill et al. (2002) was used to embed our results into the more general prediction of BNPP from climatically quite contrasting environments. The original algorithm (Model 1) was developed to predict BNPP/NPP of grassland of different climatic zones and it would be surprising, if the robust and effective approach were able to detect grazing effects within one small-scale region. In both years, predicted BNPP/NPP of site UG79 was similar to that experimentally determined by the ingrowth core method (f_{ARB}) and illustrates that Model 1 apparently is able to predict BNPP/NPP of grassland under the long-term exclosure condition in this region, at least for the two dry years investigated. Obviously, predicted BNPP/NPP at sites WG and HG was overestimated by Model 1. This discrepancy can be due to erroneous estimation of BGB as a linear function of ANPP, Live BGB/BGB or turnover. A correction of Live BGB/BGB (Model 2) did not improve the prediction, resulted in substantially lower estimates of BNPP/NPP and, again, predicted increases of BNPP/NPP under grazing. In order to test, if the turnover prediction is compatible within this grassland system, Model 3 was applied and gave values of BNPP/NPP which agreed more or less well with f_{ARB}. Considering the turnover, the empirical estimation based on ARB (Table 2) and maximum live root DW, varied from 0.23-0.33 yr^{-1}, was lower in 2005 than in 2006 and basically quite similar to the value of 0.3 of the empirical model of Gill et al. (2002) (Table 4). Consequently, the predicted BGB of that model must be different from the experimental data. As summarized in Table 4, predicted maximum BGB was roughly only half of that found at the three sites (Table 1). From these findings we conclude that the model of Gill et al. (2002) needs to be parameterized for the relationship between ANPP and BGB in this steppe ecosystem.

Finally, it must be stated that any rigorous test of BNPP estimates must include a detailed analysis of aboveground biomass and photosynthetic capacity. Any increase of BNPP/NPP for a given ANPP will require a substantial increase of photosynthetic carbon gain. With leaf area size and leaf N in combination with seasonal temperature and light and water availability, the potential of total biomass production can be roughly estimated. Furthermore, data from wet years are highly required in order to test if BNPP/NPP is lower compared to the dry years 2005 and 2006.

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Belowground Net Primary Productivity and Biomass Allocation in relation to Nitrogen and Water Supply

Introduction

The productivity of the Inner Mongolian semi-arid grassland ecosystem is mainly depending on rainfall amount and distribution (Bai et al., 2004). Additionally, aboveground net primary productivity (ANPP) of this grassland system can be increased by additional N application (Zhang et al., 2004). Similar responses of grassland systems to increased precipitation or N supply have been illustrated by DiTommaso and Aarssen (1989), Ram et al. (1991), Seagle and McNaughton (1993), Fahnestock and Detling (1999), and Camill et al. (2004). However, responses of belowground net primary productivity (BNPP) to N and water supply under field conditions have been investigated rarely and reported effects are inconsistent. Ram et al. (1991) found a decrease of root biomass after two-year's N application, while Camill et al. (2004) found no fertiliser effect on BNPP.

Root growth, morphology and physiology are affected by drought and N fertiliser application (Hayes and Seastedt, 1987; Lauenroth et al., 1987; Boot and Mensink, 1990; Ryser and Lambers, 1995; Craine et al., 2001). Under conditions of low water and nutrient availability, above- and belowground biomass is lower in absolute terms, and the portion of carbon allocation to belowground organs is usually increased (Poorter and Nagel, 2000). Therefore, we suppose that NPP is not as much affected as ANPP by N fertiliser and water input due to the shift in relative allocation of carbon between shoot and root, and the reported increase of ANPP by N supply combined with irrigation is partially based on reduced investment into BNPP.

Root traits of grassland species contrast each other in terms of resource acquisition and respond to soil and climatic variation (Zobel, 1992; Busso et al., 2001; Craine et al., 2001). This can finally lead to site differences in productivity (Wilson and Tilman, 1991). As grazing affects the species composition, information about N and water effects on BNPP and biomass partitioning must consider the interaction between resource manipulation (by N and water application) and grassland management.

Studies on effects of small amounts of N fertiliser application and irrigation and the interaction of these resources manipulations on BNPP and carbon partitioning have significant implications for the management of Inner Mongolia grassland. In the past four decades, this ecosystem has been increasingly degraded due to drastic increases of livestock (Xie and Wittig, 2004; Zhou et al., 2006). 80% of natural grassland has exhibited certain degradation and 42% of the area is already badly degraded. From a practical point of view, de-stocking to low, sustainable grazing intensity is one restoration strategy (Katoh et al., 1998), however, for severely degraded sites, other measures, such as prohibition of grazing or application of small amounts of N fertiliser may accelerate the restoration processes (Zhang et al., 2004). We suppose that small amount of N fertilizer application can enhance NPP, which in turn would speed up the restoration process. However, N effects strongly depend on the soil water availability and, in order to consider this aspect, N effects were investigated on control and irrigated plots. It must be mentioned that irrigation was only intended to simulate wet year's precipitation and is not considered as a realistic management option. To the best of our knowledge, there is no systematic field study on the combined effect of N and water supply on BNPP, NPP and biomass allocation of native semiarid grassland. Therefore, we hypothesize that (1) low amounts of N fertiliser increase ANPP, BNPP and NPP under dryland conditions, where no additional water was supplied; and (2) NPP is not as much affected as ANPP by N fertiliser and water input due to the shift in relative allocation of carbon between shoot and root, and the reported increase of ANPP is partially due to reduced investment into BNPP.

Results

Belowground biomass (BGB) and live root fraction

BGB was significantly higher at site MG than at HG, while live root fraction exhibited the reverse trend and was significantly higher at site HG than at site MG (Tables 1 and 2). BGB was lower with N fertiliser application compared to unfertilised plots when sites were irrigated ($P = 0.0499$).

ANPP, BNPP and NPP

ANPP was interactively affected by N and water supply (Table 1), N addition significantly increased ANPP under irrigated but not dryland conditions (Fig. 1 a). Irrigation significantly increased ANPP, irrespective of N levels. For BNPP, no two-factor interactions were found (Table 1). BNPP significantly decreased from 168 g m^{-2} to 148 g m^{-2} with N supply ($P = 0.0068$) and the decrease of BNPP without

Table 1 The probability (Pr>F) of three factors ANOWA results on belowground biomass (BGB) (g m^{-2}), live root proportion (LRP) (%), aboveground net primary productivity (ANPP), belowground net primary productivity (BNPP), total net primary productivity (NPP), the fraction of BGB (f_{BGB}), live root biomass (f_{LR}) and BNPP (f_{BNPP}). S = site, N = nitrogen, W= water. *P < 0.05, ** P < 0.001 and *** P < 0.0001, NS: no significant difference.

Sources	Df	BGB	LRP	ANPP	BNPP	TNPP	f_{BGB}	f_{LR}	f_{BNPP}
S	1	*	*	NS	NS	NS	NS	NS	NS
N	1	*	NS	**	*	NS	*	*	***
W	1	NS	NS	**	***	***	**	**	***
S*N	1	NS	NS	NS	NS	NS	NS	NS	NS
S*W	1	NS	NS	*	NS	NS	NS	NS	NS
W*N	1	NS	NS	*	NS	NS	*	*	**
S*W*N	1	NS	NS	NS	NS	NS	NS	NS	NS

Table 2 Belowground biomass (g m^{-2}) and live root fraction were affected by irrigation and N fertiliser. Significant differences between sites are indicated by different small letters, n = 4. MG = moderately grazed site; HG = heavily grazed site.

	MG					HG				
	W0N0	W0N1	W1N0	W1N1	Mean	W0N0	W0N1	W1N0	W1N1	Mean
BGB	1479	1476	1754	1523	1558a	1291	1263	1497	1386	1359b
LRP	0.28	0.36	0.43	0.35	0.36b	0.43	0.43	0.48	0.47	0.45a

irrigation was less proounced than that with irrigation (Fig. 1b). BNPP significantly increased from 109 g m^{-2} to 207 g m^{-2} with water supply ($P < 0.001$) (Fig 1 b). Irrigation significantly increased NPP irrespective of N levels ($P < 0.0001$), while N supply had no significant effect on NPP ($P = 0.1119$) (Table 1, Fig 1 c).

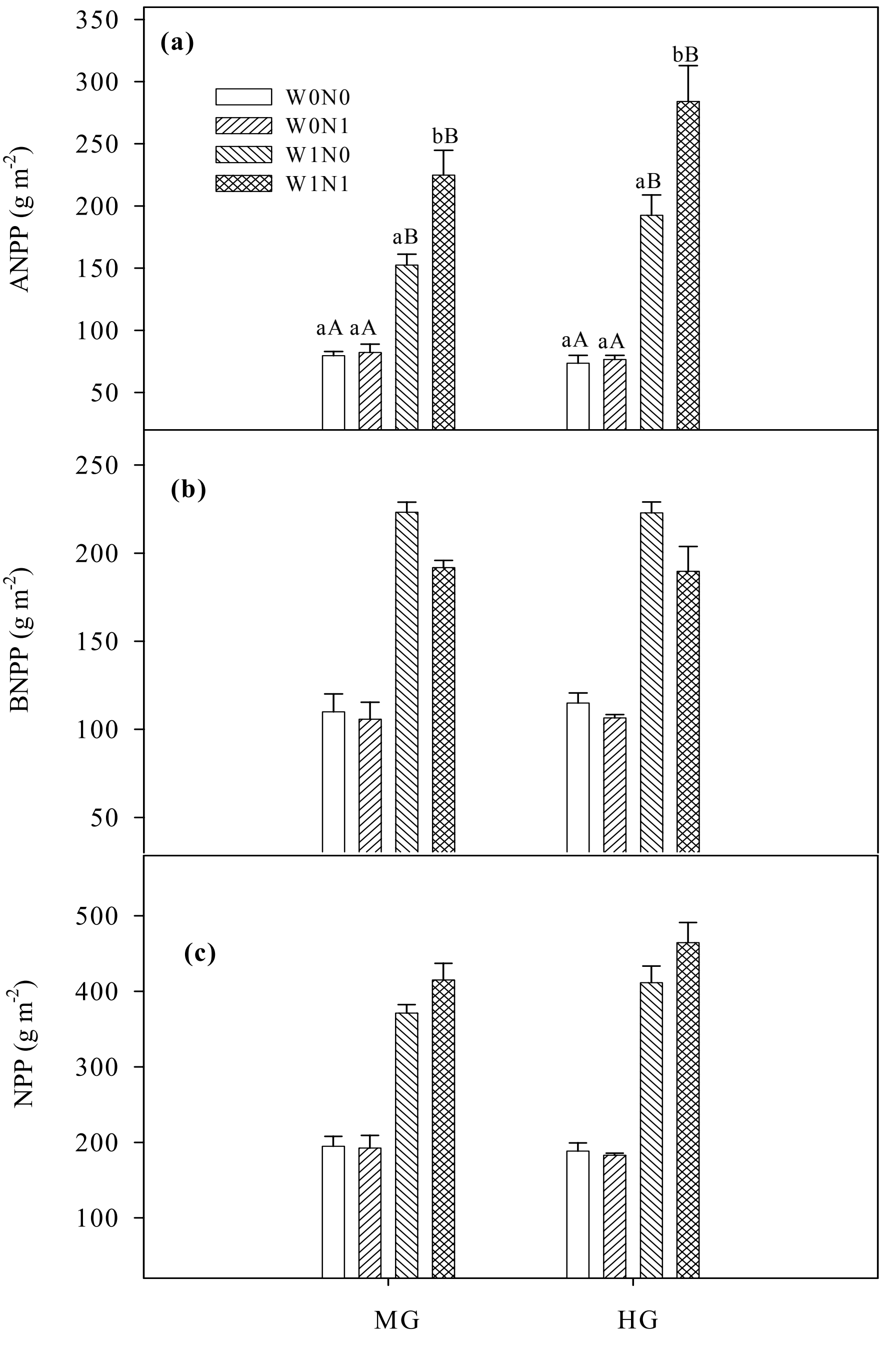

Figure 1 Aboveground net primary productivity (ANPP), belowground net primary productivity (BNPP) and total net primary productivity (NPP) as affected by irrigation and N fertiliser treatments (a-c) at two sites, respectively. Error bars denote standard errors. The unit of the data is g m^{-2}. Significant differences between N and water effects are indicated by different small and capital letters within one site, respectively, n= 4. MG = moderately grazed site; HG = heavily grazed site.

Root crop growth rate

Root growth exhibited distinct seasonal dynamics (Fig. 2). In general, crop growth rate (CGR) of roots was low at the beginning and end of the growing season. The highest CGR occurred at the second sampling date before grass anthesis at site MG, while it occurred at the third sampling date before main forbs anthesis at site HG. The highest CGR was found in treatment W1N0 with 3.0 and 3.4 g m^{-2} d^{-1} at sites MG and HG, respectively. Irrigation had significant effects on CGR. In general, CGR of the irrigated treatments was significant higher than that of non-irrigated treatments throughout the growing season. No significant difference of CGR between N1 and N0 was observed at all the sampling dates under the non-irrigated condition. CGR of W1N0 was significantly higher than that of treatment W1N1 at site WG at the third sampling date and at site HG at the second sampling date. BNPP of treatment W1N0 was the highest at both sites.

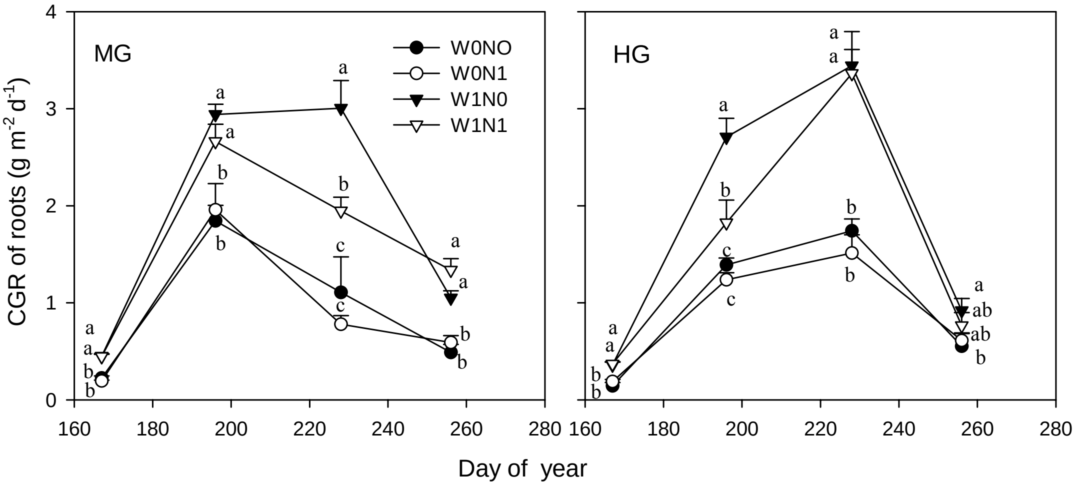

Figure 2 Crop growth rate (CGR) (g m^{-2} d^{-1}) of roots in ingrowth cores was affected by irrigation and N fertiliser at two sites. The error bars represent standard error. ANOVA was performed for each sampling date, and different small letters indicate significant differences between treatments. MG = moderately grazed site; HG = heavily grazed site.

Fraction of BGB (f_{BGB}), live root biomass (f_{LR}) and BNPP (f_{BNPP})

f_{BGB} varied from 0.85 to 0.95 was interactively affected by water and N (Tables 1 and 3). Water supply significantly decreased f_{BGB} and was stronger reduced with than without N supply (N1: $P < 0.0001$; N0: $P = 0.0063$). N supply had no significant effect on f_{BGB} without irrigation ($P = 0.8657$), whereas f_{BGB} significantly decreased with irrigation ($P < 0.0017$). Compared to f_{BGB}, f_{LR} was numerically lower and varied from 0.69 to 0.86 and was also interactively affected by water and N. Treatment effects on f_{LR} were identical to that on f_{BGB} (Table 3). Compared to f_{BGB} and f_{LR}, f_{BNPP} was substantially lower and ranged from 0.43 to 0.60. N had no effect on f_{BNPP} of dryland plots, while it was significantly reduced under irrigated conditions (Table 3). Irrigation resulted in significant reduction of f_{BNPP} of fertilised plots, while the irrigation effect on f_{BNPP} of unfertilised plots was not significant.

Table 3 The fraction of belowground biomass (f_{BGB}), live root biomass (f_{LR}) and belowground net primary productivity (f_{BNPP}) at different managed conditions. The values are the average of two sites. Significant differences between N fertiliser and water effects are indicated by different small and capital letters, respectively, n = 4.

	W0N0	W0N1	W1N0	W1N1
f_{BGB}	0.95aA	0.94aA	0.90aB	0.85bB
f_{LR}	0.86aA	0.86aA	0.80aB	0.69bB
f_{BNPP}	0.60aA	0.58aA	0.56aA	0.43bB

Root distribution

Most roots were found in the first 10 cm of soil at both sites (Fig 3 a, b). There were small, though, significant differences between sites for root distribution in the 0-10 cm soil layer ($P = 0.0659$). Pooled over all treatments, 60 % and 55 % of roots were found in the first 10 cm soil at sites MG and HG, respectively. Only small effects of water or N supply on root distribution were observed in the 0-10 cm soil layer and irrigation tended to increase the root portion at both sites (Fig. 3). Sites and irrigation significantly interacted on root portion in 10-20 cm soil depth layer ($P = 0.0137$). Water supply had no significant effect on root distribution at site MG ($P = 0.513$), whereas a significantly higher portion of roots was found with water supply at site HG ($P = 0.005$). The portion of roots in soil depth layer 10-20 of irrigated plots was

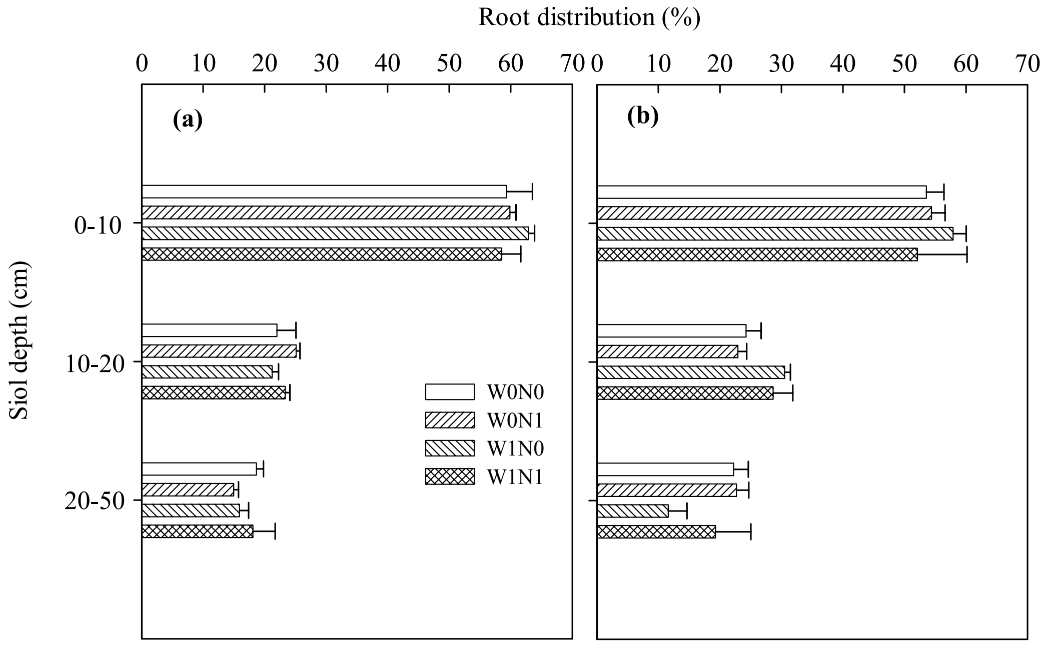

Figure 3 Root distribution based on total root dry matter (%) in different irrigation and fertiliser treatments along the soil profile at two sites. (**a**) a moderately grazed site (**b**) a heavily grazed site. Error bars denote standard errors.

significantly higher at site HG than at site MG. (HG = 30%; MG = 23%). Water supply had significant effects on root distribution in soil layer 20-50 cm ($P = 0.0456$). Root distribution in this layer was reduced by water supply (20% with water, 16% without water). Pooled over all treatments, 17% and 19% of root were distributed in this layer at MG and HG sites, respectively. However, only around 12% of root was distributed in this soil layer in treatment W1N0 at site HG.

Discussion

Irrigation and fertiliser effects on BGB and Live root fraction

After irrigation and N fertiliser application on sites protected from grazing, N supply had no effect on BGB in dryland plots, while irrigation alone or in combination with N supply tended to increase BGB at both sites (Table 2). These findings agree with those of Tilman and Wedin (1991), Hansson et al. (1992) and Fahnestock and Detling (1999), who reported positive effects of irrigation and N application on BGB of semiarid grasslands. However an increase of BGB with increasing resource availability cannot always be expected (Ram et al., 1991; Bowman et al., 1993). The high values of BGB of this semi-arid grassland with more than 1200 g DW m^{-2} can be explained by the low turn-over of root biomass due to extended periods of low soil water potential during the short growing season and very cold temperatures during the rest of the year (Milchunas and Lauenroth, 2001). As indicated by the low proportion of live root dry matter (0.28 to 0.43, and 0.43 to 0.48 at sites MG and HG, respectively), a substantial portion of BGB represents necromass, which is not functionally related to nutrient and water uptake and, thus, makes BGB to a parameter, that is only marginally reflecting grassland responses to irrigation and N supply.

Independent of irrigation and N supply, BGB was significantly lower at site HG compared to MG (Fig. 1). This finding agrees with reports of long-term decreases of BGB under heavy grazing conditions (Milchunas and Lauenroth, 1989; Snyman, 2005; Chen et al., 2006) and can be explained by the use of root carbohydrates for re-growth of shoot organs, essentially decreasing BNPP of grazed compared to ungrazed sites (Chapter 5). Further, grazing-induced changes in species composition must be considered (Snyman, 2005; Zhou et al., 2006), especially as grazing-tolerant species with lower carbon root allocation (Richards, 1993) may become dominant. At our experimental sites, the semi shrub *Artemisia frigida* and the sedge *Carex spp.* were dominant on site HG, while grasses *Cleistogenes squarrosa* and *Stipa grandis* were dominant at site MG. Information about root growth at the species level is highly required in order to dissect direct grazing effects on BGB from indirect effects via changes of species composition.

Contrary to differences in BGB between both sites, BNPP was not significantly different between site MG and HG (Fig. 1c). This discrepancy can be explained by the comparably small annual contributions of BNPP to BGB and differences between both sites in root turnover, which showed significant higher live root portion at site HG than MG (Table 2).

Irrigation and fertiliser effects on root distribution

Root distribution over depth is affected by water regimes in semi-arid zones, such that frequent irrigation or precipitation results in more shallow depths of root growth, as root grow only as deep as needed to fulfil plant resource requirement (Schenk and Jackson, 2002). Additionally, a shallow root system will establish on soil profiles, which are characterised by permanently low soil water potential of deeper soil layers.

On the other hand, rooting depth is known as one of the central adaptation mechanisms of dryland plant species and rooting depth at both sites of this study was at least 150 cm (data not shown). Our results show that root biomass in all treatments was not uniform over depth and greatest near the surface (around 60%). This result is agreement with other studies (Fitter et al., 1997; Snyman, 2005). However, the two sites have different responses to water and N supply. The effects of water and N supply on root distribution were not significant at site MG, while a trend towards a higher proportion of roots in the upper soil layers with an increasing water supply, especially at 10-20 cm soil layer, was observed at site HG (Appendix 11). These findings partially support the hypothesis that roots grow only as deeply as needed to fulfil plant resource requirement (Schenk and Jackson, 2002).

Irrigation and fertiliser effects on ANPP, BNPP and NPP

Increasing water supply by 170 mm increased ANPP more than two times compared to dryland plots, while no significant N effect was found under dryland plots, which is contrary to our hypothesis that N supply can increase ANPP at dryland conditions. On the other hand, this observation fully agrees with the contention that positive effects of N supply on ANPP can only be expected if other resources (in this case water) are not a limiting growth factor. It has also been reported that productivity (referred to ANPP in most cases) of short- and tallgrass steppe is primarily limited by precipitation and secondary by N (Lauenroth et al., 1992; Seagle and McNaughton, 1993, Varnamkhasti, 1995). A similar result was found by Zhang et al. (2004), who reported that N supply is an expedient measure to increase ANPP of this grassland system, if soil water availability is not limited during the growing season. However, it need to be stressed that irrigation is not at all a practical management option in this huge semiarid grassland but was only used in order to investigate the effect of water availability on N fertiliser effects.

BNPP is expected to be sensitive to environmental changes (e.g. annual precipitation, irrigation or fertilisation), but effects of irrigation and fertiliser application on BNPP have been reported almost exclusively in forests and agricultural crops (Ahlström et al., 1988; Majdi and Nylund, 1996; Steingrobe et al., 2001; Vamerali et al., 2003). To our best knowledge, no work considered the combined effects of water and N supply on BNPP in native grasslands. At both sites, water supply significantly increased BNPP, which was reflected by significant differences of

CGR between no-irrigated and irrigated treatments throughout the growing season (Fig. 2). However, it is in opposite to our hypothesis that N supply can significantly increase BNPP and NPP, and N supply significantly decreased BNPP and had no significant effect on NPP, which indicates a sensitive regulation of carbon allocation between shoot and root with less investment to nutrient-absorbing organs under improved nutrient supply. The increase in ANPP under irrigated conditions was mainly due to a substantial shift in carbon allocation, which is consistent with our hypothesis that N supply in combination with water had a more pronounced effect on the pattern of biomass allocation than on NPP.

Irrigation and fertiliser effects on dry mass partitioning

Carbon allocation to the root system is controlled to meet the transpirational water demand of the canopy and the nutrient uptake (Nadelhoffer and Raich, 1992; Poorter and Nagel, 2000). The C allocation to roots basically increases with decreasing nutrient and water availability (Poorter and Nagel, 2000; Schenk and Jackson, 2002). In our experiment, f_{BGB}, f_{LR} and f_{BNPP} were used to reflect carbon allocation to roots. However, from the physiological point of view, the amount of carbon allocated to roots was highly overestimated using f_{BGB} and f_{LR} due to big necromass in belowground biomass pool and perennial roots which can survive quiet long in semi-arid grasslands (Milchunas et al., 2005). Therefore we strongly argue that f_{BGB} and f_{LR} obviously are not suitable parameters to estimate the fraction of dry matter invested to the roots. In contrast to f_{BGB} and f_{LR}, f_{BNPP} is a good parameter to reflect the real carbon investment into roots. Although N fertiliser had no significant effect on f_{BNPP} under drylands conditions, and water supply had no significant effect on f_{BNPP} in un-fertilisered plots, N fertiliser with irrigation had significant influence on C partitioning between shoot and root. The total plant C used for root production was around 60% in treatments W0N0 and W0N1 at both sites, while only 43% of total carbon gain was used for root production with N supply under irrigated conditions. This result was supported by Ram et al. (1991) who found 33%-46% of the total carbon gain was used for root production in an alpine grassland of Central Himalaya, and N fertilizer can significantly reduce the root carbon investment under favourable soil moisture. Compared to some intensively managed crops, which invest only around 20% of dry matter to root system (Bolinder et al., 1999), grassland species in this semi-arid environment apparently invest carbon to roots as much as to shoot.

Conclusions and implication

Application of small amounts of N is one option for restoration of grassland, especially when restoration focuses on protection from grazing with extensive hay production, from which farmers will benefit. This could only be occurred at the precipitation rich years, which the occurring frequency is statistically every 4 years. However, the increase in ANPP by N supply is partially attributable to decreases in BNPP under irrigated conditions. Further, root turnover may potentially be increased by N supply and irrigation, and the species composition will also change with N application. Therefore, long-term data for such aspects are needed for a systematic evaluation of N effect on ecosystem stability, productivity and diversity.

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Summary and Conclusions

Aboveground and belowground productivity of the Inner Mongolia steppe ecosystem are interlinked through complex feedback loops involving plants, sheep, soil and environmental factors. Due to the shift of land use in combination with climatic change, it is important to understand the response of this steppe system to these new conditions. We gave the following summary about the results based on three year's data:

Species diversity, composition and functional groups

Drought stress and grazing disturbance interactively control species diversity, species composition and functional groups. Species diversity tended to decrease with drought and species richness and diversity in the long term enclosure were significantly higher than at the wintergrazed (WG) and heavily grazed (HG) sites, while there was no significant difference between sites WG and HG in all three years. Compared to sites WG and HG more species contributed to total biomass at site UG79. Perennial grasses and forbs had greater contribution to total biomass at site UG79 and exhibited high fluctuation in abundance and relative biomass between years; perennial grasses contributed more than 97% of total biomass at site WG in all three years. Annual forbs and semi-shrub significantly increased the contribution to total biomass, while perennial forbs sharply decreased the contribution to total biomass after two dry years at site HG. *Cleistogenes squarrosa* (C_4, bunchgrass) had a high abundance at site HG in all three years. The decrease in *Potentilla acaulis* , basically an indicator or heavy grazing and the increases in annual species biomass suggest that the perennial vegetation of this ecosystem is in high danger of degradation under prolonged drought periods.

ANPP, BNPP and belowground allocation

ANPP and BNPP of a long-term grazing enclosure were significantly higher than at the long-term heavily grazed site in all years. No significant difference of ANPP between site WG and HG was observed in 2004, a year of average rainfall, whereas ANPP at site WG was significant higher than at site HG in 2005 and 2006, both years of low rainfall amount. Continuous heavy grazing also resulted in higher total plant density (small and thin tillers or stoloniferous branches) and lower community height and litter accumulation. Litter quantity at site UG79 was 1.8 and 12.7 times higher than at sites WG and HG, respectively. Water use efficiency (WUE) and rain use efficiency (RUE) generally declined with increased grazing intensity, and varied from 0.45 to 0.94 g L^{-1}, and 2.8 to 7.1 kg ha^{-1} mm^{-1} a^{-1}, respectively. The highest crop growth rate (CGR) of 3.59 g m^{-2} d^{-1} was observed in the vegetative growth phase at site UG79 in 2004. Relative growth rate (RGR) ranged from 128.2 to -25.44 mg g^{-1} m^{-2} d^{-1}, highly depending on precipitation and plant phenology. Like RGR, the value of net assimilation rate (NAR) decreased over the growing season, and this trend was more evident in 2005 and 2006 compared to 2004. Leaf area index (LAI) varied greatly between years and sites, and the peak LAI ranged from 0.41 to 0.96 m^2 m^{-2}. The highest LAI was found at site UG79 in 2004, and the lowest value was observed at site HG in 2006. Pooled over all three years data, leaf weight ratio (LWR) at site WG was significantly higher than that at sites UG79 and HG. Leaf nitrogen content (LNC) decreased over the growing season at all sites. Pooled over the data of different sampling dates in each year, LNC at sites HG and UG79 was significantly higher than at site WG in 2004 and 2005, whereas no significant difference was found between sites UG79 and HG. However, LNC at site HG was substantially higher than sites WG and UG79, whereas no significant difference between sites UG79 and WG was observed in 2006. A positive relationship between RGR with NAR and LWR was observed, while no relationship existed between RGR with specific leaf area (SLA). In addition, LNC was positively related to RGR, which can be used to explain why site WG has lower productivity in 2004, compared to site UG79.

BNPP/NPP varied between 0.5-0.7 at grazing experimental sites and was reduced under heavy grazing in 2005 but not in 2006. The positive correlation between cumulative root length density of ingrowth cores and leaf DW suggests that the ingrowth core method is suitable for studying BNPP. The comparison of experimental data with BNPP estimates from an empirical model indicates that the effect of grazing is not accurately reproduced.

BNPP of irrigated plots (W1N0 and W1N1) was almost two times higher compared to that of dryland plots W0N0 and W0N1. The portion of live roots was significantly higher on the heavily grazed site than on the moderately grazed site. The combined supply of water and N significantly reduced the portion of carbon allocated belowground (only 45%), whereas total net primary productivity (NPP) was not significantly increased, indicating that N supply in combination with water had a more pronounced effect on the pattern of biomass allocation than on NPP. Our results further suggest that grassland productivity in this ecosystem is limited by water, and by nitrogen under condition of high water availability in terms of ANPP.

Critical evaluation of the work

The strength of this study is the monitoring of characteristics of three grassland sites subjected to different land management over a long time period. However, the pseudo-replicated sampling design allows only considering this work as a case study. More general conclusions about grazing effects on grassland characteristics are problematic. Especially, short-term grazing effects and a "real" grazing gradient were not possible to be tested with this experimental design. Therefore another experiment was established within the MAGIM framework (P3 and P4) to test short-term grazing effects and to evaluate possibilities of establishing a sustainable grazing system in this semi-arid ecosystem.

My results and especially those of chapter 3 suggest that this ecosystem is quiet complex. Additionally to studies on long-term established sites, like those used in my work, factorial experiments which focus on physiological processes at the species level are highly required in order to understand the resilience and dynamics of this grassland system under variable land use and rainfall variability.

Total conclusions

From our three years' results, we reached the following conclusions about Inner Mongolia grassland: (1) rainfall variability and grazing control productivity and herbivory in an interactive manner; (2) mean annual precipitation is not always the most important factor determining the quantity of net production; distribution of precipitation and soil nutrient availability (e. g. N) can also significantly influence productivity; (3) heavy grazing leads to significant declines in ANPP, BNPP and litter biomass, no compensatory and overcompensatory growth was observed; (4) heavy grazing that lead to a removal of more than 50% of ANPP in relative normal years and even 70% under dry climatic conditions, is very detrimental to sustainability and maintenance of grassland. Risk of degradation is enhanced by prolonged drought; (5) 50-70% of carbon gain was allocated to root system; and (6) Restoration measures of degraded grassland in this steppe ecosystem can include the application of small amounts of N fertiliser, especially in years of medium to high rainfall.

Zusammenfassung und Schlußfolgerungen

Ober- und unterirdische Produktivität der innermongolischen Steppe sind durch komplexe Rückkopplungen zwischen Pflanzen, Beweidung, Boden und Umweltfaktoren miteinander verknüpft. Die Änderungen in der Landnutzung und mögliche Auswirkungen des Klimawandels machen es erforderlich, die Reaktionen des Steppe-Ökosytems auf diese Faktoren besser zu verstehen. Basierend auf 3-jährige Versuchsdaten lassen sich folgende Schlußfolgerungen ziehen:

Artendiversität, Zusammensetzung und funktionelle Gruppen

Trockenstress und Beweidung beeinflussten Diversität, Zusammensetzung und funktionelle Gruppen dieses Grasslands interaktiv. Diversität nahm mit zunehmender Trockenheit ab und Artenvielfalt und Diversität war auf der langfristig unbeweideten Fläche (UG79) höher als auf der Fläche mit Winterbeweidung (WG) und der intensiv beweideten Fläche (HG). Zwischen den Flächen WG und HG fanden sich in allen drei Jahren keine Unterschiede in Artenvielfalt und Diversität. Auf der Fläche UG79 trugen mehr Pflanzen zur Biomasse bei als auf den beiden anderen Flächen. Perennierende Gräser und Kräuter trugen auf der Fläche UG79 stärker zur Biomasse bei und wiesen dabei eine hohe Fluktuation zwischen den Jahren auf. Perennierende Gräser trugen in allen drei Jahren zu 97% zur Biomasse auf der Fläche WG bei. Nach zwei trockenen Jahren kam auf der Fläche HG annuellen Kräutern und buschigen Pflanzen eine größere Bedeutung für die Biomasse bei, während der Beitrag perennierender Kräuter drastisch abnahm. *Cleistogenes squarrosa,* ein C_4 Horstgras, wies auf der Fläche HG in allen drei Jahren eine hohe Abundanz auf. Unter Bedingungen einer langen Dürre deutet die Abnahme von *Potentilla acaulis*, einer typischen Indikatorpflanze intensiver Beweidung, sowie die gleichzeitige Zunahme annueller Arten darauf hin, dass die intensive beweidete Fläche HG bereits deutlich degradationsgefährdet ist.

Ober- und unterirdische Nettoprimärproduktion und Biomasseallokation

Ober (ANPP)- und unterirdische (BNPP) Nettoprimärproduktion auf der langfristig unbeweideten Fläche UG79 war in allen drei Jahren signifikant höher als auf der langfristig intensiv beweideten Fläche HG. In 2004, einem Jahr mit durchschnittlichem Niederschlag, fanden sich zwischen den Flächen WG und HG keine signifikanten Unterschiede in der ANPP, während die ANPP in den trockenen Jahren 2005 und 2006 auf der Fläche WG signifikant höher war als auf der Fläche HG. Kontinuierliche, intensive Beweidung bewirkte weiterhin eine höhere Pflanzendichte (kleinere und dünnere Stolonverzweigungen), sowie eine geringere Bestandeshöhe und Streumenge. Letztere war auf der Fläche UG79 1.8 bzw. 12.7 mal höher als auf den Flächen WG und HG. Die Wasser- und Regenfallnutzungseffizienz sank mit zunehmender Nutzungsintensität und variierte zwischen 0.45 und 0.94 g pro Liter (WUE) und 2.8 und 7.1 kg pro mm Hektar und Jahr. Die höchste absolute Wachstumsrate von 3.59 g pro Quadratmeter und Tag realisierte sie Fläche UG79 während der vegetativen Wachstumsphase im Jahr 2004. Die relative Wachstumsrate (RGR) variiert zwischen 128 und -25 mg pro Gramm und war hochgradig durch Niederschlag und Phänologie beeinflusst. Dieser Wachstumsparameter, wie auch die Nettoassimilationsrate (NAR), nahmen im Vegetationsverlauf ab, wobei dieser Trend in den trockenen Jahren 2005 und 2006 ausgeprägter war als im Jahr 2004. Der Blattflächenindex (BFI) wies zwischen den Flächen und Jahren eine deutliche Variation auf und erreichte Maximalwerte von 0.41 bis 0.96. Der höchste BFI wurde im Jahr 2004 auf der Fläche UG79 gemessen, der geringste auf der Fläche HG im Jahr 2006. Gemittelt über die drei Versuchsjahre war der Anteil des Blattgewichtes an der Gesamtrockenmasse (LWR) auf der Fläche WG signifikant höher als auf den beiden anderen Flächen. Auf allen Flächen nahm der Blattstickstoffgehalt (LNC) im Laufe der Vegetationszeit ab. Im Mittel der Jahre 2004 und 2005 war LNC der Flächen HG und UG79 recht ähnlich und höher als auf der Fläche WG, während er auf der Fläche HG im Jahr 2006 signifikant höher war als auf den beiden anderen Flächen. RGR war positiv mit LWR und NAR korreliert, allerdings bestand kein Zusammenhang zwischen RGR und spezifischer Blattfläche. Die positive Korrelation zwischen LNC und RGR deutet auf einen kausalen Zusammenhang zwischen N-Versorgung und Produktivität, welcher zumindest teilweise die Produktivitätsunterschiede zwischen den Flächen UG79 und WG im Jahr 2004 erklären kann.

Der Anteil an Gesamttrockenmasse der in unterirdische Organe investiert wurde variierte zwischen 0.5 und 0.7 und war unter intensiver Beweidung im Jahr 2005 geringer, nicht jedoch im Jahr 2006. Die positive Korrelation zwischen kumulativer Wurzellänge der Wurzelbeutel und Blatttrockenmasse deutet auf eine Brauchbarkeit dieser Methode zur Bestimmung der BNPP. Ein Vergleich der experimentellen Daten zur BNPP und relativen Biomasseallokation mit einem veröffentlichtem Modell deutet

darauf hin, dass das Modell den Einfluss der Beweidung nicht korrekt widergibt.
Die BNPP bewässerter Parzellen war annähernd doppelt so hoch wie die unbewässerter Parzellen. Der Anteil lebender Wurzeln war auf der intensiv beweideten Fläche signifikant höher als auf einer parallel untersuchten Fläche moderater Beweidung. Ein kombiniertes Angebot von Wasser und Stickstoff verminderte den Anteil an Trockenmasse, der in unterirdische Biomasse investiert wurde auf ca. 45%, allerdings wurde die Gesamtnettoprimärproduktion (NPP) nicht signifikant erhöht. Dies deutet darauf, dass die N-Düngung in Kombination mit Bewässerung einen deutlichen Effekt auf die Allokation hat, nicht aber einen ausgeprägten Effekt auf die NPP. Weiterhin deuten die Ergebnisse darauf, dass die Produktivität dieses Graslandsystems primär durch Wasser limitiert ist, wohingegen Stickstoff nur unter Bedingungen ausreichender Wasserversorgung von Bedeutung ist.

Schlußfolgerungen

Basierend auf 3-jährige Versuchsdaten lassen sich folgende Schlüsse für das Grasland der Inneren Mongolei ziehen:

1. Niederschlagsmenge und -variabiliät sowie Beweidungsintensität kontrollieren die Nettoprimärproduktion (NPP)
2. Der durchschnittliche jährliche Niederschlag ist nicht immer der bedeutsamste Faktor, welcher die NPP bestimmt. Vielmehr haben auch die Niederschlagsverteilung und Nährstoffverfügbarkeit einen Einfluß.
3. Intensive Beweidung führt zu einer Verminderung der ober- und unterirdischen Nettoprimärproduktion sowie der Streumenge, wobei die Hypothese der Überkompensation durch Beweidung nicht bestätigt werden konnnte.
4. Intensive Beweidung mit einem Entzug von mehr als 50% bzw. 70% (in trockenen Jahren) der jährlichen oberirdischen Aufwuchsleistung ist nachteilig unter dem Aspekt der Nachhaltigkeit und funtionalen Integrität diesen Graslandsystems. Trockenheit fördert die Wahrscheinlichkeit von Degradation.
5. 50 bis 70% der annuellen Trockenmasse werden in das Wurzelsystem investiert.

Die Ausbringung von Stickstoffdüngern kann in feuchten Jahren eine Strategie im Rahmen von Regenerationsmaßnahmen auf degradierten Flächen sein.

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“Sonntag” dinner in “Tuanbu” and barbecue in IMGERS were also indispensable to the success of this work. I liked that very much and always got a lot of fun after drinking Inner Mongolia alcohol with “hot pot”. I will miss my drinking “comrade in arms”, Marcus Giese, Thomas Glindemann and Markus Steffens, “Lao Wang”, Ying Zhao et al., and, of course, the “hot pot”.

Thanks to Kiel University for providing good study environments. I like Kiel summer– beach, sunshine and flower, although it is short duration in my life. I will miss Kiel and colleagues of Kiel University.

Thanks to my family for never losing faith and giving a consistent spirit support in life – my wife,Yanxue Li, my son, Yiwei Gao.

Finally, and most especially, to Inner Mongolia grassland, thank you for blue sky, sunshine and delicious sheep meat, and wish you “healthiness” for ever!

MEMORIAL

My tutor, Prof. Burkhard Sattelmacher, a good friend of Chinese, was unfortunately unable to see the completion of this work due to his untimely pass-away in 21 November of 2005. With this thesis, I would like to honor the efforts Prof. Sattelmacher made with the “MAGIM project” in the Inner Mongolia grassland and would like to appreciate his preeminent ideas on understanding the integration of humans and natural processes in semi-arid ecosystems globally. I will greatly miss my mentor who had great courage, discipline, moral principles, high scientific expectations and good sense of humour.

Yingzhi Gao
10 May 2007
Kiel University, Germany

Appendix 1 Precipitation recorded in 2004, 2005, 2006 and the average of 25 years

	2004	2005	2006	25 average (1982-2006)
April	6.2	1.7	2.2	9.1
May	22.8	12.8	39.8	30.3
June	28.6	38.5	60.2	55.4
July	50.2	43.2	47.0	94.2
August	133.4	22.6	17.4	69.2
September	53.3	15.3	68.4	36.7
6 Months	294.5	134.1	235	294.9
Annual	324.6	157	271.5	333.6

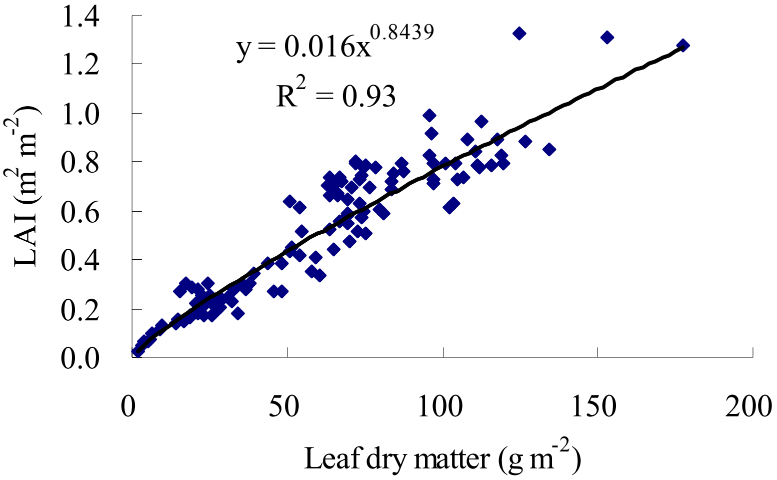
Note: the data from May 15 to September 30 in 2005 and April 1 to August 31 in 2006 are from meteorological tower located in the experimental field. All rest data are from IMGERS meteorological station.

Appendix 2 Basic soil physical and chemical properties at a moderately grazed site (MG) and a heavily grazed site (HG)

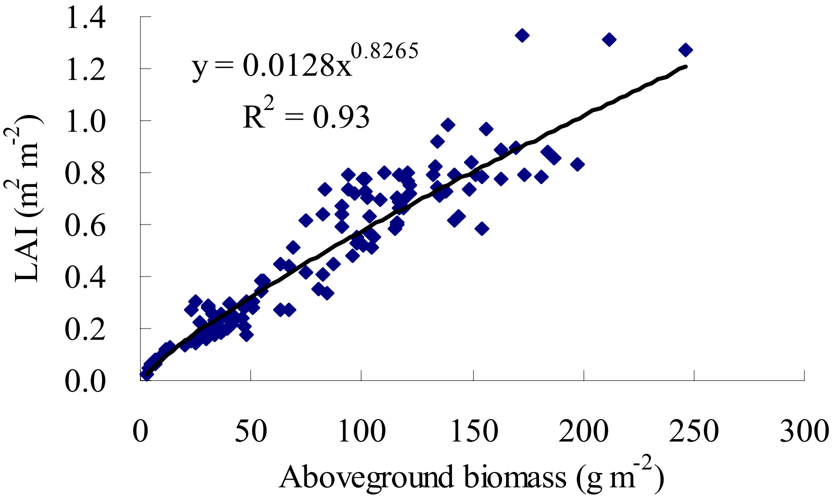
	MG			HG		
Soil depth (cm)	0-30	30-60	60-90	0-30	30-60	60-90
Sand (%)	71	76	80	81	80	72
Silt (%)	22	18	13	15	15	20
Clay (%)	6	6	6	4	4	8
Total N (%)	0.12	0.06	0.02	0.08	0.06	0.06
Total C (%)	1.2	0.6	0.4	0.9	0.7	0.7
C/N	10	10	20	11.3	11.7	11.7
Total P (mg kg^{-1})	222	159	155	224	197	272
Olsen P (mg kg^{-1})	2.0	0.3	0.3	5.9	3.3	2.2
Available K (mg kg^{-1})	152	76	60	221	235	292
PH	6.6	6.6	7.4	6.6	7.3	7.7

Appendix 3 Seasonal distribution of long term average precipitation data (1983-2001), wet year's average data, and precipitation and irrigation amount of water in 2006. The rainfall data is based on rain gauge which was installed at the experimental sites.

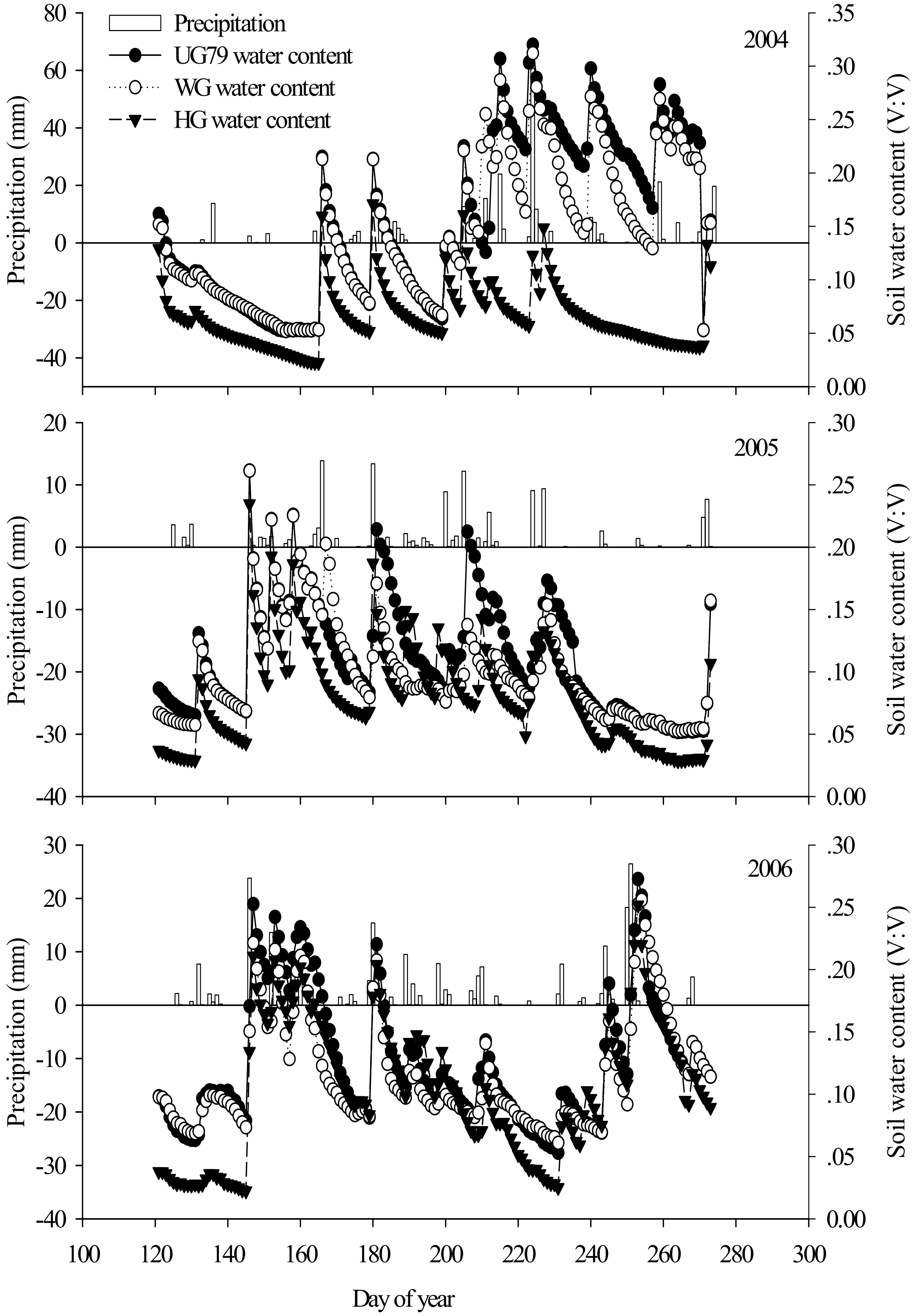
	May			June			July			August			September			May-Sept.
	0-10	11-20	21-31	0-10	11-20	21-30	0-10	11-20	21-31	0-10	11-20	21-31	0-10	11-20	21-30	
Long term data	7.0	7.8	15.3	7.0	17.2	23.9	28.6	34.6	26.0	25.2	30.0	25.2	12.7	11.4	8.3	280
Wet year data	22.6	7.7	7.9	12.6	20.4	30.6	43.3	64.3	51.7	18.4	20.0	32.8	20.9	14.7	6.9	375
2006 rainfall	3.0	7.7	26.7	24.9	5.4	21.0	13.5	18.9	8.0	3.7	8.9	24.1	47	0	6.6	219
Irrigation amount	20	0	0	0	20	10	20	35	30	15	10	10	0	0	0	170



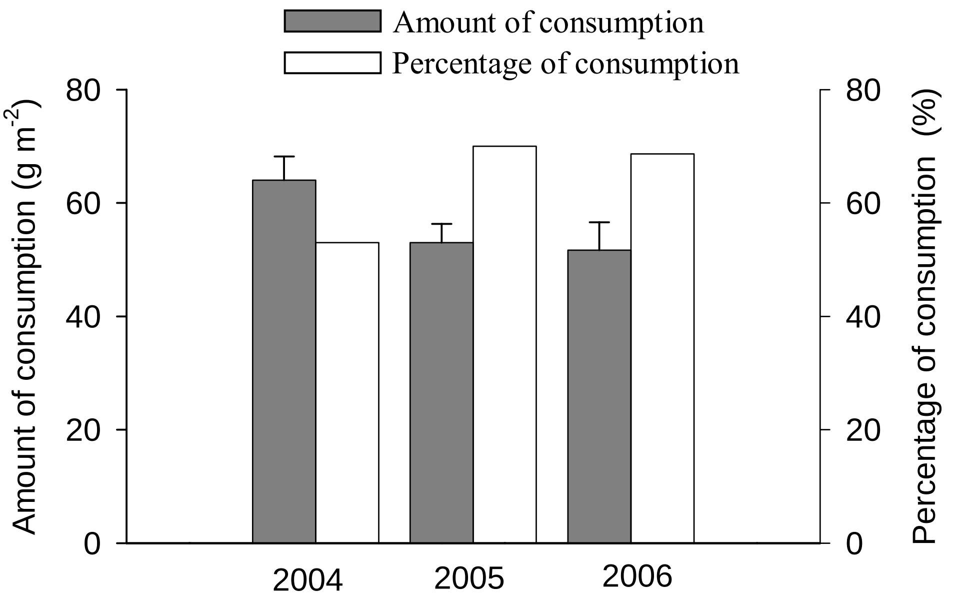
Appendix 4 The relationship of leaf area index (LAI) with leaf dry matter. ($y = 0.016 x^{0.8439}$, n =126, $R^2 = 0.93$)



Appendix 5 The relationship of leaf area index (LAI) with aboveground biomass ($y = 0.0128 x^{0.8256}$, n =126, $R^2 = 0.93$).



Appendix 6 The seasonal dynamics of precipitation and soil water content (0-5 cm) in 2004, 2005 and 2006.



Appendix 7 The amount and percentage of consumption by sheep from 2004 to 2006 at heavy grazing site.

Appendix 7 showed that 64 g m^{-2}, 53 g m^{-2} and 52 g m^{-2} of dry mass were eaten by sheep in 2004, 2005 and 2006 at site HG, respectively. Accordingly, the percentage of consumption of ANPP was lower in 2004 and higher in the dry years 2005 and 2006.

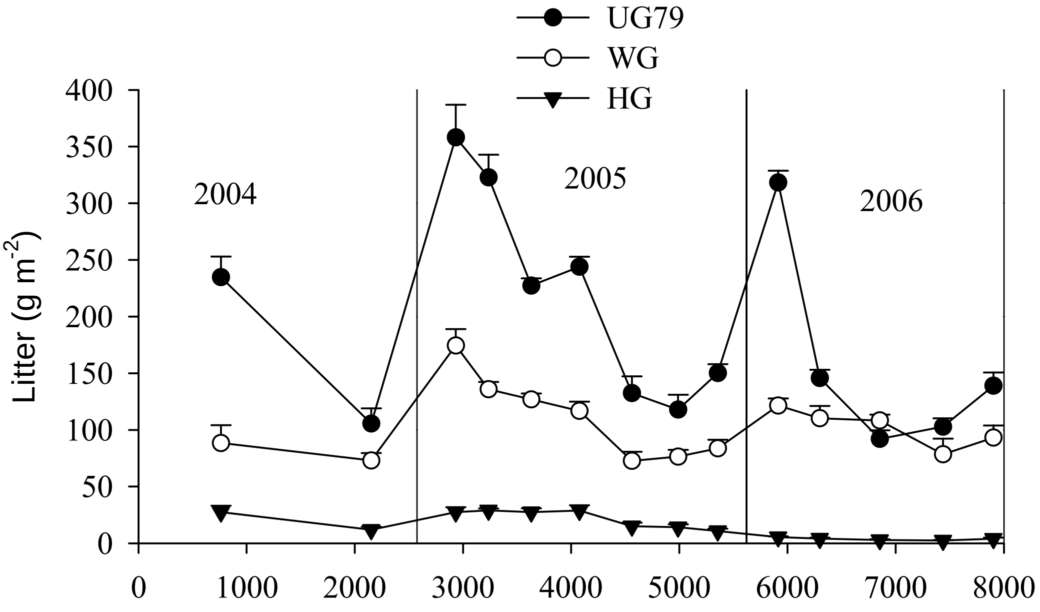
Appendix 8 Rainfall use efficiency (RUE) (kg DM ha^{-1} mm^{-1} a^{-1}) and water use efficiency (WUE) (g DM L^{-1} H_2O) at three differently managed sites

	2004		2005		2006	
	RUE	WUE	RUE	WUE	RUE	WUE
UG79	5.4	0.73	7.1	0.94	3.9	0.64
WG	3.9	0.52	6.3	0.83	3.5	0.57
HG	3.7	0.50	4.9	0.64	2.8	0.45

Water and rain use efficiency

WUE and RUE decreased with increasing grazing intensity in all three years (Appendix 8) and varied from 0.45 to 0.94 g L^{-1}, and 2.8 to 7.1 kg ha^{-1} mm^{-1} a^{-1}, respectively. The lowest amount of precipitation during the growing season was 134 mm in 2005 and the highest was 295 mm in 2004, while WUE and RUE was higher in

2005 than 2004. Accordingly, WUE and RUE tended to be higher in drier year than wet year. The values are reported here in the range of the findings from Xiao et al. (1995), who reported the long-term averages of RUE and WUE are 6.3 kg ha^{-1} mm^{-1} a^{-1} with coefficient variation of 23% and 0.69 g L^{-1} with coefficient variation of 21% at site UG79, respectively. Compared with the average value of 77 series data (RUE = 4.0) from the world arid lands (Le Houérou et al., 1988), our RUE of UG79 are higher and RUE of HG are more similar (RUE = 3.8). A decrease of WUE or RUE under at heavily grazing site was supported by Snyman (2005), who argued that high runoff and evaporation under poor condition grassland are responsible for low WUE or RUE.



Appendix 9 Seasonal dynamics of litter (g m^{-2}) with accumulated temperature under different grazing intensity, the total accumulated temperature is 2675, 2967 and 2656 °C in 2004, 2005 and 2006, respectively.

Effects of grassland management and years on litter

Appendix 10 showed litter exhibits distinctly season dynamics. The highest amounts of litter are in the early spring for all treatments, and declined with the growing season progressed, and the lowest value usually occurred at peak biomass time. Later on, litter increased again due to the newly formed litter input. The decreasing slope of UG79 is steeper than HG and WG. About 67% of litter decomposed at UG79 in 2005 and 2006, while around 58% and 35% of litter at WG, and 61% and 56% of litter at HG decomposed in 2005 and 2006, respectively. Grazing has significantly effect on the amount of litter. The quantity of litter in long term exclosure is one magnitude more than HG through all three years. On average for the trial period, compared with WG and HG site, litter quantity at site UG79 was 1.84 and 12.71 times higher than sites WG and HG. This is because heavy grazing causes reduced vegetation cover leading to litter blown away by wind in early spring and late autumn or washed away by heavy rainfall during summer.

Appendix 10 Total species were found in 2004, 2005 and 2006 at sites UG79, WG and HG.

		UG79	UG79	UG79	WG	WG	WG	HG	HG	HG
Species		2004	2005	2006	2004	2005	2006	2004	2005	2006
Melandrium apricum	AF	+	+							
Lappula redowskii	AF	+	+	+						
Axyris amaranthoides	AF	+			+			+		+
Chenopodium aristatum	AF	+		+	+		+	+		+
Salsola collina	AF	+		+	+		+	+		+
Chenopodium glaucum	AF	+			+		+	+		+
Melilotus suaveolens	AF	+		+	+					
Gentiana dahurica	PF	+	+							
Androsace longifolia	PF	+		+	+					
Allium anisopodium	PF	+	+	+	+			+	+	
Allium bidentatum	PF	+	+	+	+	+	+			
Allium tenuissimum	PF	+	+	+	+	+	+	+	+	+
Allium senescens	PF	+	+	+	+	+	+		+	
Allium ramosum	PF	+	+	+		+		+	+	+
Allium condensatum	PF	+	+	+			+		+	
Artemisia commutata	PF	+	+	+						
Heteropappus altaicus	PF	+	+	+				+	+	+
Serratula centauroides	PF	+	+	+						
Thermopsis lanceolata	PF	+	+	+						
Potentilla acaulis	PF	+	+	+				+	+	+
P. tanacetifolia	PF	+	+	+				+	+	+
Potentilla bifurca	PF	+	+	+				+	+	+
Potentilla verticillaris	PF	+	+	+						
Pulsatilla tenuiloba	PF	+	+	+						
Thatictrum petaloideum	PF	+	+		+	+	+	+	+	
Silene jenisseensis	PF	+	+	+						
Dontostemon micranthus	PF	+	+		+	+		+		
Bupleurum scorzonerifolium	PF	+	+	+	+					
Saposhnikovia divaricala	PF	+	+	+	+	+				
Haplophyllum dauricum	PF	+	+	+						

Convolvulus arvensis	PF	+	+							
Iris tenuifolia	PF	+	+	+		+	+			
Sibbardia adpressa	PF	+	+					+	+	
Anemarrhena asphodeloides	PF	+	+	+		+				
Euphorbia esula	PF	+	+	+		+	+			
Cymbaria dahurica	PF	+	+	+						
Galium verum	PF	+	+	+						
Ptilotricum canescens	PF	+		+						
Stellera chamaejasme	PF				+	+			+	
Linum stelleroides planch.	PF				+	+				
Melissitus ruthenica	PF							+	+	+
Orostachys fimbriatus	PF			+						
Filifolium sibiricum	PF	+	+	+						
Echinops latifolius	PF	+	+	+						
Oxytropis myriophylla	PF	+						+	+	+
Leymus chinensis	PG	+	+	+	+	+	+	+	+	+
Achnatherum sibiricum	PG	+	+	+	+	+	+			
Agropyron michnoi	PG	+	+	+	+	+	+	+	+	+
Koeleria cristata	PG	+	+	+	+	+	+	+	+	+
Poa argunensis	PG	+	+	+	+	+	+	+	+	
Stipa grandis	PG	+	+	+	+	+	+	+	+	+
Carex spp.	PG	+	+	+	+	+	+	+	+	+
Festuca dahurica	PG	+	+		+	+	+			
Cleistogenes squarrosa	PG	+	+	+	+	+	+	+	+	+
Artemisia scoparia	SS	+	+	+				+	+	+
Artemisia frigida	SS	+	+	+				+	+	+
Caragana microphylla	SS	+	+	+						
Kochia prostrata	SS	+		+				+	+	+
Spiraea aquilegifolia	SS	+	+	+						