

Simulating Root Responses to Grazing of a Mongolian Grassland Ecosystem Author(s): Yuxiang Chen, Pilzae Lee, Gilzae Lee, Shigeru Mariko and Takehisa Oikawa Source: *Plant Ecology*, Vol. 183, No. 2 (2006), pp. 265–275 Published by: <u>Springer</u> Stable URL: <u>http://www.jstor.org/stable/20146889</u> Accessed: 26/03/2014 08:48

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Springer is collaborating with JSTOR to digitize, preserve and extend access to Plant Ecology.

http://www.jstor.org

Simulating root responses to grazing of a Mongolian grassland ecosystem

Yuxiang Chen^{1,2,*}, Pilzae Lee¹, Gilzae Lee¹, Shigeru Mariko¹ and Takehisa Oikawa¹ ¹Institute of Life and Environmental Sciences, University of Tsukuba, Tsukuba Ibaraki 305-8572, Japan; ²College of Biological and Agricultural Engineering, Jilin University, Changchun 130022, China; *Author for correspondence (e-mail: chenyuxiang2002@hotmail.com; phone: +81-29-853-4531; fax: +81-29-853-661)

Received 18 April 2005; accepted in revised form 3 August 2005

Key words: Below-ground biomass, Below-ground net primary production, C/F, Root turnover, Stocking rate

Abstract

A new Sim-CYCLE grazing model has been obtained by combining a grazing model (Seligman et al. 1992, Ecol. Model. 60: 45-61) with the Sim-CYCLE model (Ito and Oikawa 2002, Ecol. Model. 151: 143-176). The new model has been validated against a set of field data obtained at Kherlen Bayaan-Ulaan (KBU) grassland. On the basis of the model, the root responses to grazing of KBU grassland have been studied under different conditions of stocking rates and precipitation. Model results indicate that both belowground biomass (BB) and below-ground net primary production (BNPP) generally decrease with increasing stocking rate. However, if stocking rate is not higher than 0.7 sheep ha⁻¹, a sustainable state of the grassland ecosystem can be achieved after about 100 years, which suggests that the maximum sustainable stocking rate at KBU should be 0.7 sheep ha⁻¹. At the sustainable state, the maximum BB in a year is about 11 Mg DM ha⁻¹ under non-grazing condition, 5 Mg DM ha⁻¹ under 0.4 sheep ha⁻¹ stocking rate, and 4 Mg DM ha⁻¹ under 0.7 sheep ha⁻¹ stocking rate; the BNPP is 1.3 Mg DM ha⁻¹ year⁻¹ under non-grazing condition, and 0.6 Mg DM ha⁻¹ year⁻¹ under 0.4 sheep ha⁻¹ stocking rate, and 0.4 Mg DM ha⁻¹ year⁻¹ under 0.7 sheep ha^{-1} stocking rate. Ratio of non-assimilation organ to assimilation organ (C/F) increases with increasing stocking rate. The C/F ratio is 10.99 under non-grazing conditions, and 12.11 under 0.7 sheep ha^{-1} stocking rate. Root turnover rate decreases with increasing stocking rate. The rate is 12% each year under non-grazing conditions, and 11% each year under 0.7 sheep ha⁻¹ stocking rate. In addition, the effect of grazing on the grassland ecosystem under different scenarios of precipitation is also analyzed. Both BB and BNPP increase with increased precipitation, and vice versa. When precipitation is set to be 10% higher than the averaged from 1993 to 2002, the maximum sustainable stocking rate is 0.8 sheep ha⁻¹, and when the precipitation is set to be 15% lower than the averaged, the maximum sustainable stocking rate is $0.6 \text{ sheep ha}^{-1}$.

Introduction

Plants allocate considerable part of their photosynthate for the production and maintenance of roots. Roots can be regarded as heterotrophic organs living in the soil, but in direct symbiosis with autotrophic shoots, which exchanges carbohydrate with water and soil nutrients absorbed by the roots. This ensures that the above- and belowground functions of ecosystems are linked

together. However, the integration of roots and shoots extends beyond this symbiotic exchange of and below-ground resources above-(Van Noordwijk et al. 1998). Root functions are as important for whole plant survival as aboveground functions (Buwalda 1993). Since water and nutrients are limiting factors for plant growth in many environments, root growth is particularly important for the competitive ability of plants. Ability of plants to compete for water and nutrients will be greatly hindered when root growth is reduced. This is more noticeable in semiarid and arid ecosystem where water is main factor controlling biological activity (Coronato and Bertiller 1996; Engel et al. 1998).

Carbon in a grassland ecosystem is mostly stored below ground in extensive, fibrous root system. Due to the slow rate of decay of soil organic matter, the root serves as an efficient accumulator of carbon (Hunt et al. 2002). Grasslands are usually utilized for grazing, but yet the impacts of grazing on root processes have not been understood clearly. Most studies often pay attention to above-ground response to grazing. However, it has been reported that grazing affects below-ground processes (Stanton 1983; Richards 1984).

In spite of the importance of total (above- and below-ground) net primary production (NPP) as a regulator of energy flow through ecosystems (McNaughton et al. 1989), previous studies had mostly concentrated on the above-ground net primary production (ANPP), and therefore the amount of NPP allocated below-ground remains among the most poorly understood attributes of ecosystem (Lauenroth 2000). Furthermore, there is very little information about the effects of grazing on below-ground net primary production (BNPP) (Pucheta et al. 2004). Field experiments have shown that for different grassland ecosystem, grazing could have no effect on (Milchunas and Lauenroth 1989; McNaughton et al. 1998) or increase (van der Maarel and Titlyanova 1989) or decrease root biomass and BNPP (Svejcar and Christiansen 1987; Zhang and Romo 1994; Chaieb et al. 1996; Beaulieu et al. 1996; Biondini et al. 1998; Engel et al. 1998). Nevertheless, it is widely accepted that excessive grazing is detrimental to plant communities (Cnoant and Paustian 2002). It is necessary to study the root response to grazing in a specific grassland ecosystem in order to make a right judgment. Understanding BNPP is particularly important in grassland ecosystem, because a large proportion of biomass is stored in the soil (Coupland 1992), and accurate estimation of BNPP is also essential to accurately estimate total NPP in grassland ecosystem.

Mongolia is located in northeastern Asia, where ecotones (forest-grassland-desert) are formed because of climatic shift from humid condition to arid condition. An ecotone is a transitional area between two adjacent biomes and is generally sensitive to external disturbances such as climate change, human activities, etc. (Peters 2002). Nearly 75% of Mongolia's land area is grassland and shrubland grazed by livestock all the year round. About 20% of the human population is pastoralists and half of the population depends directly or indirectly on the pastoral economy for its livelihood (Fernandez-Gimenez and Allen-Diaz 1999). About 97% of livestock forage is from natural grassland (Begzsuren et al. 2004). Grazing is the most extensive land use mode and thus the major cause of degradation in this area. Unfortunately, few researches have been conducted on grazing effect on the grassland ecosystem. This study is hopefully to improve the understanding in this respect.

In semiarid and arid regions, precipitation is a major environmental factor affecting ecosystem production, and is highly variable from year to year (Lauenroth 1979; Seligman and Van Leulen 1989). Land in Mongolia is generally categorized as semiarid and arid region (Begzsuren et al. 2004). The grassland productivity is greatly influenced by the highly variable precipitation. For example, Wang and Jiang (1982) and Chen et al. (1988) found that both above-ground biomass and belowground biomass of a semiarid Stipa grandis steppe are directly related to precipitation. In order to investigate the grazing effect on grassland at different magnitude of precipitation, modeling simulations have been performed under the 10% higher and 15% lower than the averaged precipitation from 1993 to 2002.

Simulation model is a unique tool for its diagnostic and prognostic abilities. In this study, a new Sim-CYCLE grazing model has been developed by incorporating a grazing model (Seligman et al. 1992) into the Sim-CYCLE model developed by Ito and Oikawa (2002). The main purpose of this study is to investigate the grazing effect on some aspects of root processes using the new simulation model.

Study site and methods

Study site description

The study site is Kherlen Bayaan-Ulaan (47°3' N, 108°8' E; 1300 m a.s.l.), which is located in the Hentiy province of Mongolia, 100 km east of Ulaanbaatar. The mean annual precipitation over a 10 years period (1993–2002) is 187 mm, and is concentrated in the months from June to September. The mean annual temperature is 1.4 °C. The growing season in this area is normally from late April to mid-October.

The vegetation is natural semiarid steppe, which has been grazed by livestock for thousands of years (Begzsuren et al. 2004). The grassland is under grazing pressure all the year round due to inadequate management. The livestock are mainly cattle, sheep, goats, and horses. Dominant plants are graminoids and semi-shrub accompanied by a few forbs. The graminoids are more abundant than the semi-shrub. The plants start to grow in May and reach the maximum above-ground biomass in August, when the air temperature and precipitation are optimum for plant growth. According to a 2-year field investigation conducted by us, the average height of the grassland is about 15 cm, the maximum LAI is between 0.6 and 0.7 m m⁻², mean above-ground biomass is 85-110 g m⁻², belowground biomass is about 1200 g m⁻² (0-50 cm depth), and net primary production is 230- $280 \text{ g m}^{-2} \text{ year}^{-1}$. Dominant species are *Stipa* krylovii, Artemisia frigida and Cleistogenes squarrosa. C₄ plant species occupy about 10% of total biomass (Mariko et al. 2003). The soil is chestnut soil.

Field experiment methods

Field experiments were conducted at KBU in 2003. The methods of the experiments were reported in detail by Urano et al. (2004) and Liu (2004). To facilitate an easy understanding of the present paper, a brief introduction of the experiment methods is given as bellow.

The sampling sites were carefully selected and could be regarded enough representative for the

whole KBU grassland. In order to determine the effect of grazing on the grassland ecosystem, an exclosure was made in autumn, 2002. The area of the exclosure is 200 m \times 170 m, with a fence height of 1.5 m. Livestock were restrained from entering the exclosure. The LAI, biomass and carbon fluxes were measured monthly both inside and outside of the exclosure, from June to September, 2003. LAI was measured by scanning their images with a flatbed scanner and a PC, and the images were analyzed by an image processing software (Mariko et al. 2003). Above-ground biomass (AB) was measured by the clipping method. LAI and AB were averages of measurements from 24 quadrats (Mariko et al. 2003; Urano et al. 2004). In the non-grazing site, ANPP was the summation of all positive monthly increment of total above-ground biomass (including green biomass, standing dead and litter) throughout the growing season. In the grazing site, ANPP should be the summation of all positive monthly increment in total above-ground biomass plus intake by livestock. However, since the intake by livestock was not measured, ANPP in the grazing site could not be estimated from the field experiments. Below-ground biomass (BB) was measured by the soil boring stick method. BNPP was measured by the ingrowth soil core method. BB and BNPP were measured from 12 quadrats (Liu 2004).

Model description and validation

Model description

Up to now, most carbon cycle models for grassland ecosystems have not considered grazing effect. In order to simulate grazing effect on carbon cycle of a Mongolian grassland ecosystem, we combined a carbon cycle model Sim-CYCLE with a grazing model (Seligman et al. 1992). The Sim-CYCLE model was developed by Ito and Oikawa (2002). It is a process oriented carbon cycle model, which has been successfully applied to various type of terrestrial ecosystem (Oikawa and Ito 2001; Ito and Oikawa 2004; Hazarika et al. 2005; Ito 2005). The model was developed on the basis of dry matter productivity theory. It is a compartment model: terrestrial carbon pools are conceptualized into a five-compartment system. Carbon in a given ecosystem (WE) is composed of plant biomass (WP) and soil organic carbon (WS). WP is distributed in three compartments, viz. foliage (F), stem (C), and root (R). WS is distributed in two compartments: litter (L) and humus (H).

$$WE = WP + WS$$
$$WP = WP_F + WP_C + WP_R$$
$$WS = WS_L + WS_H$$

 CO_2 exchange between atmosphere and biosphere through three major processes: gross primary production or photosynthesis (GPP), autotrophic plant respiration (AR), and heterotrophic soil respiration (HR). Autotrophic plant respiration includes maintenance respiration (ARM) and growth respiration (ARG). GPP is the ultimate origin of all organic carbon, through which atmospheric CO_2 is fixed into dry matter. Instantaneous GPP (GPP_{INS}) was calculated as follows:

$$GPP_{INS} = \int_{0}^{LAI} PCdLAI$$
$$= \frac{PC_{SAT}}{KA} [ln\{QE + KAPPFD_{TOP}\} - ln\{QE + KAPPFD_{TOP} * exp(-KALAI)\}]$$

Where PC is single-leaf photosynthetic rate, LAI is leaf area index, PC_{SAT} is the single-leaf photosynthetic rate under light-saturation, QE is light-use efficiency, KA is light attenuation coefficient and PPFD_{TOP} is the photosynthetic photon flux density at the canopy top. Photosynthate (PT) produced by leaf, in addition to supply itself, is translocated to stem and root. So the leaf, stem and root are closely inter-related through exchange of carbohydrates and water: root and stem depend on leaf for carbohydrates, and leaf and stem depend on root for water.

The net change of biomass in each compartment (Δ) during a given period are as follows,

$$\Delta WP_F = PT_F - ARG_F - LF_F$$

$$\Delta WP_C = PT_C - ARG_C - LF_C$$

$$\Delta WP_R = PT_R - ARG_R - LF_R$$

where PT_F , PT_C , and PT_R are photosynthate distributed to foliage, stem, and root. PT is the difference between GPP and ARM. LF_F , LF_C , and LF_R are litterfall of foliage, stem, and root. NPP is the difference between GPP and AR under non-grazing condition.

$$NPP = GPP - AR$$

Under grazing condition, NPP is the summation of change of plant biomass, litterfall and defoliation rate (D_r) by livestock.

$$NPP = \Delta WP + litterfall + D_r$$

We took into account of the fact that, defoliation of leaf and stem as a result of grazing by livestock will lead to a reduction in LAI and as a consequence, GPP will be affected. In addition, the amount of photosynthate to be translocated to below-ground component will also change. Therefore, the productivity of below-ground component will be affected indirectly by grazing.

The grazing model of Seligman et al. (1992) was adopted in this study. The model is suitable for semiarid grassland and was applied to a semiarid grassland ecosystem in Argentina. A brief introduction of this model is given below,

$$D_{r} = E * S_{r} * ((WP_{F} + WP_{C}) - (WP_{F} + WP_{C})_{U})$$

(0rrD_x),

Where D_r is the defoliation rate (kg ha⁻¹ d⁻¹), E is grazing efficiency of livestock (ha d⁻¹ per animal), S_r is stocking rate, (WP_F + WP_C)_u is the residual above-ground biomass unavailable to the livestock (kg ha⁻¹ dry matter), D_x is satiation consumption rate of the livestock (=2.4 kg d⁻¹ per animal) (NRC 1985).

The above-ground biomass is regarded as evenly distributed from upper layer to lower layer of the grassland. It is also assumed that there is no extreme grass clumping and no large area with bare soil.

The simulated forage intake in this model is limited to total green leaf and stem. This is because fresh green parts such as stems and leaves are highly preferred by most livestock, and the amount of green component in a plant is very critical for both processes of photosynthesis and transpiration. In this study, grazing is only limited to above-ground grazing by livestock. Although below-ground grazers are important components of the ecosystem, it has not been taken into account in this simulation. In this study, consideration of effect of grazing is still preliminary. Animals are considered as 'negative' consumers. Other possible direct or indirect effects of grazing have not been taken into account here, which, for example, include trampling by animal, changes in the nutrient cycling of grassland ecosystem, plant damage caused by animal, and changes in plant relative growth rate. Soil nutrients for plant growth were regarded as nonlimiting.

The model time step is 1 month. Model inputs include meteorological and soil data, which were obtained from a local meteorological agency by RAISE project. These data are averages over a 10-year period from 1993 to 2002 (Table 1). The model parameters have been calibrated with data from our 2 years field investigation and related work reported in the literature.

Model validation

We selected LAI, the maximum AB of a year, the maximum BB of a year, annual ANPP, and annual BNPP as index to show the grazing effect on the grassland ecosystem. The simulated results are compared with the measured data (Table 2). The simulated LAI, AB, BB and BNPP have been compared with measured data obtained under grazing condition. Because intake by livestock, one component of ANPP, was not measured in the

Table 1. Input data of major environmental factors for modeling.

Month	Environmental Factors						
	Radiation (W m ⁻²)	Soil temperature (°C)	Air temperature (°C)	Precipitation (mm)			
Jan	101.11	-15.65	-22.45	1.77			
Feb	151.65	-10.45	-14.85	1.2			
Mar	221.03	-5.75	-6.25	1.27			
Apr	283.2	4.45	5.15	1.43			
May	327.07	11.85	12.75	3.62			
Jun	327.54	17.55	18.75	25.72			
Jul	307.94	19.85	20.75	57.2			
Aug	297.38	17.35	17.65	61.18			
Sep	227.92	11.45	10.95	20.38			
Oct	167.13	3.05	1.85	4.39			
Nov	111.5	-5.35	-9.95	2.82			
Dec	85.9	-12.75	-18.95	2.19			

field experiments, the simulated ANPP has been compared with the measured data under nongrazing condition. The measured data were from outside of the exclosure, i.e., under natural grazing condition except for ANPP. The simulated results have been calculated using local stocking rate except for ANPP, which has been calculated under non-grazing condition. The values of LAI, AB, and BB presented in Table 2 are maximum values in a year, and the values of ANPP and BNPP are annual values, both for the measured and the simulated. The maximum simulated LAI and AB appeared in August and the maximum simulated BB appeared in September, all of them are matched well with the measured results. Table 2 shows the relative error (RE) between the measured data and the simulated results. The model greatly represents a real ecosystem in its simplest form. It was set up to study potential production as a function of soil water and temperature when soil nutrient did not limit plant growth in the model. In addition, there could be other sources of errors in the field experiment, for example as a result of human operations. All of these could have accounted for the deviation between simulated results and measured data. Despite these deviations, the simulated LAI, AB and BB, and annual ANPP agree well with the measured data. BNPP has a larger RE, which suggests that there are some inherent deficiencies in the model which needs to be improved upon in future. This also reveals the difficulties encountered in field work of measuring belowground items.

Results

Simulated BB and BNPP at different stocking rate

Simulated results show that BB decrease with increasing stocking rate (Figure 1). The maximum BB appears in September. The temporal dynamics of BB has been investigated here. The BB maintains constant under non-grazing condition, and the value is about 11 Mg DM ha⁻¹. The BB shows a decrease trend under stocking rates of 0.4 sheep ha⁻¹ and 0.7 sheep ha⁻¹, and the BB reaches the equilibrium after 100 years. The BB is 10.87 Mg DM ha⁻¹ under 0.4 sheep ha⁻¹ at the equilibrium state. The BB is 10.81 Mg DM ha⁻¹ under 0.7

Item	LAI (m m ⁻²)	AB (Mg DM ha ⁻¹)	BB (Mg DM ha ⁻¹)	ANPP* (Mg DM ha ⁻¹ year ⁻¹)	BNPP (Mg DM ha ⁻¹ year ⁻¹)
Measured					
Average	0.57	0.85	12.55	0.98	1.48
SD	0.10	0.19	2.50	0.23	0.39
95%CI	0.57 ± 0.06	0.85 ± 0.11	12.55 ± 1.41	0.98 ± 0.13	1.48 ± 0.22
Simulated	0.49	0.80	10.73	1.23	1.04
RE (%)	16.33	6.25	16.96	20.30	42.31

Table 2. Comparison between the measurements and the simulated results at KBU.

LAI, leaf area index; AB, Above-ground biomass; BB, Below-ground Biomass; ANPP, Above-ground Net Primary Production; BNPP: Below-ground Net Primary Production; DM, Dry Matter; SD, Standard Deviation; CI, Confidence Interval; RE, Relative Error = (Simulated – Measured)/Simulated.

*Measured data was obtained under non-grazing condition, and simulated result was also calculated under non-grazing condition.



Figure 1. Below-ground biomass at different stocking rates BB, Below-ground Biomass; DM, Dry Matter; SRn, Stocking Rate is n sheep ha^{-1}

sheep ha⁻¹ stocking rate in the first year, and 4.13 Mg DM ha⁻¹ at the equilibrium state. The BB decreases all the time under stocking rates of 0.8 sheep ha⁻¹ and 1.2 sheep ha⁻¹. The BB is 10.79 Mg DM ha⁻¹ in the first year, and decrease by 66% after 100 years under stocking rate of 0.8 sheep ha⁻¹. The BB is 10.72 Mg DM ha⁻¹ in the first year, and decrease by 82% after 100 years under stocking rate of 1.2 sheep ha⁻¹. It suggests that 0.4 sheep ha⁻¹ and 0.7 sheep ha⁻¹ stocking rates are within the grazing capacity of the KBU grassland, whereas 0.8 sheep ha⁻¹ and 1.2 sheep ha⁻¹ stocking rates are stocking rates are stocking rates are year.

Simulated BNPP also shows the same trend as BB (Figure 2). BNPP maintains the same value under non-grazing condition, and the value is about 1.3 Mg DM ha⁻¹ year⁻¹. BNPP decreases and then reaches equilibrium under stocking rates of 0.4 sheep ha⁻¹ and 0.7 sheep ha⁻¹. BNPP is 1.19 Mg DM ha⁻¹ year⁻¹ in the first year under stocking rate of 0.4 sheep ha⁻¹, and the equilibrium value is



Figure 2. Below-ground net primary production at different stocking rates BNPP, Below-ground Net Primary Production; DM, Dry Matter; SRn, Stocking Rate is n sheep ha^{-1}

0.61 Mg DM ha⁻¹ year⁻¹. BNPP is 1.13 Mg DM ha⁻¹ year⁻¹ in the first year under stocking rate of 0.7 sheep ha⁻¹, and the equilibrium value is 0.44 Mg DM ha⁻¹ year⁻¹. BNPP is 1.11 Mg DM ha⁻¹ - year⁻¹ in the first year under stocking rate of 0.8 sheep ha⁻¹, and 0.39 Mg DM ha⁻¹ year⁻¹ after 100 years, decreases by 65% compared to the first year under stocking rate of 1.2 sheep ha⁻¹, and 0.19 Mg DM ha⁻¹ year⁻¹ after 100 years, decreases by 82%. Simulated BNPP also shows that 0.8 sheep ha⁻¹ stocking rate is beyond the grazing capacity of the grassland.

Ratio of non-assimilation organ to assimilation organ (C|F) and root turnover rate

Simulated results show that the C/F increase with increasing stocking rate (Table 3). The C/F ratio is 10.99 under non-grazing condition, and 11.56

e		
Stocking rate (sheep ha ⁻¹)	C/F ratio	Root turnover rate (% year ⁻¹)
0	10.99	12
0.4	11.56	11
0.7	12.11	11
0.8	12.33	10

Table 3. The C/F ratio and root turnover rate at different stocking rates.

C/F, Ratio of non-assimilation organ to assimilation organ.

under a stocking rate of 0.4 sheep ha^{-1} , and 12.33 under 0.8 sheep ha^{-1} stocking rate.

According to Pucheta et al. (2004), root turnover rate was calculated as below,

Root turnover rate

= BNPP/mean annual live biomass

Simulated results show that 12% of the BB is renewed each year when there is no grazing (Table 3), and 11% of the BB is renewed each year under a stocking rate of 0.4 sheep ha⁻¹ and 10% of the BB is renewed each year under 0.8 sheep ha⁻¹.

Grazing effect under different precipitation scenarios

In order to investigate grazing effect under higher precipitation, the input data of precipitation has been increased by 10% of the averaged precipitation from 1993 to 2002. The BB and BNPP under different stocking rate are shown in Table 4. The responding percentages of the increased BB and BNPP are shown in Table 5. Under different stocking rates, both the BB and BNPP increase to different degree. From the Table 4, we can see that the maximum sustainable stocking rate is 0.8 sheep ha⁻¹, above which, for example 0.9 sheep ha⁻¹, the BB and BNPP decrease persistently with the year. This maximum sustainable stocking rate is 0.1 sheep ha⁻¹ higher than that under the average precipitation. When the stocking rate is lower than 0.8 sheep ha⁻¹, the highest percentage of the increased BB and BNPP is 12%, however, when the rate is 0.8 sheep ha⁻¹ or above, the effect of the elevated precipitation is particularly significant in 100 years later. This is because under the average precipitation, the stocking rate of 0.8 sheep ha⁻¹ is overgrazing, and thus the BB and BNPP decrease remarkably, especially after 100 years.

In order to investigate grazing effect under lower precipitation, the input data of precipitation has been decreased by 15% of the averaged precipitation from 1993 to 2002. The BB and BNPP under different stocking rate are shown in Table 6. The responding percentages of the decreased BB and BNPP are shown in Table 7. Under different stocking rates, both the BB and BNPP decrease to different degree. From the Table 6, we can see that the maximum sustainable stocking rate is 0.6 sheep ha^{-1} , above which, for example 0.7 sheep ha^{-1} , the BB and BNPP decrease persistently with the year. This maximum sustainable stocking rate is 0.1 sheep ha^{-1} lower than that under the average precipitation. When the stocking rate is lower than 0.6 sheep ha⁻¹, the highest percentage of the decreased BB and BNPP is 6%, however, when the rate is 0.7 sheep ha^{-1} or above, the effect of the decreased precipitation is particularly significant in 100 years later. This is because under the lower precipitation, the stocking rate of 0.7 sheep ha^{-1} is overgrazing, and thus the BB and BNPP decrease remarkably, especially after 100 years.

Table 4. BB and BNPP under different stocking rates given precipitation 10% higher than the average from 1993 to 2002.

Year	BB (Mg	$DM ha^{-1}$)				BNPP (Mg DM ha ⁻¹ year ⁻¹) SR0 SR0.4 SR0.7 SR0.8 SR				
	SR0	SR0.4	SR0.7	SR0.8	SR0.9	SR0	SR0.4	SR0.7	SR0.8	SR0.9
1	11.04	10.95	10.89	10.87	10.85	1.36	1.27	1.20	1.18	1.16
50	11.67	8.32	6.53	6.03	5.60	1.33	0.92	0.69	0.63	0.58
100	12.35	6.73	4.50	3.92	3.40	1.42	0.75	0.48	0.42	0.36
150	12.68	5.88	4.20	3.89	2.21	1.45	0.65	0.45	0.41	0.23
200	12.77	5.88	4.20	3.89	1.48	1.46	0.65	0.45	0.41	0.16
250	12.79	5.88	4.20	3.89	1.01	1.46	0.65	0.45	0.41	0.11

BB, Below-ground Biomass; BNPP, Below-ground Net Primary Production; DM, Dry Matter; SRn, Stocking Rate is n sheep ha⁻¹.

Year	Increased	l BB (%)			Increased BNPP (%)			
	SR0	SR0.4	SR0.7	SR0.8	SR0	SR0.4	SR0.7	SR0.8
1	1	2	1	1	7	7	6	6
50	4	2	3	3	3	3	5	3
100	9	5	5	7	9	7	4	8
150	11	7	2	64	12	7	2	64
200	12	7	2	148	12	7	2	141
250	12	7	2	267	12	7	2	273

Table 5. Percentage of increased BB and BNPP given precipitation 10% higher than the average from 1993 to 2002.

BB, Below-ground Biomass; BNPP, Below-ground Net Primary Production; SRn, Stocking Rate is n sheep ha⁻¹.

Table 6. BB and BNPP under different stocking rates given precipitation 15% lower than the average from 1993 to 2002.

Year	BB (Mg I	$M ha^{-1}$)			BNPP (Mg DM ha ⁻¹ year ⁻¹)						
	SR0	SR0.4	SR0.6	SR0.7	SR0	SR0.4	SR0.6	SR0.7			
1	10.92	10.84	10.80	10.78	1.24	1.16	1.12	1.10			
50	10.91	7.79	6.53	6.12	1.27	0.84	0.69	0.64			
100	10.89	6.01	4.37	3.76	1.22	0.66	0.47	0.39			
150	10.91	5.43	4.33	2.45	1.24	0.59	0.46	0.26			
200	10.91	5.43	4.33	1.69	1.27	0.59	0.46	0.18			
250	10.89	5.43	4.33	1.19	1.22	0.59	0.46	0.13			

BB, Below-ground Biomass; BNPP, Below-ground Net Primary Production; DM, Dry Matter; SRn, Stocking Rate is n sheep ha⁻¹.

Table 7. Percentage of decreased BB and BNPP given precipitation 15% lower than the average from 1993 to 2002.

Year	Decre BB (%	ased		Decreased BNPP (%) SR0 SR0.4 2 3 2 6 3 6 6 6		
	SR0	SR0.4	SR0.7	SR0	SR0.4	SR0.7
1	0	0	0	2	3	3
50	3	4	3	2	6	3
100	4	6	12	6	6	15
150	4	1	41	5	3	41
200	4	1	59	2	3	59
250	5	1	71	6	3	70

BB, Below-ground Biomass; BNPP, Below-ground Net Primary Production; SRn, Stocking Rate is n sheep ha^{-1} .

Sensitivity analysis

Model sensitivity to temperature and precipitation has been analyzed. An equilibrium state, which is at the year of 150 after start of the modeling, was chosen as the reference time. The results are shown in Tables 8 and 9. Under non-grazing condition, when the increase of temperature is from 0.25 °C to 0.75 °C compared to the long-term averaged temperature, the increase of BB is from 4% to 9%, and the increase of BNPP is from 5% to 10%;

Table 8. Sensitivity analysis to temperature.

Temperature (°C)	BB (Mg DM	ha ⁻¹)	BNPP (Mg DM ha ⁻¹ year ⁻¹)		
	0 sheep ha ⁻¹	0.4 sheep ha ⁻¹	0 sheep ha ⁻¹	0.4 sheep ha ⁻¹	
$T_0 + 0.00$	11.41	5.49	1.30	0.61	
$T_0 + 0.25$	11.92	5.73	1.37	0.64	
$T_0 + 0.50$	12.36	6.02	1.42	0.67	
$T_0 + 0.75$	12.48	6.31	1.43	0.71	
$T_0 - 0.25$	11.10	5.47	1.26	0.61	
$T_0 - 0.50$	10.98	5.46	1.25	0.60	
$T_0 - 0.75$	10.94	5.38	1.25	0.59	

 T_0 , the averaged temperature from 1993 to 2002; BB, Belowground Biomass; BNPP, Below-ground Net Primary Production; DM, Dry Matter.

When the decrease of temperature is from 0.25 °C to 0.75 °C, the decrease of BB is from 3% to 4%, and the decrease of BNPP is also from 3% to 4%. Under stocking rate of 0.4 sheep ha⁻¹, when the increase of temperature is from 0.25 °C to 0.75 °C, the increase of BB is from 4% to 15%, and the increase of BNPP is from 5% to 16%; When the decrease of temperature is from 0.25 °C to

All use subject to JSTOR Terms and Conditions

Table 9. Sensitivity analysis to precipitation.

Precipitation (mm)	BB (Mg DM	ha ⁻¹)	BNPP (Mg DM ha ⁻¹ year ⁻¹)		
	0 sheep ha ⁻¹	0.4 sheep ha ⁻¹	0 sheep ha ⁻¹	0.4 sheep ha ⁻¹	
$ \frac{P_0 \times (1+0\%)}{P_0 \times (1+10\%)} $ $ \frac{P_0 \times (1+10\%)}{P_0 \times (1-15\%)} $	11.41 12.68	5.49 5.88 5.43	1.30 1.45	0.61 0.65	

 P_0 , the averaged precipitation from 1993 to 2002; BB, Below-ground Biomass; BNPP, Below-ground Net Primary Production; DM, Dry Matter.

0.75 °C, the decrease of BB is from 0% to 2%, and the decrease of BNPP is from 0% to 3%. The results show that BB and BNPP are sensitive to increase of temperature, especially under grazing condition.

Under non-grazing condition, when precipitation increase by 10% compared to the long-term averaged precipitation, BB increase by 11%, and BNPP increase by 12%; when precipitation decrease by 15%, BB decrease by 4%, and BNPP decrease by 5%. Under 0.4 sheep ha⁻¹ stocking rate, when precipitation increase by 10%, BB increase by 7%, and BNPP also increase by 7%; when precipitation decrease by 15%, BB decrease by 1%, and BNPP decrease by 3%. The results show that BB and BNPP are more sensitive to the increase of precipitation than to the decrease of precipitation.

Discussion

The results of the study show that grazing acts as a negative force to the productivity of grassland ecosystem. The grassland ecosystem can maintain a much higher BB and BNPP under non-grazing condition than under grazing condition. However, the BB and BNPP decrease under grazing condition, especially under high grazing intensity. The reduction of above-ground biomass resulting from consumption by livestock will lead to a decrease in canopy photosynthesis and thus a reduction in translocation of photosynthate from shoot to root (Wang and Ripley 1997). Therefore, the root biomass and BNPP also decreases, though root has not been directly grazed (Smit and Kooijiman 2001).

Although there are evidences suggesting that grazing produces undetectable or positive effects on BNPP (McNaughton et al. 1998; van der Maarel and Titlyanova 1989), a general opinion is that clipping or grazing reduces root growth (Sundriyal 1992; Beaulieu et al. 1996; Biondini et al. 1998). Our simulated results are consistent with this opinion. Furthermore, the simulated BNPP decreases with increasing stocking rate, which agrees with the finding from a *Stipa breviflora* steppe by Zhang and Li (1997).

Simulated results show that the C/F ratio increase with increasing stocking rate, that is, the proportion of assimilation organs (leaves) decrease, and the proportion of non-assimilation organs (root and stem) increase. As a result of that, photosynthesis of plant also decreases. This also indicates that grazing has a negative effect on plant productivity. Brouwer (1963) put forward an opinion that plants maintain a 'functional equilibrium' between shoot and root growth. The opinion emphasizes the eco-physiological functionality of shift in allocation of current growth resources over above- and below-ground parts during the development of an individual plant, depending on the relative supply of above- (light, CO_2) and below-ground (water, nutrients) resources (Van Noordwijk et al. 1998). Allocation over above- and below-ground biomass may change rapidly, which reflect changes in the environment or external disturbances of the shoot to root equilibrium, such as grazing of root or shoot (Van Noordwijk et al. 1998). Biomass allocation ratio to root increases with increasing stocking rate, which is an adaptive response of plant to grazing. High proportion of BB in the total biomass can enhance the capacity of water uptake from soil and the ability of root water storage, and increase carbohydrate storage and the capacity to tolerate environmental stresses, which is favorable for grassland restoration (Wang et al. 2003).

Root turnover plays a critical role in regulating ecosystem carbon balance and nutrient cycling (Pendall et al. 2004), and is important for accurately evaluating carbon budget as well as nutrient cycling in ecosystems (Eissenstat et al. 2000). Our simulation results show that root turnover rate decreases with increasing stocking rate, which agrees with the results from a *Stipa breviflora* steppe in western Inner Mongolia (Zhang and Li 1997).

In general, there is a strong, positive correlation between root turnover and mean annual temperature for grassland (Gill and Jackson 2000). In our study, the mean annual temperature is 1.4 °C at KBU. This low temperature could be one of the reasons why the turnover rate is relatively lower at KBU grassland. In addition, root turnover is also affected by grazing. Reduction of the above- and below-ground biomass resulted from grazing will lead to reduction of input of litter and nutrients to the soil, and thus the overall nutrient availability decreases. As a consequence, the decomposability of litter decreases (Hobbs 1996). Nutrient losses in the form of removed biomass by animal can be partly compensated by urine and feces deposition, but this compensation is only effected for limited area (Smit and Kooijiman 2001).

In this study, the effect of precipitation variation has been evaluated based on simple assumptions of precipitation scenarios. Although the assumptions are somewhat arbitrary, they are the possible situations from the viewpoint of long-term climate change. Many uncertainties must have involved in our results. For example, feedback mechanism for water cycle has not been inadequately considered in the present model, the increased biomass resulted from the elevated precipitation might have been overestimated. This should be one of the major respects for which the model will be improved in our future work.

Conclusions

The maximum sustainable stocking rate at KBU is estimated to be 0.7 sheep ha⁻¹. With increasing stocking rate, both BB and BNPP decrease, the C/F ratio increases, and the root turnover rate decreases. The productivity and grazing capacity of the grassland are affected remarkably by precipitation variation. To prevent further degradation of the grassland, it is extremely imperative for the governments and all the stakeholders to take effective measures to keep an appropriate stocking rate. Only in this way can the goal of a sustainable grassland ecosystem be hopefully achieved.

Acknowledgements

This study has been supported by the CREST project (The Rangelands Atmosphere – Hydro-

sphere – Biosphere Interaction Study Experiment in Northeastern Asia) of JST. The authors are thankful for the helpful suggestions provided by Drs. Qingeng Wang and Wenhong Mo. The authors are also thankful to Dr. Japhet for kindly checking English. The authors are very grateful to two anonymous referees for their valuable comments on the manuscript.

References

- Beaulieu J., Gauthier G. and Rochefort L. 1996. The growth response of graminoid plants to goose grazing in High Arctic environment. J. Ecol. 84: 905–914.
- Begzsuren S., Ellis J.E., Ojima D.S., Coughenour M.B. and Chuluun T. 2004. Livestock responses to droughts and severe winter weather in the Gobi Three Beauty National Park, Mongolia. J. Arid Environ. 59: 785–796.
- Biondini M.E., Patton B.D. and Nyren P.E. 1998. Grazing intensity and ecosystem processes in a northern mixed-grass prairie, USA. Ecol. Appl. 8: 469–479.
- Brouwer R. 1963. Some aspects of equilibrium between overground and underground plant parts. Jaarboek IBS 1953: 31-39.
- Buwalda J.G. 1993. The carbon costs of root systems of perennial fruit crops. Environ. Exp. Bot. 33: 131–140.
- Chaieb M., Henchi B. and Boukhris M. 1996. Impact of clipping on root systems of 3 grasses species in Tunisia. J. Range Manage. 49: 336–339.
- Chen Z.Z., Huang D.H. and Zhang H.F. (1988). A study on the model of interrelation between underground biomass and precipitation of *Aneurolepidium chinense* and *Stipa grandis* grassland in Inner Mongolia region. In: Academia Sinica (ed.), Inner Mongolia Grassland Ecosystem Research Station, Research on Grassland Ecosystem (2). Science Press, Beijing, pp. 20–25.
- Cnoant R.T. and Paustian K. 2002. Potential soil carbon sequestration in overgrazed grassland ecosystems. Global Biogeochem. Cycles 16: 1143-1151.
- Coronato F.R. and Bertiller M.B. 1996. Precipitation and landscape related effects on soil moisture in semi-arid rangelands of Patagonia. J. Arid Environ. 34: 1–9.
- Coupland R.T. 1992. Mixed prairie. In: Coupland R.T. (ed.), Grasslands of the World, Elsevier, The Netherlands, Amsterdam, pp. 151-182.
- Eissenstat D.M., Wells C.E., Yanai R.D. and Whitbeck J.L. 2000. Building roots in changing environment: implications for root longevity. New Phytol. 147: 33-42.
- Engel R.K., Nichols J.T., Dodd J.L. and Brummer J.E. 1998. Root and shoot responses of sand bluestem to defoliation. J. Range Manage. 51: 42–46.
- Fernandez-Gimenez M.E. and Allen-Diaz B. 1999. Testing a non-equilibrium model of rangeland vegetation dynamics in Mongolia. J. Appl. Ecol. 36: 871-885.
- Gill R.A. and Jackson R.B. 2000. Global patterns of root turnover for terrestrial ecosystems. New Phytol. 147: 13-31.
- Hazarika Manzul Kumar, Yasuoka Y., Ito A. and Dye D. 2005. Estimation of net primary productivity by integrating

remote sensing data with an ecosystem model. Remote Sens. Environ. 94: 298-310.

- Hobbs N.T. 1996. Modification of ecosystems by ungulates. J. Wildlife Manage. 60: 695-713.
- Hunt J.E., Kelliher F.M., McSeveny T.M. and Byers J.N. 2002. Evaporation and carbon dioxide exchange between the atmosphere and a tussock grassland during a summer drought. Agri. For. Meteorol. 111: 65–82.
- Ito A. 2005. Modelling of carbon cycle and fire regime in an east Siberian larch forest. Ecol. Model. 187: 121–139.
- Ito A. and Oikawa T. 2002. A simulation model of carbon cycle in land ecosystems (Sim-CYCLE): a description based on dry-matter production theory and plot-scale validation. Ecol. model. 151: 143-176.
- Ito A. and Oikawa T. 2004. Global mapping of terrestrial primary productivity and light-use efficiency with a process-based model. In: Shiyomi M. (ed.), Global Environmental Change in the Ocean and on Land, Terrapub, pp. 343-358.
- Lauenroth W.K. 1979. Grassland primary production: North American grassland in perspective. In: French N.R. (ed.), Perspective in Grassland Ecology, Vol. 32. Springer-Verlag, New York, USA, pp. 3–24.
- Lauenroth W.K. 2000. Methods of estimating belowground net primary production. In: Sala O.E., Jackson R.B., Mooney H.A. and Howarth R.W. (eds), Methods in Ecosystem Ecology, Springer, New York, pp. 58-71.
- Liu J.J. (2004). Influence of grazing pressures on belowground biomass and productivity in Mongolia steppe. Japan Earth and Planetary Science Joint Meeting.
- Mariko Shigeru, Urano Tadaaki and Oikawa Takehisa (2003). Biomass and carbon fluxes in a Mongolian grassland. The second workshop on terrestrial change in Mongolia. Ulaanbaatar, Mongolia.
- McNaughton S.J., Banyikwa F.F. and McNaughton M.M. 1998. Root biomass and productivity in a grazing ecosystem: the Serengeti. Ecology 79: 587–592.
- McNaughton S.J., Oesterheld M., Frank D.A. and Williams K.J. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. Nature 341: 142–144.
- Milchunas D.G. and Lauenroth W.K. 1989. Three-dimensional distribution of plant biomass in relation to grazing and topography in the shortgrass steppe. Oikos 55: 82-86.
- NRC 1985. Nutrient requirements of sheep 6th ed. National Academic Press, Washington, p. 46.
- Oikawa T. and Ito A. (2001). Modeling carbon dynamics of terrestrial ecosystems in monsoon Asia. In: Matsuno T. and Kida H. (eds), Present and Future of Modeling Global Environmental Change: Toward Integrated Modeling. Terrapub, pp. 207–219.
- Pendall E, Bridgham S., Hanson P.J., Hungate B., Kicklighter D.W., Johnson D.W., Law B.E., Luo Y, Megonigal J.P., Olsrud M., Ryan M.G. and Wan S. 2004. Below-ground process response to elevated CO₂ and temperature: a discussion of observations, measurement methods, and models. New Phytol. 162: 311–322.

- Peters D.P.C. 2002. Plant species dominance at a grassland shrubland ecotone: an individual-based gap dynamics model of herbaceous and woody species. Ecol. Model. 152: 5-32.
- Pucheta E., Bonamigi I., Cabido M. and Diza S. 2004. Belowground biomass and productivity of a grazed site and a neighbouring ungrazed exclosure in a grassland in central Argentina. Austral Ecol. 29: 201–208.
- Richards J.H. 1984. Root growth response to defoliation in two *Agropyron* bunchgrasses: field observations with an improved root periscope. Oecologia 64: 21–25.
- Seligman N.G. and Van Leulen N 1989. Herbage production of a Mediterranean grassland in relation to soil depth, rainfall and nitrogen: a simulation study. Ecol. Model. 47: 303-311.
- Seligman N.G., Cavagnaro J.B. and Horno M.E. 1992. Simulation of defoliation effects on primary production of warmseason, semiarid perennial-species grassland. Ecol. Model. 60: 45-61.
- Smit A. and Kooijiman A.M. 2001. Impact of grazing on the input of organic matter and nutrients to the soil in a grassencroached Scots pine forest. For. Ecol. Manage. 142: 99-107.
- Stanton N.L. 1983. The effect of clipping and phytophagous nematodes on net primary production of blue grama, *Bouteloua gracilis*. Oikos 40: 249–257.
- Sundriyal R.C. 1992. Structure, productivity and energy flow in an alpine grassland in the Garhwal Himalaya. J. Veg. Sci. 3: 15–20.
- Svejcar T. and Christiansen S. 1987. The influence of grazing pressure on rooting dynamics of Caucasian bluestem. J. Range Manage. 40: 224–227.
- Urano Tadaaki, Mariko Shigeru, Kiyokaza Jawada. (2004). Seasonal dynamics of biomass and carbon fluxes in a Mongolian grassland. Japan Earth and Planetary Science Joint Meeting.
- Van der Maarel E. and Titlyanova A. 1989. Above-ground and below-ground biomass relations in steppes under different grazing intensities. Oikos 56: 364–370.
- Van Noordwijk M., Martikainen P., Bottner P., Cuevas E., Rouland C. and Dhillion S.S. 1998. Global change and root function. Global Change Biol. 4: 759-772.
- Wang R.Z and Ripley E. A. 1997. Effects of grazing on a Leymus chinensis grassland on the Songnen plain of northeastern China. J. Arid Environ. 36: 307–318.
- Wang R.Z., Gao Q. and Chen Q.S. 2003. Effects of climate change on biomass and biomass allocation in *Leymus chinensis* (Poaceae) along the Northeast China Transect (NECT). J. Arid Environ. 54: 653–665.
- Wang Y.F. and Jiang S. 1982. The effect of arid climate on the community structure and aerial biomass of *Stipa Grandis* Steppe. Acta Phytoecologica Et Geobotanica Sinica 6(4): 333–338 (In Chinese).
- Zhang J. and Romo J.T. 1994. Defoliation of a northern wheatgrass community: above- and belowground phytomass productivity. J. Range Manage. 47: 279–284.
- Zhang S.Y. and Li D. 1997. Effect of grazing on underground productivity and nitrogen turnover of *Stipa breviflora* steppe. Grassland of China 1: 13–18 (in Chinese with English abstract).