

Model analysis of grazing effect on above-ground biomass and above-ground net primary production of a Mongolian grassland ecosystem

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Summary In this study, we have analyzed the productivity of a grassland ecosystem in Kherlenbayan-Ulaan (KBU), Mongolia under non-grazing and grazing conditions using a new simulation model, Sim-CYCLE grazing. The model was obtained by integrating the Sim-CYCLE [Ito, A., 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. Ecological Modeling, 151, pp. 143–176] and a defoliation formulation [Seligman, N.G., Cavagnaro, J.B., Horno, M.E., 1992. Simulation of defoliation effects on primary production of warm-season, semiarid perennial- species grassland. Ecological Modelling, 60, pp. 45-61]. The results from the model have been validated against a set of field data obtained at KBU showing that both above-ground biomass (AB) and above-ground net primary production ($N_{p,a}$) decrease with increasing grazing intensity. The simulated maximum AB for a year maintains a nearly constant value of 1.15 Mg DM ha^{-1} under non-grazing conditions. The AB decreases and then reaches equilibrium under a stocking rate (S_r) of 0.4 sheep ha⁻¹ and 0.7 sheep ha⁻¹. The AB decreases all the time if S_r is greater than 0.7 sheep ha⁻¹. These results suggest that the maximum sustainable S_r is 0.7 sheep ha⁻¹. A similar trend is also observed for the simulated $N_{p,a}$. The annual $N_{p,a}$ is about 1.25 Mg DM ha⁻¹ year⁻¹ and this value is also constant under non-grazing conditions. The annual $N_{p,a}$ decreases and then reaches equilibrium under an S_r of 0.4 sheep ha⁻¹ and 0.7 sheep ha⁻¹,

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but the $N_{p,a}$ decreases all the time when S_r is greater than 0.7 sheep ha⁻¹. It also indicates that the maximum sustainable S_r is 0.7 sheep ha⁻¹. Transpiration (E_T) and evaporation (E_E) rates were determined by the Penman–Monteith method. Simulated results show that E_T decreases with increasing S_r , while E_E increases with increasing S_r . At equilibrium, the annual mean evapotranspiration (E) is 189.11 mm year⁻¹ under non-grazing conditions and 187.46 mm year⁻¹ under an S_r of 0.7 sheep ha⁻¹. This indicates that the water budget of the KBU grassland ecosystem is not significantly affected by grazing.

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Introduction

Mongolia is located in northeastern Asia, where ecotones (forest-grassland-desert) are formed because of the climatic shift from humid to arid conditions. An ecotone is a transitional area between two adjacent ecological communities. It is generally sensitive to any external disturbance of the environment, both natural and human, such as climate change or human activities (Pogue and Schnell, 2001; Peters, 2002). About 75% of the total land area in Mongolia is made up of grasslands and shrublands, which have been freely grazed by livestock all year round (Fernandez-Gimenez and Allen-Diaz, 1999). Moreover, the number of livestock increased significantly in recent years (Sugita et al., 2006). Grazing is the main activity in these grasslands. The effect of grazing on the ecosystem cannot be neglected. However, little information on the effect of grazing on grassland ecosystems is currently available. Overgrazing easily induces grassland ecosystem degradation. The establishment of an appropriate stocking rate (S_r) is essential if Mongolia is to maintain a sustainable grassland ecosystem.

Above-ground biomass (AB) is a direct indicator of grassland productivity. Net primary production (N_p) is the carbon fixed by plants per unit time and space and is an important component of carbon cycle research (Lobell et al., 2002). Since Mongolian grasslands are subjected to grazing all year round, the effect of grazing should be taken into account in order to accurately understand the carbon cycle of the Mongolian grassland ecosystem. The sustainable S_r for a certain grassland ecosystem varies with the above-ground net primary production $(N_{p,a})$. Therefore $N_{p,a}$ is directly related to the grazing capacity of the grassland and is also influenced by grazing. Grazing has been generally regarded as detrimental to plants because the living tissue is removed by the animals, although it has been observed that $N_{\rm p}$ can be maintained or stimulated in response to grazing, namely compensatory or overcompensatory growth (Hik and Jefferies, 1990; Biondini et al., 1998). Response to grazing varies from one grassland ecosystem to another. In general, however, it is a widely accepted opinion that $N_{p,a}$ or N_p will decrease significantly if Sr exceeds the grazing capacity of the grassland (Conant and Paustian, 2002). Direct measurement of $N_{\rm p}$ is only practical for relatively small field plot experiments. For larger areas, a simulation model should be able to provide a better estimate of N_p since plant growth and defoliation dynamics are very difficult to monitor in a freely grazed rangeland, partly because of the large area and relatively long duration of active interaction between animals and plants, and partly because of the difficulties encountered in measuring the forage consumed by free-ranging animals (White, 1984). In addition, well-controlled grazing experiments require an monetary investment which often makes their implementation impractical. It is also helpful to use a simulation model for grazed grassland to identify the problems that may be involved in grazing experiments and eventually to supply some useful suggestions for grazing management (Ungar and Noy-Meir, 1988; Hart, 1989).

Grazing may also affect the water cycle of the grassland ecosystem. Mongolia is classified as an arid and semi-arid region (Begzsuren et al., 2004). Water is one of main factors controlling biological activity in arid ecosystems. Precipitation in any ecosystem may either be intercepted by plants, infiltrated into soil or run off the ground surface. All of these depend on vegetation cover, soil characteristics and topography (Coronato and Bertiller, 1996). The study site, Kherlenbayan-Ulaan (KBU), has a very flat relief that overrules the possibility of runoff from the ground surface. Water infiltrated into soil can be absorbed by roots and utilized by plants. Therefore, most of the precipitation is eventually lost by evaporation (E_E) from bare soil or transpiration $(E_{\rm T})$ from plants. This implies that precipitation and evapotranspiration (E) contribute the largest proportion of the water budget in KBU. Overgrazing will cause serious damage to the grassland canopy, change soil properties and water loses (Gao et al., 1996; Gao et al., 1998). This will, of course, influence E_{T} and E_{E} .

There were three objectives for this study. The first was to analyze the response of AB and $N_{p,a}$ to different grazing intensities. The second was to establish an appropriate S_r for KBU grasslands. The third was to investigate how grazing intensity influences E_T and E_E of the KBU grassland ecosystem.

Study site and description of field experiments

Study site

The study site was KBU ($47^{\circ}3'N$, $108^{\circ}8'E$), in Hentiy province of Mongolia, 100 km east of Ulaanbaatar. The altitude is 1235 m above sea level. The mean annual precipitation and temperature are respectively 187 mm and 1.4 °C according to the Meteopost station data for the period of 1993–2002 of the Institute of Meteorology and Hydrology of Mongolia. The majority of the precipitation is concentrated in the months of June to September. The growing season is from late April to mid October.

The vegetation is a natural semi-arid steppe, which has been subjected to grazing by livestock for thousands of years (Begzsuren et al., 2004). The livestock are mainly cattle, sheep, goats and horses which graze freely all year

round. According to the Statistical Office of Mongolia, the present grazing intensity is 0.7 sheep ha^{-1} and this intensity represents the whole of Dergelthaan soum (a Mongolian administrative unit equivalent to a county or prefecture) which includes KBU village. However, the grazing intensity for KBU village has been found to be 2.3 sheep ha^{-1} in summer (Sugita et al., 2006), but since we are not very certain that all the livestock are limited to the grasslands of KBU, we use the Dergelthaan soum grazing intensity to represent the KBU grazing intensity in our simulation. Dominant plants are graminoids and semi-shrubs, accompanied by a few forbs. According to two years' investigation by our project group (Mariko et al., 2003), the average height of the grassland is about 15 cm, the maximum leaf area index (L) is 0.6–0.7 m m⁻², the mean AB is 85–110 g m⁻², and N_p is 230-280 g m⁻² year⁻¹. Dominant species are Stipa krylovii, Artemisia frigida and Cleistogenes squarrosa. C₄ plant species occupy about 10% of the total biomass. The soil is chestnut soil.

Field experiments

Measured data were obtained by field experiments at KBU. The methodologies have been reported in detail by Mariko et al. (2003) and Urano (2005). In order to facilitate an easy understanding of the present paper, a brief introduction to the experimental methods is given as bellow.

The field experiment sites were carefully selected and could be regarded as sufficiently representative of the whole KBU grassland. In order to determine the effect of grazing on the grassland ecosystem, an enclosure was made in autumn 2002. The area of the enclosure was 200 m \times 170 m and the fence height was 1.5 m. Livestock was restrained from going into the enclosure. The value of L, biomass and carbon fluxes were measured both inside and outside the enclosure during each growing season from 2003. The items were measured monthly from June to September. The value of L was measured by scanning the images of leaves with a flatbed scanner and a computer and analyzing the image by a kind of image processing software (Mariko et al., 2003). The value of AB was measured by the clipping experiment as described by Urano (2005). The values of L and AB were averages of measurements from 24 quadrats. In the non-grazing site, the value of $N_{p,a}$ was the summation of the increase of the total above-ground biomass (including green biomass, standing dead matter and litter) throughout the growing season. In the grazing site, the value of $N_{p,a}$ was the summation of the increase in total AB plus the intake by livestock.

Model description

The model structure of the Sim-CYCLE grazing is shown in Fig. 1. Until now, most carbon cycle models for grassland ecosystems have not considered the grazing effect. In order to simulate the grazing effect on carbon cycle of a Mongolian grassland ecosystem, we combined a carbon cycle model, Sim-CYCLE (Ito and Oikawa, 2002) with a grazing formulation (Seligman et al., 1992). Sim-CYCLE is a process-oriented carbon cycle model, which has been successfully applied to various types of terrestrial ecosystem (Hazarika et al., 2005; Ito, 2005; Ito and Oikawa, 2004; Ito and Oikawa, 2002; Oikawa and Ito, 2001). Sim-CYCLE was developed on the basis of dry-matter productivity theory (Monsi and Saeki, 1953). The carbon cycle is simulated as in Fig. 1a. In this model, terrestrial carbon dynamics is conceptualized as a five-compartment system. Carbon in a given ecosystem (C_E) is composed of that in the plant biomass (C_P) and that in the soil organic carbon (C_S). C_P includes three compartments: foliage, stem and root; C_S includes two compartments: litter and humus as shown in Eqs. (1)–(3)

$$C_{\rm E} = C_{\rm P} + C_{\rm S} \tag{1}$$

$$C_{\rm P} = C_{\rm P,F} + C_{\rm P,C} + C_{\rm P,R} \tag{2}$$

$$C_{\rm S} = C_{\rm S,Li} + C_{\rm S,H} \tag{3}$$

where the subscripts, F, C, R, Li and H stand for foliage, stem, root, litter and humus respectively.

Gross primary production (G_p) is the ultimate origin of all the organic carbon, through which atmospheric CO_2 is fixed into dry matter. Instantaneous G_p ($G_{p,ins}$) is expressed as follows:

$$G_{p,ins} = \int_{0}^{L} AdL$$

= $\frac{A_{MAX}}{k_{b}} [ln\{\alpha + k_{b}Q_{P}\} - ln\{\alpha + k_{b}Q_{P}\exp(-k_{b}L)\}]$ (4)

where A is the single-leaf photosynthetic rate, A_{MAX} is the single-leaf photosynthetic rate under light-saturation, α is the light-use efficiency, $k_{\rm b}$ is the light attenuation coefficient, $Q_{\rm P}$ is the photosynthetic photon flux density at the canopy top. The daily $G_{\rm p}$ rate can be obtained by integrating $G_{\rm p,ins}$ for day length.

The grazing effect has been neglected in Sim-CYCLE. N_p is the difference between G_p and plant autotrophic respiration (R_{plant}) under non-grazing conditions. In the present study, grazing using a defoliation formulation (Seligman et al., 1992) has been integrated into Sim-CYCLE in order to simulate the effect of grazing on the carbon cycle of grassland ecosystems. N_p is the summation of the increase of $C_P(C'_P)$, litterfall and defoliation rate (D_r) by livestock under grazing conditions.

$$N_{\rm p} = G_{\rm p} - R_{\rm plant} = C_{\rm p}' + {\rm litterfall} + D_{\rm r}$$
 (5)

The same formulation for grazing by Seligman et al. (1992), which is suitable for semiarid grasslands and which was successfully applied to a semiarid grassland ecosystem in Argentina, was adopted in this study. A description is as follows:

$$D_r = G_e S_r((C_{P,F} + C_{P,C}) - (C_{P,F} + C_{P,C})_U) \quad (0 < D_r < S_r D_x)$$
(6)

where D_r is defoliation rate (kg ha⁻¹ d⁻¹), G_e is the grazing efficiency of the livestock (ha d⁻¹ per sheep unit), S_r is the stocking rate, $(C_{P,F} + C_{P,C})_U$ is the residual above-ground biomass that is unavailable to the livestock (kg ha⁻¹ dry matter) and D_x is the satiation consumption rate of the livestock (NRC, 1985).

In the grazing formulation of Seligman et al. (1992), the grassland structure is assumed to be evenly distributed vertically from upper to lower layers when the effect of grazing



Figure 1 Model structure of Sim-CYCLE grazing (a), carbon cycle. G_p : gross primary production; N_p : net primary production; ARM: maintenance respiration; ARG: growth respiration; HR: soil heterotrophic respiration; $C_{P,F}$: carbon in foliage; $C_{P,C}$: carbon in stem; $C_{P,R}$: Carbon in root; $C_{S,Li}$: carbon in litter; $C_{S,H}$: carbon in humus; HF: humus formation; D_r : defoliation rate; PT_F, PT_C and PT_R: photosynthate translocated to foliage, stem and root; (b), water cycle. $R_{n,o}$: canopy radiation; $R_{n, s}$: soil surface radiation; E_T : transpiration; E_E : evaporation; $M_{s,u}$: upper layer soil water; $M_{s,l}$: lower layer soil water; I_{int} : rain interception by canopy.

is simulated. It is also assumed to be evenly distributed horizontally over the site without extreme grass clumping and without large areas of bare soil. These assumptions are actually feasible during the peak growing season. But in other seasons, the intake by animals will be overestimated, and the maximum S_r will be underestimated. In our present model, we just simulate the grazing effect in the growing season, thereby minimizing this error.

No attempt has been made to separate the grass into palatable and unpalatable species.

The simulated forage intake is limited to green leaves and stems only. This is based on the assumption that not only is the green biomass highly preferred by most livestock but that the amount of green biomass is a critical component in the plant system that controls both assimilation and transpiration.

In this study, the effect of grazing has been primarily simulated. Animals are regarded simply as consumers. Many other possible direct or indirect effects of grazing, such as trampling by animals, changes in the nutrient cycling of grassland ecosystems, plant damage caused by animals, changes in plant relative growth rates etc., have not been taken into account here. Soil nutrients for plant growth are regarded as non-limiting. The effect of grazing animals is not only harmful, but also beneficial. For example, excretion from animals can add nitrogen to the soil, which is helpful for grass growth. In our present model, in addition to soil water, other soil nutrients are regarded as non-limiting, so the animal is a negative consumer. The water cycle in the grassland ecosystem is simulated as in Fig. 1b. The water component is classified as soil water in the upper layers ($M_{s,u}$), soil water in lower layers ($M_{s,l}$) and snow accumulation (S_A). Precipitation includes rain and snow fractions. The fraction of snowfall in the total precipitation is a function of air temperature and the thawing of snow is also a function of the ground surface temperature (Ito, 2000).

$$P_{\rm snow} = \frac{P}{1 + \exp[0.75(T_{\rm a} - 2)]} \tag{7}$$

$$S_{T} = \frac{S_{A}}{1 + \exp(-0.375T_{g})}$$
 (8)

where P_{rain} and P_{snow} are the rain and snow fractions of the total precipitation (*P*) respectively, S_T is snow thaw, T_a and T_g are the air and ground surface temperatures respectively.

The actual *E* is mainly composed of E_E from the soil surface and E_T from the grassland canopy. The transpired water is from the lower layer soil water. For each water component, the net balance of water content during a given period is as follows:

$$M'_{\rm s,u} = P_{\rm rain} + S_{\rm T} - E_{\rm E} - M_{\rm p} \tag{9}$$

$$M_{\rm sl}' = M_{\rm p} - E_{\rm T} \tag{10}$$

$$S'_{A} = P_{snow} - S_{T}$$
(11)

where $M_{\rm p}$ is the water penetration from the upper to lower layers.

In order to estimate the $E_{\rm E}$ from the soil surface and the $E_{\rm T}$ from the grassland canopy, the soil surface net radiation $(R_{\rm n,s})$ and the canopy net radiation $(R_{\rm n,o})$ separated from the total net solar radiation are required. The potential transpiration $(E_{\rm T,P})$ and evaporation $(E_{\rm E,P})$ have been estimated by the Penman–Monteith method (Monteith, 1981).

$$E_{\mathrm{T,P}} = \frac{\Delta R_{\mathrm{n,o}} + \rho_{\mathrm{a}} c_{\mathrm{p}} g_{\mathrm{v}} D}{\lambda [\Delta + \gamma (g_{\mathrm{v}} / g_{\mathrm{a}})]}$$
(12)

$$E_{\mathsf{E},\mathsf{P}} = \frac{\Delta R_{\mathsf{n},\mathsf{s}} + \rho_{\mathsf{a}} c_{\mathsf{p}} g_{\mathsf{g}} D}{\lambda [\Delta + \gamma (g_{\mathsf{g}}/g_{\mathsf{a}})]}$$
(13)

where Δ is the slope of the saturated vapor pressure which is a function of temperature, ρ_a is the air density, c_p is the specific heat of air, D is the vapor pressure deficit, g_v is the single-leaf conductance, g_a is the aerodynamic conductance and g_g is the ground conductance for water vapor. λ is the latent heat of water vaporization and γ is the psychrometer constant.

The actual transpiration (E_T) and evaporation rates (E_E) are as follows:

$$E_{\rm T} = \frac{(M_{\rm s,l} + E_{\rm T,P}) - \sqrt{(M_{\rm s,l} + E_{\rm T,P})^2 - 4C_{\rm v}M_{\rm s,l}E_{\rm T,P}}}{2C_{\rm v}}$$
(14)

$$E_{\rm E} = \frac{(M_{\rm s,u} + E_{\rm E,P}) - \sqrt{(M_{\rm s,u} + E_{\rm E,P})^2 - 4C_{\rm v}M_{\rm s,u}E_{\rm E,P}}}{2C_{\rm v}}$$
(15)

where C_v is the convexity of the $M_{s,l} - E_T$ and $M_{s,u} - E_E$ curves.

The actual evapotranspiration rate (E) is

$$\boldsymbol{E} = \boldsymbol{E}_{\mathrm{T}} + \boldsymbol{E}_{\mathrm{E}} \tag{16}$$

The model time step is one month. Model input data include meteorological and soil data. The model input data are given in Table 1. The data, except the radiation, were obtained from the KBU meteorology station operated by the Institute of Meteorology and Hydrology, Mongolia (Sugita et al., 2006). These data are an average of the 10-year period from 1993 to 2002. The radiation data is estimated from the NCAR and NCEP datasets (Ito and Oikawa, 2002). The parameters of the model are listed in Table 2.

Table 1	Major model input data					
Month	Precipitation	Radiation $(W m^{-2})$	2 m height specific	Soil t		

Results

Model validation at KBU

The simulated results are compared with the measured data in Fig. 2 and Table 3. The measured data are those from outside of the enclosure, i.e., under natural grazing conditions. The simulated results were calculated using the local S_r (0.7 sheep ha⁻¹). The values of L and AB were validated using data obtained under grazing conditions. Reference $N_{p,a}$ was deduced from the standing crop and standard sheep unit intake (NRC, 1985), because intake by livestock has not been measured in field experiments and this is one component of $N_{p,a}$. Simulated $N_{p,a}$ was validated by this deduced $N_{p,a}$. The measured maximum L and AB in each year were observed in the month of August, and the values were, $0.57 \text{ m}^2 \text{ m}^{-2}$ and $0.85 \text{ Mg DM ha}^{-1}$ respectively. The simulated maximum L and \overrightarrow{AB} were also found in August, and the values were $0.63 \text{ m}^2 \text{ m}^{-2}$ and $0.89 \text{ Mg DM ha}^{-1}$ respectively. The values of the reference annual $N_{p,a}$ and the simulated annual $N_{p,a}$ are shown in Table 3. There are some observed differences between the simulated results and the measured data. The model greatly simplified the real ecosystem. It was set up to study potential production as a function of soil water and temperature when soil nutrients did not limit plant growth. In addition, there was also error in the field experiment because of human operation, for example, the error in selecting quadrat. Any of these could account for the differences between the simulated results and measured data. Despite these differences, the trends in the simulated L, AB and $N_{p,a}$ agree with those of the measured data.

AB at different stocking rates

A preliminary study has indicated that it will take 100-150 years for the productivity of the grasslands to reach an equilibrium state under an S_r lower than 0.7 sheep ha⁻¹. Thus 150 years should be long enough to investigate the grassland. Therefore in this study, we decided to run the model for 250 years. We simulate AB under S_r values of 0, 0.4, 0.7, 0.8, and 1.2 sheep ha⁻¹. Simulated results show that the AB

Table 1 Major model input data							
Month	Precipitation	Radiation (W m ⁻²)	2 m height specific humidity (kg kg ⁻¹)	Soil temperature (°C)		Air temperature (°C)	
	(mm)			10 cm depth	200 cm depth	Ground surface	2 m height
January	1.77	101.11	0.001	-15.65	-12.55	-22.45	-23.35
February	1.20	151.65	0.001	-10.45	-8.65	-14.85	-15.65
March	1.27	221.03	0.002	-5.75	-7.05	-6.25	-6.65
April	1.43	283.20	0.003	4.45	-1.75	5.15	5.55
May	3.62	327.07	0.004	11.85	1.05	12.75	13.75
June	25.72	327.54	0.006	17.55	3.25	18.75	20.35
July	57.20	307.94	0.008	19.85	6.15	20.75	22.25
August	61.18	297.38	0.007	17.35	8.05	17.65	18.75
September	20.38	227.92	0.004	11.45	9.45	10.95	11.45
October	4.39	167.13	0.003	3.05	3.85	1.85	1.85
November	2.82	111.50	0.002	-5.35	1.85	-9.95	-10.55
December	2.19	85.90	0.001	-12.75	-8.15	-18.95	-19.75

Table 2 Parameters in Sim-CYCLE grazing

Symbol	l Description			Unit	Reference
		C ₃	C4		
AMAX	Light-saturated photosynthetic rate	20	30	μ mol CO ₂ m ⁻² s ⁻¹	lto (2000)
	Light-use efficiency	0.05	0.05	mol CO ₂ mol ⁻¹ photon	lto (2000)
, b	Light attenuation coefficient	0.38	0.40	Dimensionless	lto (2000)
R,L	Albedo of leaf surface	0.16	0.15	Dimensionless	lto (2000)
- ´ n	Minimum temperature for photosynthesis	0	6	°C	lto (2000)
o	Optimum temperature for photosynthesis	18	30	°C	lto (2000)
x	Maximum temperature for photosynthesis	45	50	°C	lto (2000)
sens,CO ₂	CO ₂ sensitivity of photosynthetic rate	40	10	ppmv	Lee (2006)
a	Photosynthate allocation ratio for above-ground assimilation organ	0.24	0.30	Dimensionless	Lee (2006)
n,a	Photosynthate allocation ratio for above-ground non-assimilation organ	0.05	0.10	Dimensionless	Lee (2006)
s	Specific leaf area	125	110	cm ² g ⁻¹ dry weight	Lee (2006)
0	Stomatal conductance at the light compensation point	50	10	mmol $H_2O m^{-1} s^{-1}$	lto (2000)
1	Empirical coefficient of Ball-Berry-Leuning model	58,000	55,000	Dimensionless	lto (2000)
2	Empirical coefficient of Ball-Berry-Leuning model	5	7	Dimensionless	lto (2000)
,max	Maximum stomatal conductance	0.4	0.2	mol $H_2O m^{-1} s^{-1}$	lto (2000)
	CO ₂ compensation point	50	5	ppmv	lto (2000)
.10	Temperature sensitivity of respiration	2	2	Dimensionless	lto (2000)
M,F	Specific maintenance respiration rate of leaf at 15 °C	1.75	1.60	mg C g C $^{-1}$ day $^{-1}$	Lee (2006)
M,C	Specific maintenance respiration rate of stem at 15 °C	0.10	0.30	mg C g C $^{-1}$ day $^{-1}$	Lee (2006)
M,R	Specific maintenance respiration rate of root at 15 °C	0.03	0.56	mg C g C $^{-1}$ day $^{-1}$	Lee (2006)
G,F	Specific growth respiration coefficient of leaf at 15 °C	0.35	0.52	g C g C ⁻¹	Lee (2006)
G,C	Specific growth respiration coefficient of stem at 15 $^\circ C$	0.18	0.32	$ m g~C~g~C^{-1}$	Lee (2006)
G,R	Specific growth respiration coefficient of root at 15 °C	0.29	0.41	g C g C $^{-1}$	Lee (2006)
F	Specific litter fall rate of foliage	3.5	3.2	mg C mg C $^{-1}$ day $^{-1}$	Lee (2006)
İc	Specific litter fall rate of stem	0.23	0.23	mg c mg C $^{-1}$ day $^{-1}$	Lee (2006)
R	Specific litter fall rate of root	1.4	1.4	mg c mg C $^{-1}$ day $^{-1}$	Lee (2006)
v	Convexity of water availability- evapotranspiration rate curve	0.85		Dimensionless	lto (2000)
R,S	Soil surface albdo	0.05		Dimensionless	lto (2000)
Li	Litter specific respiration rate at 15 °C	1.45		mg C g C $^{-1}$ day $^{-1}$	Lee (2006)
н	Humus specific respiration rate at 15 °C	0.11		mg C g C $^{-1}$ day $^{-1}$	Lee (2006)
l _w	Parameter of soil moisture on microbial activity	0.20		Dimensionless	lto (2000)
la	Parameter of soil air space on microbial activity	0.10		Dimensionless	lto (2000)
7 _f	Mineral soil formation ratio to litter decomposition	1.2		Dimensionless	Lee (2006)
e	Grazing efficiency of livestock	0.011		ha day ⁻¹ per sheep unit	Seligman et a (1992)
) _X	Satiation consumption rate of the livestock	2.4		kg d $^{-1}$ per sheep unit	NRC (1985)

decreases with increasing grazing intensity (Fig. 3). The maximum AB of the year appears in August, and is maintained at a constant value of about 1.15 Mg DM ha⁻¹ under non-grazing conditions. The maximum AB decreases and then reaches an equilibrium state under an S_r of 0.4 sheep ha⁻¹ and 0.7 sheep ha⁻¹. The value of AB is 0.99 Mg;DM ha⁻¹ under an S_r of 0.4 sheep ha⁻¹ in the first year and 0.50 Mg DM ha⁻¹ in the equilibrium state. The value of AB is 0.89 Mg DM ha⁻¹ in the equilibrium state. The AB decreases all the time at an S_r of 0.8 sheep ha⁻¹ in the first year and 1.2 sheep ha⁻¹. The value of AB is 0.87 Mg DM ha⁻¹ under an S_r of 0.8 sheep ha⁻¹ in the first year and sheep ha⁻¹ in the first year and 1.2 sheep ha⁻¹. The value of AB is 0.87 Mg DM ha⁻¹ under an S_r of 0.8 sheep ha⁻¹ in the first year and is 0.19 Mg DM ha⁻¹ after 150 years, showing a decrease of 78% compared to the first year. Similarly, the value of AB is 0.80 Mg DM ha⁻¹ under

der an S_r of 1.2 sheep ha⁻¹ in the first year, and becomes 0.07 Mg DM ha⁻¹ after 150 years, showing a 91% decrease compared to the first year. These results suggest that the maximum sustainable S_r is 0.7 sheep ha⁻¹. Here the sustainable state stands for the condition in which the grassland productivity, the values of AB or $N_{p,a}$ maintain nearly constant values.

We have also investigated the ratio of AB to the total biomass (TB). Both the measured and the simulated ratio show a decreasing trend with increasing grazing intensity. The measured data shows that the ratio of AB/TB is 7% under non-grazing conditions, and 6% under an S_r of 0.7 sheep ha⁻¹. The simulated results show that the ratio of AB/TB is 9% under non-grazing conditions, 8% under an S_r of 0.7 sheep ha⁻¹, and 7% under an S_r of 1.2 sheep ha⁻¹. This sug-



Figure 2 Measured data and simulated results at KBU (a), *L*: leaf area index; (b), AB: above-ground Biomass; DM: dry Matter.

Table 3 simulated N	Comparison betv V _{p,a} at KBU	ween the	reference	and the
Item	$N_{ m p,a}$ (mg DM ha $^{-1}$ yea	SD ar ⁻¹)	95%CI	RE
Reference	1.07	0.20) 1.07 ± 0.	11 –
Simulated	1.13	_	-	5%

 $N_{p,a}$: above-ground net primary production; DM: dry matter; SD: standard deviation; CI: confidence interval; RE: relative error = (simulated – measured)/simulated; ''-'': not available.



Figure 3 Effect of grazing on AB simulated by Sim-CYCLE grazing AB: above-ground Biomass; DM: dry matter; S_r n: stocking rate is *n* sheep ha⁻¹.

gests that the ratio of AB to TB decreases with increasing grazing intensity. The results show that biomass allocation to roots increases with increasing S_r . This is one of the adaptive responses of plants to grazing. High proportions of below-ground biomass in the total biomass can enhance the capacity of water uptake from soil and below-ground water storage ability, increase carbohydrate storage and the



Figure 4 Effect of grazing on $N_{p,a}$ simulated by Sim-CYCLE grazing $N_{p,a}$, above-ground net primary production; DM, dry matter; S_rn : stocking rate is *n* sheep ha⁻¹.

capacity to tolerate environmental stresses. This improves the potential for grassland restoration from disturbance (Wang et al., 2003a; Wang, 2004).

$N_{p,a}$ at different stocking rates

Simulated results show that the annual $N_{p,a}$ decreases with increasing S_r (Fig. 4). The annual $N_{p,a}$ maintains a constant of about 1.25 Mg DM ha⁻¹ year⁻¹ under non-grazing conditions. At S_{rs} of 0.4 sheep ha⁻¹ and 0.7 sheep ha⁻¹, the value of $N_{p,a}$ decreases and then reaches an equilibrium state. Under an S_r of 0.8 sheep ha⁻¹, the value of $N_{p,a}$ is 1.12 Mg DM ha⁻¹ year⁻¹ in the first year and 0.25 Mg DM ha⁻¹ year⁻¹ in the 150th year showing a decrease of 78% compared to the first year. Under an S_r of 1.2 sheep ha⁻¹, $N_{p,a}$ decreases by 92% when the 150th year is compared to the first year. These results also indicate that the maximum sustainable S_r is 0.7 sheep ha⁻¹.

E_T and E_E

 $E_{\rm T}$ and $E_{\rm E}$ have been simulated under different values of $S_{\rm r}$ to investigate the impact of grazing on the soil hydrologic characteristics. Simulated results show that $E_{\rm T}$ decreases with increasing $S_{\rm r}$. In the equilibrium state, the annual $E_{\rm T}$ is about 15.08 mm year⁻¹ under non-grazing conditions. It is 3.84 mm year⁻¹ when the $S_{\rm r}$ is 0.4 sheep ha⁻¹ and 2.11 mm year⁻¹ under an $S_{\rm r}$ of 0.7 sheep ha⁻¹. Simulated results show that $E_{\rm E}$ increases with increasing $S_{\rm r}$. The annual $E_{\rm E}$ is 174.03 mm year⁻¹ under non-grazing conditions, 183.63 mm year⁻¹ under an $S_{\rm r}$ of 0.4 sheep ha⁻¹ and 185.35 mm year⁻¹ under an $S_{\rm r}$ of 0.4 sheep ha⁻¹. In our present simulation, E is the summation of $E_{\rm T}$ and $E_{\rm E}$. The annual E is 189.11 mm year⁻¹ under an $S_{\rm r}$ of 0.7 sheep ha⁻¹. On the whole, the water budget of the KBU grassland ecosystem is not significantly influenced by grazing.

Discussion

The simulated results show that both the value of AB and $N_{p,a}$ decrease with increasing S_r. The most productive one is under non-grazing conditions. The value of *L* decreases when grass is defoliated by animals. The grass growth rate has been hampered by grazing. The productivity of

grasslands consequently decreases. The total intake by animals increases with increasing S_r . Therefore $N_{p,a}$ decreases due to all the above-mentioned reasons. The value of AB decreases with increasing S_r . The reduction of AB is not only due to consumption by livestock but also due to a decrease in shoot productivity.

The present simulation results show that grazing has a negative effect on the KBU grassland ecosystem. There is no compensatory growth in this grassland ecosystem. Experimental results from other grassland ecosystems and model simulations have shown that N_p can be maintained (compensatory growth) or stimulated (overcompensatory growth) in response to grazing (McNaughton, 1979, 1983; Biondini et al., 1998; Mazancourt et al., 1998), but there is no grazing optimization in the KBU grassland ecosystem. The main compensatory mechanisms are as follows.

The first is the grazing modification of light availability. Grazing decreases the standing crop, improves light absorption efficiency and reduces self-shading (Jameson, 1963). The second is that the biomass allocation pattern between aboveground and belowground has been changed. Partial defoliation has a strong effect on the allocation of assimilate within the plant (Caldwell et al., 1981; Holland et al., 1992; Leriche et al., 2001). The third mechanism is the reduction of water loss and water stress. Reduction of plant above-ground biomass decreases canopy $E_{\rm T}$ and reduces the intensity and duration of water stress for plants (Rauzi, 1963; Archer and Detling, 1986).

The first mechanism is not effective in the KBU grasslands since the maximum *L* is lower than 0.7 m m⁻² (Urano, 2005; Kojima, 2004) and thus the self-shading effect could have been negligible.

For the second mechanism, this response depends on the plant species. Some species increase their investment in the above-ground part, whereas other plant species increase their investment to the below-ground part as a response to increasing grazing intensity. Changes in the shoot/root allocation pattern could play a major role in determining the response of the grassland to grazing (Leriche et al., 2001). Our simulated result of decreasing of shoot/root ratio in response to increasing grazing intensity is consistent with results reported for Artemisia frigida under grazing conditions (Wang et al., 2003b). Unfortunately, we have been unable to obtain information from the literature about the Stipa krylovii allocation ratio under grazing conditions. Biomass allocation to roots increased with increasing S_r , and this is also one reason why there is no compensatory above-ground growth under grazing conditions.

As for the third mechanism, although $E_{\rm T}$ decreases due to removal of the canopy, the area of bare ground increases simultaneously, and the $E_{\rm E}$ from the soil surface increases. The removal of the vegetation canopy by grazing reduces the transpiration leaf area, and results in a reduction of $E_{\rm T}$, but the reduction of vegetation canopy also results in the exposure to sun and wind of a larger ground area and leads to higher surface temperatures. As a result, the $E_{\rm E}$ from soil surface increases. Also, trampling by animals compacts the topsoil, and reduces the soil porosity (Zhang and Gao, 1994). This leads to a much lower water infiltration rate. The soil surface $E_{\rm E}$ also increases due to the lower infiltration (Wang and Ripley, 1997). For the above-mentioned reasons, the reduction of $E_{\rm T}$ is largely compensated for by an increase in $E_{\rm E}$. The water budget is not significantly influenced by grazing. This is consistent with the results obtained by Coronato and Bertiller (1996) and Chen and Wang (2000).

In order to make sustainable use of grasslands and to avoid degradation, as well as to maintain a high level of production from ecosystems, an appropriate S_r is necessary. Our simulated results show that the S_r at KBU should not be higher than 0.7 sheep ha^{-1} in the growing season which coincides with the data reported by the Statistical Office of Mongolia. Therefore the S_r of 0.7 sheep ha⁻¹, which represents the whole of Dergelthaan soum, is safe in summer for KBU grasslands according to our present simulation. However further studies need to be carried out to ascertain if this stocking rate is appropriate for KBU in winter. The data of grazing intensity only for KBU village is found to be 7.3 sheep ha^{-1} in winter (Sugita et al., 2006). This high grazing intensity could be the result of migration by other animals into KBU from other villages of Dergelthaan soum because of the comparably more favorable climate at KBU in winter. As a result of this, the grazing management system makes the S_r much higher than 0.7 sheep ha⁻¹. The $N_{\rm p,a}$ of the grasslands of western Inner Mongolia, China is about 0.96 Mg DM ha^{-1} year⁻¹. Field experiments have shown that 6.67 sheep ha^{-1} is too high a stocking rate for this type of grassland (Wang et al., 2003b). The $N_{\rm p,a}$ of the grassland of KBU is about 0.98 Mg DM ha⁻¹ year⁻¹ which is similar to that of the grassland of western Inner Mongolia. We conclude that an S_r of 7.3 sheep ha⁻¹ is too high for KBU and beyond its carrying capacity. Hence the grassland ecosystem is under threat of serious degradation if the present management system is not improved upon.

The effect of grazing on the water cycle is not significant from the result of this preliminary simulation. Many field study results show that grazing influences the soil water content and many other soil physical properties relative to hydrologic characteristics (Warren et al., 1986; Abdelmagid et al., 1987a; Abdel-magid et al., 1987b; Wang and Ripley, 1997; Li et al., 2000). Continuous overgrazing is detrimental to soil hydrologic characteristics, while moderate to light grazing is less harmful to the soil (Gifford and Hawkins, 1978; Stroosnijder, 1996; Wang and Ripley, 1997). These changes have not been reflected in our present model. We will improve on our model to reflect the effects of the aforementioned factors and make it better express the grazing effect on the water cycle of grassland ecosystems.

Conclusions

Simulated results show that AB and $N_{p,a}$ decrease with increasing S_r . To maintain the sustainable grassland ecosystem, the S_r of KBU grasslands in the growing season should not be higher than 0.7 sheep or sheep equivalents per hectare. A preliminary simulation of the water budget shows that E_T decreases with increasing S_r , and E_E increases with increasing S_r . The water budget of the KBU grassland ecosystem is not significantly influenced by grazing. Further investigations of the effect of grazing on the water budget of this grassland ecosystem will be needed.

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References

- Abdel-magid, A.H., Schuman, G.E., Hart, R.H., 1987a. Soil buck density and water infiltration as affected by grazing systems. Journal of Range Management 40, 307–309.
- Abdel-magid, A.H., Trlica, M.J., Hart, R.H., 1987b. Soil and vegetation responses to simulated trampling. Journal of Range Management 40, 303–306.
- Archer, S., Detling, J.K., 1986. Evaluation of potential herbivore mediation of plant water status in a North American mixed-grass prairie. Oikos 47, 287–291.
- Begzsuren, S., Ellis, J.E., Ojima, D.S., Coughenour, M.B., Chuluun, T., 2004. Livestock responses to droughts and severe winter weather in the Gobi Three Beauty National Park, Mongolia. Journal of Arid Environments 59, 785–796.
- Biondini, M.E., Patton, B.D., Nyren, P.E., 1998. Grazing intensity and ecosystem processes in a northern mixed-grass prairie, USA. Ecological Applications 8, 469–479.
- Caldwell, M.M., Richards, J.H., Johnson, D.A., Nowak, R.S., Dzurec, R.S., 1981. Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. Oecologia 50, 14–24.
- Chen, Z.Z., Wang, S.P., 2000. Chinese Typical Grassland Ecosystem. China Science Press, pp. 106–109.
- Conant, R.T., Paustian, K., 2002. Potential soil carbon sequestration in overgrazed grassland ecosystems. Global Biogeochemical Cycles 16, 1143–1151.
- Coronato, F.R., Bertiller, M.B., 1996. Precipitation and landscape related effects on soil moisture in semi-arid rangelands of Patagonia. Journal of Arid Environments 34, 1–9.
- Fernandez-Gimenez, M.E., Allen-Diaz, B., 1999. Testing a nonequilibrium model of rangeland vegetation dynamics in Mongolia. Journal of Applied Ecology 36, 871-885.
- Gao, Q., Yang, X., Yun, R., Li, C., 1996. MAGE, a dynamic model of alkaline grassland ecosystems with variable soil characteristics. Ecological Modelling 93, 19–32.
- Gao, Q., Yu, M., Li, C., Yun, R., 1998. Effects of ground water and harvest intensity on alkaline grassland ecosystem dynamics-a simulation study. Plant Ecology 135, 165–176.
- Gifford, G.F., Hawkins, R.H., 1978. Hydrologic impact of grazing on infiltration: a critical review. Water Resources Research 14, 305–313.
- Hart, R.H., 1989. SMART: a simple model to assess range technology. Journal of Range Management 42, 421–424.
- Hazarika, M.K., Yasuoka, Y., Ito, A., Dye, D., 2005. Estimation of net primary productivity by integrating remote sensing data with an ecosystem model. Remote Sensing of Environment 94, 298– 310.
- Hik, D.S., Jefferies, R.L., 1990. Increases in the net above-ground primary production of a salt-marsh forage grass: a test of the predictions of herbivore-optimization model. Journal of Ecology 78, 180–195.
- Holland, E.A., Parton, W.J., Detling, J.K., Coppock, D.L., 1992. Physiological responses of plant populations to herbivory and

their consequences for ecosystem nutrient flow. American Naturalist 140, 685–706.

- Ito, A., 2000. The relationship between atmospheric change and carbon dynamics in terrestrial ecosystems: a global study using a mechanistic model, Sim-CYCLE. Ph.D. thesis, Doctor's Program in Biological Sciences, the University of Tsukuba.
- Ito, A., 2005. Modelling of carbon cycle and fire regime in an east Siberian larch forest. Ecological Modeling 187, 121–139.
- Ito, A., 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. Ecological Modeling 151, 143–176.
- Ito, A., 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.
- Jameson, D.A., 1963. Response of individual plants to harvesting. Botanical Review 29, 532-594.
- Kojima, T., 2004. Investigation into the factors that determine the evapotranspiration in Kherlen river basin in Mongolia. MS thesis, Master's Program in Environmental Sciences, the University of Tsukuba, p. 85.
- Lee, P., 2006. Estimation and validation of carbon/water cycles in Mongolian grassland ecosystem under non-grazing condition using Sim-CYCLE. MS thesis, Master's Program in Environmental Sciences, the University of Tsukuba. p. 23, p. 106.
- Leriche, H., LeRoux, X., Gignoux, J., Tuzet, A., Fritz, H., Abbadie, L., Loreau, M., 2001. Which functional processes control the short-term effect of grazing on net primary production in grasslands? Oecologia 129, 114–124.
- Li, S.G., Harazono, Y., Oikawa, T., Zhao, H.L., He, Z.Y., Chang, X.L., 2000. Grassland desertification by grazing and the resulting micrometeorological changes in Inner Mongolia. Agricultural and Forest Meteorology 102, 125–137.
- Lobell, D.B., Hicke, J.A., Asner, G.P., Field, C.B., Tucker, C.J., Los, S.O., 2002. Satellite estimates of productivity and light-use efficiency in United States agriculture, 1982–1998. Global Change Biology 8, 722–735.
- Mariko, S., Urano, T., Oikawa, T., 2003. Biomass and carbon fluxes in a Mongolian grassland. Proceedings of the Second Workshop on Terrestrial Change in Mongolia, 97–99, available from Institute of Meteorology and Hydrology of Mongolia, Ulaanbaatar.
- Mazancourt, C. de, Loreau, M., Abbadie, L., 1998. Grazing optimization and nutrient cycling: when do herbivores enhance plant production? Ecology 79, 2242–2252.
- McNaughton, S.J., 1979. Grazing as an optimization process: grassungulate relationships in the Seregeti. American Naturalist 113, 691–703.
- McNaughton, S.J., 1983. Compensatory plant growth as a response to herbivory. Oikos 40, 329–336.
- Monsi, M., Saeki, T., 1953. Über den Lichtfaktor in den Pfanzengesellschaften und seine Bedeutung für die Stoffproduktion. Japanese Journal of Botany 14, 22–52.
- Monteith, J.L., 1981. Evaporation and surface temperature. Quarterly Journal of the Royal Meteorological Society 107, 1–27.
- NRC, 1985. Nutrient requirements of sheep, sixth revised edition, Committee on Animal Nutrition, National Research Council. National Academic Press, Washington, DC, p. 46.
- Oikawa, T., Ito, A., 2001. Modeling carbon dynamics of terrestrial ecosystems in monsoon Asia. In: Matsuno, T., Kida, H. (Eds.), Present and Future of Modeling Global Environmental Change: Toward Integrated Modeling. TERRAPUB, pp. 207–219.
- Peters, D.P.C., 2002. Plant species dominance at a grasslandshrubland ecotone: an individual-based gap dynamics model of herbaceous and woody species. Ecological Modelling 152, 5–32.
- Pogue, D.W., Schnell, G.D., 2001. Effects of agriculture on habitat complexity in a prairie-forest ecotone in the Southern Great

PLns of North America. Agriculture, Ecosystems and Environment 87, 287–298.

- Rauzi, F., 1963. Water intake and plant composition as affected by differential grazing on rangeland. Journal of Soil and Water Conservation 18, 114–116.
- Seligman, N.G., Cavagnaro, J.B., Horno, M.E., 1992. Simulation of defoliation effects on primary production of warm-season, semiarid perennial-species grassland. Ecological Modelling 60, 45–61.
- Stroosnijder, L., 1996. Modelling the effect of grazing on infiltration, runoff and primary production in the Sahel. Ecological Modelling 92, 79–88.
- Sugita, M., Asanuma, J., Tsujimura, M., Mariko, S., Lu, M., Kimural, F., Azzaya, D., Adyasuren, Ts., 2006. An Overview of the Rangelands Atmosphere—Hydrosphere—Biosphere Interaction Study Experiment in Northeastern Asia (RAISE), Journal of Hydrology, this issue.
- Ungar, E.D., Noy-Meir, I., 1988. Herbage intake in relation to availability and sward structure: grazing processes and optimal foraging. Journal of Applied Ecology 25, 1045–1062.
- Urano, T., 2005. Seasonal dynamics of above-ground biomass and CO_2 flux under grazing and non-grazing conditions of a semiarid steppe in Mongolia. MS thesis, Master's Program in Environmental Sciences, the University of Tsukuba, pp 23.

- Wang, R.Z., 2004. Responses of *Leymus chinensis* (Poaceae) to longterm grazing disturbance in the Songnen grassland of northeastern China. Grass and Forage science 59, 191–195.
- Wang, R.Z., Ripley, E.A., 1997. Effects of grazing on a *Leymus* chinensis grassland on the Songnen pLn of north-eastern China. Journal of Arid Environments 36, 307–318.
- Wang, R.Z., Gao, Q., Chen, Q.S., 2003a. Effects of climate change on biomass and biomass allocation in *Leymus chinensis* (Poaceae) along the Northeast China Transect (NECT). Journal of Arid Environments 54, 653–665.
- Wang, S.P., Wang, Y.F., Chen, Z.Z., 2003b. Grazing Ecosystem Management. Science Press, China, p.19; p. 48–53.
- Warren, S.D., Thurow, T.L., Blackburn, W.H., Garza, N.E., 1986. The influence of livestock trampling under intensive rotation grazing on soil hydrologic characteristics. Journal of Range Management 39, 491–495.
- White, E.G., 1984. A multispecies simulation model of grassland producers and consumers. I. Validation. Ecological Modelling 24, 137–157.
- Zhang, W.Z., Gao, Q., 1994. Exploration of the movements of water and dissolved salts in soils under different plant community in *Aneurolepidium chinense* grassland of Songnen pLn. Acta Phytoecologica Sinica 18, 132–139, In Chinese with English abstract.