

## Synergistic effects of climate change and grazing on net primary production of Mongolian grasslands

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**Abstract.** In arid and semi-arid regions, grassland degradation has become a major environmental and economic problem, but little information is available on the response of grassland productivity to both climate change and grazing intensity. By developing a grazing module in a process-based ecosystem model, the dynamic land ecosystem model (DLEM), we explore the roles of climate change, elevated CO<sub>2</sub>, and varying grazing intensities in affecting aboveground net primary productivity (ANPP) across different grassland sites in Mongolia. Our results show that both growing season precipitation totals and average temperature exert important controls on annual ANPP across six sites over a precipitation gradient, explaining 65% and 45% of the interannual variations, respectively. Interannual variation in ANPP, measured as the ratio of standard deviation among years to long-term mean, increased from 9.5 to 18.9% to 23.9–32.5% along a gradient of high to low precipitation. Historical grazing resulted in a net reduction in ANPP across all sites ranging from 2% to 15.4%. Our results further show that grassland ANPP can be maintained at a grazing intensity of 1.0 and 0.5 sheep/ha at wet and dry sites, respectively, indicating that dry sites are more vulnerable to grazing compared to wet sites. In addition, precipitation use efficiency (PUE) decreased while nitrogen use efficiency (NUE) increased across a gradient of low to high precipitation. However, grazing resulted in a net reduction in both PUE and NUE by 47% and 67% across all sites. Our results indicate that seasonal precipitation totals, average temperatures and grazing are important regulators of grassland ANPP in Mongolia. These results have important implications for grassland productivity in semi-arid regions in Central Asia and beyond.

**Key words:** aboveground net primary production (ANPP); climate change; ecosystem modeling; grassland vulnerability; grazing.

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### INTRODUCTION

Recent studies have shown that semi-arid ecosystems are an important driver of global carbon cycle (Poulter et al. 2014, Ahlström et al. 2015). The grasslands of Mongolia (41.6–52.2° N and 87.6–119.9° E) are located in arid and semi-arid regions and represent roughly 2.6% of the global grassland vegetation (Li et al. 2005). These

grasslands are ecologically fragile and are sensitive to changing climatic conditions (Qi et al. 2012), particularly precipitation. Vegetation activity and productivity in Mongolia have declined in recent decades (Lu et al. 2009, John et al. 2013) associated with extreme winters (referred to as *dzud* in Mongolia) and summer droughts. Declines in grassland productivity have also been attributed to increasing human activity

associated with higher livestock numbers and changes in herd composition (Hilker et al. 2013), and to a lesser extent by conversion to agriculture, increasing urbanization, and mining (Addison et al. 2012, Leisher et al. 2012). Ground-based measurements have also confirmed that human activity coupled with warmer climatic conditions have resulted in declines in both biodiversity and ecosystem function within the region (Li et al. 2008, Zhang et al. 2011). Satellite-based studies are less consistent, showing both declines and increases in vegetation cover and production in the Mongolian grasslands in response to climate and grazing (Sternberg et al. 2011, Li et al. 2012). Changes in the ecology of the extensive grasslands in Mongolia affect local pastoralists, distant cities through dust transport and could alter regional carbon budgets.

The response of grassland ANPP to climate change, grazing, and other environmental factors has been the subject of much debate across the Mongolian Plateau (Fernandez-Gimenez and Allen-Diaz 1999). Many methods, such as environmentally controlled field experiments, long-term monitoring, and ecosystem modeling, have been employed to explore the responses of ANPP to changing climatic conditions (Lauenroth and Sala 1992, Knapp et al. 2008) and grazing by domestic herbivores (Chen et al. 2007, Schönbach et al. 2011). Notably, exploring the response of ANPP to climate change and grazing along a precipitation gradient is a critical approach to understand the mechanisms for grassland degradation in Mongolia.

Mongolia has shown a remarkable linear increase in mean annual temperature since 1940, which could have a substantial negative impact on pasture productivity (Hilker et al. 2013) and by extension, animal husbandry (Nandintsetseg and Shinoda 2013). Evidence from Mongolia meteorological stations show that the annual mean temperature has increased by 2.14°C from 1940–2009 (Dagvadorj et al. 2009) with warming more pronounced in winter than summer. Recent meteorological records also indicate an increasing hot and dry summers and cold winters, particularly in the mountain and forest steppe in Mongolia (Fernandez-Gimenez et al. 2015). There appears to have been little abatement of these trends in recent years. In fact, a paleoclimatic reconstruction of summer temperatures indicates

that 2000–2005 period is estimated to have been the warmest since at least 931 CE (Davi et al. 2015). The most pronounced warming has been in the high mountains (Batima et al. 2005). Increased summer temperatures are likely to cause more frequent heat waves resulting in an overall decline in productivity (Craine et al. 2012). On average, heat wave duration has increased by 8–18 days while cold wave duration has decreased by 20 days in Mongolia (Batima et al. 2005). Although increased winter temperatures and decreased cold wave duration have a positive effect on pasture productivity, some unexpected climate signals such as sudden warming in winter, high snowfall, and wind storms have taken place during the past decade resulting in an overall negative effect on pasture production and animal husbandry (Nandintsetseg and Shinoda 2013).

Unlike temperature, total precipitation in Mongolia has not changed linearly. However, there has been a large reduction in precipitation over much of Mongolia. In fact, between 1980 and 2010, 63 lakes >1 km<sup>2</sup> disappeared in Mongolia, which equates to a loss of 17.6% of lakes (Tao et al. 2015). In addition, extreme weather events such as droughts, harsh winters, and dust storms are of particular concern in the Mongolian grasslands because of their negative consequences on pasture production and livestock subsistence (Nandintsetseg et al. 2007). For instance, the 1999–2002 *dzud* constituted the most severe climatic conditions of the last 50 years (Severinghaus 2001) that resulted in the death of 30% of Mongolian livestock (Fernandez-Gimenez et al. 2012). Recently, the 2009–2010 winter *dzud* resulted in a death of 8.5 million livestock representing 20% of the national herd size (Fernandez-Gimenez et al. 2012). Paleoclimatic reconstruction of seasonal temperature and precipitation also indicate that changes in the ecosystem and societies in Mongolia have been associated with unusual climatic conditions, favoring the formation of political and military power during warm and persistently wet periods (Pederson et al. 2014). Therefore, changing climatic conditions, including extreme climatic events, have a significant impact on ecosystem and societies, with potentially severe consequences on the ecology of Mongolia.

Another key factor shaping the structure and function of Mongolian steppe is livestock herbivory. Grazing by domestic herbivores resulted in a dramatic decline in plant diversity, vegetation cover, primary production (Fensham 1998) and seed production (Coffin and Lauenroth 1989). Mongolia has also experienced a remarkable increase in livestock numbers (Gong Li et al. 2000) from 26 million in 1990 to about 45 million in 2012 (National Statistical Office of Mongolia – NSO, 2012), which equates to a total increase of approximately 73% since 1990. Livestock grazing resulted in 80% decline in Normalized Difference Vegetation Index (NDVI) across Mongolia during 2002–2012 (Hilker et al. 2013). However, Liu et al. (2013b) found that increases in goat numbers was secondary to precipitation in explaining variation in satellite-based vegetation optical depth. While site-level studies indicate that climate has a greater influence on grassland productivity compared to grazing intensity in arid sites (Fernandez-Gimenez and Allen-Diaz 1999), a recent study indicates that grazing may result in an overall decline in productivity (Chen et al. 2007). Therefore, there is still a considerable debate about the response of grassland ANPP to the combined effect of climate change and livestock grazing in Mongolia (Addison et al. 2012).

The debate about the responses of ANPP to climate change and grazing might be related to the possibility that various factors can drive ANPP, synergistically or negatively. Additional factors beyond climate and grazing include vegetation composition, edaphic condition, and biogeochemical constraints (Huxman et al. 2004). Previous studies report that mesophytic grasslands are more productive and less variable in terms of productivity than xerophytic grasslands (Chen et al. 2007, Bai et al. 2008) indicating a dominant role of soil moisture limitations on ANPP. In arid and semi-arid grasslands, ANPP is usually limited or co-limited by nitrogen availability, which itself is tightly coupled with water availability (Holdo et al. 2007). Local environmental characteristics such as water holding capacity, texture, permeability and bulk density are considered important determinants of soil moisture and nutrient availability. All these factors could substantially alter ANPP at the site level suggesting that a multi-factorial approach is needed to better understand the drivers of ANPP.

We investigate the grassland responses to changes in climate and grazing and their underlying mechanisms based upon a long-term dataset (1981–2010) that spans a precipitation gradient in arid and semiarid ecosystems in Mongolia. We chose sites with varying grazing intensity to better understand the plant physiological effect on ANPP. In addition, we separated the climate variables into periods of high and low biological activity to examine how growing season precipitation totals and mean growing season temperature affect annual ANPP along a precipitation gradient. We also quantify precipitation-use efficiency (ANPP/precipitation) and nitrogen-use efficiency (ANPP/available nitrogen) here because local environmental conditions including vegetation composition, edaphic condition, and biogeochemical constraints may limit ANPP through its effect on plant water and nitrogen uptake.

Our primary objectives are to (1) quantify the magnitude and temporal variation in ANPP induced by climate change (seasonal and annual temperature and precipitation changes) combined with increasing atmospheric CO<sub>2</sub> along a precipitation gradient in Mongolia; (2) quantify how growing season mean temperature and precipitation totals affect grassland ANPP (3) assess how livestock grazing affects ANPP; (4) examine the compensatory or over-compensatory growth response of grasslands under different grazing intensities; and (5) investigate how moisture and nutrient limitations affect ANPP along a precipitation gradient. To accomplish these tasks, we use the dynamic land ecosystem model (DLEM, (Tian et al. 2011a)), which has been improved to include the effects of grazing on carbon, nitrogen and water balance. The model was first validated with and without grazing in Inner Mongolia and then applied at six sites in Mongolia along a precipitation gradient.

## MATERIALS AND METHODS

### Study area

The study areas were selected based on three different grassland types along a precipitation gradient from north to south (Table 1; Fig. 1). The grassland types are categorized as wet, moderately wet, and dry grasslands. Wet grasslands annually receive precipitation totals of

Table 1. Grassland information under traditional grazing systems in Mongolia during 1981–2010.

Grasslands	Site	Lon	Lat	Altitude (m)	Grazing (Sheep/ha)	Climate Conditions	
						Tair (°C)	Prec (mm)
Wet	Tsetserleg (TC)	101.5° E	47.5° N	1865	2.0	0.91	335.95
Wet	Bulgan (BC)	103.6° E	48.8° N	1176.23	1.6	-0.6	329.54
Moderately wet	Uliastai (UC)	96.9° E	47.8° N	2096.16	1.3	-1.65	214.24
Moderately wet	Altai (AC)	96.15° E	46.4° N	2176.9	0.9	-0.17	177.70
Dry	Dalanzadgad (DG)	104.4° E	43.6° N	1524.79	0.12	5.26	120.32
Dry	Tsogt-ovoo (TO)	105.4° E	44.5° N	1245.5	0.34	4.47	97.37

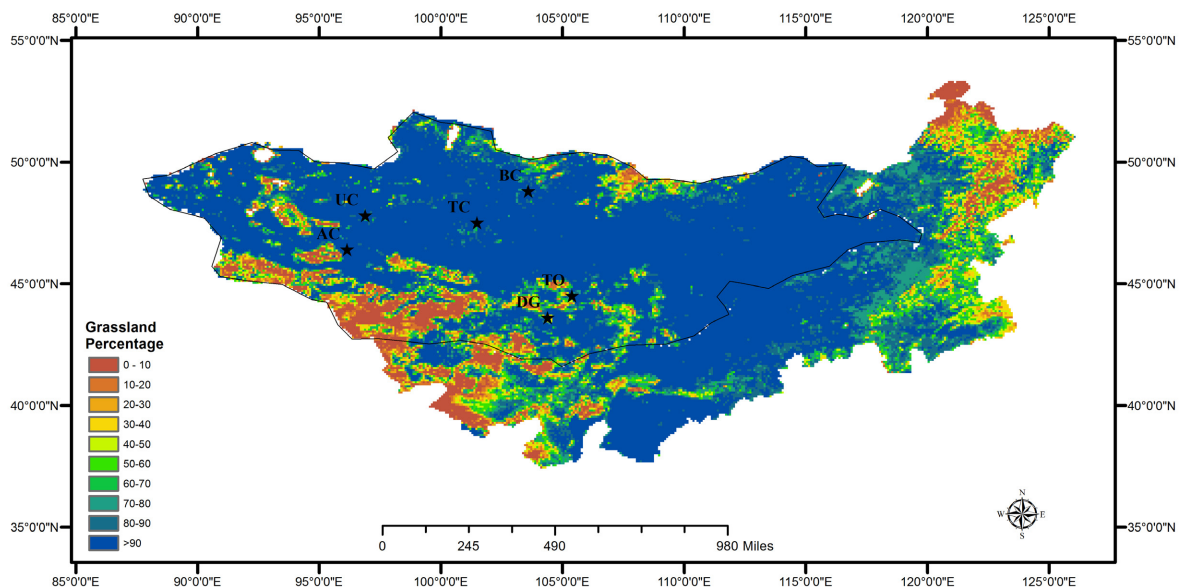


Fig. 1. Percentage of area covered by grasslands in the Mongolian Plateau based on 5-min HYDE v3.1 (Klein Goldewijk et al. 2011) land cover datasets. The symbols on the map represent the location of study sites considered in this study. BC: Bulgan; TC: Tsetserleg; UC: Uliastai; AC: Altai; DG: Dalanzadgad; TO: Tsogt-ovoosum.

>300 mm, while moderately wet and dry grasslands receive precipitation totals of 150–300 and 50–150 mm/yr, respectively (Fig. 1). Bulgan (BC) and Tsetserleg (TC) are grasslands that receive the highest annual precipitation of about 330 and 336 mm/yr, respectively. The average grazing intensity for the period 1981–2010 are 1.6 and 2.0 sheep/ha at BC and TC, respectively. Uliastai (UC) and Altai (AC) are moderately wet grasslands receiving total annual precipitation of about 214 and 178 mm/yr, respectively. Grazing intensity is about 1.3 and 0.9 sheep/ha at UC and AC, respectively. The drier site Dalanzadgad (DG) receives total annual precipitation of about 120 mm/yr while Tsogt-ovoo

(TO) receives total annual precipitation of about 97 mm/yr. Grazing intensity is about 0.34 and 0.12 sheep/ha at TO and DG, respectively.

#### Model description

The DLEM is a highly integrated, process-based terrestrial ecosystem model that simulates the structural and functional dynamics of terrestrial ecosystems affected by multiple factors including climate, atmospheric composition ( $\text{CO}_2$ , nitrogen deposition, and tropospheric ozone), land-use and land-cover (LULC) change, and land management practices (e.g., harvest, rotation, irrigation, fertilizer use, etc.). The DLEM has five core components: (1) biophysics,



(2) plant physiology, (3) soil biogeochemistry, (4) vegetation dynamics, and (5) land use and management (Tian et al. 2010). This model has been extensively calibrated against various field data in typical vegetation types including forest, grassland, and cropland from the Chinese Ecological Research Network, the US Long-Term Ecological Research (LTER) sites, and the AmeriFlux network (Tian et al. 2010, Lu et al. 2012, Pan et al. 2014). The DLEM has been used to simulate the effects of climate variability and change, atmospheric CO<sub>2</sub>, tropospheric ozone, nitrogen deposition, and LULC change on the pools and fluxes of carbon and water in China (Ren et al. 2007, 2012, Tian et al. 2011a, b, Lu et al. 2012), the United States (Tian et al. 2010, 2012, Song et al. 2013) and North America (Xu et al. 2010). The detailed information on how DLEM simulates these processes are available in Tian et al. (2010). We recently

updated the model to DLEM 2.0, which is characterized by cohort structure, multi-soil layer processes, coupled carbon, water and nitrogen cycles, multiple GHG emissions simulation, enhanced land surface processes such as vegetation dynamics and soil moisture movement by improved representation of surface heterogeneity, and dynamic linkages between terrestrial and riverine ecosystems (Liu et al. 2013a, Pan et al. 2014, 2015, Tian et al. 2014). In this study, we have improved the DLEM 2.0 by incorporating a grazing module that accounts for the effect of grazing on carbon, nitrogen, and water balance in grassland ecosystems (Fig. 2).

#### Development of grazing module in the DLEM

The grazing module used in this study is based on Seligman et al. (1992). In its simplest form, the module is dependent on four

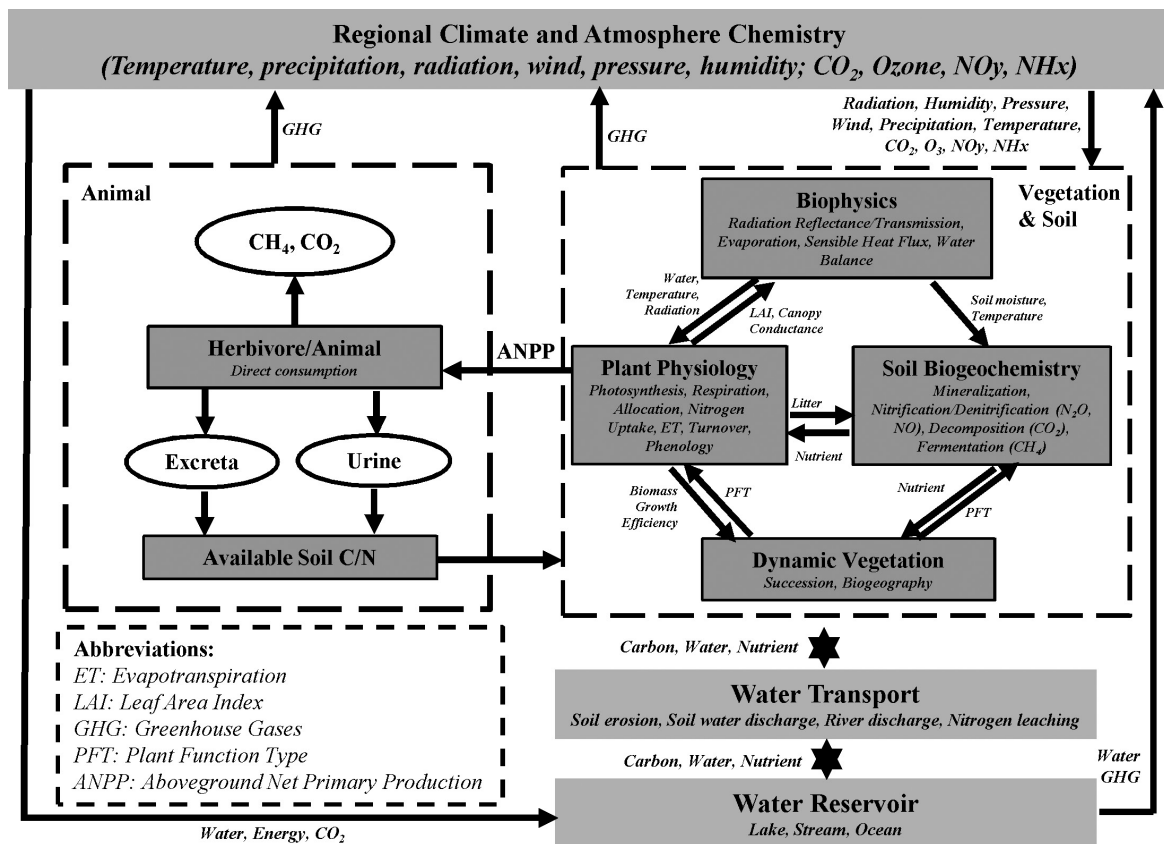


Fig. 2. The simplified framework of Dynamic Land Ecosystem Model (DLEM) for assessing the effects of grazing on carbon, nitrogen and water balance in arid- and semi-arid environments.

parameters that control the amount of biomass uptake by herbivores. The four parameters include amount of biomass available for grazing by herbivores, the grazing efficiency of the herbivores (maximum area grazed by herbivores per day), the satiation consumption rate of the herbivores, and the density of herbivores (grazing intensity). Biomass intake by herbivores is a minimum function of herbivore forage demand and the available aboveground forage per unit area. The amount of biomass consumed by herbivores is then divided into different parts using an energy flow approach. These parts include: carbon losses during respiration, assumed to be 50% (Minonzio et al. 1998); carbon losses during methane release by ruminants, assumed to be 4% (Vuichard et al. 2007); and carbon losses through excretory processes, assumed to be 30% (Schimel et al. 1986). The amount of carbon and nitrogen lost through excreta is further separated into urine and feces assuming that the nitrogen in urine is readily available for plant use. Other processes such as volatilization and ammonia emission are based on Jarvis et al. (1989). A detailed description of the grazing module is available in Appendix S1.

It is important to recognize that the grazing module used in this study has both negative and positive effects on grassland ANPP. First, biomass uptake by herbivore reduces both sunlit and shaded leaf area index resulting in an overall decline in carbon assimilation rate. Second, reduction in leaf area improves light absorption and reduces self-shading (Jameson 1963) which has a stimulatory effect on plant performance. Third, reduction of water loss through transpiration makes more water available for plant growth resulting in an overall decrease in plant water stress (Turner et al. 1993). Fourth, accelerated nutrient cycling as a result of increased nitrogen mineralization with additional nutrient inputs in the form of excreta has a positive effect on the growth rate of grassland communities (Noy-Meir 1993). While biomass uptake by herbivores has a short-term negative effect on grassland ANPP, three other mechanisms, (improved light efficiency, accelerated nutrient cycling and improved plant water status), have a positive effect on grassland ANPP. The positive effect implies that ANPP can be maintained

(compensatory growth) or stimulated (over-compensatory growth) in response to grazing.

#### Input datasets

The model input data include annual historical land cover maps, daily climate data, monthly atmospheric CO<sub>2</sub> concentrations, soil properties and topography data for each site. The vegetation map for each site was extracted from a global vegetation distribution map based on National Land Cover Data (NLCD, 2001) at a resolution of 30 × 30 m. We further developed a continuous gap filled daily pattern of average, maximum, and minimum temperature, and precipitation during the 1981–2010 using CRUNCEP and meteorological observations obtained from National Climate Data Center (NCDC; <http://www7.ncdsc.noaa.gov>). We then used the site level monthly observations based on National Agency for Meteorology, Hydrology & Environment Monitoring (<http://env.env.pmis.gov.mn/>) to restrict the mean temperature and total amount of precipitation during a particular month in the daily climate datasets (Appendix S1: Fig. S1). Monthly atmospheric CO<sub>2</sub> concentration data were derived from Multi-scale Synthesis and Terrestrial Model Intercomparison Project (MsTIMP, <http://nacp.ornl.gov/MsTMIP.shtml>). Soil property data including soil texture, pH, and bulk density were extracted from Global Soil Data Task (<https://daac.ornl.gov/SOILS/guides/igbp.html>).

In addition to the above datasets, DLEM now requires grazing intensity (sheep/hectare) data as a part of model inputs. Official records of animal population at *aimag* (similar to province) level are available from the National Statistical Office (NSO) of Mongolia. These data include the number of animal head units by species (horse, cattle, sheep, goat, and camel). We used a conversion scheme based on USDA National Range and Pasture Handbook to convert different animal species into a sheep unit based on body weight. These conversions are: 1 horse is equivalent to 6.25 sheep units, one cattle to four sheep units, one goat to 0.75 sheep unit, and one camel to 6.75 sheep units. After these initial conversions, we estimated the grazing intensity by dividing the total number of sheep unit in a particular *aimag* by total grassland area of that *aimag*.

### *Model parameterization, calibration and evaluation*

In this study, we parameterized the model against long-term observational data for grassland ecosystems in Inner Mongolia, China. During calibrations, we tune the parameters (Appendix S1: Table S1) such that the simulated carbon and nitrogen stocks and fluxes are close to observations. The calibrated model is then implemented at other sites for evaluating its performance.

We evaluated the DLEM performance in Inner Mongolia (116.7° E, 43.6° N) under both grazing and non-grazing conditions. We first carried out a comparison of simulated NPP with observations based on Ma et al. (2008) for temperate steppe in Inner Mongolia (Appendix S1: Fig. S2) under non-grazing conditions. These comparisons indicate that DLEM captures both the magnitude and temporal variation of ANPP in grassland sites. We further evaluated DLEM-simulated ANPP against observations from Schönbach et al. (2011) at the same site with five different grazing intensities (Appendix S1: Fig. S3, Table S2). Simulated ANPP are within the range of -2.8% to 20% at different grazing intensities when compared to observations based on Schönbach et al. (2011). In particular, the DLEM over-estimates ANPP response at high grazing intensity of 7.5 sheep/ha compared to Schönbach et al. (2011) (Appendix S1: Table S2). This is primarily because we assumed that nitrogen returned to the soil in the form of excreta and urine is uniformly distributed across the landscape. Grazing, however, is not uniformly distributed in space with a matrix of grazed and ungrazed patches (Semmartin and Oesterheld 2001). Bai et al. (2010) found that external nitrogen inputs increased aboveground biomass in the range of 41% to 199%, indicating that nitrogen limitations exert an important control on ANPP at the study sites. Therefore, our assumptions of uniform distribution of excreta and urine in the landscape could have resulted in the over-estimation of ANPP response at high grazing intensity.

### *Model implementation*

The model simulation at the site level follows a two-step procedure: an equilibrium simulation and a transient simulation. The model simulation begins with an equilibrium stage with

long-term average climate data for the period 1981–2010, and 1981 levels of atmospheric CO<sub>2</sub> concentrations and vegetation cover. The equilibrium run is carried out for 10,000 yr at most or until the net carbon exchange between the atmosphere and the site is less than 0.1 g C/m<sup>2</sup>, the change in soil water pool is less than 0.1 mm, and the change in soil total nitrogen content is less than 0.1 g N/m<sup>2</sup> during 10 consecutive years. We carry out an equilibrium simulation without grazing assuming that there is no effect of herbivory during the start of our simulation. After the equilibrium simulation, the transient simulation is conducted using daily climate data and monthly atmospheric CO<sub>2</sub> concentration with time-series vegetation cover maps. The transient simulation consists of two important scenarios. The first simulation reflects the evolution of ANPP during the period 1981–2010 in the absence of livestock grazing. The second simulation reflects the evolutionary response of ANPP with increasing livestock pressure.

We further separated our climatic variables into period of high and low biological activity to quantify how seasonal precipitation distribution affects grassland annual ANPP across six sites. We defined growing season for our study sites as 1 May – 31 August based on Begzsuren et al. (2004), although growing season length likely varies across our study sites. We then quantified the contribution of growing vs. non-growing season precipitation totals and average temperatures to annual ANPP during the study period.

We also investigated whether there is compensatory response of ANPP across a precipitation gradient in Mongolia using five hypothetical grazing intensities. The first two represent low grazing intensity (0.25 and 0.50 sheep/ha), while the other three (1, 3, and 4.5 sheep/ha) represent moderate and high grazing intensity. We simulated the ANPP response to hypothetical grazing intensity across all sites along a precipitation gradient to examine whether ANPP can be maintained (compensatory growth) or stimulated (over-compensatory growth) in response to grazing. In this study, we only simulated grazing during the peak biomass accumulation period (June–Sept.) because information of grazing timing for the study sites was unavailable.

## RESULTS

### *Inter-annual and temporal variation in ANPP induced by climate change*

With the exclusion of grazing, the DLEM-simulated ANPP showed that climate change exerts an important control on terrestrial ANPP in Mongolian grasslands (Table 2). ANPP across six grassland sites ranged from 27.18 g C·m<sup>-2</sup>·yr<sup>-1</sup> at the dry site to 84.15 g C·m<sup>-2</sup>·yr<sup>-1</sup> at the wet site from 1981 to 2010. Grassland ANPP was significantly correlated with annual precipitation totals across all sites, explaining 67% of the variation in ANPP ( $y = 0.16x$ ;  $P < 0.05$ ). Our site-specific comparisons, however, showed that annual precipitation may not have the same positive association with ANPP at individual sites largely due to differences in local environmental conditions (Fig. 3). Across individual sites, grassland ANPP was significantly correlated with precipitation explaining 28–49% of the variation ( $P < 0.05$ ). But at BC, grassland ANPP was significantly correlated with previous year precipitation ( $R^2 = 0.30$   $P < 0.05$ ). Interestingly, DLEM-simulated ANPP showed larger inter-annual variation at drier sites compared to moist sites. The coefficient of variation (CV), measured as the ratio of standard deviation among years to long-term mean, across all sites showed that drier sites (DG and TO) have the largest inter-annual ANPP variations of 23.9 and 32.5%, respectively. However, at wetter sites (BC and TC), the CV in ANPP was 9.5 and 18.9%, respectively (Table 2).

Cross-site analysis further showed that inter-annual variation in ANPP decrease with increasing precipitation ( $R^2 = 0.63$ ;  $y = -0.06x$ ;  $P < 0.05$ ).

The DLEM-simulated ANPP further showed that mean annual temperature had a significant negative correlation with grassland ANPP across all six sites ( $R^2 = 0.48$ ;  $y = -5.2x$ ;  $P < 0.05$ ). At individual sites, however, the DLEM-simulated ANPP showed varying responses to changes in mean annual temperature. The negative correlation between ANPP and mean annual temperature was prevalent across all sites except the wetter BC site. At BC, mean annual temperature had a positive association with grassland ANPP ( $R^2 = 0.26$ ;  $y = 4.98x$ ;  $P < 0.05$ ), indicating that temperature limitations may constrain grassland productivity in areas with abundant rainfall.

### *The impact of climate seasonality on annual ANPP*

Growing season precipitation had a significant positive effect explaining 65% of the variation in annual ANPP across the six sites (Fig. 4). Our site specific comparison showed that growing season precipitation explained 40–65% of the variation in annual ANPP at UC, AC, DG, and TO. Annual ANPP at BC showed a weak correlation with growing season precipitation; however, non-growing season precipitation had a significant effect on the following year annual ANPP ( $P < 0.05$ ), explaining 26% of the variation. Our further analysis at BC suggested that there is a different water use pattern compared to

Table 2. Climate controls on annual aboveground net primary production (ANPP) during the 1981–2010 period.

Site	ANPP (g C·m <sup>-2</sup> ·yr <sup>-1</sup> )				R <sup>2</sup>		
	Mean	Max	Min	CV (%)	ANPP-Prc	ANPP-Prev. Year Prc	ANPP-Tair
BC	84.15	98.09	64.52	9.5	0.001	0.30*	0.26*
TC	64.14	88.07	40.74	18.9	0.28*	0.001	-0.003
UC	59.27	91.01	41.89	17.8	0.28*	-0.12	-0.03
AC	57.98	79.24	41.61	16.7	0.49*	-0.02	-0.01
DG	36.93	58.18	24.31	23.9	0.44*	0.02	-0.02
TO	27.18	57.91	16.78	32.5	0.49*	0.05	-0.01

Note: R<sup>2</sup> represent the percentage variation in ANPP in response to annual precipitation (Prc) totals or mean annual temperature (Tair).

\* Indicates a significant effect at 5% level of significance.



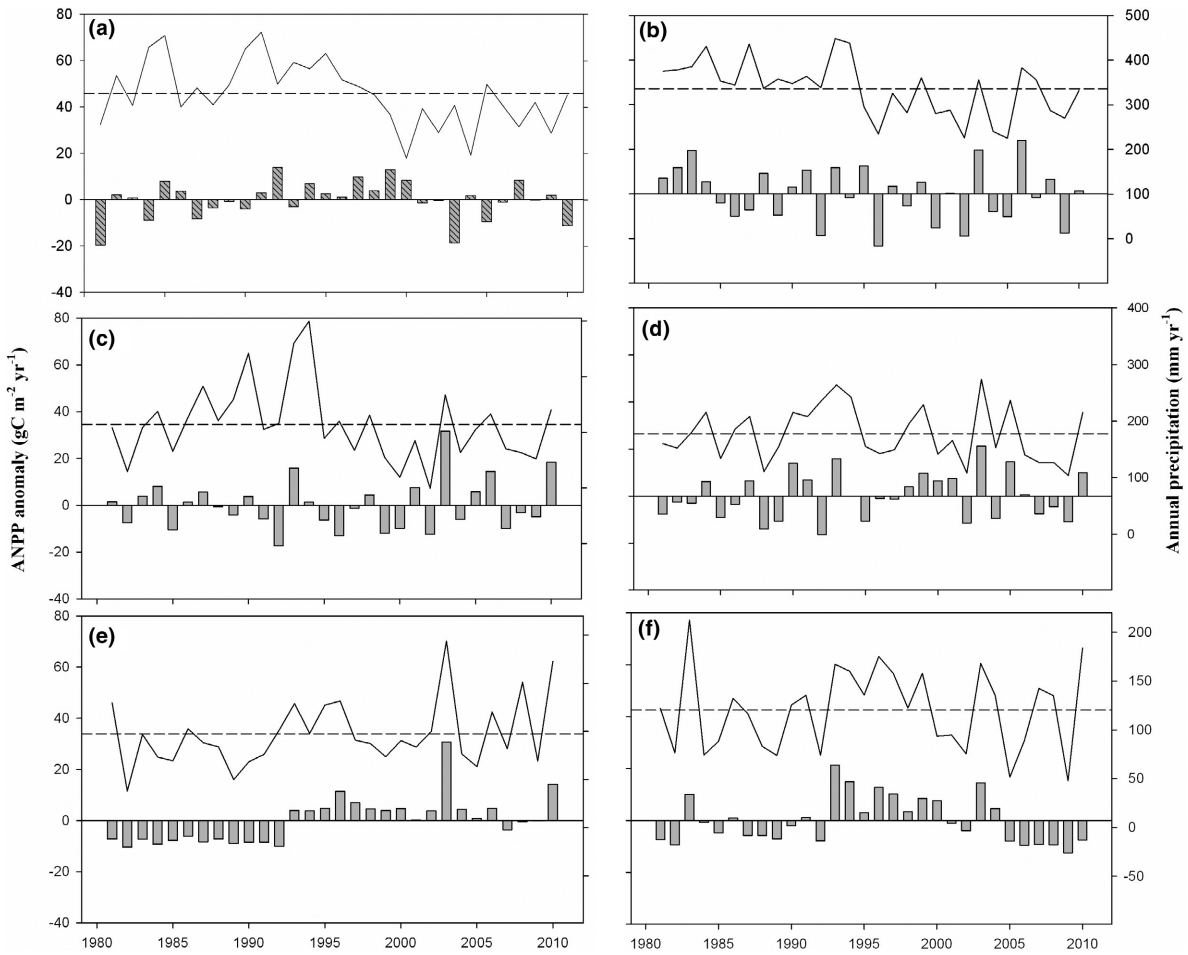


Fig. 3. The DLEM-simulated ANPP (bars) driven by multiple environmental changes during 1981–2010 at Bulgan (a), Tsetserleg (b), Uliastai (c), Altai (d), Tsogt-Ovoosum (e) and Dalanzadgad (f). The solid line represents inter-annual variation in precipitation while the dashed line represents 30-yr (1981–2010) mean precipitation.

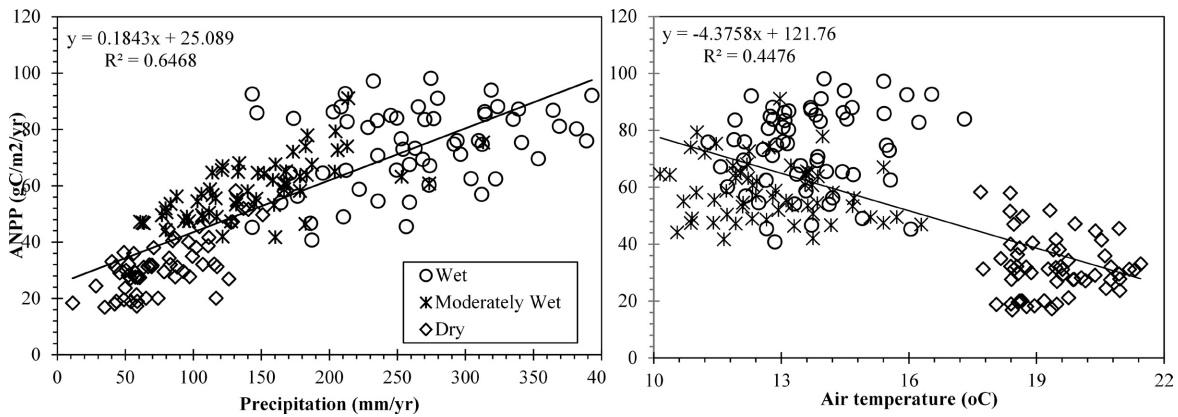


Fig. 4. Effect of growing season precipitation totals (left panel) and average temperature (right panel) on grassland annual ANPP across six sites in Mongolia.

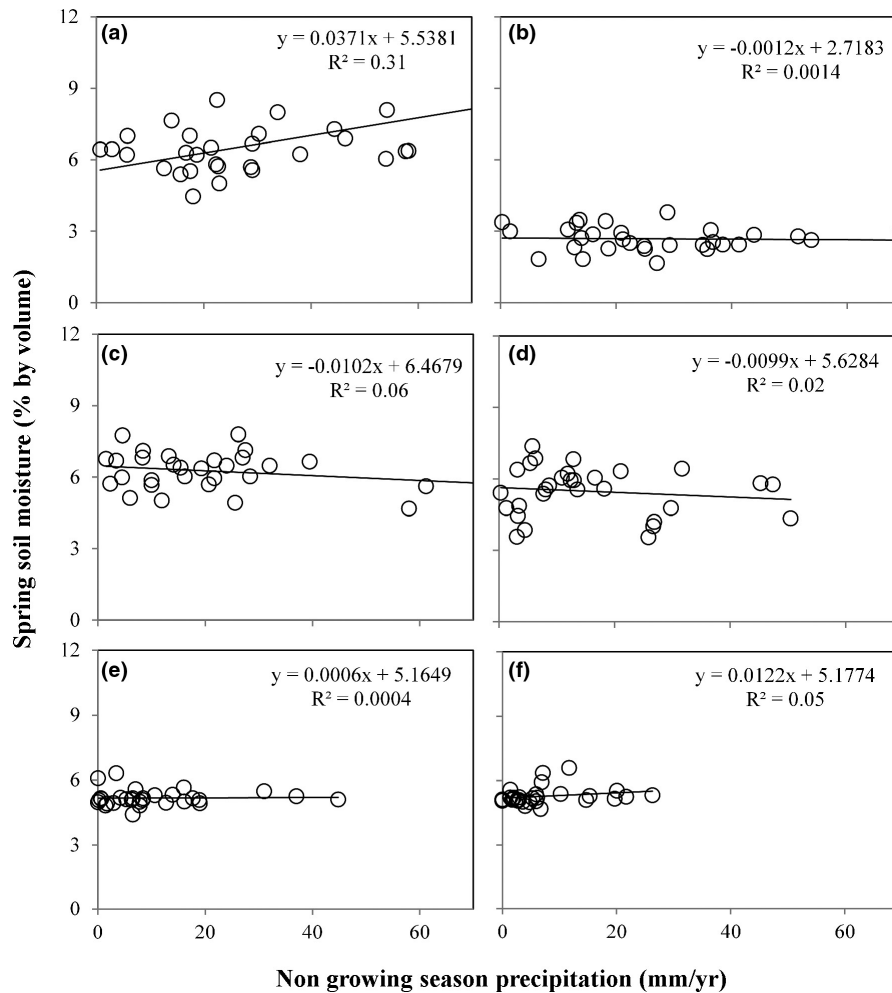


Fig. 5. Correlation between annual non-growing season precipitation totals and spring soil moisture across six sites in Mongolia. Bulgan (a), Tsetserleg (b), Uliastai (c), Altai (d), Tsogt-Ovoosum (e) and Dalanzadgad (f).

other sites. First, the water table at BC is higher compared to other similar sites, which allowed plants to access deep groundwater. Second, precipitation (as snow) during the non-growing season at BC showed a significant correlation with soil moisture content at the top 20 cm of the soil during the month of May ( $P < 0.05$ ;  $R^2 = 0.31$ ; Fig. 5a). However, this soil moisture memory mechanism was not evident at other sites.

Growing season temperatures had a significant negative effect across the six sites, explaining 45% of the variation in annual ANPP ( $P < 0.05$ ). Our site specific comparisons showed that growing season temperatures had a positive effect on annual ANPP

at wetter sites (BC and TC), indicating that increasing temperature may promote ANPP at sites where moisture is not limiting. However, moderately wet and dry sites showed a negative association with temperature. Drier sites (DG and TO) are likely more sensitive to temperature changes because growing season temperature at these sites often reaches  $\sim 21^\circ\text{C}$  compared to other wet sites where growing season temperatures are in the range of  $13\text{--}15^\circ\text{C}$ . It is also likely that wet sites experience less heating compared to dry sites due to high rates of evapotranspiration. Low growing season precipitation totals combined with warm temperatures at the drier sites (DG and TO) resulted in low annual ANPP compared to wetter sites.

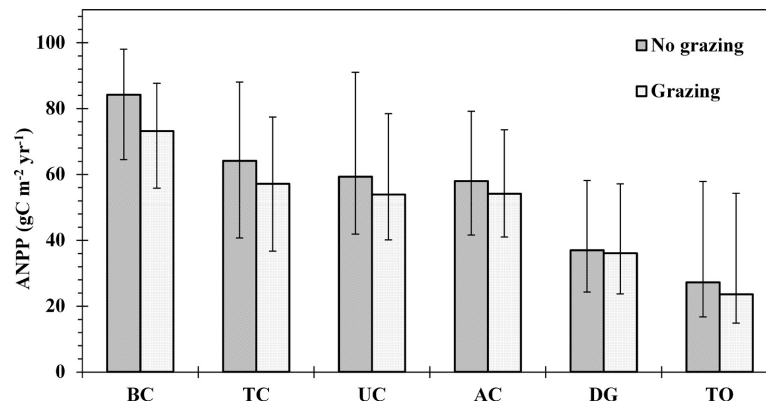


Fig. 6. Effects of grazing on ANPP across a precipitation gradient in Mongolia. We used realistic grazing intensity during 1981–2010 to simulate the effects of historical grazing intensity at each sites. Error bars represent the maximum and minimum ANPP during 1981–2010. BC: Bulgan; TC: Tsetserleg; UC: Uliastai; AC: Altai; TO: Tsogt-Ovoosum; DG: Dalanzadgad.

#### Variations in grassland ANPP induced by climate change and grazing

When including historical site-level records of grazing intensity as an input driver, DLEM simulations showed a net reduction in grassland ANPP across all sites (Fig. 6). The reduction ranged from 2% to 15.4%, depending on local conditions and grazing intensity among sites studied here. Our analysis showed that the simulation with grazing is significantly different from the simulation without grazing at BC, TC, UC and TO ( $P < 0.05$ ), indicating that historical grazing intensity at these sites have a negative effect on grassland ANPP. At other sites (AC and DG), simulated ANPP with grazing was not significantly different from the simulation without grazing, although there was a net reduction in ANPP following grazing. Compared to the non-grazing simulation, the largest ANPP reduction of 11.0 g C/m<sup>2</sup> and 3.6 g C/m<sup>2</sup> (equivalent to a decrease of 15.0 and 15.4%) occurred at BC and TO, respectively.

#### Compensatory growth response

We further examined the response of grassland ANPP to five different hypothetical grazing intensities (0.25, 0.5, 1.0, 3.0, and 4.5 sheep/ha) to determine whether there is the compensatory mechanism in response to grazing. None of our study sites experienced over-compensation in response to grazing, indicating that grazing had an overall negative influence on grassland

ANPP (Fig. 7). Our simulation with different grazing intensities showed that grassland ANPP decreased from no grazing to grazing intensity of 4.5 sheep/ha by 27.7% across all sites. The largest reductions occurred in TO and DG (drier sites) by 50.7% and 46.7% respectively. There was no significant reduction in annual ANPP at grazing intensity of 0.25, 0.5 and 1.0 sheep/ha at wet and moderately wet sites. At dry sites, however, grazing resulted in a significant reduction in ANPP when the grazing intensities were 1.0, 3.0 and 4.5 sheep/ha. Although all sites experienced a net reduction in ANPP due to grazing, ANPP response to grazing suggest that ANPP can be maintained at grazing intensity of 1.0 sheep/ha for wet and moderately wet sites and at 0.5 sheep/ha for dry sites, indicating that compensatory growth response is possible at low grazing intensity at all sites (Fig. 8).

#### Effect of moisture and nutrient limitations on ANPP

We further examined how moisture and nutrient limitations affect ANPP along a precipitation gradient with and without grazing. Our simulation without grazing showed that precipitation use efficiency (PUE), measured as a ratio of ANPP to annual rainfall, decreased with increasing precipitation ( $R^2 = 0.42$ ;  $P < 0.05$ ), indicating that plants would be able to utilize water more efficiently under conditions of moisture stress (i.e. drought) (Fig. 9). For instance,

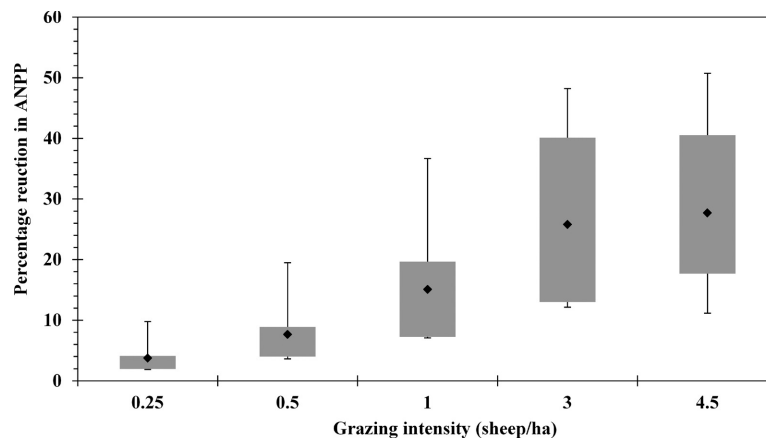


Fig. 7. Percentage reduction in ANPP as a function of grazing across six different sites in Mongolia. The box length represents the range of the first and the third quartile. The error bar represents the maximum and minimum percentage reduction in ANPP during 1981–2010 and the black dot represents an overall mean reduction in ANPP.

when the mean annual precipitation was between 50–100 mm/yr, the average PUE was  $0.37 \text{ g C}\cdot\text{m}^{-2}\cdot\text{mm}^{-1} \text{ H}_2\text{O}$ ; however, the average PUE decreased to  $0.17 \text{ g C}\cdot\text{m}^{-2}\cdot\text{mm}^{-1} \text{ H}_2\text{O}$  when the mean annual precipitation was 500–600 mm/yr. In contrast, nitrogen use efficiency (NUE) measured as a ratio of ANPP to available nitrogen in soil, showed the opposite pattern compared to PUE. For instance, NUE was  $7.54 \text{ g C/g N}$  when the precipitation was between 50–100 mm/yr; however, the average NUE increased to  $14.97 \text{ g C/g N}$  when the precipitation increased to 500–600 mm/yr. This suggests that plants will use nutrients more efficiently when water is not limiting, and vice versa.

Our results also showed that grazing resulted in an overall reduction in PUE and NUE across the study sites (Fig. 10). With grazing, the largest reduction in PUE occurred at the dry sites compared to the wet sites, indicating that dry sites are more vulnerable to grazing because grazing not only removes aboveground biomass, but also limits plants' capability in using water. For example, in wet and moderately wet areas (BC, TC, UC, and AC), PUE declined by 16% at most at the grazing intensity of 4.5 sheep/ha; however, PUE declined by 47% at most at the grazing intensity of 4.5 sheep/ha at dry sites (DG and TO). On the other hand, there was an overall decline in NUE by 67% at a grazing intensity of 4.5 sheep/ha compared to the no grazing simulation. This is primarily because plants' capacity to translate

nitrogen into photosynthetic products decreases with increasing nitrogen availability associated with high excretal return at higher grazing intensity. Across different sites, the largest decline in NUE occurred at dry sites where NUE declined by 82% at the grazing intensity of 4.5 sheep/ha compared to the non-grazing experiment.

## DISCUSSION

### Temperature control on grassland ANPP

In general, mean annual temperature has a negative relationship with ANPP in arid and semiarid grasslands (Bai et al. 2000, Ni 2004) because elevated temperatures have been found to increase evaporation, intensify drought, and reduce biomass production. Our results across all sites also suggest that mean annual temperature and mean growing season temperature resulted in a significant decline in grassland ANPP by  $5.2 \text{ g C/m}^2$  per  $1^\circ\text{C}$  increase in temperature. Temperature effects on ANPP can vary with total soil moisture content such that warm temperatures positively affect ANPP in areas with abundant moisture, but have negative effects during periods of moisture stress (i.e. drought) (Zhou et al. 2008). The decline in ANPP at higher temperatures as evident in this study suggests that increased evaporation and associated water stress may offset any positive effects of higher temperatures on plant growth (Dulamsuren et al. 2013, Xu et al. 2013).



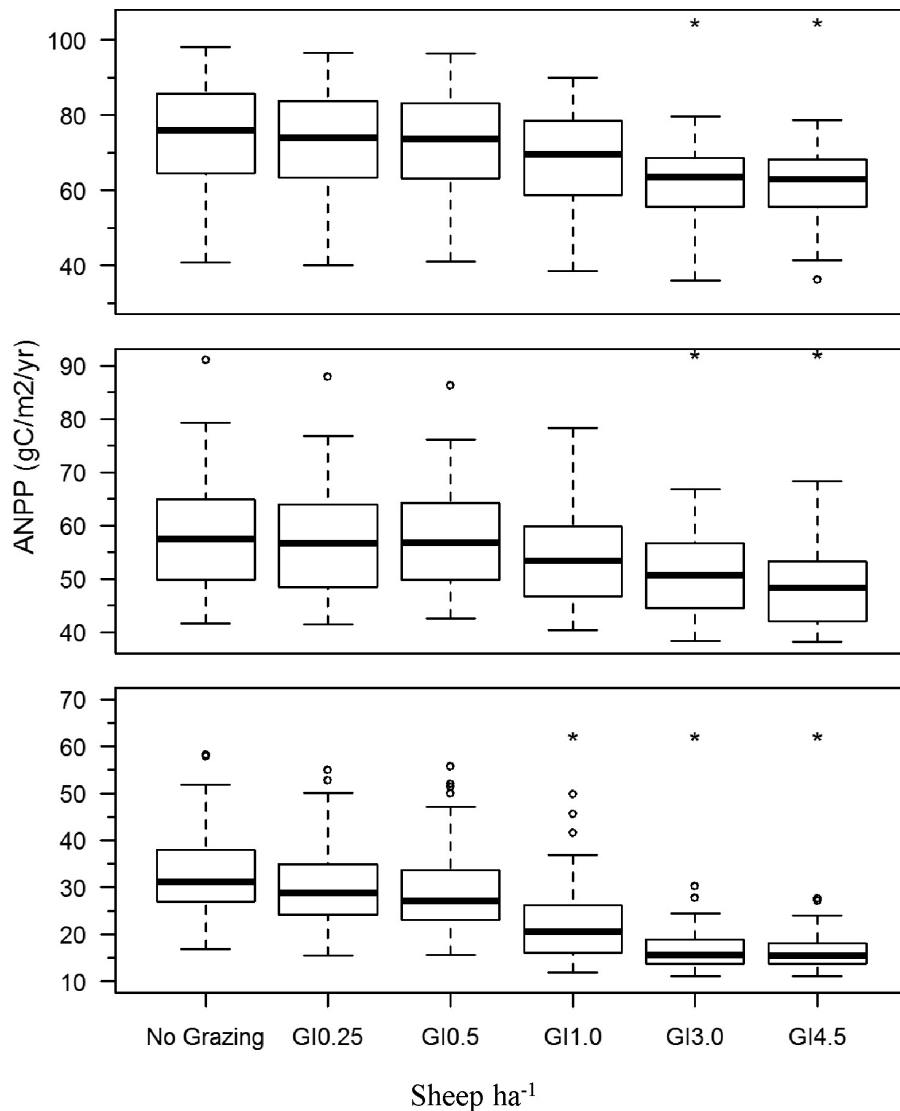


Fig. 8. Sensitivity of grassland annual ANPP to different grazing intensity across a precipitation gradient. An asterisk indicates a significant difference in annual ANPP between grazing and no grazing simulations at 5% level of significance. The top, middle, and bottom panels represent the ANPP response to different grazing intensities at wet, moderately wet, and dry sites, respectively.

Munkhtsetseg et al. (2007) found that seasonal change in temperature had a strong association with ANPP across three sites in southern Mongolia. Interestingly, the response of ANPP to temperature changes varied across individual sites, with one site (BC) showing a clear positive association. At BC, an increase in mean annual temperature resulted in a significant increase in ANPP by 4.98 g C/m<sup>2</sup> per 1°C increase in temperature ( $P < 0.05$ ). Our analysis further indicated that the positive influence of mean

annual temperature at BC is because warming, particularly during the early part of growing season, promotes ANPP by increasing snow melt and indirectly modifying soil water availability. Therefore, warmer springs seem to enhance ANPP early in the growing season at BC.

#### *Precipitation control on grassland ANPP*

Both growing season and annual precipitation totals have a substantial impact on grassland productivity (Knapp and Smith 2001, Huxman

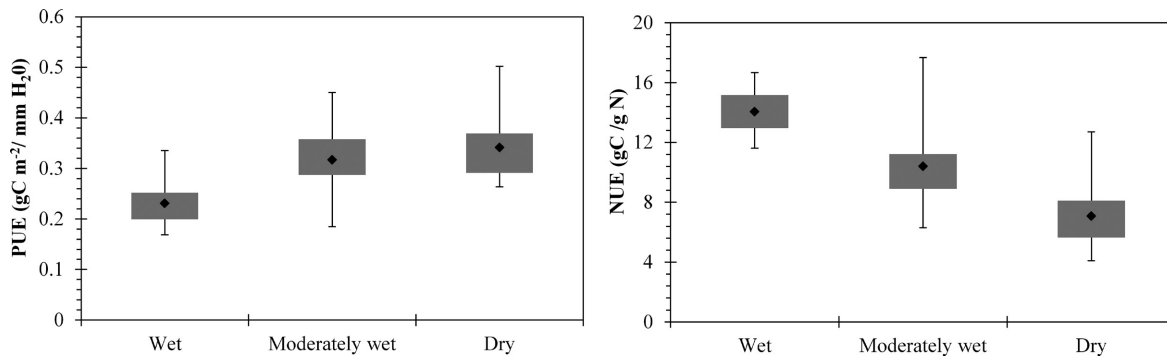


Fig. 9. Precipitation use efficiency (PUE) and nitrogen use efficiency (NUE) along a precipitation gradient in Mongolia. The box length represents the first and third quartile. The error bar represents the maximum and minimum values for PUE and NUE during 1981–2010 and the black dot represents the mean PUE and NUE during 1981–2010.

et al. 2004, Bai et al. 2008, Craine et al. 2012). Previous studies have shown that annual precipitation totals can explain 51–90% of the variation in ANPP for grassland ecosystems (Lauenroth 1979, Sala et al. 1988). Similarly, Thomey et al. (2011) confirmed that more concentrated precipitation distribution during the summer season promotes ANPP by alleviating water stress. In arid- and semi-arid grasslands, ecological processes are more sensitive to within-season dynamics primarily due to intense water limitations (Schwinning et al. 2004). Our study also found that precipitation during the growing season accounted for 60–72% of the annual precipitation totals across sites which resulted in the largest proportion of carbon accumulation as annual ANPP. However, at individual sites, growing season precipitation

explained only 28–49% of the variation in ANPP. In particular, growing season precipitation was weakly correlated with annual ANPP at BC because of the complex relationship among factors that determine soil water availability. At BC, precipitation concentrated during the non growing season (September–April) was significantly correlated with spring soil moisture content in the top 20 cm soil layer, indicating a carryover of non-growing season precipitation to the subsequent spring. This antecedent precipitation provides a basis for initial vegetation growth earlier in the spring (Shinoda and Nandintsetseg 2011). Antecedent precipitation or soil moisture conditions have the potential to stimulate or inhibit ecosystem processes (Potts et al. 2006, Sponseller 2007). For example, Potts et al. (2006) has shown that the ability of

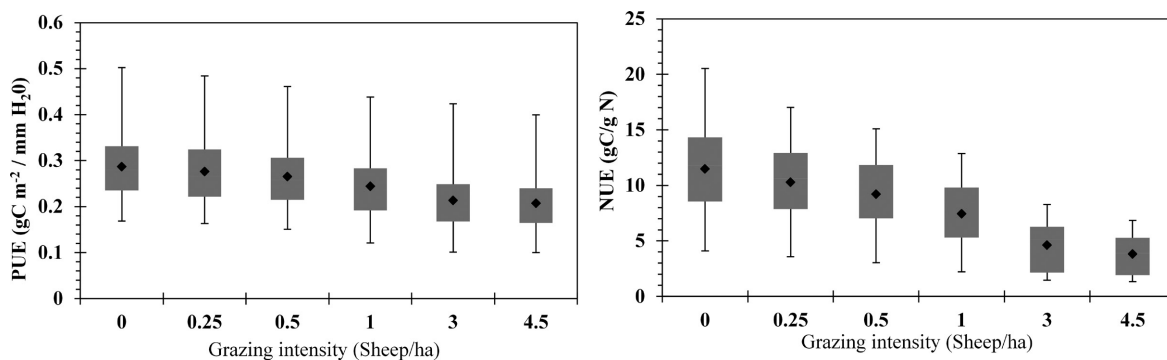


Fig. 10. Precipitation use efficiency (PUE) and nitrogen use efficiency (NUE) as a function of grazing intensity in Mongolia. The box length represents the first and third quartile. The error bar represents the maximum and minimum values for PUE and NUE during 1981–2010 and the black dot represents the mean PUE and NUE during 1981–2010.

semi-arid grasslands to assimilate carbon is strongly influenced by antecedent precipitation, which has a substantial effect on soil moisture conditions.

It is important to recognize that at other sites (TC, UC, AC, DG and TO) this kind of memory mechanism in hydrology was not evident. Similarly, spring soil moisture had little or no effect on grassland ANPP at these sites. The DLEM simulates effective root distribution across different soil layers as a function of root vertical distribution and moisture status in each layer, which determines the amount of water used by plants. To assess the soil water use at each site, we compared the DLEM simulated BNPP (estimated as a difference between NPP and ANPP) across each site as a measure of belowground biomass. Although the proportion of belowground biomass compared to total biomass was not significantly different across all sites, the total belowground biomass content differed across sites with the highest belowground biomass at BC (75 g C/m<sup>2</sup>) compared to TC (66 g C/m<sup>2</sup>), UC (66 g C/m<sup>2</sup>), AC (59 g C/m<sup>2</sup>), DG (34 g C/m<sup>2</sup>) and TO (25 g C/m<sup>2</sup>). Because the amount of carbon allocated belowground at BC site is higher compared to other sites, it is possible that the distribution of effective roots into deeper soil layers has led to the extraction of water from deeper soil horizons and increase ANPP early in the spring. However, the effective root distribution at other sites is more concentrated in the upper soil horizons, resulting in a stronger ANPP response to summer precipitation compared to spring soil moisture content. Interestingly, we did not observe any ANPP response to summer precipitation at BC. It is likely that at such wet climatic conditions, there is a threshold level of soil moisture beyond which any changes in soil moisture does not necessarily increase ANPP due to other plant constraints such as active root area, plant density, and nutrient limitations.

#### *Grazing effect on grassland ANPP*

Grazing by domestic herbivores is one of the primary factors influencing vegetation structure and function of grassland ecosystems (McNaughton 1985, Oesterheld and Sala 1990, Han et al. 2008). The DLEM simulated results showed that ANPP decreased with increasing grazing intensity across all sites. Milchunas and Lauenroth (1993), in a global meta-analysis of

the effects of grazing on ANPP, found that grazing had a negative effect on ANPP, particularly in grasslands with high ANPP. While our study found that historical grazing resulted in an overall reduction in ANPP at all sites, there was no significant reduction at AC and DG, indicating that compensatory growth response resulted in maintaining ANPP at these sites. Experimental results from other grassland ecosystems and model simulations suggested that ANPP can be maintained or stimulated in response to grazing (Biondini et al. 1998, de Mazancourt et al. 1998). Our study support the findings that ANPP can be maintained at sites that experienced low evolutionary grazing particularly due to improved plant-water and plant-nutrient status in response to grazing. However, at sites that experienced high grazing intensity, improved plant-water or plant-nutrient status does not maintain grassland ANPP, because grazing has a much larger effect on grassland biomass.

#### *Compensatory growth response*

Grassland NPP could be maintained, or even stimulated, in response to grazing. At sites where water is not limiting, low grazing intensity may alleviate nitrogen limitation by stimulating nitrogen mineralization and nitrogen uptake. But, this finding may not be the case at drier sites, because moisture limitation regulates net primary production, resulting in no net gain in ANPP. Our study, based on different hypothetical grazing intensities suggests that the net reduction in ANPP due to grazing is larger at drier compared to moderately wet and wet sites. Compared to the no grazing simulation, grazing resulted in a net reduction in ANPP by 50.7% at most at drier sites, while 11.2–22% at wet sites. This is primarily because at low to moderate grazing intensity, decrease in ANPP can be more than compensated by increasing net nitrogen mineralization rates, with additional nutrient inputs from excretal return at wet and moderately wet sites. However, at drier sites, moisture exerts an important control on ANPP and the associated feedback between warming, soil moisture, and available nitrogen results in a larger reduction in ANPP. Therefore, precipitation, through its effect on available soil moisture and net nitrogen mineralization, is an

important regulator of ANPP in grazed arid and semiarid grasslands.

In arid and semiarid grasslands, there has been no consistent evidence of grazing induced compensatory or over-compensatory effects on grassland ANPP. While numerous studies were conducted on the effect of grazing on ANPP (Chen et al. 2007, Bat-Oyun et al. 2010) in Mongolia, there have been no reports of over-compensatory or compensatory growth response. This is primarily because these studies do not include the feedback of livestock to the soil properties and plant growth or simulate grazing as a disturbance. Our study indicates that ANPP can be maintained at a grazing intensity of  $\leq 1.0$  sheep/ha in areas that experience growing season precipitation totals of 130 mm or more. However, the optimal grazing intensity for dry sites receiving growing season precipitation totals of  $< 130$  mm is 0.5 sheep/ha. We did not find any over-compensatory growth response that resulted in a stimulation of ANPP at all sites. Grazing may improve light absorption and reduce self-shading (Jameson 1963), which could have a positive effect on plant performance. Similarly, excretal nutrient inputs in the form of urine and dung would increase decomposition rates, making more nutrient available for plant growth (McNaughton 1979, Turner et al. 1993). Decreasing senescence of young grown leaves increases photosynthetic efficiency, promoting ANPP after grazing (Van Stalduinen and Anten 2005). In addition, reduction in water loss through stomatal pores improves short-term plant water relations, promoting compensatory growth (Turner et al. 1993). In light of the mechanisms explained above, our simulation considers the beneficial effect of grazing on ANPP, such as improved plant nutrient status due to increased nitrogen inputs in the form of excretal return, improved plant water efficiency due to reduction in leaf area index, and improved light absorption due to reduced shading.

While we were able to quantify the effects of climate and grazing on grassland ANPP and the associated changes in nitrogen and water use by plants, there are several limitations that need to be addressed in our future work. First, our grazing module does not account for the allocation of carbohydrates reserves following grazing as empirical evidence of such mechanisms is still not available. Second, we have not considered

how grazing affects soil properties, including soil structure and texture through trampling. Third, we have assumed that nitrogen inputs following excretal return is evenly distributed in space. However, excretal return from livestock often occurs in patches (Afzal and Adams 1992). Finally, regional validation with and without grazing is required to support current results and to better understand system interaction under changing climatic conditions.

## CONCLUSIONS

Our study identified that the interaction between climate and grazing was a major driver of inter-annual variations in ANPP over the previous 30 yr. Notably, total growing season precipitation and average growing season temperature were important factors determining the magnitude of ANPP in a particular year. Given the rise in temperature of  $2^{\circ}\text{C}$  since the 1940s and decrease in annual precipitation totals by 7% (Badarch et al. 2009), our results indicate that both decreased precipitation and increased temperature have negatively affected ANPP, with growing season average temperature alone contributing to approximately  $11 \text{ g C/m}^2$  decline in ANPP across the region.

Our findings further suggest that plants in the driest regions are more vulnerable to grazing compared to plants in wetter regions because of different water and nitrogen use patterns. Therefore, grazing management strategies across precipitation gradients should consider not only stocking rate and biomass productivity, but also how plants change their resource (nitrogen and water) use with grazing. In addition, our results show that the optimal stocking rate for areas experiencing high seasonal precipitation totals is 1.0 sheep/ha, while the optimal stocking rate for areas experiencing low seasonal precipitation totals is 0.5 sheep/ha. Our results indicate that moisture limitation is an important regulator of grazing optimization (or compensation) across Mongolian grasslands, given that traditional pastoral techniques, including mitigation strategies against overgrazing such as animal movement, are not considered.

Climate change models predict increased mean annual temperature both during winter and summer, slightly elevated but changing precipitation patterns (Dagvadorj et al. 2009),



and decreases in summer soil moisture of up to 6% (Hansen et al. 2007) in Mongolia. Even with existing observations from experimental manipulations, it is challenging to verify how climate and grazing or their interactions affect grassland productivity. Therefore, experimental studies focusing on grazing and climate manipulations are needed to better represent the range of climate and grazing conditions. These kinds of studies will provide insights for model development and evaluation, and predict the vulnerability of Mongolian grasslands in a changing global environment.

## ACKNOWLEDGMENTS

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