Interactive Effects of Climate Change and Grazing on Ecosystem Productivity and Greenhouse Gas Balance at Multiple Scales from Landscape to Global

by

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Abstract

The Anthropocene is facing several critical challenges in the 21st century due to increasing impacts of human activities such as deforestation, urbanization, agriculture and fossil fuel burning. Human activities alter surface aerodynamic, thermodynamic, radiative, hydrological and vegetative properties of the terrestrial biosphere with substantial impact on biogeochemical cycles and the global climate system. It is essential to understand the processes and dynamics that affect land transformation and how they mediate complex ecosystem processes in order to examine the impact of human activities on the terrestrial biosphere and their feedback to the global climate system.

This study focuses on the impact of human land use (grazing and livestock production) and climate on terrestrial ecosystems and feedback of livestock production to the climate system. Although numerous studies have examined the role of grazing and climate on terrestrial ecosystems, few, if any have simultaneously investigated the impact of grazing on carbon storage and their contribution to greenhouse gas balance using an integrated modeling approach. In this study, I used a process-based (The Dynamic Land Ecosystem Model) and an empirical model to investigate the impacts of grazing and climate on terrestrial carbon budget at site, regional and global scales. In addition, I examined the consequences of increasing livestock production on global greenhouse gas balance.

Results show that livestock grazing has a significant impact on aboveground NPP (-12%) and heterotrophic respiration (-12.4%), but did not alter net ecosystem productivity and

evapotranspiration across different sites in the Northern Hemisphere. In Mongolia, historical grazing reduced aboveground NPP by up to 15.4%, with larger reduction in dry sites compared to wet sites. Regional simulation across the Mongolian Plateau show that 83% of the grassland area has experienced decline in aboveground NPP, largely due to climate change (-61.4%) and grazing (-23.2%) since the 1990s. In addition, climate change increased livestock mortality by 28% due to combined drought and extreme winter condition. At a global level, livestock grazing and climate change reduces soil organic carbon (SOC) at the rate of 13.4 PgC/yr and 2.0 PgC/yr, respectively ($p < 0.05$). Likewise, grazing reduced net primary productivity (NPP) by 4.3 PgC/yr, while climate change increases NPP by 1.6 PgC/yr.

The results also indicate that livestock production plays an important role in regulating the concentration of greenhouse gases globally. Methane (CH_4) emissions from the global ruminant livestock sector accounted for 47-54% of all non-CO_2 GHG agricultural emissions. Since the 1890s, CH_4 emission from the ruminant livestock sector has increased by 2.06 Gt CO_2-eq (332%), with the largest contribution from dryland ecosystems (347%). Global drylands has 36% higher emission intensity (CH_4 emissions/km2) compared to non-drylands in the recent decades. In addition, developing countries experienced the largest percentage increase in CH_4 emissions from 51.7% in the 1890s to 72.5% in the 2010s.

Nitrous oxide (N_2O) emissions from the global grasslands increased significantly from 1.41 Tg N_2O-N/yr in 1961 to 1.89 Tg N_2O-N/yr in 2014. Managed pastures dominated N_2O emissions contributing to up to 68% of the total grassland emissions. Among different sources, manure left on pastures contributed to ~40% of the total emissions, followed by manure applied

to pastures (20%) and fertilizer applied to pastures (10%). Regionally, Asia dominated N_2O emission contributing to 31% of the total emission, followed by North America (25%), Europe (20%) and Africa (13%).

The results also indicate a positive cumulative impact of three greenhouse gases (CO_2, CH_4 and N_2O) in the global grasslands. Grassland ecosystems were a net source of greenhouse gas of about 434 Tg CO_2-eq/yr during 1960-2014. CH_4 and N_2O emissions contributed to 60% and 40% of the total GHG sources, respectively. Across different continents, southern Asia was the major source of GHG, followed by North America and Europe. In particular, managed pastures in southern Asia, Europe and North America dominated N_2O emissions, which largely controlled the net GHG balance in these regions.

Overall, the results of this study demonstrate that increasing livestock production and climate change (increasing heat waves, higher temperatures) have profound impacts on climate and the environment. In order to mitigate CH_4 emissions from the livestock sector, direct and indirect approaches that relies on animal (improving feed quality, feed additives, animal productivity) and land (grazing optimization, transition to extensive system) based mitigation approaches and policy (imposing tax on conventional ranching) efforts can promote sustainable intensification. Likewise, improvement in genetic production potential of livestock and their feed composition can reduce nitrogen losses via urine and feces and application of manure to croplands and pastures based on specific plant nitrogen demand could potentially reduce N_2O emissions.

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Chapter 1. Introduction

The terrestrial biosphere plays an essential role in regulating the concentration of atmospheric greenhouse gases providing climate change mitigation benefits (IPCC 2014). Recent observations indicate that the terrestrial biosphere sequestered 3.1 $GtCyr^{-1}$, offsetting approximately 30% of the net carbon dioxide (CO_2) emissions during 2006-2015 (Quéré et al. 2016). However, the terrestrial biosphere acts as an overall carbon source when three major greenhouse gas [CO_2, methane (CH_4) and nitrous oxide (N_2O)] are considered together (Tian et al. 2016a). The net source or sink strength of greenhouse gases is ultimately determined by both natural and anthropogenic drivers, which mediate complex biogeochemical and hydrological processes (Vitousek et al. 1997b, Schimel et al. 2001, Canadell et al. 2007, Tian et al. 2015b, Keenan et al. 2016). Understanding both natural and anthropogenic drivers and their contribution to greenhouse gas balance is crucial to develop prudent short-term actions and long-term strategies in coping with climate change.

The terrestrial biosphere also plays a fundamental role in providing goods and services that are vital for the functioning of ecosystems and societies (Melillo et al. 1993, Costanza et al. 1997). These ecosystem services include provisioning (food, timber, firewood), regulating (climate regulation, water quality, insect/pest control), supporting (soil formation and nutrient cycling) and cultural (recreation, aesthetics) (MEA 2005b). In particular, terrestrial ecosystems contribute to biomass production (Net Primary Production; NPP) by fixing atmospheric CO_2

through photosynthesis, after accounting for losses associated with plant respiration and microbial decomposition (Pan et al. 2011, Pan et al. 2014a). However, the amount of biomass sequestered by terrestrial ecosystems are largely influenced by both natural and anthropogenic factors, which includes climate, land cover land use change (LCLUC), tropospheric ozone, nitrogen deposition and land management (Field et al. 1995, Ellis and Ramankutty 2008, Felzer et al. 2011, Tian et al. 2016a, Zhu et al. 2016b). Quantifying the terrestrial NPP, both in time and space, and their response to multiple environmental changes is crucial for assessment of physiological and ecological processes that controls the timing and magnitude of biomass production, which ultimately determine the planetary boundaries of safe operating space.

The Anthropocene is facing several critical challenges in the 21st century due to increasing impacts of human activities such as land use, deforestation, fossil fuel burning and manufacturing of hazardous chemical compounds (Crutzen 2006, Steffen et al. 2007). Among these human activities, agricultural practices and the combustion of fossil fuels have a significant negative impact on the environment and natural resources (Scheffer et al. 2001, Hertwich 2010, Tian et al. 2016a). For example, human appropriation of net primary productivity (HANPP), which measures the impact of human on the biosphere has reached 25% of the potential net primary productivity, and is expected to rise up to 44% by 2050 (Haberl et al. 2007, Krausmann et al. 2013). Agricultural lands are the major source of HANPP, which provides food, feed and fuel to meet the demands of the growing population (Foley et al. 2005). However, unsustainable farming not only degrade ecosystem services (Tian et al. 2012b) but also increases the risk of operating outside the planetary boundaries that define the safe operating space (Rockström et al. 2009).

The global agricultural sector therefore must operate within the available finite resources and boundaries to sustain food production and ecosystem services (Dietz and O'Neill 2013). Currently, approximately 37% of the terrestrial surface is occupied by some form of agricultural practices, which includes croplands (11%) and rangelands (26%) (FAO 2009b). Global cropland area has grown by 12% over the last 50 years, while agricultural intensification due to “Green Revolution” (Tilman 1998) has led to an increase in agricultural production between 2.5 and 3 times (FAO 2011). The larger increase in agricultural production has been associated less with bringing new land into cultivation and more with the use of irrigation, fertilizers, pesticides, herbicides and improved crop varieties (Tilman et al. 2002). For example, agricultural area has increased considerably in South America (83%), Africa (46%), and Asia (36%), but it has declined in North America (4%) and Europe (25%) since 1960 (FAOStat 2010). The expansion of agricultural area coincides with alarming rates of deforestation, which could substantially impair the ability of natural systems to provide ecosystem goods and services (Donald 2004, Isbell et al. 2013, Newbold et al. 2015). Consequently, a better understanding of the impact of agricultural expansion and intensification on both natural and managed ecosystems is paramount to develop strategies necessary for maintaining biodiversity ecosystem functions for future generations (Norris 2008).

The livestock sector is one of the major driver of land use changes, which occupies approximately 30% of the ice-free terrestrial surface (Steinfeld et al. 2006a), and 70% of global agricultural land (Gerber et al. 2013a). It also consumes about 60% of the global biomass harvest (Krausmann et al. 2008), uses around 30% of the agricultural water withdrawals (Peden et al. 2007, Mekonnen and Hoekstra 2010) and alter the global nutrient cycle (Bouwman et al. 2013). A recent estimate suggest that beef production has more than doubled, while chicken meat production has increased by a factor of 10 since the 1960s (Thornton 2010). In particular, developing regions experience the largest increase in livestock products, accounting for 50% of the beef, 41% of the milk, 72% of the lamb, 59% of the pork and 53% of the poultry globally (Steinfeld et al. 2006a). This rapidly evolving livestock system has a substantial impact on the environment including water and biodiversity (Ripple et al. 2014). The impact of livestock sector on the natural resources and the environment can be broadly grouped into two categories: 1) direct impact, which includes grazing and its resultant effect on grassland resources and 2) indirect impact, which includes land conversion for producing livestock feed (for example, replacing forests to produce soybean in South America), which ultimately leads to loss of biodiversity (Cardinale et al. 2012).

The livestock sector is also a major driver of climate change, contributing between 16% to18% of all greenhouse gas emissions (Steinfeld et al. 2006a, O'Mara 2011). In particular, the livestock sector accounts for 9%, 37% and 65% of anthropogenic CO_2, CH_4 and N_2O emissions, respectively (Steinfeld et al. 2006a). The large part of livestock related anthropogenic CO_2 comes from land use changes, particularly deforestation due to expansion of pastures and arable land for feed crops, while the large part of CH_4 and N_2O emissions come from enteric fermentation by ruminant livestock and livestock waste in the form of manure, respectively (IPCC 2007b, Saunois and Kleinen 2016). Given the projected increase in demand of global meat production and milk consumption by 68% and 57%, respectively between 2000-2030 (FAO 2006), it is anticipated that the global livestock sector may occupy the majority of or surpass the safe operating space and contribute more to anthropogenic climate change by 2050 (Pelletier and Tyedmers 2010). Hence, there is an urgent need to develop strategies and management practices that focus on sustainable livestock production to better cope with the effects of climate change (Thornton et al. 2009).

Although numerous studies have quantified grassland response to livestock grazing and the impact of livestock production on greenhouse gas emissions, few, if any, have examined the impact of livestock grazing on ecosystem function and greenhouse gas balance at regional to global scales simultaneously. For example, Herrero et al. (2013) quantified biomass use, feed efficiencies and greenhouse gas emissions (CH_4 and N_2O) globally, but the effect of grazing on ecosystem functions such as NPP and NEP were not included. Bouwman et al. (2013) examined the impact of livestock production on global nitrogen and phosphorus cycles during 1900, 1950, 2000 and 2050, but did not include the effects of livestock production on greenhouse gas balance and ecosystem productivity. Other studies have attempted to quantitatively investigate the impact of grazing and management (fertilization, mowing and irrigation) on biomass production and soil carbon, but the effect of livestock production on greenhouse gas emissions was not included (Parton et al. 1995, Piñeiro et al. 2010, McSherry and Ritchie 2013, Chang et al. 2016). Although these studies consider different scenarios of livestock production, which affect ecosystem services and greenhouse gas emissions, simultaneous estimates of livestock contribution to greenhouse gas balance and their impacts on ecosystem function are lacking.

Likewise, studies on the impact of global livestock sector on ecosystem structure and function has been limited from few years to decades and site to regional scales (Burke et al. 1989, Cui et al. 2005, He et al. 2011, Lezama et al. 2014). However, the long-term trend, impacts and drivers of livestock grazing on ecosystem attributes such as ANPP and soil organic carbon has not been investigated well at the global scale. For example, grazing affect ecosystem function synergistically or negatively depending on climate, site quality and other environmental factors (Dangal et al. 2016). 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 McNaughton (1983) found a compensatory plant growth in response to herbivory. The likely differences on the impact of grazing might be associated with the range of factors that drive grazing induced changes in plant growth. 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 plants growth (McNaughton 1979, Turner et al. 1993a). Decreasing senescence of young grown leaves increases photosynthetic efficiency promoting ANPP after grazing (Van Staalduinen and Anten 2005). In addition, reduction in water loss through stomatal pores improves short-term plant water relation promoting compensatory growth (Turner et al. 1993a). Quantifying the long-term grazing induced changes in primary production and soil organic carbon is crucial to understand the impact of grazing on both vegetation and soil carbon.

Additionally, livestock related greenhouse gas emissions are quantified using different approaches following IPCC guidelines (O’Mara 2011, Herrero et al. 2013, Tubiello et al. 2013). These studies either quantify GHG emission at a country scale since 1960 (Tubiello et al. 2013) or provide one time estimates of CH_4 and N_2O emission based on gridded livestock data (Herrero et al. 2013). In particular, we have no clear understanding of how livestock related GHG emission has changed over a century long time scales. Also, global gridded livestock data has only been reported for year 2006 (Robinson et al. 2014), although livestock sector has evolved rapidly over the past 50 years (Steinfeld et al. 2006a). There is need to develop the spatial distribution of global livestock population over longer time scales to understand the dynamics and processes controlling GHG emissions. This approach will further allow identifying hotspots of GHG emissions and developing short-term actions and long-term strategies to mitigate GHG emissions.

We applied both empirical and process-based modeling approaches: 1) to investigate the spatial and temporal dynamics of grazing induced variation in ANPP and SOC at landscape to global scales; and 2) to quantify the contribution of livestock sector (ruminants) to greenhouse gas balance (CH_4 and N_2O emissions) at the global level. In particular, this study uses a process based ecosystem model [the Dynamic Land Ecosystem Model; Tian et al. (2010a)] to investigate grazing impacts on ANPP and SOC, and the contribution of global livestock sector to N_2O emissions from both pastures and rangelands. For CH_4 emissions, this study uses empirical approach by following IPCC guidelines to quantify the evolution of CH_4 emission associated with ruminant production and manure management.

1.1 Objectives

The overarching goal of this study is to examine the response of grassland ecosystems to livestock grazing at landscape to global scales and assess the contribution of livestock production to CH_4 and N_2O emissions. The specific objectives of this study are to:

1. Develop a comprehensive modeling approach to include the impacts of livestock into the global land model, and their associated feedback to the climate system.
2. Develop gridded livestock data for ruminant livestock during 1890-2014 to assess the impacts of grazing on climate and the environment.
3. Assess the impacts of climate change and livestock grazing on carbon and water cycles across several sites in Northern Hemisphere.

4. Quantify the impact of climate change and livestock grazing on terrestrial ANPP across several sites in the Mongolian Plateau.
5. Examine the grassland ecosystem response to climate and livestock grazing by integrating livestock population dynamics with a global land model in the Mongolian Plateau.
6. Quantify the long-term impact of climate change and grazing on grassland ANPP and SOC at the global scale.
7. Quantify the trend and driver of CH_4 emissions from the global livestock sector during 1890-2014 using empirical approach.
8. Assess the contribution of global livestock sector to N_2O emission from pasture and rangelands.

1.2 Hypotheses

1. Rising air temperatures can reduce primary production by increasing plant respiration and evapotranspiration rates, which can ultimately drive a decrease in stomatal conductance and photosynthesis in areas with limited soil moisture supply (Objective 3, 4, 5 and 6).
2. Altered precipitation pattern and its timing and magnitude would affect primary production through soil moisture changes. Areas experiencing decline in growing season precipitation would show reduction in primary production due to decreased leaf water potential as a result of low soil moisture (Objective 3, 4, 5 and 6).
3. Regardless of elevated temperatures and altered precipitation, physiological differences among plant functional types (C3 vs C4; deep-rooted vs shallow-rooted) could alter biomass production differently. In areas with low soil moisture, C3 and shallow-rooted plants would experience higher decline in primary production due to low water use efficiency and lower root biomass, respectively (Objective 3, 4, 5 and 6).

4. Livestock grazing would have a significant impact on primary production and soil organic carbon, but the magnitude and direction of the impact would depend on grazing intensity. Grassland ecosystems would be more vulnerable and less resilient with increasing grazing intensity, largely due to reduction in leaf biomass, low litter input to soil and changes in biomass allocation among different plant parts (Objective 3, 4, 5 and 6).
5. The global livestock sector would have a significant impact on CH_4 emissions, with larger emissions in region that experience low grass quality, low feed efficiency and higher livestock density (Objective 7).
6. Managed pastureland would result in higher N_2O emissions compared to unmanaged pastures. Irrigated pastures with higher amount and frequency of fertilizer application would result in greater N_2O emissions compared to non-irrigated pastures that receive low amount and frequency of fertilizer (Objective 8).

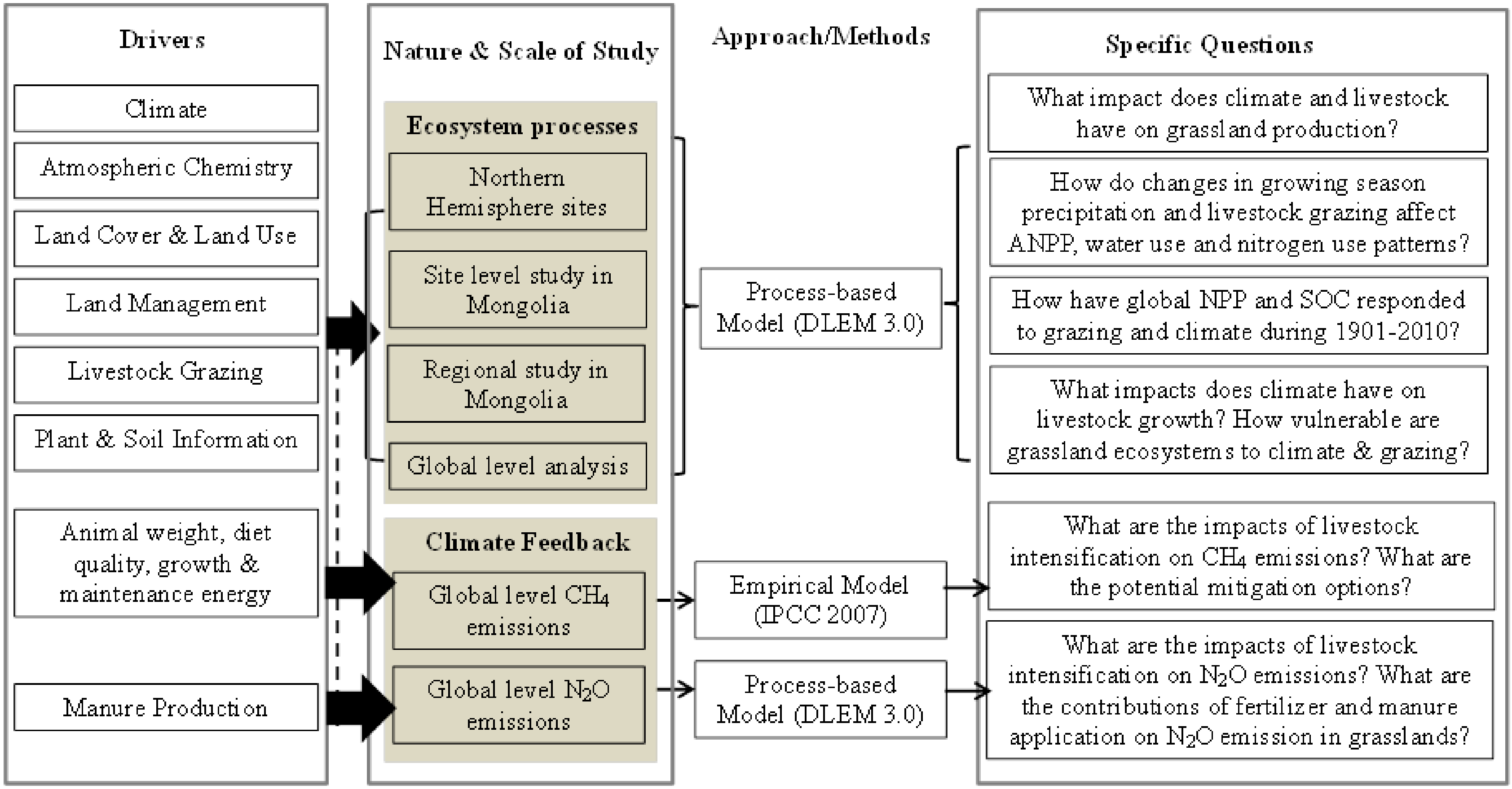


Figure 1-1Detailed Framework of the research used in this study.
DLEM: Dynamic Land Ecosystem Model; IPCC: Intergovernmental Panel on Climate Change; ANPP: Aboveground Net Primary Productivity; NEP: Net Ecosystem Productivity; Rh: Heterotrophic Respiration; ET: Evapotranspiration

1.3 Approaches

To address the objectives and test the hypotheses listed above, the study is conducted by using both empirical and process-based modeling approaches (Figure 1-1). First, we developed the animal component within the process-based model (the Dynamic Land Ecosystem Model; Tian et al. (2010a)) using an integrated approach that considers the underlying mechanisms of both livestock population dynamics (natality, growth, mortality and energetics) and their impact on terrestrial ecosystems (carbon, nitrogen and water cycles). We then applied the model at landscape to regional and global scales to examine the response of terrestrial ecosystems to climate change and grazing. Finally, we estimate CH_4 and N_2O emissions associated with the global livestock sector using empirical and process-based model, respectively. Below are the detailed steps on how the study was carried out:

1.3.1 Data collection

- Reconstructed gridded grazing intensity (heads/ha) data at global scales based on FAO and other sources (for example, National Statistics of Mongolia).
- Reconstructed gridded managed pasture vs rangeland distribution at $0.5^o \times 0.5^o$ resolution
- Model input datasets on climate, atmospheric CO_2 concentration, tropospheric O_3, nitrogen deposition, land cover land use change (LCLUC) and other stationary datasets (soil texture, bulk density, slope etc)
- Site level observation datasets to evaluate the model performance

1.3.2 Model development

- Develop livestock population dynamics model within the framework of the DLEM (DLEM 3.0)
- Calibrate and validate the livestock population dynamics across different sites in North America
- Evaluate the impacts of livestock on carbon dynamics at site to regional and global scales

1.3.3 Model application

- Use grazing intensity as an input to the DLEM to simulate the impacts of climate change and grazing at site level in semi-arid grassland ecosystems
- Regional scale simulation of livestock population dynamics in response to multiple environmental changes, and their associated impacts on biomass production
- Global level simulation of climate change and grazing impacts on ANPP and SOC during 1901-2010
- Global level simulation of the impacts of grassland management (fertilization and manure deposition) on N_2O emissions

1.3.4 Estimate livestock contribution to CH_4 emissions using IPCC (tier II) guidelines

To quantify the contribution of ruminant livestock on CH_4 emissions, we used IPCC tier II approach (Dong et al. 2006), which requires information on different sources of energy required by livestock category. While DLEM has the capability to provide CH_4 estimates at sites to regional level using a detailed animal physiology, it does not explicitly simulates dairy vs nondairy cattle, which could potentially alter CH_4 emissions. Therefore, we relied on IPCC tier II approach to simulate CH_4 emissions. The study first developed a spatially disaggregated global dataset of ruminant livestock during 1890-2014. This dataset along with the energy requirement and feed digestibility information were feed into empirical models (IPCC tier II) to estimate CH_4 emission.

1.4 Dissertation structure

Chapter 1 gives a background on the significance, objectives, research hypothesis and approaches used in this study.

Chapter 2 provides a much more detailed literature review on the impacts of multiple environmental changes including livestock production on ecosystem productivity and multiple greenhouse gas emissions across different scales. It also provides an overview of the importance of using process-based models in quantifying the impacts of climate change and grazing on ecosystem function and multiple greenhouse gas emission.

Chapter 3 presents the detailed mathematical approach describing DLEM 3.0 animal population dynamics module by including processes to estimates the growth, development and mortality of specific mammalian livestock, and their impact on carbon and water cycles.

Chapters 4-6 investigate the impacts of climate change and grazing on ecosystem carbon dynamics at site to regional and global scales. Chapter 4 uses site level livestock density data as input to DLEM to quantify the impacts of climate change and grazing on terrestrial ANPP in semi-arid grassland ecosystems. Chapter 5 simulates livestock population dynamics using DLEM 3.0, and investigate the impact of livestock grazing in combination with climate and other environmental factors on grassland ANPP at the regional scale in the Mongolian Plateau. Finally, chapter 6 applies the approach similar to chapter 4 to provide estimates of the impact of grazing in combination with climate change/variability on ANPP and SOC at the global level.

Chapters 7-8 examines the impact of global livestock sector on greenhouse gas emissions (CH_4 and N_2O). Chapter 7 uses an empirical approach based on IPCC guidelines to quantify CH_4 emissions from ruminant livestock and manure management. Chapter 8 investigates the impact of livestock manure deposition/application and fertilizer application on N_2O emissions from managed grassland (pastureland) at the global scale.

Chapter 9 summarizes the key findings and list uncertainties and improvements needed in the future work.

Chapter 2. Literature Review

2.1 Overview of the response of the terrestrial biosphere to multiple environmental changes

The terrestrial biosphere responds strongly to both natural and anthropogenic peturbation, which not only impact the cycling of carbon, water and nitrogen but also affect regional and global climate by changing the concentration of greenhouse gases in the atmosphere (Vitousek et al. 1997a, Falkowski et al. 2000, Vörösmarty et al. 2000, Gordon et al. 2005, Scholze et al. 2006, Tian et al. 2016a). In the absense of anthropogenic perturbations, two opposing processes determine the land-atmosphere carbon exchange: plants accumulate carbon in both vegetation and soils by fixing atmospheric CO_2, but the accumulated carbon are lost through respiratory processes from autotrophs and heterotrophs (Costanza et al. 1997, Valentini et al. 2000). Under stable climatic conditions, carbon exchange between the atmosphere and terrestrial biota are in equilibrium, with steady carbon pools in vegetation and soil. However, changes in climate and increasing atmospheric CO_2 concentration alter the equilibrium condition, making the terrestiral biosphere a net sink of atmospheric CO_2 (Luyssaert et al. 2008, Pan et al. 2011, Quéré et al. 2016).

Carbon exchange between the terrestrial biosphere and atmosphere is also strongly affected by soil water availability, which is ultimately determined by temperature and precipitation changes. In response to soil water deficit, photosynthesis is limited first by reduced rates of CO_2 supply due to declining stomatal conductance (Tuzet et al. 2003, Harris et al. 2004, Berry et al. 2010), but continued soil water deficit ultimately leads to reduction in cell expansion and growth (Hsiao 1973). Ecosystem respiration, on the other hand, is primarily dominated by belowground processes such as root and microbial decomposition (Eissenstat and Yanai 1997, Silver and Miya 2001). Soil water deficit may constrain root production, and microbial and root decomposition (Boone et al. 1998, Davidson et al. 2000b, Suseela et al. 2012) and strongly influence net exchange of carbon between the terrestrial biosphere and atmosphere. The overall soil water storage is determined by altered precipiation and elevated temperatures (Koster et al. 2004, Seneviratne et al. 2010). In particular, changes in the timing and amount of precipitation has an overwhelming influence on soil moisture dynamics (Eltahir 1998, Huxman et al. 2004b). Low precipitation totals during the growing season negatively impact soil moisture content (Knapp et al. 2002, Heisler-White et al. 2008) and elevated temperatures further amplify soil moisture deficit by increasing reference evapotranspiration and atmospheric water demand (Immerzeel et al. 2012). Water availability is therefore an important driver of plant carbon uptake and plays a paramount role in the global carbon cycle.

The natural interaction of climate-vegetation-soil and the coupled carbon and water cycle systems have been dramatically altered by anthropogenic modification fo the earth’s surface (IPCC 2014, Hautier et al. 2015). Humans have transformed nearly 37% of earth’s land surface (NRC 2010), in the process of providing essential goods and services such as food, fiber and wood products. These land cover land use change (LCLUC) are driven by a suite of factors (social, political and economic factors) that operate at local to regional and global scales

(Lambin et al. 2001, Rudel et al. 2005). LCLUC (conversion of natural landscapes for human use) and land management (harvest, irrigation and fertilization practices) affect terrestrial carbon, nitrogen and water flows and the exchange of carbon, water and energy between the terrestrial biosphere and the atmosphere (Houghton 1995, Tilman et al. 2001, Schlesinger 2005, Liu et al. 2008, Tian et al. 2011a, Tian et al. 2015d). For example, LCLUC and intensive land management practices have led to a net release of 1 Gt CO_2 yr^{-1} to the atmosphere (Quéré et al. 2016), doubled the reactive nitrogen on land (Galloway and Cowling 2002, Gruber and Galloway 2008, Schlesinger 2009), altered the global water cycle (Oki and Kanae 2006, Gerten et al. 2008, Vörösmarty et al. 2010) and resulted in considerable biodiversity loss (Thomas et al. 2004, Pereira et al. 2010).

In particular, agricultural practices (culitvation of crops and pastures) are the dominant form of land use occupying approximately 37% of the terrestrial surface (FAO 2009b) driven by the growing needs of the rapidly increasing world population (Ramankutty et al. 2002, Banger et al. 2015). However, increasing agricultural practices carries an environmental cost (Foley et al. 2005). Agricultural land use significantly affect carbon pools of both vegetation and soils (Bondeau et al. 2007, Dangal et al. 2014), mostly in a negative way (Dixon et al. 1994, Murty et al. 2002). It also reduces the carbon sequestration capacity of the land surface by reducing the turnover time of vegetation and soil pools because large proportion of NPP are removed during harvest and returned to the atmosphere via consumption and respiration (Gitz and Ciais 2003, Erb et al. 2016). Likewise, agricultural land use can disrupt the water balance by increasing surface runoff and river discharge, particularly when natural vegetation are cleared for human uses (Costa et al. 2003, Piao et al. 2007, Tao et al. 2014). Increase in surface runoff and river discharge is likely due to a decline in plant transpiration and interception (Zhang et al. 2001). Also, agricultural practices including land cover changes affect surface albedo and alter latent and sensible heat fluxes, which likely affect the global climate system (Bonan 2008).

Despite the overwhelming influence of climate and LCLUC on global carbon, water and nutrient flows, other environmental factors such as changes in atmospheric chemistry (elevated CO_2 and tropospheric O_3) and nitrogen deposition may potentially bring complex interacting impacts on ecosystem functioning (Hyvönen et al. 2007, Reay et al. 2008, Leakey et al. 2009). Elevated atmospheric CO_2 concentration may potentially increase photosynthetic response (Keenan et al. 2016, Zhu et al. 2016b) and water use efficiency of C3 plants (Tian et al. 2011a, Battipaglia et al. 2013). Nitrogen deposition, on the other hand, could alleviate nutrient limitation and increase carbon storage of the terrestrial biosphere (Luo et al. 2004, LeBauer and Treseder 2008), although excessive nitrogen enrichment in the form of synthetic fertilizer would not significantly influence productivity in managed ecosystem (Tian et al. 2012b). For example, a recent study show that elevated atmospheric CO_2 concentration and atmospheric nitrogen deposition accounted for 70% and 9% of the greening effect, respectively (Zhu et al. 2016b). But, a recent Free Air CO_2 Enrichment (FACE) experiment does not support the sustained CO_2 fertilization effect, because nitrogen limitation constrained the plant growth response to elevated CO_2 (Norby et al. 2010).

Tropospheric O_3 is a damaging and second most important air pollutant (after particulate matter) that significantly affect the terrestrial biosphere, including both plants and animals

(Chappelka and Samuelson 1998, Fuhrer and Booker 2003, Ainsworth et al. 2012). Long-term exposure to tropospheric O_3 concentration, particulalry during the growing season have negative impact on plant growth and productivity (Adams et al. 1989, Barbo et al. 1998). Plant growth in chronic tropospheric O_3 is characterized by low rates of CO_2 assimiation at the leaf level, which limits carbon sequestration across all biomes (Sitch et al. 2007, Talhelm et al. 2014). In addition, tropospheric O_3 induces changes in foliary chemistry and shifts in community richness (Power and Ashmore 2002), which may result in a decrease in nutritive quality of forage for mammalian herbivores (Krupa et al. 2004, Muntifering et al. 2006, Gilliland et al. 2016). Large scale studies, which are parametrized for O_3 impact using the physiological response observed in seedlings and saplings indicate a decrease in carbon storage by up to 7.7% (Felzer et al. 2005, Sitch et al. 2007, Ren et al. 2011), but the magnitude of this impact likely varies across biome type and tropospheric O_3 concentration.

2.2 Global climate change and its impact on natural and managed ecosystems

Accumulating evidence suggests that the global climate system is changing as a result of human activities, largely due to emissions of greenhouse gases (Karl and Trenberth 2003, IPCC 2014). The most recent report on IPCC (IPCC 2014) estimates that the globally averaged combined land and ocean surface air tempature has increased by 0.85 ^{o}C during 1880-2012. The increase in surface temperature is attributed to GHG emissions, particularly CO_2, CH_4 and N_2O. The cumulative anthropogenic CO_2 emissions between 1750 and 2011 has reached 2040 Gigatons (Gt) CO_2 (1 Gt = 10^{15} g) of which approximately 40% (880 $GtCO_2$) have remained in the atmosphere, while the remaining 60% were equally shared by land and ocean uptake (IPCC

2014). Atmospheric CH_4 and N_2O concentrations have increased by 150% and 20%, respectively since the start of industrial era (Montzka et al. 2011). Of the total CH_4 emissions (8.5 $GtCO_2$-eq yr^{-1}), two-third of the increase in CH_4 (5.8 $GtCO_2$-eq yr^{-1}) has been attributed to agriculture and fossil-fuel exploitation, while natural sources account for the remaining one-third dominated by wetlands and variations in temperature and water table depth (Montzka et al. 2011). Similarly, anthropogenic N_2O account for 40% of all N_2O emissions and is dominated by agricultural activites (1.9 $GtCO_2$-eq yr^{-1}). Collectively, the increase in the atmospheric concentration of GHG (CO_2, CH_4 and N_2O) has resulted in a net positive cumulative impact on the planetary energy budget (Tian et al. 2016a), largely dominated by anthropogenic sources.

Climate change will likely alter the supply of ecosystem services from natural ecosystems through changes in rates of primary productivity, plant abundance and their distribution in a complex way (Grimm et al. 2013). NPP of C3 grassland is expected to decline by >50% over the four decades, due to increasing aridity and declining late-summer precipitaiton (Brookshire and Weaver 2015). Forest ecosystems in the tropics and temperate regions would be increasingly vulnerable to climate related temperature and moisture stress (Dale et al. 2001, Bonan 2008), while boreal forest would experience an increase in tree growth due to extended growing season, and increased tree recruitment (Ruckstuhl et al. 2008). More extensive and severe wildfires would affect burned areas, with resultant impact on NPP, biodiversity and net carbon exchange (Littell et al. 2009, Yang et al. 2015). Climate change will also alter the growth and reproduction of forest pests and insects, which ultimately increases the extent of insect outbreaks with significant impact on tree mortality and carbon balance (Logan et al. 2003, Kurz et al. 2008, Raffa et al. 2008, Ghimire et al. 2015). These impacts will be further amplified due to widespread tree mortality triggered by drought, heat waves, tropical cyclones and tornadoes (Zeng et al. 2009, Anderegg et al. 2012).

Climate change will also have a signficant impact on managed ecosystems. Food security would be increasingly under pressure as human population will surpass 9 billion by 2050, with likely decline in crop yield for major crops in some regions (Schmidhuber and Tubiello 2007, Teixeira et al. 2013, Tai et al. 2014, Tian et al. 2016b). Although temperate and higher latitude will experience an increase in crop yield and food production, the tropics and subtropics will experience the largest reduction in crop yield (McMichael et al. 2004, Lobell and Field 2007, Challinor et al. 2014). Food security will be further aggravated as the livestock products would become more costlier due to climate induced agricultural disruption, which will drive an increase in grain prices (Steinfeld et al. 2006a). Climate change will also increase soil moisture stress particularly in tropics and temperate croplands and affect the distribution of arable land, irrigation requirement and fresh water availability (Schmidhuber and Tubiello 2007, Zhang and Cai 2013, Pan et al. 2015c).

2.3 Global agriculture and food security

Global agricultural practices (crops and pastures), which occupies 37% of the terrestrial biosphere, is the largest user of land and water. It also plays a key role in feeding the growing population by producing agricultural and livestock products, which are determined by a range of biophysical and socioeconomic forces (Tilman et al. 2011). Biophysical forces include climate, soils, topography, water availability and site management practices, while socioeconomic forces include changes in human population density, demand of food products, and their availability and access (Ericksen 2008). While global cropland area has increased by only 12% over the past 50 years, agricultural production (grain harvests) has increased by a factor of two, exceeding 2 billion tons per year (Mann 1999). The larger proportion of an increase in food production is driven by “Green Revolution” technologies, which includes cultivation of high-yielding varieties, application of chemical fertilizers and animal manure, use of pesticides, and mechanization and irrigation (Matson et al. 1997, Evenson and Gollin 2003, Pingali 2012). Over the previous 40 years, fertilizer application has increased by nearly 700% and irrigated cropland area has increased by nearly 70% (Foley et al. 2005). This has resulted in a significant increase in food production but at high environmental cost (Tilman et al. 2001, Fedoroff et al. 2010).

While the “Green revolution” has been successful in increasing agricultural production, it has also caused detrimental impact on the environment and societies (Borlaug 2002, Tilman et al. 2002). High fertilizer use has degraded water quality (Hamilton and Helsel 1995), by polluting ground and surface water (Peel et al. 2013), and irrigated area has experienced increased salinization resulting in large loss of arable land annually (Wood et al. 2000). In addition, areas that rely heavily on ground-water for irrigation show a significant decline at a mean rate of 4.0 cm yr^{-1} (Rodell et al. 2009). Intensive agricultural practices have also increased soil erosion and reduced fertility (Power 2010). Collectively, global increase in food production comes at a high environmental costs, with significant negative impact on freshwater resources, water quality and land degradation.

The global demand for food production is expected to roughly double by 2050, owing to an increase in population growth and changes in diet associated with rising incomes (Godfray et al. 2010). Agricultural management practices that led to an increase in food production by two fold over the past 50 years would likely not help anymore because some of the cropland area has already reached its production potential. For example, Tian et al. (2012b) show that nitrogen fertilizer induced crop yield have reached their peaks, while Ray et al. (2012) found that crop yield of 24-39% of the four key global crops (maize, rice, wheat and soybean) would never improve, stagnate or even collapse. Thus, there is increasing concern that future global food security is only possible at the expense of land conversion because reduction in productivity due to land degradation can drive expansion of croplands into natural habitats.

2.4 The importance of livestock sector and its impact on global food security

Although livestock production is driven by socio-economic factors that operates at local to regional scales (Thornton 2010), it is currently considered as a force of global importance (Steinfeld et al. 2006a), which significantly interacts with many earth system processes. Globally, it accounts for 40% of the agricultural GDP, and also provides 17% of food calories and one-third of protein to human diets (Herrero et al. 2009). While providing food benefits and improving people's livelihood, it also consumes 60% of the global biomass harvest (Krausmann et al. 2008), uses 30% of agricultural water withdrawals (Peden et al. 2007) and substantially alter the global nitrogen cycle (Bouwman et al. 2013). It is also responsible for up to 18% of all anthropogenic GHG emissions, which is dominated by CH_4 and N_2O (Steinfeld et al. 2006a, Tubiello et al. 2013).

As the impact of livestock on ecosystem and the environment differ as a function of livestock type (monogastrics and ruminants) and the way they are produced, the global livestock sector has been broadly divided into two different production systems (Steinfeld and Mäki-Hokkonen 1995): 1) Solely livestock system; and 2) Mixed crop-livestock farming system. Solely livestock production system are those in which > 90% of the livestock feed comes from rangeland, pastures, annual forages and purchased feed, while < 10% of the feed comes from non-livestock farming practices. Mixed farming system are those in which >10% of livestock feed comes from crop by-products, stuble or non-livestock farming practices. The solely livestock system is further divided into grassland-based and landless livestock systems. Grassland-based system are those in which >10% of the livestock feed comes from farm and stocking rates are <10 temperate livestock units per hectare of agricultural land. The landless livestock system are those in which <10% of the livestock feed comes from farm and stocking rates are >10 temperate livestock units per hectare. The mixed livestock system, on the other hand, are categorized as rain-fed mixed farming and irrigated mixed farming. The landless livestock system further include landless monogastric (chicken, pigs) and landless ruminant (cattle, sheep, goat) production systems.

Based on the production system, ruminant livestock can be produced as landless, grassland based and mixed farming systems. Landless ruminant production system are those in which livestock feed is mainly introduced from outside the farm system. These are highly concentrated system, and are particularly found in eastern Europe and Commonwealth of the Independent States (CIS). The grassland based ruminant production system rely primarily on free grazing practices whether rangeland or pasture land for their feed. But, the mixed ruminant production system rely on both on farm and non farm production for their feed.

The interaction of ruminant livestock with the ecosystem is complex because of their dependence on different production system for feed. Most traditional ruminant system are resource driven in which ruminants make use of available resources, with limited alternative uses (Abraham and Kepford 2000), while mixed system are integrated together closely, with livestock providing input to the crop system in the form of manure and crop system providing necessary feed to the livestock. Regardless, ruminants that rely primarily on rangeland and pastureland have the potential to alter ecosystem structure, function and biodiversity (Asner et al. 2009, Alkemade et al. 2013), but the magnitude and direction of such effect is driven by intensity of grazing (Schönbach et al. 2011).

2.4.1 Livestock and land degradation

Livestock-related land use change also contribute to land degradation with substantial impact on plant and animal biodiversity, and ecosystem services (Petz et al. 2014). There are three potential mechanisms through which livestock contribute to land degradation (Steinfeld et al. 2006a): 1) expansion into natural ecosystems; 2) rangeland degradation; and 3) pollution, productivity losses and soil degradation. Expansion of crop and pasture by replacing native vegetation would lead to biodiversity losses (MEA 2005b). For example, Brazil is the largest beef exporter where one-fourth of Brazil’s beef production comes from the Amazon, which drives deforestation to grow pastures and feed crops (Cederberg et al. 2011, Ometto et al. 2011). The destruction of natural vegetation cover to produce pasture and livestock feed alter biogeochemical cycles. In addition, conversion of natural vegetation to pasture and croplands affect surface energy balance through changes in evapotranspiration, infiltration, water storage and runoff (Ward and Robinson 2000).

Rangeland degradation can primarily occur through overgrazing when there is a mismatch between ecosystem carrying capacity and livestock density (Weber and Horst 2011, Hilker et al. 2014). Livestock density can exceed ecosystem carrying capacity particularly in semi-arid and arid grassland ecosystems, where biomass production is erratic due to large inter-annual variation in growing season precipitation totals (Abel 1993). The exceedance of ecosystem carrying capacity (overgrazing) could ultimately lead to a series of environmental problems such as soil erosion, vegetation degradation, biodiversity loss and water resource depletion (Snyman and Du Preez 2005, Han et al. 2008b).

Likewise, livestock grazing affect grassland productivity, plant species composition and soil organic input, depending on the herbivore and ecosystem type, with impacts on both vegetation and soil (Bardgett and Wardle 2003, Augustine and McNaughton 2006, Irisarri et al. 2016). Some empirical and modeling studies suggest that herbivory reduces primary productivity and decreases nutrient cycling rates (Pastor and Cohen 1997, Schönbach et al. 2011, Dangal et al. 2016), while other studies indicated that herbivory can stimulate primary productivity and promote nutrient cycling (McNaughton et al. 1997, Frank et al. 2002). Livestock grazing also influence soil processes by altering the quantity and quality of resource inputs (exudation, litter inputs) and functional composition of vegetation, which may enhance or reduce litter quality and soil decomposition (Bardgett and Wardle 2003). Finally, nutrient overloads and changes in nutrient cycling rates coming from crop-livestock system have deleterious impact on water quality and other ecosystem services including eutrophication of surface water, leaching of nitrates and nitrites and excess accumulation of nutrients in system with high doses of manure (Steinfeld et al. 2006a).

2.4.2 Livestock and multiple GHG emissions

The livestock sector is also a source of GHG that pollute the atmosphere and contribute to climate warming, either directly (e.g. enteric fermentation, excretal return) or indirectly (e.g. feed-production activities, clearing native vegetation for pastures) (Thornton 2010). There are three main sources of GHG emissions from the livestock sector (Steinfeld et al. 2006a): 1) land use change, which drives CO_2 emission; 2) enteric fermentation dominated by ruminants, which drives CH_4 emissions; and 3) manure management, which drives both N_2O and CH_4 emissions. The global warming potential (GWP) of non-CO_2 gases (CH_4 and N_2O) is much higher than CO_2, which makes non-CO_2 gases an important contributor to climate warming, although their concentration in the atmosphere is not higher. The GWP can be used to measure the impact of multiple GHG emission on the planetary energy budget and is a metric to compare all GHG together. At a 100-year time horizon, the GWP of CH_4 and N_2O is 28 and 265, respectively (Myhre et al. 2013, Tian et al. 2016a).

Livestock-related CO_2 emission primarily comes from land use change when native vegetation are cleared to grow livestock feed (IPCC 2007b). Carbon dioxide emission associated with clearing of natural vegetation is more complex and varies as a function of type of natural vegetation, climatic condition and modes by which CO_2 is released (i.e. burning or decay)

(Steinfeld et al. 2006a). Livestock induced CO_2 emission from deforestation account for approximately 2.4 billion tonnes (9%) of CO_2 per year. The largest proportion of this comes from Latin America where Amazon forests are cleared to grow pastures and feed crops for beef production (Ometto et al. 2011). Likewise, although livestock respiratory process releases substantial amount of carbon (Steinfeld et al. 2006a), it is not considered as a net source but a part of rapidly cycling biological system in which biomass consumed was itself created through photosynthesis, sequestering CO_2 in the process (Herrero et al. 2011). But, considering animal respiration as a part of rapidly cycling biological system has recently been contested (Goodland and Anhang 2009). Other studies such as the Kyoto Protocol and IPCC (2007b) also does not consider livestock respiration as a source of CO_2 because part of carbon consumed is stored in the live tissue of the growing animal, which could even be considered as a carbon sink. Collectively, land use change related CO_2 fluxes due to converstion of natural vegetation to pasture and feed is only considered as a net source based on IPCC inventory guidelines, which account for 9% of anthropogenic CO_2 emissions (Steinfeld et al. 2006a).

Livestock related CH_4 emissions are associated with two major processes: 1) enteric fermentation; and 2) manure management. During enteric fermentation, the ruminant livestock (for example, cattle, buffalo, sheep, goats and camel) emit CH_4 as a by-product of the normal digestive process, due to fermentation of feed consumed by livestock (Dangal et al. 2017). The emission of CH_4 from enteric fermentation of ruminant livestock is influenced by feed quantity and quality, body weight, feeding level and the activity and health of livestock (Johnson and Johnson 1995, Shibata and Terada 2010). The amount of CH_4 emissions from manure depend on the decomposition process, which is influenced by climate, and the manner in which manure are collected and stored before its application (Chadwick et al. 2011). Manure management related CH_4 emission requires anaerobic, water-based environment, high level of nutrient for bacetrial growth, a neutral pH and high temperatures.

Livestock related N_2O emissions are primarily driven by animal manure application to crops and pastures and urine deposition by grazing livestock in rangelands (Brown et al. 2001, De Klein et al. 2006). Unlike CH_4 production, N_2O production during storage and treatment of animal manure can occur as a result of combine nitrification-denitrificaiton processes. Nitrification involves transformation of ammonium to nitrates under aerobic conditions, while denitrification involves conversion of nitrates into dinitrogen and subsequent release of N_2O under anaerobic conditions (Jose et al. 2016). Factors that drive N_2O production include temperature, pH, biochemical oxygen demand (BOD), and nitrogen concentration (IPCC 2007b). Globally, livestock related N_2O emission account for 65% of the anthropogenic N_2O emission (Steinfeld et al. 2006a).

2.5 An integrated modeling approach for global livestock sector

Computer models that explain physical, chemical and biolgocial processes within the earth system are an essential and inseparable part of the earth system analysis that provide need based information by integrating different components of the terrestrial biosphere (Claussen et al. 2002, Dunne et al. 2012). In particular, ecosystem models with explicit representation of different plant and animal processes can serve as an important tool to quantify the impact of livestock on terrestrial ecosystems and their feedback to climate change (Rotz et al. 2005, Freer et al. 2012, Pachzelt et al. 2013). These models allow the scientific community to conceptualize and measure complex system and quantify both historical and future changes in different ecosystem attributes (Ollinger and Smith 2005).

Ecosystem models are also invaluable in providing both individual factor and interactive effects and the response of different ecosystem attributes to change in those factors (Melillo et al. 1993, McGuire et al. 2001, Pan et al. 2014a). In assessing the interactive effect, ecosystem models can provide meaningful interpretation of the complex system involving nonlinear interaction, which is not possible with single factor experiments (Pan et al. 2014a). For example, grazing may promote ANPP by increasing nutrient cycling rates and making more nitrogen available for plant use. However, grazing also reduces the aboveground photosynthetic tissue, which ultimately leads to reduction in LAI and less carbon uptake during photosynthesis. The net impact of these processes are inturn driven by grazing intensity, ecosystem carrying capacity, ecosystem type and local environmental conditions. While experimental studies can provide information on the impact of grazing, these results are just suited for one specific environment and cannot be extrapolated at the global scale. Unlike the experimental studies, ecosystem models uses spatially explicit information by separating the terrestrial biosphere into grid cells, which require information on soil, climate and land use practices. Therefore, ecosystem models are powerful tool that allows us to investigate different types of effect and evaluate the response of terrestrial ecosystem to multiple environmental changes.

Chapter 3. Integrating Herbivore Population Dynamics into a Global Land Biosphere Model: 1. Model Development and Evaluation

Abstract

Mammalian herbivores are an essential component of grassland and savannah ecosystems, and therefore affect these ecosystems interacting with the climate system. To date, the response and feedback of mammalian herbivores to changes in both abiotic and biotic factors are poorly quantified and not adequately represented in current global land modeling framework. In this study, we coupled herbivore population dynamics into a global land model (the Dynamic Land Ecosystem Model; Tian et al. 2010) to simulate herbivore dynamics and their responses to changes in multiple environmental factors at site level across different Continents. We simulated population dynamics of horse, cattle, sheep and goat in Mongolia, Africa, and North America during 1980-2010. Our results showed that the model is capable of reproducing observed herbivore populations across all sites for these animal groups. Our simulated results also indicated that climate extremes led to a maximum mortality of 53% of the total herbivores in Mongolia. In addition, herbivore had a negative impact on grassland production and heterotrophic respiration, but a positive feedback to the climate through methane emission. However, herbivores did not have a significant impact on net ecosystem productivity and evapotranspiration. With adequate parameterization, the model can be used for historical assessment and future prediction of mammalian herbivore population and their relevant impact on biogeochemical cycles and other land surface processes. Our results demonstrate a strong coupling between primary producers and consumers, indicating that inclusion of herbivores into

global land ecosystem modeling framework is essential to better understand the effect of herbivores on biogeochemical and hydrological processes.

3.1 Introduction

Mammalian herbivores are an essential component of the terrestrial biosphere, and therefore affect the exchanges of energy, water, carbon and greenhouse gases between land and the atmosphere (Herrero et al. 2009, Steinfeld and Gerber 2010, Tian et al. 2016a). Changes in herbivore abundance can lead to dramatic direct and indirect effect on plant composition, above- and below-ground productivity, nutrient cycling and other ecosystem processes (Augustine and McNaughton 1998, Steinfeld and Wassenaar 2007, Piñeiro et al. 2010). Quantifying the overall impact of herbivores on forage productivity and diversity have been limited due to mixed results ranging from positive to neutral and negative effects of herbivores on ecosystem processes (Hoshino et al. 2009, Schönbach et al. 2011). Therefore, a better understanding of herbivore population dynamics and their impact on ecosystem processes is essential to enhance the capability on how herbivores regulate carbon, nitrogen and water cycles at different scales.

Biotic factors such as species composition, plant morphology, productivity, and forage quality may affect the population size and spatial distribution of mammalian herbivores (Bailey et al. 1996). In areas with stable forage resources, mammalian herbivores are regulated in a density-dependent manner (Illius and O'connor 1999, 2000b). As the herbivore population exceeds ecological carrying capacity, increased competition among herbivores for forage resources may lead to a reduction in herbivore productivity (Vetter 2005), provided that supplemental feeding from stored forage resources are not taken into account. However, if herbivore populations are below carrying capacity, mortality during unfavorable years is reduced due to availability of greater forage and body fat reserves (Vetter 2005). Thus, the availability of forage resources, both in terms of quality and quantity, may directly influence herbivore population dynamics.

Abiotic factors such as climate, topography, soil characteristics, and distance to water can directly (for example, feed intake, water intake, growth and reproduction) or indirectly (for example, feed supply, parasites and diseases, shelter) influence mammalian herbivore population (Williamson and Payne 1978, Morignat et al. 2015, Rao et al. 2015, Reeves and Bagne 2016). Seasonal variation in climate creates alternating wet and dry periods, which forces herbivore to migrate (Owen-Smith et al. 2010) or lose weight (Illius and O'Connor 2000b) during periods of low resource availability. Likewise, extreme climatic condition such as drought and severe cold has been linked with a decline in herbivore numbers (Begzsuren et al. 2004, Rao et al. 2015). However, these effects are largely dependent on the type of herbivores, their foraging behavior, and distribution pattern.

We also have limited understanding about how mammalian herbivores affect ecosystem processes, given existing result indicating both positive and negative effects on forage productivity, plant species composition and soil organic input (Bardgett and Wardle 2003, Augustine and McNaughton 2006, Irisarri et al. 2016). Some empirical and modeling studies suggest that herbivory reduces primary productivity and decreases nutrient cycling rates (Pastor and Cohen 1997, Schönbach et al. 2011, Dangal et al. 2016), while other studies indicate that herbivory can stimulate primary productivity and promote nutrient cycling (McNaughton et al. 1997, Frank et al. 2002). Likewise, herbivore populations may influence soil processes by altering the quantity and quality of resource inputs (exudation, litter inputs) and functional composition of vegetation, which may enhance or reduce litter quality and soil decomposition (Bardgett and Wardle 2003). While previous experimental and modeling studies have quantified the effect of herbivore on individual carbon components such as ANPP, soil organic carbon and methane emission (Milchunas and Lauenroth 1993, Herrero et al. 2013, Dangal et al. 2016), these studies does not account for population dynamics of herbivores, and therefore, cannot quantify the feedback among climate, herbivores and ecosystem processes.

Ecosystem models with explicit representation of herbivore population dynamics and their response and feedback to changes in both biotic and abiotic factors serve as an important tool to quantity the tradeoffs and synergies related to herbivore and forage productivity across temporal and spatial scales (Freer et al. 1997, Rotz et al. 2005, Pachzelt et al. 2013). Most population dynamics models lack generality as they are parameterized for particular systems and for particular species and simulate herbivore population dynamics using an individual based modeling (models that simulates autonomous individual organisms as a function of intake rates and energetics) approach (Turner et al. 1993b) or statistical approach, which relies on modeling annual changes in population dynamics as a function of abundance level, rainfall and mean annual temperature (Ogutu and Owen-Smith 2003).The earliest approach to modeling herbivore dynamics and their response to environmental factors depended on multiple regression, which linked herbivore numbers and productivity to climate and forage availability (Gillen et al. 1984, Smith 1988, Senft 1989). However, these models were only applicable at a particular site and could not be extrapolated to other sites due to limited inclusion of detailed mechanism of foraging, herbivore growth and reproduction. Other models such as GrazPLAN (Freer et al. 1997) and Growth, Metabolism and Mortality (GMM) model (Owen-Smith 2002) have been used to model population dynamics with detailed animal physiology. For example, GrazPLAN include detailed animal and plant physiology operating at a daily time step, but can only be applied to sheep or cattle (Moore et al. 1997, Gill et al. 2010a, King et al. 2012). Similarly, GMM model does not explicitly consider resource and climatic constraints on different age classes of herbivores (Owen-Smith 2002). Therefore, it is imperative to improve current population dynamics models by including explicit representation of different herbivore types for quantifying herbivores dynamics in response to changes in both biotic and abiotic factors.

The purpose of this study is to explicitly integrate herbivore population dynamics into the global land modeling framework so that we can evaluate herbivore impacts on ecosystem dynamics and the climate system. In particular, we attempt to model the growth, mortality, and reproduction of specific herbivores as a function of available forage, climate, and other environmental factors. The herbivore population dynamics model was then linked to a global land ecosystem model (the Dynamic Land Ecosystem Model) to quantify the impact of herbivores on carbon, nitrogen and water cycles through aboveground biomass and the associated feedback of herbivores to vegetation and soil. Our primary objectives are to: (1) develop the capability to simulate global mammalian herbivore population dynamics as a function of resource and environmental constraints; (2) evaluate model performance and quantify herbivore population dynamics across multiple sites in Asia, Africa, and North America; (3) quantify climate and environmental controls over herbivore population dynamics at the study sites; and (4) examine the impact of herbivores on aboveground net primary productivity (ANPP), net ecosystem productivity (NEP), heterotrophic respiration (Rh) and evapotranspiration. We hypothesize that the incorporation of herbivore population dynamics into the global land modeling framework will have a significant impact on terrestrial biogeochemistry, and the magnitude and direction of the impact will depend on the relative abundance of herbivores at a given location.

3.2 Materials and methods

3.2.1 The Dynamic Land Ecosystem Model (DLEM)

The DLEM is a highly integrated global land ecosystem model that simulates the interactions and feedbacks among multiple ecosystem components to estimate the stocks and fluxes of carbon, nitrogen and water from site to region to globe (Tian et al. 2010a, Pan et al. 2014b). The DLEM is driven by changes in atmospheric chemistry (nitrogen deposition, tropospheric ozone concentration and atmospheric CO_2 concentration), climate, land-use and land-cover (LULC) and disturbances (e.g., fire, timber harvest). The model has been extensively used to quantify carbon stocks (vegetation carbon, soil carbon) and fluxes (net primary productivity, net ecosystem productivity) and the exchanges of methane and nitrous oxide between multiple terrestrial ecosystems and the atmosphere (Ren et al. 2012, Pan et al. 2015a, Pan et al. 2015b, Pan et al. 2015d, Tian et al. 2015a, Tian et al. 2015b, Yang et al. 2015). Detail description of the processes for simulating vegetation dynamics and biogeochemical cycles are available elsewhere (Tian et al. 2010a, Pan et al. 2014a).

The basic simulation unit in the DLEM is a grid cell at a certain resolution, which is covered by a mixture of vegetation cover, impervious surface, lake, stream, bare land, and glacier. The vegetation cover in the DLEM includes five plant functional types (PFTs) of which four are reserved for natural vegetation and one for crops. The grid at a certain resolution is assumed to have identical environmental conditions including climate, soil and topography.

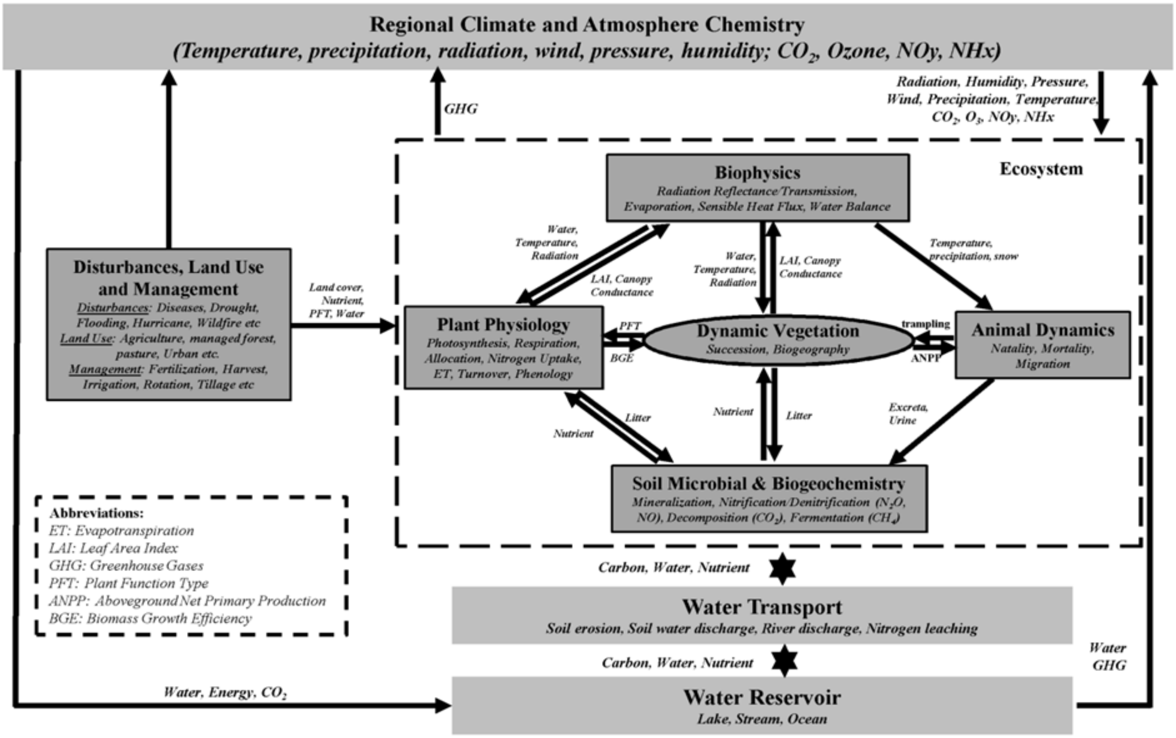


Figure 3-1The simplified framework of the Dynamic Land Ecosystem Model (DLEM3.0; Tian et al. 2010) for modeling herbivore population dynamics in terrestrial ecosystems

In this study, we simulated forage productivity for three major PFT's, i.e., C3 grass, C4 grass and savannas, within a grid assuming that steppe and savannas biomass are the most preferred resources for mammalian herbivores at the study sites. In the new version of the DLEM (DLEM 3.0), we included the fifth core component (The Animal Dynamics Module; Figure 3.1). The animal dynamics module includes four major processes: (1) energy intake; (2) energy expenditure; (3) reproduction; and (4) mortality including both ordinal mortality (base mortality that occurs every year) and mortality associated with extreme climatic conditions (such as drought and freezing winter). We simulated the dynamics of cattle, horse, sheep and goat during the course of this study. The detailed processes that regulate natality, mortality and reproduction of herbivores are described in section 2.2.

3.2.2 Modeling Herbivore Population Dynamics

The representation of herbivore population dynamics in the DLEM 3.0 is based on several previous modeling studies (Illius and O'Connor (2000b), Konandreas and Anderson (1982) and Freer et al. (1997) (Figure 3.2). The basic simulation unit for herbivore population dynamics is a grid, in which the maximum of four different herbivore types can co-exist at a time. Although we attempted to simulate the population dynamics of four herbivores at site level in this study, the simulation scheme makes the model applicable to any herbivore type and at regional to global scales. Using the DLEM 3.0, we simulated the population dynamics of cattle, horse, goat and sheep in Mongolia, Africa and the United States. However, in this version of the DLEM, we have not considered the epidemic disease or mortality of livestock. Below we describe the detailed model structure and algorithms through which we model energy intake, energy expenditure, reproduction and mortality among different herbivores within each grid cell.

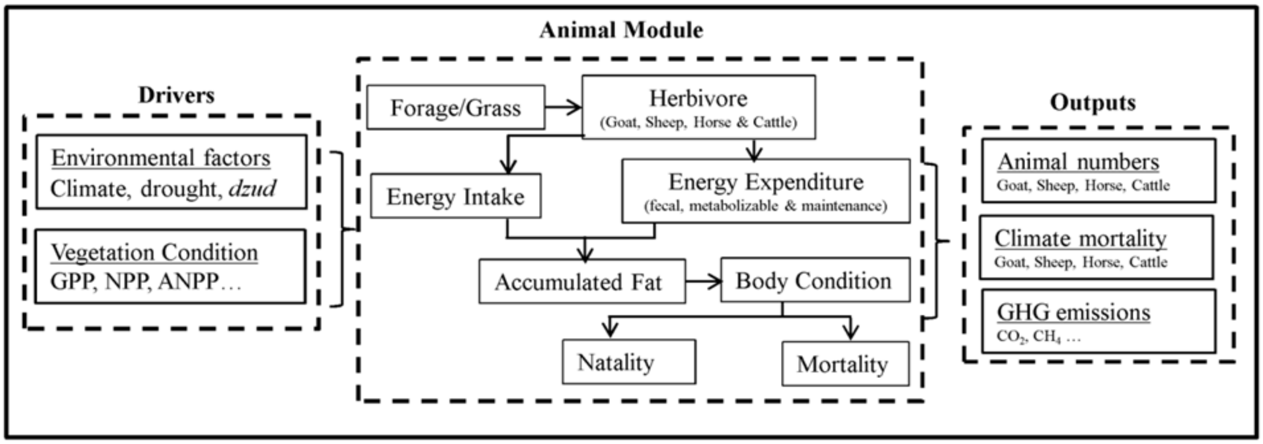


Figure 3-2 Modeling framework showing the input drivers, herbivore dynamics and outputs from the coupled herbivore-land model (DLEM3.0)

Table 3-1 Key parameters controlling the herbivore population dynamics in the DLEM

Parameters	Horse	Cattle	Sheep	Goat	Remarks	References
A	400	400	65	65	Mature Mass (kg)	FAO and Illius and O'Connor (2000b)
β	240	240	308	308	Half saturation intake rate (kg/ha)	Wilmshurst et al. (2000)
b, c	b = 15, c = 0.3				Parameters controlling effect of body reserves on birth	Illius and O'Connor (2000b)
i,j,k	0.034, 3.565, 0.077				Ruminant intake const.	Shipley et al. (1999)
i,j,k	0.108,3.284,0.08				Hindgut intake const.	Shipley et al. (1999)
p	0.8				Intrinsic rate of increase	Illius and O'Connor (2000b)
C_e	0.7	0.9	0.9	0.9	Chewing efficiency	Freer et al. (2012) for cattle and goats
C_c	0.02	0.025	0.02	0.02	Chewing cost (MJ/kg)	Freer et al. (2012) for cattle and goats
S_{thres}	5	5	40	40	Threshold stocking rate (heads/ha)	Freer et al. (2012) for cattle and goats
M_{base}	0.00003	0.00003	0.00003	0.00003	Basal rate of mortality (frac)	Pepper et al. (1999) for Sheep
F_{max}	0.3	0.3	0.3	0.3	Maximum body fat (fraction of mature weight)	Illius & O'Connor 2000

Forage Intake and Digestibility

Potential Forage Intake by Herbivores

Potential intake (I_{max}) is defined as the amount of forage eaten when there is no limitation of feed and its digestibility (Freer et al. 1997). In the DLEM 3.0, potential forage intake is related to animal size and food digestibility (measured in proportion), and is expressed as the maximum daily net energy intake (MJ/day) based on the relationship among physical and chemical properties of food, animal mass, and type of digestive system (Illius and Gordon 1991, 1992, Shipley et al. 1999). The maximum intake rate (MJ/day) for different herbivore types (ruminants vs. hindgut) were regressed against the body weight (kg) to derive the following equation:

$$I_{max} = i \times exp^{j \times d} \times A_{lt}^{(k \times \exp(d) + 0.73)} \times u_g \tag{1}$$

Where *i*,*j*,*k* are parameters that control the potential intake rates for different herbivores; *d* is digestibility of the biomass (measured in fraction) based on equation (4); A_{lt} is mature body mass of each animal type (kg); u_g is a scalar to define the gut capacity of each age class of herbivores, and is expressed as:

$$u_g = \left(\frac{W}{A}\right)^{0.75} \tag{2}$$

Where W is body mass (kg) of herbivores in each age group and A is mature mass (kg) of herbivores.

The expression $i \times exp^{j \times d}$ allows for the conversion of body mass (kg) to energy intake (MJ/kg of body weight) such that for hindgut herbivore *i* is 0.108, while for ruminant herbivore *i* is 0.034. The higher conversion coefficient (*i*) of hindgut herbivore assumes higher potential intake rate per unit body weight compared to ruminant herbivore. For example, comparison of ruminant and hindgut herbivore of similar body weights indicated that the ratio of horse to cattle dry matter and metabolizable energy intake averaged 1.73 and 1.48, respectively (Johnson et al. 1982).

Forage Digestibility

The digestibility of the consumable forage ($V_{consume}$) in the DLEM is separated into the proportion of living and dead forage, with their respective digestibility rate (fraction). The digestibility of the dead forage is assumed to be 0.4 (Illius and O'Connor 2000b), while the digestibility of the living forage is a function of quantity of available live forage at any time period and is modeled similar to Pachzelt et al. (2013):

$$d_{living} = 0.4605 + 0.239106 \times V_{living}^{-0.1697} \tag{3}$$

Where,

d_{living} is digestibility of live forage on offer (fraction)

V_{living} is live aboveground forage (Kg DM/ha)

Equation (3) is derived by combining the dependence of digestibility on crude protein content of forage (Prins 1996) and the exponential decrease of crude protein content with increasing biomass (van Wijngaarden 1985), such that the coefficient 0.239106 allows for the conversion of living biomass (kg DM/ha) to digestibility (fraction). The negative power (-0.1697) assumes that the digestibility of living biomass decreases with increasing biomass production (van Wijngaarden 1985).

The overall digestibility of the total available forage (both dead and living) is modeled as:

$$d = d_{living} \times B_d + 0.4 \times (1 - B_d) \tag{4}$$

Where,

B_d and $1-B_d$ represent the proportion of functional (live) and non-functional biomass, respectively. B_d in the DLEM is based on Illius and O'Connor (2000b), and is expressed as:

$$B_d = \left(\frac{V_{living}}{V_{total}}\right)^{0.2} \tag{5}$$

The exponent 0.2 is used to describe diet selection during progressive defoliation by herbivores, such that herbivore tend to prefer green material and avoid dead (Chacon and Stobbs 1976). Illius and O'Connor (2000b) found that the standard error for the exponent was 0.032, with the correlation coefficient (r) of 0.79.

Relative Intake by Herbivores

The proportion of the potential intake that a herbivore can satisfy depends on two attributes of forage supply: (1) relative availability; and (2) relative ingestibility (Freer et al. 1997). In the DLEM, relative availability of the forage is measured as a function of model simulated aboveground biomass ($V_{consume}$), while relative ingestibility is a saturating function of available plant biomass (Illius and O'Connor 2000b). Thus, daily forage intake (MJ/day) is modeled as a function of maximum daily intake rate (MJ/day) based on equation (1) and the saturating function of available aboveground biomass:

$$I_{daily} = I_{max} \times \left(\frac{Vconsume}{\beta + Vconsume}\right) \tag{6}$$

Where,

I_{daily} is Actual daily intake (MJ/day)

$V_{consume}$ is total available forage biomass for animal consumption (Kg/ha/day)

β is half maximum intake rate (Kg/ha/day)

Table 3-2 Site information used for model evaluation during 1980-2010 in Mongolia, Africa and the United States

Site Location	lon, lat	Elev (m)	Climate		Dominant	
			Tair (^{o}C)	Prec (mm)	PFT	Herbivore
Arxangai, MN	101.5^{o}E, 47.5^{o}N	1865	0.91	335.95	C3 grass	Sheep
Bulgan, MN	103.6^{o}E, 48.8^{o}N	1176	-0.6	329.54	C3 grass	Sheep
Zavxan, MN	96.60^{o}E, 47.7^{o}N	2547	-1.65	211.91	C3 grass	Sheep
Selenge, MN	105.3^{o}E, 49.1^{o}N	926	-0.64	325.84	C3 grass	Sheep
Ethiopia	39.1^{o}E, 9.1^{o}N	1263	16.63	1131.2	Savanna	Cattle
Zimbabwe	31.1^{o}E, 20.2^{o}S	941	19.1	667.9	Savanna	Cattle
South Africa	29.2^{o}E, 30.5^{o}S	1203	13.6	795.4	Savanna	Sheep
Texas, US	99.9^{o}W, 32.8^{o}N	504	17.3	673.8	C3 grass	Goat
Kansas, US	98.8^{o}W, 38.4^{o}N	330	17.6	659.5	C4 grass	Cattle

Energy Intake and Expenditure

Metabolizable Energy Intake by Herbivores

Metabolizable energy (ME) is the energy remaining after urinary and gaseous energy resulting from fermentation are subtracted from the total digestible energy in the digestive system (Weiss 2016). The total metabolizable energy intake in the DLEM 3.0 is a function of forage intake and its digestibility, and is mathematically expressed based on Freer et al. (1997):

$$MEI_f = (17.2 \times d - 1.71) \times I_f \qquad (7)$$

Where,

MEI_f is metabolizable energy intake from forage (MJ)

I_f is forage intake (kg DM)

Equation (7) was estimated by regression based on 55 roughage feeds in Givens and Moss (1990), such that the expression (17.2 × d – 1.71) allows for the conversion of dry matter intake (Kg DM/day) to metabolizable energy (MJ/day). However, we did not attempt to quantify the metabolizable energy intake for supplemental feeds and milk in this study.

To obtain the amount of grass (Kg DM) necessary for daily energy intake, the intake energy (I_{daily}) is divided by the net grass energy content (MJ/Kg DM). Mathematically,

$$I_f = \frac{I_{daily}}{N_e} \qquad (8)$$

Maintenance Energy of Herbivores

In the DLEM 3.0, total energy costs is simulated as the sum of energy required for maintenance, grazing and travel (Freer et al. 1997). The metabolic energy required for maintenance (E_{daily}) is based on Corbett et al. (1985), which considers the effect of different feeding level on metabolic energy requirements. The ME_m is expressed as:

$$E_{daily} = \left(\frac{E_{metab}+E_{graze}}{K_m} + L_w \times MEI_f\right) \qquad (9)$$

Where,

E_{daily} is metabolic energy required for maintenance (MJ)

E_{metab} is basal metabolic energy required for each herbivore (MJ)

E_{graze} is energy required for grazing and distance walked by herbivores (MJ)

L_w is daily liveweight gain (0-1)

K_m = efficiency of use of ME for maintenance (0-1)

The basal metabolic energy requirement (E_{metab}) is a function of body weight, age, sex and milk intake and is expressed based on Freer et al. (2012):

$$E_{metab} = B_s \times S_s \times M_s \times W_s \times W^{0.75} \times \max(\exp(A_s \times age), 0.84) \qquad (10)$$

Where,

B_s is basal metabolism scalar for metabolic energy requirement (0-1)

S_s is effect of sex on metabolic energy requirement

M_s is effect of milk production on metabolic energy requirement

W_s is effect of weight on metabolic energy requirement (0-1)

W is weight of each age classes of herbivores (kg)

A_s is effect of age on basal metabolism (day^{-1})

age is age of herbivores (days)

The effect of sex on metabolic energy requirement (S_s) is obtained from Wheeler (2015). We used an S_s value of 1.075, assuming a 50:50 ratio of male and female herbivores.

The effect of milk production on metabolic energy requirement (M_s) is based on Freer et al. (1997) and is estimated as:

$$M_s = 1 + B_{milk} \times P_{milk} \tag{11}$$

Where,

B_{milk} is basal metabolism for milk intake (0-1)

P_{milk} is proportion of diet as milk (0-1)

Energy required for grazing is a function of distance walked by herbivores for grazing, which is reduced to zero, in case when herbivores are not grazing. Mathematically,

$$E_{graze} = C_c \times W \times I_f \times \left(C_e - DMD_f\right) + E_{move} \tag{12}$$

Where,

C_c is Chewing cost of herbivores (MJ/kg)

C_e is Chewing efficiency (0-1)

E_{move} is energy required for movement (MJ), and is expressed as:

$$E_{move} = E_h \times D_c \times W \tag{13}$$

Where,

E_h is energy cost for walking (MJ/km/kg)

D_c is distance covered (km)

The distance covered (D_c) depends on the steepness of the land (L_{steep}) and the amount of green and dead forage available for herbivores:

$$D_c = \begin{cases} L_{steep} \times \frac{\min\left(1.0, \frac{S_{thres}}{S_{actual}}\right)}{(W_c \times V_{living} + W_e)} & V_{living} \geq 100 \\ L_{steep} \times \frac{\min\left(1.0, \frac{S_{thres}}{S_{actual}}\right)}{(W_c \times V_{dead} + W_e)} & V_{living} < 100 \; and \; V_{dead} \geq 100 \\ 0 & V_{dead} < 100 \end{cases} \tag{14}$$

Where,

D_c is distance covered as its horizontal equivalent (km)

L_{steep} is steepness of the land on a scale of 1-2

S_{thres} is threshold stocking rate of herbivores (head/ha)

S_{actual} is actual stocking rate of herbivores (head/ha)

W_c is walking cost of herbivores (kg/km)

W_e is walking efficiency of herbivores (0-1)

Growth and Reproduction of Herbivores

In the DLEM 3.0, growth of herbivores is calculated at a daily time step as the difference between the amount of energy gained and the amount of energy lost by herbivores (Illius and O'Connor 2000b, Pachzelt et al. 2013). The net change in daily energy flux is further used to update the fat reservoir, which is given by:

$$\frac{df}{dt} = \frac{(I_{daily} - E_{daily})}{m} \tag{15}$$

Where,

m = metabolic coefficient for the conversion between energy (MJ/day) and fat (kg/day). The value of m is based on Blaxter (1989), such that m = 39.5 MJ net energy/kg for $I_{daily} < E_{daily}$ (catabolism) and m = 54.6 for $I_{daily} > E_{daily}$ (anabolism).

Daily change in fat (df/dt) in equation (15) is used to update the fat pool, which determines the overall body condition (B_{con}) of the herbivores.

$$B_{con} = \frac{F}{F_{max}} \tag{16}$$

Where,

F is total fat reserve during a year (kg)

F_{max} is maximum fat reserves for each age class of herbivores (kg)

For newly born offspring, the initial body fat (F) is set to 15% of the mature body fat (Pachzelt et al. 2013).

Body condition (B_{con}) in the previous year is then used to determine the number of offspring born in the current year. The number of newly born offspring is based on the number of mature herbivore and their body condition. Mathematically,

$$B_h = \frac{N \times p}{l * (1 + \exp(-b(Bcon - c)))} \tag{17}$$

Where,

B_h is birth rate of specific herbivores (numbers/year)

N is number or individuals in a mature class of animal in previous year (heads)

p is population maximum annual intrinsic rate of increase (proportion)

l is length of birth season (fraction of a year)

b,c are constants that control the effect of body reserves on reproductive rate (unitless)

The value of p in equation (17) is set to 0.8, which implies a male to female ratio of 1:4, with every female having the possibility of giving birth to one offspring. B_{con} is based on the net changes in body fat condition of mature age class of herbivores, such that a B_{con} of 0.3 would result in a breeding of 50% of the female while a B_{con} of 0.5 would result in a breeding of 95% of the female.

The length of birth season l allows to capture differences in breeding rates among different herbivores. In the absence of l, equation (17) assumes that all herbivores have the potential to reproduce only one offspring in a given year. However, to allow for birth rates to vary depending on specific herbivores, the birth rate function in equation (17) is divided by the length of breeding season (l), which is expressed in fraction of year. The l of 1.0 ensures that every female has the possibility of giving birth to one offspring during a year, while the l of 0.5 results in a birth of 2.0 offspring during a year.

Mortality

In the DLEM 3.0, we account for two potential causes of herbivore mortality. One is an annual mortality that occurs under normal conditions (base mortality). The other is mass herbivore mortality as a result of extreme climatic conditions such as summer drought and extreme winter (Begzsuren et al. 2004, Rao et al. 2015).

Base Mortality of Herbivores

The mortality of herbivores is predicted daily as a function of basal rate and body condition, which varies based on specific herbivore type (Freer et al. 1997, Pepper et al. 1999). The model assumes that there is a greater risk of death in herbivores, if the body condition is below a nominated threshold. The basal mortality rate is expressed based on Pepper et al. (1999):

$$MR_{base} = \begin{cases} M_{base} + 0.3 \times \left(1 - \frac{BC}{BC_{crit}}\right) & BC < BC_{crit} \;\&\; W_{daily} < 0.2\delta N \\ M_{base} & else \end{cases} \tag{18}$$

Where,

MR_{base} is basal rate of herbivore mortality (fraction)

M_{base} is basal mortality constant for specific herbivores (fraction)

W_{daily} is daily weight gain (kg)

BC is relative body condition, and is expressed as a ratio of base weight (kg) of herbivore to normal weight (kg) of herbivore

BC_{crit} is threshold body condition below which death is assumed to occur at a higher rate. BC_{crit} in the DLEM is expressed as:

$$BC_{crit} = 1 - 0.2 \times (1 + Z) \qquad (19)$$

Where,

Z is given by:

$$Z = min\left(1, \frac{N_w}{A}\right) \qquad (20)$$

Where,

N_w is normal body weight for each age class (kg)

A is mature body weight (kg)

The normal body weight (Nw) is expressed as a function of mass, age and weight at birth of specific herbivores and is given by:

$$N_w = A - (A - W_{birth}) \times \exp(-0.0157 \times \frac{age}{A^{0.27}})) \qquad (21)$$

Where,

W_{birth} is weight at birth (kg)

Climate Related Mortality of Herbivores

It has been suggested that climate has a direct effect on herbivore health, growth and reproduction, particularly during years of extreme events (Oba 2001, Tachiiri et al. 2008, Rao et al. 2015, Vitali et al. 2015). In the DLEM 3.0, we modeled herbivore mortality as a function of climatic conditions, which is based on seasonal (summer vs winter) precipitation in the form of rain or snow. We developed a scalar to first identify whether drought or extreme winter condition occur in a given year based on Batima (2006). The summer and winter scalar is expressed as:

$$S_s = \sum\left(\frac{T_s - \overline{T_s}}{\sigma_{Ts}}\right) - \sum\left(\frac{P_s - \overline{P_s}}{\sigma_{Ps}}\right) \tag{22}$$

$$S_w = \sum\left(\frac{T_w - \overline{T_w}}{\sigma_{Tw}}\right) - \sum\left(\frac{P_w - \overline{P_w}}{\sigma_{Pw}}\right) \tag{23}$$

Where,

S_s *and* S_w are scalar to identify summer drought or extreme winter condition in a given year, respectively. A value of S_s greater than zero indicates an occurrence of drought, while a value of S_w less than zero indicates extreme winter condition.

T *and* P are annual temperature and precipitation respectively

$\overline{T}$ *and* $\overline{P}$ are 30-year (1980-2009) average temperature and precipitation, respectively

σ_T *and* σ_P are standard deviation of temperature and precipitation

We then use a formulation based on Begzsuren et al. (2004), to implement mortality rates during drought and extreme winter year, separately.

$$MR_{clm} = \begin{cases} 26.11 - 0.13 \times prec_s & S_s > 0.0 \\ -3.45 + 0.49 \times prec_w & S_w > 0.0 \\ 16.9 - 0.1 \times prec_s + 0.35 \times prec_w & S_s > 0.0 \text{ and } S_w > 0.0 \\ 0 & S_s \leq 0.0 \; or \; S_w \leq 0.0 \end{cases} \tag{24}$$

Where,

MR_{clm} is climate related mortality expressed as percentage of individuals in each age classes

$prec_s$ is daily summer precipitation (mm)

$prec_w$ is daily winter snowfall (mm)

Methane emission from herbivores

Methane emission from herbivore is a function of daily gross energy expenditure, forage digestibility and liveweight of herbivore (IPCC 2007). Mathematically, we first calculate the gross energy requirement of herbivore based on daily net energy expenditure and the percentage of digestible energy in the diet:

$$GE = \frac{\frac{E_{daily}}{REM}}{\frac{DE\%}{100}} \tag{26}$$

Where,

GE is gross energy, MJ/day

E_{daily} is daily energy expenditure obtained from (9)

REM is ratio of net energy available for growth in a diet to digestible energy consumed

$DE\%$ is digestible energy expressed as a percentage of gross energy

We then calculate the methane emission factor for each herbivore category, which is then multiplied by the total number of herbivores to estimate total methane emission within each grid cell. Mathematically,

$$E_f = \frac{GE \times Y_m}{55.65} \tag{28}$$

Where,

E_f is emission factor (kg CH4/head/yr)

Y_m is methane conversion factor

55.65 is is the energy content of methane (MJ/kg CH_4)

It should be noted that equation (28) provides estimates of methane emission for mature herbivore types, which likely differs for lower age classes. In the DLEM 3.0, we obtain methane emission from small age classes by scaling the emission obtained for mature herbivore type as a function of their mature body weights for different herbivore types.

3.2.3 Modeling plant production and the feedback of herbivores

The representation of primary productivity in the DLEM is based on several previous studies (Farquhar et al. 1980, Collatz et al. 1991, Bonan 1996, Sellers et al. 1996) and are described in detail elsewhere (Tian et al. 2010a). Here we only describe the major plant production processes that affect herbivore dynamics and the feedback of herbivore to carbon, nitrogen and water cycles.

Primary production

The gross primary production (GPP) is modeled using a modified Farquhar's model (Farquhar et al. 1980), where the whole plant canopy is divided into sunlit and shaded layers. For each of the two layers, GPP (gC/m2/day) is calculated by scaling leaf level assimilation rates to the whole canopy. Mathematically,

$$GPP_{sun} = 12.01 \times 10^{-6} \times A_{sun} \times plai_{sun} \times dayl \times 3600 \qquad (25)$$

$$GPP_{shade} = 12.01 \times 10^{-6} \times A_{shade} \times plai_{shade} \times dayl \times 3600 \qquad (26)$$

$$GPP_{total} = GPP_{sun} + GPP_{shade} \qquad (27)$$

Where,

GPP_{sun} and GPP_{shade} are GPP of sunlit and shaded canopy, respectively (gC/m2/yr).

A_{sun} and A_{shade} are leaf level assimilation rates of sunlit and shaded canopy, respectively (µmol $CO_2/m^2/s$).

$plai_{sun}$ and $plai_{shade}$ are projected leaf area index of sunlit and shaded canopy, respectively (fraction).

dayl is daytime length (second) in a day.

12.01×10^{-6} is a constant to change the unit from µmol CO_2 to gram C.

The carbon assimilation rate is a minimum function of three limiting rates: a) photosynthetic enzyme (rubisco) limited; b) photosynthetically active radiation (light) limited; and c) photosynthetic product utilization (export) limited. In case of C4 species, the export limitation (c) refers to the Phosphoenolpyruvate (PEP) carboxylase limited rate of assimilation. Mathematically,

$$A = \min\left(w_c, w_j, w_e\right) \times Index_{gs} \tag{27}$$

$$w_c = \begin{cases} \dfrac{(c_i - \Gamma_*)V_{\max}}{c_i + K_c(1 + o_i / K_o)} & for\ C_3\ plants \\ V_{\max} & for\ C_4\ plants \end{cases}$$
$$w_j = \begin{cases} \dfrac{(c_i - \Gamma_*)4.6\phi\alpha}{c_i + 2\Gamma_*} & for\ C_3\ plants \\ 4.6\phi\alpha & for\ C_4\ plants \end{cases}$$
$$w_e = \begin{cases} 0.5V_{\max} & for\ C_3\ plants \\ 4000V_{\max}\dfrac{c_i}{P_{atm}} & for\ C_4\ plants \end{cases} \tag{28}$$

Where,

w_c, w_i *and* w_e are rubisco, light and export (for C3) or PEP carboxylase (for C4) limited assimilation rates, respectively

c_i is internal leaf CO_2 concentration (Pa)

*o*i is O_2 concentration (Pa)

Γ_* is CO_2 compensation point (Pa)

K_c and K_o are Michaelis-Menten constants for CO_2 and O_2, respectively

α is quantum efficiency

$\o$ is absorbed photosynthetically active radiation (watt/m^{-2})

V_{max} is maximum rate of carboxylation, which varies as a function of temperature, foliage nitrogen concentration, and soil moisture (Bonan 1996) and is expressed as:

$$V_{\max} = V_{\max 25} a_{v\max}^{\frac{T_{day}-25}{10}} f(N) f(T_{day}) \beta_t \tag{29}$$

Where

V_{max25} is rate of carboxylation at 25^{o}C

a_{vmax} is temperature sensitivity parameter

$f(Tday)$ is function of temperature related metabolic processes

$f(N)$ is adjustment of photosynthetic rate for foliage nitrogen

β_t is soil moisture and low temperature effects on stomatal resistance and photosynthesis (0-1)

The net primary production (NPP) in the DLEM is estimated as the net carbon gain after carbon losses through plant respiration and expressed as:

$$NPP = GPP - Mr - Gr \tag{30}$$

Where,

NPP is net primary production (gC/m2/day)

Mr is maintenance respiration of plants (gC/m2/day)

Gr is growth respiration of plants (gC/m2/day)

In the DLEM, Gr is calculated by assuming that the fixed part of assimilated C will be used to construct new tissue (for turnover or plant growth). During these processes, 25% of assimilated carbon is supposed to be used as growth respiration. However, maintenance respiration is a function of surface air temperature and biomass nitrogen content and is expressed as:

$$Mr_i = rf \times R_{coeff} \times N_i \times f(T) \tag{31}$$

Where,

i is carbon pool of different plant parts including leaf, sapwood, fineroot and coarseroot

Mr_i is maintenance respiration (gC/m2/day) of different pools

rf is growing season index with 0.5 indicating non-growing season and 1.0 indicating growing season

R_{coeff} is plant functional type specific respiration coefficient

N_i is nitrogen content (gN/m2) of vegetation pool i

The aboveground NPP (g C/m^2/day) in the DLEM 3.0 is estimated as a ratio of aboveground carbon pools to the total carbon pools and is expressed as:

$$ANPP = \frac{leafC + sapwoodC + reprodC + heartwoodC}{leafC + sapwoodC + reprodC + heartwoodC + rootC} \times NPP \qquad (32)$$

The ANPP calculated in equation 32 represent the consumable forage (*Vconsume*) for herbivores explained in section 2.2.1.2.

Herbivore impacts on grassland/savannah ecosystems

The impact of herbivores on carbon, nitrogen and water cycles is simulated similar to our previous study (Dangal et al. 2016) as a function of relative supply and demand of forage resources at a daily time step. The maximum dry matter demand per unit area is dependent on the number of herbivore and the amount of food required by herbivore on a daily basis and is estimated as:

$$C_{demand} = 0.05 \times D_x \times G_I \qquad (33)$$

Where,

C_{demand} is the maximum amount dry matter required by herbivores (gC/day)

D_x is satiation consumption rate (2.4 kg dry matter/day) expressed in per unit of sheep

G_I is herbivore intensity expressed in sheep units/ha

0.05 is factor to convert kg/ha to gC/m2/day

The demand of forage by herbivore is restricted by the amount of forage produced per unit area. Thus, the dry matter supply is modeled as a function of grazing efficiency and the amount of forage available from a unit area of land. Mathematically,

$$C_{supply} = 0.7 \times G_e \times (C_{leaf} + C_{stem} + C_{reprod}) \quad (34)$$

Where,

G_e is grazing efficiency expressed in ha/day/sheep. The grazing efficiency is assumed to be 0.011 ha/day/sheep (Seligman et al. 1992b)

C_{leaf}, C_{stem} *and* C_{reprod} are carbon in leaf, stem and reproduction pool, respectively.

Combining equation (33) and (34), the daily impact of herbivore on primary production is estimated as:

$$Intake_{daily} = fmin\,(C_{demand}, C_{supply}) \quad (35)$$

The biomass consumed by herbivores (*Hc*) is then further separated 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 (Dangal et al. 2016).

3.2.4 Model parameterization and calibration

In this study, we parameterized and calibrated both vegetation and herbivore components of the model (Table 3.1). Based on existing and previous studies, we first determined the reasonable range of key model parameters that control the growth and productivity of both vegetation (White et al. 2000) and herbivores (Freer et al. 1997, Illius and O'Connor 2000b, Pachzelt et al. 2013). Within these ranges, we allow DLEM parameters to vary such that the parameters were optimized to fit the simulated carbon, nitrogen and water fluxes with observation for specific plant functional types (PFTs). Similarly, in case of herbivores, the parameters were assumed to be optimized when the simulated herbivore numbers are close to observation for specific herbivore types. During the start of simulation, we assumed that the total number of herbivores for each cohort is evenly distributed across all the age classes. The DLEM, however, updates the number of herbivores in each class annually assuming that the small herbivore has the maximum of three age classes, while the large herbivore has the maximum of four age classes.

3.2.5 Simulation protocol

Input datasets

The model input data include daily climate datasets (daily mean-, maximum- and minimum-temperature, daily precipitation), monthly atmospheric CO_2 concentrations, annual land cover and land use (LCLU) maps, nitrogen deposition (Dentener 2006), tropospheric ozone concentration (Felzer et al. 2004), soil properties (texture, pH, and bulk density) and topographical information (e.g., elevation, slope and aspect). Daily climate data at our study sites were developed as follows: In Mongolia, we used site level monthly climate data from National Statistics of Mongolia, Institute of Meteorology and Hydrology. These monthly climate data were allowed to follow the daily precipitation pattern based on CRUNCEP by restricting the total precipitation during a month based on monthly meteorological observation. In Africa, we extracted daily climate data for the sites based on CRUNCEP global datasets. In the United States, we downloaded daily meteorological data from NOAA National Centers for Environmental Information (https://www.ncdc.noaa.gov). LCLU map for site level was extracted from the global LCLU maps, which was constructed by combining Synergetic Land Cover Product (SYNMAP) (Jung et al. 2006) and HYDE 3.1 land use data (Klein Goldewijk et al. 2011). Monthly atmospheric CO_2 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, bulk density were extracted from Global Soil Data Task (www.daac.ornl.gov), site level elevation, slope, and aspect were extracted from Global 30 Arc-Second Elevation product (GTOPO30) (https://lta.cr.usgs.gov/GTOPO30).

Model simulation and implementation

The model simulation follows a three-step procedure: an equilibrium run, a spin-up, and a transient simulation. The model simulation begins with an equilibrium run driven by a 30-year (1980-2009) average climatic condition and 1980 levels of atmospheric CO_2 concentration and vegetation cover, assuming no herbivores exist in the system. The equilibrium run is carried out for the maximum of 10,000 years or until the net carbon exchange between the atmosphere and the site is less than 0.1 g C m^{-2}, the change in soil water pool is less than 0.1 mm, and the change in total nitrogen content is less than 0.1 g N m^{-2} during two consecutive 20 years. The purpose of the equilibrium run is to get the initial condition for the spin-up and transient simulations. After the model spin-up, we carry out a transient simulation using daily climate data, monthly atmospheric CO_2 concentration, and time-series LCLU maps.

For the simulation of herbivore population dynamics in Mongolia, we developed a scalar that accounted for anthropogenic changes associated with policy shifts (Chen et al. 2015a). After the collapse of former Soviet Union in the early1990s, Mongolia transitioned to private herd ownership, which resulted in a dramatic increase in herbivore populations (Johnson et al. 2006). At present, 95% of herbivores are privately owned with the largest increase in the number of sheep and goat due to rapid growth of cashmere industry that provides high economic return (Arulpragasam et al. 2004, Berger et al. 2013). In the DLEM 3.0, the transition from central to market economy is represented by developing a scalar, which accounts for the rapid increase in number of herbivores and changes in herd composition during the post-Soviet Union period. The scalar is derived as a ratio of 30-year average (1961-1990) herbivore numbers to annual herbivore numbers during the market economy to account for changes in herbivore dynamics following economic transition in Mongolia. In the DLEM 3.0, the scalar is directly applied to the herbivore pool. Applying a similar approach, Shabb et al. (2013) used different parameters developed through optimization to simulate herbivore populations by separating the study area into seven different time periods during 1970-2011. The time periods were categorized into socialist, post-socialist, extreme winter condition (*dzud*), and drought years, such that each time period assumed a separate set of parameters to simulate herbivore numbers. Meanwhile, to make the model applicable at different scales, we developed a regional parameter in Mongolia that accounts for the effect of policy shifts and economic transitions on Mongolian herbivores. However, in Africa and the United States, the scalar that accounts for policy shifts and economic transitions was set to 1.0.

In this study, we specifically performed two different simulations. The first simulation was carried out in the absence of feedback of herbivores to ecosystems in order to quantify the evolution of herbivore in response to climate, forage availability and local environmental conditions. In the second simulation, we introduced the feedback of herbivores to terrestrial ecosystems to quantify the effect of herbivores on carbon and water cycles at the study sites.

3.2.6 Model Evaluation

Model evaluation in the DLEM 3.0 follows a two-step procedure: 1) evaluation of simulated carbon pools and fluxes and 2) evaluation of simulated herbivore density against observations at the study sites. Our study sites in Mongolia, Ethiopia, South Africa, Zimbabwe and the United States were dominated by C3 grass, C4 grass and savannas (Table 3.2). The detailed description of the study sites used to evaluate carbon fluxes is available in supplementary material (Text S1). The comparison of simulated carbon fluxes with observation was performed in the absence of herbivory. After the evaluation of carbon fluxes against observations, we simulated the evolution of herbivores as a function of DLEM-estimated ANPP and prevailing climatic and environmental conditions. The simulated herbivore density was then compared with observations at the study sites. The detail description of study sites used to evaluate herbivore populations performance is available in supplementary material (Text S2).

To quantify the CH_4 fluxes from the fermentation of different livestock, we first estimated the CH_4 emission factor for each livestock category, which was then multiplied by the total number of livestock at the specific sites to obtain the net CH_4 emission. While evaluating the CH_4 emission from different livestock category, we compared emission factor estimated for each livestock category against IPCC tier I emission factor in Mongolia, Africa and the United States (Table S1).

Evaluation of DLEM-simulated carbon fluxes

In Inner Mongolia, DLEM-simulated ANPP showed a good agreement with observed ANPP (observed = 1.11 × simulated; $p\text{-value} < 0.05$; $r = 0.9$). In Kansas, comparison of daily gross primary production (GPP), ecosystem respiration (ER) and net ecosystem productivity (NEP) are in reasonable agreement with EC measurements ($r = 0.2\text{-}0.9$; $p\text{-value} < 0.05$). Overall, DLEM over-estimated daily GPP and ER by 4% and 4.6%, respectively. In particular, DLEM-simulated ER was not able to capture the low respiration of 2011, likely due to variation among root classes not adequately represented in the model. For example, Thorn et al. (2015), at the Konza Prairie site, found that PnET-CN over-estimated the contribution of root respiration to ER and associated that to metabolic variation among different root classes. In the DLEM, we broadly categorize roots into two major classes (fine and coarse roots). It is possible that DLEM over-estimates the contribution of roots to ecosystem respiration likely due to different root classes not included in the model. Likewise, DLEM-simulated a daily NEP close to zero, compared to observations of 0.3 gC/m2/day. Overall, DLEM tended to under-estimate NEE during high precipitation years (2009, 2010 and 2011). Our results showed that during high precipitation years, increased runoff and leaching enhanced nitrogen limitation associated with a decrease in plant available nitrogen (LeBauer and Treseder 2008). Burke et al. (2002) found that nitrogen, particularly in the form of nitrates is vulnerable to leaching with maximum leaching rates during wet seasons. Nitrogen limitation was the major factor that resulted in a NEP close to zero at Konza Prairie.

In Africa, we found both simulated GPP and NEP to be significantly correlated with observations ($r = 0.51$ for GPP and $r = 0.45$ for NEP; $p\text{-value} < 0.05$). Overall, DLEM tended to under-estimate daily GPP by 7.7%, but over-estimate NEP by 0.38 gC/m2/day when compared to observations. The over-estimation of NEP by 0.38 gC/m2/day is due to some of the factors not included in the model. For example, fire and herbivory are two important factors that drive carbon fluxes in savannas ecosystems. At Skukuza site, large mammalian herbivore consists of 14 species, which translates into a herbivore flux (both from respiration and decomposition of dung) of 0.03 gC/m2/day (Archibald et al. 2009). However, we did not include the effect of different herbivores while simulating carbon fluxes because data on different herbivore types and their exact number were not available. Other important factor not included is fire, which releases carbon at a rate of 0.11 gC/m2/day in Skukuzu (Archibald et al. 2009).

Evaluation of DLEM-simulated herbivore density

DLEM simulations tend to agree well with observations at both spatial (Figure 3.3) and temporal scales. In general, DLEM simulation was able to capture the mean herbivore numbers across all sites in Mongolia, Africa and North America ($r = 0.84$; observed = 1.01 × simulated; p-value < 0.05). In Mongolia, the simulated herbivore density showed a good agreement with observations ($r= 0.83$; observed = 1.07 × simulated; p-value < 0.05). The simulated herbivore density showed a tendency of under-prediction by 12%. The slight under-prediction is likely due to how mortality related with extreme winter (*dzud*) is included in the model. DLEM simulates mortality associated with *dzud* as a function of snow accumulation and winter temperatures, but does not take into account how different classes of *dzud* affect herbivore mortality. For example, Rao et al. (2015) identified five different types of *dzud* (white, black, iron, storm and combined), which likely affect herbivore mortality at different rates. Instead, we simulated mortality as a function of snow accumulation, with higher snow resulting in high mortality (Begzsuren et al. 2004). But, we did not attempt to simulate different types of *dzud*, which would likely result in different mortality rates of herbivores.

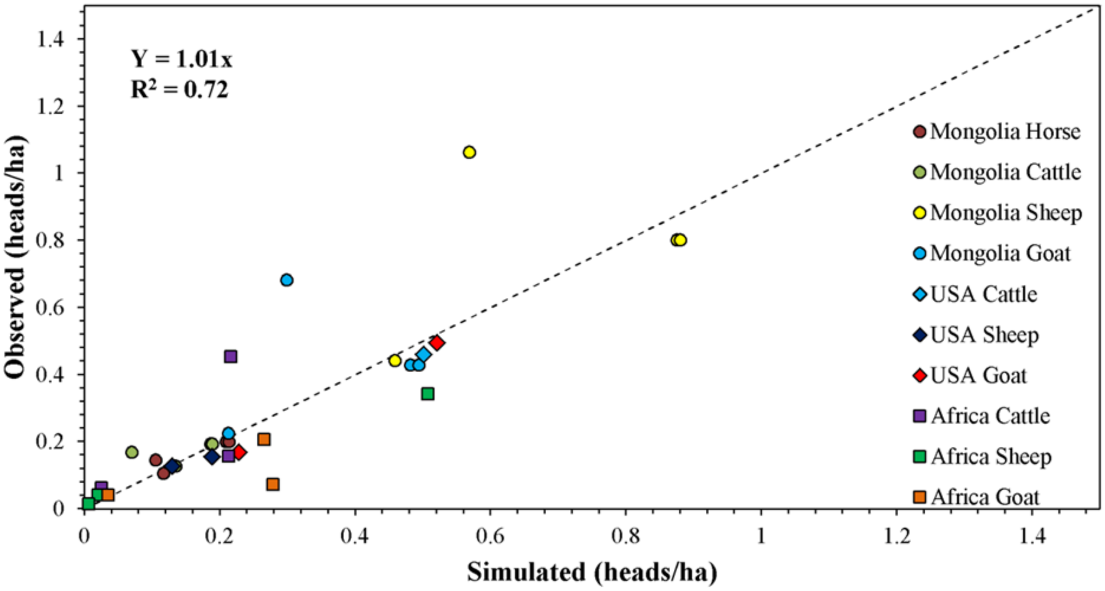


Figure 3-3 Comparison of simulated vs observed population of horse, cattle, sheep and goat across all sites in Mongolia, the United States and Africa

In the United States, overall model simulated results were in reasonable agreement with observations (r = 0.99; observed = 0.92 × simulated; p-value < 0.05), with a slight over-prediction (11.2%) This is likely due to reported decline of sheep density in Texas and Kansas. Although climatic condition and forage productivity were favorable at the study sites, which resulted in an increase in the number of cattle and goat, we found no link between climate and sheep population in the United States. Previous study indicated that sheep number in Texas and Kansas has declined by 61% and 59%, respectively since 1975 (Jones 2004). Decline in sheep number has been attributed to low demand of wool products from sheep due to availability of less expensive synthetic fibers (Jones 2004). In the current version of DLEM, we have not included how demand and supply of wool products from sheep could affect sheep productivity in the United States.

In Africa, however, model simulated mean herbivore density show a tendency of over-prediction (observed = 0.77 × simulated), but simulated herbivore density was not significantly different from observations (r= 0.65, p-value < 0.05). DLEM showed a tendency of over-prediction by 11.3%. This over-prediction is because we did not included predation (Ogada et al. 2003, Patterson et al. 2004) in the model, which has been suggested to reduce herbivore numbers annually by up to 2.4% in south-eastern Kenya (Patterson et al. 2004), 5% in Zimbabwe's community lands (Butler 2000) and 8% in South Africa (Van Niekerk 2010).

To account for how market/policy changes have altered herbivore density in Mongolia, we simulated herbivore dynamics with and without the market/policy changes. Our results show that simulated herbivore density after the inclusion of policy changes were closer to observations compared to simulation without policy changes (Figure 3.4). We also found that the simulated herbivore density with policy changes were not significantly different from simulation without policy changes for sheep, cattle and horse. However, we found a significant difference in goat density between the simulation with and without policy changes (p-value < 0.05), indicating that policy changes strongly affect the abundance of herbivores. Overall, our results show that policy changes resulted in an increase in horse, cattle, sheep and goat density by 14%, 8%, 6% and 75%, respectively.

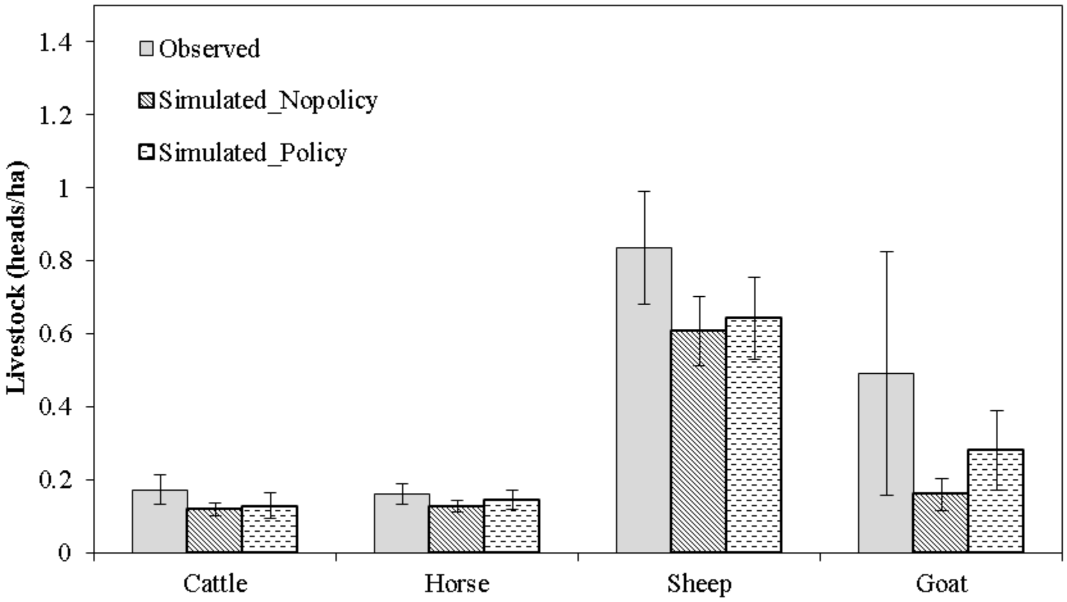


Figure 3-4 Comparison of simulated vs observed population of different herbivores with and without policy changes in Mongolia

3.3 Results:

3.3.1 Herbivore response to resource availability and climate change:

Our results show that the temporal change in mean herbivore density across sites was significantly correlated with both annual ANPP and growing season precipitation (p-value < 0.05; Figure 3.5). Changes in annual ANPP and growing season precipitation explained 43% and 21% of the variation in herbivore density during 1980-2010 (Figure 3.5b, 3.5d), indicating that both forage availability and climatic conditions were an important regulator of the abundance of herbivores at the study sites. We further separated the changes in herbivore abundance as a function of annual precipitation gradient across all sites, and found that at low annual precipitation totals, changes in growing season precipitation and ANPP explained 48% and 53% of the variation in herbivore density. However, at higher annual precipitation, ANPP had a significant influence on herbivore density, accounting for 82% of the variation.

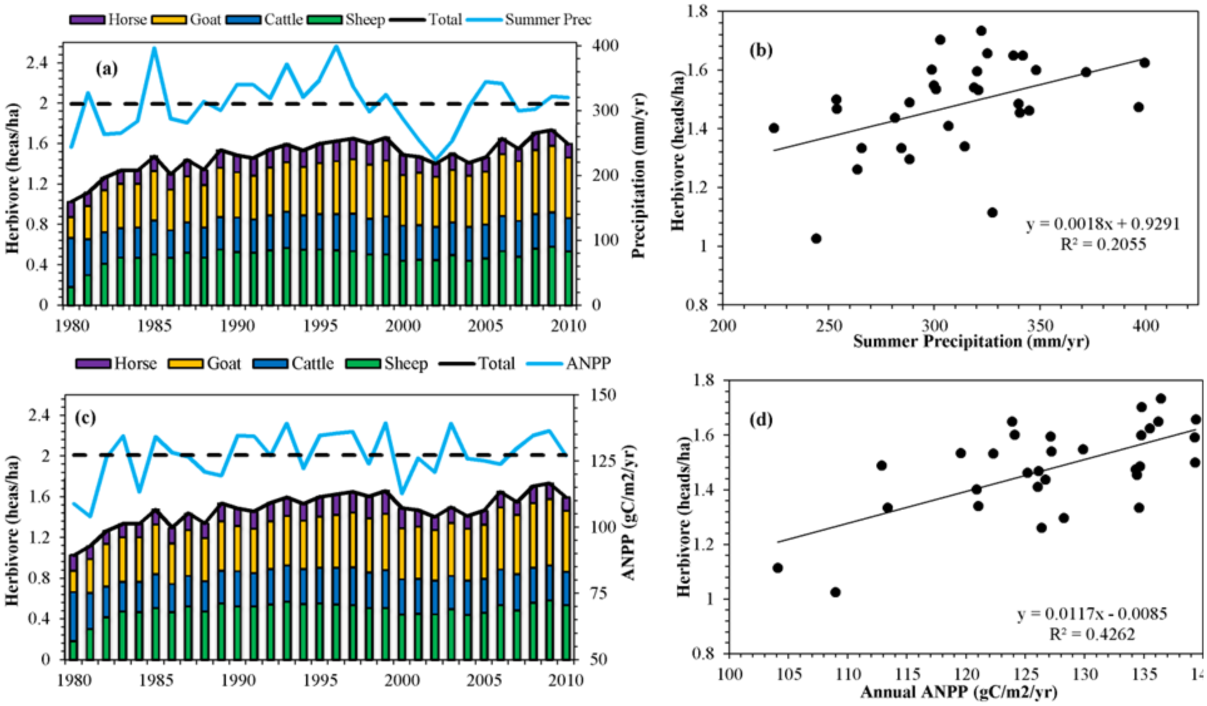


Figure 3-5 Temporal pattern of herbivore vs precipitation change (a) and herbivore vs ANPP change (c), and one-to-one comparison between herbivore and growing season precipitation (b) and herbivore and annual ANPP (d)

3.3.2 Herbivore response to extreme climatic conditions

In Mongolia, we found that the herbivore experienced a highest mortality of 24.7% and 27.3% during drought only and drought and *dzud* years (Figure 3.6a). During *dzud* years, however, the mortality was only 8.6%. The temporal pattern of total mortality during 1980-2010 indicate that the total herbivore mortality in Mongolia has been increasing significantly at a rate of 0.009 heads/ha (p-value < 0.05; R^2 = 0.34; Figure 3.7). In 2000-2002, our results suggest a consecutive drought and *dzud* year at all sites, while in 2007 and 2010, our results indicate that there was a drought only, and drought and *dzud* year, respectively. At the study sites in Africa and North America, we only analyzed the effect of drought on herbivore density because all sites had a mean winter temperature higher than 0^{o}C. Our results show that drought resulted in the mean mortality of 24.7% of the herbivores, while the nominal mortality was 3.1% (Figure 3.6b). During 1980-2010, we did not find a significant increase in herbivore mortality in Africa and North America (p-value = 0.12).

3.3.3 Herbivore feedback to carbon and water fluxes

We found that the introduction of herbivory feedback to ecosystem resulted in a significant decline in ANPP and Rh by 12.4% and 12%, respectively (p-value < 0.05; Figure 3.8a and 8b). When investigating NEP, we found that herbivory resulted in an increase in NEP by 17%, although the effect was not statistically significant (p-value = 0.72; Figure 3.8c). Similarly, herbivore did not significantly alter ET across our study sites (p-value = 0.53; Figure 3.8d), largely due to increase in evaporation and decrease in transpiration following herbivory.

3.3.4 Herbivore effect on CH_4 fluxes through enteric fermentation

Across different livestock category, cattle contributed to the largest source of CH_4 emission (61.7%), followed by horse (24.8%), sheep (7.1%) and goat (6.5%) (Figure 3.9). Overall, CH_4 emission from the herbivores did not increase significantly due to control of continuous increase in herbivore numbers during drought and *dzud* year, particularly in Mongolia. Similarly, herbivore density in the United States did not increase significantly, resulting in no significant effect on CH_4 emission. However, in Africa, we found a significant increase in CH_4 emission at a rate of 0.05 kg CH_4/ha/yr (p-value < 0.05; R^2 = 0.37).

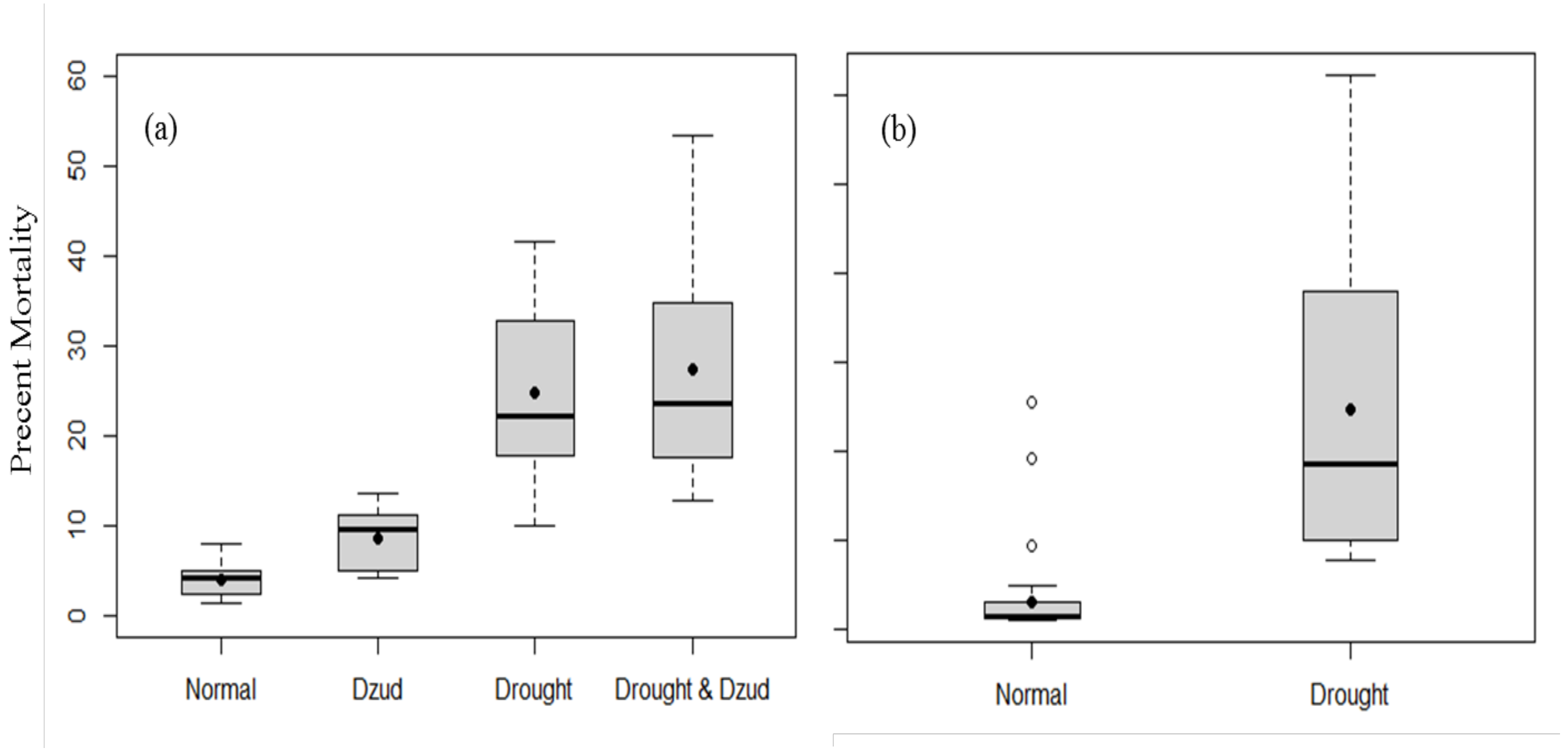


Figure 3-6 Effect of summer drought and winter *dzud* on herbivore mortality (a) and effect of summer drought on herbivore mortality in the United States and Africa (b) estimated as the percentage of total herbivores

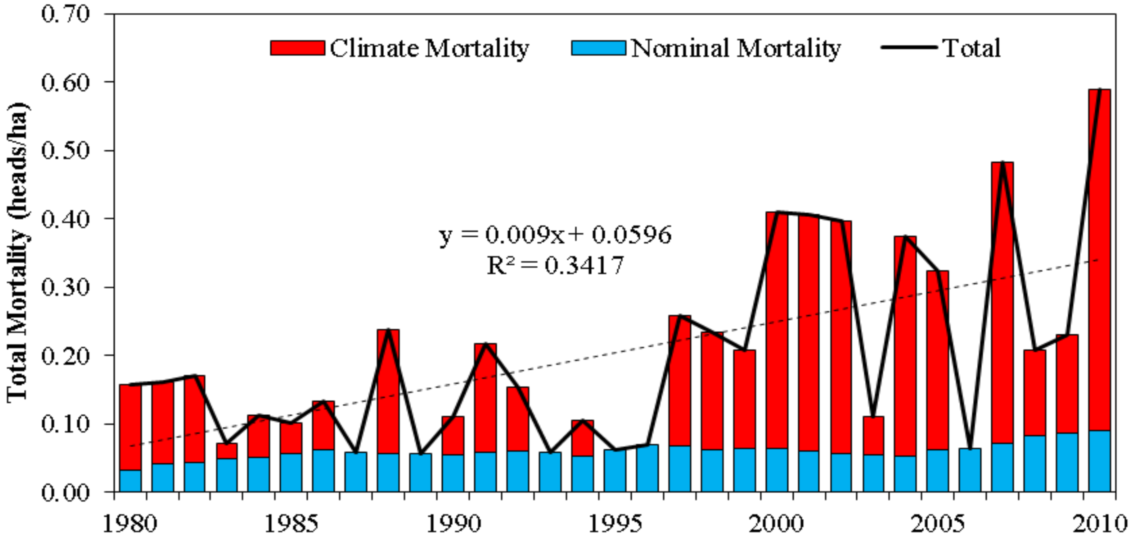


Figure 3-7 Temporal pattern of total herbivore mortality (nominal + climate) in Mongolia during 1980-2010. The equation represents the annual decline (heads/ha/yr) associated with combined (nominal + climate) mortality.

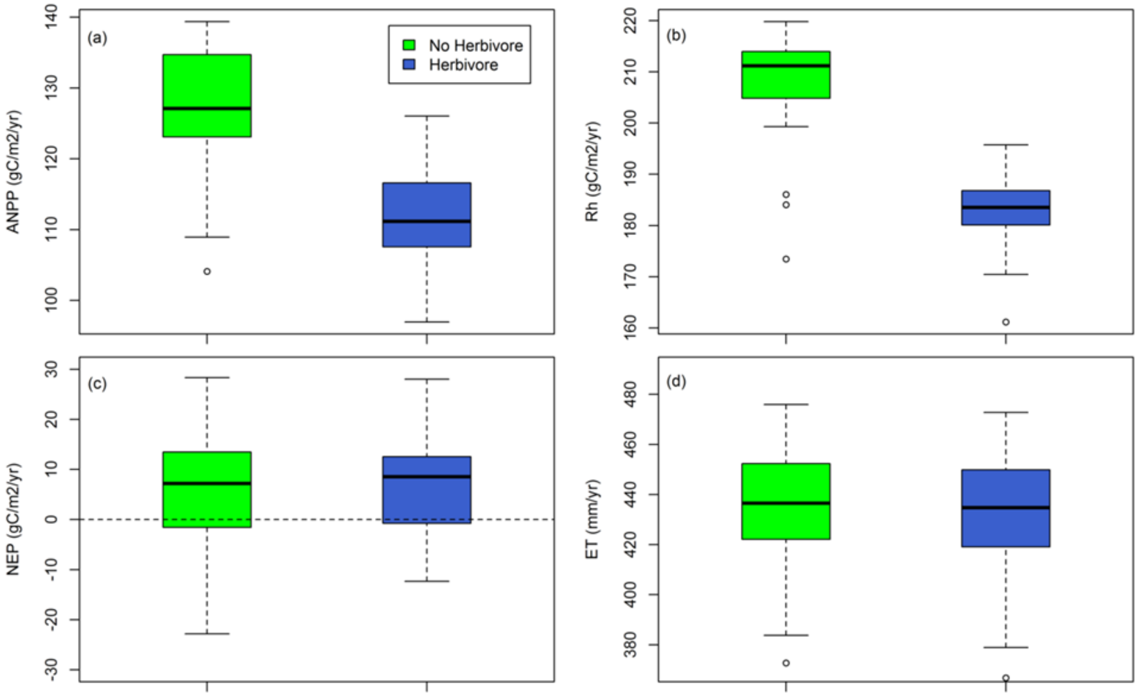


Figure 3-8 Effect of herbivores on ANPP (a), Rh (b), NEP (c) and ET (d) across all sites in Mongolia, Africa and North America

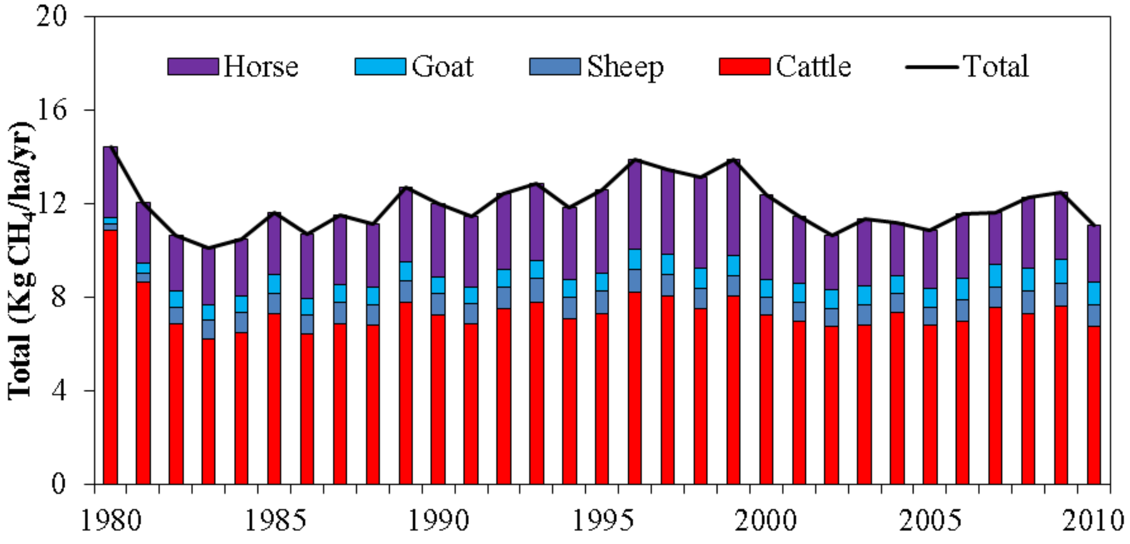


Figure 3-9 Methane emissions from herbivores across all sites in Mongolia, Africa and North America

3.4 Discussion

3.4.1 Simulation of herbivore density in Mongolia, Africa and North America

We implemented a global land ecosystem model by incorporating herbivore population dynamics to examine the response of herbivores to climate and other environmental factors, and their feedbacks to the climate system. In the model, we simulated herbivore density as a function of initial herbivore numbers, forage availability and digestibility, forage demand, herbivore energetics, natality and mortality. Herbivore cohorts are separated as a function of body weight and their respective intake constant, which determines the maximum rate of intake for different herbivores (see equation 1). Actual daily intakes for respective herbivore are then predicted as a saturating function of modeled aboveground biomass. The daily growth of herbivores is simulated as a difference between energy intake and energy expenditure, which determines the amount of fat reserves. Energy costs include basal metabolic expenditure made energy maintenance (section 2.2.2). The fat reserve pool is updated daily, which is further used to determine the birth rate of respective cohorts. Birth is assumed to occur only once in a year, but is scaled as a function of length of birth season (see equation 17) of the respective cohorts such that sheep and goat are assumed to give birth to more individual compared to large herbivores such as horse and cattle. Within each herbivore cohort, we assumed a maximum of three age classes for small herbivores (goat and sheep) and four age classes for large herbivores (cattle and horse). The newly born individuals are assumed to the first age classes with a maximum fat depot.

The population dynamics model shown here captured the annual variation in herbivore density reasonably well across all sites in Mongolia, Africa and North America (Figure 3.3). We did not expect the model to exactly reproduce the observations because we only simulated herbivore density as a function of climate and environmental conditions, but did not include other factors such as predation and diseases in Mongolia and market-policy changes, demand and supply of herbivore products, predation and diseases in Africa and North America. For example, we found that transition from central to market economy in 1993 resulted in a rapid increase in herbivore numbers in Mongolia (Johnson et al. 2006), while low demand of wool products due to increased availability of synthetic fibres (Jones 2004) resulted in a decline in sheep numbers in the United States.

To account for the shortcomings associated with market-policy changes, we tested the effect of transition from central to market economy in Mongolia to look at how great the effect of market/policy changes will have on herbivore numbers (see section 2.5.2). Our results further indicate that the transition from central to market economy resulted in an increase in horse, cattle, sheep and goat density by 14%, 8%, 6% and 75%, respectively. The largest increase in goat numbers was due to increasing demand of cashmere (Berger et al. 2013). Unlike the goats, market economy did not have a significant influence on cattle, sheep and horse, although it had a small positive effect on their numbers. Our study, therefore, indicated that market/policy changes have the potential to significantly influence herbivore density, but such effect are not only region specific but also depend on the demand/supply of type of herbivore.

3.4.2 Herbivore response to climate and forage availability

The response of herbivores to climate change or forage availability has been a subject of ongoing debate over the last few decades (Fernandez-Gimenez and Allen-Diaz 1999, Illius and O'connor 1999, Sullivan and Rohde 2002, Vetter 2005). This debate focuses on two important aspect of rangeland ecology, i.e., density-dependent interactions and controls of abiotic factor in determining herbivore size, reproduction, and mortality. In areas with predictable annual rainfall, herbivore densities are regulated by forage availability, with increased competition for resources leading to reduction in herbivore size and productivity (Illius and O'Connor 2000b). But, in areas with high rainfall variability, herbivore density is driven by rainfall through its direct effect on resource availability (Ellis and Swift 1988). Our simulated results indicated that at low precipitation totals, both ANPP and climate are important regulators of herbivore density, which accounted for 48% and 53% of the variation in herbivore density, respectively. However, at high precipitation totals, the influence of ANPP became more important, explaining 82% of the variation in herbivore density. Our results thus support both equilibrium (resource dependent) and non-equilibrium (rainfall dependent) processes in determining herbivore density at the study sites, indicating that even in areas with low precipitation totals and higher inter-annual variations, the importance of available resources cannot be neglected.

3.4.3 The role of extreme events on herbivore mortality

Extreme events such as maximum temperatures and drought can either result in mortality of herbivore or lead to reduction in their productivity through adjustment in metabolic rate to cope with maximum temperatures (Coulson et al. 2001, Nardone et al. 2010, Walthall et al. 2013). Climate related mass mortality of herbivores has been strongly linked to summer droughts in Mongolia, Africa and the United States (Nardone et al. 2010, Key et al. 2014, Kgosikoma and Batisani 2014, Megersa et al. 2014, Rao et al. 2015). Similarly, extreme winter condition has also been linked to mass herbivore mortality, particularly in countries like Mongolia (Begzsuren et al. 2004, Fernandez-Gimenez et al. 2012b, Rao et al. 2015). Winter weather disasters associated with deep snow and severe cold makes forage resources inaccessible, which increases the risk of herbivore mortality (Rao et al. 2015). But mortality could vary depending on herbivore types, their feeding behavior and how quickly they can recover from extreme winter condition. In the DLEM 3.0, drought related herbivore mortality is a function of summer precipitation. If summer precipitation is below a certain threshold precipitation, mortality associated with drought is assumed to occur in the model. Similarly, winter weather related mortality is a function of winter snow accumulation. If the winter snow accumulation is above a certain threshold, mortality related to extreme winter conditions is implemented.

In Mongolia, we found that both summer drought and extreme winter conditions could lead to a mean and maximum mortality of 27% and 53% of the total herbivores, respectively. In Africa and the United States, summer drought could lead to a mean and maximum mortality of 25% and 62%, respectively. Our result is consistent with previous studies, which report that the consecutive drought and extreme winter (*dzud*) event of 1999-2002 had resulted in a mass mortality of 30% of the herbivores in Mongolia (Fernandez-Gimenez et al. 2012b). The highest mortality rates during consecutive drought and *dzud* event is because prior summer drought and upcoming winter temperatures, which determines snow accumulation, have been linked to intensifying mortality rates (Begzsuren et al. 2004, Rao et al. 2015). Similarly, high mortality rates of cattle population in the range of 37-42% has been reported in semi-arid Ethiopia, during drought years (Desta and Coppock 2002, Alemayehu and Fantahun 2012). In United States, decrease in herbivore productivity and increase in mortality rates due to increasing heat waves and maximum temperatures have been reported (Nienaber and Hahn 2007, Key et al. 2014).

3.4.4 Herbivore feedback to carbon and water fluxes

It has been recognized that herbivores have a substantial impact on the flow of energy and nutrients (McNaughton et al. 1997, Bardgett and Wardle 2003, Augustine and McNaughton 2006), but the magnitude and direction of this effect vary widely across ecosystems (Milchunas and Lauenroth 1993, Augustine and McNaughton 1998). In many ecosystems, herbivore has been found to reduce ANPP, but there are also report of an increase in ANPP following herbivory (McNaughton 1979, Milchunas and Lauenroth 1993). The differences among studies are likely due to differences in herbivore density and how they affect litter inputs and nutrient cycling in different ecosystems (Asner et al. 2004). For example, Irisarri et al. (2016) found that doubling grazing intensity resulted in a reduction in ANPP by 25%, while our results indicate an overall reduction in ANPP by 12%. Similarly, exclosure experiment in Mongolia, Africa and the United States has indicated that herbivore reduce ANPP in areas with low rainfall, regardless of nutrient availability (Augustine and McNaughton 2006, Schönbach et al. 2011, Irisarri et al. 2016), because moisture limitation is an important determinant of plant production in such ecosystems (Dangal et al. 2016). Our results are consistent with the findings that herbivore has a negative impact on ANPP, but the magnitude of this impact largely depends on the density and type of herbivores and the ecosystem considered.

Likewise, our results also indicated that herbivore reduces Rh by 12% across the study sites. In semiarid grasslands, Kang et al. (2013) found that herbivory resulted in a significant reduction in Rh by 33%, which is higher than our estimate. Kang et al. (2013) used a moderate herbivore density to quantify the effect of grazing on Rh, while we used a dynamic approach to simulate herbivore density and its effect on Rh. The reduction in Rh in the DLEM is due to reduced litter input (Savadogo et al. 2007), which has been indirectly linked to increase soil temperature and evaporation, which could suppress soil organic matter decomposition (Raiesi and Asadi 2006, Piñeiro et al. 2010). In addition to reduction in litter pools, herbivore can reduce canopy photosynthesis and slow down the translocation of carbon to the rhizosphere resulting in an overall reduction in annual soil respiration by 18% (Bremer et al. 1998). The DLEM 3.0 accounts for changes in LAI following herbivory, which ultimately drives canopy photosynthesis. Also, changes in allocation of carbohydrates occur due to grazing induced reduction in canopy photosynthesis, which affect Rh at the study sites.

Net ecosystem productivity is an essential component of the carbon cycle, which determines whether an ecosystem is a source or a sink of atmospheric CO_2 (Law et al. 2000). The change in NEP following herbivory depends on several factors such as soil water content, soil temperature and soil properties (Potts et al. 2006, Zhao et al. 2011), and biomass and litter inputs including other vegetation characteristics (Frank 2002, Risch and Frank 2006). Our results indicated that herbivory resulted in an increase in NEP by 17%, but it was not statistically significant. In a recent study in semiarid steppe, Kang et al. (2013) found that moderate grazing increased NEP significantly shifting the ecosystem from negative to positive carbon balance. This was likely due to a slight increase in GPP combined with a significant reduction in Rh. Meanwhile, other studies report no significant effect of herbivory on NEP (Lecain et al. 2000, 2002, Hou et al. 2016), although the general trend was an increase in NEP due to reduction in ecosystem respiration, open canopy structure and the presence of young, photosynthetic leaves that enhances carbon uptake (Owensby et al. 2006). Our study is consistent with the finding that decrease in Rh is responsible for an increase in NEP, but our results also showed a significant decrease in ANPP following herbivory. While both ANPP and Rh decreased, the reduction in Rh was larger than the reduction in ANPP, which resulted in an increase in NEP in this study.

Methane emission from herbivores through the fermentation of food reserves has significant impact on the environment and also regulates atmospheric composition and climate (Lassey 2008, Steinfeld et al. 2012, Herrero et al. 2013, Ripple et al. 2014). Our results indicated that cattle were the largest source of CH_4 emission, followed by horse, sheep and goats, which is similar to Crutzen et al. (1986) reporting higher emission per individual in cattle and horse compared to sheep and goats. Our results are also consistent with previous findings that live body weight is an important factor affecting CH_4 emission from herbivores (Chang et al. 2015). While fermentation of food products and their quality also played a dominant important role in determining the net emissions (Moss et al. 2000), we found that larger herbivores (cattle and horse) had more CH_4 emission compared to smaller herbivores (sheep and goats). In the current modeling framework, we used the Intergovernmental Panel on Climate Change (IPCC) tier II guideline, which relies on estimating different components of energy expenditure (lactation, feeding, work, wool and pregnancy) and digestibility of forage to quantify the CH_4 emission.

Evapotranspiration is a key component of the water cycle regulating the net amount of water available for plant growth (Parton et al. 1981, Frank and Inouye 1994, Pan et al. 2015c, Bhattarai et al. 2016). In grassland ecosystems, reduction in plant surface area and LAI following herbivory would result in a decline in transpiration rates and retain more soil moisture for plant growth (Naeth and Chanasyk 1995, Bremer et al. 2001). Meanwhile, herbivory also increase bare soil surface area, which ultimately leads to an increase in surface evaporation (Bremer et al.

2001). The net effect of herbivory on ET depends largely on the balance between lower transpiration rates due to reduction in vegetation cover and LAI and higher soil evaporation rates due to increase in bare surface area (Naeth and Chanasyk 1995). Our results indicated that decrease in transpiration was compensated by increase in evaporation due to reduction in vegetation cover, resulting in no net change in ET following herbivory. In a recent study, Wang et al. (2012) found that the direct effect of herbivory induced reduction in LAI on ET was not significant is semiarid ecosystem because soil evaporation compensated most of the losses in plant transpiration. Likewise, in a modeling study with different herbivore density, Zhao et al. (2010) showed that moderate herbivore density had no significant effect on water budget components, while high herbivore density resulted in a significant reduction in transpiration by 39% and increase in evaporation by 45%. It is likely that herbivore densities at the study sites are lower than the maximum carrying capacity due to which we did not find any significant effect of herbivore on ET.

3.4.5 Implications of coupling herbivore feedbacks into the global land ecosystem model

By incorporating herbivore dynamics in the global land ecosystem model, we aimed at quantifying the response of herbivores to climate change and resource availability and their effect on ecosystem and climate. Regarding similar work, Pachzelt et al. (2013) coupled LPJ-GUESS with the grazer model to simulate the population of large ungulates in African savannas. However, factors such as migration, and mortality associated with extreme climatic conditions were not represented in such model. The version of LPJ-Guess also does not account for the effect of herbivores on biogeochemistry and other land surface processes. Similarly, Kooijman (2010) had a detailed animal physiology but was not explicitly linked to population dynamics. Shabb et al. (2013) used a Leslie-Gower difference equation competition model to simulate the population dynamics of horse, cattle, sheep and goat in Mongolian steppes; however, the model is not explicitly linked to plant physiology. Here we present the global land model that explicitly accounts for both animal and plant physiology and simulate the effects of climate and other environmental factors on herbivore population and vice versa. The herbivore model is parameterized for specific herbivore type (similar to specific plant function types in the DLEM) which makes the model applicable across the globe. In this study, we only used horse, cattle, sheep and goat dynamics as a case study. However, with adequate parameters and data, the model can be applied for other mammalian herbivores and at multiple spatial scales.

Current land ecosystem models simulate ecological and ecosystem processes without considering the effect of herbivores, although herbivore has been recognized as an important factor that alter carbon, nitrogen and water cycles (Knapp et al. 1999, Hopcraft et al. 2010). By linking the DLEM plant model with the herbivore dynamics in this work, we demonstrate that herbivore has a substantial effect on ANPP, Rh, NEP and ET, although the magnitude of their effect largely varies by ecosystem type and prevailing climatic conditions. In the absence of herbivore dynamics and their effect on biogeochemical processes, current land models may over-estimate ANPP and Rh by up to 12.4%, while under-estimate NEP by 17%. But, the extent to which these site level responses would scale up to regional and global effect remains a subject of future investigation.

3.5 Uncertainty and Future Needs

The study incorporated a simplified herbivore dynamics model into a land ecosystem model (DLEM) to simulate the population of herbivores in response to climate and other environmental factors at site level. Although we attempted to include major processes that affect herbivore dynamics and how they alter carbon, nitrogen and water cycles, there are several limitations that need to be addressed in the future work. The largest uncertainty in the model comes from how markets, policy and economic activity (change in demand and supply of products) affect population dynamics of herbivores. While we have shown the effect of market/policy changes in Mongolia, we did not attempt to quantify the effect market/economic changes in Africa and North America. Our model can be used to quantify how great the effect of market/ policy changes will have on herbivore production (see section 4.1), but future work is needed to accurately estimate the effect of policy, market and economic changes on livestock production. Likewise, we have only included four herbivores (horse, cattle, sheep and goat) in Mongolia, while three herbivores (cattle, sheep and goat) in Africa and the United States. We have also not considered herbivore migration in the current modeling framework. However, the simulated results were calibrated to fit observed herbivores numbers.

Our study also recognizes that mortality associated with climate extremes is not adequately represented in the current modeling framework. For example, extreme heat wave has been linked to high mortality of herbivores (Crescio et al. 2010, Morignat et al. 2014); however, we have not included the effect of heat waves on herbivore mortality in the current modeling framework. We need more experimental studies to model the complexity associated with summer heat waves, and its subsequent impact on herbivore population.

3.6 Conclusions

In this study, we integrated a mammalian herbivore population model into the global land model (DLEM) and quantified the effects of both biotic and abiotic factors on herbivore growth and productivity in Mongolia, Africa and the United States. In addition, we simulated the impact of herbivores on carbon, water and greenhouse gas fluxes, which influence the ecosystem-climate feedback. The generalized model was able to capture the observed values of herbivore population at all sites. Likewise, our results demonstrated that herbivore has a significant impact on ANPP, Rh and CH_4 emission, but impact was largely dependent on simulated herbivore density at a given site. Our results also indicated that climate extremes (droughts and extreme winter) would result in a maximum mortality of 53% in Mongolia, while drought would result in a mortality of up to 25% and 62% in Africa and the United States, respectively.

By using spatially explicit information on climate and other environmental factors into the global land ecosystem model, we attempted to provide general insight into the growth and productivity of herbivores and their response to climate extremes. In addition, we examined the effect of herbivores on terrestrial ecosystems and the climate system. Our results demonstrated a strong coupling between primary producers and consumers, indicating that the inclusion of herbivores in the current land ecosystem model is essential to understand the biogeochemical processes (for example: carbon sequestration, evapotranspiration, CH_4 emission). To our best knowledge, this is the first attempt to couple a global land model with herbivore population dynamics with detailed animal physiology. Although the current work focused on model development and its application at site level, with adequate parameterization the model can be applied at regional and global scales to understand the complex interactions among climate, grazing systems and mammalian herbivores provided that adequate data and parameters to represent the biology of different herbivores are available.

Chapter 4. Synergistic effects of climate change and grazing on net primary production in the grasslands of Mongolia

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 intensities. By developing a grazing module in a process-based ecosystem model, the dynamic land ecosystem model (DLEM), we explore the role of climate change with elevated CO_2 at varying grazing intensities in affecting aboveground net primary productivity (ANPP) across different grassland sites in Mongolia. Our results showed that both growing season precipitation totals and average temperature exert an important control 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 along a gradient of high (9.5-19.9%) to low (23.9-32.5%) precipitation. Historical grazing resulted in a net reduction in ANPP across all sites ranging from 2% to 15.4%. Our results further showed that grassland ANPP can be maintained at a grazing intensity of 1.0 sheep ha^{-1} and 0.5 sheep ha^{-1} 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, respectively. Our results

indicated 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.

4.1 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^{o}N and 87.6-119.9^{o}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 (*dzud*) and summer droughts. Declines in grassland productivity has also been attributed to increasing human activity which is associated with higher livestock numbers and changes in herd composition (Hilker et al. 2013), and to a lesser extent by grasslands conversion to agriculture, increasing urbanization, and mining (Addison et al. 2012, Leisher et al. 2012). Ground-based measurement has also confirmed that human activities coupled with warmer climatic conditions have resulted in a decline in both biodiversity and ecosystem function within the region (Li et al. 2008, Zhang et al. 2011), while satellite based studies have shown both declines and increases in vegetation cover and production in the Mongolian grassland (Sternberg et al. 2011, Li et al. 2012). Changes in the ecology of grassland ecosystem 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 a 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 and by extension, animal husbandry (Nandintsetseg and Shinoda 2013). Evidence from Mongolia shows that the annual mean temperature has increased by 2.17 ^{o}C from 1940-2009 with warming more pronounced in winter than summer. 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 (1.9 ^{o}C - 2.28 ^{o}C). Hilker et al. (2013) suggest that increases in air temperature negatively affect plant growth in Mongolia. However, the extent to which temperature contributes to grassland ANPP is still unknown.

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^2 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 (referred as *dzuds* in Mongolia), 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. 2012a). 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. 2012a). Therefore, changing climatic conditions, including extreme climatic events, have a significant impact on grassland ANPP and the associated feedbacks on the carbon balance, hydrological cycles and livestock productivity in 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), seed production and the amount of seeds in the soil (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). 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. (2013) found that dramatic increases in goat numbers was an important factor 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. 2004a). 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 and 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 natural arid and semiarid ecosystems sites in Mongolia. We choose 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 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. 2011b)), 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.

4.2 Materials and methods

4.2.1 Study area

The study areas were selected based on three different grassland types along a precipitation gradient from north to south (Table 4.1; Figure 4.1). The grassland types are categorized as wet, moderately wet, and dry grasslands. Wet grasslands annually receive precipitation totals of > 300mm, while moderately wet and dry grasslands receive precipitation totals of 150-300 and 50-150 mm yr^{-1}, respectively (Figure 4.1). Bulgan (BC) and Tsetserleg (TC) are grasslands that receive the highest annual precipitation of about 330 and 336 mm yr^{-1}, respectively. The average grazing intensity for the period 1981-2010 are 0.12 and 0.66 sheep/hectare 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^{-1}, respectively. Grazing intensity is about 0.38 and 0.17 sheep ha^{-1} at UC and AC, respectively. The drier site Dalanzadgad (DG) receive total annual precipitation of about 120 mm yr^{-1} while Tsogt-ovoosum (TO) receive total annual precipitation of about 97 mm yr^{-1}. The grazing intensity is 0.34 and 0.12 at TO and DG, respectively.

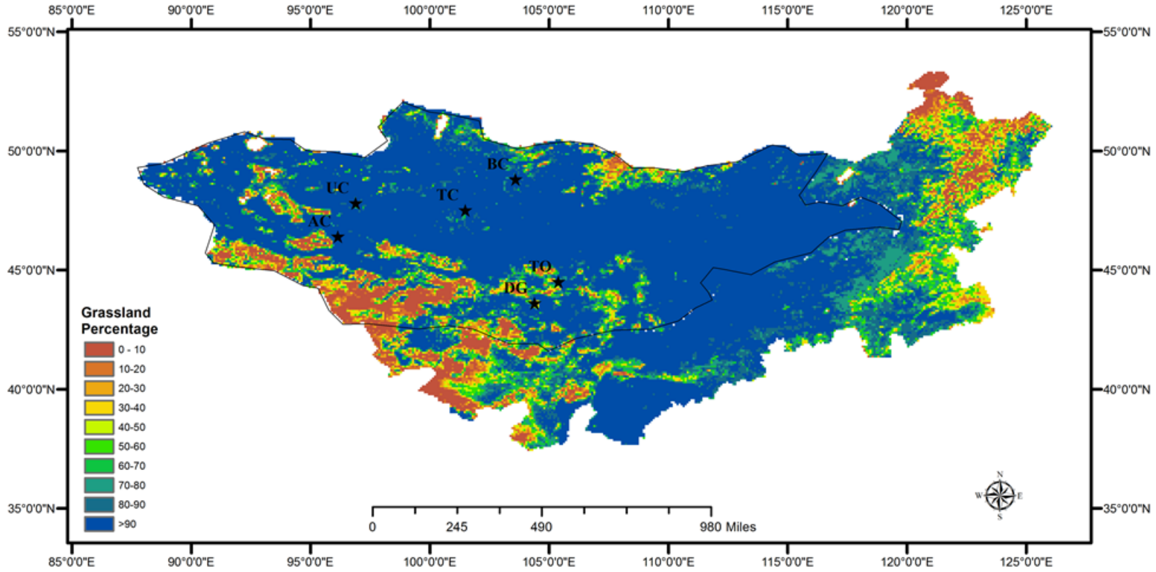


Figure 4-1 Percentage of area covered by grasslands in the Mongolian Plateau in year 1980 based on the DLEM.

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: Tsott-ovoosum.

4.2.2 Development of grazing module in the DLEM

The grazing module used in this study is based on Seligman et al. (1992a). In its simplest form, the module is dependent on four parameters that control the amount of biomass uptake by herbivores. The four parameters include amount of biomass unavailable 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 includes 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). The detailed description on how we simulate the effect of grazing is available in supplementary information.

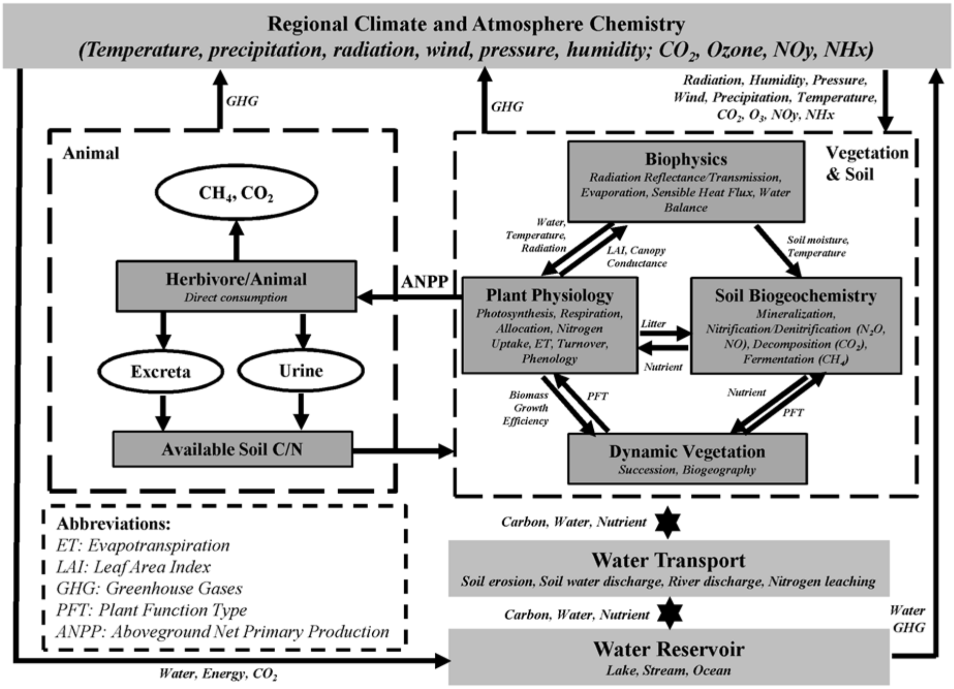


Figure 4-2 Schematic representation of grazing module in DLEM used to simulate the effects of grazing on carbon, nitrogen and water balance in arid- and semi-arid environments.

It is important to recognize that the grazing module used in this study has both a negative and positive effect 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. 1993a). 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.

4.2.3 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 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^{o}E, 43.6^{o}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 (Figure 4.3) 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 (Figure 4.4; Table 4.2). Model evaluation showed that the simulated ANPP are closer than Schönbach et al. (2011) and are within the range of -2.8% to 20% based on different grazing intensities. In particular, the DLEM over-estimates ANPP response at high grazing intensity of 7.5 sheep ha^{-1} compared to Schönbach et al. (2011) (Table 4.2). 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.

4.2.4 Model implementation

The model simulation at the site level follows 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, with 1981 levels of atmospheric CO_2 concentrations and vegetation cover. The equilibrium run is carried out for 10,000 years at most or until the net carbon exchange between the atmosphere and the site is less than 0.1 g C m^{-2}, 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^{-2} 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_2 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.

Table 4-1 Grassland information under traditional grazing systems during 1981-2010 in Mongolia

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

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 sheep ha^{-1} and 0.50 sheep ha^{-1}), while other three (1, 3, and 4.5 sheep ha^{-1}) 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.

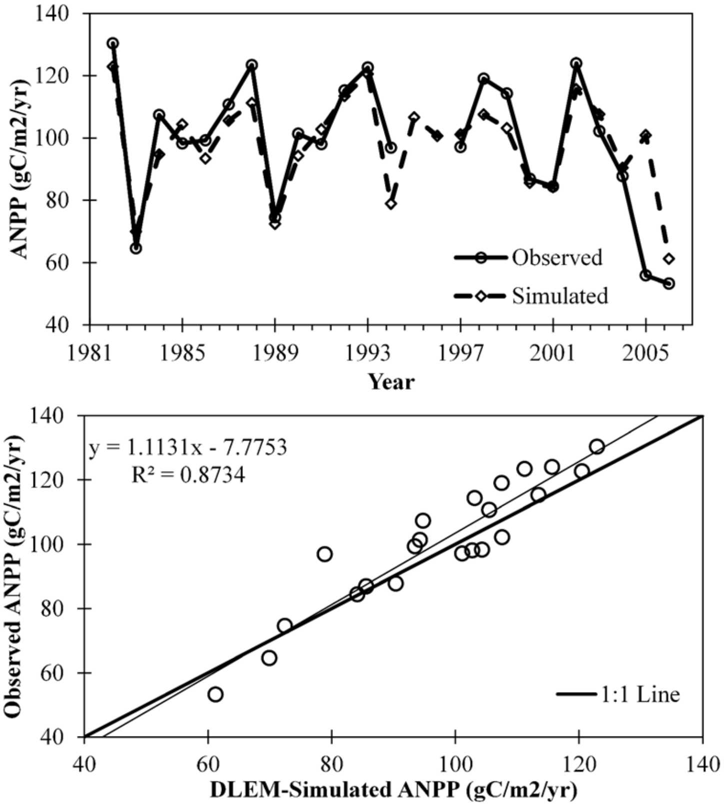


Figure 4-3 Temporal patterns (top panel) of and comparison (bottom panel) of DLEM simulated ANPP with observations at Xilingol River Basin, Inner Mongolia (116.7^{o}E, 43.6^{o}N) based on Ma et al. (2010)

Table 4-2 Climate controls on annual ANPP during the 1981-2010 period. Correlation coefficient (r) represents the correlation between annual ANPP and annual precipitation totals or mean annual temperature.

Site	ANPP (gC/m2/yr)				ANPP-Prec (r)	ANPP-Prev. Year Prec (r)	ANPP-Tair (r)
	Mean	Max	Min	CV (%)			
BC	84.15	98.09	64.52	9.5	-0.01	0.55*	0.51*
TC	64.14	88.07	40.74	18.9	0.53*	0.02	-0.05
UC	59.27	91.01	41.89	17.8	0.53*	-0.34	-0.17
AC	57.98	79.24	41.61	16.7	0.70*	-0.15	-0.12
DG	36.93	58.18	24.31	23.9	0.66*	0.15	-0.13
TO	27.18	57.91	16.78	32.5	0.70*	0.22	-0.12

* indicates a significant effect at 5% level of significance.

4.3. Results

4.3.1 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 4.3). ANPP across six grassland sites ranged from 27.18 g C m^{-2} yr^{-1} at the dry site to 84.15 g C m^{-2} yr^{-1} at the wet site from 1981-2010. Grassland ANPP was found to be significantly correlated with annual precipitation totals across all sites explaining 67% of the variation in ANPP ($y = 0.16x$; P-value < 0.05). Our site-specific comparisons, however, showed that annual precipitation may not have a same positive association with ANPP at individual sites largely due to differences in local environmental conditions (Figure 4.5). Across individual sites, grassland ANPP was found to be 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 ($r = 0.55$ P-value < 0.05). Interestingly, DLEM-simulated ANPP showed larger inter-annual variations 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 19.9%, respectively (Table 4.3). Cross-site analysis further showed that inter-annual variations in ANPP decrease with increasing precipitation ($R^2 = 0.63$; $y = -0.06x$; p-value < 0.05).

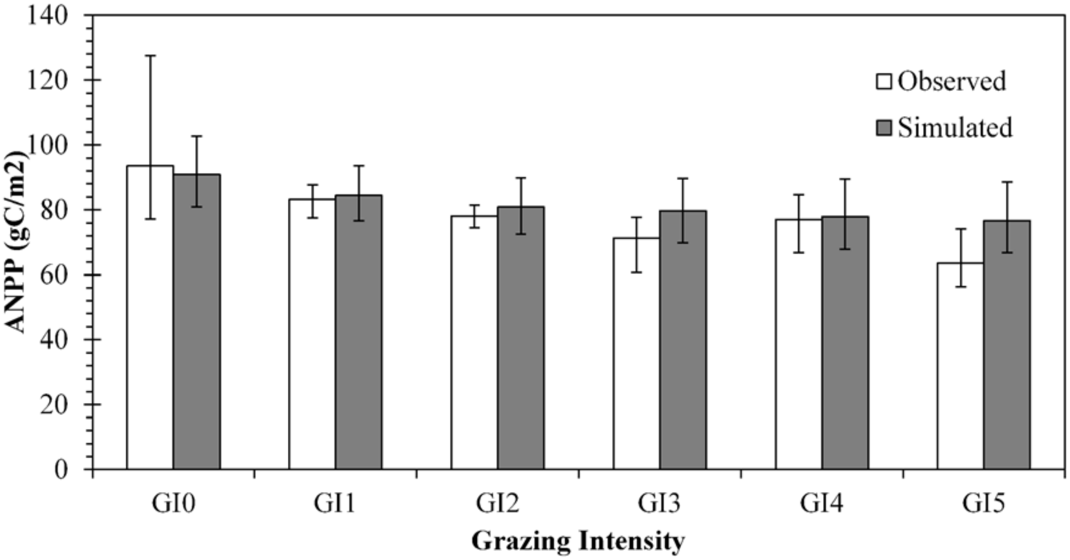


Figure 4-4 Comparison of DLEM simulated ANPP with observation at different grazing intensities based on Schönbach et al. (2011) during 2005 – 2008.
The error bars represent the maximum and minimum ANPP during 2005-2008. GI0: No Grazing; GI1: 1.5 sheep ha^{-1}; GI2: 3.0 sheep ha^{-1}; GI3: 4.5 sheep ha^{-1}; GI4: 6.0 sheep ha^{-1}; GI5: 7.5 sheep ha^{-1}.

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-value < 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 ($R^2 = 0.26$; $y = 4.98 x$; p-value < 0.05) indicating that temperature limitations may constrain grassland productivity in areas with abundant rainfall.

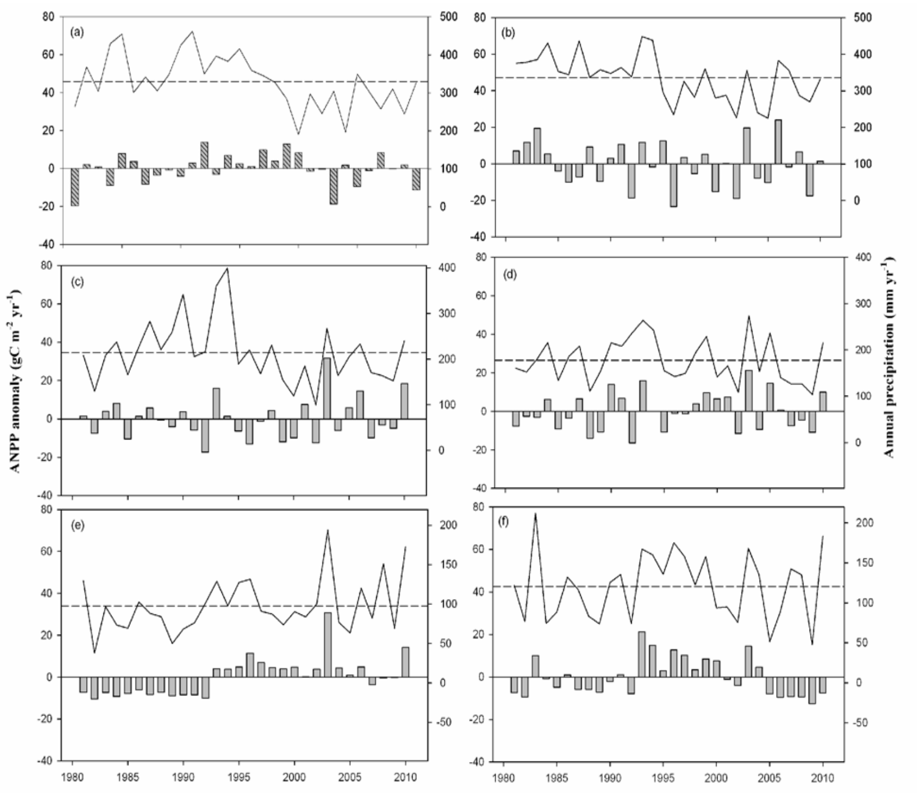


Figure 4-4 The DLEM-simulated ANPP (bars) driven by multiple environmental changes during 1981-2010 at Bulgan (a), Tsetserleg (b), Uliastai (c), Altai (d),Tsogt-Ovoosum (e) and Dalanzadgad (f).

The solid line represents inter-annual variation in precipitation while the dashed line represents 30-year (1981-2010) mean precipitation.

4.3.2 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 (Figure 4.6). 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-value < 0.05), explaining 26% of the variation. Our further analysis at BC suggested that there is a different water use pattern compared to other sites. First, 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-value < 0.05; $R^2 = 0.31$; Figure 4.7a). However, this soil moisture memory mechanism was not evident at other sites.

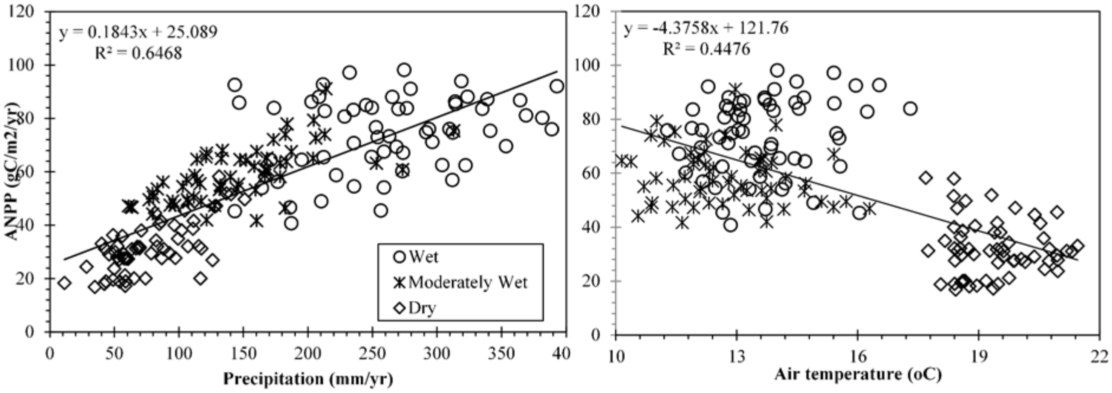


Figure 4-5 Effect of growing season precipitation totals (left panel) and average temperature (right panel) on grassland annual ANPP across 6 sites in Mongolia.

Growing season temperatures had a significant negative effect across the six sites explaining 45% of the variation in annual ANPP (p-value < 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 ~21^{o}C compared to other wet sites where growing season temperatures are in the range of 13-15^{o}C. 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.

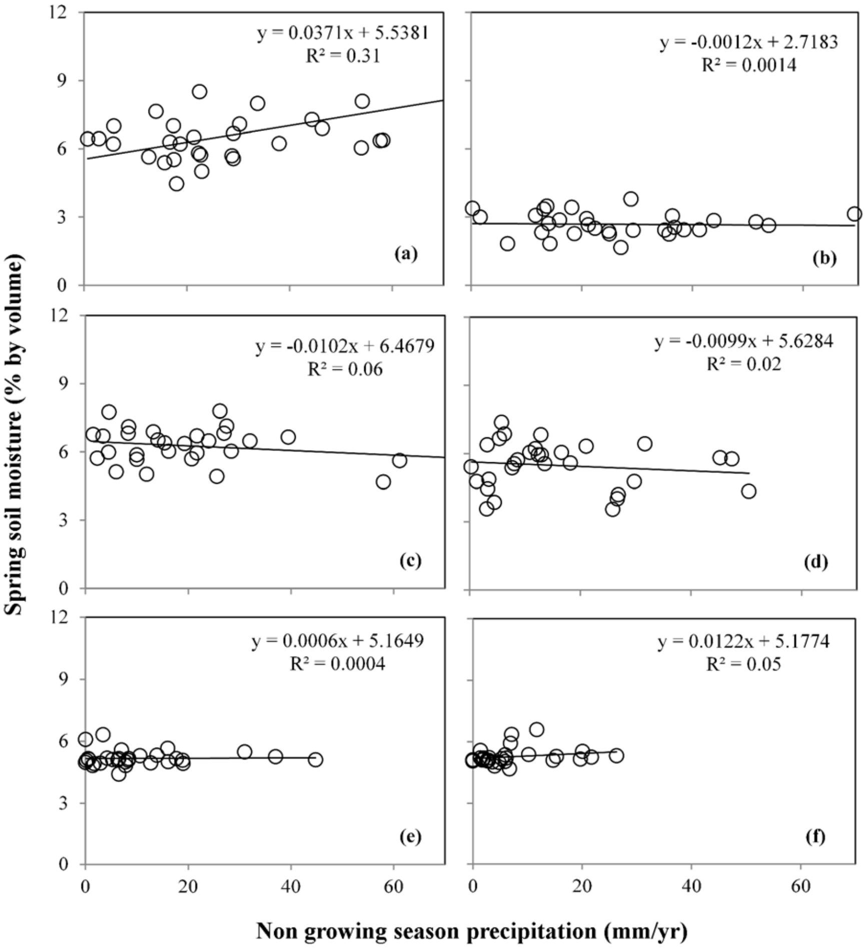


Figure 4-6 Correlation between annual non-growing season precipitation totals and spring soil moisture across six sites in Mongolia.
Bulgan (a), Tsetserleg (b), Uliastai (c), Altai (d),Tsogt-Ovoosum (e) and Dalanzadgad (f).

4.3.3 Variations in grassland ANPP induced by climate change and grazing

When including historical site-level records of grazing intensity as input driver, DLEM simulations showed a net reduction in grassland ANPP across all sites (Figure 4.8). The reduction ranged from 2% to 15.4%, depending on local condition 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-value < 0.05) indicating that historical grazing intensity at these sites has had 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^2 and 3.6 g C/m^2 (equivalent to a decrease of 15.0 and 15.4%) occurred at BC and TO, respectively.

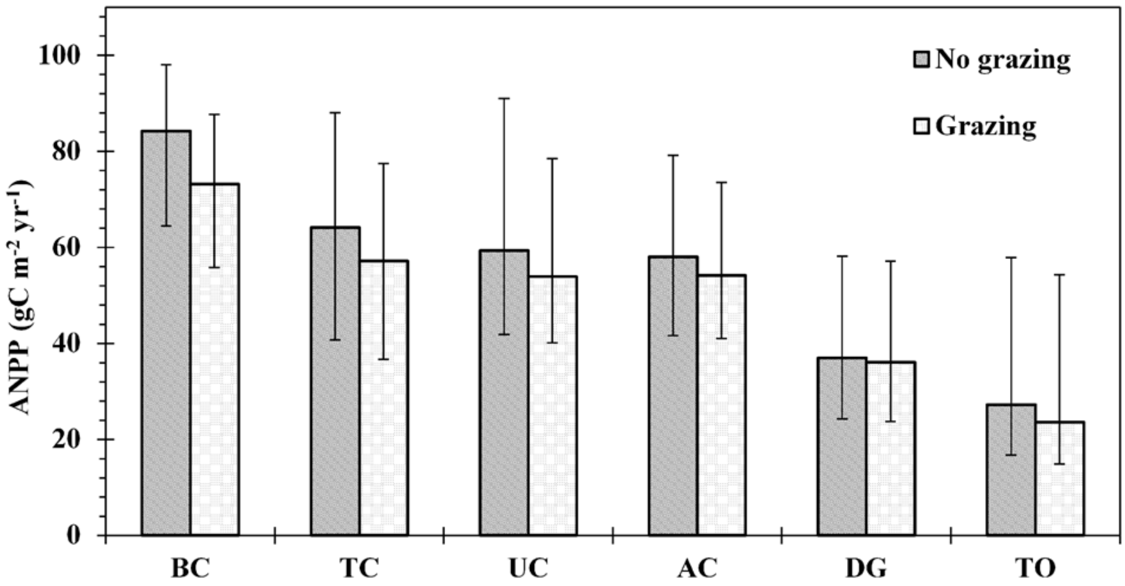


Figure 4-7 Effects of grazing on ANPP across a precipitation gradient in Mongolia.
We used realistic grazing intensity during 1981-2010 to simulate the effects of historical grazing intensity at each sites. Error bar represent the maximum and minimum ANPP during 1981-2010. BC: Bulgan; TC: Tsetserleg; UC: Uliastai; AC: Altai; TO: Tsogt-Ovoosum; DG: Dalanzadgad.

4.3.4 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^{-1}) to quantify if there is 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 (Figure 4.9). Our simulation with different grazing intensities showed that grassland ANPP decreased from no grazing to grazing intensity of 4.5 sheep ha^{-1} 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^{-1} 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^{-1}. 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^{-1} for wet and moderately wet sites and at 0.5 sheep ha^{-1} for dry sites indicating that compensatory growth response is possible at low grazing intensity at all sites (Figure 4.10).

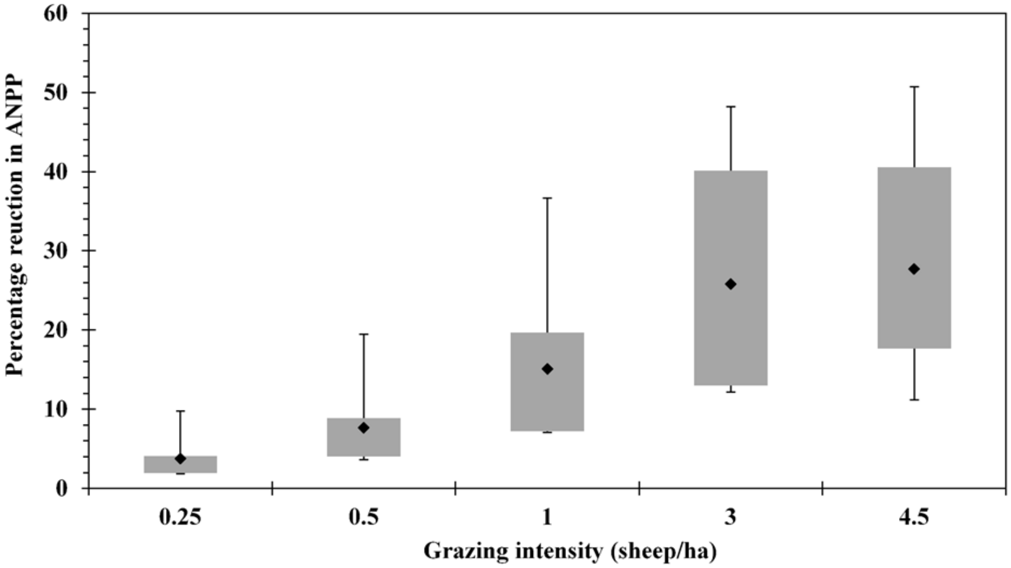


Figure 4-8 Percentage reduction in ANPP as a function of grazing across six different sites in Mongolia.

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.

4.3.5 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 simulations 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-value < 0.05) indicating that plants would be able to utilize water more efficiently under conditions of moisture stress (i.e. drought) (Figure 4.11). For instance, when the mean annual precipitation was between 50-100 mm yr^{-1}, the average PUE was 0.37 g C m^{-2} / mm H_2O; however, the average PUE decreased to 0.17 g C m^{-2} / mm H_2O when the mean annual precipitation was 500-600 mm yr^{-1}. In contrast, nitrogen use efficiency (NUE) measured as a ratio of ANPP to available nitrogen in soil showed an opposite pattern compared to PUE. For instance, NUE was 7.54 g C / g N when the precipitation was between 50-100 mm yr^{-1}; however, the average NUE increased to 14.97 g C / g N when the precipitation increased to 500-600 mm yr^{-1}. It implies plants are prone to more efficiently exploit and use nutrients when water is not limiting, and vice versa.

We also tested how grazing induced changes in nitrogen and water cycles affect ANPP across a precipitation gradient. Our results showed grazing resulted in an overall reduction in PUE and NUE (Figure 4.12). 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 since it not only removes aboveground biomass, but also limits plants' capability in using water. For example, in wet and moderately wet areas, PUE declined by 16% at the grazing intensity of 4.5 sheep ha^{-1}; however, PUE declined by 47% at the grazing intensity of 4.5 sheep ha^{-1} at dry sites. On the other hand, NUE decline by 67% at a grazing intensity of 4.5 sheep ha^{-1} compared to the no grazing simulation. This is primarily because plants' capacity to translate nitrogen into photosynthetic product 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^{-1} compared to the non-grazing experiment.

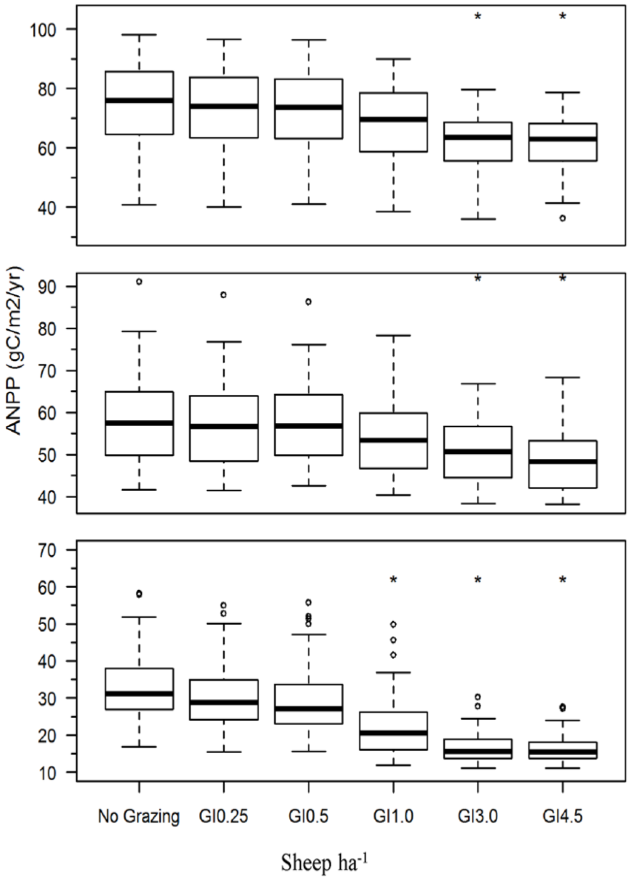


Figure 4-9 Sensitivity of grassland annual ANPP to different grazing intensity across a precipitation gradient.

* indicates a significant difference in annual ANPP between grazing and no grazing simulations at 5% level of significance.

4.4 Discussion

4.4.1 Temperature control on grassland ANPP

In general, mean annual temperature had 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 resulted in a significant decline in grassland ANPP by 5.2 g C m^{-2} per 1^{o} C increase in temperature. Temperature effects on ANPP can vary with total soil moisture content such that warm temperatures might positively affect ANPP in areas with abundant moisture, but have negative effects during period 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 the consequent water stress may offset any positive effects of higher temperatures on plant growth (Dulamsuren et al. 2013, Xu et al. 2013). 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^{-2} with per ^{o}C increase in temperature (p-value < 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 melting and indirectly modifying soil water availability. Therefore, warmer springs seem to enhance ANPP early in the growing season at BC.

4.4.2 Precipitation control on grassland ANPP

Both growing season and annual precipitation totals have a substantial impact on grassland productivity (Knapp and Smith 2001, Huxman et al. 2004a, Bai et al. 2008, Craine et al. 2012). Previous studies have shown that annual precipitation totals can explain 51% to 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 (Thomey et al. 2011). 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 of 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% to 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 providing basis for initial vegetation growth earlier in the spring (Shinoda and Nandintsetseg 2011).

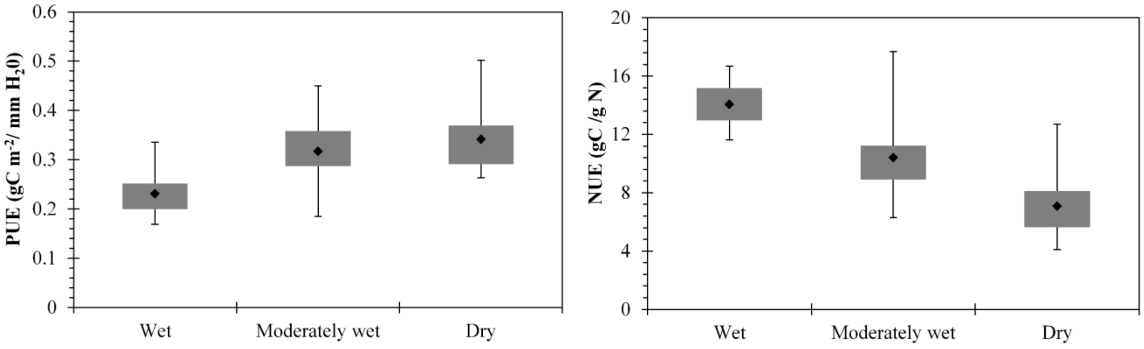


Figure 4-10 Precipitation use efficiency (PUE) and nitrogen use efficiency (NUE) along a precipitation gradient in Mongolia.
The box length represents the first and third quartile. The error bar represents the maximum and minimum values for PUE and NUE during 1981-2010 and the black dot represent the mean PUE and NUE during 1981-2010.

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. Walter (1971) suggested that partitioning of soil water resources between deep and shallow layers play an important role in determining the amount of carbon sequestered as ANPP. For example, shallow-rooted plants primarily use shallow soil water derived from growing season precipitation whereas deep-rooted plants rely on available deep soil water derived from winter precipitation. 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 aboveground biomass was similar across all sites, the total biomass content differ across sites with the highest belowground biomass at BC (75 g C m^{-2}) compared to TC (66 g C m^{-2}), UC (66 g C m^{-2}), AC (59 g C m^{-2}), DG (34 g C m^{-2}) and TO (25 g C m^{-2}). 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 have led to extract water from deeper soil horizons and increase ANPP early in the spring. However, the effective root distribution at other sites is more concentrated at top 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.

4.4.3 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. 2008b). The DLEM simulated results showed that ANPP was found to decrease 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, improve plant-water or plant-nutrient status does not maintain grassland ANPP because grazing has a much larger effect on grassland biomass.

4.4.4 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 intensity suggested 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.

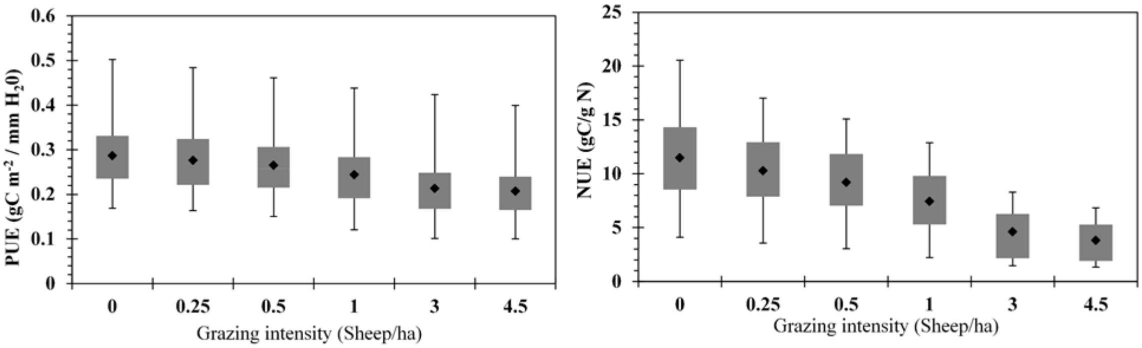


Figure 4-11 Precipitation use efficiency (PUE) and nitrogen use efficiency (NUE) as a function of grazing intensity in Mongolia.
The box length represents the first and third quartile. The error bar represents the maximum and minimum values for PUE and NUE during 1981-2010 and the black dot represent the mean PUE and NUE during 1981-2010.

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, Tserenpurev 2011) in Mongolia, there has 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 (Chen et al. 2007). Our study indicated that ANPP can be maintained at a grazing intensity of <= 1.0 sheep ha^{-1} 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 < 130mm is 0.5 sheep ha^{-1}. 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 plants growth (McNaughton 1979, Turner et al. 1993a). Decreasing senescence of young grown leaves increases photosynthetic efficiency promoting ANPP after grazing (Van Staalduinen and Anten 2005). In addition, reduction in water loss through stomatal pores improves short-term plant water relation promoting compensatory growth (Turner et al. 1993a). In light of the mechanisms explained above, our simulation considers the beneficial effect of grazing on ANPP such as improve plant nutrient status due to increased nitrogen inputs in the form of excretal return, improve plant water relation 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. Finally, regional validation with and without grazing is required to support current results and to better understand system interaction under changing climatic conditions.

4.5 Conclusions

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

Our findings further suggested that plants in the driest ends of our gradient are more vulnerable to grazing compared to plants localized at wet extremes 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 showed that the optimal stocking rate for areas experiencing high seasonal precipitation totals is 1.0 sheep ha^{-1} while the optimal stocking rate for areas experiencing low seasonal precipitation totals is 0.5 sheep ha^{-1} indicating that moisture limitations 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. 2009a), 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 alone 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.

Chapter 5. Vulnerability of grassland ecosystems to climate change and grazing in semi-arid environments

Abstract

Although many studies have examined the impact of grazing and climate on grassland ecosystems in the Mongolian Plateau, few have quantified the contribution of climate and other environmental changes on livestock production and their subsequent effect on grassland ecosystems. Here we used a process-based ecosystem model (the Dynamic Land Ecosystem Model) to investigate livestock production, biomass use and grassland vulnerability to climate and multiple environmental changes during 1950-2012. Our results show that about 83% of the grassland area in the Mongolian Plateau has experienced decline in grassland aboveground net primary productivity (ANPP), as a result of climate change (-61.4%) and grazing (-23.2%) since the 1990s. Livestock biomass use has increased from 28.8 TgC/yr to 40.6 TgC/yr, accounting for 41% of the increase, largely due to an increase in cattle, sheep and goat population by 20.2%, 14.8% and 114.5%, respectively. Transition from central (government-controlled) to market economy was the major driver of an increase in livestock population, which led to an increase in livestock biomass use by 70.3% since the early 1990s. However, grassland ANPP has declined by 15% (from 162.3 TgC/yr to 138.8 TgC/yr) during the same time period. Our results demonstrate that increased surface air temperatures, changes in precipitation patterns and livestock grazing have decreased productivity with potentially severe consequences on grassland ecosystems in the MP. Future warming and increases in livestock population may overwhelm the

adaptive capacity of ecosystems and societies in Mongolia, leading to further grassland degradation unless management strategies that focus on climate change mitigation and grazing optimization are implemented in the near future.

5.1 Introduction

The Mongolian Plateau (MP) lies in the prominent transition belt (41.6-52.2^{o}N and 87.6-119.9^{o}E) which encompasses desert ecosystems in the south and the Siberian taiga forest in the north (Batima and Dagvadorj 2000, Suttie 2010). The plateau is dominated by grassland ecosystems, which comprise approximately 72% (112.8 million hectares) and 66% (78.8 million hectares) of the total land area in Mongolia and Inner Mongolia, respectively (Bai et al. 2008, NSO 2013). Grassland productivity in the MP has declined in recent decades by over 70% (UNEP 2002), which has been attributed to climate change, intensive grazing and policy shifts (Usukh et al. 2010, Liu et al. 2013, Hilker et al. 2014, Chen et al. 2015a), but the evidence about the extent and causes of grassland degradation remains uncertain (Addison et al. 2012).

Grassland vulnerability to climate change, extreme events (droughts and extreme winters) and grazing have been studied extensively in the Mongolian Plateau using environmentally controlled field experiments (Bai et al. 2004, Schönbach et al. 2011, Khishigbayar et al. 2015), satellite observation (John et al. 2013, Liu et al. 2013, Hilker et al. 2014, Miao et al. 2015), ecosystem modeling (Lu et al. 2009, Bao et al. 2016) and other approaches (Zhang et al. 2011, Bruegger et al. 2014, Tian et al. 2014). But few studies, if any, have attempted to investigate the vulnerability of grassland ecosystem to combined effects of climate and grazing at the regional scale. For example, satellite based studies show both declines and increases in vegetation indices due to climate and/or grazing (Hilker et al. 2014, Miao et al. 2015), while ecosystem models have been used to simulate grassland productivity in the absence of grazing (Lu et al. 2009).

Although these studies consider different scenarios that alter grassland productivity and health, attributing the response of grassland aboveground net primary productivity (ANPP) to climate, grazing and other environmental factors is essential to assess the vulnerability of grassland ecosystems in the MP.

Although climate change directly influences the availability and accessibility of resources and determine carrying capacity of grasslands, grazing by domestic animals indirectly remove aboveground biomass and alter both ecological and hydrological processes (Milchunas and Lauenroth 1993, Bardgett and Wardle 2003, McSherry and Ritchie 2013, Petz et al. 2014). The impact of grazing on ecological and hydrological processes could be positive, negative and neutral, depending on herbivore density, ecosystem type and local environmental conditions (Augustine and McNaughton 2006, Bakker et al. 2006, Knapp et al. 2012, Metcalfe et al. 2014). In Mongolia, grazing resulted in a decline in vegetation cover by 9.1% and biomass by 23.1% (Dashbal 2010), with regional studies attributing up to 80% decline in vegetation index to overgrazing (Liu et al. 2013, Hilker et al. 2014). Model projections indicate that Mongolia will experience an increase in air temperature by more than 0.6-0.8^{o}C over the global average, slightly elevated annual precipitation, decreases in soil moisture by up to 37.7% (Angerer et al. 2008, Lu et al. 2009) and more than two fold increase in goat and sheep populations in the next 10 years (Shabb et al. 2013). It is likely that climate change and increased grazing pressure will further intensify grassland vulnerability (Liu et al. 2013), with potentially severe consequence on the grassland productivity. Any grassland management approach ought to therefore consider the evolution of livestock population in the context of multiple environmental changes and policy shifts, and how they influence grassland productivity.

Any assessment of climate impact on ecosystem processes must take into account how climate change and its interaction with biotic and abiotic factors drive key ecological and evolutionary processes and mediate ecosystem responses (Craine et al. 2012, Blois et al. 2013). The distribution and abundance of livestock population respond positively to increased carrying capacity of land, which is strongly influenced by changes in both biotic (abundance of resources, competitors, and predators) and abiotic (climate, slope and distance to water bodies) factors (Oesterheld et al. 1992, Kakinuma and Takatsuki 2012). Historically, increased carrying capacity of land during warm and persistently wet climatic conditions has been linked to the expansion of Mongol political and military power (Pederson et al. 2014). But, since the 1990s, increased carrying capacity of land during favorable climatic condition was overwhelmed by market/policy changes that stimulated the expansion of herd size by up to 27% (Dietz et al. 2005, Tian et al. 2014, Chen et al. 2015a). This led to the exceedance of carrying capacity of the grazing land by 32.5% (Jigjidsuren 2005) and degradation of rangeland area in some form by up to 78% (UNEP 2002, Erdenetuya 2006), with heavily degraded grassland covering approximately 31% of the land (Javzandulam et al. 2005). Decline in both the availability and accessibility of resources such as food and water [for example, 63 lakes > 1 km^2 disappeared; Tao et al. (2015)] for livestock led to a drop in livestock population size by up to 30%, particularly during extreme climatic conditions (Sternberg 2010, Fernandez-Gimenez et al. 2012b, Rao et al. 2015). Therefore, it is imperative to investigate the effects of various drivers including climate and changes in available resources on livestock population in the MP.

We used a process based ecosystem model [The Dynamic Land Ecosystem Model (DLEM); Tian et al. (2010a)], with explicit representation of different livestock, to model the growth, mortality and reproduction of specific livestock in response to climate and local environmental conditions. We introduced the impacts of simulated livestock on ecosystem processes through aboveground biomass to quantify how long-term grazing and climate change have altered grassland productivity and understand the evolutionary grassland-grazer relationship during 1950-2012. Unlike chapter 4, this chapter simulates livestock population dynamics as a function of changes in multiple environmental factors. In addition, chapter 4 uses livestock information as input to the DLEM and simulates grassland response to climate change and grazing at the site level. However, this chapter simulates dynamic changes in herbivore population density within the model and quantifies the response of grassland ecosystems to changes in herbivore density. The specific objectives of this study are to: 1) quantify the growth and productivity of livestock in response to environmental changes; 2) investigate how multiple environmental factors including livestock grazing affect grassland productivity; and 3) assess grassland vulnerability in response to both climate and grazing.

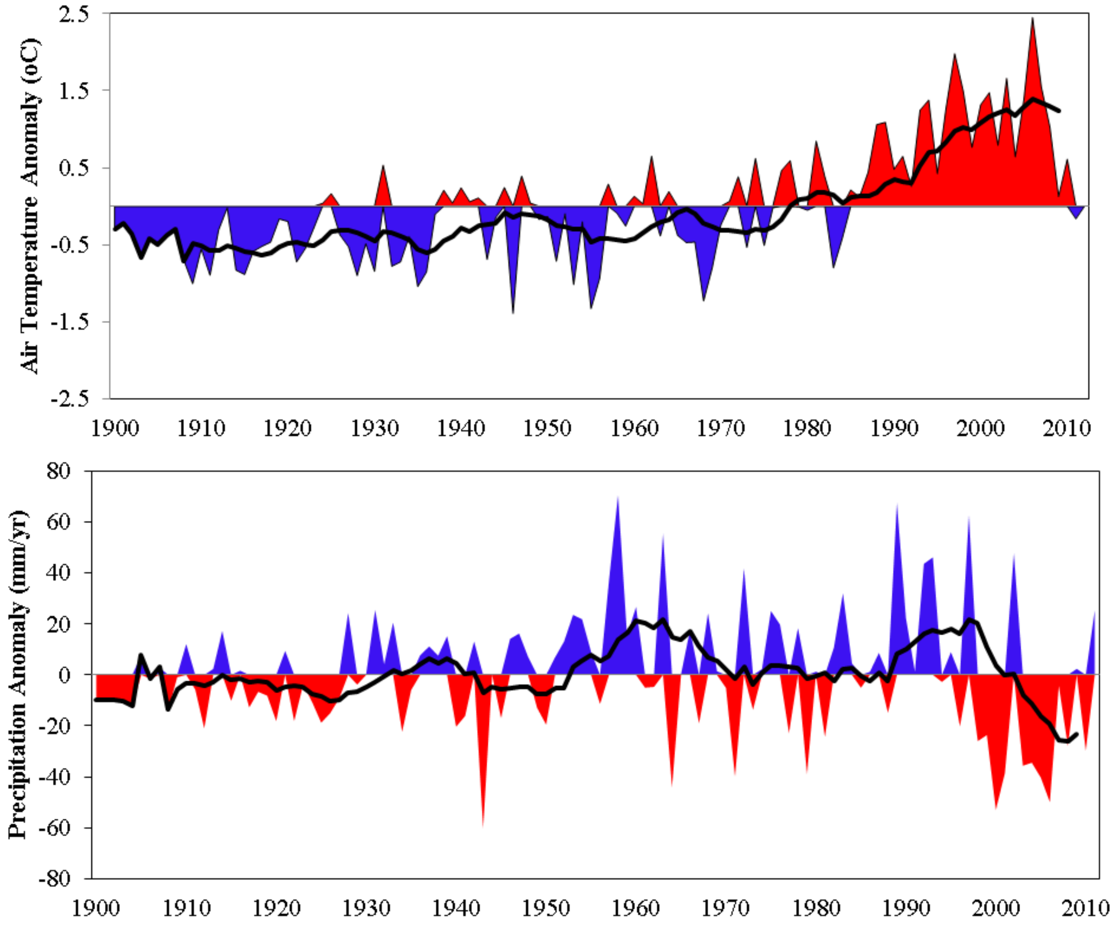


Figure 5-1 Temporal anomalies of surface air temperatures and precipitation totals in the Mongolian Plateau during 1901-2012

5.2 Methods

In the DLEM 3.0, we added a new component (livestock dynamics) to simulate the growth and mortality of specific livestock as a function of multiple environmental changes. The population dynamics model in the DLEM is based on several previous modeling studies (Konandreas and Anderson 1982, Freer et al. 1997, Illius and O'Connor 2000a), which explicitly simulates four major processes to provide daily estimates of animal population: 1) Energy Intake; 2) Energy Expenditure; 3) Natality; and 4) Mortality of specific herbivores. The basic simulation unit for population dynamics is a grid, in which the maximum of four herbivores can co-exist at a time. Large herbivore consists of a maximum of four age classes, while small herbivore has three age classes. Herbivores within each age class is assumed to have a fixed body weight, which is determined based on the mature weight of the respective herbivores (Pachzelt et al. 2013). In addition, we made two assumptions while simulating the growth and productivity of different herbivores: 1) there is no competition between different herbivore types for resources, although their growth and productivity are limited by resource availability, particularly during years of drought or *dzud* when carrying capacity is low; and 2) there is no migration of herbivores because mobility is very limited during harsh winter conditions under which long-distance movements of herbivore is not possible (Begzsuren et al. 2004), although there are some evidence of long-distance movements, particularly during drought years (Suttie and Reynolds 2003). The key parameters used for driving livestock population dynamics are provided in Table 5.1.

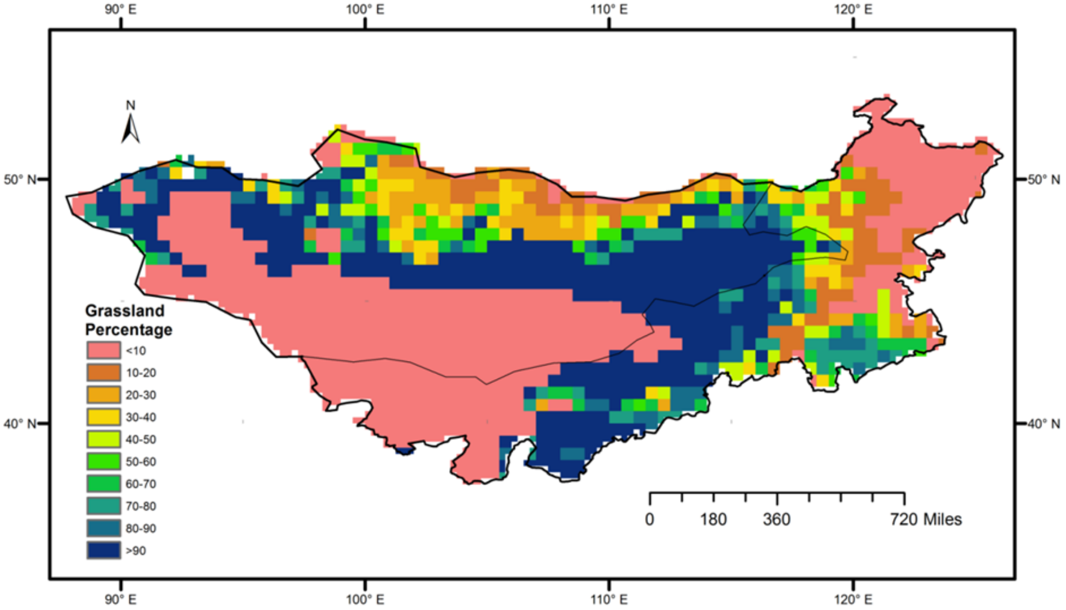


Figure 5-2 Percentage of area covered by grassland in the Mongolian Plateau in 2012

5.2.1 Modeling Protocol

Gridded, georeferenced datasets for the DLEM were compiled from various sources at a spatial resolution of $0.25^o \times 0.25^o$. These datasets include daily climate data, atmospheric chemistry (CO_2 concentration, AOT40 O_3 index, and nitrogen deposition), soil properties, land cover land use change (LCLUC), land management practices (irrigation, nitrogen fertilizer use and rotation) and other ancillary data such as river network, cropping system and topography maps. In this study, we used a derived AOT40 index as a measure of actual ozone concentration. Daily climate data during 1901-2012 were based on Asia Model Inter-comparison Project (Asia-MIP; https://sites.google.com/site/asiamipccycle/) (Figure 5.1), while atmospheric CO_2 concentration was obtained from Carbon Dioxide Information Analysis Center (CDIAC; http://cdiac.ornl.gov/). Annual nitrogen deposition was retrieved from the outputs of multiple atmospheric chemistry transport models (http://daac.ornl.gov/CLIMATE/guides/global_N_deposition_maps.html; Dentener et al. (2006)) and tropospheric ozone concentration were based on Felzer et al. (2004), while LCLUC was constructed based on Synergetic Land Cover Product (SYNMAP; Jung et al. (2006)) and HYDE3.1 land use data (Klein Goldewijk et al. 2011). Elevation, slope and aspect were derived from Global 30 arc-second elevation product (GTOPO30; https://lta.cr.usgs.gov/GTOPO30), and soil texture was derived from Food and Agricultural Organization (FAO) Soil Database System (Reynolds et al. 2000).

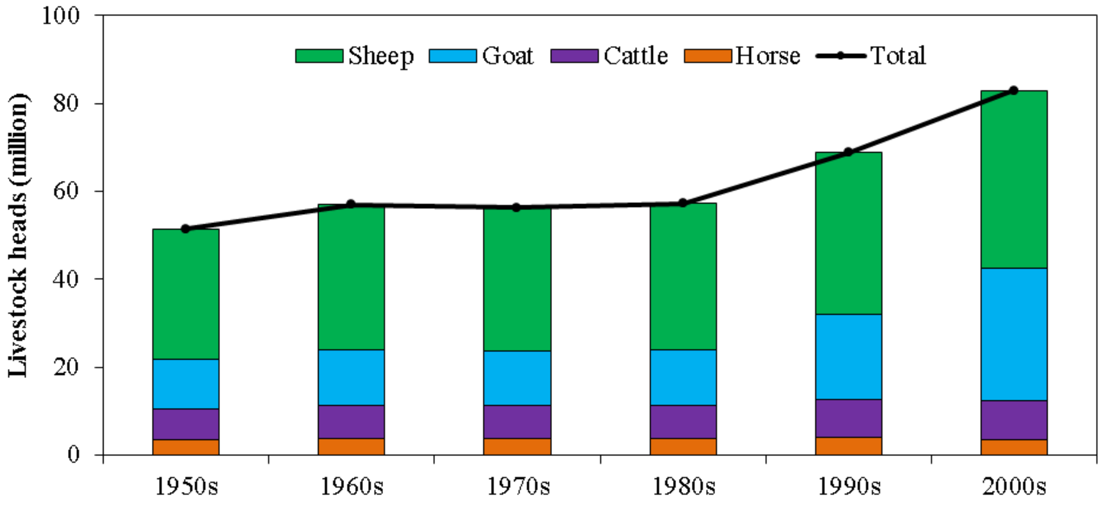


Figure 5-3 Simulated total livestock (million head) during 1950s, 1960s, 1970s, 1980s, 1990s, and 2000s

For each grid cell, we first run the DLEM to determine the equilibrium state of carbon, nitrogen and water for an undisturbed ecosystems using the long-term (30 year; 1901-1930) daily climate averages, while other input data (atmospheric CO_2, nitrogen deposition and land cover) were kept at 1901 level. The equilibrium run is carried out for the maximum of 10,000 years or until the net carbon exchange between the atmosphere and the terrestrial ecosystem is less than 0.5 g C m^{-2}, the change in soil water pool is less than 0.5 mm, and the change in total nitrogen content is less than 0.5 g N m^{-2} during two consecutive 20 years, for each grid cell. We then carried out a model spin up for 100 years by randomly selecting 20 years of climate data, repeated five times, during 1901-1930. The purpose of model spin up is to account for the influence of inter-annual variability on the initial conditions of carbon, nitrogen and water pools and to smooth the transition from equilibrium state to transient run. Both equilibrium and spin up simulation were carried out without herbivores. Following the model spin up, we carried out a transient simulation with the forcing of daily climate data and other environmental factors during 1901-2012. To account for more realistic initial (baseline) condition of herbivore population, we used a 30 year (1961-1990) average grazer numbers by different category based on FAO data (http://www.fao.org/statistics/en).

Table 5-1 Experimental Design

Simulation	Climate	Livestock	CO_2	NDEP	LCLUC	Policy
Reference (S0)	1900	1900	1900	1900	1900	1900
All-Combined (S1)	1901-2012	1901-2012	1901-2012	1901-2012	1901-2012	1901-2012
No-Livestock (S2)	1901-2012	1900	1901-2012	1901-2012	1901-2012	1901-2012
No-Climate (S3)	30-year average	1901-2012	1901-2012	1901-2012	1901-2012	1901-2012
No-CO_2 (S4)	1901-2012	1901-2012	1900	1901-2012	1901-2012	1901-2012
No-NDEP (S5)	1901-2012	1901-2012	1901-2012	1900	1901-2012	1901-2012
No-LCLUC (S6)	1901-2012	1901-2012	1901-2012	1901-2012	1900	1901-2012
No-Policy (S7)	1901-2012	1901-2012	1901-2012	1901-2012	1901-2012	1900

Multifactor includes historical changes in grazing, climate, carbon dioxide (CO_2), atmospheric nitrogen deposition (NDEP), land cover land use change (LCLUC) and policy shifts. No-Livestock is a simulation without the impacts of grazing on ecosystems

To compare the herbivore response to climate, grassland productivity and other environmental factors, we aggregated all animal groups into animal heads and examined the temporal dynamics of herbivore population to climate, grassland production and other environmental factors. We also partition the effect of climate, elevated CO_2, nitrogen deposition, land use/cover change and market/policy changes on livestock biomass use, as a measure of livestock productivity. Livestock biomass use, in this study, is measured as the annual sum of carbon intake by all animal groups during 1950-2012. In addition, we also presented the results of herbivore response by separating the simulated herbivore density into two specific periods similar to Shabb et al. (2013): 1) Soviet Union (1950-1990) and 2) Post-Soviet Union (1991-2012). The underlying assumption is that herbivore density during the socialist period are regulated by environmental factors and grassland productivity, while herbivore density in the post-socialist period are regulated by market or policy changes, which is influenced by the demand and supply of herbivore products.

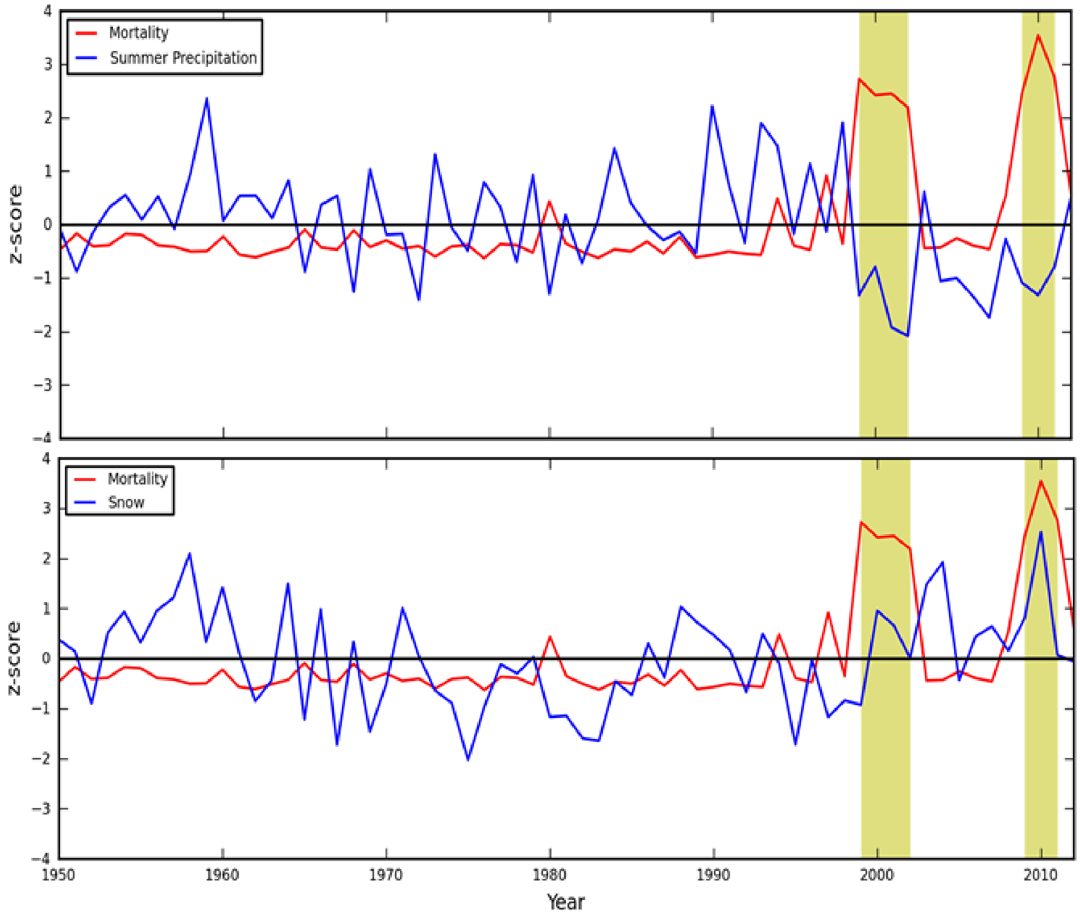


Figure 5-4 Mortality due to extreme climatic conditions (drought/dzud) in Mongolia. Comparison of mortality with summer precipitation (top) and snowfall (bottom)

5.2.2 Experimental Design

To determine the magnitude and relative contribution of different environmental factors, a total of eight simulation experiments were performed (Table 5.1). The relative contributions of each factor were calculated as a difference between "All-combined" and simulation in the absence of contributing factors (climate, CO_2, nitrogen, deposition, grazing, land cover land use change and policy shift). For example, the relative contribution of climate factors was estimated as a difference between “All-combined” and “No-climate” simulation. In addition, the overall contribution of multiple environmental changes was obtained as a difference between “All-combined” and “Reference” simulation.

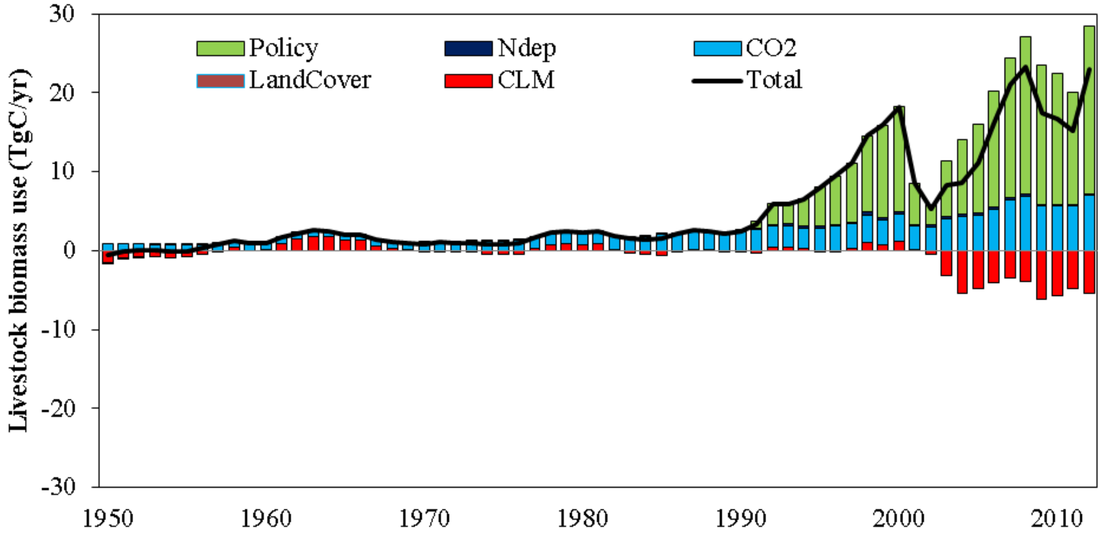


Figure 5-5 Livestock biomass use and its response to multiple environmental changes in the Mongolian Plateau

5.2.3 Statistical Analysis

In this study, we applied the non parametric Mann-Kendall method (Mann 1945, Kendall 1975) to detect statistically significant trends in simulated carbon pools and fluxes. The magnitude of trends were assessed by computing a Theil-Sen slope, which is a more robust method to estimate slope than simple least square models (Sen 1968). We used slope computed from prewhitened values using the R package “zyp” (Bronaugh and Werner 2013) to correct for the spatial autocorrelation. In addition, we used spearman correlation to quantify the relationship between environmental factors and carbon pools and fluxes. We also used R (https://www.r-project.org/) to perform regression analysis in order to understand the response of herbivores and ANPP to multiple environmental factors.

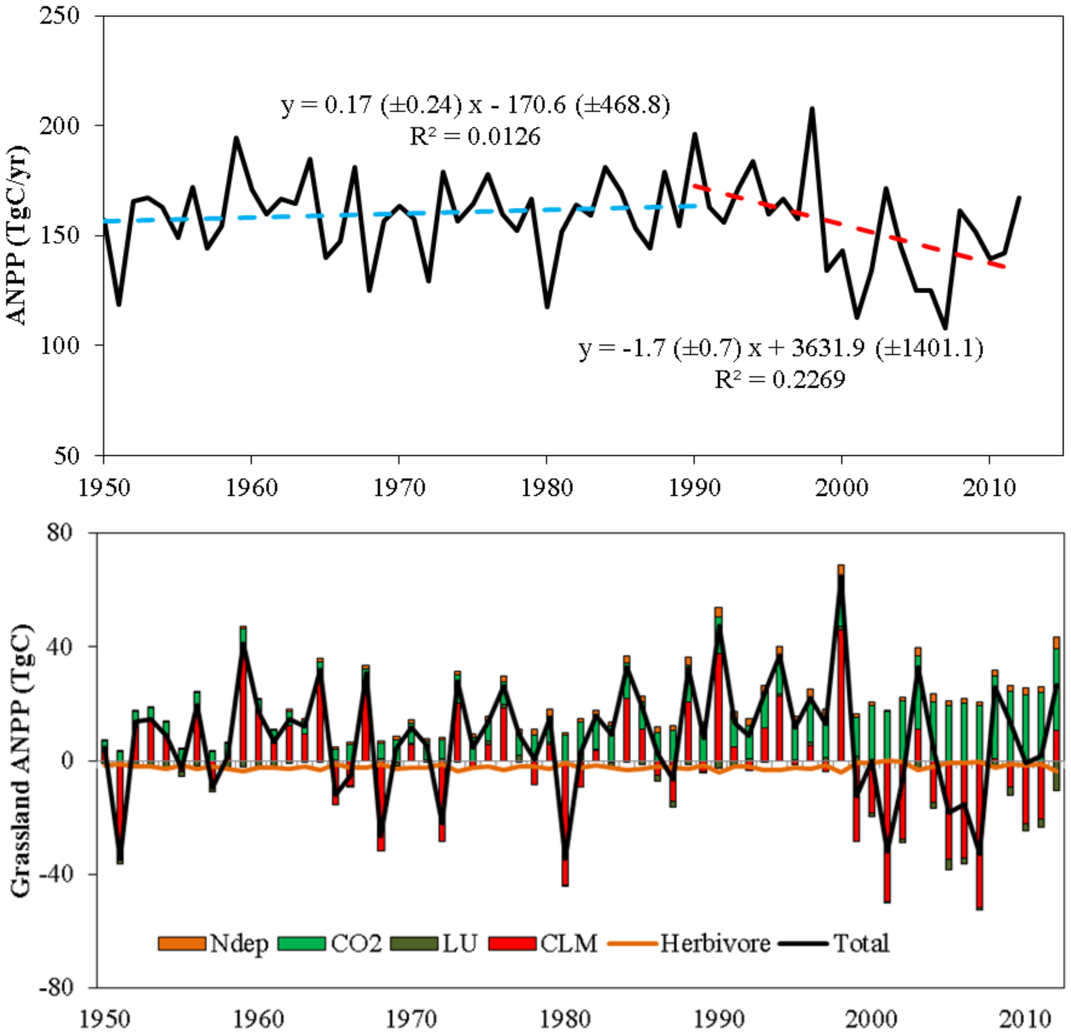


Figure 5-6 Grassland productivity (ANPP) in response to multiple environmental changes (top panel) and contribution of multiple environmental changes on ANPP (bottom panel) during 1950-2012

To estimate the effect of climate change and grazing on ANPP, we first obtained the climate and grazing induced changes in ANPP based on S1-S3 and S1-S2 simulations, respectively (see Table 5.1). We then estimated the average change in ANPP from climate and grazing effect during 2000-2012. Vulnerability to climate and grazing was measured as sum of grid cell area that has experienced negative changes in ANPP as a result of climate and grazing only effect during 2000-2012.

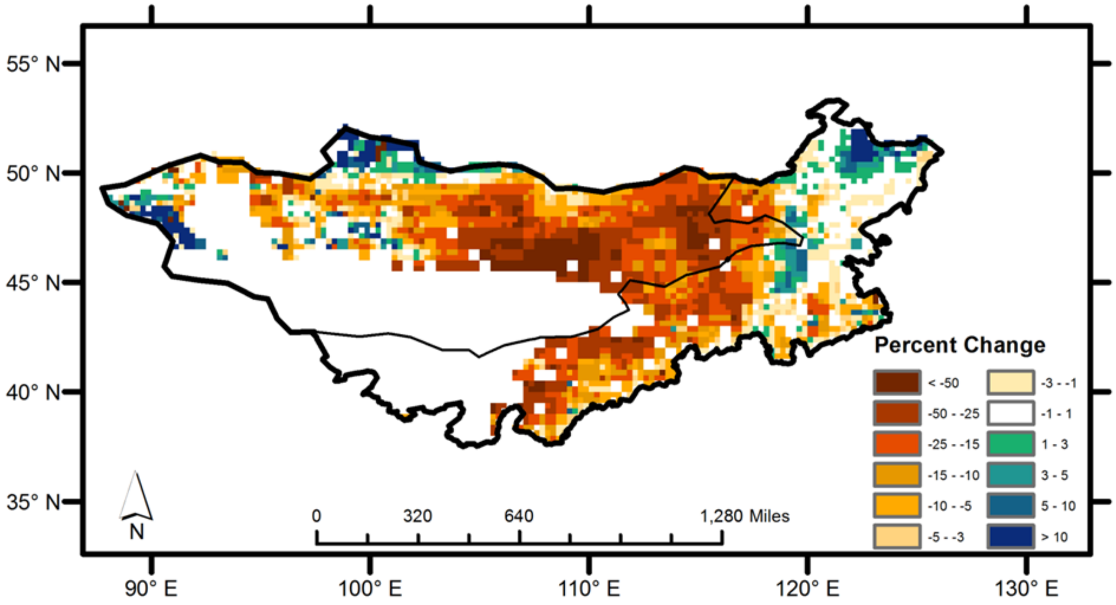


Figure 5-7 Percent change in grassland ANPP as a result of multiple environmental factors in the Mongolian Plateau during 2000-2012

5.3 Results

5.3.1 Livestock growth and productivity

The total number of livestock increased significantly during 1950-2012 at the rate of 0.6 million head/yr (p-value < 0.05; $R^2 = 0.70$) (Figure 5.3). Separation of the simulated livestock numbers into different time periods showed that livestock population increased at a rate of 0.17 and 1.5 million head/yr during the Soviet Union and post-Soviet Union period, respectively (p-value < 0.05). Across different livestock types, our results show that cattle, sheep and goat increased by 20.2%, 14.8% and 114.5%, respectively. But, horse population declined by 5.5%.

5.3.2 Livestock mortality

Our study also indicated that extreme climatic events resulted in mass mortality of livestock, particularly during the post-Socialist period due to increased livestock numbers and decreased carrying capacity of land. Extreme events (drought and/or *dzud*) resulted in the maximum mortality of up to 28% (Figure 5.4). In particular, the combination of drought and *dzud* resulted in the mortality of 8.7 million during 1999-2001 and 10.2 million livestock during 2009-2010.

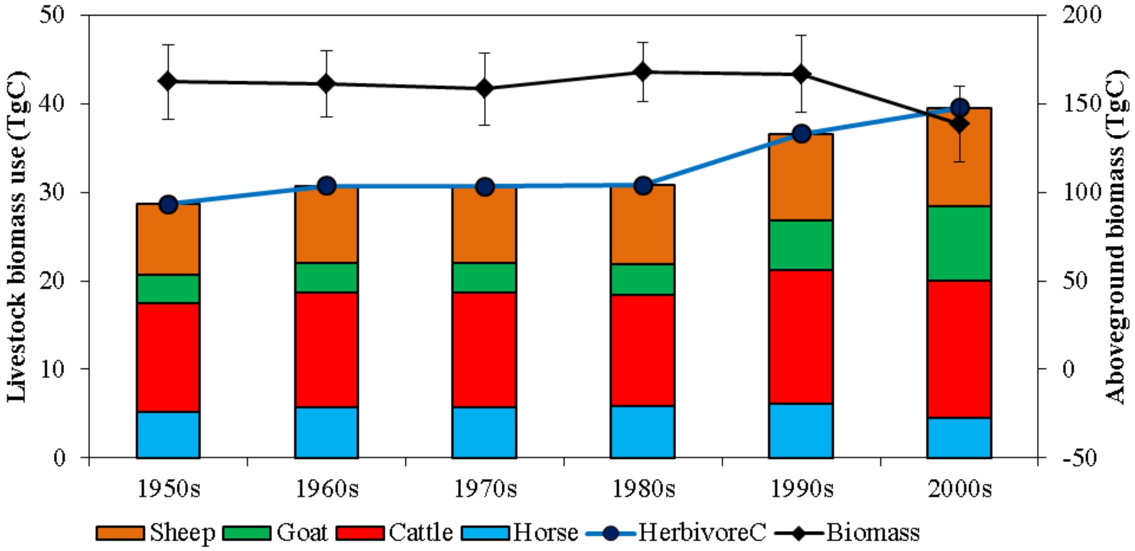


Figure 5-8 Decadal change in livestock biomass use and aboveground net primary productivity (ANPP) during 1950-2012

5.3.3 Livestock biomass use

Our results also show that biomass use has increased by 41% from 28.8 TgC/yr in the 1950s to 40.6 TgC/yr in the 2000s, largely due to an increase in the number of cattle, sheep and goat by 20.2%, 14.8% and 114.5%, respectively. The livestock biomass use was affected by changes in multiple environmental factors including climate, elevated CO_2 concentration, land use/cover change, nitrogen deposition and market/policy changes (Figure 5.5). Analysis of the contributing factors to livestock growth and biomass use showed that market/policy changes, elevated CO_2 and nitrogen deposition resulted in an increase in biomass use by 70.3%, 39.0% and 2.6%, respectively during 1950-2012. However, climate had a net negative impact on biomass use of livestock by 14.1%.

5.3.4 Grassland response to environmental changes

Simulated ANPP response to multiple environmental factors showed that ANPP has been increasing at the rate of 0.17 TgC/yr during the Soviet Union period, but the effect was not significant (p-value = 0.48). However, ANPP showed a significant decline during the post-Soviet Union period at the rate of 1.74 TgC/yr (p-value < 0.05; $R^2 = 0.23$). Assessment of the contributing factors showed that climate and grazing reduced grassland ANPP by 3.6% and 25.4% during 1950-2012 (Figure 5.6). However, elevated CO_2 and nitrogen deposition resulted in an increase in ANPP by 69% during the same time period. During the post-Soviet Union period, climate change and grazing resulted in a net reduction in ANPP by 61.4% and 23.2%, respectively.

5.3.5 Interaction among climate, grassland productivity and grazing

The combined effects of climate change and grazing resulted in a decline in ANPP over 83% of the grassland area in the MP during the 21st century (Figure 5.7). This decline in ANPP is largely due to increased grazing pressure (23.2%) and climate change (61.4%) since the 1990s. In particular, approximately 8% of the total grassland area has experienced decline in ANPP by more than 50%, indicating increased vulnerability of grassland ecosystems to climate change and grazing in the MP. Our results also show an increase in biomass use by 41%, but a decline in grassland productivity by 15% since the 1950s (Figure 5.8). When compared with the total grassland production in the MP, we found that livestock consumed 18% of the total available biomass in the 1950s, which has increased to 30% in the 2000s.

5.4 Discussion

5.4.1 Simulated livestock production and its dependence on environmental and policy factors

Livestock productivity

The existing studies on the impact of multiple environmental factors on livestock population suggests that changes in temperature, precipitation, atmospheric CO_2 concentration and nutrient availability have both direct and indirect impact on livestock growth and biomass use (McMichael et al. 2007, Backlund et al. 2008, Thornton et al. 2015). The direct impacts include changes in livestock nutritional requirement, development time and mortality during extended period of droughts and freezing winters, while the indirect impacts include changes in food quality and quantity, which ultimately determines the body condition of livestock (Gill et al. 2010b, Pachzelt et al. 2013). Likewise, the demand and supply of livestock products also affect livestock production, which could lead to changes in herd size and composition (Chen et al. 2015a). Our results indicate that both environmental and market/policy changes have resulted in a significant increase in livestock population at a rate of 0.6 million head/yr during 1950-2012. The overall increase in livestock population can be broadly categorized into two time periods: 1) Soviet Union (1950-1990) and 2) post-Soviet Union (1991-2012). We found that there was a dramatic change in herd structure and composition following the collapse of Soviet Union during the early 1990s, which led to an increase in the number of cattle, sheep and goat by 20.2%, 14.8% and 114.5%, respectively. But, horse number declined by 5.5%.

Policy impacts

Our results also indicate that market/policy changes, elevated CO_2 concentration and nitrogen deposition contributed to an increase in livestock productivity by 70.3%, 39% and 2.6%, respectively. However, climate change had an overall negative impact on livestock production by 14.1%. Market/policy changes, in particular, played an important role not only in increasing the total numbers, but also in changing the composition of livestock. For example, collapse of former Soviet Union in the early 1990s resulted in transitioning to private herd ownership, which led to a dramatic increase in livestock population and changes in their composition (Johnson et al. 2006). The largest increase in livestock productivity is linked to a significant increase in goat population by 114.5% since the 1990s due to rapid growth of cashmere industry that provides high economic return (Arulpragasam et al. 2004, Berger et al. 2013). In the DLEM 3.0, the transition from central to market economy and private herd ownership after the collapse of former Soviet Union is represented by developing a scalar that account for an increase in livestock numbers. The scalar is derived as a ratio of 30-year average (1961-1990) to country level FAO livestock numbers for different livestock groups during 1991-2012, which is applied directly to livestock pool. Our approach, although conservative, provides an estimate of how great the effect of market/policy changes will have on livestock population and their composition. For example, Shabb et al. (2013) used similar approach to simulate livestock population dynamics by separating the study area into seven different periods, such that separate set of parameters were used for each time period to simulate livestock population during socialist, post-socialist, *dzud* and drought years. Meanwhile, to make the model applicable at different scale, we developed a regional scalar to quantify the impact of market/policy changes on livestock productivity. Higher livestock population due to transition from central to market economy led to an increase in livestock biomass use by 70.3% since the 1990s. Thus, our study confirms that policy changes had a substantial impact on livestock size, composition and biomass use in the MP.

Elevated atmospheric CO_2 and nitrogen deposition

Elevated atmospheric CO_2 concentration and nitrogen deposition have the potential to affect livestock growth and biomass use by altering the quantity and quality of aboveground biomass (McMichael et al. 2007, Mader et al. 2009). Our results indicate that both elevated CO_2 and nitrogen deposition increased livestock productivity and biomass use by 69% during 1950-2012. This increase was primarily attributed to an enhancement in carbon uptake due to CO_2 fertilization effect and increased nitrogen availability for plant growth, which ultimately led to an increase in aboveground biomass (Dijkstra et al. 2008, Donohue et al. 2013) and carrying capacity of the land. Elevated CO_2 can potentially affect livestock production and biomass use in two ways: 1) an increase in non-structural carbohydrates which enhances grass quality (Barbehenn et al. 2004), thereby increasing livestock biomass production and use, and 2) a decline in plant nitrogen and crude protein content which decreases grass quality (Milchunas et al. 2005), thereby decreasing livestock production and biomass use. Our results suggest that enhancement of carbon uptake as a result of elevated CO_2 and nitrogen deposition overwhelmed any potential decline in plant nitrogen and crude protein content resulting in an overall increase in livestock production. In the DLEM 3.0, we assume an exponential decrease in crude protein content with increasing biomass (van Wijngaarden 1985) while the enhancement in carbon uptake due to CO_2 fertilization is based on a linear function of atmospheric CO_2 concentration (Ainsworth and Long 2005). Our study is similar to other studies, which found that non-structural carbohydrates increased by up to 37% compared to a decline in total nitrogen content by up to 21% (Poorter 1993, Wand et al. 1999). Similarly, at 475 ppm atmospheric CO_2 concentration expected around 2030, Newton et al. (2006) found no significant change in gross nutrient composition of grasses, although plant-level nitrogen content declined by about 11%, which was compensated by greater abundance of high nitrogen containing species. Likewise, nitrogen deposition can stimulate grassland production and improve forage quality by increases in tissue nitrogen content of grassland communities (Plassmann et al. 2009, Phoenix et al. 2012). Thus, it is likely that even under elevated CO_2 and nitrogen deposition, grassland ecosystem would not affect nutrition quality (Newton et al. 2006) or even remain more nutritious due to higher levels of protein and non-structural carbohydrates (Barbehenn et al. 2004), which could potentially increase livestock growth and biomass use as evident in this study.

Climate change

Climate change can impact livestock production in two possible ways: 1) direct effect on livestock performance due to changes in air temperature, humidity and heat waves and 2) indirect effect on livestock growth and maintenance due to changes in the quantity and quality of available biomass and changes in the distribution of livestock diseases and pests (Valtorta 2002, McMichael et al. 2007). In the DLEM 3.0, we consider both direct and indirect impact of climate on livestock population. Direct impact include extreme events such as maximum temperature, drought and *dzud*, which could lead to reduction in livestock productivity through adjustment in metabolic rate (Coulson et al. 2001, Nardone et al. 2010, Walthall et al. 2013). Indirect impacts include climate induced changes in available biomass, which ultimately determines livestock carrying capacity. Our results demonstrate that extreme events (drought/*dzud*) led to the maximum cumulative mortality of up to 28%, while climate induced changes in available aboveground biomass led to decline in livestock biomass use by 11.9%. Climate related mass mortality of livestock has been strongly linked to summer droughts across different continents (Nardone et al. 2010, Key et al. 2014, Kgosikoma and Batisani 2014, Megersa et al. 2014, Rao et al. 2015), while extreme winter condition (*dzud*) has been linked to livestock mortality in countries like Mongolia, where average winter temperatures ranges between -15^oC to -30^oC

(Dagvadorj et al. 2009b). For example, consecutive drought and *dzud* event of 1999-2002 resulted in a mortality of 30% of the livestock in Mongolia (Fernandez-Gimenez et al. 2012b), while *dzud* of 2010 resulted in a mortality of 20% of the livestock (Sternberg 2010). Our results also show that a combination of drought and *dzud* of 1999-2000 resulted in 28% mortality while *dzud* of 2010 resulted in 15% mortality of the livestock. A slight under-estimation of direct climate impacts on livestock mortality is likely due to differences in livestock management system following extreme events, which are more developed in Inner Mongolia compared to Mongolia (Chen et al. 2015b). For example, during extreme events livestock in Inner Mongolia can rely more on purchased fodder compared to Mongolia (Wang et al. 2013) suggesting that some of the factors that could dampen the direct impacts of climate on livestock are not included in the model.

5.4.2 Impact of multiple environmental changes and livestock on grassland productivity

Grassland productivity and multiple environmental changes

Quantifying the impact of multiple environmental changes on grassland productivity is challenging due to the number of factors and the possible interaction among these factors, which mediates physiological, ecological and biogeochemical aspects of ecosystem function (Shaw et al. 2002, Zavaleta et al. 2003, Zhu et al. 2016a). Our simulated results indicate that climate increased ANPP by 30% during the Soviet Union era (1950-1990), but decreased ANPP by 61.4% during the post-Soviet Union era (1991-2012). The decline in productivity due to climate effect was offset by increased CO_2 fertilization and nitrogen deposition by up to 89% during 1991-2012. Elevated CO_2 concentration can stimulate plant growth across different biomes (Norby et al. 2005, Wang 2007), although the magnitude of CO_2 fertilization effect is moderated by climate and the type of plant (Morgan et al. 2011). For example, arid and semi-arid ecosystem experience greater stimulation effect from CO_2 due to reduced evapotranspiration, which is mediated by reduction in stomatal opening (Owensby et al. 1999, Niklaus and Körner 2004). Our results suggest that CO_2 fertilization effect was more dominant during dry years accounting for up to 140% increase in ANPP. But, during wet years CO_2 fertilization effect accounted for up to 58% of the increase in ANPP. Likewise, nitrogen deposition has been found to increase net primary productivity in grassland ecosystem, but the magnitude and extent of biomass response is mediated by precipitation and soil moisture availability (Zavaleta et al. 2003, Xia and Wan 2008). Although increases in primary production has been linked to high nitrogen enrichment in grassland ecosystem, reduction in plant species diversity has often be reported (Stevens et al. 2004), with greater species loss in communities experiencing cold temperatures (Clark et al. 2007). Our study indicate that nitrogen deposition led to an overall increase in ANPP by up to 12% and 23% during dry and wet years, respectively. The higher response of ANPP to nitrogen deposition during wet years is likely because high soil moisture has been suggested to enhance nitrogen mineralization making more nitrogen available for plant use (Lee et al. 2010, Dangal et al. 2016).

Grassland productivity and grazing

Grazing by livestock has a substantial impact on primary productivity of grasslands (McNaughton et al. 1997, Bardgett and Wardle 2003, Augustine and McNaughton 2006), but the magnitude and direction of this effect vary widely across ecosystems as a function of temperature and moisture limitations, density of livestock and type of grazing management. In arid and semi-arid grasslands, there has been no consistent evidence of grazing induced changes in primary production, with studies indicating both positive and negative impacts of grazing on ANPP (Milchunas and Lauenroth 1993, Milchunas and Vandever 2013, Hilker et al. 2014).

Positive effects of grazing on ANPP are linked to faster nutrient cycling (due to livestock excretion) and reduced transpiration, which could potentially alleviate both nitrogen and moisture limitation (Augustine and McNaughton 2006, Dangal et al. 2016). But, grazing may offset any positive impact on plant growth due to faster nutrient cycling and lower transpiration by reducing litter input and increasing surface evaporation. Our results indicate that grazing resulted in a decline in ANPP by 23.2%, due to 41% increase in biomass use from 28.8 TgC/yr in the 1950s to 40.6 TgC/yr in the 2000s. Increased biomass use is associated with 2.5 fold increase in livestock numbers between the Soviet Union and post Soviet Union era. This non-linear effect is prevalent at the regional scale in MP because of the spatial variation in livestock density, with larger negative impact in areas that experience high livestock density (for example, central and north eastern Mongolia, southern Inner Mongolia), but positive impact in areas with low livestock density and favorable climatic condition.

Climate change, grazing and grassland productivity

Climate change and grazing have profound impacts on grassland productivity and vegetation greenness in arid and semiarid ecosystems (UNEP 2002, Liu et al. 2013, Hilker et al. 2014). These impacts could be positive, negative or neutral depending on ecosystem type, prevalent climatic conditions and grazing intensity (Oesterheld et al. 1999b, Christensen et al. 2004, Augustine and McNaughton 2006, Fan et al. 2010). Our results indicate that about 83% of the grassland area in the MP has experienced decline in ANPP during the 21st century. This decline is attributed to climate change and increasing grazing pressure, which resulted in a decline in grassland ANPP by 61.4% and 23.2%, respectively since the 1990s. The estimates of grassland degradation are comparable with other studies, which suggest decline in grassland resources by up to 70% (UNEP 2002, Liu et al. 2013). However, there exist considerable uncertainty regarding the contribution of climate and grazing on grassland degradation in the MP. While Liu et al. (2013) attributed 60% of the decline in vegetation optical depth to variations in rainfall and surface temperature, Hilker et al. (2014) attributed 80% of the decline in vegetation index to grazing. This seemingly contradictory finding indicate that the complex interaction among climate change, grazing and other environmental factors might be responsible for explaining the differences across studies. Our results are close to Liu et al. (2013), attributing 61.4% of the decline in grassland aboveground productivity to climate change. However, our results disagree with Hilker et al. (2014), who attributed 80% of the decline to grazing. This disagreement is likely because Hilker et al. (2014) suggests that the impact of summer precipitation on grassland regeneration was responsible for lower negative effect of climate compared to grazing on grassland vegetation index. However, we did not considered how grazing induced changes in grassland biomass affect the growth and regeneration of other plant species. Additionally, both the spatial pattern and contributing factors to grassland degradation as evident in this study are closer to Liu et al. (2013) because vegetation optical depth is a better proxy for vegetation water content and aboveground biomass.

5.5 Conclusions

In this study, we examined the interaction among climate change, grazing and livestock growth and productivity in the Mongolian Plateau during 1950-2012. We specifically assessed how multiple environmental changes and policy shifts have altered livestock growth and biomass use, and grassland productivity in the study area. We found that market/policy change, climate and increased livestock pressure have accelerated grassland degradation in the MP. Our results indicate that 1) Mongolian grasslands productivity has declined significantly during 2000-2012, with approximately 83% of the grassland area considered degraded in some form; 2) Decline in grassland productivity was increasingly controlled by livestock grazing (-23.2%) and climate change (-61.4%) since the 1990s; and 3) Livestock biomass use has increased by 41%, with the largest contribution from market/policy changes (70.3%) since the 1990s. Given the projected change in climate and more than 2 fold increase in sheep and goat numbers in the next 10 years, it is likely that the MP will experience further degradation, with potentially severe consequences on grassland ecosystems and societies. Improving the resilience of Mongolian grasslands to climate change and grazing requires sustainable management strategies that focus on both climate change mitigation and grazing optimization.

Chapter 6. Global Impacts of Climate Change and Grazing on Vegetation and Soil Organic Carbon during 1901-2010: A process-based Modeling Study

Abstract

Soils are an important reservoir of carbon, and carbon losses from soil can affect atmospheric CO_2 concentration and climate change. In particular, livestock grazing and climate warming could potentially alter soil carbon stores. But the extent to which livestock grazing and climate change affect soil organic carbon (SOC) has not been investigated well at the global scale. Here we used the Dynamic Land Ecosystem Model (DLEM) to quantify the long-term changes in SOC, and attribute those changes to grazing and climate change during 1901-2010. Results indicate that grazing and climate change reduced SOC at the rate of 242 TgC/yr and 42 TgC/yr, respectively. Over the century long time scale, livestock grazing and climate reduced SOC by 13.4 PgC (2%) and 2 PgC (0.5%), respectively. The grazing induced reduction in SOC was largely due to a decrease in litter production (12%) and belowground carbon (7%). Climate, on the other hand, decreased SOC due to low biomass production in the tropics and high soil decomposition in the temperate and boreal region. Likewise, livestock grazing decreased net primary production (NPP) at the rate of 28.5 TgC/yr, while climate change increased NPP at the rate of 10 TgC/yr during 1901-2010. Our results demonstrate that the effects of grazing on SOC and vegetation carbon are highly context specific with grazing intensity playing more important role in the dynamics of SOC compared to other environmental factors. These findings highlight the importance of including grazing as a major ecosystem processes into global land models for

accurately quantifying the impact of global changes and grazing on ecosystem processes and assessing the climate-biosphere feedbacks.

6.1 Introduction

Soil Organic Carbon (SOC) is the largest terrestrial reservoir of carbon storing about 425 - 2200 Pg C (Batjes 1996, IPCC 2007a, Tian et al. 2015c). Grassland ecosystem, in particular, store a majority of their carbon in soils (Conant et al. 2001), and are influenced by climate, grazing, land-use and management and other environmental factors. Globally, carbon sequestration in grassland vary from 0.02 to 0.08 Mg C/ha/yr in arid climates, 0.03 to 0.12 MgC/ha/yr in semiarid climates, and 0.08 to 0.2 MgC/ha/yr in semi-humid to humid climate (Lal 2000). Grazing by domestic herbivores in grassland ecosystem are considered as an important form of land use that could potentially alter carbon sequestration by modifying the structure and function of ecosystems (Milchunas and Lauenroth 1993, Piñeiro et al. 2010). While short-term effects of grazing on some ecosystem attributes (leaf area index, aboveground biomass, soil properties) at the site level have been studied extensively (McNaughton 1979, Cingolani et al. 2005), their long-effect on both vegetation and soil carbon at regional to global scale remains unclear.

Grazing by domestic herbivores influences SOC through two major pathways: 1) modifying the soil microenvironment, which control soil organic matter decomposition; and 2) changing the pattern and amount of litter inputs, which control the amount and quality of substrate necessary for soil carbon formation (Piñeiro et al. 2010, McSherry and Ritchie 2013). Previous studies have demonstrated that grazing increase soil bulk density (Neff et al. 2005, Zhou et al. 2016), increase or decrease root production (Pucheta et al. 2004), increase or decrease leaf area index and biomass production (McNaughton 1983, Bardgett and Wardle 2003) and changes biomass allocation patterns (Holland et al. 1996, Zhou et al. 2016) resulting in positive or negative effect on SOC. However, the extent to which these site level positive or negative changes in biomass production, litter inputs and carbon allocation will alter SOC at regional to global scales needs further investigation.

Grazing also has the potential to change carbon allocation patterns among different plant organs. For example, grazing effects on aboveground biomass production are variable, but mostly negative (Oesterheld et al. 1999a). However, grazing effects on SOC seems to increase, decrease or remain constant over time due to the effect of grazing induced changes in root production. For example, Piñeiro et al. (2010) found that grazing impact on SOC varied across a precipitation gradient altering the amount of carbon allocated to roots. Carbon allocation to roots mostly increased following grazing (Johnson and Matchett 2001), although the net impact depend on the intensity of grazing and how grazing induced changes in soil moisture and nutrient availability affect soil organic matter formation.

The impact of grazing on SOC is also affected by grazing intensity and the type of grasslands (Bardgett et al. 2001, Han et al. 2008a). For example, McSherry and Ritchie (2013) found that grazing increased SOC under heavier intensities in C4 dominated grasslands due to increases in fine and shallow roots, but decreased SOC in C3 dominated grasslands due to reduction in CO_2 fixation and carbon inputs to the soil. Other studies, however, indicate that light grazing contribute to an increase, but moderate and heavy grazing significantly decrease SOC regardless of the type of grasslands (He et al. 2011, Wu et al. 2012, Zhou et al. 2016). Studies that do not consider different grazing intensities suggest an increase, decrease or no change in SOC across temperature and precipitation gradients indicating that grazing influences SOC in a complex way (Han et al. 2008a, Ingram et al. 2008, Chadwick et al. 2011). While numerous studies have been conducted to quantify the response of SOC to grazing at site level, there is limited understanding of how grazing impacts SOC at regional to global scales. One way to explore how grazing affect SOC at regional to global scale is to consider grazing processes including changes in litter inputs, leaf area index and carbon allocation in the global land model.

In this study, we used the Dynamic Land Ecosystem Model (DLEM) to quantify the effects of grazing on both aboveground and belowground carbon dynamics and how that regulates long-term changes in SOC during 1901-2010. Specifically, we 1) examine global patterns of SOC and vegetation carbon changes with and without grazing; 2) quantify effect of different grazing intensities on carbon fluxes (NPP); and 3) investigate the role of multiple environmental factors on SOC. We hypothesize that higher grazing intensities decreases SOC by reducing carbon fixation due to loss of photosynthetic tissue and reducing belowground biomass due to lower litter fall. However, under low to moderate intensity, grazing would increase SOC by improving light absorption, reducing water loss through transpiration and increasing nitrogen mineralization rates making more nitrogen available for plant use.

6.2 Methods

6.2.1 Improvements in the DLEM

We specifically improved the carbon allocation routine in the DLEM by adding the relative allocation scheme developed by Friedlingstein et al. (1999). The scheme considers resource limitations (stresses) of two types: 1) aboveground limitation of resources where plants will allocate more resources to accrue more carbon if belowground resources such as nitrogen and water are not limiting; and 2) belowground limitation of resources where plants will allocate more resources to fine and coarse roots if light (aboveground resource) is not limiting. DLEM assumes that only the most limiting one of the two belowground resources drives the allocation pattern (i.e. the controlling resources are light and either water or nitrogen). In summary, the model behaves as if one above-ground resource (light) directly controls the stem (sapwood) allocation of available storage carbon and one below-ground resource (water or nitrogen) drives the root allocation of available storage carbon.

$$\rho = 3r_0 \times \{L/[L + 2 \times \min(W, N)]\}$$

$$\sigma = 3s_0 \times \{\min(W, N) /[\min(W, N) + 2L]\}$$

$$\lambda = 1 - \rho - \sigma$$

where r_0 and s_0 are the fractional carbon allocation to root and stem for non-limiting conditions, respectively. In normal conditions, both r_0 and s_0 is set to 0.3, giving a leaf allocation of 0.4 under condition where resources are totally non-limiting. L, W, and N are light, water and nitrogen availability scalars, ranging from 0.01 (severely limited) to 1(readily available).

DLEM use the canopy leaf area index (LAI) to estimate L, the light availability scalar:

$$L = \exp(-k \times LAI)$$

where k is an extinction coefficient set to 0.5. This scalar serves as an index, indicating the extent to which a plant at the base of the canopy might increase it access to light through increased stem.

The water availability scalar, W, is determined by soil moisture factor β, ranging from 0 to 1:

$$W = \beta$$

The nitrogen availability scalar, N, is determined based on the quotient of vegetation nitrogen content and maximum vegetation content,

$$N = \frac{\sum_{i=1}^{5} n_i}{\sum_{i=1}^{5} c_i / CN_{min,i}}$$

where i represent leaf, sapwood, coarse root, fine root, and reproduction pool; n_i and c_i are the amount of nitrogen and carbon in each pool; $CN_{min,i}$ is the minimum carbon to nitrogen ratio for each tissue.

The impact of grazing on carbon, nitrogen and water balance is based on Dangal et al. 2016 (Chapter 4).

6.2.2 Input datasets

The model input data include annual historical land cover maps, daily climate data, monthly atmospheric CO_2 concentrations, and soil property and topography data at each site. The vegetation map for each site was extracted from global vegetation distribution map based on National Land Cover Data (NLCD, 2001) at a resolution of 30m × 30m. We used climate data (average, maximum and minimum temperatures, precipitation totals and shortwave radiation) based on CRUNCEP. Monthly atmospheric CO_2 concentrations 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 (www.daac.ornl.gov).

In addition to the above datasets, DLEM now requires grazing intensity (livestock units/hectare) data to drive the model. Gridded data on livestock heads of dairy cattle, non-dairy cattle, sheep and goat were obtained from the previous study. In this study, livestock species are converted to LU based on the calculation of metabolisable energy (ME) requirement of each type of animal. ME (also called net energy) is the amount of energy an animal needs for maintenance and for activities such as growth, lactation and pregnancy. The total number of ruminant livestock (Ntotal; in LU) is calculated as:

$$N_{total} = \frac{ME_{total}}{ME_{LU}}$$

where ME_{LU} is the ME requirement by one LU defined in this study (an adult dairy cow producing 3000 kg milk annually, with live body weight of 600 kg; Eurostat, 2013); MEtotal is the annual total ME requirement by all major ruminants, and is given by:

$$\mathrm{ME_{total}} = \sum(\mathrm{ME_i} \times \mathrm{N_i})$$

where N_i is number of animals in category i and ME_i is the ME requirement of animals in category i. The category i indicate whether the animals are dairy cattle, non-dairy cattle, sheep or goats.

6.2.3 Model parameterization, calibration and evaluation

The DLEM has been parameterized against long-term observation data for major plant functional types and extensively applied at the stand, country, regional and continental scales (Tian et al. 2010a, Tian et al. 2011c, Lu et al. 2012, Ren et al. 2012). We calibrated the model for C3 grassland using site level ANPP data in Inner Mongolia, China. The model was then applied to evaluate its performance with and without herbivory based on observation data from Ma et al. (2010) and Schonbach et al. (2014) (see Dangal et al. 2016). In this study, to make the model applicable at global scale, we performed model evaluation by comparing simulated vegetation and soil carbon against Harmonized World Soil Database (HWSD). First we compared the vegetation carbon based on IPCC tier I global biomass carbon map for the year 2000 (http://cdiac.ornl.gov/epubs/ndp/global_carbon/carbon_documentation.html) developed by Ruesch and Gibbs (2008). The vegetation biomass carbon was estimated by combining vegetation map from the Global Land Cover 2000 Project based on SPOT-VEGETATION satellite product to identify actual biome type such as forest, grassland, shrubland, cropland, mosaics and desert. Comparison of DLEM-simulated vegetation carbon against Ruesch and

Gibbs (2008) show that DLEM tend to under-predict vegetation carbon by 15% (379 PgC based on the DLEM vs 445 PgC based on observation).

We also compared DLEM simulated SOC against estimates based on harmonized world soil database (Hiederer and Köchy 2011) for the top 100 cm soil layer in 2000. The HWSD v1.2 provides one of the most updated and coherent global datasets for SOC, which was developed by combining existing maps of soil types with soil characteristics, derived from the WISE (v2) database containing about 9600 soil profiles. The DLEM simulation under-predicted SOC by 38% when compared to HWSD (702 PgC based on DLEM vs 1141 PgC based on observation). The inconsistencies are found in the United States and Australia. This is because HWSD does not include an extensive database on soil maps and therefore fail to consider different soil types in these countries (Köchy et al. 2015). In addition, Köchy et al. (2015) found large uncertainty (in the range of -56 to 180 PgC) in the estimate of global SOC in the top 1 cm, due to differences in estimates of bulk density, which is an important variable to estimate SOC.

6.2.4 Model implementation

The model simulation at site level follows three-step procedure: an equilibrium simulation, a model-spin up and a transient simulation. The model simulation begins with an equilibrium stage with long-term average (1901-1930) climate data and 1901 levels of atmospheric CO_2 concentration and vegetation cover. The equilibrium run is carried out for 10000 years at most until the net carbon exchange between the atmosphere and the site is less than 0.1 gC m^{-2}, 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 gN m^{-2} 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 model spin-up is performed so as to remove the model bias or sudden jump from equilibrium to transient simulation. After the model spin-up, the transient simulation is conducted using daily climate data and monthly atmospheric CO_2 concentration with time-series vegetation cover maps. We performed two specific simulations during the transient phase. The first simulation was an all combined simulation in which all environmental factors including herbivory were allowed to vary during 1901-2010. The second simulation was a simulation in the absence of herbivory but all other environmental factors were allowed to vary during 1901-2010. The difference between the two simulations was used to assess the impact of herbivores on SOC pools and NPP.

6.3 Results

6.3.1 Temporal variation in SOC due to climate and grazing

The results show that changes in multiple environmental factors resulting in a significant decline in SOC at a rate of 81.0 Tg C/yr during 1901-2010 (p-value < 0.05; $R^2 = 0.62$; Figure 6.1). In particular, grazing and climate change resulted in a significant decline in SOC by 13.4 TgC/yr and 2 PgC/yr during 1901-2010 (p-value < 0.05). However, a combination of other environmental factors including elevated CO_2 concentration, nitrogen deposition, tropospheric ozone, LCLUC and land management practices resulted in a significant increase in SOC by 8 PgC/yr (p-value < 0.05; $R^2= 0.91$). Globally, grazing decreased annual SOC by 2%, while climate decreased annual SOC by 0.5%.

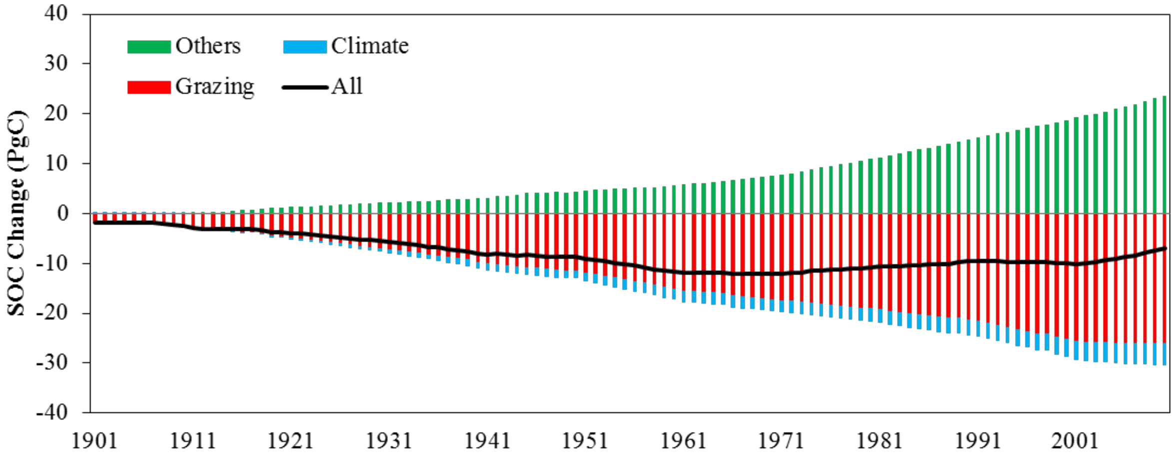


Figure 6-1Changes in SOC due to climate, grazing and other environmental factors

Other simulation includes the influence of elevated CO_2 concentration, nitrogen deposition, ozone, LCLUC and land management practices on SOC.

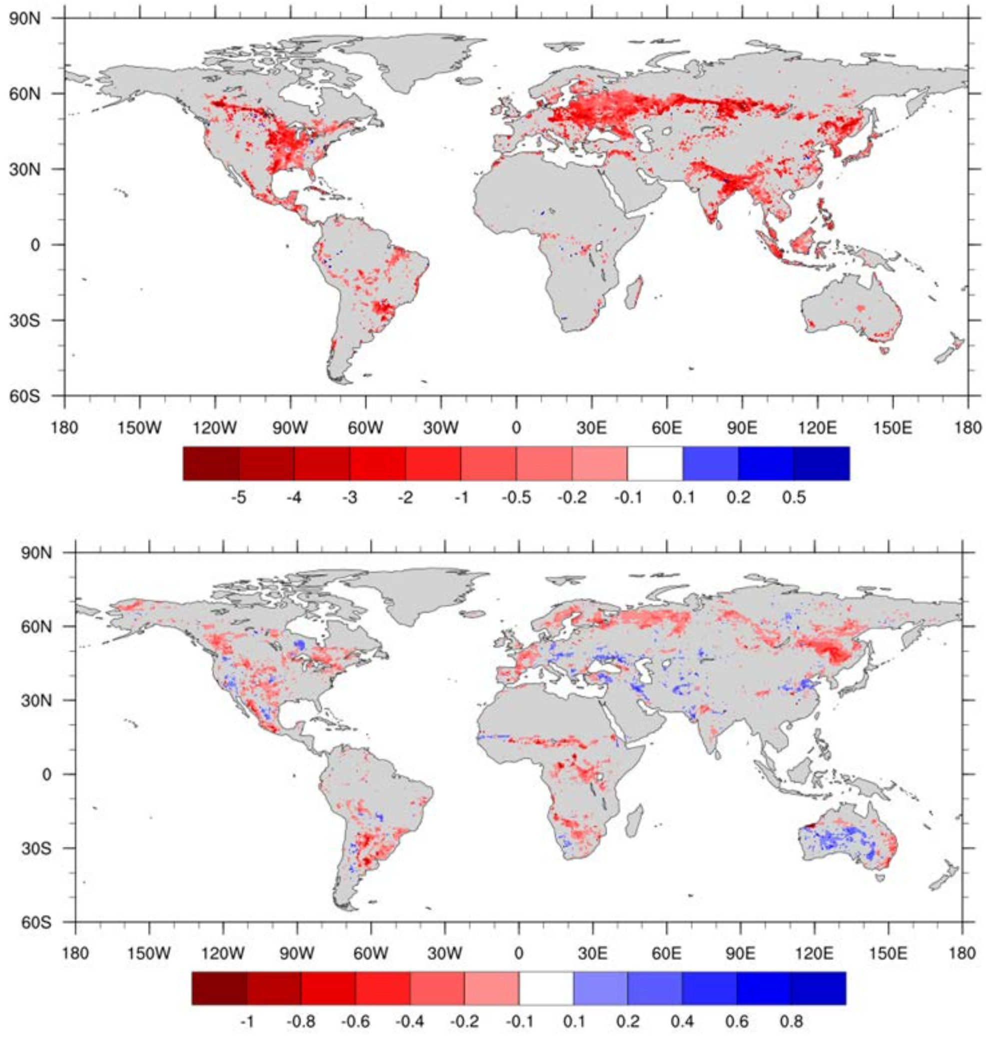


Figure 6-2 Impact of Livestock grazing (top panel) and climate change (bottom panel) on SOC calculated as a difference between 2000s and 1900s. All units are in KgC/m2.

6.3.2 Spatial and regional variation in SOC due to climate and grazing

We found large spatial variation in SOC due to climate and grazing during 1901-2010. In response to grazing, SOC show a maximum reduction of 5kg C/m2 in Europe, North America and south Asia (Figure 6.2). In response to changing climatic condition, SOC declined over most of the land surface, with larger decline in high latitude ecosystem compared to temperate and the tropics. Regionally, North America experienced the largest reduction in SOC due to livestock grazing (7.1 Pg C/yr), followed by Asia (5.4 Pg C/yr), East Europe (2.6 Pg C/yr), Latin America

(2.2 Pg C/yr), West Europe (0.85 Pg C/yr), Africa (0.81 Pg C/yr) and Oceania (0.16 PgC/yr) (Figure 6.3). Climate reduced SOC in Africa (0.60 Pg C/yr), Latin America (0.40 Pg C/yr), Asia (0.27), North America (0.26) and Europe, but increased SOC in Oceania (0.13 Pg C/yr) and Middle East (0.02 Pg C/yr).

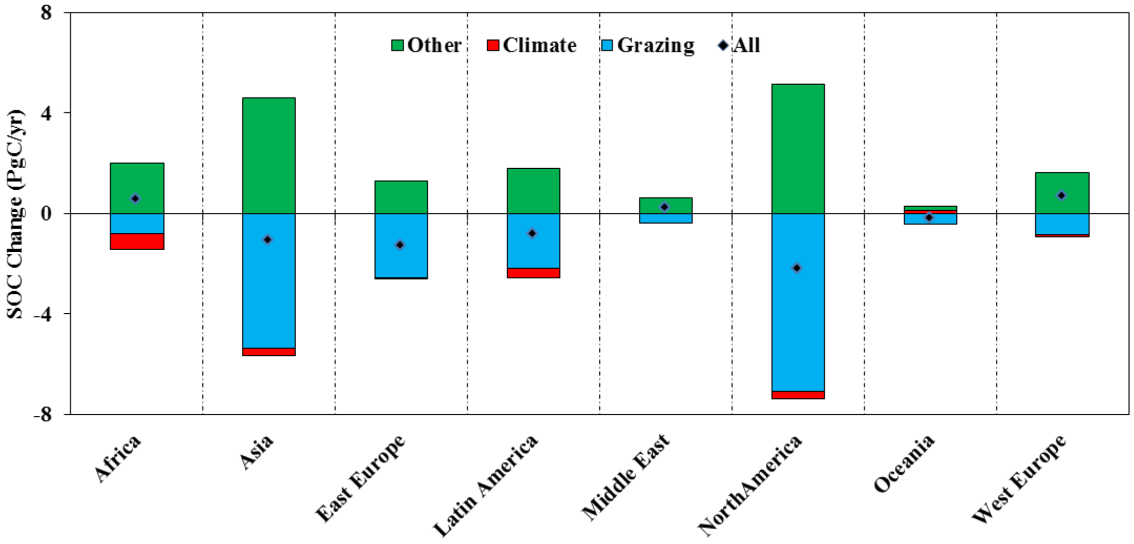


Figure 6-3 Regional impact of livestock grazing and climate change on SOC.

6.3.3 Temporal change in NPP due to climate and grazing

The results show a significant increase in NPP at the rate of 46.7 TgC/yr due to changes in multiple environmental factors (p-value < 0.05; R^2 = 0.68; Figure 6.4). Climate change increased NPP significantly at a rate of 1.6 PgC/yr (p-value < 0.05; R^2 = 0.27), while grazing declined NPP by 4.3 PgC/yr (p-value < 0.05; R^2 = 0.94). Other environmental factors including a combination of elevated CO_2, nitrogen deposition, tropospheric ozone, LCLUC and land management practices increased NPP by 8.6 PgC/yr during 1901-2010 (p-value < 0.05; R^2= 0.90).

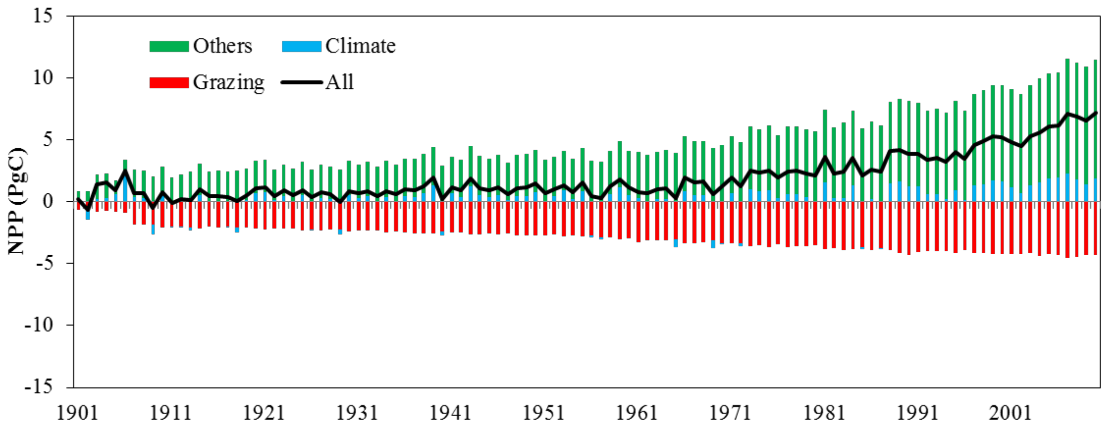


Figure 6-4 Changes in NPP due to climate, grazing and other environmental factors

Other simulation includes the influence of elevated CO_2 concentration, nitrogen deposition, ozone, LCLUC and land management practices on SOC.

6.3.4 Spatial and regional variation in NPP due to climate and grazing

The results show that livestock grazing resulted in a decline in NPP by a maximum of 350 gC/m^2, which dominated mostly in south Asia, East Europe and the central United States (Figure 6.5). Climate change had a positive effect on NPP, particularly in high latitude ecosystems, with a maximum increase of 200 gC/m^2 (Figure 6.5). Regionally, livestock grazing resulted in the largest NPP reduction in Asia (0.98 PgC/yr), followed by North America (0.52 PgC/yr), Latin America (0.27 PgC/yr), West Europe (0.23 PgC/yr), East Europe (0.20 PgC/yr) and Middle East (0.05 PgC/yr). In response to climate change NPP decreased in Latin America (0.15 PgC/yr), Oceania (0.12 PgC/yr), Asia (0.06 PgC/yr), North America (0.05 PgC/yr), while Africa experienced a marginal increase of 0.04 PgC/yr (Figure 6.6).

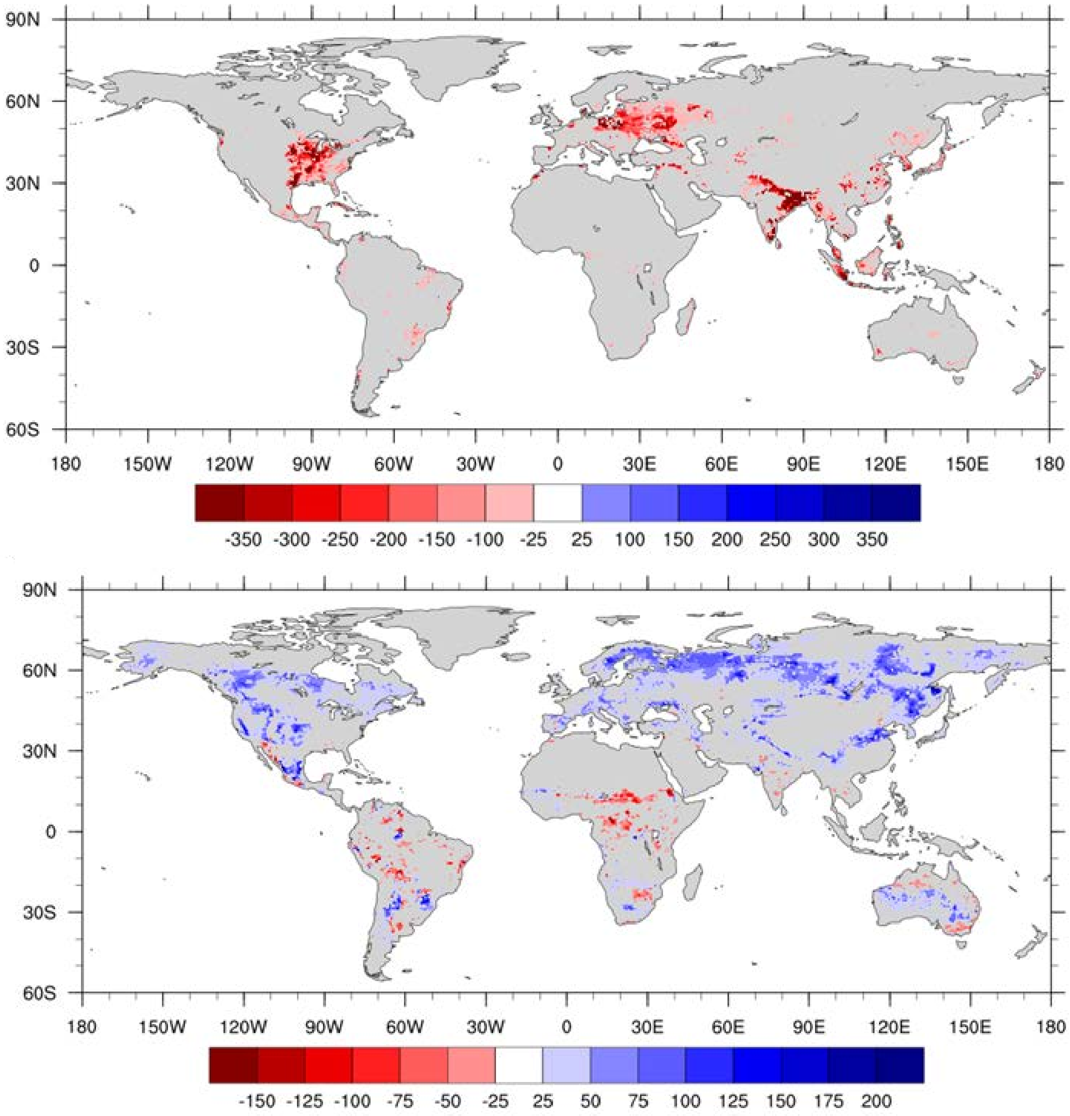


Figure 6-5 Impact of livestock grazing (top panel) and climate change (bottom panel) on NPP calculated as a difference between 2000s and 1900s. All units are in gC/m2.

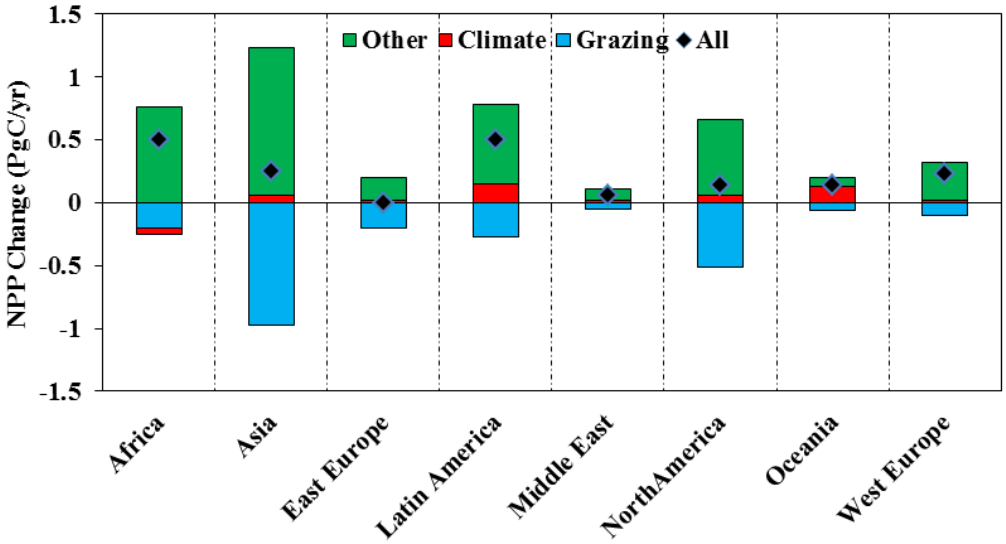


Figure 6-6 Regional impact of livestock grazing and climate change on NPP.

6.4 Discussion

6.4.1 Comparison with previous SOC and NPP estimates

Our estimates of global SOC for year 2010 (746 Pg) are in the range of historic global SOC estimates between 504 and 3000 PgC based on Scharlemann et al. (2014). The global SOC simulated by the DLEM also agrees well with 10 terrestrial biosphere models (TBMs) ensembles that range from 425 to 2111PgC based on Tian et al. (2015c). Estimating global SOC rely on measurements, inventories and empirical/process based ecosystem models. Measurement and inventory approach relies on estimating SOC at a site level, which are then extrapolated by relating it with soil structure, bulk density and soil texture information. Ecosystem models, on the other hand, rely on physical and biological processes including photosynthesis, respiration and the exchanges of carbon, water and energy across the atmosphere-soil surface. But, both inventories and modeling based approaches to estimate SOC have their own limitations. At the global level, an inventory may not be reliable particularly when the measurements are well distributed across the terrestrial surface. Similarly, large uncertainty associated with model structure, parameterization and input datasets could provide different estimates of SOC (Tian et al. 2015c). For example, uncertainties in the representation of belowground carbon processes have been found to vary significantly across different ecosystem models (Johnston et al. 2004, Schimel and Schaeffer 2015). It is possible that some of the model parameters used while simulating SOC could increase uncertainty in the model estimates of SOC.

6.4.2 Livestock grazing impact on SOC

Grazing impact on SOC through changes in plant processes

Grazing by domestic livestock has been suggested to significantly affect SOC by changing aboveground processes such as carbon uptake, litter fall rates and carbon allocation, which ultimately controls the amount of substrate entering the soil pool (Piñeiro et al. 2010). Previous studies report several mechanisms that lead to the reduction of SOC following grazing by livestock. First, decrease in SOC has been attributed to reduction in leaf area index and the resultant decline in ANPP due to removal of aboveground biomass by grazing (Bagchi and Ritchie 2010). Second, grazing affect the rate of litter fall indirectly by consuming aboveground biomass, which could potentially decrease substrate necessary for soil carbon formation (Liu et al. 2015). Third, increased grazing pressure reduces carbon allocation to roots (McSherry and Ritchie 2013) resulting in a decline in root elongation and biomass (Gao et al. 2008, Bagchi and Ritchie 2010). In this study, decline in SOC due to grazing was largely due to decrease litter inputs (12%) and belowground carbon pool (7%). While decline in litter inputs following grazing are consistent with previous studies (Christie 1979, Ingram et al. 2008), root production has been found to either increase or decrease (Klumpp et al. 2009, McGranahan et al. 2014), which is ultimately determined by the stocking rates (Potter et al. 2001), type of grass (C3 or C4)

(McSherry and Ritchie 2013) and prevalent climatic and environmental conditions (Fitter et al. 1998). In this study, we did not attempt to quantify how different stocking rates affect root production and SOC changes, but only focused on the overall impacts of grazing on SOC changes. In addition, our dynamic carbon allocation routine based on Friedlingstein et al. (1999) considers resource limitations as a function of aboveground (light) and belowground (nitrogen and water) resource pool. In the model, aboveground resource limitation directly control the sapwood or stem allocation, while belowground resource limitation drives more allocation of reserves to roots. The light availability scalar that drives aboveground allocation is a function of LAI (see Methods) in the DLEM. Following grazing, there is a decrease in LAI such that plant allocates more resources aboveground to accrue more carbon given that belowground resources such as nitrogen and water are not limiting.

Grazing impact on SOC through changes in soil processes

Livestock grazing also affects soil processes as determined by the complex interactions among factors that control SOC formation (Schuman et al. 1999, Savadogo et al. 2007). For example, grazing by large herbivores has been found to accelerate nutrient cycling, increase soil temperature and changes in soil water content (Odriozola et al. 2014). While increased nutrient cycling may alleviate plant nutrient availability resulting in enhanced plant growth, increased soil temperature and soil moisture following grazing could potentially increase soil decomposition resulting in no net gain in SOC. For example, an increase in soil temperature due to grazing (Bremer et al. 2001) increase soil respiration (Cao et al. 2004), which could ultimately lead to soil carbon losses associated with enhanced decomposition rates. In this study, however, we found a significant decline in decomposition rates, which is largely due to the fact that substrate necessary for microbial activities declined due to lower litter inputs. It is likely that soil decomposition rates may increase over the short term due to increase in soil moisture and soil temperature. In the long term, our results indicate that decrease litter fall and substrate input, particularly in intensively grazed areas experience a significant reduction in SOC.

The impact of grazing intensity on SOC

The mechanism of grazing controls on SOC as mediated by changes in soil temperature, nutrient cycling rates and soil water content are also dependent on stocking rate (density) and the evolutionary history of grazing (Cingolani et al. 2005). High grazing intensity lead to a decline in microbial respiration because of depletion of substrate pool, while grazing under low intensity increases microbial activities due to an enhancement of substrate input (Zhou et al. 2016). For example, light grazing compared to moderate and heavy grazing could increase soil moisture (Thomey et al. 2011, Zhang et al. 2015), favoring the abundance of microbial populations leading to an increase in soil respiration (Savadogo et al. 2007). In a 10-year study, Ingram et al. (2008) found a 30% reduction in SOC at the heavily grazed (50% utilization rate) site, indicating the dominant role of grazing intensity on SOC. Although we did not attempt to quantify how different grazing intensity alter SOC, our results indicate that areas that experience high grazing intensity such as Europe, central United States, South Asia and Latin America show the larges reduction in SOC by up to 5kgC/m2/yr (Figure 6.2).

6.4.3 Climate change impact on SOC

SOC in soils result from the balance between inputs (leaves and root detritus) and output (decomposition and leaching) (Davidson and Janssens 2006). Climate warming has the potential to enhance decomposition rates leading to a decline in SOC stocks (Jones et al. 2005), but the overall response can be altered by soil properties and hydrological conditions. Our results indicate that climate change decreases SOC due to low NPP in the tropics and higher decomposition rates in the temperate and boreal regions. For example, we found that low NPP resulted in lower litter input, which is a substrate necessary for SOC formation. The NPP-dominated reduction in SOC due to climate was prevalent in the tropics. Unlike the tropics, NPP increased due to climate warming in both temperate and boreal regions, which also enhanced decomposition rates. Relative increases in decomposition were greater than increases in NPP resulting in an overall decline in SOC in temperate and boreal regions.

6.5 Conclusion and Limitation of the study

The study demonstrated that grazing led to a significant reduction in SOC at the rate of 13.4 PC/yr during 1901-2010. This decreased was largely attributed to low litter fall rates and root production, which reduced the amount of substrate input necessary for SOC formation. However, the negative impact of grazing were more localized with regions such as the central United States, Europe and south Asia experiencing the largest reduction due to the high livestock density. Given the projected increase in per capita meat and milk production by 20% and 25% by 2050 compared to the 2015 level (Steinfeld et al. 2006b), it is likely that the increasing livestock production will have large adverse effect on SOC unless policies that enforce grazing regulation and optimization are implemented in areas that have experienced high grazing intensities. Likewise, our results demonstrate that climate change also resulted in a significant reduction in SOC by 2 PgC/yr, largely due to decline in NPP in the tropics and an increase in heterotrophic respiration in the temperate and boreal regions.

There are several study limitations that need to be addressed in the future work. First, we did not quantify the response of SOC to livestock grazing at different grazing intensities (light, moderate and high). Second, we have not considered how increasing grazing intensity alter soil structure and processes. For example, it has been suggested that grazing increases soil bulk density and reduces soil water holding capacity (Neff et al. 2005). It is therefore important to include the effect of grazing on soil bulk density and their impact on soil moisture dynamics to accurately capture the response of soil respiration to grazing and their effect on SOC at the global scale. Finally, there is need to conduct long-term manipulative experiments to understand the SOC dynamics following grazing because current grazing enclosure studies in most cases are less than 10 years.

Chapter 7. Methane emission from the global livestock sector during 1890-2014: magnitude, trends and spatio-temporal patterns

Abstract

The livestock sector occupies 30% of the global terrestrial surface and contributes 33-50% of agricultural gross domestic product (GDP) and 18% of all anthropogenic greenhouse gas (GHG) emissions. Demand of livestock products has increased rapidly during the past few decades largely due to dietary transition and population growth, with significant impact on climate and the environment. The contribution of livestock sector to GHG emissions has been studied extensively from regional to global scale, but the magnitude, long-term trend and driver of methane (CH_4) emission from the global livestock sector remains unclear. In this study, we use Intergovernmental Panel on Climate Change (IPCC) tier II guidelines to quantify the long term trend, regional variation and drivers of CH_4 emission during 1890-2014. We estimate a total CH_4 emission of 2.72 Gt CO_2-eq (1 Gt = 10^{15} g) from ruminant livestock sector in 2014, which accounted for 47-54% of all anthropogenic non-CO_2 GHG from the agricultural sector. We find that CH_4 emission from the livestock sector in global land surface has increased by 2.06 Gt CO_2-eq (332%) since the 1890s. During the same time period, however, CH_4 emission in global drylands increased by approximately 347%. Our results further indicate that drylands, in particular, have 36% higher emission intensity (CH_4 emissions/km^2) compared to non-drylands during recent decades, largely due to the combined effect of higher rate of increase in livestock

population and low diet quality in drylands. The results also suggest that the contribution of developing regions (Africa, Asia and Latin America) has increased from 51.7% in the 1890s to 72.5% in the 2010s. A future increase in livestock production due to increasing human demand of livestock products with projected changes in climate would likely have larger adverse effect on the environment, unless both land and animal based mitigation options focused on sustainable intensification of livestock sector are implemented.

7.1 Introduction

The livestock sector occupies 30% of the global terrestrial surface (excluding ice) and contributes to 33-50% of agricultural gross domestic product (GDP), with significant impact on people's livelihood, environment and economic activity (Thornton 2010, Herrero et al. 2016). Over the past few decades, livestock sector is growing at an unprecedented rate driven by increasing demand for livestock products associated with an increase in human population, urbanization rate and people's income (WHO 2009). The acceleration of livestock sector has significant impact on the environment including land and water, and also regulates atmospheric composition and climate by contributing to an estimated 18% of all anthropogenic greenhouse gas (GHG) emission (Steinfeld et al. 2006a, Herrero et al. 2013, Ripple et al. 2014). GHG emission from global livestock sector include carbon dioxide (CO_2) associated with deforestation to produce feed and pasture for livestock, energy used during feed production, processing and transportation of grains and meat, nitrous oxide (N_2O) and methane (CH_4) due to management of livestock manure and CH_4 emission associated with enteric fermentation (Steinfeld et al. 2006a, McMichael et al. 2007, Zhang et al. 2016). Among the three major GHGs, the global livestock sector overall account for up to 28% of CH_4 emission from agriculture (Caro et al. 2014, Tian et al. 2016a). In particular, ruminant livestock dominate CH_4 emission, due to fermentation of food reserves in the rumen, which vary as a function of ruminant type, their live weight and the quantity and quality of consumed feed.

Ruminant livestock also play a fundamental role in food security by providing both live and processed livestock products (Godfray et al. 2010). Between 1961-2007, global meat and milk production have increased by 186 and 320 million tonnes, accounting for an estimated 3.6 and 2 fold increases, respectively (Alexandratos and Bruinsma 2012). Compared to 2010, the global meat and milk production will increase by 73% and 58%, respectively in 2050 (Estrada et al. 2011). Although livestock products provide an important source of high quality protein essential for human diets (Tilman and Clark 2014), projected increase in their demand even after adoption of high productivity systems is expected to approach or surpass some of the planetary boundaries of the safe operating space by 2050 (Pelletier and Tyedmers 2010). For example, an increase in livestock products (milk, meat and egg production) may increase livestock-related GHG emission in the order of 39% by 2050. Given the projected intensification of livestock sector, it is crucial to develop mitigation strategies, which allows for transition toward more efficient production system by avoiding negative impacts on people's livelihood, economic activity and the environment (Havlík et al. 2014, Thornton et al. 2014, Herrero et al. 2016).

Among livestock, ruminants are the primary emitter contributing to the largest anthropogenic source (25-40%) of CH_4 emission (Clark et al. 2005, Ripple et al. 2014, Saunois et al. 2016). The emissions from ruminant livestock are driven by two major processes: enteric fermentation and manure production and management (Popp et al. 2010, O'Mara 2011). During enteric fermentation, the ruminant livestock (for example, cattle, buffalo, sheep, goats and camel) emit CH_4 as a by-product of the normal digestive process, due to fermentation of feed that they consume. The emission of CH_4 from enteric fermentation of ruminant livestock is influenced by feed quantity and quality, body weight, feeding level and the activity and health of livestock (Johnson and Johnson 1995, Shibata and Terada 2010). The amount of CH_4 emission from manure depend on the decomposition process, which is influenced by climate, and the way in which manure are collected and stored before its application (Chadwick et al. 2011). Quantifying the long-term trend and spatial pattern of CH_4 emission from enteric fermentation and manure management is crucial to (1) understanding the environmental impacts of livestock sector at a global scale and (2) developing mitigation strategies to reduce emission from the livestock sector.

Livestock production also has a wide range of impact on environment and CH_4 emission. Growing demand for livestock products and technological changes has resulted in an increase in livestock production and widespread changes in the production system (FAO 2009a). Grazing systems, both intensive and extensive are characterized by consumption of native or permanent pastures, while mixed systems rely on both crop by-products and grassland resources, where crop by-products are consumed by livestock and livestock waste are used as input for crop production (Seré and Steinfeld 1996). On the other hand, confined or industrial systems rely mainly on concentrate feeds and are mostly dominated by single species of monogastrics (pigs or poultry) and beef cattle (Otte et al. 2007). Confined or industrial systems, in particular, are responsible for more than 40% of the global meat production, and are the fastest growing production system worldwide (Hudson 2009). Although these conventional production system has played a fundamental role in the supply of livestock products to the growing population, it has also increased the environmental costs with significant negative impact on the ecosystem (Hilker et al. 2014), water quality (Hooda et al. 2000), biodiversity (Steinfeld et al. 2006a) and climate system (Ripple et al. 2014). Unlike the conventional system, organic livestock farming has been generally perceived to have beneficial impact on the environment allowing for free-range of livestock to emulate natural systems by promoting the use of organic and biodegradable inputs from the ecosystem for livestock production (Sundrum 2001, Gracia and de Magistris 2008). But, the extent to which conventional and organic systems of livestock production differ in terms of energy use and GHG emission per unit production is still contentious (McMichael et al. 2007). For example, a recent meta-analysis in Europe indicate that ammonia emission, nitrogen leaching and nitrous oxide emission per product unit were higher in organic compared to conventional system (Tuomisto et al. 2012). In addition, organic feed insufficiency, market condition and prevalence of infectious diseases (mastitis, lameness and metabolic disease) could potentially make organic farming less feasible, particularly in developing regions (Kijlstra and Eijck 2006, Taji and Reganold 2006, Chander et al. 2011).

Likewise, drylands cover approximately 40% of the global land area and support 50% of the global livestock (Bregas 1998) and are highly sensitive to climate change and human activities (Reynolds et al. 2007). Drylands include land areas with the precipitation and potential evapotranspiration ratio of less than 0.65, which constitutes dry sub-humid, semi-arid, arid and hyper-arid regions (Feng and Fu 2013). Climate change and increasing livestock numbers have further resulted in the degradation of 10-20% of the global drylands (MEA 2005a). Methane emissions from livestock in the global drylands would be higher compared to non-drylands due to significant differences in the diet, with lower digestibility and crude protein content, and slower fiber and nitrogen degradation rates in dry regions compared to humid or temperate regions (Herrero et al. 2013). However, until recently there is no clear understanding of the contribution of livestock related CH_4 emission from the global drylands, although they provide much of the world's grain and livestock (MEA 2005a) and play an important role in the global carbon cycle (Poulter et al. 2014).

Mitigation strategies aimed at reducing the environmental cost of livestock sector intensification focuses on two options (Herrero et al. 2015): 1) animal based mitigation; and 2) land-based mitigation. Animal based mitigation primarily rely on changing feed additives and feed quality to lower CH_4 emission from enteric fermentation (Gill et al. 2010b), and improving livestock productivity through a combination of genetics, animal health, nutrition and reproductive efficiency (Havlík et al. 2014). On the other hand, land-based mitigation practices such as carbon sequestration in grazing lands, improved grazing management and optimization of livestock grazing can help to reverse carbon losses due to grazing (Smith et al. 2008). In addition, transition from lagoons and liquid toward dry manure management systems could help to reduce anaerobic digestion of manure resulting in a reduction in CH_4 emission (Clemens et al. 2006). Beside land and animal based mitigation strategies, indirect approach such as implementing polices that focus on sustainable livestock intensification by imposing tax on conventional ranching and subsidies on semi-intensive ranching can cut deforestation rate by half and reduce GHG emission by 25% in Brazil (Cohn et al. 2014). However, such practices have been found to be less profitable in the western Andes of Colombia (Gilroy et al. 2014). While both direct (animal and land based) and indirect (policy changes) approaches help to mitigate the impact of livestock, in this study, we only focused on animal based direct impact on CH_4 emission, and their potential mitigation options.

A wide range of methods are available to measure CH_4 emission from ruminant livestock, which include chamber based approach, SF_6 tracer, *in vitro* gas production and CH_4 emission models (Johnson et al. 1994, Grainger et al. 2007, Storm et al. 2012). CH_4 emission using chamber based approach is estimated based on the difference between outgoing and incoming amount of CH_4 from the chamber (Takahashi et al. 1999), while SF_6 technique relies on the measurement of CH_4:SF_6 concentration by dosing a SF_6 (non-toxic, physiologically inert gas) permeation tube into the rumen (Pinares-Patiño et al. 2011). *In vitro* technique relies on fermentation of feed under controlled laboratory condition by employing natural rumen microbes and measurement of the total CH_4 produced during incubation (Rymer et al. 2005). In cases when measurement of CH_4 from ruminants are not possible, particularly when regional and global level estimates are required, prediction models become increasingly important (Moraes et al. 2014). The standard prediction model used is issued by the Intergovernmental Panel on Climate Change (IPCC), which are based on three different levels (Tiers I, II and III) depending on data availability to estimate CH_4 emission (Storm et al. 2012). Tier I requires less information compared to tier II and tier III approach and the choice of prediction model depend on the level of information available (IPCC 2006). Use of higher Tier approach is generally considered more appropriate given that sufficient information are available because transition toward efficient production system and introduction of new breeds are not fully accounted in Tier I approach (Tubiello et al. 2013).

Here, we used the IPCC recommended methods (see Table 10.9, Dong et al. (2006)) to estimate total CH_4 emission from the ruminant livestock sector (enteric fermentation and manure management) during 1890-2014. To quantify the spatio-temporal patterns of CH_4 emission from the livestock sector, we first created a spatially disaggregated data on livestock (dairy cattle, non-dairy cattle, sheep and goat) population (heads/km^2) at a spatial resolution of 5’ × 5’ during 1890-2014. The disaggregation was performed by using estimates of annual livestock population for dairy cattle, non-dairy cattle, sheep and goat based on subnational and country level FAO

(Food and Agricultural Organization) data for 192 countries during 1961-2014 (see Table S1). For years prior to 1961, we used Mitchell (1993) livestock data available for 17 different regions. To estimate CH_4 emissions from enteric fermentation and manure management, we used IPCC tier II guideline. Our objectives are (1) to develop a high resolution spatially explicit data on livestock numbers during 1890-2014; (2) to quantify the trend and driver of CH_4 emission from the livestock sector during 1890-2014; (3) to estimate CH_4 emission across different regions; and (4) to assess and identify hotspots of CH_4 emission from the global livestock sector during the contemporary (2000-2014) period. We hypothesize that large ruminants (dairy and other cattle) will contribute to higher CH_4 emissions due to higher energy demand and manure production compared to small ruminants (sheep and goat). CH_4 emission from manure production will also depend on average air temperature and manure management practices, with lagoons and liquid management yielding higher emission compare to dry management. In addition, drylands would be characterized by larger emission per unit area compared to other lands, largely due to lower digestibility and crude protein concentration, and slower fiber and nitrogen degradation rates.

7.2 Methods

To estimate CH_4 emission from enteric fermentation following IPCC Tier II guidelines, we need data on livestock size, function, feed management and energy requirements. The feed and energy requirement differ based on livestock category and their live weight. In this study, we obtained country level livestock data by each category from the FAO database. The FAO statistical year book (FAOSTAT) database provides annual estimates of ruminant livestock by category at a country level since 1961, while Mitchell (1993) and Mitchell (1998a) provides annual estimates of livestock population by different category at every 10-year interval since 1890. We disaggregated the country level estimates of livestock heads by each category at a grid level during 1890-2014 based on gridded livestock of the world version 2.0 available at a resolution of 3-arc minute for the year 2006 (Robinson et al. 2014). To estimate CH_4 emission from manure management using IPCC tier II approach, we need information on excretion rates by livestock category, maximum methane producing capacity, methane conversion factors for each manure management system, livestock fraction handled using specific manure management system and mean annual temperature.

7.2.1 Collection of sub-national level and country level livestock numbers

We first collected livestock numbers on smaller administrative region for countries that have official estimates of livestock heads by different category at province or state level. These countries included the United States, Australia, Brazil, Canada, China and Mongolia. For the United States, we used state level livestock numbers from United States Department of Agriculture National Agricultural Statistics Service (https://quickstats.nass.usda.gov/). For Australia, we obtained data from Statistical Database of Meat & Livestock Australia Limited (http://statistics.mla.com.au/Report/List) available at 6 different regions (New South Wales, Northern Territory, Queensland, South Australia, Tasmania, Victoria and Western Australia). For Brazil, we collected data from Brazilian Institute of Geography and Statistics at a Federation Unit level (http://www.sidra.ibge.gov.br/bda/tabela/listabl.asp?c=73&z=p&o=34) (total of 28 federation unit exist in Brazil). For Canada, we used provincial level data on cattle, sheep and goat statistics from Agriculture and Forestry Ministry (http://www1.agric.gov.ab.ca/$department/deptdocs.nsf/all/sdd10294). For China, we used provincial level cattle, sheep and goat inventory data available from United States Department of Agriculture Economic Research Service (http://www.ers.usda.gov/data-products/china-agricultural-and-economic-data/national-and-provincial-data.aspx). The data in China were available for only contemporary period (1998-2009) for Anhui, Beijing, Chongqing and Fujian province. For Mongolia, we used National Statistics of Mongolia data to obtain livestock number data at provincial level (total of 22 provinces; http://www.1212.mn/en/). For countries that do not have a complete data during 1961-2014 (for example, China), we obtained the proportion of livestock for each lower administrative unit based on available livestock inventory data and applied the same proportion to missing years based on country level FAO estimates. Mathematically,

$$Proportion_{ijk} = \frac{Inventory_{ijk}}{Country_{jk}} \tag{1}$$

Where,

$Proportion_{ijk}$ = proportion of livestock numbers for county/province *i*, country *j* and livestock category *k*

$Inventory_{ijk}$ = observed livestock totals for county/province *i*, country *j* and livestock category *k*

$Country_{jk}$ = observed country level totals for country *j* and livestock category *k*

For the rest of the countries that do not have estimates of livestock heads at the lower administrative units, we used country level livestock heads from Food and Agricultural Organization (http://www.fao.org/faostat/en/#data).

7.2.2 Disaggregation and development of gridded livestock data during 1961-2014

To disaggregate the provincial/state and country level livestock data obtained in section 2.1, we used annual livestock density of cattle, sheep and goat based on Global Livestock Impact Mapping System (GLIMS) available at a spatial resolution of $0.0083^o \times 0.0083^o$ for year 2006 (Robinson et al. 2014). The gridded livestock data provide the spatial variation for each livestock category, which was developed by using environmental variables to spatially distribute sub-national data to grid level. This dataset was first corrected to match polygon (lower administrative unit) values of the inventory data based on sub-national statistics and then to match the FAO country level totals (Robinson et al. 2014). Because spatial data for year 2006 in Robinson et al. (2014) was obtained using sub-national livestock totals, we first attempted to disaggregate the livestock data into grid level by using smaller administrative/provincial units based on data obtained in section 2.1. Overall, we controlled annual change based on state or provincial level inventory estimates of livestock numbers for the United States, Brazil, Australia, China, Mongolia and Canada. However, for other countries we used country level FAO estimates during 1961-2014 to generate annual variation. This approach assumes that spatial variation within state or province is controlled by GLIMS for countries that have data available at lower administrative units.

To create a gridded database of livestock numbers for each category, we first calculated the total number of livestock at country/state/province level based on GLIMS. Mathematically,

$$GLIMS_{i/j,ref} = \sum_{n=1}^{o} (Area_n \times Livestock_{n,i/j}) \qquad (2)$$

Where,

$GLIMS_{i/j,ref}$ = Total number of livestock in county /province i or country j for reference year (2006)

$Area_n$ = Area of grid cell n in km^2

$Livestock_{m,i/j}$ = density of livestock in heads/km^2 in grid cell n for county/province i or country j based on reference year 2006

o = total number of grid cells in county/province i or country j

We then obtained the annual change of livestock proportion at a country/state/province level during 1961-2014 as given by:

$$Scalar_{m,i/j} = \frac{Inventory_{m,i/j}}{GLIMS_{i/j,ref}} \qquad (3)$$

Where,

$Scalar_{m,i/j}$ = ratio of total livestock heads obtained from inventory or FAO for year *m* county/province *i* or country *j*

$Inventory_{m,i/j}$ = total number of livestock heads obtained from livestock survey or FAO database for year *m* in county/province *i* or country *j*

To create a gridded map of annual change in total livestock numbers for each livestock category, we took the product of $scalar_{m,i/j}$ obtained in each year to the reference year total livestock numbers, which is given by:

$$LT_{m,n} = Scalar_{m,n} \times Area_n \times Livestock_n \quad (4)$$

Where,

LT_{mn} = livestock totals (heads/grid cell) for year m and grid cell *n*

$Livestock_n$ = livestock density in heads/km^2 for grid *n*

7.2.3 Development of gridded livestock data prior to 1961

To develop a gridded datasets of livestock population prior to 1961, we used livestock information available at 10 year interval (Mitchell 1993, 1998b) for 17 different regions during 1890-1960. The datasets are available at (http://themasites.pbl.nl/tridion/en/themasites/hyde/landusedata/livestock/index-2.html), and was scaled in 1961 to match the FAO data (Mitchell 1998a). Annual time series data of livestock population was developed by using linear interpolation technique based on statistical package "zoo" (R software; https://cran.r-project.org/). First, we developed an annual time series of cattle, sheep and goat population and then disaggregated the total cattle into dairy and non-dairy cattle following approach in section 2.4.

7.2.4 Disaggregation of gridded cattle into dairy and non-dairy cattle

The GLIMS provided data of total cattle, which needs to be disaggregated into dairy and other cattle to quantify CH_4 emission from enteric fermentation because dairy vs other cattle have different rates of CH_4 emission (IPCC, 2014). To disaggregate the gridded livestock totals of cattle obtained above, we used country level FAO data on the number of dairy cattle, which are expressed as livestock heads producing milk and can be retrieved from the FAOSTAT database by selecting cow milk, whole fresh producing animals. We disaggregated cattle into dairy and non-dairy components by subtracting dairy cattle from total cattle. Finally, we obtained the annual ratio of dairy to non-dairy cattle during 1961-2014 at the country level, and applied this ratio to $LT_{m,i}$ obtained in (4) to create a gridded livestock total data for dairy and other cattle. For years prior to 1961, we used a 30-year (1961-1990) average dairy and non-dairy cattle population obtained from FAO data to create the proportion of dairy vs non-dairy cattle and used the same proportion to disaggregate the total cattle into dairy and non-dairy categories. While this approach attempt to reflect the overall proportion of dairy vs non-dairy cattle, there is uncertainty associated with annual changes in their proportion due to changes in dairy and non-dairy industry (Thornton 2010).

7.2.5 CH_4 emission from enteric fermentation

To estimate CH_4 emission, we used IPCC Tier II approach, which relies on the estimation of net energy requirement and energy availability of the diet (Table 7.1). This includes energy for maintenance, work, activity, lactation, pregnancy, growth and wool production (for sheep only). We used IPCC (2006) equation 10.16 to estimate the gross energy requirement of each animal category, which is calculated as a sum of maintenance, work, activity, lactation, pregnancy and growth. The most important parameters that affect quantification of energy requirements of each livestock category are the live weight and milk production of the animals because energy requirement has been found to vary significantly for different categories of livestock or for different live weight even within same category.

Table 7-1 Livestock emission category and equations used to estimate CH_4 emissions in this study. Equations are based on IPCC (2006)

Emission type	Variable	Equation	Livestock type
Enteric Fermentation	Maintenance Energy	10.3	All
	Activity Energy	10.4	Non-dairy, Dairy Cattle
	Activity Energy	10.5	Sheep, Goat
	Growth Energy	10.6	Non-dairy, Dairy Cattle
	Growth Energy	10.7	Sheep, Goat
	Lactation	10.8	Non-dairy, Dairy Cattle
	Lactation Energy	10.9	Sheep, Goat
	Work Energy	10.11	Non-dairy, Dairy Cattle
	Wool Energy	10.12	Sheep
	Pregnancy	10.13	All
	Ratio of net energy for maintenance	10.14	All
	Ratio of net energy for growth	10.15	All
	Gross energy	10.16	All
Manure Management	Emission factor	10.23	All

7.2.6 CH_4 emission from manure management

To estimate CH_4 emission from manure management, we used IPCC tier II guidelines, which rely on two primary types of input that affect emissions (IPCC 2006): 1) manure characteristics and 2) manure management system. Manure characteristics include total volatile solids produced in the manure, while manure management practices include different types of system used to manage manure and a system specific methane conversion factor. For dairy and non-dairy cattle, we used IPCC recommended guidelines (Table 10A-4, 10A-5; IPCC 2007) to develop total volatile solids and manure conversion factors for different systems. For sheep and goat, we used Table 10A-9 (IPCC 2007), which differentiates volatile solid produced and methane conversion factor by developed and developing regions. In addition, mean annual temperature play an important role in driving CH_4 emission from livestock manure. We used CRUNCEP daily climate data (ftp://nacp.ornl.gov/synthesis/2009/frescati/model_driver/cru_ncep/analysis/readme.htm) to obtain the global gridded mean annual temperature at $0.5^o \times 0.5^o$ spatial resolution. The CRUNCEP data were only available since 1901, so we used 1901 air temperature data for the period 1890-1900 while estimating CH_4 emission related to manure management. We then used equation 10.23 (Table 1) to estimate CH_4 emission from manure management using an IPCC tier II approach.

7.2.7 Contribution of drylands to global methane emission

To quantify the temporal evolution of CH_4 emission in the global drylands, we used global mean aridity index maps based on Trabucco and Zomer (2009). The global mean aridity index is a measure of a ratio of precipitation availability to potential evapotranspiration over the period 1950-2000. The global aridity index was modeled using climate data available from WorldClim (Hijmans et al. 2004) at a resolution of ~1km × 1km at the equator. To separate drylands from the global aridity index map, we selected all pixels with aridity index less than 0.65 (Feng and Fu 2013, Huang et al. 2015). We then extracted the CH_4 emission for all pixels with aridity index less than 0.65 to quantify the evolution of CH_4 emission from the livestock sector in global drylands.

7.2.8 Calculation of methane (CH_4) emission and emission intensity

In this study, we calculated the CO_2 equivalents of the methane emission from the global livestock sector by adopting a 100-year global warming potential (GWP) of 28 (Myhre et al. 2013, Tian et al. 2016a). Global warming potential is a metric used to define the cumulative impact of 1g CH_4 on radiative forcing relative to 1g of CO_2 gas over a certain time period. We also quantified emission intensity associated with ruminant livestock using two approaches: 1) emission per unit area; and 2) emission per livestock unit (LU). Emission per unit area was estimated as a ratio of total CH_4 emissions to total area, while emission per LU was estimated as a ratio of total CH_4 emission to standardized total livestock heads. Standardized livestock heads refers to the exchange ratio of different livestock category, which is derived based on the relationship between animal body weight and metabolic weight. The exchange ratio to convert different livestock species into one standardized LU was obtained from Chilonda and Otte (2006).

7.2.9 Statistical analysis

We use mean ± standard deviation (s.d.) to provide the best possible estimate of CH_4 emission and their ranges. We perform simple linear regression by using total CH_4 emission as a dependent variable and time as an independent variable based on statistical package R. We also examined whether there is a significant change in CH_4 emission over time at 5% level of significance.

7.3 Results

7.3.1 Temporal evolution of CH_4 emission during 1890-2014

Our results show that the total amount of CH_4 emission from the livestock sector was 2.72 Gt CO_2-eq in year 2014, which accounted for 47-54% of the total anthropogenic non-CO_2

GHG from the agricultural sector (5-5.8 Gt CO_2-eq/yr; Smith et al. (2014)). The overall CH_4 emission from the livestock sector (both enteric fermentation and manure management) has increased from 0.62 Gt CO_2-eq in the 1890s to 2.68 Gt CO_2-eq in 2010s, accounting for an increase of 332% since 1890s (Figure 1a). This increase represents an annual increment of 17.1 Tg CO_2-eq/yr emission during 1890-2014. Emission associated with enteric fermentation showed a continuous and significant increase (p-value < 0.05; $R^2 = 0.98$), while emission associated with manure management showed a significant increase at a rate of 5 Tg CO_2-eq/yr until 1960 but then remained steady with no substantial changes thereafter. In particular, emission related to manure management after 1960 showed both declines and increases in CH_4 emissions. For example, there was a period of decline in CH_4 emission during 1961- 1971, followed by an increase during 1972-1990. From 1991-2001, there was a significant decline in methane emission from manure management (p-value < 0.05), and then a significant increase during the recent decade (2002-2014; p-value < 0.05).

When disaggregated across different livestock category, non-dairy cattle accounted for the majority of CH_4 emission (67%) followed by dairy cattle (20%), sheep (9%) and goat (4%) during 1890-2014 (Figure 7.1a, 7.1c). Compared to the 1890s, CH_4 emission from non-dairy cattle increased by 410%, while that of dairy cattle increased by 336%. While sheep and goats made a minor contribution to the global total, CH_4 emission increased by 615% for goats and 78% for sheep in the 2010s compared to the 1890s. In case of emission from manure management, dairy cattle and non-dairy cattle contributed to approximately 38% and 55% of CH_4 emissions, respectively during 1890-2014.

7.3.2 Spatial and regional variation in CH_4 emission during 1890-2014

Africa, Asia and Latin America shared the majority of global CH_4 emission, accounting for approximately 51-73% of the total emission during 1890-2014 (Figure 7.1b, Figure 7.2). The contribution from developing regions (Africa, Asia and Latin America) increased from 52% in the 1890s to 73% in the 2010s, while the contribution from other regions has declined from 48% in the 1890s to 28% in the 2010s. In developed regions such as North America, eastern Europe and western Europe, our results show substantial changes in emissions largely associated with the change in livestock numbers across different time periods. For example, the eastern Europe experienced a significant decrease in CH_4 emission from enteric fermentation after the 1980s, largely associated with a 68% decrease in the number of dairy cows (Figure 1b; Figure S4). Likewise, we found slowing down emissions in North America and western Europe during the 1970s and the 1980s, respectively associated with a corresponding decrease in livestock numbers. Spatial pattern of total CH_4 emissions from enteric fermentation indicate an overall increase, particularly in Latin America, Africa, south Asia and eastern China (Figure 7.2a, 7.2b).

Unlike the overall increasing trend of CH_4 emissions from enteric fermentation, emissions from manure management has been declining in eastern Europe, western Europe and North America at the rate of 0.17, 0.16 and 0.20 Tg CO_2-eq/yr (p-value < 0.05), respectively since 1961. But, the contribution of eastern Europe, western Europe and North America to total CH_4 emission from manure management is still higher (41.7%) in 2014 compared to other regions. In addition, most of the developing regions such as Asia, Latin America and Africa experienced a significant increase in emissions from manure management at the rate of 0.32, 0.11 and 0.11 Tg CO_2-eq/yr (p-value < 0.05), respectively since 1961.

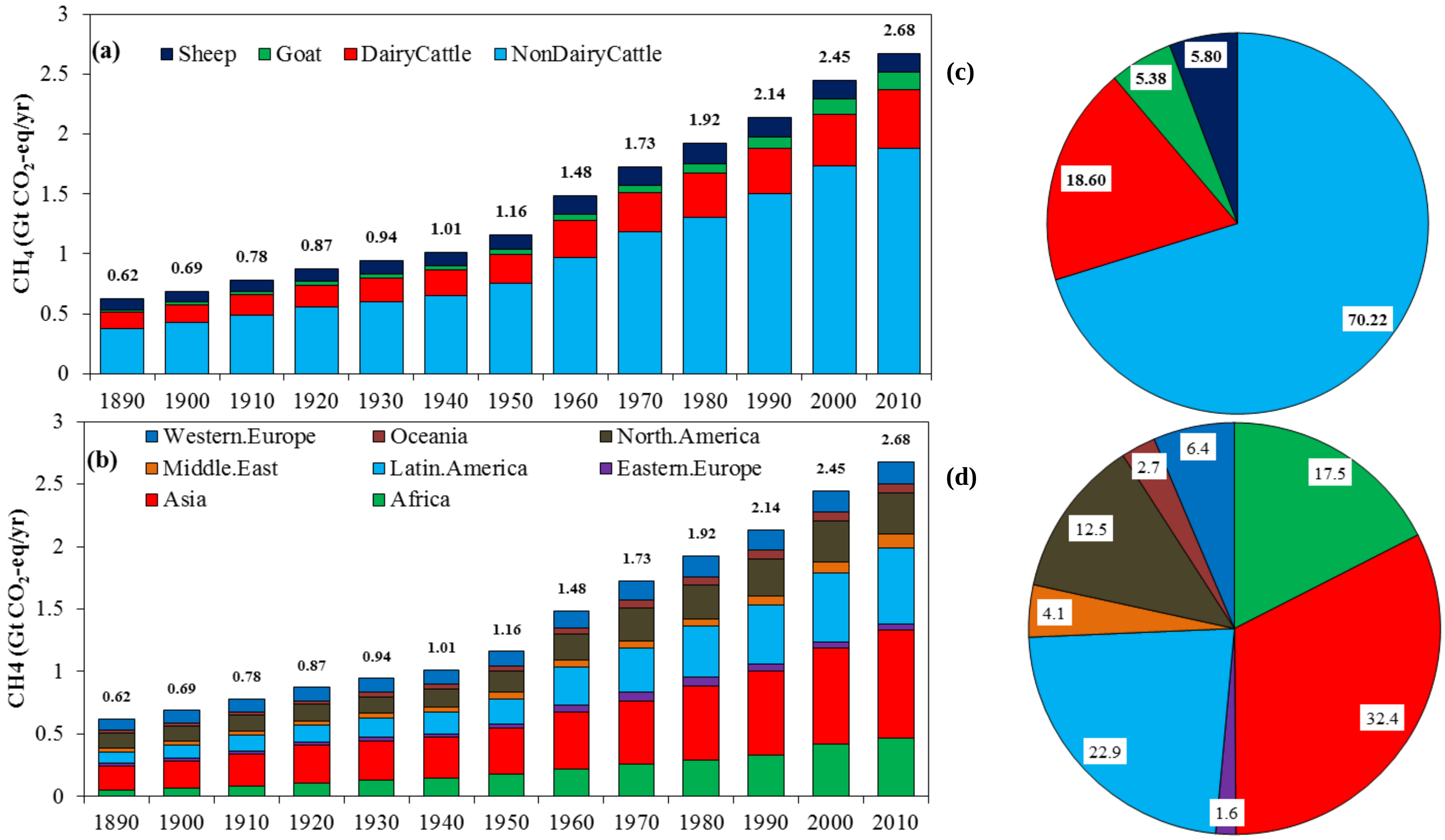


Figure 7-1Temporal evolution of CH$_4$ emission from global livestock sector by livestock category (a) and regions (b) during the 1890s-2010s, and percentage contribution of different livestock category (c) and regions (d) to total CH$_4$ emissions in the 2010s. Livestock related CH$_4$ emission grew by 332% globally since 1890s, with increasing contribution from Asia (31.8%), Latin America (23.1%) and Africa (17.6%) in the 2010s.

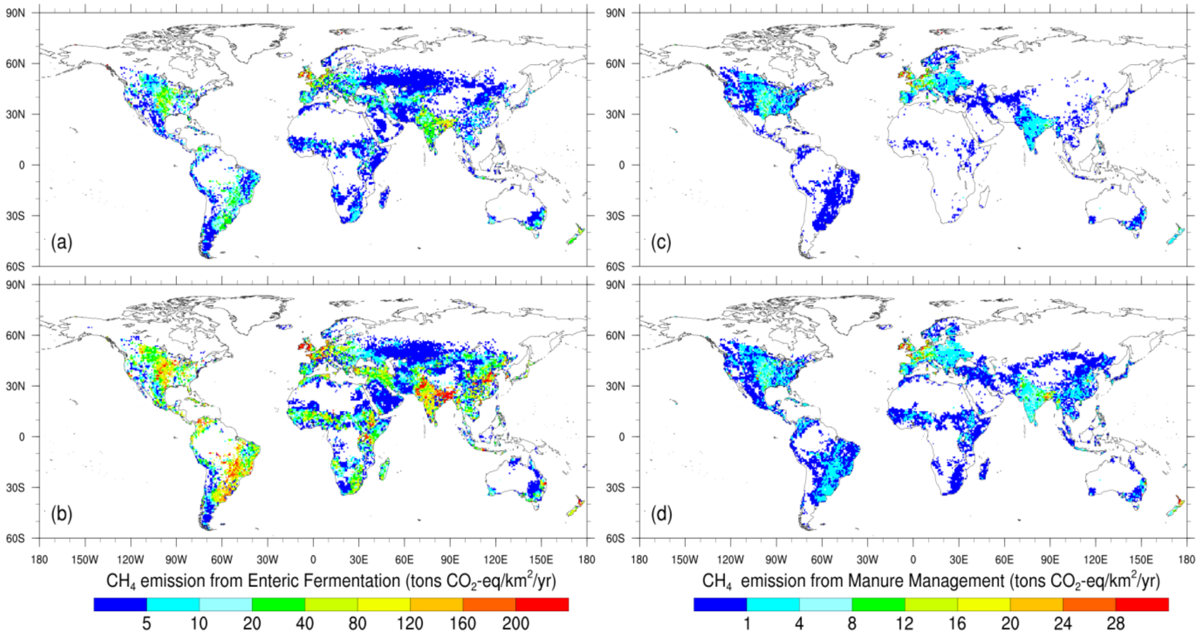


Figure 7-2 Spatial variation of CH_4 emission from enteric fermentation during 1890s (a) and 2010s (b), and CH_4 emission from manure management during 1890s (c) and 2010s (d). Latin America and Asia dominated CH_4 emissions from enteric fermentation, while western Europe dominated CH_4 emissions from manure management between 1890s and 2010s.

7.3.3 Contribution to CH_4 emission from global drylands during 1890-2014

Our results show that the livestock CH_4 emission from global drylands have experienced an increase of approximately 347% since the 1890s (Figure 7.3a). The global drylands CH_4 emission increased significantly from 0.29 Gt CO_2-eq/yr during the 1890s to 1.28 Gt CO_2-eq/yr during the 2010s. Our results also indicate that emission intensity (CH_4 emissions per unit area) is 36% higher in drylands compared to other lands in the 2010s (Figure 7.3b). Although emission intensity was similar in drylands and other lands in the 1890s, changes in livestock abundance and the quality of feed had resulted in large differences in emission intensity during 1890-2014. For example, CH_4 emission in global drylands increased from 5 tons CO_2-eq/km^2 in the 1890s to

24 tons CO_2-eq/km^2 in the 2010s. In contrast, CH_4 emission in other lands increased from 4 tons CO_2-eq/km^2 in 1890 to 18.89 tons CO_2-eq/km^2 in 2014.

7.3.4 CH_4 emission and emission intensity during the contemporary period (2000-2014)

Our results showed that during the contemporary period, total CH_4 emission from the livestock sector increased at a rate of 36 Tg CO_2-eq/yr/yr, with positive contribution from both enteric fermentation (96%) and manure management (4%) (Table 7.2). Non-dairy cattle contributed to the majority of CH_4 emission (70%), followed by dairy cattle (19%), sheep (6%) and goat (5%) (Figure 7.1c). In particular, emission from manure management showed a significant annual increase at a rate of 0.6 Tg CO_2 eq/yr/yr (p-value < 0.05) during the contemporary period, although its contribution to the total CH_4 emission represented only 4% of the global total. Likewise, emission from enteric fermentation showed a significant increase at a rate of 35.4 Tg CO_2 eq/yr/yr (p-value < 0.05) during the contemporary period, accounting for 96% of the global total.

Across regions, North America and eastern Europe experienced no significant change in CH_4 emission, largely due to reduction in livestock numbers (Table 7.2). All other regions showed a significant increase in CH_4 emission during the contemporary period (p-value < 0.05). Asia and Latin America were the major contributors to CH_4 emission, accounting for 54% of the global total emission from the livestock sector (Figure 7.1b). Other important regions in terms of contribution to global total were Africa (18%), North America (13%) and Europe (9%).

Our results also showed that emission intensity measured as CH_4 emission per unit area and per livestock unit (LU) vary substantially across regions. CH_4 emission per LU was higher in Middle East (3.11 tons CO_2-eq), North America (3.02 tons CO_2-eq), Asia (2.44 tons CO_2-eq) Africa (2.22 tons CO_2-eq), while lower in eastern Europe, Oceania and western Europe (Table

7.3). Likewise, CH_4 emission per km^2 was found to be higher in western Europe (46.99 tons CO_2-eq), Asia (37.56 tons CO_2-eq) and Latin America (28.41 tons CO_2-eq), but lower in Oceania, Africa, Middle East, North America and eastern Europe. Our results also showed that regions that experience higher livestock density had higher CH_4 emission per km^2 compared to regions that experience low livestock density. For instance, CH_4 emission was highest (46.99 tons CO_2-eq) in western Europe, which was particularly due to high livestock density of 22.1 LU/km^2 in the region.

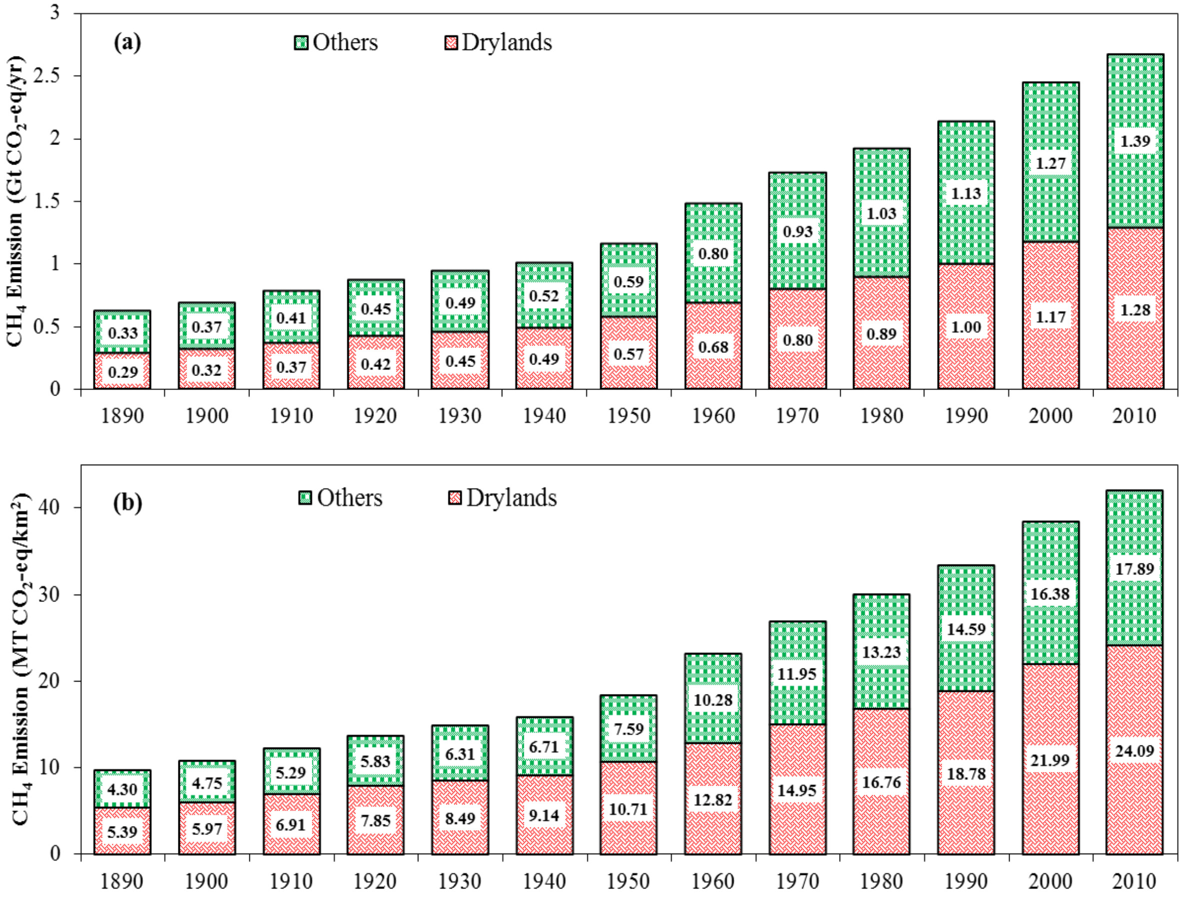


Figure 7-3 Temporal evolution of ruminant livestock CH_4 emission from global drylands and non-drylands (a) and emission intensity (CH_4 emission per unit area) in global drylands vs non-drylands (b) during the 1890s to 2010s. CH_4 emission increased by 347% in the drylands since the 1890s, while emission intensity was 36% higher in drylands compared to non-drylands in 2010s. Numbers on bars indicate CH_4 emission (in Fig a) and emission intensity (in Fig b) on drylands and non-drylands

Table 7-2 Methane emission from enteric fermentation and manure management during the contemporary period (2000-2014). The values presented are mean ± s.d.

Regions	Enteric Fermentation ($TgCO_2$ eq/yr)				Manure Management ($TgCO_2$ eq/yr)				Total ($TgCO_2$ eq/yr)
	Dairy Cattle	Nondairy Cattle	Sheep	Goat	Dairy Cattle	Nondairy Cattle	Sheep	Goat	All
Africa	84.9±10.9	270.6±20.7	32.6±2.8	45.2±5.9	1.8±0.2	3.6±0.3	1.3±0.1	1.6±0.2	441.60
Asia	119.4±17.8	534.5±33.3	43.3±4.3	68.8±4.4	14.1±2.0	14.5±0.5	1.0±0.1	2.0±0.1	787.53
East Europe	17.6±1.5	14.3±1.5	3.9±0.1	1.1±0.0	3.5±0.5	2.3±0.1	0.1±0.0	0.0±0.0	42.89
Latin America	65.5±4.9	488.8±29.6	11.7±0.3	4.0±0.2	1.8±0.1	9.1±0.4	0.3±0.0	0.14±0.0	581.26
Middle East	25.3±4.4	35.5±7.6	23.1±1.6	8.7±0.3	0.5±0.0	0.4±0.0	0.4±0.0	0.2±0.0	94.20
North America	29.1±1.3	283.8±8.1	0.8±0.1	0.0±0.0	14.5±0.2	3.3±0.1	0.0±0.0	0.0±0.0	331.60
Oceania	9.1±0.7	42.2±2.5	14.2±2.1	0.4±0.1	3.7±0.1	1.3±0.0	0.7±0.1	0.0±0.0	71.70
West Europe	34.9±1.1	99.8±3.4	12.1±1.0	0.8±0.0	11.1±0.6	10.1±0.3	0.4±0.0	0.0±0.0	169.16
Total	385.8±35.1	1759.7±98.7	141.7±4.9	129.0±10.4	50.9±1.7	44.6±0.8	4.2±0.1	4.0±0.4	2519.94
Sector Total	2416.2 (95.9%)				103.74 (4.1%)				

7.4 Discussion

7.4.1 Comparison with previous estimates

We compared our results with studies based on FAOSTAT database (Tubiello et al. 2013, Caro et al. 2014), Environmental Protection Agency (EPA; (EPA 2012)), JRC/PBL Emissions Database for Global Atmospheric Research (EDGAR 2016), and a higher tier (tier III) estimates based on Herrero et al. (2013). Our global estimates of CH_4 emission from livestock sector (enteric fermentation and manure management) are in broad agreement with EPA (2012), FAOSTAT and EDGAR (2016), which provides estimates in the range of 2.1 – 3.1 Gt CO_2-eq in year 2010. Our estimate during the year 2010 was 2.7 Gt CO_2-eq, which closely matches with the above global level estimates. However, there are differences in the approach that has been used to estimate CH_4 emission from the global livestock sector. For example, EPA (2012) uses country-prepared emissions reports, activity data and default emission factors, while Tubiello et al. (2013) and Caro et al. (2014) used IPCC tier I approach to estimate CH_4 emission from the global livestock sector. Similarly, Herrero et al. (2013) used tier III approach and estimated a global CH_4 emission from livestock sector in 2000 to be 1.6 Gt CO_2-eq, which is lower than estimates based on this study and other studies using IPCC tier I and tier II approach (EPA 2012, Tubiello et al. 2013, Caro et al. 2014). Herrero et al. (2013) suggested that lower estimates of CH_4 emissions from enteric fermentation is likely due to the use of more aggregated methods for calculation of CH_4 emission. Here, we used tier II approach to provide improved estimates of CH_4 emission from the global livestock sector during 1890-2014.

Table 7-3 Emission intensity measured as total CH_4 emission/km^2 and total CH_4 emission/LU during the contemporary period (2000-2014). The values are mean ± standard deviation (n = 15).

Region	CH_4 Emission (tons CO_2-eq/LU)	CH_4 Emission (tons CO_2-eq/km^2)
Africa	2.22 ± 0.04	14.82 ± 1.28
Asia	2.44 ± 0.05	37.56 ± 2.93
Eastern Europe	1.38 ± 0.09	18.35 ± 0.40
Latin America	2.05 ± 0.06	28.41 ± 1.69
Middle East	3.11 ± 0.22	15.46 ± 2.18
North America	3.02 ± 0.12	17.50 ± 0.47
Oceania	1.52 ± 0.05	8.49 ± 0.27
Western Europe	1.95 ± 0.08	46.99 ± 0.63

Tier II approach uses a more detailed methodology by allowing for inclusion of information other than livestock population data such as estimation of energy intake and energy loss, diet quality and body weight and better representing the complexity of the system, which may lead to a 10-20% decrease in uncertainty (IPCC, 2006). However, it is possible that spatial and temporal aggregation of some of the variables used to estimate energy content, milk yield, diet quality and body weight may result in an overall increase in uncertainty. To assess the uncertainty associated with the estimated variables used to drive CH_4 emission, we compared emission by different livestock category against FAOSTAT based on Tier I approach during 1961-2014. Our results show that CH_4 emission from cattle, sheep and goats were higher by 25%, 9% and 35%, respectively. The higher estimate in this study is largely due to inclusion of variables that control feed intake, energy content and diet quality unlike the Tier I, which primarily relies on livestock numbers to estimate CH_4 emission. For example, IPCC Tier II approach provides 10-30% higher CH_4 emission compared to Tier I in western Canadian feedlots (Beauchemin and McGinn 2006), and 31% higher for individual dairy cattle (Ellis et al. 2010). While Tier II approach may perform well compared to other approaches at individual animal level, it does not have the full capacity to consider compositional changes in diet making it less applicable while estimating the impact of varying nutritional strategies on emissions (Ellis et al. 2010). In addition, temporal and spatial aggregation of some of the variables used to estimate CH_4 emission may add uncertainty in our results.

7.4.2 Global and regional trends in CH_4 emission from the livestock sector

Global emission from the livestock sector, the largest in agriculture, increased from 0.60 to 2.72 Gt CO_2-eq/yr during 1890-2014. Although there was an overall increasing trend during 1890-2014, we found that emissions slowed down during 1990-1999 (19.7 Tg CO_2-eq/yr), and later increased at the rate of 36.0 Tg CO_2-eq/yr during 2000-2014. In a similar study, using Tier I approach, Tubiello et al. (2013) found the slowing of emission during the 1990s, which then increased during the 2000s. The slowing of emission is due to the slowing of an increase in livestock numbers during the 1990s, particularly in developed countries. Globally, dairy and non-dairy cattle represent the largest source of CH_4 emissions, accounting for 89% of the total emission from the livestock sector in the 2010s (Figure 7.1c). The dominance of cattle toward global emission is due to higher energy demand (maintenance, growth, activity) and body weight resulting in higher emission per unit livestock (Caro et al. 2014). While CH_4 emission from the global livestock sector is closely linked to livestock numbers, other factors such as size, energy demand and diet quality also affect feed intake, resulting in substantial impact on CH_4 emission (O'Mara 2011). In the Tier II approach used here, we considered variation in gross energy demand by livestock category as a function of animal body weight, amount of milk produced per day, energy required for maintenance, activity, lactation and work, and the digestibility of forage, which varies annually during 1961-2014. But, for years prior to 1961 we used a 30-year average condition to determine the gross energy demand by livestock category while estimating CH_4 emissions.

By developing gridded livestock data at a global scale, we seek to estimate livestock related CH_4 emission by regions and livestock category. Across different regions, livestock related CH_4 emissions showed an increasing trend until 1990, but there was substantial difference in emission across regions after 1990. Developing region such as Latin America, Asia and Africa showed increasing contribution to CH_4 emission compared to developed region such as North America, Europe and Oceania (Figure S4). The beginning of the 1990s was characterized by ideological and economic changes, with most of the developing countries transitioning toward export oriented policies (Narula and Dunning 2000, Caro et al. 2014). The export oriented market policy ultimately affected the livestock production, resulting in large increase in CH_4 emission after 1990 in developing countries (Moran and Wall 2011). But, in

North America, western Europe, eastern Europe and Oceania, we found a level-off or even decline in emissions after 1990, largely due to decline in livestock numbers (in LU units) by 8%, 14%, 47% and 8%, respectively. In particular, our study found that eastern Europe showed an increasing trend until 1990, after which it declined significantly at a rate of -0.93 Tg CO_2-eq/yr/yr (p-value < 0.05) due to 47% decline in livestock numbers.

CH_4 emission also differ based on different livestock category, with ruminant livestock producing more CH_4 than non-ruminants and livestock with higher body weight producing more CH_4 within same groups (Moss et al. 2000). Across different livestock category, we found that non-dairy cattle were the largest contributor to CH_4 emission (67%), followed by dairy cattle (20%), sheep (4%) and goat (9%) during 1890-2014. Comparison of the share of CH_4 emission with Tier I estimates based on FAOSTAT show similar contribution across different livestock category. For example, estimation based on FAOSTAT suggests that non-dairy cattle and dairy cattle contributed to 62% and 25%, respectively. The higher contribution from non-dairy cattle is largely driven by an increase in global non-dairy cattle emission by 59%, with developing regions alone responsible for 94% of an increase during 1961-2010 (Caro et al. 2014). During the same time period, our results suggest contribution from global non-dairy cattle to be 78%, which is associated with the largest increase in livestock numbers in Africa (120%), Latin America (67%) and Asia (62%) between the 1960s and the 2010s. Interestingly, our results also indicate that emissions associated with goat increased by 615%, while sheep increased only by 79% between the 1890s and the 2010s. Since the 1890s, there has been a rapid increase in goat numbers in the developing regions, particularly in Asia and Africa, while North America has experienced a significant decline (-87%) in sheep numbers. For example, Jones (2004) found that sheep numbers peaked from 7 million heads in the early 1800s to 56 million head in 1945, then declined to less than 7 million head in 2003 in the United States. This decline is driven by contraction of sheep and wool industries owing to lesser demand of sheep products. However, goat numbers have increased by 146% during 1990-2008 (Aziz 2010). This increase is more prevalent in developing regions because small farm owners rely on goats as a way of boosting their income (Peacock 2005). In addition, goats can utilize poor quality forage and has faster reproduction rates playing an important role in people's livelihood in developing region (Peacock 1996). Also, countries like China have the highest population of goats accounting for an export of 65% of the cashmere (Dubeuf et al. 2004, Berger et al. 2013). Also, emission per unit head of goat did not change significantly (p-value < 0.05), while there was substantial variation in the emission per unit head of sheep over the 1890-2014 period. This implies that large increase in emission from goat was due to dramatic increase in goat numbers, while low contribution from sheep was due to both decline in their number and low emission per unit head of sheep after 1990.

Using higher tier approach has been suggested to reduce bias and better represent the complexity of the system while estimating CH_4 emission (IPCC 2006). Our approach to estimate CH_4 emission from the global livestock uses feed quality and livestock characteristics such as body weight and energy requirements of different livestock category, which has been found to regulate feed intake, livestock productivity, CH_4 emission and manure production (Herrero et al. 2013). For example, diet quality is an important parameter that affects CH_4 production in ruminants. By using digestibility percentage that varies across 10 different regions, we found that Europe and North America have higher digestibility resulting in lesser emission and greater livestock productivity. But in regions such as south Asia with low feed digestibility and lower milk yield per unit livestock, our results showed higher emission implying less productivity per livestock unit.

7.4.3 Drylands as an important contributor to CH_4 emission from the livestock sector

Drylands are highly sensitive to changing climatic conditions and human activities (Reynolds et al. 2007), with projection indicating 78% of the dryland expansion occurring in developing regions compared to 1961-1990 level by 2100 (Huang et al. 2015). In addition, about two-third of the drylands are occupied by rangelands, which support approximately 50% of the world's livestock (Bregas 1998). Climate change and increasing livestock population have led to the degradation of approximately 10-20% of the global drylands (MEA 2005a). Although drylands play a major role in driving the inter-annual variability of land CO_2 sink (Poulter et al. 2014, Ahlström et al. 2015), changing climatic condition and increasing livestock pressure would likely have negative effect on dryland ecosystem, both in terms of net carbon balance and CH_4 emission. Our results showed that 1) CH_4 emission from the livestock sector in drylands has increased by 347%, which is higher than the estimate of 330% increase from the global land surface since the 1890s and 2) emission intensity of the livestock sector in drylands is 36% higher than non-drylands in 2014. The increase of CH_4 emission and higher emission intensity in drylands are associated with changes in the relative abundance of total livestock numbers, low diet quality and low milk production per unit livestock during 1890-2014.

7.4.4 Contemporary CH_4 emission and emission intensity from the global livestock sector

During the contemporary period, CH_4 emission from enteric fermentation and manure management was 2.72 Gt CO_2-eq in year 2014. CH_4 emission increased at a rate of 36.0 Tg CO_2-eq/yr/yr during 2000-2014; however, the magnitude and driving factors of increase in CH_4 emission vary across different regions. Developing regions accounted for the majority of emission (72%) during the 2000s. This is due to relatively higher rates of an increase in ruminant livestock, particularly cattle numbers in the region (Delgado 2003). Unlike the developing regions, developed regions such as North America and Europe showed a decrease in total livestock numbers. Although low livestock numbers resulted in a slowing of emission in Europe, we found that North America experienced an increase in CH_4 emission. Our results are consistent with a slowing of emission as reported by Chang et al. (2015) for European grasslands due to decline in livestock numbers after 1990. But, for North America we found a slight increase in CH_4 emission despite a decline in livestock numbers after 2000 (Figure S7). In the IPCC Tier II approach, emission factor is directly proportional to animal weight, which drives energy demand but inversely proportional to feed digestibility. Higher CH_4 emission in North America despite improved feed quality is due to higher animal live weight, which increases the net energy demand of individual livestock resulting in higher emission.

In case of manure management, Asia, North America and Europe shared a majority of CH_4 emissions. Three key factors affect emission from manure management: manure treatment, climate and type of manure (Opio et al. 2013). In Asia, large increase in animal abundance has rapidly increased CH_4 emission from manure management despite the fact that emission per unit animal is low in Asia due to dominance of dry manure management practices (IPCC 2006). However, in North America and Europe, higher emission are associated with liquid manure management system, which create condition favorable for anaerobic digestion (Opio et al. 2013). In most of the developing regions, livestock manure are either used as fuel or handled in dry systems resulting in lower emissions per livestock unit.

Our results also indicate that there are large differences in CH_4 emission per unit area and per LU, which if managed properly, could facilitate in mitigation of livestock related CH_4

emissions (Avetisyan et al. 2011). Overall, our results showed higher emission per unit area and per LU in developing regions except in western Europe and North America. In western Europe, we found higher emission per unit area because Europe has one of the highest livestock density in the world, although it has fallen by 10% in recent decades (FAOSTAT), particularly in eastern Europe. Our results suggest that livestock density was significantly and positively correlated with emissions per unit area ($p\text{-value} < 0.05$), with high livestock density resulting in higher emission. Africa, Asia, Latin America experienced the largest increase in emission intensity (emission/km^2) by 112%, 120%, 91% and 121% during 1960-2014. However, developed regions showed an increase by up to 56% in North America and decline by up to 32% in eastern Europe. Likewise, emission per LU was higher in North America compared to other regions. This increase was driven by higher live weight of animal, which regulates the maintenance energy requirement of livestock (NRC 1981). For example, comparison of live weight based on FAOSTAT in North America suggests that animal live weight increased from 378.2 to 580.1 kg per cattle, which intensified CH_4 emission, despite higher feed digestibility in the region. It is important to recognize that this increase in CH_4 emission per LU cannot be detected using Tier I approach because of limitation of using a fixed emission factor without considering changes in animal body weight and milk production over time.

7.4.5 Implications for food security and environmental sustainability

The livestock sector is rapidly evolving driven by increased demand for livestock products associated with an increase in population, urbanization and people's income. Our results indicated that the livestock sector has contributed to 47-54% of global anthropogenic non-CO_2 GHG emission from agriculture in 2014. In the future, the environmental costs of increasing livestock production would be large with significant impact on biogeochemical cycles and GHG emission. For example, Pelletier and Tyedmers (2010) found that the global livestock sector will get close to or even surpass some of the planetary boundaries of the safe operating space in the areas of climate change, human appropriation of biomass productivity and nitrogen mobilization. While there is little doubt that the current environmental cost of livestock sector is already large, measures such as shift in diet and increase feed conversion and efficiency could potentially reduce environmental impact of livestock production (Steinfeld and Gerber 2010, Herrero et al. 2016). Livestock systems are an important user of natural resources and also contribute significantly to the livelihoods of people, particularly in developing countries (Thornton 2010). It is therefore imperative to focus on sustainable intensification of the livestock production, which should acknowledge not only on improving livestock production and efficiency, but also on developing regulations and limits for system that has experienced unprecedented ecological changes (Bellarby et al. 2013).

A range of mitigation options exist in reducing the environmental cost of livestock sector (Key and Tallard 2012, Bellarby et al. 2013, Gerber et al. 2013b), which could represent up to 50% of the global mitigation potential from agriculture, forestry and land use sector (Herrero et al. 2016). The mitigation option can be broadly categorized into direct and indirect mitigation practices. The direct mitigation effort include animal based and land based management practices, which focuses on sustainable intensification of the global livestock sector (Herrero et al. 2015), while indirect mitigation effort focuses on policy changes that promote the transition from intensive to extensive production system (Lamb et al. 2016). Animal based mitigation strategies relies on improving feed quality, feed additives, animal productivity and their reproductive efficiency (Gerber et al. 2013b). For example, our results indicated that higher emission per unit area from the global drylands and developing countries is linked to low diet quality and feed inefficiency, and higher livestock numbers. Improving diet quality and feed efficiency in these regions help to reduce the proportion of energy lost as CH_4, which ultimately lead to reducing livestock related GHG emission by 25% (Valin et al. 2013). Using FAOSTAT database, we found that milk yield has increased by 131% between 1961 and 2014, but dairy cattle population has declined by 21% in North America. This implies that improving the production output per unit livestock could play an essential role in mitigating CH_4 emission.

Land based mitigation efforts focuses on increasing the carrying capacity of grassland ecosystem through grazing optimization practices that promote sustainable use of grassland resources (Dangal et al. 2016), and transitioning from intensive to extensive production system (Neely et al. 2010). For example, improve grazing practices can sequester an average of 0.54 Mg C ha^{-1} yr^{-1} globally (Conant et al. 2001), while transitioning from heavy to moderate grazing can sequester 0.21 and 0.69 Mg C ha^{-1} yr^{-1} in Africa and South America, respectively (Conant and Paustian 2002). But, the extent to which grazing intensity can promote or reduce carbon sequestration capacity is still contentious (Milchunas and Lauenroth 1993, McSherry and Ritchie 2013). In case of CH_4 emission associated with manure management, preventing anaerobic digestion of manure that practices lagoons and liquid manure can be beneficial particularly in regions such as Europe and North America (Clemens et al. 2006).

Indirect mitigation option include the policy efforts that promote sustainable intensification of livestock production by imposing tax on conventional ranching and subsidies on semi-intensive and extensive ranching (Smith et al. 2013, Cohn et al. 2014). For example, Cohn et al. (2014) found that semi-intensive production system can cut deforestation rate by half and reduce GHG emission by up to 25% in Brazil. But, such practices have also been suggested to be not profitable in other regions (Gilroy et al. 2014) indicating that the extent to which policy that promote sustainable intensification of livestock production provide long-term carbon benefits may vary by regions. While we did not consider the indirect effects associated with policy changes, our results indicate that an increase in feed efficiency, diet quality and changes in manure management practices to reduce anaerobic digestion has the potential to sustainably intensify global livestock production.

7.4.6 Sources of Uncertainty

In this study, we followed IPCC 2006 guidelines to estimate CH_4 emission from the global livestock sector during 1890-2014. While the use of IPCC tier II to reduce bias and better represent the complexity of ecosystem while estimating CH_4 emission, there are two known uncertainties in terms of development of gridded data for livestock and animal energy requirements, which could possibly introduce uncertainty in our estimation of CH_4 emissions. First, we assumed that the gridded livestock data follows a same spatial pattern based on Robinson et al. (2014), but the temporal pattern are controlled by country level estimates of annual livestock numbers based on FAO during 1961-2014 and Mitchell (1993) for years prior to 1961. It is likely that the spatial distribution of livestock might change during 1890-2014. To reduce the uncertainty associated with spatial distribution of livestock numbers, we collected animal data at lower administrative units for countries such as China, the United States, Australia, Brazil, Mongolia and Canada (see methods for detail) during 1961-2014. Second, we have not considered other livestock such as horses, camels and buffalo, which could influence CH_4 emissions. In addition, the Tier II approach used here does not account for compositional changes in diet and the resultant impact of varying nutritional strategies on CH_4 emissions (Ellis et al. 2010).

Chapter 8. Nitrous oxide (N_2O) emission from global grasslands: contribution from manure and nitrogen fertilizer

Abstract

Manure production and their application to grassland ecosystems play an important role in the global N_2O emission, but relatively little attention has been given to attributing different sources of N_2O emissions from animal agriculture. In this study, we use the Dynamic Land Ecosystem Model (DLEM) to quantify the evolution of N_2O emission from global grassland ecosystems and attributed the contribution of manure deposition/application and fertilizer application during 1961-2014. Our results show that N_2O emission from global grasslands increased significantly from 1.41 Tg N_2O-N/yr in 1961 to 1.89 Tg N_2O-N/yr in 2014. Among different sources, manure left on pastures contributed to ~40% of the total emissions, followed by manure applied to pastures (20%) and fertilizer applied to pastures (10%). Regionally, Asia dominated N_2O emissions contributing to 31% of the emission, followed by North America (25%), Europe (20%) and Africa (13%). Our results indicate that although managed grasslands occupy 24% of the global grassland area, they contribute up to 68% of the total emissions, primarily due to high levels of nitrogen inputs in the form of urine, feces in the form of animal manure and mineral nitrogen. It is likely that future increases in livestock production would increase manure production, which could ultimately lead to increases in N_2O emissions. Improvement in genetic production potential of livestock and their feed composition can reduce nitrogen losses via urine

and feces and collection of manure and their application to croplands and pastures based on specific plant nitrogen demand could potentially reduce N_2O emissions.

8.1 Introduction

Nitrous oxide (N_2O) is considered to be a potent greenhouse gas (GHG), with a 100 year global warming potential 265-298 times that of carbon dioxide (CO_2) (Myhre et al. 2013). The terrestrial biosphere emitted 12.6-15.2 Tg N_2O-N yr^{-1} during the 2000s, with human activities contributing to ~45% of the total emissions (Tian et al. 2016a). Among the anthropogenic sources (agriculture, industry, biomass burning and indirect emissions from reactive nitrogen), agriculture plays a fundamental role in driving emission growth (Mosier et al. 1998, Davidson 2009), contributing to ~25-30% of all terrestrial biogenic emission (Tian et al. 2016a). The dominant contribution from agricultural soil is attributed to the expansion of agricultural land area and high fertilizer use since the pre-industrial era (Forster et al. 2007, Reay et al. 2012).

Nitrous oxide emissions are driven by two biological processes of nitrification and denitrification (Davidson 1991, Senbayram et al. 2009). Nitrification involves the oxidation of ammonium (NH_4^+) to nitrate with N_2O as the by product, while denitrification involves the reduction of nitrate (NO_3^-) into dinitrogen (N_2), with N_2O as an intermediate product. These processes are regulated by many factors, particularly soil water content, soil temperature, soil pH, aeration and substrate (NH_4^+ and NO_3^-) availability (Bouwman 1990, Granli and Bøckman 1994, Dobbie et al. 1999). Although both nitrification and denitrification occur simultaneously within soils, low soil water content and coarse texture soil favor nitrification, while high soil water content and fine texture soil with high organic content promote denitrification (Davidson 1991). In addition, field measurements suggest that high N_2O emissions are generally associated with soil condition that promotes denitrification (anaerobic with adequate NO_3^- supply) (De Klein and Eckard 2008).

Animal agriculture has been identified as an important source of N_2O contributing up to 50% of total agricultural emissions (De Klein and Eckard 2008). The sources of N_2O emission from animal agriculture include nitrogen fertilizer application for feed crops, indirect fertilizer emission due to losses, manure management, manure application/deposition and indirect manure emission. In particular, manure management, manure application/deposition and indirect losses from manure are responsible for ~80% of the total emissions from animal agriculture (Steinfeld et al. 2006a). However, with respect to the contribution of manure management and manure application/deposition to N_2O emissions, contrasting results have been reported (Steinfeld et al. 2006a, De Klein and Eckard 2008, Davidson 2009). Therefore, a better understanding of the contributing factors to N_2O emissions from animal agriculture is needed, which could potentially help to reduce uncertainties in emission estimates.

The largest source of N_2O emissions from animal agriculture comes from manure left on pasture and manure applied to soils (Steinfeld et al. 2006a), with emissions from manure left on pasture 6 fold higher than that applied to croplands (Tubiello et al. 2013). But, there is considerable uncertainty regarding which factor dominates emission. For example, Oenema et al. (2005) found that manure applied to land and manure left on pasture resulted in the emission of 45 and 183 Tg CO_2-eq, respectively in 2010. In contrast, Tubiello et al. (2013) found that manure applied to soils and manure left on pasture resulted in the emission of 116 Tg CO_2-eq and 764 Tg CO_2-eq, respectively in the same year. These inconsistencies in the estimation of N_2O emission from manure comes from differences in animal categorization and nitrogen excretion rates per animal species, disaggregation of total manure nitrogen production to manure left on pasture, manure lost through leaching, manure applied to croplands and burning of dung, and spatial and temporal aggregation of data used to estimate emissions (Bouwman et al. 1995).

One approach to reduce uncertainty in the estimates of N_2O emission from livestock manure production is to use a process-based model, with explicit representation of nitrification and denitrification mechanism (Bouwman et al. 2002, Stehfest and Bouwman 2006, Tian et al. 2015b). However, this approach requires spatially explicit estimates of manure production and their attribution to different sources including indirect (volatilization and leaching) and direct (manure left on pasture and that applied to croplands/pastures, waste in storage and burning of dung) sources (Oenema et al. 2005). For example, Bouwman et al. (2013) developed a spatially explicit dataset on global nitrogen inflows and outflows including manure applied to croplands and that left on pasture from the land biosphere for 1900, 1950, 2000 and 2050, but continuous time-series were not available. Perhaps a more reliable dataset would be that from Food and Agriculture Organization (FAOSTAT 2017), but manure production data are available only since 1961 and are aggregated at a country level making it difficult to use as input to the process based land model. In a recent study (Zhang et al. Under Review), spatially explicit dataset on global manure production and their attribution to rangeland and croplands has been achieved for over a century long time scale (1860-2014), which could be used as an input to the ecosystem model in estimating N_2O emissions.

Here we used the Dynamic Land Ecosystem Model [DLEM; Tian et al. (2010a)] in conjunction with newly developed datasets on manure applied to cropland and pastures (Zhang et al. Under Review) to estimate N_2O emission from global grasslands during 1901-2010. Objectives of this study are to (1) investigate the evolution of N_2O emission from global grasslands (both managed pastures and rangelands) during 1961-2014; (2) attribute N_2O

emissions to climate and grassland management (fertilization and manure deposition) during 1961-2014; (3) identify the hotspots of N_2O emission during the contemporary period (2001-2014); and (4) discuss the mitigation options for N_2O emission from fertilization and manure application in global grasslands.

8.2. Materials and methods

8.2.1 The Dynamic Land Ecosystem Model (DLEM)

The DLEM is a process-based ecosystem model that uses spatially explicit information on climate (mean, maximum and minimum air temperatures, precipitation, wind speed and shortwave radiation), vegetation (four natural vegetation and one crops) and soil (texture, bulk density and pH) to make estimates of carbon, nitrogen and water pool sizes and fluxes at regional to global scales (Tian et al. 2012a, Pan et al. 2015c, Tian et al. 2015b). Briefly, the DLEM consists of five core components: 1) biophysics; 2) plant physiology; 3) soil biogeochemistry; 4) dynamic vegetation; and 5) disturbance, land use and management. The structure, algorithm, parameterization and evaluation of the model has been documented elsewhere (Tian et al. 2010a, Tian et al. 2010b, Ren et al. 2012, Pan et al. 2014c, Pan et al. 2015a, Tian et al. 2015d). In this study, we used DLEM (version 2.0), which explicitly simulates N_2O emissions from croplands in response to nitrogen fertilization and manure deposition/application. The model was further improved to allow for fertilization and manure deposition in grasslands, and to make estimates of N_2O emissions during 1901-2010.

8.2.2 Model improvements

In the previous version of the DLEM 2.0 (Tian et al. 2010), management practices including fertilization and manure application were only implemented for croplands, while grasslands were broadly categorized as C3 and C4 grass. In this version, we improved the model by representing processes for four different grassland types: 1) C3 pastures; 2) C3 rangelands; 3) C4 pastures; and 4) C4 rangelands. We assumed that pastures are intensively managed, while rangelands receive no management. Grassland carbon and nitrogen cycling in and out of the grassland ecosystems is modeled similar to our previous work (Ren et al. 2007, Tian et al. 2010a, Herrero et al. 2013, Pan et al. 2014c). The availability of substrate (inorganic nitrogen) plays an important role in determining the nitrification and denitrification processes. These processes are assumed to occur only in the top 50 cm soil surface. Nitrification and denitrification processes are simulated similar to Chatskikh et al. (2005).

Nitrification process

Nitrification, in the DLEM, is a function of maximum daily nitrification rates regulated by soil temperature, soil moisture and ammonium content. Mathematically,

$$N_{nit} = k_{nit} f(T_{soil}) f(w) av_{NH4} \qquad (1)$$

Where,

K_{nit} is the daily maximum fraction of ammonia that is converted into nitrate and nitrogen gases, which is set to be 0.1/day

$f(T_{soil})$ is the effect of soil temperature on nitrification

$f(w)$ is the effect of soil moisture on nitrification

av_{NH4} is the soil available ammonium content

The soil temperature effect ($f(T_{soil})$) on nitrification is based on Kirschbaum (1995) and Petersen et al. (2005):

$$f(T_{soil}) = 7.24 \times e^{-3.432+0.168 \times T \times (1-0.5 \times T/36.9)} \qquad (2)$$

Where,

T is the soil temperature in ^{o}C for the top soil layer

The soil moisture effect on nitrification is estimated as:

$$f(w) = -12.904 \times wfp^4 + 17.651 \times wfp^3 + 5.5368 \times wfp^2 + 0.9975 \times wfp - 0.0243 \quad (3)$$

Where,

wfp is the percentage of soil porosity that are filled by water

The total nitrogen gas production from nitrification is then estimated as:

$$Ngas_{nit} = k_{np} f(T) wfp \, N_{nit} \quad (4)$$

Where

k_{np} is the proportion of N intermediates resulting in N_2O emissions from nitrification

f(T) is the temperature function based on Li et al. (2000) and is given by

$$f(T) = e^{-0.5((T-34.2)/17.1)^2} \quad (5)$$

Denitrification process

Denitrification is a function of potential denitrification rate regulated by soil temperature, soil water content and soil available nitrates. The process of denitrification results in three types of nitrogen gases, which includes nitric oxide (NO), nitrous oxide (N_2O) and dinitrogen (N_2), and is modeled as:

$$N_{denit} = N_{pot,denit} f(T_{soil}) f(w) f(c_{av_{NO_3}}) \quad (6)$$

where,

f(w) is the soil water effect

$f(C_{avNO3})$ is the effect of nitrate concentration on denitrification

$N_{pot,denit}$ is the potential denitrification rate

The soil water effect is given by:

$$f(w) = 0.0116 + 1.36/(1 + e^{-\frac{wfp-0.815}{0.0896}}) \quad (7)$$

The effect of nitrate concentration on denitrification is calculated as:

$$f\left(c_{av_{NO_3}}\right) = 1.17 \, c_{av_{NO_3}}/(32.7 c_{av_{NO_3}}) \quad (8)$$

The potential denitrification rate is calculated as:

$$N_{pot,denit} = (0.151 + 0.015 \times P_{clay}) \times Rh \times kden$$

(9)

Where,

P_{clay} is the percentage clay content

Rh is the soil respiration rate

Kden is a biome dependent parameter that affects the potential denitrification rate

The total nitrogen gas production from denitrification is equal to the denitrification rate

$$Ngas_{denit} = N_{denit} \qquad (10)$$

Estimation of N_2O emission from nitrification and denitrification

Nitrous oxide (N_2O) emission is a function of total nitrogen gas produced by nitrification (N_{gasnit}) and denitrification ($N_{gasdenit}$) modified by functions of temperature, soil water content and soil texture. Mathematically,

$$N_2O = (Ngas_{nit} + Ngas_{denit})f(T)(1 - f(w))f(clay) \qquad (11)$$

where,

f(T) is the temperature effect

f(w) is the soil water effect

f(clay) is the soil texture effect

The temperature effect (*f(T)*) is given by

$$f(T_{soil}) = \frac{1}{1+e^{-0.64+0.08T_{soil}}} \qquad (12)$$

The soil water effect (*f(w)*) is given by

$$f(w) = 0.0116 + 1.36/(1 + e^{-\frac{wfp-0.815}{0.0896}}) \qquad (13)$$

The soil texture effect (*f(clay)*) is given by

$$f(clay) = 1.26e^{-0.0116P_{clay}} - 0.249 \tag{14}$$

Nitric oxide (NO) is calculated based on the empirical relationship between N_2O, NO and water filled pore space (Davidson et al. 2000a), which is given by

$$NO = N_2O/10^{2.6wfp-1.66} \tag{15}$$

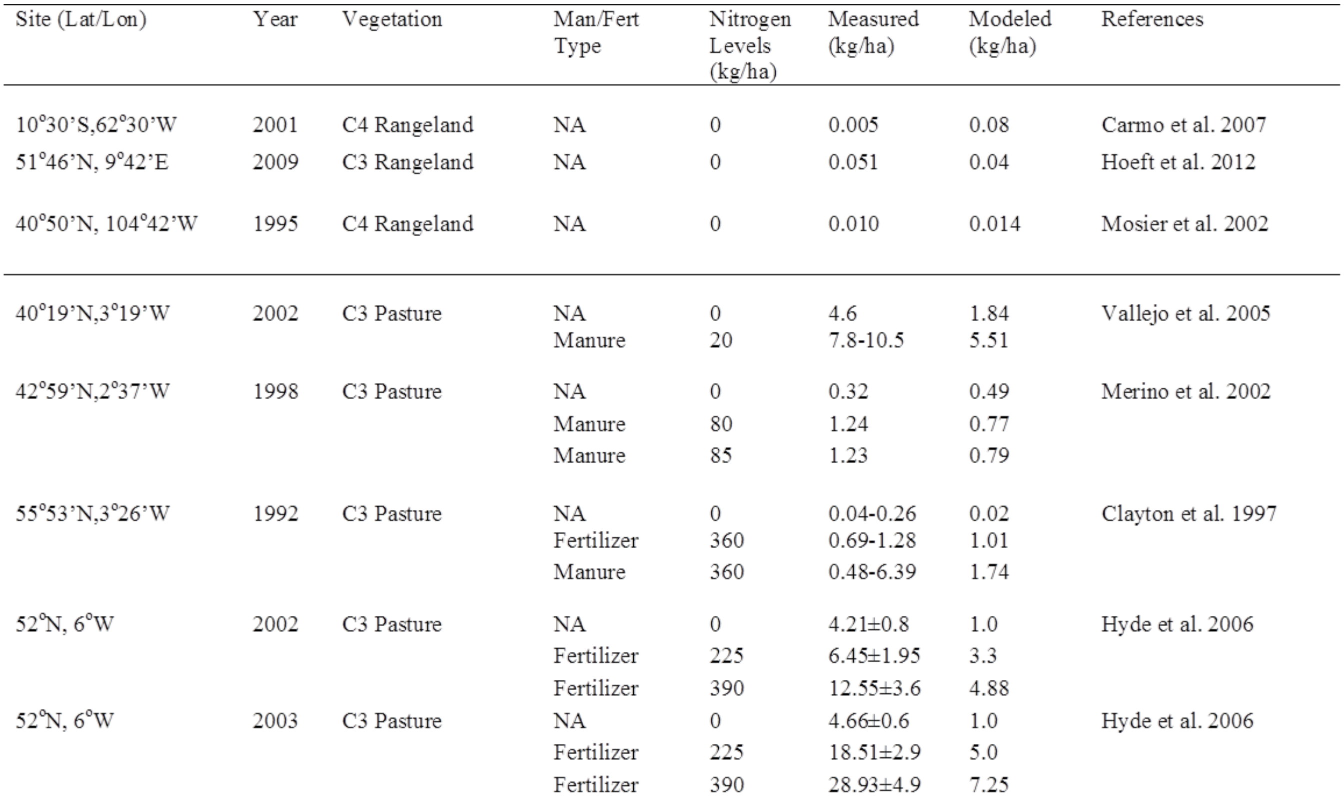
The remaining gas from nitrification and denitrification is then assumed to be lost as dinitrogen (N_2)

$$N_2 = Ngas_{nit} + Ngas_{denit} - N_2O - NO \tag{16}$$

Table 8-1 Simulation design used in this study

Simulation	Climate	Fertilizer	Manure Applied	Manure Left	Other factors
Reference	1900	1900	1900	1900	1900
All Combined	1900-2014	1961-2014	1900-2014	1900-2014	1900-2014
Climate only	1900-2014	1900	1900	1900	1900
Fertilizer only	1900	1900-2014	1900	1900	1900
Manure Applied Only	1900	1900	1900-2014	1900	1900
Manure Left Only	1900	1900	1900	1900-2014	1900

Table 8-2 Comparison of DLEM simulated N_2O emission against observations in rangelands and pastures



Site (Lat/Lon)	Year	Vegetation	Man/Fert Type	Nitrogen Levels (kg/ha)	Measured (kg/ha)	Modeled (kg/ha)	References
10°30’S,62°30’W	2001	C4 Rangeland	NA	0	0.005	0.08	Carmo et al. 2007
51°46’N, 9°42’E	2009	C3 Rangeland	NA	0	0.051	0.04	Hoeft et al. 2012
40°50’N, 104°42’W	1995	C4 Rangeland	NA	0	0.010	0.014	Mosier et al. 2002
40°19’N,3°19’W	2002	C3 Pasture	NA	0	4.6	1.84	Vallejo et al. 2005
			Manure	20	7.8-10.5	5.51	
42°59’N,2°37’W	1998	C3 Pasture	NA	0	0.32	0.49	Merino et al. 2002
			Manure	80	1.24	0.77	
			Manure	85	1.23	0.79	
55°53’N,3°26’W	1992	C3 Pasture	NA	0	0.04-0.26	0.02	Clayton et al. 1997
			Fertilizer	360	0.69-1.28	1.01	
			Manure	360	0.48-6.39	1.74	
52°N, 6°W	2002	C3 Pasture	NA	0	4.21±0.8	1.0	Hyde et al. 2006
			Fertilizer	225	6.45±1.95	3.3	
			Fertilizer	390	12.55±3.6	4.88	
52°N, 6°W	2003	C3 Pasture	NA	0	4.66±0.6	1.0	Hyde et al. 2006
			Fertilizer	225	18.51±2.9	5.0	
			Fertilizer	390	28.93±4.9	7.25	

8.2.3 Modeling Protocol

Gridded, georeferenced datasets for the DLEM were compiled from various sources at a spatial resolution of $0.5^o \times 0.5^o$. These datasets include daily climate data, atmospheric chemistry (CO_2 concentration, AOT40 O_3 index, and nitrogen deposition), soil properties, land management practices (irrigation, nitrogen fertilizer use and rotation) and other ancillary data such as river network, cropping system and topography maps. Daily climate data during 1901-2014 were based on CRU-NCEP climate forcing (ftp://nacp.ornl.gov/synthesis/2009/frescati/model_driver/cru_ncep/analysis/readme.htm), while atmospheric CO_2 concentration was obtained from Carbon Dioxide Information Analysis Center

(CDIAC; http://cdiac.ornl.gov/). Annual nitrogen deposition was retrieved from the outputs of multiple atmospheric chemistry transport models [http://daac.ornl.gov/CLIMATE/guides/global_N_deposition_maps.html; Dentener et al. (2006)] and tropospheric ozone concentration were based on Felzer et al. (2004), while LCLUC was constructed based on Synergetic Land Cover Product (SYNMAP; Jung et al. (2006)) and HYDE3.1 land use data (Klein Goldewijk et al. 2011). Elevation, slope and aspect were derived from Global 30 arc-second elevation product (GTOPO30; https://lta.cr.usgs.gov/GTOPO30), and soil texture was derived from Food and Agricultural Organization (FAO) Soil Database System (Reynolds et al. 2000).

In this study, to account for more realistic estimates of carbon and nitrogen cycling in grassland ecosystems, we classified grassland into two different categories based on HYDE 3.2 (Klein Goldewijk et al. Under Review). The grazing lands are categorized into more intensively used pastures and less intensively used rangelands as a function of aridity index and population density. A grid is categorized as rangeland when the aridity index is less than 0.5 or when the aridity index is higher than 0.5 but the population density is less than 5/km^2. This approach assumes that more intensively managed pastures are found closer to populated areas and are representative of wetter grazing lands, while less/no managed grasslands are found in drier areas. The global distribution of pastures and rangelands for 2014 is provided in Figure 8.1 We further categorized both pastures and rangelands into C3 and C4 category by overlaying the global distribution of C3 and C4 grasslands based on Still et al. (2003).

In addition to the global distribution of pastures and rangelands, we developed spatially explicit datasets on manure left on pastures, and manure and fertilizer applied to pastures/rangelands. Manure left on pastures was developed based on country level FAOSTAT during 1961-2014. Manure applied to pastures was based on Zhang et al. (Under Review), while fertilizer applied to pastures was developed by combining FAOSTAT country level fertilizer data against country level total fertilizer allocated to grasslands (Lassaletta et al. 2014).

For each grid cell, we first run the DLEM to determine the equilibrium state of carbon, nitrogen and water for an undisturbed ecosystems using the long-term (30 year; 1901-1930) daily climate averages, while other input data (atmospheric CO_2, nitrogen deposition and land cover) were kept at 1900 level. The equilibrium run is carried out for the maximum of 10,000 years or until the net carbon exchange between the atmosphere and the terrestrial ecosystem is less than 0.5 g C m^{-2}, the change in soil water pool is less than 0.5 mm, and the change in total nitrogen content is less than 0.5 g N m^{-2} during two consecutive 20 years, for each grid cell. We then carried out a model spin up for 100 years by randomly selecting 20 years of climate data, repeated five times, during 1901-1930. The purpose of model spin up is to account for the influence of inter-annual variability on the initial conditions of carbon, nitrogen and water pools and to smooth the transition from equilibrium state to transient run. Following the model spin up, we carried out five transient simulations with the forcing of daily climate data and other environmental factors during 1901-2014 (Table 8.1).

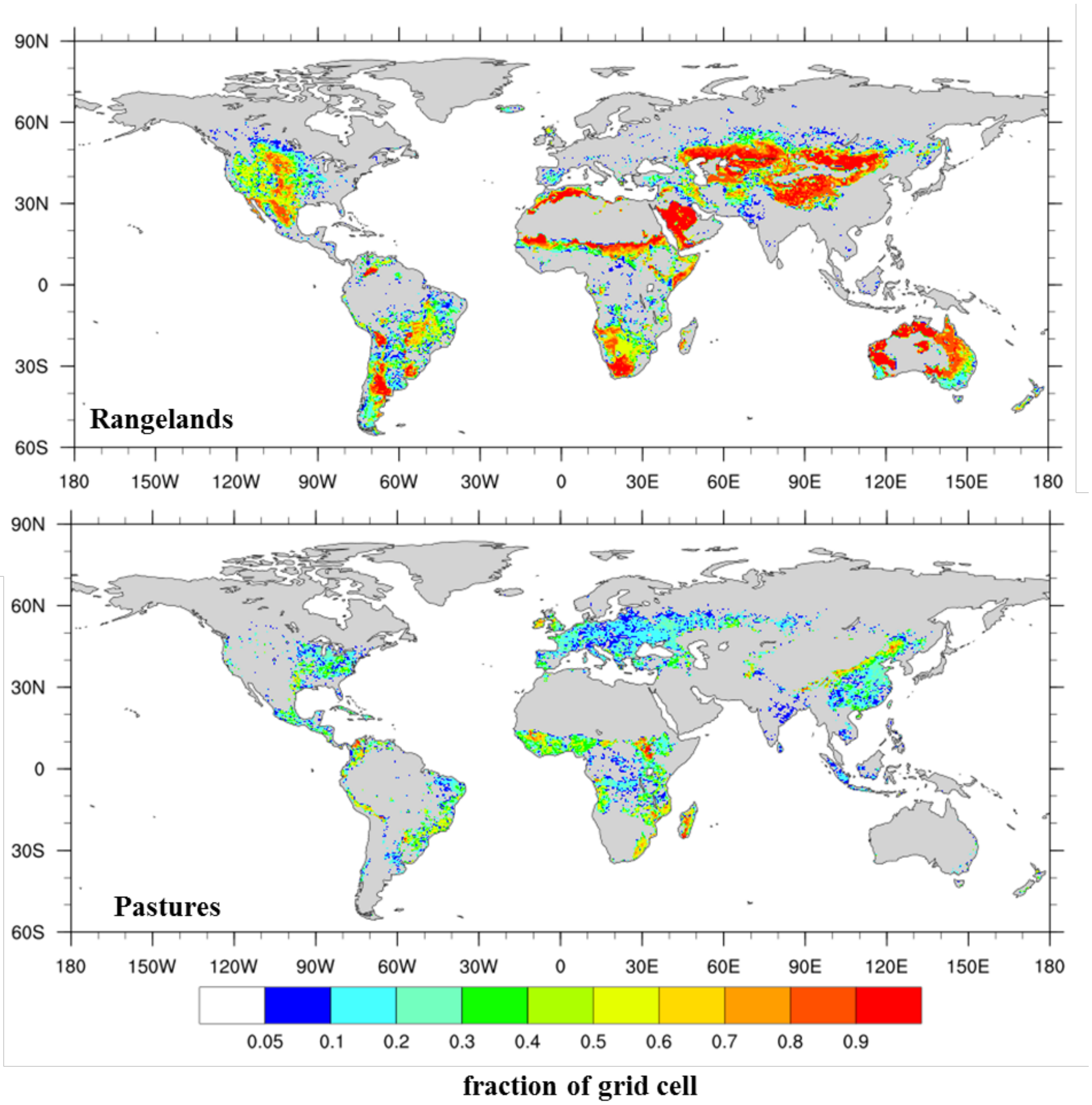


Figure 8-1 The global distribution of pastures and rangelands in year 2014

8.2.4 Model evaluation

We compared the simulated N_2O emission for different grassland type and at different levels of nitrogen application across seven sites. Our results showed that the DLEM simulated N_2O fluxes are in agreement with observations, particularly for rangelands. In case of pastures, DLEM showed a reasonable agreement with different levels of fertilizer and manure application at Edinburgh (Clayton et al. 1997) and Basque County, Spain (Merino et al. 2002), but there was a tendency of under-prediction at other sites (Table 8.2). However, DLEM has a tendency of under-prediction when compared to observations under different levels and type of nitrogen applications. For example, at Arganda del Rey (Madrid) site, DLEM under-predicted N_2O emissions by 2.76 kg N_2O-N/ha and 2.29-4.99 kg N_2O-N/ha for control and manure application scenario, respectively (Vallejo et al. 2005). This is because we did not irrigate the pastures in the DLEM, but Vallejo et al. (2005) irrigated the pastures for both control and fertilized scenario. In addition, the grassland was cut six times over the study period, which would likely lead to differences in N_2O emissions. While it is tempting to irrigate the pastures and investigate the response of N_2O emissions, the extent to which irrigation, its timing and amount affect N_2O emission is still contentious (Davidson 1992, Bollmann and Conrad 1998). Increased frequency of irrigation may promote anaerobic condition and N_2O reductase enzyme activity which reduces N_2O to dinitrogen during denitrification (Knowles 1982), while irrigation after dry periods increases N_2O production by enhancing the microbial activity (Garcia-Montiel et al. 2003).

At a site in Wexford, Ireland (Hyde et al. 2006), DLEM indicates large under-estimation under both control and different levels of fertilizer application (Table 8.2). This is because the site has experienced 21-day rotational grazing with a total of 42 animals (300-350 kg liveweight) over the experimental area. It is likely that nitrogen inputs in the form of urine and excreta led to large emissions under both control and fertilized treatments at the study sites. However, in the DLEM, we did not include the manure deposition following rotational grazing at Wexford site because the total manure deposition data at the study site were not available.

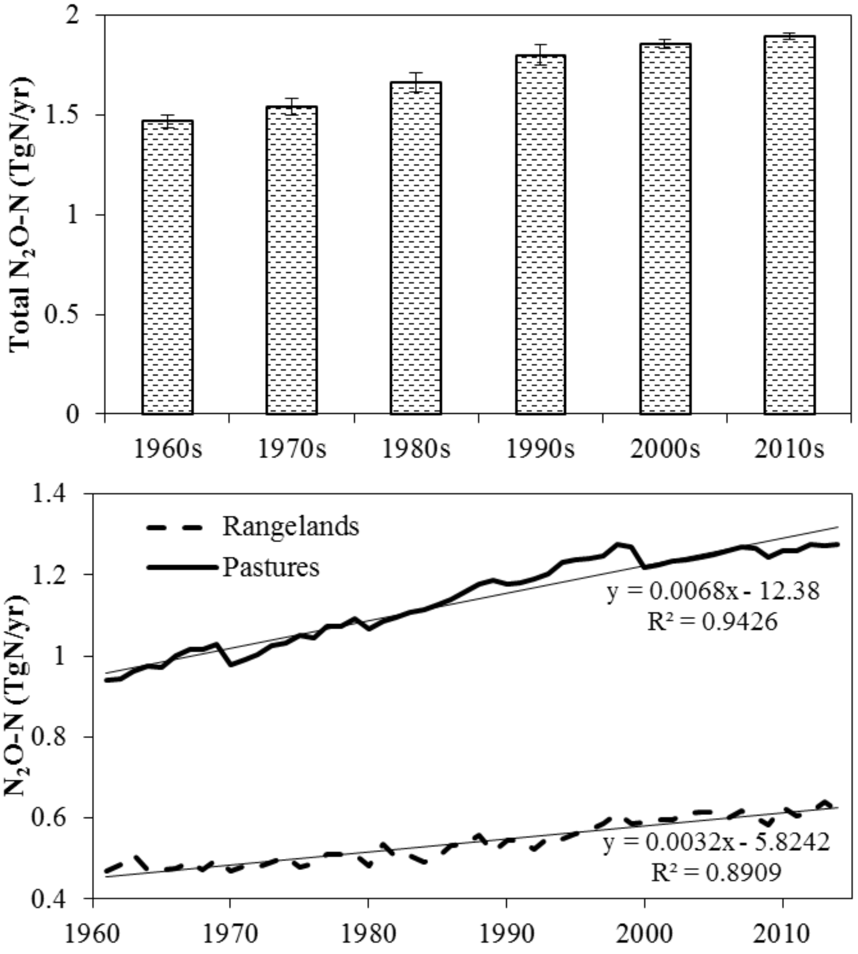


Figure 8-2 Decadal changes in N_2O emissions from global grasslands during 1961 to 2014 (top panel) and temporal change in N_2O emissions from rangelands and pasturelands during 1961 to 2014 (bottom panel).

8.3 Results

8.3.1 Temporal pattern of N_2O emission from pastures and rangelands

The DLEM simulated results showed that the influence of multiple environmental factors including land management practices such as fertilization, manure left on pastures and manure application resulted in a significant increase in N_2O emissions from 1.41 Tg N_2O-N/yr in 1961 to 1.89 Tg N_2O-N/yr in 2014 (p-value < 0.05; R^2= 0.96; Figure 8.2). Managed pastures contributed

68% of the total emissions (1.14 Tg N_2O-N/yr), while rangelands contributed to 32% (0.54 Tg N_2O-N/yr). Both pastures and rangelands show a significant increase in N_2O emission at the rate of 0.007 Tg N_2O-N/yr and 0.003 Tg N_2O-N/yr, respectively (Figure 8.2). Although pastures occupy approximately 24% of the global grassland area, they contributed to 68% of the total N_2O emissions from grassland ecosystems.

8.3.2 Spatial and regional variation in N_2O emissions

Our results indicated large spatial variability in N_2O emission as a result of multiple environmental changes and pasture management practices such as fertilization, manure left on pastures and manure application (Figure 8.3). Europe, North America and Asia dominated N_2O emissions at a rate of up to 1 TgN_2O-N, with increasing contribution from Asia due to higher livestock numbers, which ultimately lead to an increase in manure production. Regionally, Africa, Asia, Latin America, Middle East, North America and Oceania showed a significant increase in N_2O emissions (p-value < 0.05), while Europe experienced a decline in N_2O emissions, but the effect was not statistically significant (p-value $= 0.4$). Asia dominated N_2O emission from grassland contributing to 31% of the emissions, followed by North America (25%), Europe (20%) and Africa (13%) (Figure 8.4).

8.3.3 Effect of climate and pasture management on N_2O emissions

Among different sources of N_2O emissions, manure left on pastures contributed to a largest emission source of 0.43 Tg N_2O-N/yr, followed by manure applied on pastures (0.26 Tg N_2O-N/yr), fertilizer application (0.13 Tg N_2O-N/yr) and climate (0.03 Tg N_2O-N/yr) (Figure 8.5) during 1961-2014. Manure left on pastures resulted in the largest rate of increase in N_2O emissions (0.0024 Tg N_2O-N/yr), followed by climate change (0.001 Tg N_2O-N/yr), manure application (0.0005 Tg N_2O-N/yr) and fertilization (0.0002 Tg N_2O-N/yr) (p-value < 0.05).

Overall, manure left on pastures contributed to ~40% of the total N_2O emissions from global grassland ecosystems.

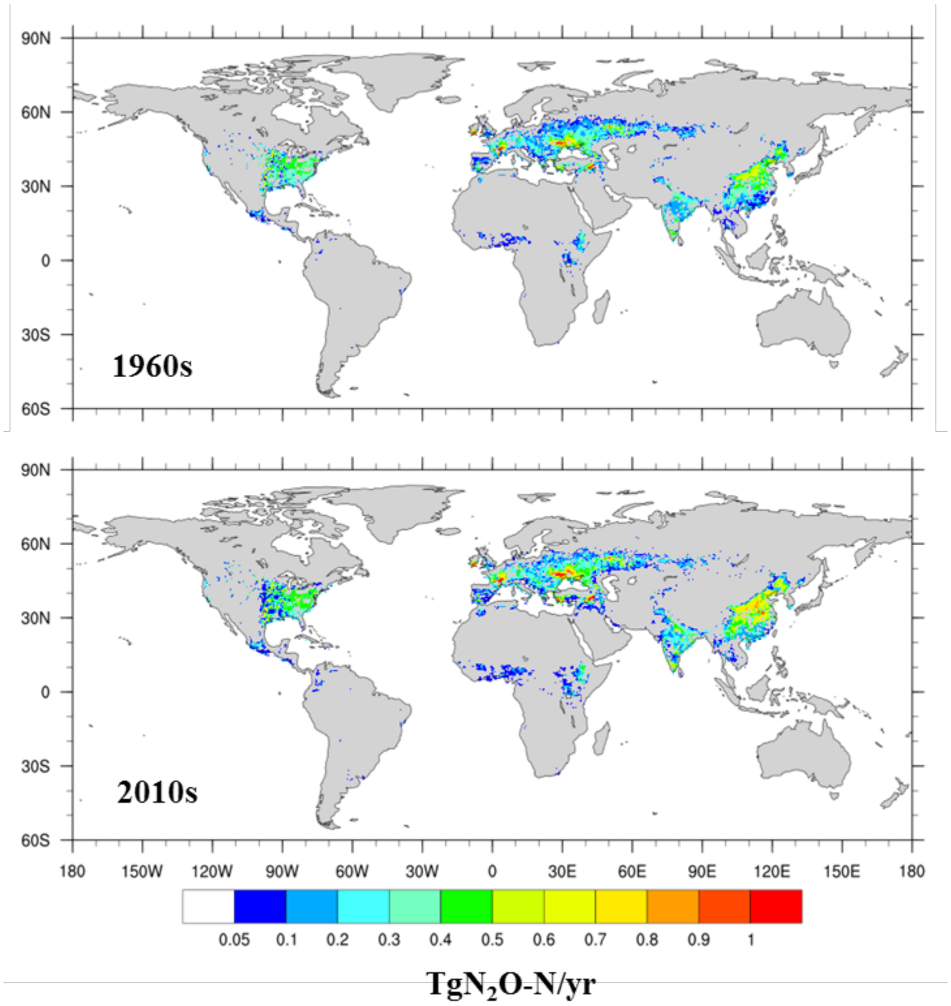


Figure 8-3 Spatial pattern of change in N_2O emissions in the 1960s and the 2010s

8.3.4 Contemporary changes in N_2O emissions

During the contemporary period (2001-2014), grassland ecosystems was a source of 1.86 (1.82-1.91) Tg N_2O-N, with a significantly increasing trend at a rate of 0.0051 Tg N_2O-N/yr (p-value < 0.05; $R^2 = 0.59$). Among different sources, manure left on pastures contributed to 36% of the total N_2O emissions, while manure and fertilizer applied on pasture contributed to 20% and 10% of the total N_2O emissions (Figure 8.6). Pastures were the dominant source contributing to 67% (1.25 Tg N_2O-N/yr) of the total N_2O emissions from grassland ecosystems during 2001-2014.

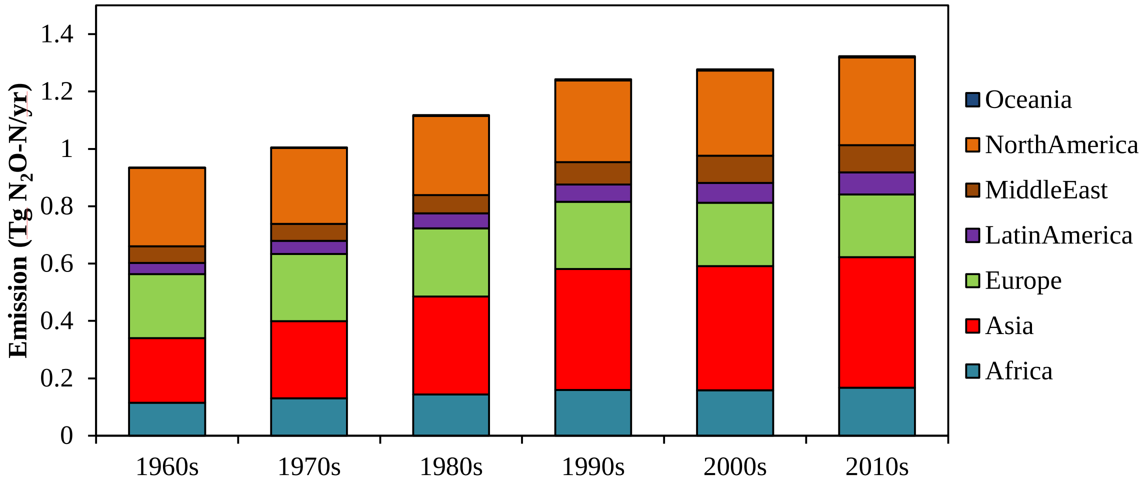


Figure 8-4 Regional changes in N_2O emissions during 1961-2014

8.4. Discussion

8.4.1 Comparison of emission sources to previous studies

We compared our results of emission from manure left on pastures against IPCC tier I studies based on Steinfeld et al. (2006a) and Tubiello et al. (2013). Steinfeld et al. (2006a) provide emission estimates from manure deposition of about 2.24 Tg N_2O-N (not including emission from intensive practices), while Tubiello et al. (2013) provide estimates of about 2.07 Tg N_2O N/yr during 1961-2014. We provide estimate of about 1.5 Tg N_2O-N during 1961-2014 due to manure left on pastures, which is similar to total N_2O emissions of 1.5 Tg N2O-N from animal production systems based on Oenema et al. (2005). The discrepancy between IPCC tier I and this study is because IPCC tier I approach relies on using a default emission factor of 1-2%

for emissions from manure left on pasture, with higher emission factor for manure produced from dairy, non-dairy, buffalo, poultry and pigs, but lower emission factor for sheep and other animals. Using a default emission factor assumes a linear relationship between nitrogen input and N_2O emissions, but does not account for the effect of soil conditions, climate and vegetation type, which varies considerably across different regions (Stehfest and Bouwman 2006, Philibert et al. 2012). However, recent studies suggest that the relationship between nitrogen inputs and N_2O emissions can be linear, exponential or hyperbolic (Bouwman et al. 2002, Shcherbak et al. 2014), depending on whether the soil condition is nitrogen limited or carbon limited (Kim et al. 2013). In a recent meta-analysis study, Shcherbak et al. (2014) found that N_2O response to nitrogen enrichment increased significantly faster compared to the linear response for synthetic fertilizer and different crop types. This implies that using a default emission factor for global extrapolations of N_2O emissions as a function of nitrogen inputs in the form of manure and fertilizer does not accurately capture the biological thresholds that occur when nitrogen inputs exceeds plant nitrogen demands (Shcherbak et al. 2014).

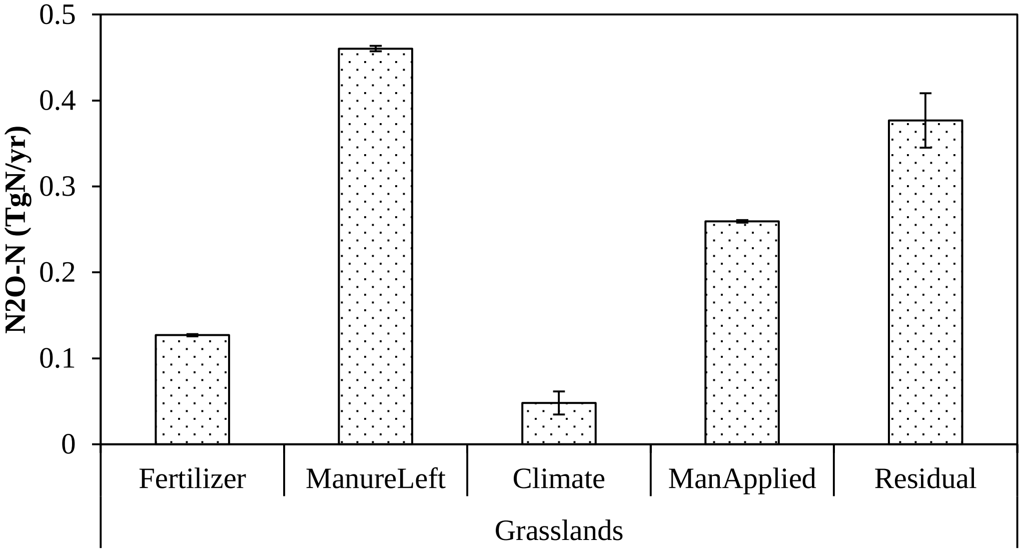


Figure 8-5 Contemporary changes in N_2O emissions due to fertilizer application, manure left on pastures, climate and manure application.

Nitrous oxide emission show a non-linear relationship response to increasing nitrogen inputs (Bouwman et al. 2002, Zebarth et al. 2008, Hoben et al. 2011). This non-linear response of N_2O emission to different rates of nitrogen application can be best captured using a process-based model with explicit representation of nitrification and denitrification mechanisms modified by soil moisture availability, soil temperature, soil bulk density, soil pH and topography (Schmid et al. 2001, Herrero et al. 2013). In this study, we used a process-based model to quantify the evolution of N_2O emission by including nitrification and denitrification processes following manure deposition/application and fertilizer application during 1961-2014. The DLEM simulated N_2O emissions were lower than IPCC tier I (Dong et al. 2006) approach by 28-33% for manure left on pastures. This result is not surprising given that IPCC tier I uses aggregated nitrogen input data to generate a default emission factor applicable at the global scale regardless of differences in soil conditions, climate and plant cover type. For example, using a non-linear model, Gerber et al. (2016) found 18-34% lower N_2O emissions compared to estimates based on linear response for global croplands. The reduced emissions compared to the linear response was attributed to negative –concave model fit, which show reduced low emissions at lower nitrogen fertilizer application rates. In studies that consider manure application on grasslands (Velthof et al. 1996, Chadwick et al. 2000), relatively low N_2O emission (<1% of total nitrogen inputs) has been found for manure applied in grasslands, which agrees with our estimates of lower emissions following manure application compared to linear response emission estimates. It is also likely that the lower N_2O emissions based on this study is due to differences in manure deposition rates, climate, soil conditions and plant functional types.

8.4.2 Variation in N_2O emissions from grassland ecosystems during 1961-2014

Grassland ecosystems are considered an important source of N_2O (Mosier et al. 1991, Dobbie and Smith 2003). In this study, we estimated global N_2O emissions of 1.89 Tg N_2O-N in 2014, with a significant increasing trend during 1961-2014 (p-value < 0.05). Managed grasslands (pastureland) alone contributed to 68% of the N_2O emissions from global grassland ecosystems. Although managed grasslands only covered 24% of the total grassland area, their contribution toward N_2O emission is much higher compared to rangeland due to higher nitrogen inputs to soil in the form of fertilizer and manure deposition/application. The higher rate of increase in N_2O emissions during 1961-2010 can be explained based on two reasons. First, manure left on pastures increased significantly at a rate of 0.67 Tg N/yr, contributing to ~40% of the total N_2O emissions from grasslands. For example, Tubiello et al. (2013) found that manure left on pastures is the second largest source GHG emissions after enteric fermentation. Second, both air temperature and precipitation increased significantly at a rate of 0.04^{o}C/yr and 0.53mm/yr (p-value < 0.05) in pastures, which led to higher emissions in pastures compared to rangelands. It is possible that higher temperature and higher soil water content led to a conversion of organic manure to mineral form, providing the substrate necessary for denitrification (Butterbach-Bahl et al. 2013). However, the effect of precipitation on N_2O emissions has been found to be non-linear (Chatskikh et al. 2005), where period of high rainfall increase N_2O emissions from denitrification due to presence of anaerobic conditions, while increased rainfall also increases nitrate leaching reducing the concentration of nitrates necessary for denitrification (Saggar et al. 2007). In our study, although temperature and precipitation increased significantly, the contribution of climate to N_2O emissions was 4% of the total emissions. It is likely that significant increase in precipitation led to an increase in nitrate leaching resulting in lower N_2O emissions.

8.4.3 Sources of N_2O emissions

It is apparent that quantifying N_2O emissions from the land biosphere is extremely complex, due to variety of nitrogen forms and microbial processes that need to be considered (Davidson 2009, Butterbach-Bahl et al. 2013). In addition, climate, soil conditions and vegetation type and soil management practices (fertilization, manure application) would result in complex interaction among the driving factors with large temporal and spatial variations in the magnitude of N_2O emissions (Bouwman et al. 2002). The complex interaction among soil, climate factors and vegetation type determine nitrification and denitrification rates, which are further influenced by the abundance of soil nitrogen relative to assimilatory demand by microorganisms and plants (Weier et al. 1993). One of the largest source of uncertainty in N_2O emissions comes from management practices which includes manure deposited in pastures, manure applied to soils and fertilizer applied to soils (Steinfeld et al. 2006a, Tubiello et al. 2013). The uncertainty arises due to two reasons. First, different approaches used to estimate total manure production and their allocation to different uses including croplands and pasturelands

(Bouwman et al. 2013). Second, N_2O emission vary as a function of manure type, with cattle manure yielding higher emission compared to sheep (Velthof et al. 2003). In our study, we first estimated total manure production and manure applied to croplands and pastures, and manure deposition in pastures to provide the first estimate of N_2O emission from different sources in global grasslands. Our results indicate that manure left on pastures is the dominant source of N_2O contributing to 36% of the total N_2O emissions in the 2010s. Manure applied to pastures was the second largest source contributing to 20% of the emissions, followed by fertilizer application (10%). The largest contribution from manure left on pastures is associated with a significant increase in manure production as a result of an increase in livestock numbers (FAOSTAT). For example, manure left on pastures increased from around 48 TgN in 1961 to 87 Tg N in 2014, while nitrogen fertilizer and manure applied to grassland showed an increase of up to 8 Tg N/yr.

8.4.4 Mitigation options

Grasslands are an important source of N_2O emissions, largely due to nitrogen input and rapid cycling of carbon and nitrogen in the form of animal dung and urine (Jarvis et al. 1995, Ussiri and Lal 2013). Animal excreta, which includes urine and dung left in grazed pastures and in animal housing/shelters account for 70% of global N_2O emissions from livestock production (Oenema et al. 2005). The estimated global amount of manure production ranges between 80-130 TgN/yr, with the largest contribution from cattle (60%), sheep (12%) and pigs (6%) (Oenema and Tamminga 2005). Following manure application to land, the efficiency of conversion of nitrogen to plant production ranges from 0-60%, while the other 40-100% is lost via NH_3 volatization, denitrification, leaching and run-off (Oenema and Tamminga 2005). These losses can be reduced by collecting manure rapidly in water-tight basins and applying to croplands and pastures in proper amounts based on specific plant nitrogen demands. In addition, animal based mitigation strategies such as improvement in genetic production potential of the herd and composition of animal feed could potentially lead to higher conversion of plant protein nitrogen to animal nitrogen and reduces losses via urine and feces (Ussiri and Lal 2013).

8.4.5 Uncertainties

Our study estimates the magnitude and spatio-temporal pattern of N_2O emissions from different sources, but the following uncertainties should be considered while interpreting the results from this study. Uncertainties in our estimation on N_2O fluxes are mainly derived from several sources including input datasets, model structure and the simplification of manure allocation procedures. First, input datasets and changes in model structure could potentially change N_2O emissions from global grasslands. Second, although parameters were well calibrated based on existing field observations, second order microbial processes with explicit representation of nitrifying and denitrifying bacteria has not been included in this study. Third, we used aggregated data on manure deposition and fertilization based on FAO and other data sources, which could add uncertainty in N_2O emissions. Therefore, future research must take into account explicit representation of specific microbes in the current land model framework with high resolution datasets on manure production and their allocation to pastures to accurately model N_2O emissions from global grasslands

8.5 Conclusions

Grassland management practices including manure deposition, and manure and fertilizer application have remarkably altered the global nitrogen budget (Bouwman et al. 2013)with large increase in N_2O emissions. In this study, we used the process based model to quantify the contribution of global grassland ecosystems to N_2O emission by using spatially explicit datasets on different sources on nitrogen inputs to soil. As a result of multiple environmental changes and grassland management practices, N_2O emission increased significantly from 1.41 Tg N_2O-N/yr in 1961 to 1.89 Tg N_2O-N/yr in 2014. Managed pastures dominated N_2O emissions contributing to 68% of the total, while rangeland contributed to 32% of the total emissions.

Our results also indicate that manure left on pastures is the dominant source of N_2O emissions contributing to ~40% of the total emissions during 1961-2014. Similarly, manure application to pastures is the second largest source contributing to 20%, followed by fertilizer application (10%). Regionally, Asia dominated N2O emissions contributing to 31% of the emissions, followed by North America (25%), Europe (20%) and Africa (13%). To reduce emissions associated with livestock manure, special attention should be focused on manure deposition and manure handling systems in the context of multiple environmental changes.

Chapter 9. Conclusion and Future Research Needs

9.1 Net greenhouse gas balance in global grasslands

This study examined the net greenhouse gas (GHG) balance in the global grasslands by using independent estimates of CO_2, CH_4 and N_2O emissions using process-based and empirical models. Our results indicate that grasslands (both pastures and rangelands) are a net source of GHG to the atmosphere (Figure 9-1). Since the 1960s, grassland ecosystems are a source of 434 Tg CO_2-eq/yr. Methane emission due to enteric fermentation and manure management contributed to 60% of the source, while N_2O emission due to pasture management (fertilization and manure deposition/application) contributed to 40% of the source.

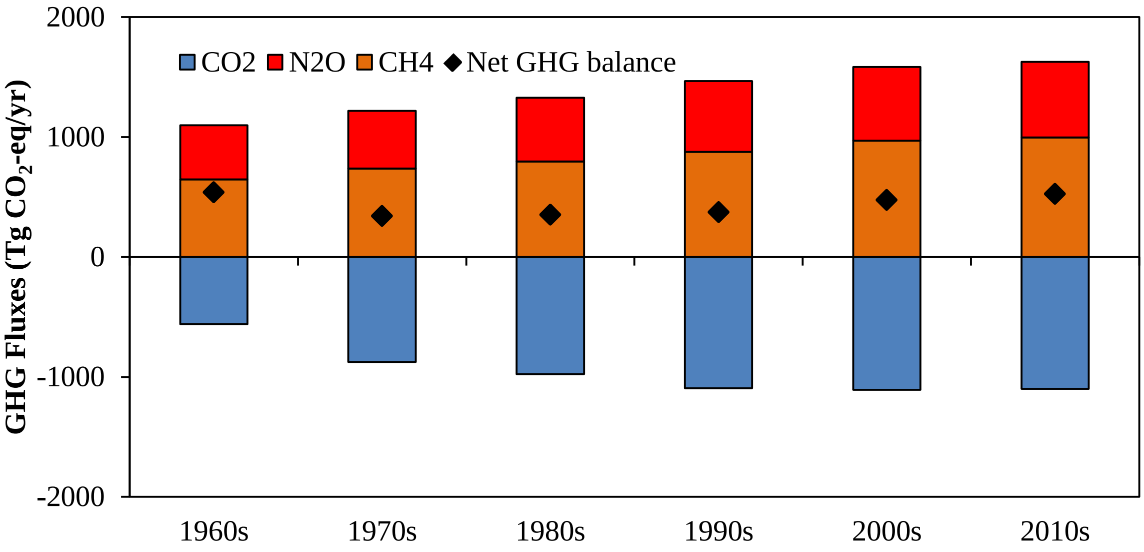


Figure 9-1 Net greenhouse gas balance in the global grasslands during the 1960s to the 2010s.

At the continental scale, southern Asia was the major source of GHG emissions from both pastures (273.8 Tg CO_2-eq/yr) and rangelands (184.8 Tg CO_2-eq/yr). North America and Europe also contributed substantially to GHG source, largely due to increasing N_2O contribution from managed pastures. Interestingly, rangelands were in balance of net flux of GHG at all the continents expect North America and South America. This is likely due to increasing contribution of CH_4 emissions from rangelands. We also found that managed pastures in Africa were a net sink of GHG, which is likely due increasing carbon sequestration in grasslands.

9.2 Climate and grazing impact on ecosystem productivity and greenhouse gas emissions

In this study, landscape to global level impact of grazing, livestock production and climate change were investigated by using process-based ecosystem model and empirical approach. A process based ecosystem model (DLEM 3.0) was developed to examine the trends and patterns of livestock growth and their impact on ecosystem carbon using Mongolia as a case study. Spatially-explicit ruminant livestock numbers were used as input in the DLEM to explore the role of grazing and climate change on soil organic carbon and net primary productivity during 1901-2010. In addition, the study used gridded livestock and pastures fertilization and manure application data to investigate the role of increasing livestock production and grassland management on nitrous oxide emissions.

The major conclusions from this study are as follows:

1. Site level studies in the Northern Hemisphere showed that climate extremes led to a maximum mortality of 53% of the total livestock in Mongolia. In addition, herbivore had a negative impact on grassland production (12.4%) and heterotrophic respiration (12%), and a positive feedback to the climate through methane emission. However, herbivores did not have significant impact on net ecosystem productivity and evapotranspiration.

2. The site level study in the Mongolian Plateau showed that historical grazing resulted in a net reduction in ANPP across all sites ranging from 2% to 15.4%. The results also found that grassland ANPP can be maintained at a grazing intensity of 1.0 sheep ha^{-1} and 0.5 sheep ha^{-1} at wet and dry sites, respectively, indicating that dry sites are more vulnerable to grazing compared to wet sites. In addition, grazing resulted in a net reduction in both PUE and NUE by 47% and 67% across all sites, respectively. Overall, site level study in the Mongolian Plateau indicated that seasonal precipitation totals, average temperatures and grazing are important regulators of grassland ANPP in Mongolia.

3. The regional level study in the Mongolian Plateau showed that 83% of the grassland area has experienced decline in ANPP, as a result of climate change (61.4%) and grazing (23.2%). Livestock biomass use has increased by 41% (from 28.8 TgC/yr to 40.6 TgC/yr), while grassland ANPP has declined by 15% (from 162.3 TgC/yr to 138.8 TgC/yr). At the regional level, extreme climatic events including the drought and dzud of 1999-2002 and the dzud of 2009-2010 resulted in a cumulative mortality of 28% of the livestock.

4. At a global level, grazing and climate change reduced SOC at the rate of 2 PgC/yr and 13.4 PgC/yr, respectively ($p<0.05$). The reduction in SOC due to grazing was largely attributed to decrease in litter production (12%) and belowground carbon (7%). Climate, on the other hand, decreased SOC due to low biomass production in the tropics and high soil decomposition in the temperate and boreal region. Likewise, livestock grazing decreased net primary production (NPP) at the rate of 28.5 TgC/yr, while climate change increased NPP at the rate of 10 TgC/yr.

5. Global level analysis based on IPCC tier II empirical approach showed a total CH_4 emission of 2.72 Gt CO_2-eq (1 Gt = 10^{15} g) from ruminant livestock sector in 2014, which accounted for 47-54% of all non-CO_2 GHG from the agricultural sector. The results also show

that CH_4 emissions from the livestock sector in global land surface has increased by 2.06 Gt CO_2-eq (332%) since the 1890s. During the same time period, however, CH_4 emission in global drylands increased by approximately 347%. The results indicate that drylands, in particular, have 36% higher emission intensity (CH_4 emissions/km^2) compared to non-drylands during recent decades, largely due to the combined effect of higher rate of increase in livestock population and low diet quality in drylands. In addition, contribution of developing regions (Africa, Asia and Latin America) has increased from 51.7% in the 1890s to 72.5% in the 2010s.

6. Nitrous oxide emissions from global grassland ecosystems increased significantly from 1.41 Tg N2O-N/yr in 1961 to 1.89 Tg N2O-N/yr in 2014. Among different sources, manure left on pastures contributed to ~40% of the total emissions, followed by manure applied to pastures (20%) and fertilizer applied to pastures (10%). Regionally, Asia dominated N_2O emissions contributing to 31% of the emissions, followed by North America (25%), Europe (20%) and Africa (13%). Although managed grassland occupy 24% of the global grassland area, they contribute up to 68% of the total emissions, primarily due to high level of nitrogen inputs in the form of urine, feces and mineral nitrogen.

9.3 Sources of uncertainty

While this study simultaneously investigated the role of grazing and climate change on primary production and the feedback of increasing livestock production to the global climate system through CH_4 and N_2O emissions, there are various uncertainties that need to be addressed in the future work. First, there is need to improve the spatial resolution of the input data to more accurately quantify the impact of grazing and climate change on grassland productivity. Second, model representation of market/policy changes and their influence on population dynamics are parameterized in the current study. But, in realty market/policy changes requires information on the demand and supply of livestock products. Thus, there is need to develop a dynamic approach by including both demand and supply of livestock products to assess the influence of livestock production on grassland ecosystems Third, livestock impact on soil properties are not adequately represented in the current modeling framework. For example, livestock tramping, particularly in areas with high livestock density could has a substantial influence on soil texture and structure. Fourth, while estimating CH_4 emissions from the global livestock sector, we assumed that the gridded livestock data follows a spatial pattern similar to benchmark data. It is likely that the spatial distribution of livestock might change during 1890-2014, which could introduce additional uncertainty in CH_4 emissions.

Nevertheless, this study is the first attempt to simultaneously estimate the impact of livestock on terrestrial ecosystem and their feedback to the global climate system through GHG emissions. These findings could provide insights to stakeholders interested in understanding the impact of grazing and climate change on ecosystem functions and how grazing and livestock production feedback to climate system through CH_4 and N_2O emissions.

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