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Soil Ecosystem Responses to Climate Change and Land-Use Simulations and Estimation of Carbon Stocks in Steppe and Forest Ecosystems in Northern Mongolia

Anarmaa Sharkhuu
University of Pennsylvania, anarmaa@sas.upenn.edu

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Abstract

Northern Mongolia currently sequesters 31 Tg C yr^{-1} but it may become a carbon source if respiration rates increase due to climate change and overgrazing, or if projected boundary shifts between forest and steppe cause a change in the carbon storage of ecosystems. The objectives of the thesis are to study soil ecosystem response to simulated climate change and grazing, and to assess C stocks in the steppe and forest. Open-top chambers (OTCs) have been frequently used for simulating climate change. However, the pattern of temperature increase by OTCs contradicted the IPCC predictions. An alternative method, open-sided chambers (OSCs), was evaluated based on its effects on abiotic and biotic factors. The results indicated that OSCs manipulated air temperature in a pattern that was predicted by IPCC models, but the overall effect was too small, hence it is not an optimal device. In the subsequent study, OTCs were used to study soil respiration response to experimental warming in three ecosystems. Temperature increase by OTCs had no effect on soil respiration in the steppe but increased soil respiration in the forest (by 0.20 g CO_2 m^{-2} h^{-1}), demonstrating the importance of ecosystem setting. Although warming increased soil respiration, it decreased its temperature sensitivity as well (Q_{10} = 5.82 in control versus 2.22 in OTC). In addition to OTCs, watering and grazing effects on CO_2 effluxes (ecosystem and soil respiration) were studied across the topographical gradients in the steppe. Our results show a robust, positive effect of soil moisture on CO_2 effluxes across topography, and the contrasting effects of grazing on CO_2 effluxes. Interactive effects of the treatments were minimal. Soil carbon of the forest was the same (8.3 kg C m^{-2}) as the steppe (8.1 kg C m^{-2}) but aboveground carbon in the forest (2.9 kg C m^{-2}) was 3-7 times greater than that in the steppe. In summary, the results show that warming will slightly increase soil respiration in the forest, but in steppe precipitation will have stronger effect on CO_2 flux than temperature change. The results also indicated that overgrazing and deforestation could trigger a greater loss of carbon

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SOIL ECOSYSTEM RESPONSES TO CLIMATE CHANGE AND LAND-USE SIMULATIONS AND ESTIMATION OF CARBON STOCKS IN STEPPE AND FOREST ECOSYSTEMS IN NORTHERN MONGOLIA

Anarmaa Sharkhuu

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Supervisor of Dissertation

____

Dr. Alain F. Plante, Assistant Professor, Department of Earth and Environmental Science

Graduate Group Chairperson

____

Dr. Arthur H. Johnson, Professor, Department of Earth and Environmental Science

Dissertation Committee

Dr. Alain F. Plante, Assistant Professor, Department of Earth and Environmental Science

Dr. Arthur H. Johnson, Professor, Department of Earth and Environmental Science

Dr. Brent R. Helliker, Associate Professor, Department of Biology

SOIL ECOSYSTEM RESPONSES TO CLIMATE CHANGE AND LAND-USE SIMULATIONS AND ESTIMATION OF CARBON STOCKS IN STEPPE AND FOREST ECOSYSTEMS IN NORTHERN MONGOLIA

To my biology teachers Ms. Davaajav and Ms. Erdenetsetseg

who inspired me to seek hidden secrets of mother nature

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ABSTRACT

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BACKGROUND

1. Terrestrial ecosystem carbon, its fluxes and impacts of climate change

Carbon (C) stored in terrestrial ecosystems and C fluxes between the atmosphere and terrestrial ecosystems are important and dynamic components of global carbon cycling. Terrestrial ecosystems contain considerably more C (2100-3600 Pg C) than the surface layer of the ocean (700 Pg C) and the atmosphere (750-800 Pg C) (Amundson 2001; Houghton et al. 2003; Denman et al. 2007). C fluxes between terrestrial ecosystems and the atmosphere are also large. Terrestrial ecosystems annually sequester ~60 Pg C and release ~120 Pg C to the atmosphere, of which ~60-70 Pg C comes from soil (Schlesinger 1997; Houghton et al. 2003). The majority of C in terrestrial ecosystems is stored in soil. Soil contains 2300 Pg C in the top 3 m of which 1500 Pg C is in the top 1 m. Additionally, 450 Pg C and 400 Pg C is stored in wetlands and permafrost soil (Amundson 2001; Johnson and Matchett 2001).

Currently terrestrial ecosystems sequester 0.3-1.0 Pg C, mainly into soil, thereby mitigating climate change (Denman et al. 2007; Grace 2004; Houghton 2003). Whether terrestrial ecosystems continue to sequester C or not will be determined by the rate of photosynthesis and ecosystem respiration that consists of aboveground (canopy) respiration and soil respiration (Janzen et al. 1998; Schlesinger 1999; Smith et al. 2008). As biochemical processes, soil and ecosystem respiration respond positively to temperature increase (Rustad et al. 2001; Wu et al. 2011). Meta-analysis has showed that soil respiration increased with increasing air temperature on a global scale over the last two decades (Bond-Lamberty and Thomson 2010). Therefore the projected global air temperature increase of 2.2 °C (Solomon et al. 2007) may increase ecosystem and soil respiration, and potentially create a positive feedback to climate change (Heimann and Reichstein 2008).

Shifts in the boundary between forest-grassland and forest-tundra boundaries, induced by climate change and human activities, have been reported around the world (Devi et al. 2008; Field et al. 2007; Saxe et al. 2001; Mast et al. 1997). These changes in dominant functional types of plants or shift in vegetation zones can alter terrestrial C dynamic and storage (Luo 2007). Meta-analysis and prior researches suggest that woody plant encroachment to grassland causes a net loss of carbon (Guo and Gifford 2002) due to loss of large amount of organic carbon contained in the grassland soils (Jackson et al. 2002). However, some studies have demonstrated that expansion of forest can lead to carbon accumulation (Devi et al. 2008) or conversion from forest to grassland can result in net loss of carbon (Bradley et al. 2006; Guo and Gifford 2002). Understanding the responses of terrestrial carbon cycling to climate and land-use change, particularly regarding the significance of climate-carbon coupling and the nature of ecosystem as a potential carbon sink, has become a major question in terrestrial ecology (Luo 2007).

2. Experimental methods to study impacts of climate change

Experimental warming is frequently used to study responses of ecosystems to potential climate change. Several techniques have been proposed to manipulate air temperature in field conditions, which can be divided into two broad categories: (1) active warming techniques, including heating cables (Peterjohn et al. 1993) and infra-red lamps (Harte et al. 1995), and (2) passive warming techniques, including infra-red reflective curtains (Beier et al. 2004), closed greenhouses (Hobbie and Chapin 1998), unvented open-top chambers (Marion et al. 1997) and ventilated, regulated open-top chambers (Godfree et al. 2010). The main disadvantages of the active warming techniques are the need for external power and an automated temperature regulation system, which are logistically problematic to use in remote areas (Aronson and McNulty 2009). On the other hand, passive open-top chambers (OTC) have been proposed as an inexpensive, effective, non-destructive method to induce warming, and have been effectively used in a number of ITEX (International Tundra Experiment) experiments to raise air and soil temperatures (Marion et al. 1997). However, the specific pattern of temperature manipulation caused by OTCs differs from that predicted by the IPCC (Solomon et al. 2007). Open-sided chambers (OSC) with a louvered top have been suggested as an alternative passive warming method (Germino and Smith 1999). To determine the whether OSCs can overcome the shortcomings of OTCs, the effects of OSCs on abiotic and biotic factors needed to be tested in the field setting.

3. Soil and ecosystem respiration responses to climate change simulations

The majority of warming experiments has found that warming increased ecosystem and soil respiration (Rustad et al. 2001; Wu et al. 2011). However, some studies have shown that warming decreases soil and ecosystem respiration (Liu et al. 2009) or does not affect (Wan et al. 2007). The different responses of ecosystem and soil respiration to warming could arise due to differences in ecosystems studied or warming techniques used, presence of unmeasured direct and indirect experimental effects, and duration of experimental manipulation(Klein et al. 2005; Rustad et al. 2001; Shaver et al. 2000). It has been suggested to conduct experimental warming studies in different ecosystems using the same warming technique (Klein et al. 2005; Rustad et al. 2001; Shaver et al. 2000).

Some ecosystems, such as temperate and boreal forest ecosystems, regions at higher latitude with low precipitation, and arid and semi-arid ecosystems, are underrepresented in experimental warming and soil respiration studies (Aronson and McNulty 2009; Raich and Schlesinger 1992; Rustad 2008). The majority of warming studies using passive experimental warming have been conducted in moist tussock tundra, wet sedge tundra of North American or European Arctic (Aronson and McNulty 2009; Rustad 2008; Rustad et al. 2001). Experimental warming studies using OTC in coniferous temperate forest and mountain semi-arid steppe grassland are rare. There are only two published studies using OTCs to manipulate temperature in forest ecosystems (De Frenne et al. 2010; Xu et al. 2010). Warming experiments in semi-arid grasslands have been concentrated in western USA, except some studies in northern China (Harte et al. 1995; Liu et al. 2009; Xia et al. 2009; Wu et al. 2010).

Warming can also indirectly affect soil and ecosystem respiration by increasing evapotranspiration and thus decreasing soil moisture. Soil moisture limitation can decrease soil respiration and its temperature sensitivity by limiting substrate diffusion rate (Moyano et al. 2012; Schmidt et al. 2004; Suseela et al. 2012). Besides of temperature change, precipitation amount and timing can affect soil and ecosystem respiration. Experimentally reduced rainfall (by 30%) and altered rainfall timing decreased soil respiration by 8% and 13%, respectively (Harper et al. 2005).

Climate change does not involve only temperature change; often several environmental factors are involved in climate change. Hence, the net effect of climate change on soil and ecosystem respiration will depend not only on independent effects of climate variables but also their interactive effects. Results of field experiments and modeling studies show that experimental treatments could have strong interactive effects on CO_2 effluxes (Luo et al. 2008; Selsted et al. 2012), while other studies suggest that the interactive effects of warming and precipitation are minor compared to the main factors (Zhou et al. 2006). Hence, it is important to evaluate interaction effects of multiple factors involved in climate change on CO_2 effluxes along with main independent effects in boreal forest and semi-arid temperate grassland ecosystems.

4. Study area: Hövsgöl region

The Hövsgöl region of northern Mongolia is located on the southern fringe of Siberian continuous permafrost, and represents a transition zone of Siberian boreal forest to Central Asian steppe grassland. Due to topography, solar radiation and presence of permafrost, three ecosystems have developed in close proximity: (1) semi-arid mountain steppe on permafrost-free south-facing slopes, (2) shrub-dominated riparian zone, underlain by permafrost in the valley bottom, and (3) larch forest, underlain by permafrost on the north-facing slope (see Figure 1). It is a unique and important region where soil carbon stocks and soil respiration can be studied in both forest and grassland ecosystems which have same climate and soil parent material. Furthermore, the forest in this region is underlain by permafrost with very low ice content which makes this region different from other high-latitude regions.

The climate of this region is harsh continental, with high annual and diurnal temperature amplitudes, and low annual precipitation (Nandintsetseg et al. 2007). Mean annual air temperature is -4.5 °C, with the coldest average temperature of -21 °C in

January, and the warmest average temperatures of 12 °C in July (Nandintsetseg et al. 2007). Mean annual rainfall is 290-300 mm (Namkhaijantsan 2006). Grassland in northern Mongolia has been subject to grazing for centuries. Like many other places in Mongolia, grazing has recently become a serious issue in the region. Since the experimental site is a part of the Hövsgöl national park grazing is not as intensive as in other valleys in the region, though the steppe on the south-facing slope has been used as pastureland.

5. Observed and predicted climate change in Mongolia

Study of climate change impacts on carbon dynamics in northern Mongolia is of particular interest because the area is expected to undergo greater climatic changes than global average (Dagvadorj et al. 2009b; Meehl et al. 2007). The mean annual temperature in northern Mongolia has been increased by 1.8 °C for 1963-2002 (Nandintsetseg et al. 2007), greater than the global average temperature increases in that period (IPCC 2007). Air temperature is predicted to increase by < 1 °C in winter and 2 °C in summer within 80 years (Sato and Kimura 2006). Precipitation is projected to increase according to global models (IPCC 2007), however the opposite has been predicted by a regional model (Sato et al. 2007). It is predicted that increased evapotranspiration caused by air temperature increase (Dagvadorj et al. 2009b) or simultaneous changes in temperature and precipitation (Sato and Kimura 2006; Sato et al. 2007) will worsen water stress. Currently, higher evapotranspiration has been observed over the last 60 years (Batima et al. 2005) while the mean annual precipitation over this region has not significantly changed over the last 40 years (Nandintsetseg et al. 2007). The observed climate change in Mongolia have already induced other ecological changes, including the thaw of discontinuous permafrost, disappearance of water bodies and shift in biomes (Batima et al. 2005; Sato et al. 2007; Sharkhuu et al. 2007). Evaluation of NDVI data showed that desert area has increased and forest area has decreased overall in Mongolia (Dagvadorj et al. 2009b). According to model simulation, taiga forest and semi-desert biome will increase while semi-arid mountain-steppe and steppe will decrease (Dagvadorj et al. 2009b). The projected boundary shifts between ecosystems due to climate change are expected to be more prominent in the transition zones of the forests; forest-tundra and forest-steppe (Walker et al. 2006).

6. Climate change and grazing effects on carbon dynamics

Temperature and evapotranspiration increases in this semi-arid region, coupled with human activities such as overgrazing can trigger significant changes in C dynamics of this region. For instance, Lu et al. (2009) modeled C dynamics in Mongolia and concluded that this region was a sink of 31 Tg C yr^{-1} in the 1990s. They proposed that this sink will decline because of enhanced soil respiration caused by temperature increase. This proposal has not been tested in this region. Alternatively, water stress due to temperature increase may suppress soil respiration. Furthermore, changes in the forest-steppe boundary are likely to influence C storage and C and nutrient cycling processes such as litter production and decomposition, and soil respiration over a long term. However how this projected shift would affect C stored in the ecosystems is highly uncertain for this region due to lack of data on current C stocks.

Previous research demonstrated that grazing reduces soil respiration (Cao et al. 2004; Johnson and Matchett 2001; Stark et al. 2003) by decreasing substrate supply (Rees et al. 2005; Stark et al. 2003). Alternatively, light grazing increased carbon allocation into roots, belowground biomass and root deposition (Hafner et al. 2012; Sjögersten et al. 2012), which may enhance soil respiration. Grazing also alters vegetation composition (Frank et al. 1995), removes live biomass and affects soil temperature and moisture (Klein et al. 2005), and thus indirectly affects ecosystem and soil respiration. However, current results contradict with each other and no clear trend has been observed. Furthermore, no experiments have been conducted to address the response of carbon efflux to direct and interactive effects of grazing and warming in this region.

7. Objectives/questions

The general objective of this thesis is to study soil ecosystem responses of different ecosystems to simulated climate change and land-use, and to assess carbon stocks in steppe and forest ecosystems in northern Mongolia. Within this general objective, I had the following objectives, structured into thesis chapters:

Chapter 1: test whether open-side chambers, suggested as an alternative passive warming method, can overcome the known shortcomings of OTCs and perform better in field setting.

Chapter 2: study how experimental warming will affect microclimatic variables, and how experimental warming and subsequent changes in environmental variables affect soil respiration and its temperature sensitivity in three ecosystems.

Chapter 3: study how experimental warming, watering, grazing and topography affect soil and ecosystem respiration, whether the effects of experimental warming on soil and ecosystem respiration differ across topographical gradient, and how interactions of main treatments affect soil and ecosystem respiration.

Chapter 4: assess aboveground and soil carbon stocks in the forest and the steppe in order to determine whether or not the projected ecotonal shift will result in carbon loss.

Figure 1.

Dalbay Valley in northern Mongolia. Lake Hövsgöl is behind the viewer. Numbers indicate ecosystems; (1) grassland, (2) riparian area and (3) forest.

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CHAPTER 1

Abiotic and biotic responses to open-top versus open-sided passive warming chambers in the semi-arid mountain steppe of northern Mongolia

Anarmaa Sharkhuu[1], Alain F. Plante[1], Brenda B. Casper[2], Matthew J. Germino[3], Brent R. Helliker[2], Pierre Liancourt[2], Bazartseren Boldgiv[4], Peter S. Petraitis[2]

[1] Department of Earth & Environmental Science, University of Pennsylvania, Philadelphia, PA 9 19104-6316, USA

[2] Department of Biology, University of Pennsylvania, Philadelphia, PA 19104-6018, USA

[3] United States Geological Survey, Boise ID 83717, USA

[4] Department of Ecology, National University of Mongolia, Ulaanbaatar 210646, Mongolia

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Abstract

Passive open-top chambers (OTC) increase air temperature mainly by decreasing convective cooling, resulting in daily maximum temperature increases, whereas IPCC models predict daily and seasonal minimum temperature increases. Passive open-sided chambers (OSC) have been suggested as an alternative method to manipulate air temperature and create the pattern of temperature change predicted by IPCC models with minimal artifacts. We monitored abiotic and biotic factors to compare the effectiveness of these two chamber designs in the semi-arid steppe of northern Mongolia during two consecutive growing seasons. OTCs increased mean daily air temperature by 0.8 °C, mainly as a result of an increased daily maximum air temperature of 2.4 °C. OSCs did not increase either daily air temperature or maximum temperature, though they slightly increased night-time air temperature by 0.2 °C in 2010. Neither chamber design affected soil temperatures. Incident rainfall in the chambers was 52% of that received in control plots, and soil moisture was 1.6-4.1 % VWC less in the chambers. The biotic responses in the two chamber designs were similar: both OTCs and OSCs delayed the flowering of graminoids and accelerated the flowering of forbs, while flower production of either forbs or graminoids was unaffected by chamber design. Our study suggests that decreases in soil moisture rather than temperature increases were likely the key factor driving the observed biotic responses in this semi-arid steppe system.

1.1. Introduction

Experimental manipulation of temperature in-situ is an important tool for investigating climate change impacts on ecosystem functions and processes (Rustad et al. 2001). Passive open-top chambers (OTC) have been frequently used to for this purpose because they are inexpensive, non-destructive, and suitable for remote areas where it is logistically challenging to supply electricity (Aronson and McNulty 2009; Marion et al. 1997). OTCs are effective at raising daily mean air and soil temperatures (Marion et al. 1997; Yin et al. 2009), but the specific pattern of temperature manipulation caused by OTCs differs from that predicted by the IPCC (Solomon et al. 2007). OTCs significantly increase daily maximum temperature and amplify diurnal temperature range (Kennedy 1995; Klein et al. 2005) whereas IPCC predictions are for a reduced diurnal temperature range due to increased night-time temperatures. In addition, OTCs may have other confounding effects, including changes in convective air flow, interception of precipitation, and decreases in soil moisture (Kennedy 1995; Marion et al. 1997).

Open-sided chambers (OSC) with a louvered top have been suggested as an alternative passive warming method (Germino and Smith 1999). OSCs are designed to accomplish predicted temperature patterns of increased (night-time) minimum temperature by decreasing losses of long-wave radiation, thus reducing diurnal temperature range. Their open sides and louvered tops also help to minimize adverse effects on wind and water regimes. Studies examining the abiotic response to the two chamber designs, set side by side, are needed to determine the relative performances of two chambers.

Since the primary interest of ecosystem experimentation is to find impacts of climate manipulation on ecosystem functions and biological processes, in addition to examining the relative abiotic changes caused by passive warming, it is useful to assess the biological responses to the two chamber designs. Studies of plant responses to warming have shown that flowering phenology and flower production are sensitive to temperature increase (Henry and Molau 1997; Arft et al. 1999; Walker et al. 2006; Hudson and Henry 2010; Liancourt et al. 2012b). Hence we have chosen flowering phenology and flower production as biological responses to our treatments. Particularly, flowering phenology and flower production have responded more positively to spring temperature manipulation and snow melt than summer warming (Aerts et al. 2004; Dunne et al. 2003), which could be related to more frequent occurrence of frost during spring at high latitudes and altitudes. In this respect, OSCs may have a more positive effect on flowering than OTCs if they increase night-time temperature to a greater extent. However, to our knowledge, the biological responses to these two chamber designs have never been compared.

In this study, we compare the effects of the two passive warming chamber designs, OTCs and OSCs, on abiotic (air and soil temperatures, rainfall interception and soil moisture) and biotic factors (flowering time and flower production) in a mountain steppe area in Northern Mongolia. We hypothesized that (1) both chamber designs would increase air and soil temperatures relative to the control, with OTCs increasing mainly day-time air and soil temperatures and OSCs increasing mainly night-time air and soil temperatures. We also predicted that (2) both chamber designs would affect the spatial distribution of rainfall within the chambers but would not necessarily affect overall soil moisture; and that (3) both chamber designs would advance flowering time and increase flower production, with OSCs generating a larger positive effect if OSCs would increase nighttime temperature during early spring, and thus decrease the number of cold nights.

1.2. Materials and methods

1.2.1 OTC and OSC construction

Hexagonal open-top chambers (OTCs) were built to International Tundra Experiment specifications (Marion et al. 1997). The frame was constructed of clear acrylic panels that were 1 ± 0.1 mm thick and had 95% transparency to visible shortwave radiation, but near blackbody absorbance and emissivity in the long wavelengths (Sun-Lite HP©, Solar Components Corp, Manchester NH, USA). Each trapezoidal panel was 58 cm long at the top and 87 cm long at the base, and was inclined inward at approximately 60° from the ground surface. This created a hexagonal chamber with a footprint of 1.96 m2 and an opening 0.87 m2 at 40 cm above the ground surface.

Louvered open-side chambers (OSCs) were built according to a design by Germino & Demshar (pers. comm.). Frames were constructed of lumber (4.5 × 4.5 cm) and were 1.2 m long × 1.2 m wide, with the roof positioned at 50-52 cm height. The 3.2 mm thick acrylic strips comprising the roofs of louvered OSCs were 1.2 m long and 10.2 cm wide, and inserted at 7 cm spacing between strips with each strip inclined 45° towards the center of the frame (i.e., the slope aspect of the strip faced away from plot center).

1.2.2 *Experimental site*

The experimental site is located in Dalbay Valley, part of the Lake Hövsgöl International Long-Term Ecological Research (ILTER) site on the eastern shore of the lake in northern Mongolia (51° 01.405' N 100° 45.600' E; 1670 m asl). The climate of the Hövsgöl region is described as harsh continental, with high annual and diurnal temperature amplitudes (Nandintsetseg et al. 2007). Regionally, mean annual air temperature is −4.5 °C, with the coldest average temperature of −21 °C in January, and the warmest average temperature of 12°C in July (Nandintsetseg et al. 2007), and mean annual rainfall ranges between 290-300 mm in lower altitudes (Namkhaijantsan 2006). A U30 HOBO weather station (Onset Computers Inc., Bourne MA) was installed approximately 300 m from the experimental blocks to collect local meteorological data as supplemental data to the control plots. Air temperature (2 m above ground), relative humidity, precipitation, wind speed and direction, soil temperature and moisture at 10 cm depth, and photosynthetically active radiation were recorded continuously (five-minute frequency) during two growing seasons (June 1 to August 31).

Experimental blocks are located on the south-facing slope of the valley, where vegetation is dominated by sedges (e.g., *Carex pediformis*), grasses (e.g., *Festuca lenensis*, and *Koeleria macrantha*), forbs (e.g., *Potentilla acaulis*, and *Artemisia commutata*) and dwarf shrubs (e.g., *Thymus gobicus*) (Ariuntsetseg et al. 2005). Average vascular plant cover in each block was 95% (unpublished data). Soils are non-calcareous sandy loams, classified as dark Kastanozems (Aridic Borolls or Typic Ustolls). Permafrost exists in the north-facing slopes of the region, but not under the plots (Sharkhuu et al. 2007).

Eight 9 × 9 m blocks, each consisting of an OTC, an OSC, and a non-warmed control plot area, were installed at ~40 m spacing on the toe-slope position of the south facing slope of the valley. Blocks were fenced to exclude livestock throughout the year. The passive warming chambers were in place for the 2009 (June 10 to August 16, 67 days) and 2010 (June 2 to August 16, 75 days) growing seasons.

1.2.3 *Environmental monitoring*

Air temperature at 15 cm height and soil temperature at 10 cm depth were recorded for each treatment (control, OTC and OSC) in four of the eight replicate blocks by HOBO dataloggers (Pro v2 or Pendant, Onset Computers Inc., Bourne MA) at ten-minute intervals. Air temperature sensors were placed inside RS3 radiation shields (Onset Computer Corporation, Pocasset MA). They were located randomly either on the west or east sides of the chambers but away from side walls to avoid sheltering. Instruments were installed in early June (June 12, 2009 and June 3, 2010) and recorded until mid-August (Aug 15 in both 2009 and 2010).

Rainfall inside and outside the chambers was assessed during three storms in the 2010 summer season. Rainfall was collected by 9-cm diameter cups placed in each treatment in the evening of July 7, August 10 and 16, and retrieved the following mornings. For OTCs and control plots, two cups were placed on the east and two on the west side of chambers or control plots (~40 cm away from the corner), and three cups were placed in the middle. OSCs were divided into four equal quadrats, such that one cup was placed in the center of each quarter of the plot (NW, NE, SW and SE). The volume of incident rainfall collected in the cups was summed, normalized to the total surface area of cups within each plot, and expressed in units of mm.

Single, daily (between 10am and 12pm) soil moisture measurements (volumetric water content – VWC%) were taken manually for each treatment in all eight blocks using a WET sensor connected to a HH2 handheld recording device (DeltaT Devices Ltd., Cambridge England). Measurements began on June 26, 2009 and June 7, 2010, and continued until August 13, 2009 and August 17, 2010 (Liancourt et al. 2012a).

1.2.4 *Flowering phenology and production*

Flowering phenology and flower production were assessed weekly from June 20 to August 10, 2009, and from June 4 to August 11, 2010 by counting the number of flowers or inflorescences in a 50 × 100 cm subplot centered in each chamber or control plot. For forbs, only fully opened flowers, or for some species, inflorescences with at least one fully open flower were counted (Appendix 1). For graminoids, inflorescences were counted as “flowering” from the beginning of the transition to reproductive stage (i.e., bolting stage) to the anthesis stage, but not after anthesis (Liancourt et al. 2012b). Vegetative cover of each species in each subplot was also calculated in mid-July each year and used to weight flower number per plot for each species. The sampling subplot was divided into fifty 10 x 10 cm cells, and percentage cover per species was estimated to the nearest 10% in each cell and averaged to estimate percentage cover per plot. Flower counts and % cover of three co-occurring *Carex* spp. were combined due to difficulty in distinguishing between them when not in flower.

1.2.5 *Data analyses*

Daily sinusoidal fluctuations in measured air and soil temperatures were removed using Fourier transform and applying high frequency filters (MATLAB v5, MathWorks, Inc, Natick, MA). Data points that fell outside of three standard deviations from mean-normalized data were considered erroneous and excluded from analysis. The proportion of erroneous temperature measurements was typically < 1 %, however one OTC treatment had ~30% erroneous measurements in 2010 and was excluded from analysis. Air and soil temperature data were split into night-time (9 pm – 6 am) and day-time (6 am – 9 pm) data sets based on solar radiation measurements. Mean daily day- and night-time temperatures were then computed and used for separate, further analyses.

Effects of treatments on air and soil temperatures, and soil moisture were evaluated separately for each year using repeated-measures ANOVA, with blocks as a random factor, chamber treatment, date expressed as Julian days, and all their interactions as fixed factors (JMP v8, SAS Institute, Cary, NC). Planned contrasts (OTC vs. control, and OSC vs. control) were carried out with Bonferroni-corrected *P*-values. Differences in rainfall interception among treatments were assessed by one-way ANOVA, with blocks as a random factor, cup location as a nested random factor, and Tukey's HSD test for mean separations.

The effects of chamber treatment (OTC, OSC, and control), year, and the interaction between treatment and year on the date of peak flowering and on flower/inflorescence production were examined at the plant community level, separately for graminoids and for forbs. For each species within each plot, flowering date was calculated as $\sum_j F_{ij} T_j / \sum_j F_{ij}$ where Fij is the number of flowers produced by species i on a given plot in week j, and Tj is the Julian day on which the count of week j was performed. Flower production was calculated as $\sum_j (F_{ij}/P_i)$ where Pi is the percentage cover by species i in a given plot. The summation included the week of peak flowering, and one week before and after the peak.

Canonical analysis of principal coordinates (CAP, see Anderson and Willis 2003) was used to examine plant community-level responses. Data matrices contained 48 objects - eight replicates of the three treatments sampled in two years. Species were only included if they occurred in more than eight objects. This resulted in seven graminoid species, including the *Carex* spp., and 15 forbs (Appendix 1), all of them perennial except for the single annual forb *Draba nemorosa*. Species present on a plot, but not flowering, were assigned the average value for that treatment and year in the timing data set and the value of zero in the flower production data set. Distances were calculated using Gower's dissimilarity, which can handle the inclusion of objects (plots) in which some species were not present or present without flowering. Effects of treatment, year, and their interaction were analyzed using permutation ANOVAs performed using the R statistical package (R Development Core Team 2011) with the FD (Laliberte and Legendre 2010) and Vegan (Oksanen et al. 2011) packages. When either the treatment effect or the treatment × year interaction was significant, differences among treatments within a year were tested using Tukey's HSD tests with Bonferroni correction after ANOVA using R.

Differences in peak flowering date and peak flower production between chamber treatments and years, as found in the CAP analysis, are visualized as mean values (±

standard error) for each treatment-year combination, graphed in two-dimensional space, using the two (of five) axes accounting for greatest proportions of variation explained by the model. Contours representing the average Julian date of flowering or the average number of flowers/inflorescences were fitted to these plots.

1.3. Results

1.3.1. Environmental variables

Compared to the 2010 growing season, the 2009 growing season was cooler (9.8 °C in 2009 vs. 10.2 °C in 2010). Mean night-time temperatures were warmer in 2009 (6.9 °C) than in 2010 (5.3 °C), and day-time temperatures were cooler in 2009 (11.3 °C) than in 2010 (13.1 °C). Although total rainfall amounts were similar (200 mm in 2009 vs. 178 mm in 2010), they were not similarly distributed through the growing seasons (Figure 1.1). Average wind speeds were 1.6 m s^{-1} in 2009 and 1.7 m s^{-1} in 2010.

Mean day-time air temperatures were significantly warmer in OTCs than control plots in 2009 (+1.6 ± 0.05 °C, $P < 0.001$), and 2010 (+1.2 ± 0.09 °C; $P < 0.05$), but mean day-time air temperature of OSCs did not differ significantly from control plots in either year (Figure 1.2 and Table 1.1). Maximum day-time temperatures in OTCs were also significantly warmer than control plots in 2009 (+3.3 ± 0.10 °C, $P < 0.001$) and 2010 (+2.5 ± 0.16 °C; $P < 0.001$), but there was no significant difference in maximum day-time temperature between OSC and control plots (Table 1.1). The warming effect of OTCs on day-time air temperature decreased through the season in both years, corresponding to decreased solar radiation through the growing season (Figure 1.2; repeated measures ANOVA date and date × treatment, $P < 0.0001$).

Mean night-time air temperatures in OTCs were significantly cooler than control plots in each year (-0.3 ± 0.02 °C, *P* < 0.025). Mean night-time temperatures of OSC were not statistically different from control plots in 2009 (0.1 ± 0.01 °C warmer in OSC, *P* = 0.25), but were significantly warmer than control plots in 2010 (0.2 ± 0.01 °C warmer in OSC, *P* = 0.03, Figure 1.2). The maximum and minimum night-time air temperatures in OTCs and OSCs were not statistically different from control plots in either year of the study (Table 1.1), although the minimum night-time air temperature was always warmer in OSCs than in OTCs and control plots (0.2-0.3 °C in 2009 and 0.3-0.5 °C in 2010). In addition, there were no seasonal trends of increase or decrease in warming by any of the treatments (Figure 1.2).

Neither chamber design generated soil temperatures that were statistically different from the control plots (Figure 1.3). Mean daytime soil temperatures in 2009 and 2010 combined were 13.1 ± 0.1 °C in the control plots, 12.8 ± 0.1 °C in the OTCs (*P* = 0.5, compared to control) and 13.6 ± 0.1 °C in the OSCs (*P* = 0.3, compared to control). Mean nighttime soil temperatures in 2009 and 2010 were 13.5 ± 0.1 °C in the control plots, 13.1 ± 0.1 °C in the OTCs (*P* = 0.4, compared to control) and 13.6 ± 0.1 °C in the OSCs (*P* = 0.6, compared to control). Differences in mean daily minimum and maximum soil temperatures between the control plots and chamber treatments were also non-significant (*P* values were between 0.2-0.8).

Overall, both chamber designs significantly decreased incident rainfall in the three observed rainfall events (*P* < 0.005): OTCs received 41% and OSCs received 52% of the 2.9 ± 0.16 mm rainfall received in the control plots. Differences in incident rainfall between OTCs and OSCs were not statistically significant for the events of July 7 and

August 11, but were statistically significant on August 17 (Tukey HSD, $P < 0.05$), likely due to differences in rainfall intensity and wind speed and direction among the individual events.

Incident rainfall within the OTCs and OSCs was also spatially heterogeneous, with some locations appearing to receive less than 5% of available precipitation. Although the centers of the OTCs received similar amounts of rainfall compared to control plots in the three events (2.6 ± 0.23 mm in control vs. 2.6 ± 0.25 mm in the center of OTCs), the western and eastern sides received less precipitation (0.2-0.4 ± 0.1 mm, $P < 0.001$). Depending on wind direction and strength (as measured by the local meteorological station), rainfall was also unequally distributed in the OSCs in all three events (0.9 ± 0.19 mm in NE, 2.2 ± 0.56 mm in NW, 1.1 ± 0.24 mm in SE, and 1.8 ± 0.50 mm in SW, $P < 0.001$). It should also be noted that these results may have been affected by evaporation because no oil was used in the collection cups to prevent evaporation during the relatively long (overnight) collection period.

Soil moisture in our system is relatively sensitive to precipitation events because the soil is a well-drained sandy loam. Hence, it seemed that rainfall interception by the chambers resulted in significantly drier (by 1.6-4.1 VWC%) conditions in both OTCs and OSCs compared to control plots ($P < 0.01$) in both growing seasons (Table 1.2). Differences among treatments were highly variable over the growing season due to pulses from precipitation events (Figure 1.4). Soil moisture in OSCs was significantly lower than OTCs (by 2 ± 0.2 VWC%, $P < 0.001$) and controls (by 4.1 ± 0.2 VWC%, $P < 0.001$) in 2009. In contrast, soil moisture in OTCs was significantly lower than OSCs (by 2.5 ± 0.1 VWC%, $P < 0.001$) and controls (by 4.1 ± 0.1 VWC%, $P < 0.001$) in 2010.

1.3.2. *Flowering timing and production*

Chamber treatment altered the timing of flowering of both graminoids and forbs but more so in 2009 than in 2010, resulting in a chamber × year interaction (Table 1.3). In general, the OSCs and OTCs changed flowering times in similar ways. Both chamber designs delayed flowering time of graminoids in 2009 (Figure 1.5a, Table 1.3), each differing significantly from controls ($P < 0.01$ in each case, Tukey's HSD test) but not from each other. There was no effect of chamber treatment on the timing of flowering for graminoids in 2010. In contrast, both the OTC and OSC treatments (Figure 1.5a) caused forbs to flower earlier in comparison to control plots in 2009 ($P < 0.01$ in each case), and flowering time did not differ significantly between the two chamber designs. In 2010, forbs flowered earlier in the OSCs in comparison to controls ($P < 0.05$), but their flowering time in the OTCs was intermediate between the OSCs and the controls and not significantly different from either.

Flower production at the time of peak flowering, weighted by percent cover of the species, did not respond to chamber treatment in either graminoids or forbs in either year (Figure 1.5c, d). Overall, there were differences between years in both the timing of flowering and flower production (Table 1.3): flowering was earlier in 2010 than in 2009 for both graminoids and forbs (Figure 1.5a, b), and flower production was greater in 2010 than in 2009 for graminoids (Figure 1.5c) but greater in 2009 for forbs (Figure 1.5d).

1.4. Discussion

The first objective of this study was to assess the relative effects of two passive warming devices, open-top chambers (OTCs) and open-sided chambers (OSCs), on air and soil temperatures and soil moisture, and to determine whether OSCs overcome previously identified shortcomings of OTCs. Results corroborated previous findings that OTCs increased mean day-time temperature by increasing maximum day-time temperature rather than a small, constant amount of warming throughout the day (Marion et al. 1997). However, OTCs decreased night-time mean temperature, which is consistent with some previous observations (Danby and Hik 2007; Shen et al. 2009), though other studies report either warming or no effect of OTCs on night-time temperature (Charles and Dukes 2009; Hoffmann et al. 2010). This pattern of maximum and minimum temperature change by OTCs differed from the IPCC projections. Models predicted a greater increase in daily minimum temperature than daily maximum temperature (Solomon et al. 2007). Nevertheless, OTCs increased daily air temperature (day- and night-time together) by 0.7 °C which is realistic compared to the observed global air temperature increase of 0.6 °C in the last century (Solomon et al. 2007).

OSCs, in contrast, had no effect on maximum day-time temperature and increased night-time mean air temperature in 2010 by decreasing radiative losses (Germino and Smith 1999), similar to studies using passive reflective curtains (Mikkelsen et al. 2008). OSCs increased minimum daily temperature rather than maximum temperature, similar to the projected pattern of temperature change, but this night-time air temperature increase by OSCs was less than the reported range of warming (0.7-1.2 °C) by passive reflective curtains (Beier et al. 2004; Mikkelsen et al. 2008). OSCs may not provide the desired warming effect of bulk air or soil in the chamber, but have been shown to effectively warm biological and soil surfaces (Germino and Smith 1999). The observed differences in warming patterns were caused by the different chamber designs, where warming in OTCs is caused by decreased convective cooling (Marion et al. 1997; Kennedy 1995), while convective flows are largely unaffected by the OSC design. Instead, the OSCs were designed to warm surfaces at night, which may substantially change the number of frost-free nights during the growing season.

Observed soil temperature changes were not statistically significant, but were of the same magnitude as those reported in previous studies with similar increases in air temperature (Beier et al. 2004; Hollister et al. 2006). These differences among studies indicate that it is important to consider other site-specific factors, including vegetation cover, soil moisture, or a potential temperature inversion at night, rather than only the magnitude of air temperature increase (Dabros et al. 2010; Hollister et al. 2006; Klein et al. 2005; Marion et al. 1997).

Soil moisture in the chambers was significantly less than in control plots due to the interception of precipitation, but evapotranspiration rates may also have been affected. Plant biomass, convective air flow and relative humidity differences among chamber designs and control plots may further reduce soil moisture by increasing evapotranspiration. Chambers can increase evapotranspiration through increased temperatures, and thus decreasing relative humidity (Dabros et al. 2010; Marion et al. 1997). Conversely, OTCs can decrease evapotranspiration by increasing relative humidity by shielding near surface wind (De Frenne et al. 2010; Gedan and Bertness

2009). OSCs likely have less effect on evapotranspiration rates than OTCs because they allow convective air flow.

The primary objective of using passive warming chambers was to observe the biotic responses of plant communities in response to changes in abiotic conditions. Both OTCs and OSCs delayed the flowering of graminoids but accelerated flowering of forbs, regardless of their different effects on air and soil temperatures. This is in contrast to some previous warming studies using either OTCs, corner passive chambers or infra-red heaters conducted in tundra or subalpine systems, which documented advancement of flowering in both forbs and graminoids (Dunne et al. 2003; Arft et al. 1999; Hollister and Webber 2000; Hoffmann et al. 2010). It is possible that snow melt or spring temperature manipulation in those studies may have had a stronger effect than summer warming (Dunne et al. 2003; Aerts et al. 2004). Other warming studies conducted in temperate deciduous forest and prairie grassland showed either no effect of warming on flowering time, or advancing flowering and fruiting time of some species as well as delaying flowering and fruiting time of other species (De Frenne et al. 2010; Sherry et al. 2007). Our results where neither chamber design (OTC, OSC) affected flower production contrast with some studies showing an increase in flower production in response to warming (Aerts et al. 2004). However, it is possible that we did not observe larger differences because of the relatively short duration of the experiment, which captured only short-term effects (Arft et al. 1999). In general, warming has a cumulative effect over time that is more evident for some species than others (Elmendorf et al. 2012; Hoffmann et al. 2010).

Similar biological responses to the OTC and OSC treatments, regardless of their differing effects on air and soil temperature, suggest that there is another abiotic factor controlling the biotic responses. Decreased soil moisture in both chambers could explain the similar flowering responses to the OTCs and OSCs. Although temperature may be the main controlling factor of plant phenology and growth at higher latitude (e.g. Menzel et al. 2006; Aerts et al. 2004; Wielgolaski 2001), Elmendorf et al. (2012) demonstrated that soil moisture modulates the warming effect on plant phenology and that vegetation therefore exhibits strong regional variation to warming. At the sites reviewed by Elmendorf et al. (2012), gravimetric soil moisture of 20% or less was considered to be dry. By comparison, gravimetric soil moisture measured in the current study was considerably drier: ~10% in the control plots and ~8-9% in the chambers. These results and similar studies in semi-arid and arid environments such as xeric Mediterranean or steppe areas, suggested that plant phenology might be more responsive to water availability or rainfall events rather than temperature (Ma and Zhou 2012; Liancourt et al. 2012b; Shinoda et al. 2007; Llorens and Peñuelas 2005).

Results of previous warming experiments suggest that plant phenology would advance by 1.9-3.3 days per degree Celsius of warming, while results from observational studies predict that phenology advancement would be 2.5-5 days per degree Celsius. This timing disparity between observational study and warming experiments may be caused by co-changing multiple drivers in the observational data, or by artifacts in the experiments. De Valpine and Harte (2001) noted that abiotic factors other than warming that are manipulated unintentionally or intentionally by the warming devices may play a more important role than the warming itself. Similar to our study, some warming studies reported the artifact of drying (e.g. Xu et al. 2010). Such artifacts of experimental warming may attenuate the positive effect of warming on plant phenology and result in underestimate of the advancement of plant phenology in experimental studies.

The comparison between OTC and OSC provided useful information to interpret biological responses to chamber designs. OTCs had a complex effect on abiotic environmental variables while OSCs largely affected soil moisture only. Although OSCs manipulated air temperature in a similar pattern that was predicted by IPCC models, the overall effect was too small. Hence it may not optimal device to simulate air temperature increase. Instead, OTCs might be better option, although it generates some adverse effects and increase daily maximum temperature rather than minimum temperature. However, both of them decreased soil moisture. The similar responses of biological variables to OTC and OSC treatments suggest that flower phenology might have been more strongly affected by soil moisture and precipitation regime which altered by chamber rather than its warming effect. The observed biological responses to simulated climate change have important implications in predicting the productivity of the Mongolian steppe and potential impacts on herders’ livelihoods.

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Table 1.1

Day-time and night-time mean, minimum, and maximum, and seasonal minimum and maximum air temperature (°C) in open-top chamber (OTC), open-side chamber (OSC) and control plots (n = 4). Statistically significantly different values in chambers from those in controls are shown in bold.

		Day-time (6am - 9pm)			Night-time (9pm - 6am)		
		Control	OSC	OTC	Control	OSC	OTC
2009 (Jun 13-Aug 15)	Seasonal minimum	4.5	4.5	5.6	-5.4	-5.0	-5.5
	Mean daily minimum	3.8±0.2	4.0±0.2	3.9±0.3	2.2±0.2	2.3±0.2	2.0±0.2
	Mean daily	14.2±0.2	14.3±0.2	**15.8±0.2**	5.6±0.2	5.7±0.2	**5.4±0.2**
	Mean daily maximum	19.7±0.3	19.8±0.3	**23.0±0.3**	11.0±0.2	11.1±0.2	10.8±0.2
	Seasonal maximum	21.2	21.4	23.7	11.1	11.2	10.7
2010 (Jun 5-Aug 15)	Seasonal minimum	3.9	3.9	3.9	-2.2	-2.2	-2.8
	Mean daily minimum	3.2±0.2	3.4±0.2	3.2±0.3	1.4±0.2	1.7±0.2	1.2±0.2
	Mean daily	15.5±0.2	15.2±0.2	**16.9±0.3**	5.2±0.2	**5.5±0.2**	**5.0±0.2**
	Mean daily maximum	22.1±0.3	21.3±0.3	**25.0±0.3**	11.0±0.2	11.3±0.2	11.0±0.2
	Seasonal maximum	24.0	23.3	26.3	15.3	15.4	14.8

Table 1.2

Volumetric soil moisture content (% VWC) in open-top chambers (OTC), open-side chambers (OSC) and the control plots (n = 4). Statistically significantly different values in chambers from those in controls are shown in bold. All *P*-values were highly significant ($P < 0.0001$), except *P*-value of comparison of OSC and OTC in 2010 ($P < 0.01$)

	Control	OSC	OTC
2009 (Jun 26-Aug 13)	17.3 ± 0.3	**13.2 ± 0.3**	**15.2 ± 0.3**
2010 (Jun 7-Aug 17)	12.1 ± 0.2	**10.5 ± 0.2**	**8.0 ± 0.2**

Table 1.3

P-values of permutation tests for the community-level CAP analysis examining the date of peak flowering and flower production weighted by percent cover of each species (n = 8). Graminoids and forbs were examined separately. In parentheses, percentage of variance explained by each model. Statistically significant values are shown in bold.

Treatment	Date of peak flowering		Flower production	
	Graminoids (29.7%)	Forbs (33.3%)	Graminoids (25.8%)	Forbs (13.0%)
Chamber	**< 0.001**	**< 0.001**	0.872	0.685
Year	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**
Chamber × year	**0.013**	**0.024**	0.296	0.985

Figure 1.1

Growing season meteorological data for 2009 and 2010. Lines represent mean daily air temperature in 2009 (closed symbols) and 2010 (open symbols). Bars represent rainfall in 2009 (black) and 2010 (open). Data between June 12 and June 24 in 2009 are missing due to device failure.

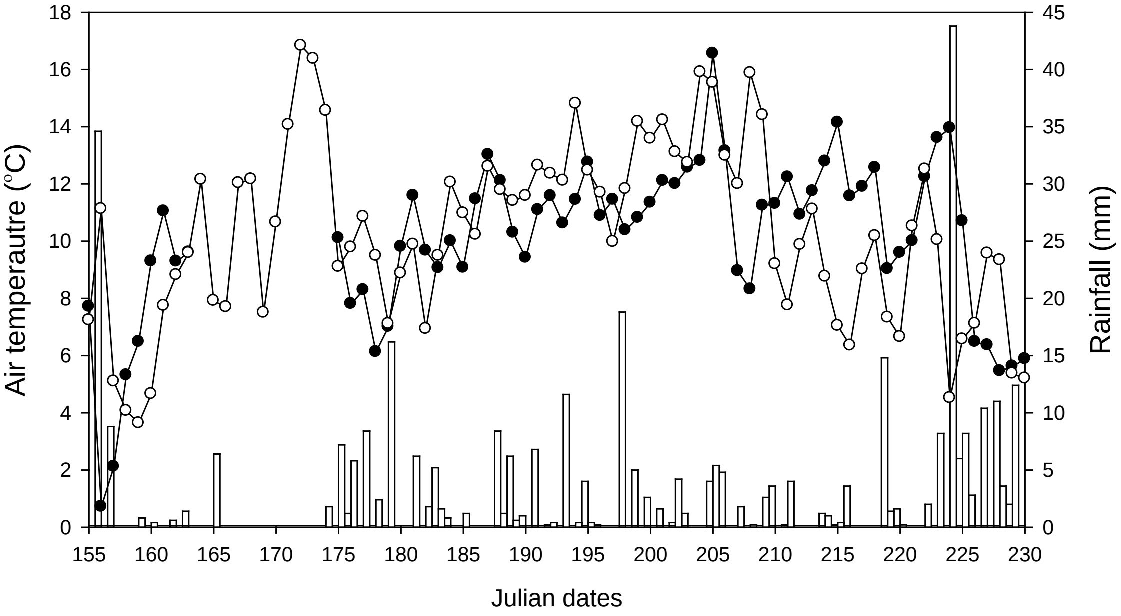


Figure 1.2

Differences in air temperature at 15 cm height between open-side chambers (OSC) or open-top chambers (OTC) and controls (n = 4) during the day (left panels) and night (right panels) in 2009 and 2010. See Table 0.1 for summary descriptive statistics.

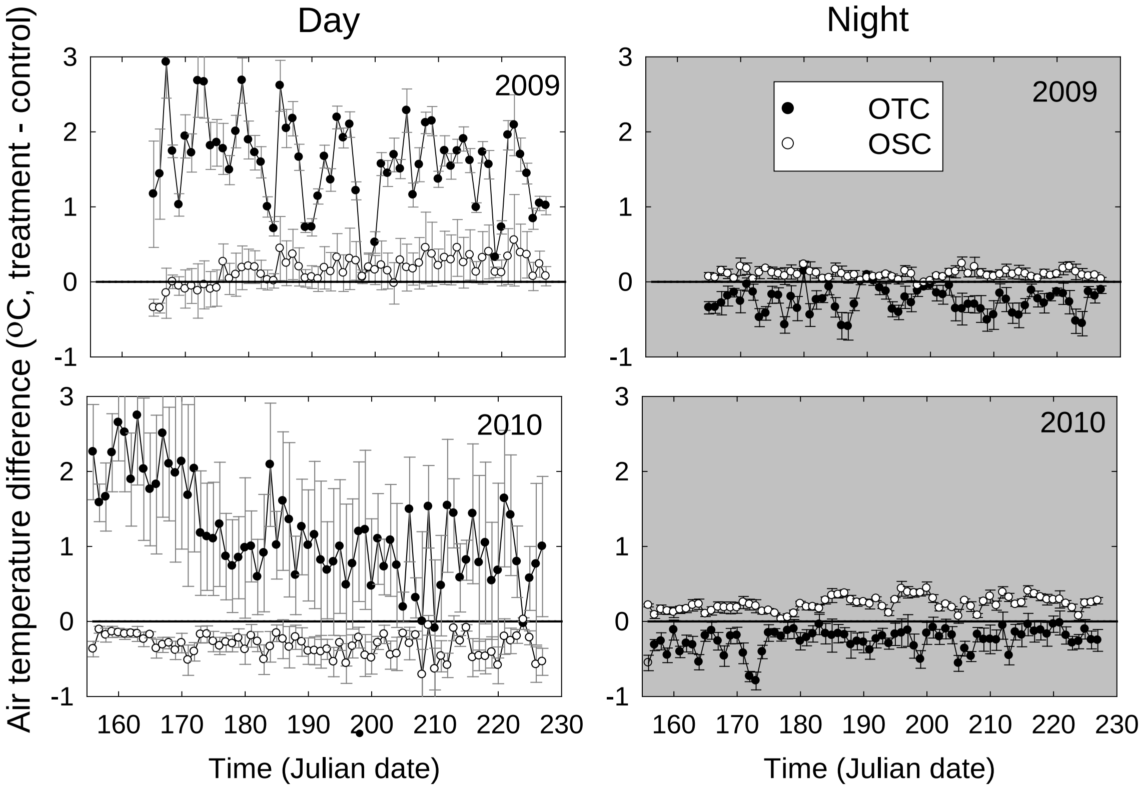


Figure 1.3

Differences in soil temperature at 10 cm depth between open-side chambers (OSC) or open-top chambers (OTC) and control (n = 4) during the day (left panels) and night (right panels) in 2009 and 2010.

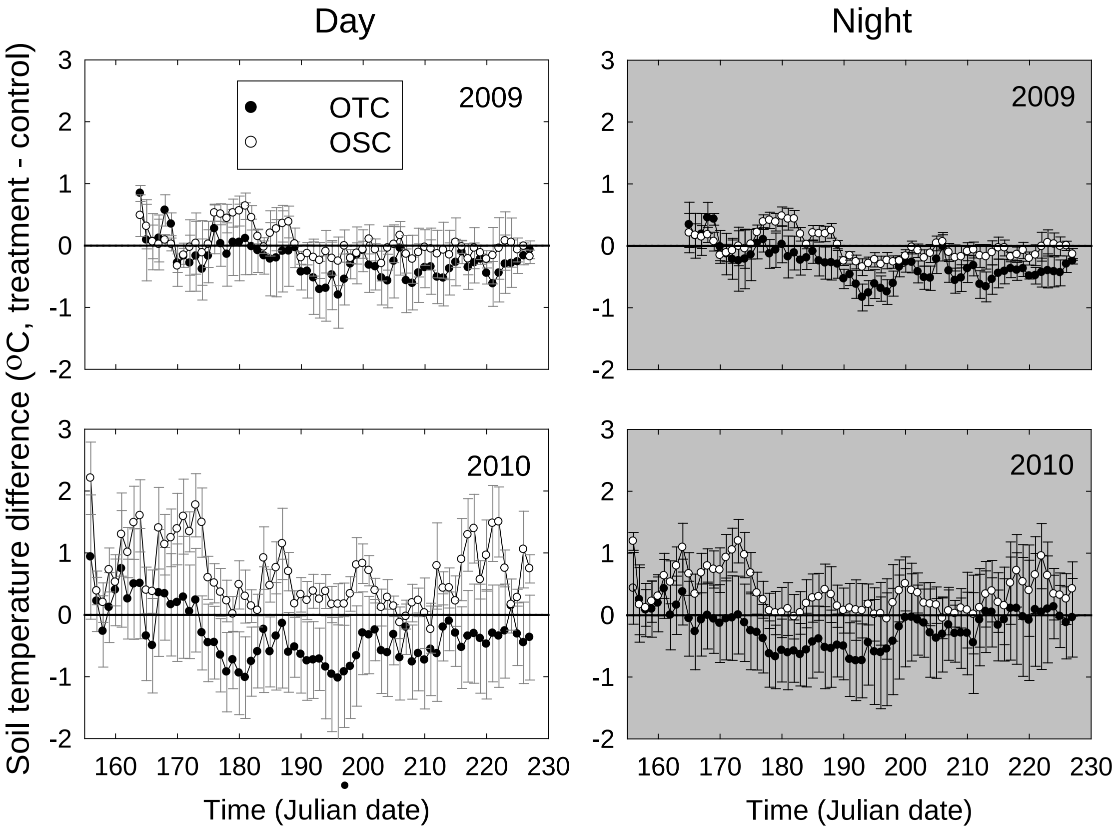


Figure 1.4

Differences in volumetric soil moisture (VWC %) at 5 cm depth between open-side chambers (OSC) or open-top chambers (OTC) and control plots (n = 8) and rainfall (mm) in 2009 and 2010.

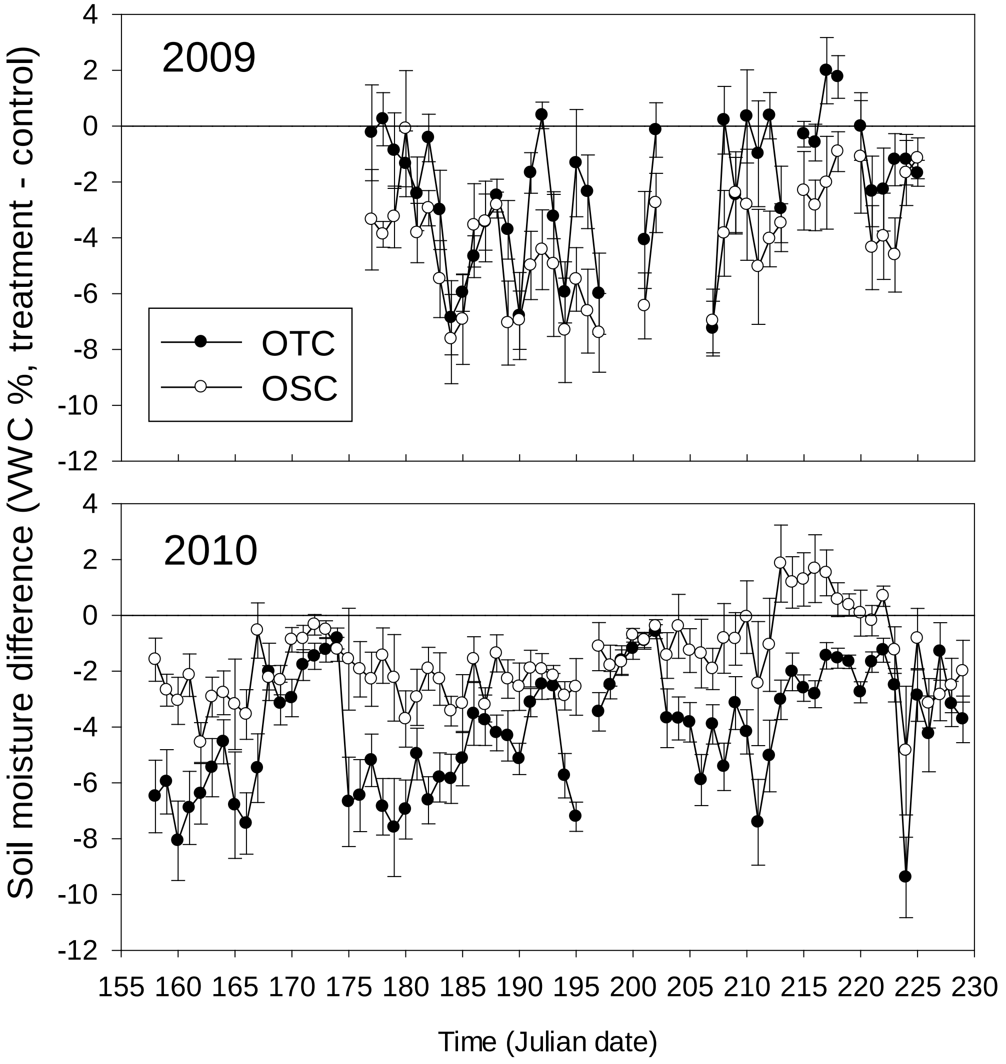
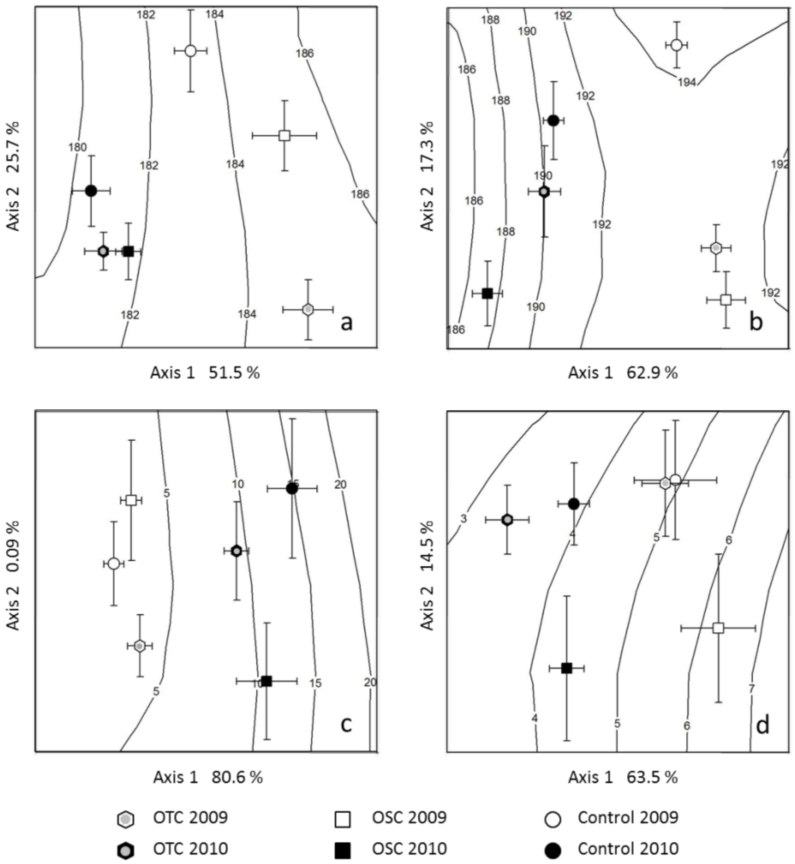


Figure 1.5

Canonical analysis of principal coordinates (CAP) output plots for the average date of peak flowering for graminoids (a) and forbs (b) and the mean (± standard error) flower production at the peak of flowering for graminoids (c) and forbs (d) for the three chamber treatments in both 2009 and 2010 (n = 8). The overall pattern is visualized by overlaying the plots of the first two CAP axes upon the gradient (contour plots) of the averages of either flowering time in Julian date or flower production. Shown also is the percentage of explained variation attributable to each of the first two axes. Abbreviations for treatments are OTC-open-top chamber and OSC- open-side chamber



CHAPTER 2

Effects of open-top passive warming chambers on soil respiration in the semi-arid steppe to taiga forest transition zone in northern Mongolia

Anarmaa Sharkhuu[1], Alain F. Plante[1], Orsoo Enkhmandal[2], Brenda B. Casper[3], Brent R. Helliker[3], Bazartseren Boldgiv[2], Peter S. Petraitis[3]

[1] Department of Earth & Environmental Science, University of Pennsylvania, Philadelphia, PA 19104-6316, USA

[2] Department of Ecology, National University of Mongolia, Ulaanbaatar 210646, Mongolia

[3] Department of Biology, University of Pennsylvania, Philadelphia, PA 19104-6018, USA

Submitted to Biogeochemistry

Abstract

The response of soil respiration to warming has been poorly studied in regions at higher latitude with low precipitation. We manipulated air and soil temperature using passive, open-top chambers in three different ecosystem settings in close proximity (boreal forest, riparian area, and semi-arid steppe) to investigate how experimental warming would affect environmental factors and soil respiration across different ecosystems for 2009-2011 growing seasons. The results indicate that OTCs significantly increased air and soil temperature in areas with open canopy and short-statured vegetation (i.e., riparian and steppe areas). OTCs affected not only air and soil temperature but also soil moisture; however, the sign of change in soil moisture in OTCs depended on the ecosystem, and the magnitude of change was highly variable. Generally, OTCs did not affect soil respiration in steppe and riparian areas. Although soil respiration was slightly greater in OTCs of the forest, the difference was not statistically significant. Analyses of relationship between soil respiration and environmental variables suggested that different factors control soil respiration in different ecosystems. Results indicated that soil temperature was main controlling factor for soil respiration in the forest, which was supported by stronger seasonal fluctuation in soil respiration. In contrast, soil respiration in steppe responded to rainfall events rather than temperature, creating respiration pulses. Our results suggest that soil respiration rate will increase in the forest in response to warming but the warming effect on soil respiration will likely to lessen due to lower temperature sensitivity of soil respiration in warmer condition. In the steppe, soil respiration will be regulated by soil moisture availability rather than temperature change. These contrasting responses highlight the importance of taking account of biome shifts in

C cycling modeling to generate more accurate predictions of responses to anticipated climate change.

2.1. Introduction

Soil respiration plays an important role in terrestrial ecosystem carbon cycling. Globally, the flux of C to the atmosphere from terrestrial respiration is 6-7 times larger than current anthropogenic emissions (~60 Pg C yr^{-1} versus ~9 Pg C yr^{-1}, IPCC 2007). As a major component of ecosystem respiration, soil respiration accounted for 71% of terrestrial ecosystem respiration in a mixed hardwood (Curtis et al. 2005) and 52% of ecosystem respiration in an alpine grassland (Zhang et al. 2009), and was positively correlated with litterfall amount in forests (Schlesinger 1977) and with net primary productivity in grasslands (Raich and Schlesinger 1992; Raich and Tufekcioglu 2000). Soil respiration measurement may therefore represent a good proxy for ecosystem carbon cycling.

On a global scale, soil respiration increases with increasing air temperature (Bond-Lamberty and Thomson 2010), and thus potentially generates a positive feedback with warming (Heimann and Reichstein 2008). However, responses of carbon cycling to climate change varied drastically among different modeling simulations (Heimann and Reichstein 2008) and among experimental warming studies. Some field studies have shown that soil respiration increases (Biasi et al. 2008; Wan et al. 2005), while other studies have shown that it decreases (Liu et al. 2009) or does not change (Wan et al. 2007).

These varying results highlight that effects of climate change on ecosystem processes, including carbon cycling, can be complex and obscured by differences in the main driving factors of soil respiration in different environments. For instance, soil respiration in a grassland was 20% greater than in a forest under similar conditions

(Raich and Tufekcioglu 2000) due to higher input of carbon in grassland, but the effect size of experimental warming on soil respiration was greater in the forest than in the grassland (Rustad et al. 2001). Previous studies have shown that experimental warming changes not only soil temperature, but also soil moisture (Dabros et al. 2010; Xu et al. 2010). Soil moisture affects soil respiration and its temperature sensitivity by changing oxygen availability or by alleviating substrate diffusion limitation (Moyano et al. 2012; Schmidt et al. 2004; Suseela et al. 2012). The reduced effect of experimental warming on soil respiration in grassland compared to forest could have been caused by a soil moisture limitation in grassland, occurring either naturally or caused by experimental warming.

Although no significant difference has been found between responses to various warming techniques (Rustad et al. 2001), most studies in the Arctic region have used open-top chambers, while most studies in grasslands have used infra-red radiator and passive nighttime warming chambers (Aronson and McNulty 2009). This suggests that varying responses between ecosystems might have been caused by methodological differences (Klein et al. 2005). The way different ecosystems respond to warming and the soil respiration response to those environmental changes can be studied using one experimental warming technique in different ecosystems. In addition, temperate and boreal forest ecosystems, regions at higher latitude with low precipitation, and arid and semi-arid biomes are underrepresented in experimental warming and soil respiration studies (Aronson and McNulty 2009; Rustad 2008; Raich and Schlesinger 1992). Most experimental warming studies have been conducted in North America and Europe, in mid- to high latitudes and moderate to high annual precipitation.

We conducted an experimental warming study in northern Mongolia. Our study site is located at the southern fringe of Siberian continuous permafrost and comprised of three ecosystems in close proximity: Siberian boreal forest, tussocky peat, and Central Asian semi-arid steppe. This allowed us to compare the microclimatic responses of different ecosystems to experimental warming without regional climatic variation. Our study across three ecosystem types was carried out to answer to the following questions: (1) how does experimental warming affect environmental variables, and (2) how does experimental warming and subsequent changes in environmental variables affect soil respiration.

Aside from being an under-studied area, study of climate change impacts in northern Mongolia are of particular interest because the area is expected to undergo larger than global average changes in climate (Dagvadorj et al. 2009b; Meehl et al. 2007). The observed temperature increase in northern Mongolia has been 1.8 °C for years between 1963-2002 (Nandintsetseg et al. 2007), greater than the global average temperature increases (IPCC 2007). Air temperature in this region is predicted to increase an additional 1-2 °C within the next century (Sato and Kimura 2006). Precipitation is projected to increase according to global models (IPCC 2007), however it has been projected to decrease by regional model, causing decreases in soil moisture (Sato et al. 2007). This region currently acts as a carbon sink (Lu et al. 2009), however, this may be at risk due to climate change.

2.2.Methods

2.2.1. *Study site*

The study site is located in the Dalbay valley, in the Lake Hövsgöl International Long-Term Ecological Research (ILTER) site, in northern Mongolia (51° 01.405' N, 100° 45.600' E; 1670 m asl). The mean annual temperature of this region is -4.5 °C, with the coldest average temperature of -21 °C in January, and the warmest average temperature of 12°C in July (Nandintsetseg et al. 2007). The mean annual rainfall ranges between 290-300 mm in lower altitudes (Namkhaijantsan 2006).

The experiment was performed in three ecosystems located in close proximity to each other within Dalbay valley: (1) semi-arid steppe, located on the south-facing slope, which is free of permafrost, (2) shrub-dominated riparian zone, located in the valley bottom with underlying permafrost, and (3) larch forest, with underlying permafrost, on the north-facing slope (Figure 2.1). Of two commonly occurring trees, Siberian larch (*Larix sibirica*) and Siberian pine (*Pinus sibirica*), Siberian larch is the dominant tree in the forest. Dominant understory species in the forest are sub-shrub (*Vaccinium vitis-idaea*), moss (e.g., *Rhytidium rugosum*), grass (*Festuca lenensis*) and forbs (e.g., *Galium boreale, Chrysanthemum zawadskii*, *Peucedanum sp*.). The riparian zone where our experimental blocks were located is characterized by tall shrubs (*Salix sp.*) up to a height of 1.8 m and clear patches dominated by forbs (e.g., *Artemisia tanacetifolia*, *Silene repense*, *Myosotis sylvatica*), grass (e.g., *Leymus chinensis*, *Poa subfastigiata*, *Agrostis mongolica*) and sedges (e.g., *Carex melanocephala*, *Carex sp*.). The foot of the south-facing slope of the valley where our steppe experimental blocks were located is dominated by sedges (*Carex pediformis*), grasses (e.g., *Festuca lenensis*, *Helictotrichon* *schellianum*, *Koeleria macrantha*), forbs (e.g., *Potentilla acaulis, Aster alpinus, Artemisia commutata*) and sub-shrubs (*Thymus gobicus*).

Dominant soil texture is sandy loam in all three ecosystems; however ecosystems differ by their dominant soil types and their total organic carbon contents. The dominant soil type is Mountain taiga-derno (Cryept) in the forest, Alluvial meadow boggy cryomorphic soil (Fluvent) in the riparian area, and non-calcareous dark Kastanozem (Aridic Borolls or Typic Ustolls) in the steppe (Batkhishig 2006). Since the study area became a national park, land-use has been minimized, though the steppe on the south-facing slope has been used as grazing pasture and some parts of the riparian area has been used for hay preparation.

Four replicate transects across the three ecosystems were established in mid-June of 2009, yielding 12 blocks (Figure 2.1). The distances between blocks are approximately 1 km in the same environmental setting and approximately 300-700 m along the cross-section of Dalbay valley. In each block, International Tundra Experiment (ITEX)-style open-top passive warming chambers (OTC) and a non-warmed control area were installed. The OTCs were consistently installed in the same locations for three growing seasons beginning in June in the summers of 2009, 2010 and 2011 and retrieved at the end of August of each year. Forest blocks were located under larch forest canopy. The vegetation inside OTCs and control plots were typical understory vegetation of the forest, and the average coverage was 74.5% according to 2009 and 2011 plant cover estimates. Riparian blocks had no shrub inside chambers or control plots but had dense cover of vegetation with 99.9% coverage. Vegetation grew taller than OTCs in two riparian blocks. The steppe blocks were characterized by vegetation with short stature and sparse coverage of 68.5%.

2.2.2. Environmental monitoring

Air temperature, soil temperature and soil moisture were measured to record changes in environmental variables in response to the chamber treatment. Above-ground air temperature (15 cm) was continuously recorded in each treatment (OTC and control) using HOBO pendant dataloggers (± 0.5 °C accuracy; Onset Computers Inc., Bourne, MA, USA) at intervals of 30 minutes. The air temperature dataloggers were placed inside of RS3 radiation shields (Onset Computer Corporation, Pocasset, MA), which were placed in the middle of plot. Soil temperature and moisture were measured and recorded using EC-TM sensors (± 1 °C and 1-3% VWC accuracy) and EM50 dataloggers (Decagon Devices Inc., Pullman, WA, USA) at intervals of 30 minutes in each treatment of blocks. The soil temperature and moisture sensors were placed horizontally at depths of 10 cm.

To determine how experimental warming and subsequent changes in environmental variables affect soil respiration, surface CO_2 efflux was measured using a portable infra-red gas analyzer (IRGA, EGM-4, PP Systems Inc.) and soil respiration chamber (SRC-1, PP Systems Inc.) in consistently the same location, where green and standing dead plants were removed before measurements. Plant material was returned to the measurement location immediately after analysis to avoid changes in surface temperature, moisture and decomposition regime. Soil respiration was measured three times per treatment per block, and the mean was used for statistical analyses. Each measurement lasted three minutes. It was possible to measure only three blocks per day without introducing diurnal variation in the soil respiration measurements. Therefore, one block (out of four) was chosen randomly from each ecosystem, and these three blocks were measured in a given day. In subsequent days, additional sets of three blocks were randomly chosen (one from each ecosystem, and previously sampled blocks left out of the selection), until all 12 blocks are sampled in a four-day span before restarting the random selection process. The order of measurement of these three blocks was randomized to avoid a measurement order bias. During each growing season, 13-15 measurements were taken in each block.

2.2.3. *Data analysis*

Daily sinusoidal fluctuations in measured air and soil temperatures were removed using Fourier transform and applying high frequency filters (MATLAB v5, MathWorks Inc, Natick, MA) to identify outliers in the environmental data set caused by instrumental errors. Data points that fell outside of three standard deviations from mean-normalized data were considered erroneous and excluded from analysis. The proportion of erroneous temperature measurements was typically 0.6% for air temperature data and 1.0-1.3% for soil temperature data. A small proportion (< 0.5%) of soil moisture data were negative values and thus considered erroneous and excluded. Mean daily values were calculated from non-transformed outlier-free data and used for further statistical analyses.

Chamber effects on environmental variables (air temperature, soil temperature and moisture) and CO_2 efflux rates were evaluated using repeated-measures ANOVA with ecosystems, chamber treatment, and all their interactions as fixed factors, and blocks as a random factor nested within ecosystems. Significant inter-annual variability was detected, and therefore the effects of the chamber treatment and ecosystems were evaluated separately for each year. When analyzing CO_2 efflux response to chamber treatment, the four-day span required for measuring CO_2 efflux in all replicate blocks was considered the time unit for the repeated measures analyses. Mean daily values were time units for other analyses. When differences among ecosystems were statistically significant, these differences were tested using Tukey's HSD test. All ANOVA analyses were carried out with JMP v8 (SAS Institute, Cary, NC).

The relationship between soil temperature at 10 cm depth and soil respiration was modeled by fitting an exponential function to the OTC and control data of each ecosystem, pooled across years:

$$R_{ij} = b_0 e^{b_1 T_{ij}}$$

where: R_{ij} is the soil respiration rate (g CO_2 m^{-1} h^{-1}) in either chamber or control plot (i) of one of ecosystems (j), T_{ij} is the soil temperature (°C) at 10 cm depth recorded at the same time as the respiration measurement, b_0 is the modeled intercept of soil respiration, and b_1 is the modeled temperature sensitivity coefficient. The b_1 values were used to calculate apparent Q_{10} values of each data set using the following equation:

$$Q_{10} = e^{10 b_1}$$

Nonlinear regression curve fitting and corresponding parameters and goodness-of-fit tests were carried out using SigmaPlot v12 (Systat Software Inc. San Jose, CA).

The model selection method using AICc was used to determine relationships between soil respiration and environmental variables, and to test the relative importance of environmental variables. We used model selection instead of stepwise multiple linear analyses because of high correlation between soil temperature and moisture. Relationships between soil respiration and soil temperature, soil moisture, and a combination of soil temperature and moisture were described by linear models. These models were assessed based on Akaike weights (i.e., model probabilities) and evidence ratios of the ranked models according to AICc, such that models with less plausible AICc weights and evidence ratios compared with model with minimum AICc among set of models were discarded. Estimates of environmental variables were computed by weighing partial regression coefficients of the linear models by corresponding Akaike weights. To test the relative importance of each environmental variable, standardized partial regression coefficients (b′) were computed and reported. Model selection, and estimation of coefficients of environmental variables were carried out using the R statistical package (R Development Core Team 2011) with the AICcmodavg package (Mazerolle 2012).

2.3.Results

2.3.1. *Environmental variables*

Ambient air temperatures differed among the forest, riparian and steppe areas ($P < 0.001$) and among the three years ($P < 0.001$, Figure 2.2). OTCs significantly increased air temperature in 2010 and 2011 ($P < 0.01$) but not in 2009 ($P = 0.25$) across the three ecosystems. The magnitude of the increase in air temperature by OTCs also differed among ecosystems (OTC × zones, $P < 0.05$). The air temperature increase by OTCs was greatest in the steppe compared to other ecosystems (1.0-2.1 °C, $P < 0.05$ in 2010 and 2011). In contrast, the air temperature increase by OTCs was smallest (0.2-0.4 °C, $P =$

0.4-0.8), and was followed by shrub-dominated riparian areas (0.5-0.6 °C, $P = 0.3\text{-}0.6$). The magnitude of warming by OTCs significantly decreased in the riparian area after mid of June ($P < 0.001$), but this trend was not consistently observed in the forest and steppe (data not shown).

Mean daily soil temperatures at 10 cm depth were lowest in the forest, followed by the riparian zone, and were greatest in the steppe, but no interactive effect between ecosystem and chamber treatment was observed (Figure 2.3). Although soil temperature appears greater in OTCs than in controls (by 0.6-1.4 °C in forest, and by 1.0-1.7 °C in steppe), the differences were not statistically significant. Soil temperature differences due to the chamber effect in the riparian zone were highly variable (positive in some blocks and negative in others) and therefore not statistically significant overall.

Soil moisture differed significantly among ecosystems ($P < 0.05$), where it was greatest in the riparian area, followed by the forest, and was least in the steppe. Due to high spatial variability among replicate blocks (65% of total variance) and of treatments × blocks (26-28%), chambers had no statistically significant effect on soil moisture. However, soil moisture was less in OTCs than in control of the steppe (by 3.0-6.2 %), and riparian area (by 1.6-2.3 % in 2009 and 2010, and by 11.1% in 2011), but greater in OTCs in the forest (by 3.9-10.6 ± 0.6 in 2009 and 2010, with no difference in 2011) (Figure 2.4).

2.3.2. *Soil respiration*

Soil respiration rates in the control plots varied significantly across ecosystems ($P < 0.05$) and years ($P < 0.05$) (Figure 2.5; Figure 2.6). The largest soil respiration rates were observed in the riparian area (0.73 ± 0.02 – 1.14 ± 0.03 g CO_2 m^{-2} h^{-1}), followed by the forest (0.59 ± 0.02 – 0.81 ± 0.03 g CO_2 m^{-2} h^{-1}), and was least in the steppe (0.43 ± 0.01 – 0.62 ± 0.01 g CO_2 m^{-2} h^{-1}). Soil respiration rates were greatest across all ecosystems in 2009 (18.9 – 20.1% greater than average), were least in 2010 (11.4 – 22.7% less than average), and varied considerably in 2011 (9.7% less than average in the forest, but 14.7% and 1.9% greater than average in the riparian area and the steppe, respectively). The greater variability in 2011 is likely attributable to fewer and sporadic measurements due to equipment problems.

Soil respiration rates were greater by 0.20 g CO_2 m^{-2} h^{-1} in OTCs than in controls only in 2009 in the forest, although statistically, the difference was marginally non-significant ($P = 0.08$). Soil respiration rates in OTCs and controls were similar in the riparian area and steppe (Figure 2.5). The lack of differences between OTCs and controls are likely to be attributable to the high variability among interactions between blocks (16-41%), blocks × measurement dates (21-70 % of total variance), and blocks × treatment × measurement dates (20-64%) (Figure 2.6).

The temperature sensitivity of soil respiration varied widely among treatments and ecosystems, with estimated Q_{10} values ranging from 1.3 to 5.8 (Table 2.1). In the forest, the OTC and control treatments generated different temperature sensitivity coefficients. The upper 95% confidence intervals of the temperature sensitivity coefficient of control did not overlap with lower confidence limit of coefficient of OTCs. These coefficients yielded different apparent Q_{10} values. Conversely, 95% confidence limits of temperature sensitivity coefficients of control and OTC treatments overlapped with each other in both the riparian and steppe blocks. The 95% confidence intervals also showed that temperature sensitivity coefficients of the forest plots were consistently greater than those of the riparian and steppe plots, with the exception of the control-steppe plots. Hence, Q_{10} values for the riparian and steppe blocks were smaller than the Q_{10} values for forest blocks (Table 2.1).

Relationships between soil respiration and environmental variables were tested two ways: by ecosystem with annual data pooled, and by year with ecosystems pooled. Separating data by ecosystem allowed us to explore the main driving factors within each ecosystem, while separating data by year allowed us to examine driving factors among years, which varied by their climatic combinations. In the first approach, soil respiration rate was positively correlated with soil temperature ($b' = 0.49$) and negatively correlated with soil moisture ($b' = -0.13$) in forest blocks. Among tested models, a linear model with both soil temperature and moisture was the best-fit model and the second best fit was a linear model with soil temperature only, indicating that soil respiration in the forest was more responsive to soil temperature (Table 2.2). In the riparian zone, the best-fit model was a linear model with both soil temperature and moisture, indicating the importance of both variables. Soil temperature ($b' = 0.67$) and moisture ($b' = 0.60$) contributed almost equally to soil respiration variation (Table 2.2). Similarly, the best-fit model for soil respiration in the steppe was a linear model with both soil temperature and moisture, and other linear models could not compete. However, the soil moisture partial regression coefficient ($b' = 0.50$) was greater than soil temperature ($b' = 0.39$), suggesting that soil moisture might be more important than soil temperature in the semi-arid steppe.

When relationships between soil respiration and environmental variables were tested for each year with ecosystems pooled, the partial regression coefficient of soil moisture (b′ = 0.27 in 2010 and b′ = 0.70 in 2011) was greater than the partial regression coefficient of soil temperature (b′ = 0.08 in 2010 and b′ = 0.19 in 2011), except in the cooler, wetter growing season of 2009. Both 2010 and 2011growing seasons were drier and hotter, therefore best-fit models were a model containing soil moisture only and a model with both soil moisture and temperature. In 2009, both soil temperature (b′ = -0.15) and moisture (b′ = 0.10) were relatively poorly correlated with soil respiration. None of the competing models for 2009 data were the best-fit model since main driving factors varied across ecosystems.

2.4.Discussion

We assessed the performance of OTCs in three ecosystems (i.e., forest, riparian and steppe) differing by their microclimatic conditions. The comparable soil texture in the forest and steppe ecosystems allowed us to examine soil respiration responses to changes in climatic conditions as a proxy of ecosystem response to warming and drying.

To the best of our knowledge, there are only two published studies using OTCs in forested systems. Compared to these studies air temperature increase in our study was smaller: 0.2-0.4 °C in our study versus 0.4 °C in a deciduous forest (De Frenne et al. 2010) and 1.2 °C in a spruce-fir forest (Xu et al. 2010). Conversely, soil temperature increase by OTCs was greater in our study (0.6-1.4 °C) compared to previously reported values (0.25-0.6 °C; De Frenne et al. 2010; Xu et al. 2010). In contrast, warming by OTCs in the steppe in our study (1.0-2.1 °C for air temperature and 1.0-1.7 °C for soil temperature) was slightly greater than the warming of OTCs in similar open systems with short stature vegetation (0.7-1.4 °C for air temperature and 0.2-0.8 °C for soil temperature; Carlyle et al. 2011; Kudernatsch et al. 2008).

Results showed that warming by OTCs was affected by the openness of canopy surrounding the blocks and stature of the vegetation inside of the chamber, which differed among ecosystems. Forest canopy might have limited direct sunlight, shifted spectrum of solar radiation, or reduced wind speed (De Frenne et al. 2010). Thus, OTCs did not significantly increase air and soil temperature in forest. Unlike the forest, the riparian area had no initial limitation or change in solar radiation, but air and soil temperature were cooler in OTCs during the mid- and latter-part of the growing season when vegetation grew taller than the chambers. In those blocks, vegetation might have also reflected much of the solar radiation and decreased turbulence, as observed in studies using OTCs in Alaska (Callaghan and Jonasson 1995; Van Wijk et al. 2004). In contrast, OTCs achieved the greatest warming in the steppe, where vegetation was short and coverage was not dense.

Our results also showed that OTCs altered soil moisture depending on the ecosystem, indicating the importance of ecosystem setting (Shaver et al. 2000). Soil moisture decreases in OTCs in the steppe and riparian blocks can be attributed mainly to reductions in incident rainfall and were consistent with other studies (Carlyle et al. 2011; Kudernatsch et al. 2008; Xia et al. 2009). In contrast, soil moisture was greater in OTCs in the forest compared to control plots. De Frenne et al. (2010) also reported soil moisture increases in OTCs, though the amount of soil moisture increase was smaller than in our study.

Soil respiration rates were comparable to previously reported values, and differed significantly among ecosystems. Overall mean soil respiration rates in forest blocks were similar to reported values of 0.57-0.78 g CO_2 m^{-2} h^{-1} in a boreal forest (Hibbard et al. 2005; Kang et al. 2003), but measured values in the steppe blocks were slightly greater than reported values of 0.27-0.41 g CO_2 m^{-2} h^{-1} in a temperate semi-arid grassland (Hibbard et al. 2005; Liu et al. 2009; Xia et al. 2009).

The causes of the differences of soil respiration among the ecosystems in our study may be threefold. First, soil C content in the surface horizon (0-10 cm) was 5.8 ± 0.7 kg C m^{-2} in riparian, 3.7 ± 0.9 kg C m^{-2} in forest and 3.0 ± 0.3 kg C m^{-2} in steppe, thus decreasing in the same order as soil respiration. However, it is interesting to note that when normalized to soil C concentrations, the overall mean respiration rates of riparian and steppe were similar while respiration in the forest was slightly higher (0.16 mg CO_2-C g^{-1} soil C h^{-1} in riparian, 0.17 mg CO_2-C g^{-1} soil C h^{-1} in steppe and 0.20 mg CO_2-C g^{-1} soil C h^{-1} in forest). Second, these ecosystems differ in their aspects, which affect solar radiation, evapotranspiration, and subsurface water level, and thus energy and water balance of the systems. Kang et al. (2003) showed that a more mesic, north-facing slope had greater soil respiration rates than less mesic, south-facing slope in a temperate forest. Third, some studies have shown that canopy had a strong indirect positive effect on soil respiration particularly in semi-arid areas by slightly decreasing soil temperature and increasing moisture and soil C pool (Conant et al. 1998; Matías et al. 2012). In our studies, canopy openness and structure differences may have interfered with incident rainfall, solar radiation and wind. If canopy openness and structure affected climatic variables, this would create soil temperature and moisture differences between chamber and control treatments, as well as different responses to the chamber treatment between ecosystems.

In our studies, slightly higher soil respiration rates were observed in response to OTCs in the forest due to compounding effects of OTCs on environmental factors. Soil temperature increases in OTCs in this study were comparable to other studies in which soil respiration was stimulated by OTCs (Biasi et al. 2008; Welker et al. 2004). However, the observed slight but consistent increase in soil respiration rates in OTCs of the forest in 2009 and 2010 was not statistically significant in our study. Nevertheless, temperature sensitivity of soil respiration in OTCs has been decreased drastically compared to control plots in the forest, and it is more likely to be attributable to soil temperature increase in OTCs. Contrary to our expectations, soil moisture and respiration had negative relationship in the forest in 2009 and 2010, but not in 2011. In general, soil moisture increases soil heat capacity and decreases thermal diffusivity in sandy soil when moisture content is higher than 20% (Abu-Hamdeh 2003; Oke 1979), and thus wetter soil would be more resistant to warming. We observed strong negative relationship between soil moisture and temperature in the forest. Therefore increases in soil moisture in OTCs in cooler years of 2009 and 2010 potentially could have counteracted against warming by OTCs, and could have affected negatively on soil respiration.

In addition, we found that the factors governing soil respiration also varied across ecosystems. Soil respiration was mainly regulated by temperature in the forest, which is consistent with other studies (Bergner et al. 2004; Pan et al. 2008; Xu et al. 2010). The dominance of temperature as a controlling factor for soil respiration in the forest was also illustrated by greater Q_{10} values compared to those from the riparian and steppe blocks.

Meanwhile, soil respiration in the steppe was mainly affected by soil moisture, which is also consistent with many studies in arid and semi-arid systems (Davidson et al. 2006; Lellei-Kovacs et al. 2008; Liu et al. 2009; Luo et al. 2001; Matías et al. 2012). In the steppe, the soil moisture limitation caused by OTCs (Liancourt et al. 2012a) probably counteracted with the warming effect on soil respiration (Liu et al. 2009; Niu et al. 2008). Furthermore, soil respiration in steppe responded to timing and amount of precipitation events, which caused variation in baseline soil moisture (Liancourt et al. 2012a). Such a pattern of coupling soil respiration pulse after rainfall was not observed in the forest and riparian area. Instead, soil respiration rates in the forest seemed to respond to seasonal temperature variation. These different variations of background environmental factors should be taken into account to understand how ecosystems might respond to warming experiments.

When the relationship between soil respiration and environmental variables were analyzed across ecosystems, it indicated that precipitation may have a stronger impact than future warming in northern Mongolia. Although it is not conclusive, changes in precipitation may have stronger effects on soil respiration than warming by affecting primary productivity (Knapp et al. 2002), substrate supply and drought stress (Davidson et al. 2006), particularly in semi-arid systems.

2.5.Conclusions

Identifying the relevant environmental factors that govern soil respiration in different ecosystem is of importance for predicting potential changes in carbon cycling in different ecosystems in response to anticipated climate change. Ecosystem boundaries may change due to direct and indirect effects of climate change, further altering the potential carbon balance of a given area. Evaluation of normalized difference vegetation index (NDVI) data showed that desert area has increased and forest area has decreased overall in Mongolia (Dagvadorj et al. 2009b), and this trend may continue in the future. Lu et al. (2009) modeled C dynamics in Mongolia and concluded that this region was a sink of 31 Tg C yr^{-1} in the 1990s. They proposed that this sink will decline because of enhanced soil respiration caused by temperature increases. However, soil respiration rates may not increase if semi-arid steppe and desert area increases. Our results highlight the necessity of taking into account the heterogeneity of ecosystems to more accurately predict carbon flux responses to global change.

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Table 2.1

Temperature sensitivity coefficients (b_1 ± standard error) of soil respiration and apparent Q_{10} values calculated by fitting an exponential function to the relationship between soil respiration and soil temperature at 10 cm depth.

Ecosystem	Treatment	b_1	R^2	*P*	Q_{10}
Forest	Control	0.176 ± 0.025	0.32	<0.0001	5.82
	OTC	0.080 ± 0.017	0.16	<0.0001	2.22
Riparian	Control	0.023 ± 0.010	0.04	0.03	1.26
	OTC	0.0311 ± 0.013	0.05	0.02	1.36
Steppe	Control	0.0562 ± 0.014	0.12	0.0002	1.75
	OTC	0.0305 ± 0.015	0.03	0.04	1.36

Table 2.2

Linear regression equations relating soil respiration rate (Soil resp, g CO_2 h^{-1} m^{-2}) to both soil temperature (Temp, °C) and moisture (Moist, % VWC) at a depth of 10 cm, to soil temperature only, and to soil moisture only. The relationships between soil respiration and environmental variables in each ecosystem were expressed by the standardized partial regression coefficients of environmental variables, weighed by Akaike weights. The models in each ecosystem are listed according to their rank given using AICc weight and evidence ratio.

Forest

$(\boldsymbol{Soil\,resp\ =\ 0.49\times Temp - \ 0.13\times\ Moist})$

	K	AICc	ΔAICc	AICc Weight	Evidence ratio
Soil resp ≈ Temp + Moist	4	62.67	0.00	0.82	
Soil resp ≈ Temp	3	65.74	3.08	0.18	4.66
Soil resp ≈ Moist	3	122.56	59.89	0.00	1.01e+13

Riparian

$(\boldsymbol{Soil\,resp\ =\ 0.67\times Temp + \ 0.60\times\ Moist})$

	K	AICc	ΔAICc	AICc Weight	Evidence ratio
Soil resp ≈ Temp + Moist	4	255.65	0.00	1	
Soil resp ≈ Temp	3	306.56	50.90	0	1.13e+11
Soil resp ≈ Moist	3	318.47	62.81	0	4.36e+13

Steppe

$(\boldsymbol{Soil\,resp\ =\ 0.39\times Temp + \ 0.50\times\ Moist})$

	K	AICc	ΔAICc	AICc Weight	Evidence ratio
Soil resp ≈ Temp + Moist	4	-126.28	0.00	1	
Soil resp ≈ Moist	3	-82.24	44.04	0	3.66e+9
Soil resp ≈ Temp	3	-56.66	69.62	0	3.66e+9

Figure 2.1

Schematic map of the study site on the eastern shore of Lake Hövsgöl in northern Mongolia. The site is framed in rectangle in the inset map. Forested area is represented by dark grey shading, the riparian zone by light grey shading, and the white area represents the steppe area. The four transects are represented by dotted lines.

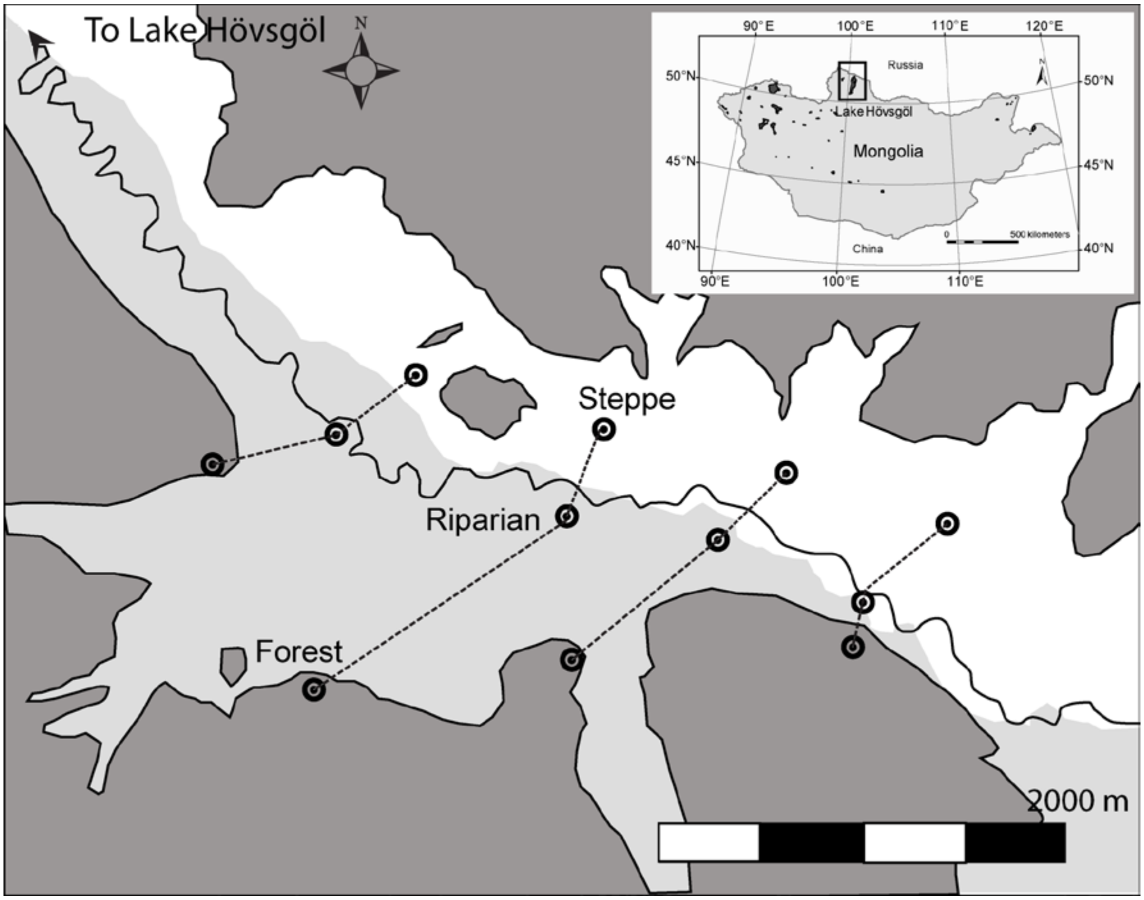


Figure 2.2

Seasonal mean air temperature (°C, mean ± standard error) in open-top passive warming chambers (OTC, solid bars) and control plots (open bars) in three ecosystems (n = ~280).

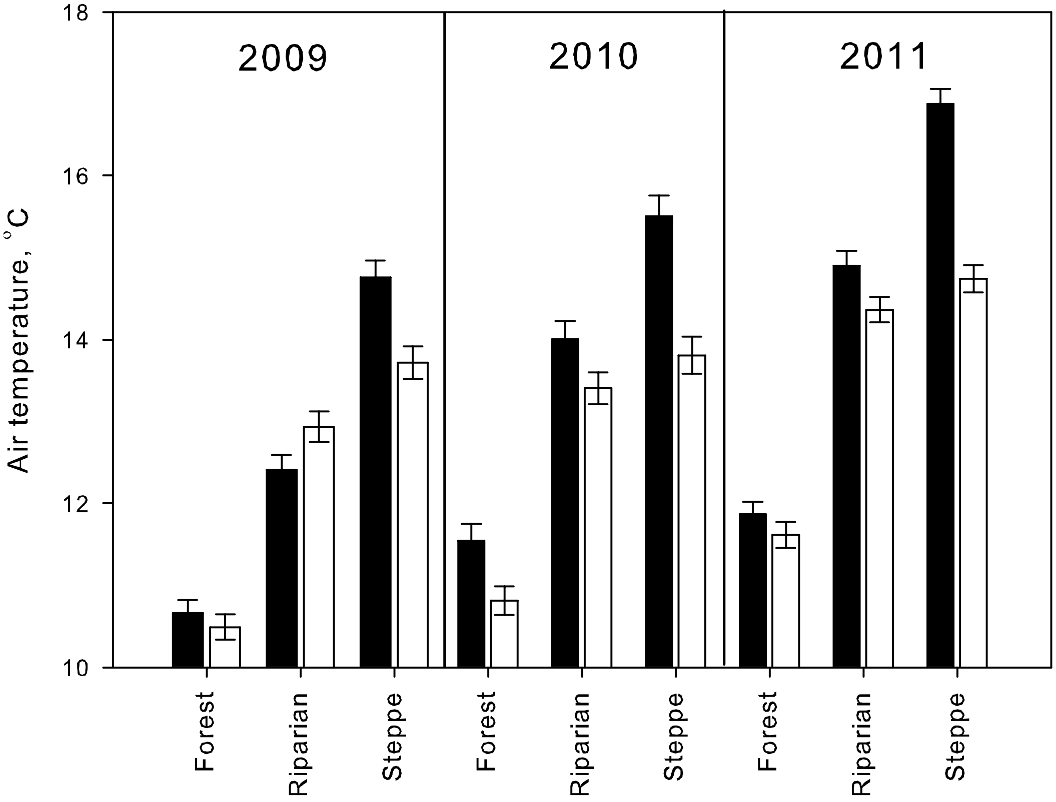


Figure 2.3

Seasonal mean soil temperature (°C, mean ± standard error) at 10 cm depth in open-top passing warming chambers (OTC, solid bars) and control plots (open bars) in three ecosystems (n = ~280).

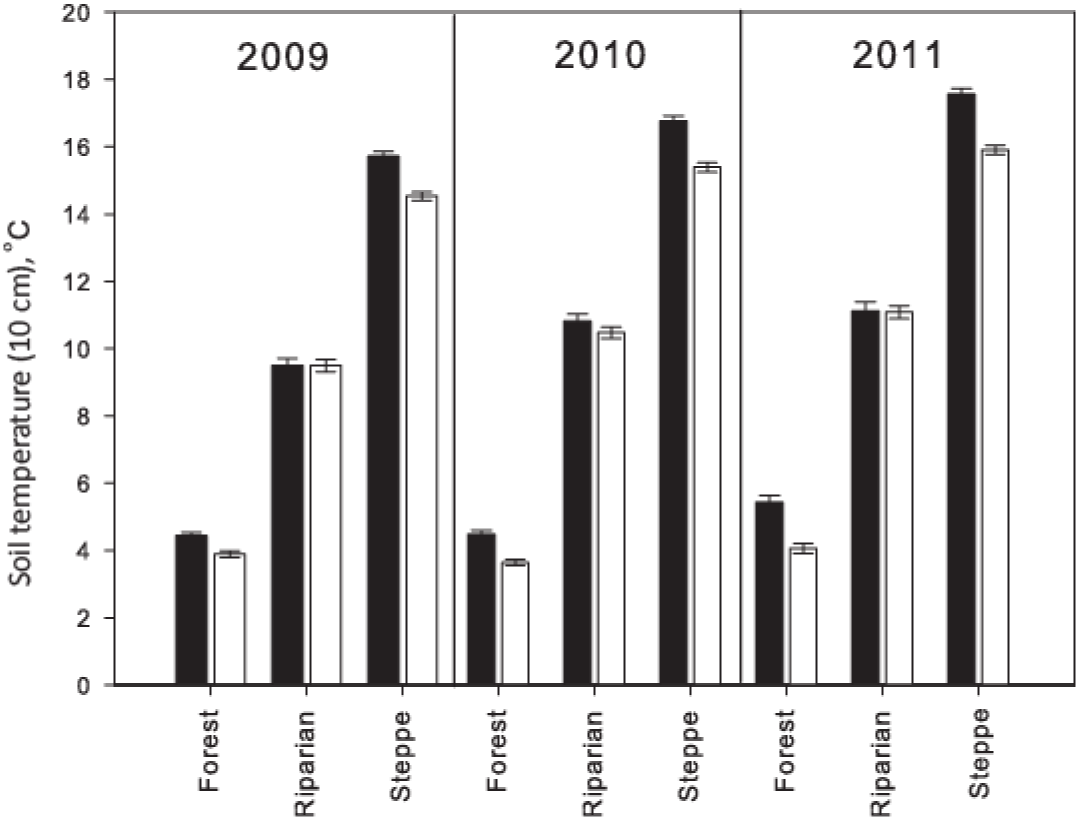


Figure 2.4

Seasonal mean soil moisture (%VWC, mean ± standard error) at 10 cm depth in open-top passive warming chambers (OTC, solid bars) and control plots (open bars) in three ecosystems (n = ~280).

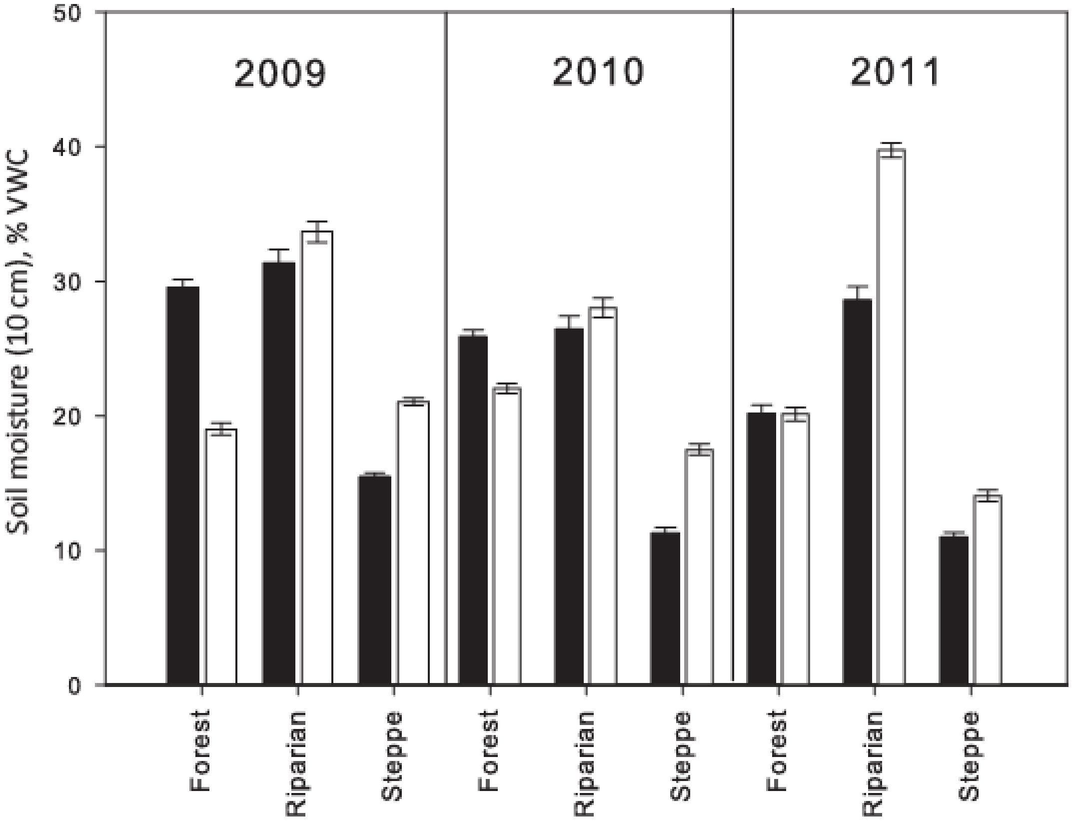


Figure 2.5

Seasonal mean soil respiration rates (g CO_2 m^{-2} h^{-1}) in open-top passive warming chambers (OTC, solid bars) and control plots (open bars) in three ecosystems.

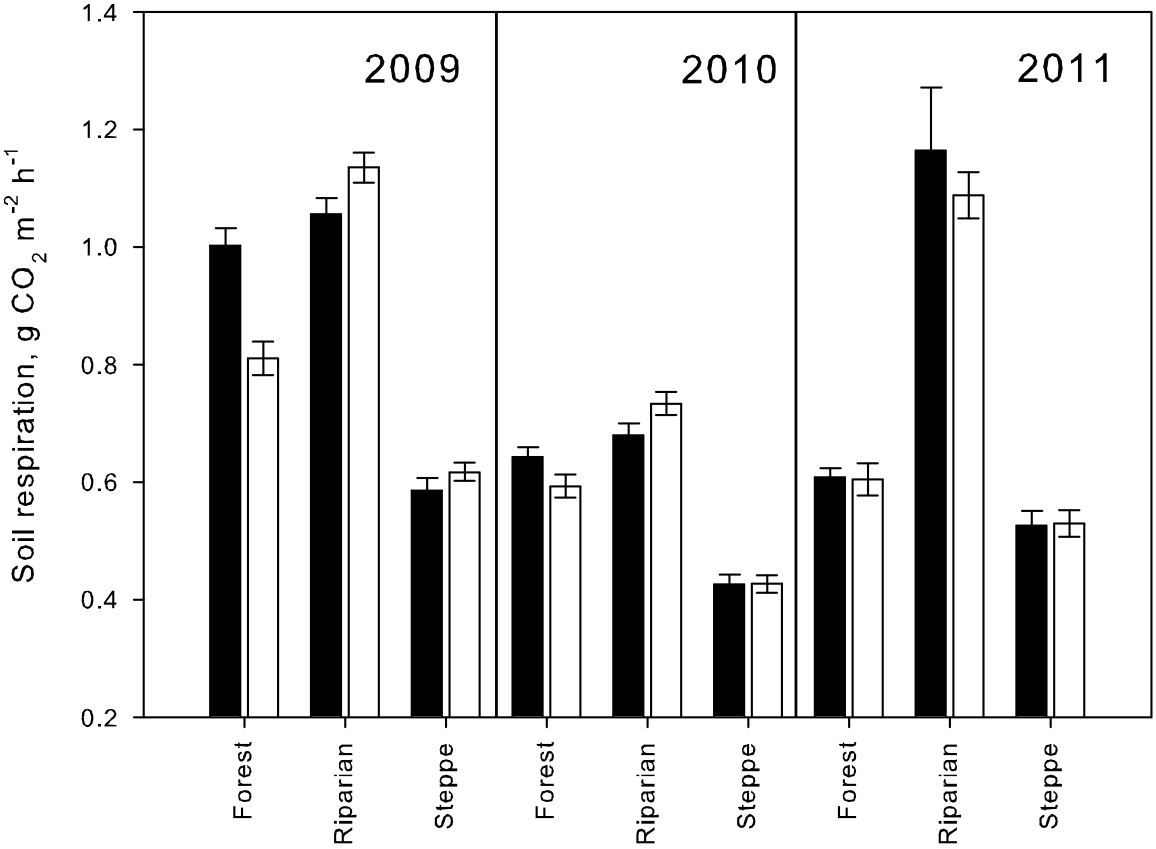
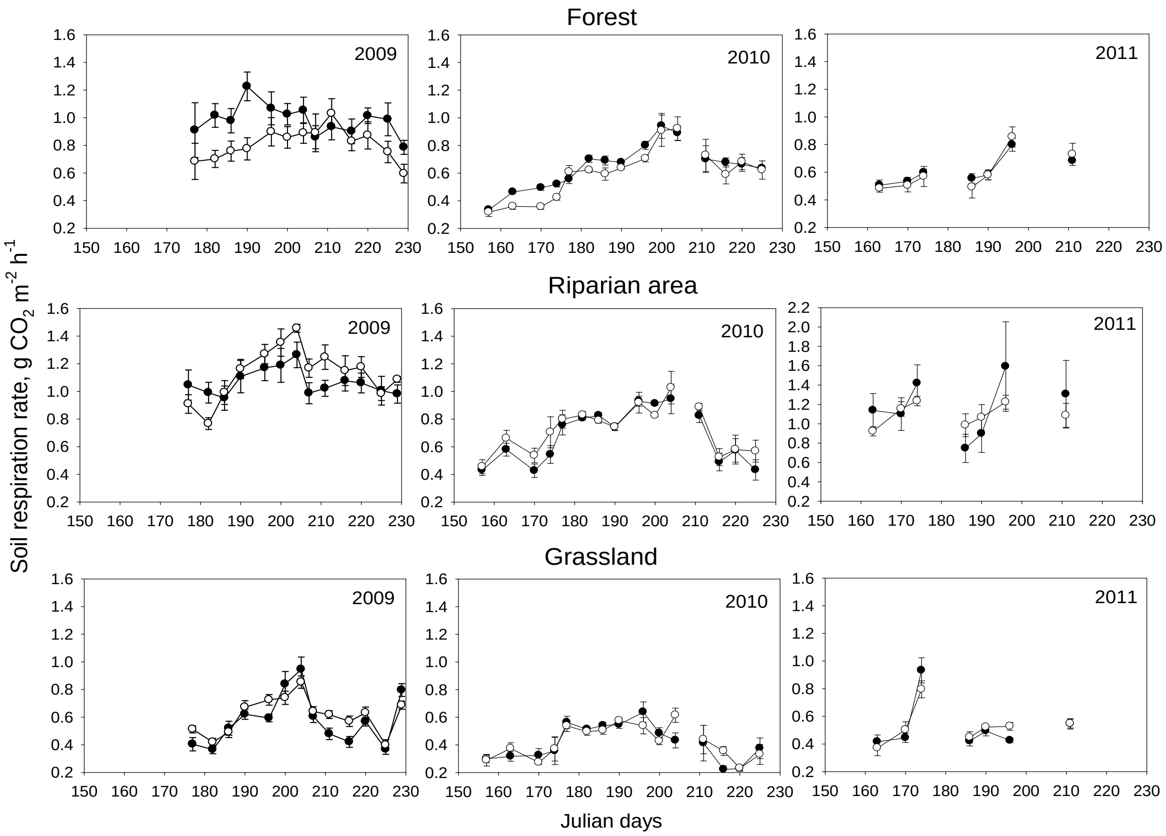


Figure 2.6

Soil respiration rates (g CO_2 m^{-2} h^{-1}) in open-top passive warming chambers (OTC, closed symbols) and control plots (open symbols) in three ecosystems over three growing seasons (n = 4).



CHAPTER 3

Soil and ecosystem respiration responses to grazing, watering and experimental warming treatments across topographical gradients

Anarmaa Sharkhuu[1], Alain F. Plante[1], Orsoo Enkhmandal[2], Pierre Liancourt[3], Daniel S. Song[3], Brenda B. Casper[3], Bazartseren Boldgiv[2], Peter S. Petraitis[3]

[1] Department of Earth & Environmental Science, University of Pennsylvania, Philadelphia, PA 19104-6316, USA

[2] Department of Ecology, National University of Mongolia, Ulaanbaatar 210646, Mongolia

[3] Department of Biology, University of Pennsylvania, Philadelphia, PA 19104-6018, USA

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Abstract

We conducted a number of experiments to study independent and combined impacts of warming, watering and grazing manipulations on soil and ecosystem respiration in northern Mongolia, which is highly vulnerable region to climate change and overgrazing. In addition, we investigated whether warming effect on soil carbon effluxes was altered by topographic gradients across the landscape. Our results indicated that warmed plots using open-top passive warming chambers (OTCs) had 10-12% and 12-16% lesser soil and ecosystem respiration than in control plots. These decreases could be attributed to soil moisture decrease in OTCs. Watering treatment significantly enhanced ecosystem and soil respiration, although watering slightly decreased soil temperature. Grazing decreased ecosystem respiration but increased soil respiration rate, indicating different impacts of grazing on above- and belowground parts. Vegetation cover and soil moisture decreased and plant available nutrient increased from lower to upper slope across the landscape. Greater vegetation cover and soil moisture in the lower slope could have caused greater ecosystem respiration compared with the upper slope. Although the upper slope had greater plant available nitrate and ammonia, it had lesser ecosystem respiration. The responses of ecosystem respiration to OTCs differed between the upper and the lower slopes, while the responses of soil respiration to OTCs did not differ between the upper and the lower slopes. We found no interactive effects of main treatments, but OTCs on the upper slope increased ecosystem respiration if not watered. Our results suggest that the soil and ecosystem respiration in this semi-arid steppe is more sensitive to soil moisture change and grazing pressure than temperature change.

3.1.Introduction

Ecosystem respiration is the largest C flux (~120 Pg C yr^{-1}) in terrestrial carbon cycling (Schlesinger 1997). A relatively minor disturbance could trigger the loss of significant amounts of CO_2 to the atmosphere, and potentially create a positive feedback to climate change. Hence, understanding responses of the terrestrial carbon cycle to climate change and land-use at the landscape scale becomes a major question in terrestrial ecosystem ecology (Luo 2007).

Soil and ecosystem respiration rates vary across the landscape in response to spatial variations in microclimate, topography, soil and vegetation characteristics and disturbance regime (Luo and Zhou 2006). It has been demonstrated that soil and ecosystem respiration respond positively to temperature increase (Rustad et al. 2001; Wu et al. 2011) but negatively to alteration of precipitation timing and decrease in soil moisture in semi-arid grassland (Liu et al. 2002; Harper et al. 2005). Temperature and moisture vary with topographic gradients, resulting in spatial variability in CO_2 production and efflux (Pacific et al. 2008; Sotta et al. 2006). In addition, plant species diversity (Fu et al. 2004), productivity (Nippert et al. 2011) and nutrient availability (Fisk et al. 1998; Hook and Burke 2000; Casper et al. 2012) also vary along topography. Plant and soil nutrients can affect ecosystem and soil respiration (see Chapin III et al. 2009; Bardgett et al. 2009) directly by regulating substrate supply, or indirectly by altering temporal dynamics of soil moisture (Liancourt et al. 2012a). These topographically induced microsite conditions may introduce increased uncertainty due to their interactions. However, little is known about how topographical variation might alter temperature effects on carbon fluxes.

Land-use change also affects soil and ecosystem respiration at the landscape level. Previous research demonstrated that a substrate supply decrease due to grazing (Stark et al. 2003; Rees et al. 2005) can reduce soil respiration (Cao et al. 2004; Johnson and Matchett 2001; Stark et al. 2003). Alternatively, light grazing increased carbon allocation into roots, belowground biomass and root deposition (Hafner et al. 2012; Sjögersten et al. 2012), which may increase soil respiration. Grazing also alters vegetation composition (Frank et al. 1995), removes live biomass and affects soil temperature and moisture (Klein et al. 2005), and thus indirectly affects ecosystem and soil respiration.

Northern Mongolia is located in the transition zone between the Siberian boreal forest and the Eurasian steppe and has experienced grazing by domestic animals for centuries. Over the last 40 years, the area experienced a significant increase in mean annual temperature (1.8 °C) (Nandintsetseg et al. 2007), which is greater than the global average temperature increases (IPCC 2007). In the future, air temperature in this region is projected to increase by 2-3 °C by the end of 2070-2080 (Sato and Kimura 2006), and simultaneously soil moisture is predicted to decrease due to the temperature increase and precipitation decrease (Sato et al. 2007, but see IPCC 2007). Thus, the net effect of climate change on soil and ecosystem respiration will depend not only on independent effects of climate variables but also their interactive effects. Results of experiments and modeling show that experimental treatments could have strong interactive effects on CO_2 effluxes (Selsted et al. 2012; Luo et al. 2008), while other experiments suggest that the interactive effects of warming and precipitation are minor compared to the independent main effects of treatments (Zhou et al. 2006). Hence, it is necessary to evaluate the interactive effects of multiple factors involved in climate change along with the independent effects to predict ecosystem response to climate change accurately.

Although northern Mongolian grasslands currently act as a carbon sink (Lu et al. 2009), the net carbon balance may change in response to climate change and intensified grazing pressure. However, no experiments have been conducted to address the response of carbon efflux to direct and interactive effects of grazing and warming in this region. We conducted a number of field experiments to determine how ecosystem and soil respiration respond to independent and interactive effects of temperature, soil moisture, and grazing manipulations across a topographic gradient. Temperature was altered using passive open-top chambers (OTCs), similar to those used in International Tundra Experiment (Marion et al. 1997). Experimental blocks with OTCs and control plots were set up on the opposite ends of the topographic gradient, which are the upper and lower slopes. While grazing effect was manipulated by fencing off the blocks on the lower slope, soil moisture was altered by weekly watering applied only on the upper slope. In this study, we aimed to answer three main questions. How do treatments of chamber, watering, grazing and topography affect soil and ecosystem respiration? Do effects of experimental warming differ between upper and lower slopes? How do these treatments interact with each other?

3.2.Methods

3.2.1. Study site

The study site is located in the Dalbay valley, in the Lake Hövsgöl International Long-Term Ecological Research (ILTER) site, in northern Mongolia (51° 01.405' N, 100° 45.600' E; 1670 m asl). The mean annual temperature of this region is -4.5 °C, with the coldest average temperature of -21 °C in January and the warmest average temperature of 12°C in July (Nandintsetseg et al. 2007). Mean annual rainfall ranges between 290-300 mm in lower altitudes (Namkhaijantsan 2006). The study area is located on the southern fringe of Siberian continuous permafrost. Forests on north-facing slopes and riparian areas in valley bottoms are underlain by permafrost, but steppe areas on south-facing slopes are permafrost free. Dominant soil texture in the steppe is sandy loam and steppe soil is classified as non-calcareous dark Kastanozem (Aridic Borolls or Typic Ustolls) (Batkhishig 2006).

The north-facing slope of the valley is covered with the taiga forest which consists of *Larix sibirica* and *Pinus sibirica*. The south-facing slope, where our experimental plots were located, is semi-arid steppe, characterized by grasses (e.g. *Festuca lenensis*, *Helictotrichon schellianum*, *Koeleria macrantha*, *Agropyron cristatum*), sedges (e.g. *Carex pediformis, Carex dichroa*) and forbs (*Potentilla acaulis, Aster alpinus*, *Artemisia commutata*). The upper slope has less total plant cover (64%) and dominated by *Potentilla acualis*, while the lower slope is characterized by greater total plant cover (78%) and dominated by *Carex spp*.

Soil moisture and soil depth gradients exist on the south-facing slope because of natural topographical variation. These gradients dictate nutrient availability, vegetation composition and plant cover percentage (Casper et al. 2012). The upper slope (elevation 1800 m asl and incline ~20°) has shallower A horizon and less soil moisture (mean summer soil moisture is 8.4% VWC) compared to the lower slope (elevation 1670 m asl and gentle to flat slope) where mean summer soil moisture is 14% VWC and A horizon of soil is depper. Since the study area is a part of the Hövsgöl national park grazing is not as intensive as other valleys in the region, though the steppe on the south-facing slope has been used as grazing pasture and some parts of the riparian area has been used for hay preparation. Cattle, yaks, and horses graze mainly on the lower slope.

3.2.2. Experimental design and measurements

Fifteen blocks were installed at ~40 m spacing on the south facing slope of the valley. Eight 9 × 13 m blocks were located on the lower slope and seven 9 × 9 m blocks were located in upper slope. All fifteen blocks had two control plots and two open-top passive warming chambers (OTCs). The OTCs were consistently set-up in the same locations in the beginning of June of 2009, 2010 and 2011 and retrieved at the end of August of each year. The chamber treatment was fully crossed with topographical locations (upper and lower slopes). This area has been grazed for centuries, and currently it is used as year-round pastureland by 1-2 families. We fenced off experimental blocks in June of 2009 to exclude grazing throughout year. On the lower slope only, we took down the fence of part of each block (9 × 4 m) in August to allow livestock to graze during fall, winter and spring and set-up the fence in June of each year. The rest of each block (9 × 9 m squares) were fenced throughout the year. Each grazed and non-grazed parts of lower blocks contained a pair of OTC and control plot. Grazing treatment was applied only on the lower slope and was fully crossed with OTCs. Soil moisture was manipulated by watering on the drier upper slope, where a pair of OTC and control plots of a block did not receive any watering, while the other pair received a weekly watering treatment equal to 4.5 mm of rainfall per week. Experimental design with watering and warming was fully factorial for the upper slope. All blocks on the upper slope was fenced to exclude livestock grazing.

A triangular area of 0.55 m^2 of bare soil within each OTC and control plot was created by removing the aboveground vegetation (Liancourt et al. 2012a). The hexagonal chamber was always positioned in a way that one side faced towards the north, while the parallel side faced towards the south. This bare soil was located in one corner of OTCs (either in east or west corner of OTCs), formed by two sides of the chamber. The same triangular bare soil was located in either the east or the west corner of the paired control plot. The bare soil was trenched to 20 cm to exclude roots, and kept vegetation-free by weekly hand weeding. CO_2 efflux measured in the vegetated area is hereafter referred to as *ecosystem respiration* because it includes CO_2 efflux originated from both plants (above- and belowground) and soil. In contrast, CO_2 efflux measurements made on the bare soil area of plots is referred as *soil respiration* because it did not include aboveground respiration but it includes root and microbial respiration.

To study direct and indirect effects of climate manipulation treatments (OTCs and watering), grazing and their interactions, we measured soil temperature and soil moisture in four of the eight blocks on the lower slope, and in three of the seven blocks on the upper slope. Soil temperature (at 10 cm depth) was monitored in each treatment by HOBO dataloggers (Pro v2 or Pendant, Onset Computers Inc., Bourne MA) at ten-minute intervals during the growing seasons. Instantaneous soil temperature and moisture (volumetric soil content, VWC %) were measured using a calibrated WET-2 sensor connected to a HH2 handheld device (DeltaT Devices Ltd., Cambridge England). These soil temperature and moisture measurements were done daily between (10 am and 12 pm) in both vegetated and bare areas of each plot in all treatments. An in-depth study of the vegetation effects on soil moisture is reported by Liancourt et al. (2012a). Vegetation decreased soil moisture by 1.5% VWC and temperature by 0.6 °C on the lower slope plots in 2009. However, the vegetation effect was not statistically significant in other years, and no statistically significant interactions were observed. Therefore, we excluded temperature and moisture data sets collected from bare areas from further analyses.

Ecosystem respiration was measured using a portable infra-red gas analyzer (IRGA, EGM-4, PP Systems Inc.) and soil respiration opaque chamber (SRC-1, PP Systems Inc.) in vegetated areas, and soil respiration was measured at bare areas of plots with the same device. Ecosystem and soil respiration were measured twice per treatment per block, and averaged for statistical analyses. Each measurement lasted three minutes. Measurements were conducted biweekly between approximately 10 am – 3 pm. Blocks were measured in completely randomized order. During each growing season, 4-5 measurements were taken in each block in 2009 and 2010, but only 3 measurements were made in 2011.

3.2.3. Data analysis

Daily sinusoidal fluctuations in soil temperatures were removed using Fourier transform and applying high frequency filters (MATLAB v5, MathWorks Inc, Natick, MA) to identify outliers. Data points that fell outside of three standard deviations from mean-normalized data were considered as outliers and excluded from analysis. The percentage of outliers was typically < 1%. However, one OTC-non-grazed plot had ~30%

erroneous data points in 2010, and therefore, the plot was excluded from the analysis. We had to exclude several data series due to datalogger malfunctions in 2011. Soil temperature data were split into night-time (9 pm – 6 am) and day-time (6 am – 9 pm) data sets based on solar radiation measurements, and only daytime soil temperature data was used for characterizing environmental conditions for CO_2 efflux and soil respiration. Mean daily daytime temperatures were then computed and used for further analyses.

We conducted three separate comparisons to evaluate treatment effects. First, we analyzed the effects of topography (upper versus lower slope) effects to determine how topographical variation alters microclimate and CO_2 efflux. In this analysis, we included only data (soil temperature, soil moisture, ecosystem and soil respiration) measured in non-grazed OTCs and control plots of lower slope, and non-watered OTCs and control plots of upper slope. In a second analysis, we focused on the grazing effect, and therefore, data (soil temperature, soil moisture, ecosystem and soil respiration) measured only in the lower slope blocks were used. The third analysis was to examine the watering effect, hence data from only the upper slope blocks were used. In all three comparisons, the main effect of OTCs and the interaction with other treatments were tested.

Main treatment effects on soil temperature, soil moisture, ecosystem and soil respiration were evaluated separately for each year using two-way, repeated-measures ANOVA with measurement dates were included as within-subject factor (SPSS v20, IBM Corp.). Treatment, date, and all interactions were included as fixed factors, and block as a random factor for all three types of comparisons. Blocks were nested within slope factor only in the first comparison. Planned contrasts were carried out with Bonferroni-corrected *P*-values if significant interactions of main treatments were detected. When a main treatment effect was consistent among years, we reported a mean of three years of response variable (i.e. mean soil respiration of 2009-2011). If a main treatment effect was not consistent among years, treatment effects were reported separately for each year.

3.3. Results

3.3.1. Soil temperature

Mean daytime soil temperatures in the non-watered upper slope plots were warmer than in the non-grazed lower slope plots by 3.3 °C in control plots and 3.7 °C in OTC plots ($P < 0.05$; Figure 3.1a and b). Grazing consistently increased mean daytime soil temperatures by 1.1 °C in OTCs and by 0.5-0.7 °C in control plots ($P < 0.05$, Figure 3.1a). Watering decreased mean daytime soil temperature, but the cooling effect was not consistent from year to year. In 2009, watering did not affect mean daytime soil temperature. In 2010 and 2011, watering decreased mean daytime soil temperature by 0.6 °C in OTCs and 0.2 °C in control plots ($P < 0.01$, Figure 3.1b).

In general, OTCs had cooler soil temperatures compared with control plots. The effect, however, was not consistent year to year, and was affected by grazing and watering treatments but not by topography. OTCs did not significantly change soil temperature in 2009. In 2010, soil temperatures were cooler by 0.3 ± 0.08 °C in the non-grazed OTCs and by 0.4 ± 0.04 °C in the grazed OTCs compared with the non-grazed and the grazed control plots, respectively ($P < 0.005$; Figure 3.1a, 2010 data). On the upper slope plots, no significant effect of OTCs on soil temperature was detected, but interactive effects of watering and OTCs were statistically significant ($P < 0.05$). Soil temperature in the watered OTCs was cooler by 0.7 ± 0.04 °C compared to the watered control plots, but it did not differ between the non-watered OTCs and the control plots (Figure 3.1b). In 2011, OTCs significantly decreased soil temperature ($P < 0.01$, Figure 3.1a and b). The effect of OTCs on soil temperature also changed due to grazing ($P < 0.05$, Figure 3.1a). OTCs decreased soil temperature by 0.5 ± 0.06 °C in the non-watered plots, by 0.6 ± 0.06 °C in the watered plots, and by 0.9 ± 0.09 °C in the non-grazed plots, but OTCs did not change soil temperature in the grazed plots ($P < 0.01$, Figure 3.1a and b).

3.3.2. Soil moisture

The non-watered plots (OTCs and control plots) of the upper slope were drier by 3.7-6.6% VWC in comparison with the non-grazed plots on the lower slope ($P < 0.01$, Figure 3.2). The mean soil moisture of non-watered control plots of upper slope was 8.6% VWC while the mean soil moisture of non-grazed control plots of lower slope was 13.5% VWC. On the lower slope, grazing did not affect soil moisture (Figure 3.2a). On the upper slope, the watering treatment increased the mean soil moisture of OTC and control plots by 2.0-2.8% VWC ($P < 0.01$, Figure 3.2b).

Mean soil moisture was consistently less in OTCs than in controls plots ($P < 0.01$, Figure 3.2). We did not observe a significant interaction between OTCs and topography in 2009 and 2011. In 2010, decrease in the soil moisture by OTCs was more prominent in non-grazed lower slope plots than in non-watered upper slope plots ($P < 0.01$, Figure 3.2). The drying effect of OTCs was negated by the watering treatment on the upper slope plots (Figure 3.2). Soil moisture was less in the non-watered OTCs than in the non-watered control plots by 2.6% VWC, while the difference between the watered

OTCs and the watered control plots was 0.9% VWC in 2009 ($P < 0.05$). A similar pattern was observed in 2010 and 2011, but the interactive effects of watering and OTCs were not statistically significant.

3.3.3. Ecosystem respiration

The largest seasonal mean ecosystem respiration rate (1.01 g CO_2 m^{-2} h^{-1}) was measured in 2009 when seasonal mean air temperature was coolest (9.8 °C), and precipitation was greatest (200 mm) among the three summers of the study. The lowest seasonal mean ecosystem respiration rate (0.78 g CO_2 m^{-2} h^{-1}) occurred in 2011, which was the hottest and driest summer (10.9 °C and 137 mm).

Ecosystem respiration varied with topography in two of the three years. In 2009 and 2010, the non-grazed OTCs and control plots of the lower slope had greater ecosystem respiration than non-watered OTCs and control plots of the upper slope, by 0.31 g CO_2 m^{-2} h^{-1} (40%) in control plots and 0.24 g CO_2 m^{-2} h^{-1} (33%) in OTCs ($P <$ 0.01, Figure 3.3a and b). Topography had no significant effect on ecosystem respiration in 2011. Grazing decreased ecosystem respiration only in 2011, by 0.11 g CO_2 m^{-2} h^{-1} (12%) in control plots and 0.07 g CO_2 m^{-2} h^{-1} (9%) in OTCs compared to non-grazed control and non-grazed OTCs (Figure 3.3a, $P = 0.02$). The watering treatment increased ecosystem respiration in 2009 and 2010 ($P < 0.01$) but not in 2011. Watering increased ecosystem respiration by 0.09 g CO_2 m^{-2} h^{-1} (12%) in control plots and 0.05 g CO_2 m^{-2} h^{-1} (7%) in OTCs (Figure 3.3b).

Across all comparisons and years, the mean ecosystem respiration was lesser by 0.08 g CO_2 m^{-2} h^{-1} in OTCs than in control plots. However, the magnitude of response, thus statistical significance, depended on a treatment and a year. In 2009, mean ecosystem respiration in OTCs were less than in control plots by 0.08 g CO_2 m^{-2} h^{-1} (7%) in non-grazed lower slope plots, by 0.12 g CO_2 m^{-2} h^{-1} (14%) in non-watered upper slope plots and 0.09 g CO_2 m^{-2} h^{-1} (10%) in watered upper slope plots ($P < 0.05$, Figure 3.3a and b). In 2010, grazed and non-grazed OTCs on the lower slope had significantly less ecosystem respiration than grazed and non-grazed control plots (by 0.12-0.13 g CO_2 m^{-2} h^{-1} or relative decreases of 12-13%, $P < 0.05$; Figure 3.3a). However, there was no significant effect of OTCs on ecosystem respiration on the upper slope plots in 2010 (Figure 3.3b). No significant difference between OTCs and control plots was detected in 2011 (Figure 3.3a and b). The interactions between topography and OTCs, and watering and OTCs were statistically significant only in 2010 ($P < 0.05$). No other interaction effects were detected.

3.3.4. Soil respiration

The seasonal mean soil respiration was 0.68 g CO_2 m^{-2} h^{-1} in 2009, the wettest summer, and 0.40 g CO_2 m^{-2} h^{-1} in 2011, the driest and hottest summer. The non-grazed OTCs and control plots of the lower slope and non-watered OTCs and control plots of the upper slope plots did not differ in soil respiration rates (P = 0.6-0.7, Figure 3.4a and b), except 2010. In 2010, mean soil respiration of the non-watered OTCs and control plots of the upper slope was 0.12 g CO_2 m^{-2} h^{-1} (23%) less than mean soil respiration of the non-grazed lower slope plots ($P = 0.014$, Figure 3.4a and b). Grazing did not affect soil respiration in 2010. However grazing increased soil respiration of OTCs by 0.11 g CO_2 m^{-2} h^{-1} (33%) and soil respiration of control plots by 0.09 g CO_2 m^{-2} h^{-1} (22%) in 2011 (P

= 0.04, Figure 3.4a). The watering treatment increased soil respiration by 0.06-0.07 g CO_2 m^{-2} h^{-1} in 2009 and 2010 ($P < 0.01$) which represents relative increases of 10-15%. The watering did not affect soil respiration in 2011 (Figure 3.4b). Mean soil respiration in OTCs was consistently less, by 0.06-0.08 g CO_2 m^{-2} h^{-1} than in control plots in 2010 and 2011 across all comparisons (P<0.05) but not in 2009 (P=0.25, Figure 3.4a and b). No significant interactions between OTCs and other treatments were observed.

The average contribution of soil respiration to ecosystem respiration declined from 75% in 2009 to 54% in 2011 (Table 3.1). The contribution of soil respiration to ecosystem respiration differed between the upper and the lower slopes only in 2009 (63% on the lower slope and 85% on the upper slope). Grazing altered the relative contribution of soil respiration to ecosystem respiration in 2011 (45% in non-grazed and 64% in grazed plots) but not in 2010. Watering did not affect the relative contribution of soil respiration to ecosystem respiration.

3.4.Discussion

We aimed to understand how microclimate manipulation, grazing and their interactions would affect soil and ecosystem respiration, and how these effects would vary along topographical gradients by conducting a multi-factor experiment for three years in the semi-arid steppe of northern Mongolia. Our results show a robust, strong positive effect of soil moisture across topography and contrasting effects of grazing on ecosystem and soil respiration. Interactive effects of climate manipulations (OTCs and watering), grazing and topography were minimal, and the combined effects of the factors were equal to the sum of their separate effects.

The results of several comparisons suggest that soil moisture is a more important driving factor for biological processes in this semi-arid environment than temperature change or nutrient availability. First, ecosystem and soil respiration were lesser in OTCs across all comparisons, which were drier than control plots. The watering treatment negated the drying effect of OTCs on ecosystem and soil respiration in watered OTCs compared with non-watered OTCs, and caused an increase in ecosystem and soil respiration in control plots compared with non-watered control plots, although watering slightly decreased soil temperature (Brown & Archer, 1999). This result is consistent with previous studies where water addition resulted in increased ecosystem respiration (Niu et al. 2008), and soil respiration (Liu et al. 2009). Second, the upper slope had less ecosystem and soil respiration compared to the lower slope, although the upper slope is warmer and has greater total plant available nitrogen (21 g per 10 cm^2 ion exchange surface per day on the upper slope vs. 13 g per 10 cm^2 ion exchange surface per day on the lower slope; Liancourt et al. in press). Third, the seasonal average of ecosystem and soil respiration decreased over three summers (by 25-42%) as rainfall amount decreased and timing of rainfall shifted in 2010 and 2011. Likewise, a reduction in soil and ecosystem respiration due to decrease in rainfall or change in rainfall timing has been observed in semi-arid grassland (Chou et al. 2008; Liu et al. 2009; Hao et al. 2010). The soil respiration decrease in response to moisture limitation could have caused either shift in soil microbial community or decrease in microbial activity due to moisture limitation (Manzoni et al. 2012; Allison and Treseder 2008), but it is impossible to discern exact mechanism involved in the process with the current data set. Alternatively, it is also possible that the soil respiration decline over years could have been caused not only by changes in rainfall timing and amount, but also by gradual root decomposition (Parton et al. 2007; Díaz-Pinés et al. 2010). Nevertheless, all our results suggest that CO_2 efflux and soil respiration will be more sensitive to soil moisture, and increasing evapotranspiration due to warming will reduce CO_2 efflux and soil respiration in semi-arid steppe.

The contrasting effects of grazing on soil and ecosystem respiration suggest these two components of CO_2 flux may be controlled by different factors. Decrease of ecosystem respiration in the grazed plots may have been caused by plant biomass reduction due to grazing (Owensby et al. 2006; Susiluoto et al. 2008). Preliminary data of plant and litter biomass suggest that they were significantly less in the grazed plots, supporting our argument. While grazing reduces aboveground plant biomass, it could increase belowground biomass (Sjögersten et al. 2012) or carbon allocation to roots (Hafner et al. 2012), and thus increase labile carbon input into soil (Hafner et al. 2012; Gao et al. 2009). These changes could cause the greater soil respiration that we observed in the grazed plots in 2011. In the future, light grazing may enhance soil respiration because light grazing in our study increased soil temperature and did not affect soil moisture. However, the effect of grazing may be cumulative and exclusion of grazing for three years is not adequate for determining the long-term effect. The effects of grazing on CO_2 fluxes may also vary depending on grazing pressure and stocking density (Sjögersten et al. 2012; Cao et al. 2004).

The results also demonstrated that the effects of climate change simulated by OTCs (temperature, moisture and wind change) on soil respiration did not vary with topography. In contrast, effects of OTCs on ecosystem respiration varied with topography and watering. In accordance with our expectation, ecosystem respiration was lesser in

OTCs than in control plots of the lower slope, but ecosystem respiration did not differ between non-watered OTCs and non-watered control plots of the upper slope although soil moisture was lesser in non-watered OTCs. Since soil respiration was lesser in non-watered OTCs than in non-watered control plots, the difference of CO_2 flux may have originated from aboveground vegetation. Likewise, Liancourt et al. (in press) found that the survival and the biomass of *Festuca lenensis* significantly increased in non-watered OTCs than in non-watered control plots. However, the unexpected positive effect of OTCs was not observed when OTCs and control plots of the upper slope were watered. This result suggests that global change involving multiple factors (temperature, precipitation and wind) could have a surprising effect on ecosystem processes, and plants could mediate environmental stress and alter sensitivity of CO_2 effluxes to environmental variables (Aanderud et al. 2011).

In summary, our results indicate that soil moisture is the key controlling factor of carbon fluxes in this semi-arid grassland, and thus changes in precipitation may have stronger effects on the ecology of the system than temperature change. However, the predicted temperature increase may exacerbate evapotranspiration and thus decrease both plant and soil respirations. Grazing could also trigger greater loss of carbon from soil if it continues to increase soil respiration, and if it decreases net primary productivity. Future research needs to investigate how grazing pressure change would alter processes of carbon allocation to roots, root deposition to soil under different precipitation regime.

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Table 3.1

Relative contribution of soil respiration to ecosystem respiration, expressed in percentage of ecosystem respiration.

	2009			2010			2011		
	Control	OTC	Mean	Control	OTC	Mean	Control	OTC	Mean
Not grazed	61	65	63	56	55	55	48	43	45
Grazed	-	-	-	57	57	57	66	62	64
Lower slope mean	61	65	63	56	56	56	56	52	54
Not watered	79	89	84	62	52	57	56	47	51
Watered	82	92	87	59	58	59	56	55	55
Upper slope mean	80	91	85	60	55	58	56	51	53
Overall mean	71	78	75	58	55	57	56	51	54

Figure 3.1

Seasonal mean soil temperature (°C, mean ± standard error) in open-top warming chambers (OTCs, solid bar) and control plots (open bar) in response to the grazing treatment on the lower slope (n=4; a panel) and the watering treatment on the upper slope (n=3; b panel).

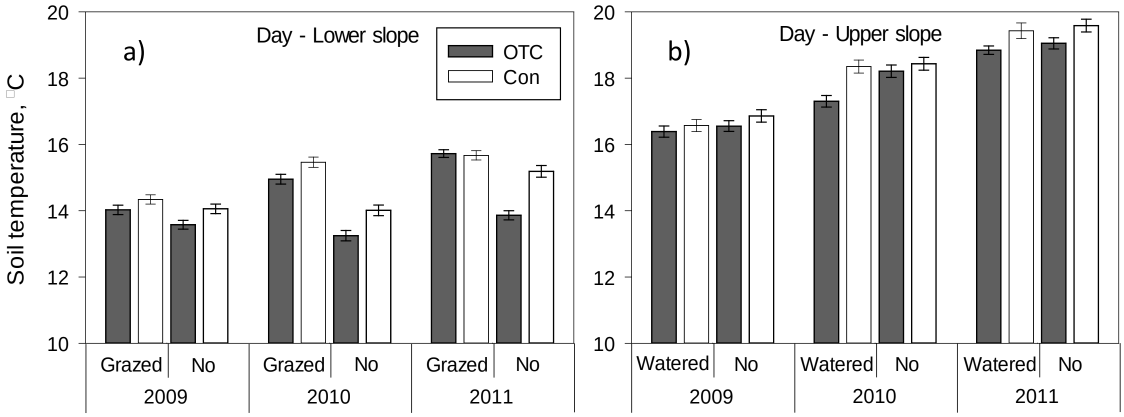


Figure 3.2

Seasonal mean soil moisture (% VWC, mean ± standard error) in open-top warming chambers (OTCs, solid bar) and control plots (open bar) in response to the grazing treatment on the lower slope (n=8; a and c panels) and the watering treatment on the upper slope (n=7; b and d panels)

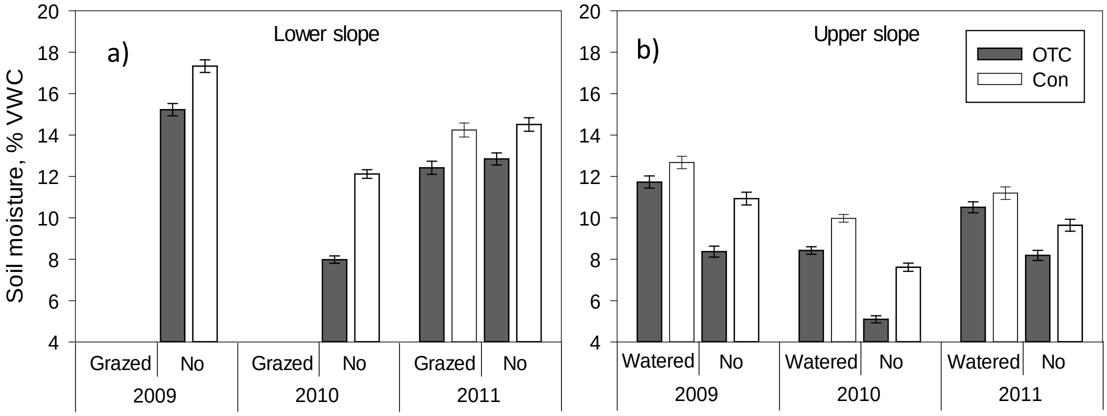


Figure 3.3

Seasonal mean ecosystem respiration (g CO_2 m^{-2} h^{-1}, mean ± standard error) in open-top warming chambers (OTCs, solid bar) and control plots (open bar) in response to the grazing treatment on the lower slope (n=4; panel a) and the watering treatment on the upper slope (n=3; panel b).

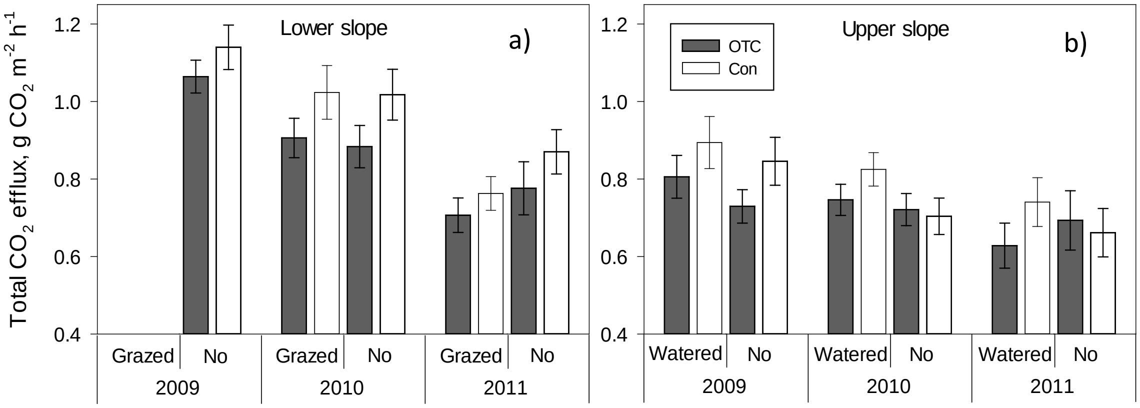
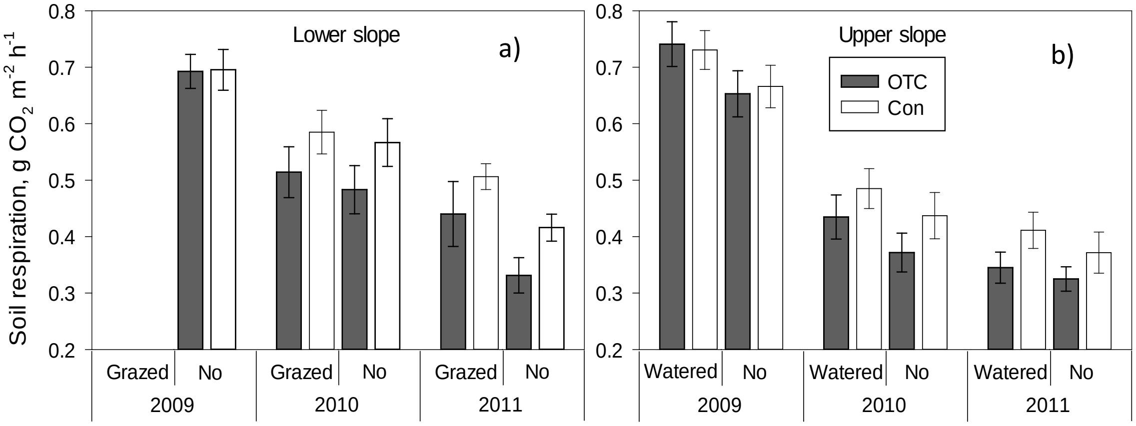


Figure 3.4

Seasonal mean soil respiration (g CO_2 m^{-2} h^{-1}, mean ± standard error) in open-top warming chambers (OTCs, solid bar) and control plots (open bar) in response to grazing (n=4; panel a) and watering treatments (n=3; panel b).



CHAPTER 4

Above- and belowground carbon storage across steppe and forest ecosystems in northern Mongolia

Anarmaa Sharkhuu[1], Alain F. Plante[1], Bazartseren Boldgiv[2], Peter S. Petraitis[3]

[1] Department of Earth & Environmental Science, University of Pennsylvania, Philadelphia, PA 19104-6316, USA

[2] Department of Ecology, National University of Mongolia, Ulaanbaatar 210646, Mongolia

[3] Department of Biology, University of Pennsylvania, Philadelphia, PA 19104-6018, USA

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Abstract

The projected conversion between forest and steppe ecosystems in Mongolia due to climate change will have a large impact on the carbon (C) balance of this region. Quantifying the current C stocks in these ecosystems is a useful initial step to determine the value of forest C and the C sequestration capacity of the systems. We estimated the aboveground C content of the forest and steppe by converting aboveground biomass data. Allometric equations for estimating biomass of stem, branch, needle and whole tree biomass were developed at the individual tree level using a tree diameter at breast height and tree height. These allometric equations were applied to estimate aboveground forest biomass. The steppe aboveground biomass data was obtained from a previous study conducted in this region. The results show that the forest contained 29.8 Mg C ha^{-1}, and the steppe contained 3.6-4.6 Mg C ha^{-1} in the aboveground biomass. Belowground C content was determined to a depth of 100 cm in the steppe and to a depth of 70 cm in the forest by excavating quantitative soil pits. The soils of the forest contained 81.4 ± 16.3 Mg C ha^{-2}, and steppe soil contained 82.9 ± 8.2 Mg C ha^{-1}. Thus, the forest contained at least 3-7 times greater C aboveground compared to the steppe, but the forest and steppe did not differ in belowground soil C content. A shift in biomes from boreal forest to steppe, which is projected to occur due to climate change, may therefore result in a significant loss of C at the ecosystems level in this area of northern Mongolia.

4.1.Introduction

Terrestrial ecosystems contain a large amount of carbon (~2100-3600 Pg C), approximately 2-4 times than in the atmosphere (Houghton 2003; Denman et al. 2007), and act as a carbon sink, sequestering 0.3-1.0 Pg C year^{-1} mostly into soil (Houghton 2003; Denman et al. 2007; Grace 2004). The amount of carbon (C) stored in terrestrial ecosystems has been subjected to the influence of natural and anthropogenic disturbances, such as climate change and land use management (Smith et al. 2008; Janzen et al. 1998; Schlesinger 1999). Climate change and land use also cause shifts of boundaries between grassland and forest (Field et al. 2007; Saxe et al. 2001), which cause a net loss or gain of C. Meta-analysis and prior research suggested woody plant encroachment into grassland causes a net loss of C (Jackson et al. 2002). Conversely, some studies demonstrated that conversion from forest to steppe can result in net loss of C or no change in C stock (Bradley et al. 2006; Devi et al. 2008; Guo and Gifford 2002). These contradictions among studies may have been caused by the climate and initial C stock of the ecosystems studied (Guo and Gifford 2002), and therefore, the extent of C loss or gain due to ecosystem boundary shift is highly uncertain in some regions (Houghton 2007).

According the climate change models, the areal extent of taiga forest in Mongolia is expected to increase by 2050, but forest at lower latitudes and altitudes is likely to be replaced by steppe due to the projected temperature increase and increase in evapotranspiration (Batima et al. 2005; Dagvadorj et al. 2009b). The majority of the conversion between forest and steppe is expected to occur in northern Mongolia because this region is located in the transition zone between the Siberian boreal forest and the

Central Asian steppe grassland, and is experiencing greater temperature change than the rest of Mongolia (Natsagdorj et al. 2000). How this projected shift would affect C stored in the ecosystems is highly uncertain for this region due to lack of data on current C stocks.

Although the concentration of soil organic matter in the Hövsgöl region was previously estimated (Batkhishig 2006), soil C stocks were not determined quantitatively and aboveground C content was never estimated. Quantifying C stocks stored in the forest and steppe of the Hövsgöl region is, therefore, of critical importance. Such estimates will help to determine a potential C gain or loss caused by the conversion between forest and steppe. Furthermore, estimating C stocks is an important initial step for implementing Reduce Emissions from Deforestation and forest Degradation (REDD) programs, which aim to evaluate the economic value of forests as well as environmental values such as C sequestration capacity (Defries et al. 2007; Baker et al. 2010).

Soil C stocks can be estimated using quantitative pits, which provide a direct measurement. In contrast, estimating aboveground C in forest typically relies on proxy data such as diameter at breast height (DBH) and height of tree. These proxy values are used to estimate species- and site-specific biomass by applying empirically developed allometric equations (Hoover 2008). Allometric equations often vary between sites and species. Using an allometric equation that is developed off-site can result in an underestimation of up 20% or an overestimation of up to 11% (Clark et al. 2001). It is therefore desirable to use allometric equations developed within a study region for a target species. However, to the best of our knowledge, no published allometric equation is available for Siberian larch (Larix sibirica) or Siberian pine (Pinus sibirica) in northern Mongolia.

The primary objective this study was to estimate aboveground and soil C stocks in the forest and the steppe ecosystems typical of the Hövsgöl region. We hypothesized that the steppe would contain more soil C than the forest because previous studies demonstrated that grassland contain more C due to deeper rooting zone (Jackson et al. 2002; Jobbagy and Jackson 2000; Stevenson 1982). We also expected that the forest would contain significantly greater C in aboveground biomass. Soil nutrients, root biomass, and soil texture were analyzed because these factors are known to affect soil C content. Previous research indicated that vegetation, particularly tree species, has a strong influence on soil C, nitrogen, phosphorus and exchangeable cations (Díaz-Pinés et al. 2011; Vesterdal et al. 2008; Shiels and Sanford Jr 2001; Berthrong et al. 2009), hence we also expected significant differences in nutrient contents among ecosystems.

4.2.Materials and Methods

4.2.1. Study site

The study area is located in the Dalbay Valley, part of the Lake Hövsgöl International Long-Term Ecological Research (ILTER) site, in northern Mongolia (51° 01.405' N, 100° 45.600' E; 1670 m asl). The climate of the Hövsgöl region is described as harsh continental, with high annual and diurnal temperature amplitudes (Nandintsetseg et al. 2007). The mean annual air temperature of this region is -4.5 °C, with the coldest average temperature of -21 °C in January, and the warmest average temperature of 12°C in July (Nandintsetseg et al. 2007). The mean annual rainfall ranges between 290-300 mm in the lower altitudes (Namkhaijantsan 2006).The topography of the study site is characterized by elongated, almost parallel valleys and ridges that run east to west due to the drainage system of Lake Hövsgöl. In this region, forest is mainly distributed on north-facing slopes, which is underlain by permafrost. On average, active layer thickness is 1.4 (Sharkhuu et al. 2007). In contrast, grassland is mainly distributed on south-facing slopes where permafrost is absent. Riparian zone, which is a boggy area characterized by vegetative tussocks and underlain by permafrost, is located between the grassland and the forest.

The dominant soil parent material at the eastern shore is Neogenic olivine basalt of volcanic origin. The northeastern shore consists of Proterozoic gneiss-slate, Late Riphean ophiolites, and Cambrian metamorphic groups with intrusions of Ordovician and Devonian granitoids and sub-alkaline granitoids (Goulden et al. 2006; Tomorhuu et al. 2004). The dominant soil type in the forest is Mountain taiga-derno (Cryept), Alluvial meadow boggy cryomorphic soil (Fluvent) in the riparian zone, and non-calcareous dark Kastanozem (Aridic Borolls or Typic Ustolls) in the steppe (Batkhishig 2006).

A distinctive tree-line is formed on the ridge tops between the north-facing forested area and the south-facing grassland. There is no definite tree-line between the riparian zone and the north-facing forest. The forest is dominated by Siberian larch (*Larix sibirica*), which composes 60-70% or more of the forest trees. At the study site, the second abundant tree species is Siberian pine (*Pinus sibirica*). Understory vegetation in the forest includes sub-shrubs (e.g. *Vaccinum vitis-idaea*), mosses (e.g., *Rhytidium rugosum*), grasses (*Festuca lenensis*) and forbs (e.g., *Galium boreale*, *Chrysanthemum zawadskii*, *Peucedanum* sp.). The vegetation on the south-facing slope is composed of sedges (e.g. *Carex pediformis*), grasses (e.g., *Festuca lenensis*, *Helictotrichon schellianum, Koeleria macrantha*), forbs (e.g., *Potentilla acaulis, Aster alpinus*, *Artemisia commutata*) and sub-shrubs (e.g. *Thymus gobicus*).

4.2.2. Belowground carbon estimation

Soil sampling:

To compare C content of the steppe and the forest, eight quantitative soil pits (50 × 50 cm) at each ecosystem were excavated in 2009 and 2010, according to a method described by Hamburg (1984). In the steppe, vegetation cover and the thin litter layer was removed before excavation. Three to five mineral soil samples were taken at depths of 0-10, 10-20, 20-30, 30-50, 50-70 and 70-100 cm during excavation of each pit in the steppe but samples from same depth and pit were composited before any analysis. Likewise, several mineral soil samples were taken at depths of 0-10, 10-20, 20-30, 30-50 and 50-70 cm of each forest pit and were composited before any analysis. In the forest, coarse woody debris and vegetation cover was removed from the surface before excavation. Organic horizons (Oi, Oe, Oa) of the forest were also weighed and subsamples were taken. Care was taken to limit error in our bulk density estimations by maintaining straight sides for each pit and by measuring profile depths as precisely as possible. During the excavations, rocks in the pit walls were removed and weighed whenever possible. Larger rocks that could not be removed during the excavations were removed and weighed afterwards. In two cases, the rocks were too large to be removed so equivalent volume of rocks was used to estimate mass. The amount of rock material within the boundaries of a profile was estimated visually in all cases. Rocks, roots and mineral soil were weighed separately. Subsamples of soil were weighed, air-dried in the field, and re-weighed to determine soil moisture content.

Soil laboratory analyses:

Whole-soil bulk density of each depth interval was estimated using the total air-dried weight of soil excavated from each depth interval. The soil samples were further separated using a 2-mm sieve into coarse (2-10 mm) and < 2 mm fractions, and the relative weight percentage of < 2 mm fraction was calculated to estimate air dried weight of the < 2 mm fraction of a depth interval. Approximately 2 g subsamples of < 2 mm soil fraction were weighed and dried at 105° for 24 hr to determine weight conversion from air-dry to oven-dry weight. Bulk density of the < 2 mm fraction of any depth interval was based on the estimated oven-dry weight of the < 2 mm fraction of that depth interval. For further chemical analyses, < 2 mm soil samples were used.

Soil texture was determined by the hydrometer method, modified from Gee and Or (1996). No pretreatment was applied to the samples. Approximately 30 g of < 2mm soil fractions were dispersed with 5% w/v Na-hexametaphosphate (HMP) by shaking for 12 hr. The soil suspensions were transferred to sedimentation columns and manually inverted end-over-end for 30 seconds prior to initiation of sedimentation. Hydrometer readings were carried out at 1.5 hr and 24 hr to determine the clay fraction. After the hydrometer reading, each soil suspension was wet sieved using a 50 µm sieve and rinsed until no visible particles passed through the sieve. The texture classification was carried out by calculating the proportions of sand by mass retained on the sieve, clay from the hydrometer data, and silt by difference, and using the USDA soil texture classification scheme (Gee and Or 1996).

Soil pH was measured using 1:1 deionized water-to-soil ratio and an OAKTON® Waterproof pH Meter (Thomas 1996). Exchangeable cations were determined by displacement of cations with 1N NH_4Cl. The extraction was carried out with 25:1 solution-to-soil ratio on an extraction machine for eight hours (Sumner and Miller 1996). The extracted solution was analyzed for concentrations of K^+, Ca^{2+}, Mg^{2+}, Na^+ and Al^+ by inductively-coupled plasma emission spectroscopy (Spectro Genesis, Mahwah, NJ). Plant available phosphorus was analyzed using the method of Kuo (1996) and Tiessen et al. (1984). Soil samples were extracted by shaking for 16 hours with 0.5 M $NaHCO_3$ (60:1 solution-to-soil ratio). Before adding sodium bicarbonate to soil, its pH was brought to pH=8 by adding 4 M NaOH. After extraction, the solution was centrifuged at 10000 rpm and -1 °C for 12 min. Due to excess Na, the supernatant was diluted before analysis and concentrations of plant available P were determined using inductively coupled plasma spectroscopy (Spectro Genesis, Mahwah, NJ).

Concentrations of organic C and total nitrogen were analyzed by dry combustion method using an elemental analyzer (Carlo Erba NA 1500 C/N Analyzer and Costech ECS 4010 CHNSO Analyzer). Prior research suggests that calcium carbonate was leached out (Batkhishig 2006), and field tests with dilute HCl suggested no presence of calcium carbonate. Therefore, we assumed that total C measurements reflected the organic C in the soil.

Statistical analysis:

The element concentrations (µg g^{-1}) as well as the C and nitrogen percentage concentrations were converted to content per meter square area (kg m^{-2} or g m^{-2}) using bulk density of the <2 mm soil fraction. Visual examination of the data suggested that assumptions of the ANOVA analysis had been violated. Therefore, normality of the data and error terms were tested using the Shapiro-Wilk's test. Homogeneity of the variance of the data and error terms were tested using O'Brien, Brown-Forsythe, Levene and Bartlett's tests. The majority of the data and error terms were neither normally distributed nor in accordance with the variance homogeneity assumption. Hence, we transformed data using Log_{10} and tested again for ANOVA assumptions. In a few cases, ANOVA assumptions had been violated. In those conditions, Welch's and Kruskal-Wallis's tests, instead of ANOVA, were used to test whether ecosystems differ in C and nutrient content. When ANOVA assumptions were met, Log_{10} transformed data were tested using a one-way ANOVA with ecosystems treated as a fixed factor for each profile depth. All these analyses were carried out with JMP v8 (SAS Institute, Cary, NC).

4.2.3. Aboveground carbon estimation

Sampling procedure:

To estimate plot-level tree biomass from DBH and height of tree using allometric equation, six blocks were randomly selected and established. Three of the blocks were located in the forest, south of the Dalbay River (south-blocks) while the other three blocks were located in the forest, north of the Dalbay River (north-blocks). In each location, two blocks were located near the forest edge (but at least 100 m away from the edge), and one block was located in the deep forest (> 400 m from the edge). Within each block, four plots with a diameter of 14.6 m and an area of 167 m^2 were established. The centers of the plots were located at least 36 m away from each other. Within the plots, one microplot with a diameter of 4 m was established to collect data on understory biomass and small trees with diameter at breast height (DBH) of 10 cm or less (U.S. Department of Agriculture Forest service 2005).The US Forest Inventory and Analysis (FIA) plot design was adapted for establishing plots.

Data collection was done in summers of 2009 and 2010. Living trees larger than 10 cm DBH at 1.3 m on each plot and saplings (DBH < 10 cm) on 4 m diameter microplot within a plot were measured. In total, data of 354 trees were collected. DBH and height of tree were used to estimate individual biomass of trees using an allometric equation. Individual biomass of trees within a plot was summed and dived by the plot area to estimate plot level biomass.

Nine trees were harvested to obtain actual biomass data to test fitness of allometric equations obtained from publications or from this study. DBH at 1.3 m and height of nine trees were measured before cutting them down. The DBH of the nine trees fell within two ranges; DBH of 11.5-13.5 cm and DBH of 21.0-21.9 cm, which represented two dominant DBH ranges of trees at the study site. For each tree, wet biomass of stem (with bark), branches and needles were measured in the field. Total biomass of each tree was obtained by adding stem, branch and needle biomass. Dry biomass of stem, branches and needles was obtained by drying them in an oven at 80 °C for 48 hours. Dry biomass of individual components (stem, branches and needles) of those three trees was used to estimate average water content. Dry biomass of the components of nine trees was estimated using the average water content of the corresponding component. Biomass was converted into C using the default IPCC value of 50% C in dry matter (Watson et al. 2000; Houghton et al. 1997).

Allometric equations

It is desirable to use allometric equations developed within a study region for a target species. However, no published site-specific allometric equations were available for Siberian larch (*Larix sibirica*) or Siberian pine (*Pinus sibirica*) in northern Mongolia. Hence, two approaches were applied to estimate aboveground biomass. The first approach was to apply allometric equations obtained from publications, in spite of the fact they were not specific to the current site or species. The second approach was to develop an allometric equation using harvested tree data.

Allometric equations from other publications

The number of allometric equations from the publications was constrained by two limitations. First, allometric equations must be developed for *L. sibirica* or *P. sibirica* specifically, regardless of growing location. Second, allometric equations must be developed for a species of *Larix* or *Pinus* genus which grows in similar ecological conditions. All allometric equations from the publications that met either of these requirements are listed in Appendix 3.

The fit of allometric equations was assessed using linear regressions of measured biomass by estimated biomass. Criteria for goodness of fit included coefficient of determination, percentage deviation, intercept and slopes of linear regressions. For estimated biomass of each component (i.e. stem, branch etc.), the average percentage deviation for each allometric equation was calculated as $Percentage\ deviation = \frac{\sum_i \frac{|B_{ij} - B_i|}{B_i} \times 100\%}{9}$ where: B_{ij} is the estimated dry biomass of tree *i* by allometric equation j, and B_i is measured dry biomass of tree *i* by harvesting. The intercepts and slopes of regressions were tested whether intercepts were significantly different than zero and slopes were significantly different than one.

Allometric equations developed in this study

The allometric equations for biomass of each component of tree was obtained by estimating coefficients of the following equations, then by determining the best equation among these equations.

$$B = b_0 D^{b_1} \quad (1)$$

$$B = b_0 D^{b_1} H^{b_2} \quad (2)$$

$$B = a + b_0 D^{b_1} \quad (3)$$

$$B = a + b_0 D^{b_1} H^{b_2} \quad (4)$$

$$B = a + b_0 D^{b_1} + c_0 H^{c_1} \quad (5)$$

$$B = a + b_0 D^{b_1} + c_0 D^{c_1} H^{c_2} \quad (6)$$

where *B* was the dry biomass (kg) of various components, *D* was the diameter at the breast height (cm), *H* was the height of tree (m), and a, b_0, b_1, b_2, c_0, c_1, c_2 were allometric coefficients calculated from a non-linear function. Some other, less frequently used, derivative forms of the above equations were neglected. To avoid introducing systematic bias, data was not transformed. Two statistical procedures were used to determine coefficients of equations and determine the best fit equation. Firstly, non-linear equation coefficients were determined by least square procedure, which were carried out using the R statistical package (R Development Core Team 2011). Adjusted coefficients of determination were obtained from the non-linear curve fitting procedure and the pseudo coefficients of determination were obtained by partitioning sums of squares manually. Goodness of fit of equations was assessed using the adjusted coefficients of determination. Secondly, equations for each biomass components were fitted using the maximum likelihood method using the R statistical package (R Development Core Team 2011) with the bbmle package (Bolker 2012). The fit of the equations was assessed based on corrected Akaike weights of the ranked models according to corrected Akaike scores. The coefficients of determinations may be misleading when used for non-linear equations. Therefore, the selection criterion was primarily based on corrected Akaike weights.

4.3.Results and discussion

4.3.1. Belowground carbon and nutrients

Soil carbon

The C concentration of each depth did not differ between the steppe and the forest, except the C concentration of the first 0-10 cm soil (Table 4.1). The C concentration of mineral soils in the forest and the steppe was comparable with the organic matter concentration of the forest and the steppe, which was determined in a previous study at this site (Batkhishig 2006). Mean soil C contents of each given depth, as well as carbon content of the whole profile, did not differ between forest and steppe (Table 4.1, Figure

4.1). Contrary to our initial hypothesis, the vertical distribution of C content of the forest was also similar to the steppe. The proportion of C in the top 20 cm to the C in the first 1 m of the steppe was 63% , which was greater than the global average value of 42% (Jobbagy and Jackson 2000) or the value of 49% in alpine steppe (Yang et al. 2010). Previous research demonstrated soil sand, silt, clay percentages, soil mass and root biomass were well correlated with soil C content (Wu et al. 2012; Parton et al. 1987; Burke et al. 1989), hence they were analyzed. Results show that these variables did not differ between the forest and the steppe soil, except at the depth of 0-10 cm (Table 4.2). Contrary to our initial hypothesis, the proportion of the root biomass of a depth of 0-30 cm compared with the total root biomass did not differ between the forest and the steppe (91% in the forest versus 93% in the steppe, Table 4.2) and a greater proportion of root biomass was found in the upper part of the steppe soil profile (Table 4.2). The proportion of root biomass in the top 30 cm of the steppe profile was 93%, which was also greater than the global average value of 65% (Jackson et al. 1996) and 90% in alpine steppe (Yang et al. 2009).

The C content of the whole soil profile in the forest (8.1 kg C m^{-2}) was slightly greater than the soil C content of the Larch forest (6.3 kg C m^{-2}) of Central Siberia (Matsuura and Hirobe 2010) but less than the soil C content of the forest (16.8 kg C m^{-2}) in northeastern Siberia. The soil C content of the steppe at depths of 0-10 and 10-20 was comparable with other alpine steppe regions where C content was 2.42-2.07 kg C m^{-2} and 1.80 kg C m^{-2} (Shi et al. 2012).

Matsuura and Hirobe (2010) concluded that the soil C storage difference among different Siberian regions caused by the difference in parent material of soil. Consistent with the results of Matsuura and Hirobe (2010), we found similar soil C content between the forest and the steppe which are underlain by the same soil parent material. Furthermore, soil of the Central Siberia and soil from the forest and steppe of our study site were both derived from basalt of volcanic origin (Goulden et al. 2006; Tomorhuu et al. 2004; Batkhishig 2006; Matsuura and Hirobe 2010) and had similar C content. In contrast, soils in the riparian zone of our study site and soils of the Northeastern Siberia were both derived from fluvial/alluvial or lacustrine deposits, having been developed during Pleistocene and Holocene by large river system (Matsuura and Hirobe 2010; Batkhishig 2006). The C content is greater in these two sites (25.5 kg C m^{-2} in the riparian zone and 16.8 kg C m^{-2} in the Northeastern Siberia) than the C content of either the steppe, forest at our study site or Central Siberian soil. Similar texture of soils, derived from the same parent material might have influenced the similarity of C content of soils with same parent material.

Soil nutrients

Soil nitrogen content was significantly greater in the steppe than that in the forest at depths of 0-10 cm, 10-20 cm and 20-30 cm (Table 4.3). We did not observe any significant difference of plant available phosphorus content between the steppe and the forest, although the mean plant available phosphorus concentration was greater in the forest than that in the steppe. Similarly, steppe and forest soil did not differ in exchangeable cations, except K^+ and Al^{3+} content in the first 10 cm soil (Table 4.3). Although the mean value of Al^{3+} and Na^+ were higher in the forest as expected, the difference was not statistically significant.

The difference in nitrogen content between the steppe and the forest was consistent with our expectations. This nitrogen content difference could have been caused by the presence of N-fixing plants, including lichens and legumes (*Oxytropsis viridiflava, Oxytropsis strobilacea, Astragalus mongolicus,* and *Vicia multifida*) in the steppe and efficiency of trees at translocating needle N before a needle senescence. The similar amount of exchangeable cations between the steppe and the forest could be the result of the similar amount of organic C content and clay fractions in the forest and the steppe soil.

4.3.2. Aboveground biomass and carbon estimation

Comparison of allometric equations developed in this study

Different allometric equations were established to predict total, stem, branch and needle biomass, using DBH and tree height in addition to the allometric equations obtained from publications. Coefficients of determination of equations for total and stem biomass were greater than 0.9 and highly significant ($P < 0.0001$, Appendix 4). Among all forms of allometric equations, developed in this study for total and stem biomass, the simplest two forms of allometric equations ($B = b_0 D^{b_1}$ and $B = b_0 D^{b_1} H^{b_2}$) had the best AICc scores and AICc weights (Appendix 4). Particularly, equations relating both height and DBH with total or stem biomass ($B = b_0 D^{b_1} H^{b_2}$) provided a better fit than the equation with only DBH ($B = b_0 D^{b_1}$). In contrast, equations relating only DBH with either branch or needle biomass ($B = b_0 D^{b_1}$) provided a better fit according to AICc score and AICc weights (Appendix 4). Adding tree height as the second independent variable slightly improved DBH only equations. However, due to the greater variability of branch and needle biomass among the sampled trees, the best allometric equations developed for branch and needle were not statistically significant (Appendix 4). The second best equations for branch and needle biomass with both tree height and DBH were statistically significant but some coefficients of the equations were not statistically significant (Table 4.4). The deviation coefficients for total and stem biomass estimated using the allometric equations developed in this study were 9% and 12% while the deviation coefficients for the branch and needle biomass were 43-44%. The biomass equations for branch and needle were the poorest among those of the biomass components. Hence, branch and needle biomass data was not used for C calculation.

There are limitations for estimating biomass of tree components. First, the number of destructively harvested trees was too few. Second, trees with bigger DBH (>25 cm) were not included in the sampling. The distribution of DBH was not normal and had long positive tail. Therefore, the number of trees with bigger DBH constituted less than 15% of the number of total trees. Hence, bigger trees were not included in the harvesting and DBH of trees that were harvested fell within two dominant ranges: DBH of 11.5-13.5 cm and DBH of 21.0-21.9 cm. However, the exclusion of trees with bigger DBH in the destructive sampling could have introduced a bias in biomass estimation of bigger trees and caused the increasing variation of total and stem biomass estimations with increasing DBH (Figure 4.2). For instance, the equation developed by Kajimoto et al. (2006) for trees of which DBH range is 2.24-18.6 cm noticeably underestimated the biomass of the trees of which DBH was around 21 cm. Therefore, it should be noted that the total or stem biomass estimation for bigger trees using equations developed in this study would be highly unreliable.

Comparison of allometric equations from other publications

The total biomass estimated using the allometric equations obtained from publications were 39-42% greater than the measured total biomass (Figure 4.3, Appendix 5). The coefficients of determination, intercepts and slopes of regressions did not vary much among allometric equations from the publications. The stem biomass estimated using equation for *L. sibirica*, growing in Iceland was relatively 13% less than the measured stem biomass, while the stem biomass using equation for *L. sibirica*, growing Manchuria region was relatively 23% more than the measured stem biomass. The stem biomasses estimated using allometric equations developed for *L. gmelinii* were either 51% less or 41% more than the measured stem biomass (Figure 4.3, Appendix 5). The goodness-of-fit indicate that the equations for *L. sibirica* performed better than the equations for *L. gmelinii*. Particularly, Snorrason and Einarsson (2006) equation provided the best fit for the measured stem biomass. All allometric equations obtained from publications resulted in poor estimation of branch and needle biomass, although the coefficients of determination were relatively high (Figure 4.3, Appendix 5). For instance, the estimated branch biomasses using equations were relatively 25-34% less than the measured stem biomass, while the estimated needle biomasses were relatively 26-71% less than the measured needle biomass.

Aboveground biomass

The plot level forest biomass and stem biomass estimated using allometric equations developed in this study ranged from 24 Mg ha^{-1} to 102 Mg ha^{-1} (Figure 4.4). The average total biomass estimated using allometric equations from this study was 59.6 ± 7.5 Mg ha^{-1}, and stem biomass was 59 ± 7.4 Mg ha^{-1}. The difference between total tree biomass and stem biomass was negligible, which could have been caused by the bias in the estimation of allometric equation coefficients and relatively small contribution of the branch and needle biomass to the total biomass (3-7% of the total biomass).

Comparisons with total and stem biomass using other equations from publications gave divergent results. The total and stem biomass estimated using the equation developed for *L. sibirica* in Iceland (Bjarnadottir et al. 2007) were comparable to the total and stem biomass estimated using our allometric equation. Other allometric equations yielded results either too greater or too lesser (Figure 4.4) compared with total and stem biomass estimated using our allometric equations. Very conservatively, the aboveground biomass in the forest was 59 Mg ha^{-1} or 5.9 kg m^{-2}.

Data of total aboveground plant biomass of the steppe was obtained from the previous study conducted in the Dalbay valley (Ariuntsetseg 2003). The average dry total aboveground biomass of seven quadrats with area of 0.25 m^2 per slope location was 230.57 ± 42.65 g per 0.25 m^2 for the upper slope and 179.55 ± 40.13 g per 0.25 m^2 for the lower slope. The dry live aboveground biomass, excluding litter biomass, was 48.36 ± 26.64 g per 0.25 m^2 for the upper slope and 23.77 ± 6.05 per 0.25 m^2 for the lower slope. The dry live aboveground biomass of the lower slope estimated in 2003 was similar to the dry live aboveground biomass of the lower slope estimated in 2010 (23.77 ± 6.05 g in 2003 versus 27.76 ± 4.28 g in 2010).

4.3.3. Comparison of carbon content between the steppe and the forest

Contrary to our initial hypothesis, C content of each depth and C content of the whole soil profile were similar between the forest and the steppe. The forest soil contained 8.14 ± 1.63 kg C m^{-2}, and the steppe soil contained 8.29 ± 0.82 kg C m^{-2} (Figure 4.5). Meta-analysis by Guo and Gifford (2002) indicated that soil C stock would increase by 8% after a land-cover conversion from forest to grassland. However, the meta-analysis also demonstrated that this soil C stock increase mainly occurred primarily in wetter ecosystem. In contrast, soil C stock was observed to decrease following a change from forest to grassland when annual precipitation was less than 1000 mm (Guo and Gifford 2002; Jackson et al. 2002). The soil C stock decrease following a change from forest to grassland in semi-arid environment could have been caused by limited C input due to shallower rooting depth as observed in our study and other studies (Schenk and Jackson 2002). Given the similar rooting depth and soil characteristics between the steppe and the forest, and low mean annual precipitation of northern Mongolia (200-400 mm), it is unlikely that the projected conversion of forest to steppe in this region (Dagvadorj et al. 2009b) will result in an increased soil C stock.

The C content of the total tree and the tree stem ranged from 12 Mg C ha^{-1} to 51 Mg C ha^{-1}, and was 29.8 ± 4 Mg C ha^{-1} (2.9 ± 0.4 kg C m^{-2}) on average. This C estimate is based on stem biomass of live trees. The biomass of branches, needles, roots of live trees, biomass of snag and biomass of understory were not included in C estimation due to great amount of uncertainty in the data collection and estimation. Therefore, the real C content in the forest would be much greater than the current estimation. The total aboveground plant biomass of the steppe measured in 2003 was 7.2 ± 0.06 Mg ha^{-1} for the lower slope and 9.2 ± 0.07 Mg ha^{-1} for the upper slope (Ariuntsetseg 2003). Using the same value of conversion factor of dry biomass to C content (0.5), steppe contained 3.6-4.6 Mg C ha^{-1} (0.36 - 0.46 kg C m^{-2}) in aboveground biomass. Compared with the C contained in the aboveground biomass of the steppe, the forest contained at least 3-7 times greater C in the aboveground tree biomass (Figure 4.5)

4.4.Concluding remarks

Data generated from this study contains considerable uncertainty due to a small number of replicates and limited areal coverage. While further research is needed to estimate C sequestration capacity of the forest accurately, our study provided initial data on above- and belowground C stocks in this region. Our estimations of aboveground biomass and above- belowground C content were comparable with the results of research conducted in similar ecosystem, suggesting the C stock estimations in this study are acceptable within the limit of the data.

Although our estimate of aboveground C content was conservative, the C stored in the forest was at least 3-7 times greater than the C stored in the steppe. Hence, the projected biome conversion from forest to steppe will result in a substantial C loss, rather than gain, in this region. Furthermore, the projected increase in temperature, evapotranspiration and dust storms (Sato and Kimura 2006; Sato et al. 2007; Dagvadorj et al. 2009a) may cause a net loss of C, considering that a larger proportion of total soil organic C is stored in near surface soil. The results of this research highlight the importance of the forest in the C balance of Mongolia.

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Table 4.1

The mean ± standard error of carbon concentration (%) and carbon content (kg m^{-2}) of each horizon of the forest and the steppe (n = 8). Bold values were significant different at $P < 0.05$ level. All data were log transformed for statistical analyses but mean and standard error of original data are reported in this table.

Depth, cm	**Concentration (%)**		**Content (kg m^{-2})**	
	Forest	*Steppe*	*Forest*	*Steppe*
0-10	**4.87 ± 1.10**	**2.63 ± 0.24**	3.68 ± 0.94	2.99 ± 0.30
10-20	1.17 ± 0.15	1.25 ± 0.16	1.74 ± 0.31	1.86 ± 0.28
20-30	0.57 ± 0.09	0.65 ± 0.10	0.93 ± 0.14	1.06 ± 0.17
30-50	0.42 ± 0.20	0.38 ± 0.08	1.16 ± 0.40	1.19 ± 0.24b
50-70	0.20 ± 0.05	0.15 ± 0.04	0.62 ± 0.12	0.53 ± 0.14
70-100		0.11 ± 0.03		0.66 ± 0.19
Total sum carbon			*8.14 ± 1.63*^{a}	*8.29 ± 0.82*^{a}

Table 4.2

The mean ± standard error of bulk density of <2 mm fraction (g cm^{-3}), soil mass of <2 mm fraction (kg cm^{-2}), coarse root biomass (g), and soil of each horizon of the forest and the steppe (n = 8). Significant differences at $P < 0.05$ level is indicated by different letters and bold face. Only root biomass data was Log$_{10}$ transformed for statistically analysis but original data is reported. All data except pH were log transformed for statistical analyses but mean and standard error of original data were reported in this table.

Depth, cm	**<2 mm fraction bulk density, g cm^{-3}**		**<2 mm fraction mass kg m^{-2}**		**Coarse root biomass, g**		**Soil texture**	
	Forest	*Steppe*	*Forest*	*Steppe*	*Forest*	*Steppe*	*Forest*	*Steppe*
0-10	**0.81 ± 0.05^{a}**	**1.24 ± 0.05^{b}**	**73.82 ± 4.94^{a}**	**113.68 ± 4.94^{b}**	**232.99 ± 54.66^{b}**	**437.08 ± 69.32^{a}**	**Sandy loam**	**Loamy sand**
10-20	1.50 ± 0.07^{a}	1.57 ± 0.07^{a}	144.87 ± 7.92^{a}	146.58 ± 7.92^{a}	48.32 ± 8.50^{ab}	18.16 ± 2.62^{b}	Sandy loam*	Loamy sand*
20-30	1.72 ± 0.10^{a}	1.52 ± 0.10^{ab}	165.31 ± 8.83^{a}	161.47 ± 8.83^{ab}	14.55 ± 3.15^{ab}	6.43 ± 1.29^{b}	Sandy loam/ Loamy sand	Sandy loam
30-50	1.65 ± 0.08^{a}	1.58 ± 0.08^{a}	330.42 ± 18.95^{a}	315.60 ± 18.95^{a}	21.15 ± 8.24^{ab}	3.80 ± 0.48^{b}	Loamy sand	Loamy sand
50-70	1.68 ± 0.13^{a}	1.68 ± 0.13^{a}	321.23 ± 31.42^{a}	329.63 ± 31.42^{a}	7.41 ± 3.89^{a}	1.44 ± 0.36^{a}	Loamy sand	Loamy sand
70-100		1.85 ± 0.13		563.22 ± 40.24	.	0.78 ± 0.22		Sand

Note: * The percentage of sand, silt and clay fractions at a depth of 10-20 cm were not statistically significantly different between the steppe and the forest. However, soil texture classification was different.

Table 4.3

The mean of pH, total nitrogen content (g m^{-2}), plant available phosphorus (g m^{-2}), exchangeable calcium (g m^{-2}), exchangeable potassium (g m^{-2}), exchangeable magnesium (g m^{-2}), exchangeable aluminum (g m^{-2}), exchangeable sodium (g m^{-2}) and effective cation exchange capacity (cmol kg^{-1}) of each horizon of the forest and the steppe (n = 8). Significant differences at $P < 0.05$ level is indicated by different letters and bold face. All data except pH were log transformed for statistical analyses but mean and standard error of original data are reported in this table.

Depth, cm	**pH**		**N (g m^{-2})**		**P (g m^{-2})**		**Effective cation exchange capacity (cmol kg^{-1})**		**K$^+$ (g m^{-2})**	
	Forest	*Steppe*	*Forest*	*Steppe*	*Forest*	*Steppe*	*Forest*	*Steppe*	*Forest*	*Steppe*
0-10	4.7	5.5	**159.9 ± 45.9^a**	**275.2 ± 31.5^b**	3.1 ± 1.4^a	2.1 ± 0.8^a	12.7 ± 2.1^a	9.1 ± 0.9^a	**6.8 ± 0.9^a**	**11.2 ± 0.7^b**
10-20	4.8	5.6	**88.8 ± 27.4^a**	**175.6 ± 26.7^b**	4.1 ± 3.1^a	1.8 ± 0.7^a	6.8 ± 0.8^a	6.3 ± 1.3^a	10.2 ± 1.3^a	7.9 ± 1.0^a
20-30	4.8	5.7	**57.1 ± 10.9^a**	**106.5 ± 16.3^b**	2.3 ± 1.5^a	1.4 ± 0.6^a	5.6 ± 0.8^a	6.0 ± 0.7^a	10.4 ± 1.1^a	10.1 ± 1.1^a
30-50	5.0	5.7	74.6 ± 14.6^a	136.1 ± 19.4^a	3.7 ± 1.8^a	3.4 ± 1.6^a	5.8 ± 1.2^a	5.7 ± 0.6^a	17.8 ± 1.2^{ab}	20.1 ± 1.1^a
50-70	5.2	6.6	49.7 ± 6.5^a	82.3 ± 17.9^a	1.7 ± 0.7^a	3.2 ± 1.5^a	6.2 ± 0.6^a	5.1 ± 0.8^a	14.6 ± 1.4^a	18.2 ± 2.4^a
70-100		5.8		105.0 ± 26.1^a		2.7 ± 1.3^a		4.6 ± 1.0^a		28.1 ± 3.2^a

Depth, cm	**Ca^{2+} (g m^{-2})**		**Mg^{2+} (g m^{-2})**		**Al^{3+} (g m^{-2})**		**Na$^+$ (g m^{-2})**	
	Forest	*Steppe*	*Forest*	*Steppe*	*Forest*	*Steppe*	*Forest*	*Steppe*
0-10	139.9 ± 32.1^a	156.3 ± 14.1^a	20.9 ± 4.5^a	23.5 ± 1.9^a	**6.1 ± 2.1^a**	**1.6 ± 0.4^b**	0.9 ± 0.4^a	0.5 ± 0.2^a
10-20	135.9 ± 22.1^a	160.2 ± 29.4^a	20.6 ± 3.1^a	26.5 ± 4.6^{ab}	10.2 ± 3.1^a	2.3 ± 0.9^a	1.2 ± 0.5^a	0.8 ± 0.3^a

20-30	123.8 ± 22.6^{a}	141.0 ± 26.4^{a}	19.6 ± 3.8^{a}	26.3 ± 5.6^{ab}	10.8 ± 3.2^{a}	3.7 ± 1.1^{a}	1.0 ± 0.4^{a}	0.8 ± 0.3^{a}
30-50	245.0 ± 43.3^{a}	241.8 ± 24.8^{a}	37.0 ± 6.7^{a}	51.4 ± 7.4^{a}	19.6 ± 6.2^{a}	8.9 ± 2.8^{a}	2.7 ± 1.0^{a}	2.4 ± 1.0^{a}
50-70	290.3 ± 29.8^{a}	217.6 ± 39.7^{a}	34.7 ± 6.2^{a}	45.6 ± 8.6^{a}	15.8 ± 5.0^{a}	12.3 ± 4.1^{a}	1.9 ± 0.7^{a}	1.5 ± 0.7^{a}
70-100		332.2 ± 76.7^{a}		73.9 ± 21.6^{a}		20.4 ± 6.4^{a}		3.3 ± 2.5^{a}

* Not normally distributed; $^{+}$ variance were heterogeneous

Table 4.4

Estimated coefficients, probability of coefficients, confidence interval of each coefficient, adjusted R^2 and probability of the allometric equation $B = b_0 D^{b_1} H^{b_2}$, used to estimate biomass of tree components. The allometric equations of tree components were fitted to the data from nine trees that were destructively harvested.

		Estimates ± Std. error	**Prob (z)**	**Confidence interval 2.5%**	**Confidence interval 97.5%**	R^2_{adj}	***P***
Total	b_0	0.03 ± 0.01	0.03*	0.01	0.05	0.98	<0.0001
	b_1	1.23 ± 0.27	<0.0001***	1.17	1.66		
	b_2	1.68 ± 0.30	<0.0001***	1.62	1.93		
Stem	b_0	0.02 ± 0.01	0.045*	0.01	0.03	0.98	<0.0001
	b_1	1.63 ± 0.27	<0.0001***	1.02	1.73		
	b_2	1.33 ± 0.30	<0.0001***	0.65	1.43		
Branch	b_0	0.004 ± 0.01	0.64	0.002	0.01	0.62	0.007
	b_1	-0.99 ± 1.39	0.48	-2.69	1.81		
	b_2	3.83 ± 1.69	0.02*	1.68	5.79		
Needle	b_0	0.002 ± 0.00	0.62	0.00	0.00	0.63	0.007
	b_1	-0.99 ± 0.39	0.01*	-1.50	-0.21		
	b_2	3.85 ± 0.31	<0.0001***	1.39	3.96		

Figure 4.1

Carbon content (kg m^{-2}) of the whole profile with a common depth of 70 cm. The boxes represent the upper and lower quartiles while solid and dashed lines represent the media and mean, respectively. The whiskers represent the 5th and 95th percentile of the data.

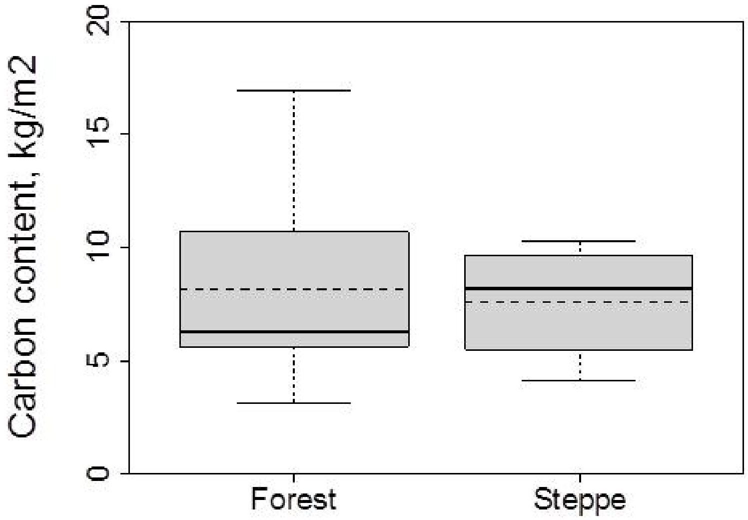


Figure 4.2

Relationships of stem biomass (kg) of individual tree against diameter at breast height. Dark circles represent stem biomass measured by destructively harvesting, grey triangles represent estimated stem biomass using DBH and height of trees that was destructively harvested, and open rhombus represent all estimated stem biomass.

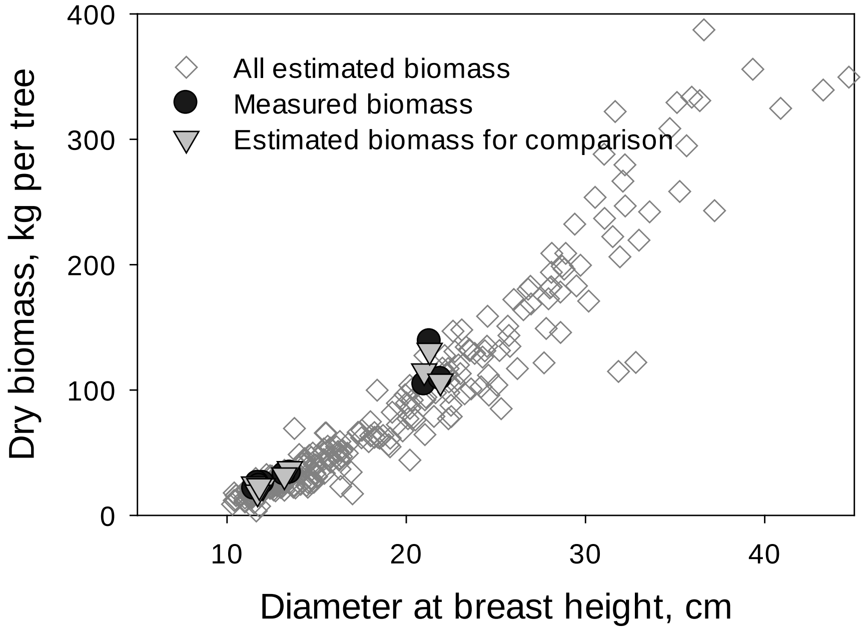


Figure 4.3

Comparisons of estimated individual tree component (needle, branch, stem and total) biomass (kg) with measured component biomass. DBH and height of trees that was destructively harvested were used to estimate the component biomasses employing allometric equations obtained from the publications (listed in the Appendix 3) and equation developed in this study.

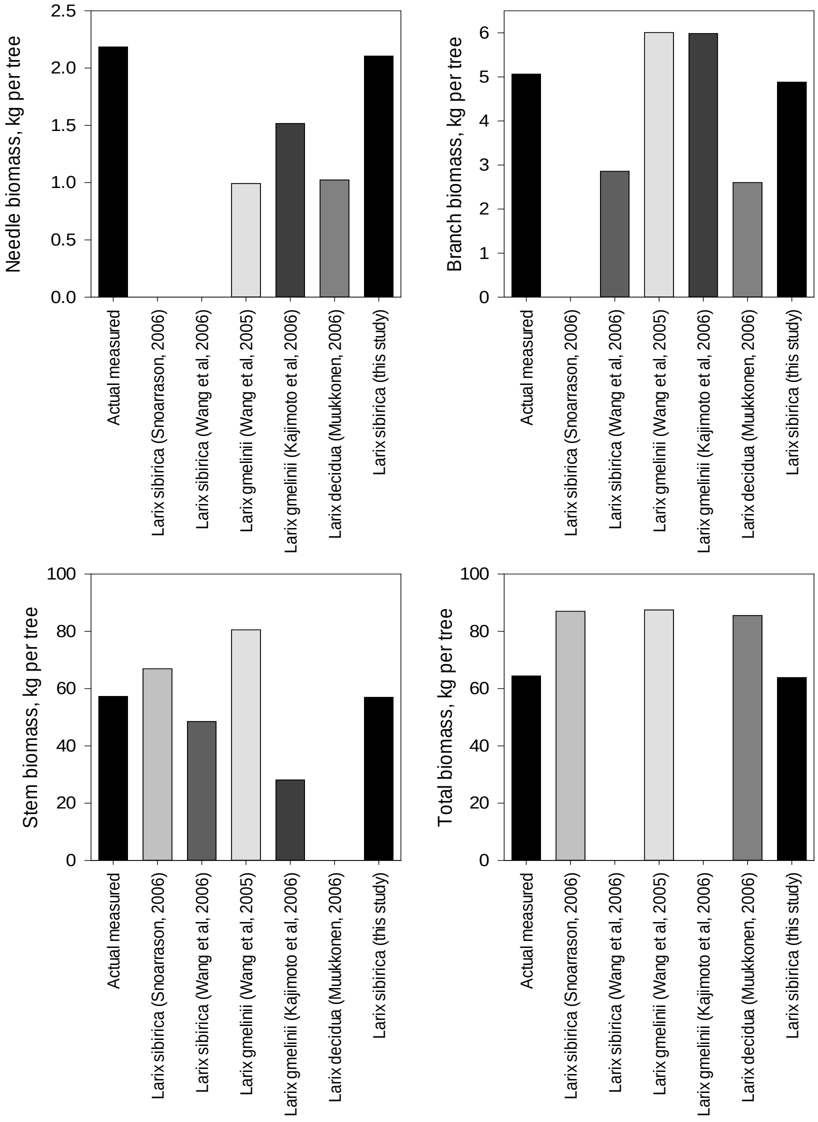


Figure 4.4

The estimated biomass (Mg ha^{-1}) for tree components (needle, branch, stem and total) employing allometric equations from the publications (listed in the Appendix 3) compared to the estimated biomass employing allometric equation developed in this study. DBH and height of trees measured in 24 sub-plots were used.

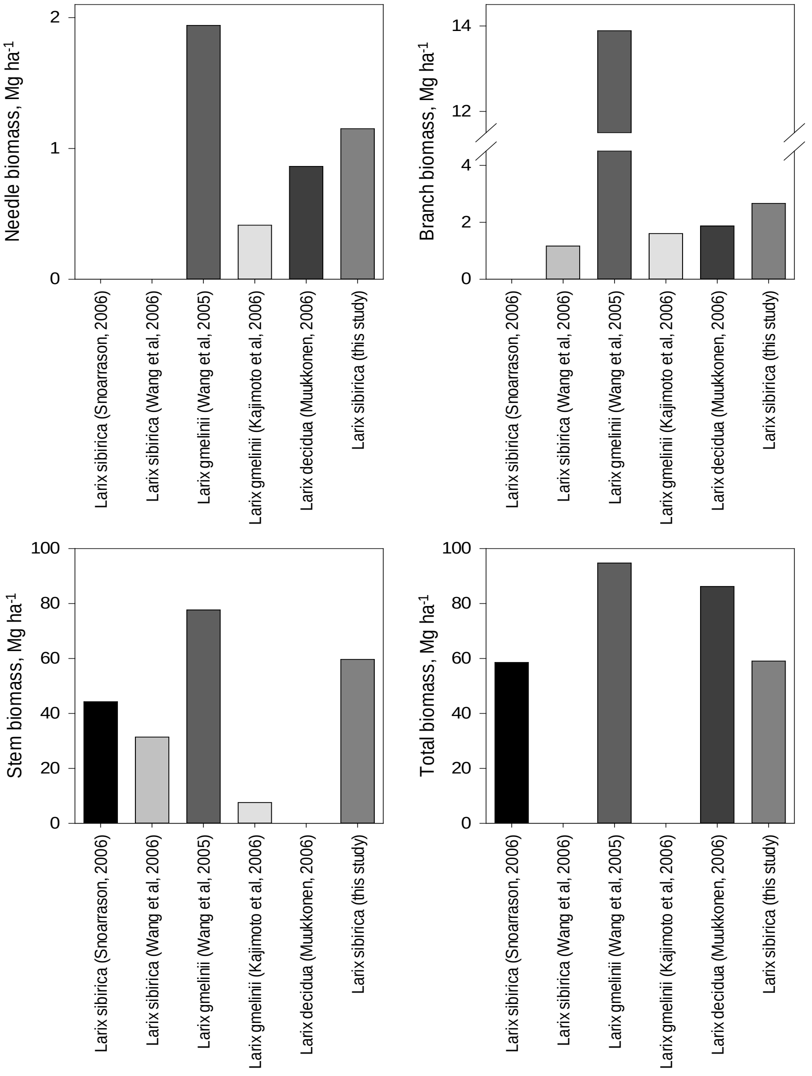
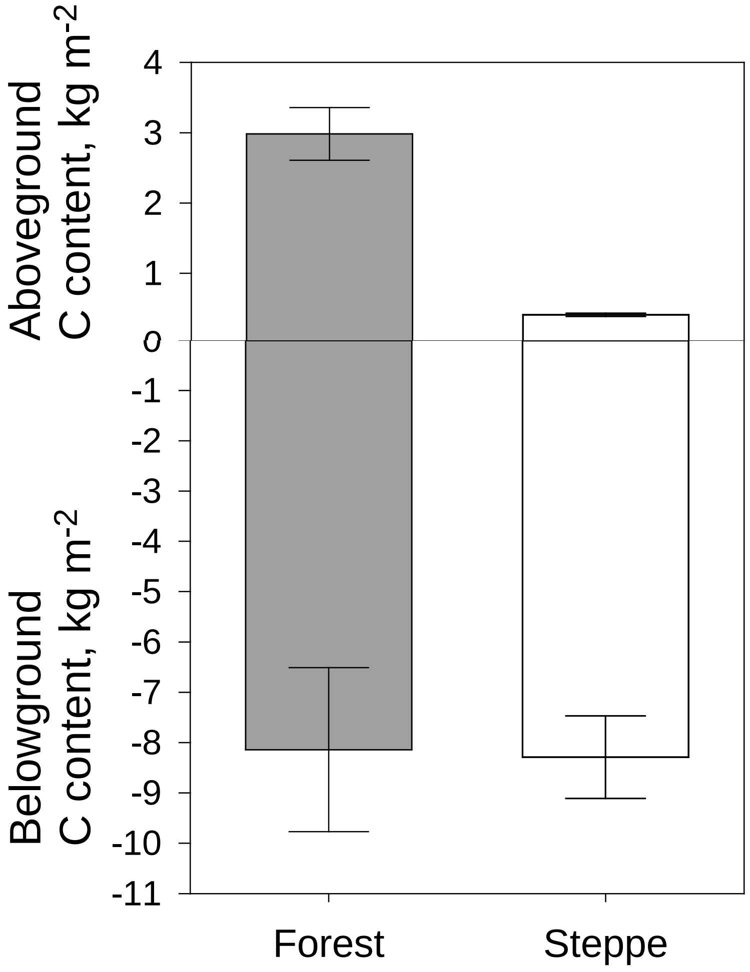


Figure 4.5

Comparison of above- and belowground carbon



SUMMARY AND CONCLUSION

Recent climate change may trigger changes in the terrestrial ecosystem's C balance, enhancing decomposition and respiration, which could cause a positive feedback to atmospheric C and climate change. The need to better understand the response of terrestrial ecosystem to climate change regarding the significance of C storage and flux of the terrestrial ecosystem in global C cycling has resulted in increased research effort at experimental warming studies. The majority of warming studies have been conducted in moist tussock tundra, wet sedge tundra of North American or European Arctic, meaning that temperate and boreal forest ecosystems, regions at higher latitude with low precipitation, and arid and semi-arid biomes are underrepresented in experimental warming studies.

The Hövsgöl region of northern Mongolia is located on the southern fringe of the Siberian continuous permafrost, and represents a transition zone of Siberian boreal forest to Central Asian steppe grassland. It is a unique and important region where soil C stocks and C fluxes can be studied in both forest and grassland that are in close proximity, and have the same climate and soil parent material. Furthermore, the forest in this region is underlain by permafrost with very low ice content which makes this region different from other high-latitude regions. This region has already experienced greater temperature increase than the global average and is under the increasing grazing pressure due to socio-economic transition. The study of climate change and grazing impacts on C dynamics in northern Mongolia is of particular interest because the area is expected to experience greater climate change than the global average and major shift in the forest and steppe boundary, and grazing pressure is expected to increase as well. However, a study on how ecosystem and soil respiration would respond to climate change and grazing pressure, and how much carbon stored in the forest and steppe ecosystems has not yet conducted in this region.

The general objective of this thesis was to study soil and ecosystem respiration responses to simulated climate change and grazing, and to assess C stocks in steppe and forest ecosystems in northern Mongolia.

Chapter 1: The objective of this chapter was to test whether OSCs, suggested as an alternative warming method, can overcome the known shortcomings of OTCs and perform better in a field setting.

Experimental manipulation of temperature *in-situ* using passive warming open-top chambers (OTCs) has been a common method to study climate change impact on soil and ecosystem respirations in a remote areas. OTCs have been used for investigating climate change impacts on ecosystem processes because they are inexpensive, non-destructive, and effective at generating temperature increase and suitable for remote areas that are logistically challenging to supply electricity. However, OTCs are known for increasing daily maximum temperature and amplifying diurnal temperature range while diurnal temperature range is predicted to decrease due to increased daily minimum temperature according to the IPCC predictions.

Open-sided chamber (OSC) with a louvered top has been suggested as an alternative passive warming method that is designed to increase daily minimum temperature by decreasing losses of long-wave radiation, thus reducing diurnal temperature range. Their open sides and louvered tops also help to minimize adverse effects on wind and water regimes. Studies examining the abiotic and biotic responses to the two chamber designs, set side by side, are needed to determine the relative performances of two chambers.

The performance of both chambers was compared with control plots. OTCs significantly increased mean daytime temperature by 1.5 °C by increasing daily maximum temperature by 2.9 °C. In contrast, OSCs had no effect on either mean daytime temperature or daily maximum temperature. Mean nighttime air temperature was significantly cooler in OTCs (by 0.3 °C) than in control plots, but it was warmer in OSCs (by 0.2 °C). Soil temperature of both chamber designs did not significantly differ from soil temperature of control plots. However, soil moisture in the chambers was significantly less than in control plots. Both OTCs and OSCs delayed the flowering of graminoids but accelerated flowering of forbs, regardless of their different effects on air and soil temperatures. This suggests that the decreased soil moisture in both chambers could be the main reason of the similar flowering responses of forbs and graminoids to OTCs and OSCs.

These results show that OSCs may not be an optimal method to simulate temperature increase, although OSCs manipulated air temperature in a similar pattern that was predicted by IPCC models. Instead, OTCs might be better option, although they generate an increase in daily temperature by increasing daily maximum temperature rather than minimum temperature.

Chapter 2: I used OTCs to simulate climate changes and aimed to study how experimental warming will affect microclimate variables, and how experimental warming and subsequent changes in environmental variables affect soil respiration and its temperature sensitivity in three ecosystems. Results of this study may allow us to discern soil respiration responses to the direct effect of climate change and indirect effect via changing microclimate of ecosystem.

OTCs significantly increased air temperatures by 1.0-2.1 °C in the steppe compared to the control plots. OTCs had slightly warmer temperatures in the forest (0.2-0.4 °C) and in the riparian (0.5-0.6 °C) compared to the corresponding control plots but the temperature increases were not statistically significant. The degree of warming by OTCs was affected by the canopy and openness and vegetation stature inside the chamber. Although soil temperature was greater in OTCs than in controls (by 0.6-1.4 °C in forest, and by 1.0-1.7 °C in steppe), the differences were not statistically significant. OTCs affected soil temperature of the riparian in not consistent manner. OTCs decreased soil moisture in the steppe (by 3-6%) and in the riparian (by 2%) but increased soil moisture in the forest (by 4-10%), indicating that responses of microclimate could vary due to ecosystem setting. Soil respiration rates were greater in OTCs than controls plots (by 0.20 g CO_2 m^{-2} h^{-1}) in the forest. Our results also indicated that soil respiration was mainly controlled by temperature in the forest, which was consistent with other studies. Meanwhile, the temperature increase by OTCs had little effect on soil respiration in the steppe, but soil moisture decrease caused by the chambers had a stronger effect, which is also consistent with many studies in arid and semi-arid systems. Although soil respiration in the forest was greater in OTCs than in control plots, temperature sensitivity of soil respiration was lower in OTCs (Q_{10} = 2.2 in OTCs versus Q_{10} = 5.8 in control). This result suggests that soil respiration may not respond to warming as strongly as anticipated. Although warming could enhance soil respiration rate in the forest, its effect would lessen due to lower temperature sensitivity. Meanwhile soil respiration may not respond to warming in the steppe due to greater water stress. Overall, our results highlight the necessity of taking into account the heterogeneity of ecosystems to predict C flux responses to global change more accurately.

Chapter 3: The ecosystems of northern Mongolia are under pressure of not only climate change but also intensified grazing due to recent socio-economic change. Livestock husbandry is the most common and important agricultural practice in Mongolia and has been part of the grassland ecosystem for thousands of years. However, no experiment has been conducted to address the response of C efflux to direct and interactive effects of grazing and warming in this region. We aimed to study how experimental warming, watering, and grazing affect soil and ecosystem respiration, whether the effect of experimental warming differs across a topographical gradient, and how interactions of main treatments affect soil and ecosystem respiration.

While OTCs had consistently less ecosystem and soil respiration, watering increased ecosystem and soil respiration regardless of the temperature decrease in watered plots. These results suggest that soil moisture is more important driving factor for biological processes in this semi-arid environment than temperature change. Grazing had contrasting effects ecosystem and soil respiration. Grazing decreased ecosystem respiration by reducing plant biomass. However, grazing increased soil respiration which could be result of greater carbon allocation to roots in response to grazing. Due to the greater plant biomass and coverage, the lower slope had greater ecosystem respiration than the upper slope, although the upper slope had greater plant available total nitrogen. Soil respiration on the other hand did not differ between upper and lower slopes. The results show a robust effect of OTCs across the topographical gradient. Interactive effects of climate manipulations (chamber and watering), grazing and topography were minimal and the combined effects of the main factors were equal to the sum of their independent effects.

The results indicate that changes in precipitation may have a stronger effect than temperature change in this semi-arid environment. However, the predicted temperature increase may exacerbate evapotranspiration and thus decrease both plant and soil respiration. Moreover, grazing could trigger greater loss of C from soil if it continues to increase soil respiration for a longer-term and if it decreases net primary productivity. Future research needs to be done on how grazing pressure would alter processes of C allocation to roots, root deposition to soil under different precipitation regimes.

Chapter 4: According climate change models, forest at lower latitudes and altitudes in Mongolia is likely to be replaced by steppe due to the projected temperature increase and change in precipitation. This projected shift in forest and steppe boundary may result in substantial changes in ecosystem C storage. Quantifying C stocks stored in the forest and steppe of the Hövsgöl region is, therefore, of critical importance. We aimed to assess aboveground and soil C stocks in the forest and steppe in order to determine potential C gain or loss caused by the conversion between forest and steppe.

Previous researches suggested that the conversion of forest to grassland could increase soil C stock because grassland can sequester more C due to deeper root penetration. Contrary to the global assessment of vertical C contentdistribution and root penetration in the grassland, no difference in vertical distributions of C and root biomass was observed between the forest and steppe. The forest and steppe soil contained 8.14 ±

1.63 kg C m^{-2} and 8.29 ± 0.82 kg C m^{-2}, respectively. Carbon stock stored in the tree biomass ranged from 12 Mg C ha^{-1} to 51 Mg C ha^{-1}, and was 29.8 Mg C ha^{-1} (2.98 kg C m^{-2}) on average. In contrast, steppe contained 3.6-4.6 Mg C ha^{-1} (0.4-0.5 kg C m^{-2}) in aboveground biomass. Compared with C contained in the aboveground biomass of the steppe, the forest contained at least 3-7 times greater C in the aboveground tree biomass but did not differ in soil C, and therefore, the projected decrease in forested area and expansion of steppe area may result in net C loss.

Conclusions

Our results have indicated that temperature increase will have different effects on soil respiration in different ecosystems, even though those ecosystems have same mean annual temperature, precipitation and soil C content. Therefore, it is important to take into account the heterogeneity of ecosystems to predict C flux responses to global change more accurately. Climate change simulation by OTCs has showed that warming is likely to increase soil respiration in the forest but that warming effect on soil respiration will be lessened due to decreased temperature sensitivity of soil respiration in warmer condition. In contrast, we found that soil moisture is the key controlling factor of C fluxes in semi-arid grassland, and thus changes in precipitation may have a stronger effect than temperature change.

Although our results demonstrated that grazing increased soil respiration, it is still inconclusive how grazing will affect soil respiration in future due to the complex responses of soil and plants to the grazing intensity change. Grazing could reduce substance supply to a root system and thus decrease soil respiration. Alternatively, grazing may induce plants to allocate more C to their root system which could enhance root exudates and soil respiration. Nevertheless grazing will likely to decrease overall CO_2 flux due to larger impact on aboveground plant biomass.

We conclude that CO_2 flux of the region will not increase as predicted due to the projected steppe area expansion and insensitivity of soil respiration to warming in the steppe. Simultaneously, the capacity for the region to absorb more CO_2 will likely to decline in both magnitude and extend due to the projected loss of forest and water stress for plants caused by temperature increase. While further research is needed to determine whether this region will act as C sink or source in future, this research provides initial data on C stocks of this region and findings of climate change and grazing impacts on C fluxes.

APPENDICES

Appendix 1

List of species, separated by graminoids and forbs, used in the analyses examining effects of chamber treatment and year on the timing of flowering and flower production. All are perennial except the annual Draba nemorosa.

Graminoids	**Structures counted**
Agrostis mongholica	Inflorescences
Carex spp.	Inflorescences
Festuca lenensis	Inflorescences
Helictotrichon schellianum	Inflorescences
Hierochloe odorata	Inflorescences
Koeleria macrantha	Inflorescences
Poa attenuata	Inflorescences
Forbs	
Amblynotus rupestris	Flowers
Androsace incana	Flowers
Arenaria capillaris	Flowers
Artemisia commutata	Inflorescences
Aster alpinus	Inflorescences
Bupleurum bicaule	Inflorescences
Draba nemorosa	Flowers
Gentiana pseudoaquatica	Flowers
Potentilla acaulis	Flowers
Potentilla bifurca	Flowers
Potentilla sericea	Flowers
Sibbaldianthe adpressa	Flowers
Thalictrum minus	Inflorescences
Thymus gobicus	Flowers
Veronica incana	Inflorescences

Appendix 2

Summary of the plots

Location	*Blocks*	*Plots*	*Slope*	*Tree density (No ha^{-1})*	*Basal area (m^2 ha^{-1})*	*Trees of which DBH is > 10 cm*		
						# of trees	*Average height (m)*	*Average DBH (cm)*
South facing slope-edge	P1	A	20	4131.74	21.3	11	12.08	18.45
		B	10	4431.14	12.0	11	11.41	14.74
		C	5	6287.43	33.6	20	12.24	17.33
		D	25	3353.29	25.5	11	13.95	21.59
South facing slope-edge	P2	A	17	4610.78	24.0	17	10.01	15.93
		B	15	9401.20	22.1	14	11.05	16.71
		C	5	1916.17	30.3	14	11.43	18.33
		D	4	8502.99	14.2	12	9.58	14.96
South facing slope-deep	P3	A	11	2275.45	33.2	16	12.23	19.06
		B	7	1377.25	18.5	12	12.11	17.52
		C	7	2095.81	25.7	15	11.71	17.65
		D	5	299.40	10.2	3	12.40	25.09
North facing slope-edge	P4	A	10	1137.72	37.7	19	13.82	19.63
		B	10	1017.96	53.8	16	15.67	25.86
		C	10	658.68	38.4	10	15.01	27.72
		D	10	538.92	20.0	8	12.18	22.83
North facing slope-deep	P5	A	34	1317.37	23.4	15	11.65	17.47
		B	32	11976.05	9.05	2	12.09	31.01
		C	45	1197.60	1.4	2	8.31	12.35
		D	30	2155.69	11.4	13	9.91	13.48
North facing slope-edge	P6	A	10	3592.81	13.9	5	14.94	24.20
		B	9	1437.13	21.3	5	15.12	28.87
		C	14	6586.83	31.4	9	16.81	23.80
		D	10	4610.78	18.8	8	11.77	21.33
Total						***268***		

Appendix 3

All available allometric functions from other publications either developed for *Larix sibirica* or *Pinus sibirica* specifically, or developed for a species of *Larix* or *Pinus* genus, growing in similar ecological condition

Species	Function	Constraints of a function	Source
Larix sibirica	$B_t = [119.734 \times D_{50}^{1.4251} \times (D_{50}^{2})^{0.2539}]/1000$	$D_{50} < 9$cm	Bjarnadottir et al. 2007
	$B_t = 102.1374 \times D^{1.8073} \times H^{0.3191}$		
Larix sibirica	$B_t = 0.1081 \times D^{1.53} \times H^{0.9482}$	3.3 cm < D < 31.6 cm	Snorrason and Einarsson 2006
	$B_s = 0.0444 \times D^{1.4793} \times H^{1.2397}$		
Pinus contorta	$B_t = 0.1429 \times D^{1.8887} \times H^{0.4332}$	4.2 cm < D < 26.3 cm	
	$B_s = 0.0669 \times D^{1.5958} \times H^{0.9096}$		
Pinus sylvestris	$B_s = [132.268 \times (D^2 \times H)^{0.9287}]/1000$	3 cm < D < 49 cm	Wirth et al. 1999
Larix sibirica	$B_s = 0.03994 \times (D^2 \times H)^{0.8718}$	Age=120	Wang et al. 2005
	$B_b = 0.03389 \times (D^2 \times H)^{0.5511}$		
Larix gmelinii	$B_t = 10^{1.977} \times D^{2.451}$	13.7 < D < 41.4 equation modified from logarithmic equation for B	Wang 2006
	$B_s = 10^{2.311} \times D^{2.154}$		
	$B_b = 10^{-1.593} \times D^{4.340}$		
	$B_n = 10^{-1.851} \times D^{3.934}$		
Larix gmelinii	$B_t = 0.439 \times D^{1.7}$	2.24 < D < 18.6; 86 < age <281	Kajimoto et al. 2006
	$B_s = 0.19 \times D^{1.81}$		
	$B_b = 0.0428 \times D^{1.79}$		
	$B_n = 0.0148 \times D^{1.68}$		
Larix decidua	$B_t = 1.3245 \times 10 + 1.8785 \times 10^{-2} \times D^2 \times H + 3.2315 \times 10^{-1} \times D$	7.7 < D < 53.9; 5.6 < H <24.9	Muukkonen and Makipaa 2006
	$B_b = -3.003 + 2.093 \times \ln(D)$ $B_b = -2.62 + 2.613 \times \ln(D) + (-0.726) \times \ln(H)$		
	$B_n = -3.201 + 1.578 \times \ln(D)$ $B_n = -2.874 + 2.021 \times \ln(D) + (-0.618) \times \ln(H)$		

Note: V – volume of stem (dm^3); D – DBH at 1.3 m (cm); D_{50} – DBH at 0.5 m (cm); H – height (m); B – biomass (kg); B_t – total aboveground biomass, B_s – stem biomass, B_b – branch biomass, B_n – needle biomass.

Appendix 4

Comparison of equations

Dependent variable	Equations	AICc	k	AICc weighs	R_{adj}	*P*
Total biomass	$B = b_0 D^{b_1} H^{b_2}$	75	3	0.96	0.98	<0.0001
	$B = b_0 D^{b_1}$	82.1	2	0.03	0.92	<0.0001
	$B = a + b_0 D^{b_1} H^{b_2}$	83.5	4	0.01	0.99	<0.0001
	$B = a + b_0 D^{b_1}$	89.2	3	<0.001	0.92	<0.0001
	$B = a + b_0 D^{b_1} + c_0 H^{c_1}$	125.1	5	<0.001	0.92	<0.0001
	$B = a + b_0 D^{b_1} + c_0 D^{c1} H^{c_2}$	179.2	6	<0.001	0.99	<0.0001
Stem	$B = b_0 D^{b_1} H^{b_2}$	73.6	3	0.85	0.98	<0.0001
	$B = b_0 D^{b_1}$	77.2	2	0.14	0.94	<0.0001
	$B = a + b_0 D^{b_1}$	84.2	3	0.004	0.95	<0.0001
	$B = a + b_0 D^{b_1} H^{b_2}$	84.5	4	0.004	0.99	<0.0001
	$B = a + b_0 D^{b_1} + c_0 H^{c_1}$	120.1	5	<0.001	0.95	<0.0001
	$B = a + b_0 D^{b_1} + c_0 D^{c1} H^{c_2}$	180.6	6	<0.001	0.99	<0.0001
Branch	$B = b_0 D^{b_1}$	55.5	2	0.76	0.35	0.055
	$B = b_0 D^{b_1} H^{b_2}$	57.9	3	0.22	0.62	0.007
	$B = a + b_0 D^{b_1}$	62.6	3	0.02	0.35	0.054
	$B = a + b_0 D^{b_1} H^{b_2}$	68.8	4	<0.001	0.66	0.005
	$B = a + b_0 D^{b_1} + c_0 H^{c_1}$	92.8	5	<0.001	0.61	0.008
	$B = a + b_0 D^{b_1} + c_0 D^{c1} H^{c_2}$	162.5	6	<0.001	0.74	0.002
Needle	$B = b_0 D^{b_1}$	40.4	2	0.75	0.35	0.055
	$B = b_0 D^{b_1} H^{b_2}$	42.8	3	0.23	0.63	0.007
	$B = a + b_0 D^{b_1}$	47.5	3	0.02	0.35	0.053
	$B = a + b_0 D^{b_1} H^{b_2}$	54.9	4	<0.001	0.62	0.007
	$B = a + b_0 D^{b_1} + c_0 H^{c_1}$	78.2	5	<0.001	0.59	0.009
	$B = a + b_0 D^{b_1} + c_0 D^{c1} H^{c_2}$	155.6	6	<0.001	0.35	0.054

Appendix 5

Comparison among available equations

		Larix sibirica (Snorrason)	*Larix sibirica* (Wang)	*Larix gmelinii* (Wang)	*Larix gmelinii* (Kajimoto)	*Larix decidua*	*Larix decidua* with height	*On-site equation*
Total biomass	Deviation	42%		39%	17%	41%		12%
	R^2	0.97		0.93	0.93	0.97		0.99
	Intercept	-6.22 ± 5.17 (*P*=0.268)		-0.73 ± 8.38 (*P*=0.933)	-28.50 ± 10.76 (*P*=0.033)	-8.68 ± 5.25 (*P*=0.142)		1.60 ± 3.59 (*P*=0.559)
	Slope	0.81 ± 0.05 (*P*=0.007)		0.74 ± 0.08 (*P*=0.014)	1.95 ± 0.20 (*P*=0.002)	0.85 ± 0.05 (*P*=0.026)		0.98 ± 0.05 (*P*=0.701)
Stem biomass	Deviation	23%	13%	56%	42%			9%
	R^2	0.98	0.98	0.95	0.95			0.99
	Intercept	-3.58 ± 3.64 (*P*=0.358)	-4.61 ± 3.98 (*P*=0.285)	-11.63 ± 6.89 (*P*=0.135)	-24.42 ± 7.81 (*P*=0.017)			0.91 ± 3.29 (*P*=0.791)
	Slope	0.91 ± 0.04 (*P*=0.082)	1.28 ± 0.07 (*P*=0.005)	0.86 ± 0.07 (*P*=0.088)	2.91 ± 0.25 (*P*=0.000)			0.99 ± 0.05 (*P*=0.847)
Branch biomass	Deviation		48%	45%	38%	43%	43%	44%
	R^2		0.87	0.93	0.91	0.87	0.91	0.67
	Intercept		-2.75 ± 1.40 (*P*=0.097)	2.23 ± 0.56 (*P*=0.007)	-2.05 ± 1.08 (*P*=0.106)	-13.06 ± 2.93 (*P*=0.004)	-14.57 ± 2.67 (*P*=0.002)	0.56 ± 1.45 (*P*=0.713)
	Slope		3.06 ± 0.48 (*P*=0.004)	0.67 ± 0.08 (*P*=0.004)	1.38 ± 0.18 (*P*=0.073)	7.29 ± 1.14 (*P*=0.001)	8.00 ± 1.05 (*P*=0.000)	0.92 ± 0.24 (*P*=0.749)
Needle biomass	Deviation			71%	39%	50%	49%	43%
	R^2			0.93	0.91	0.87	0.91	0.67
	Intercept			0.84 ± 0.25 (*P*=0.016)	-1.13 ± 0.50 (*P*=0.064)	-1.75 ± 0.69 (*P*=0.044)	-2.06 ± 0.61 (*P*=0.015	0.24 ± 0.62 (*P*=0.71)
	Slope			1.88 ± 0.21 (*P*=0.005)	2.51 ± 0.33 (*P*=0.003)	4.19 ± 0.66 (*P*=0.002)	4.65 ± 0.61 (*P*=0.001)	0.92 ± 0.24 (*P*=0.749)

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