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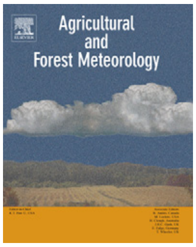

Environmental controls on photosynthetic production and ecosystem respiration in semi-arid grasslands of Mongolia

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ABSTRACT

The Mongolian steppe zone comprises a major part of East Asian grasslands. The objective of this study was to separately evaluate the quantitative dependencies of gross primary production (GPP) and ecosystem respiration (R_{eco}) on the environmental variables of temperature, moisture, radiation, and plant biomass in a semi-arid grassland ecosystem. We determined GPP and R_{eco} using transparent and opaque closed chambers in a grassland dominated by Poaceae species in central Mongolia during five periods: July 2004, May 2005, July 2005, September 2005, and June 2006. Values of GPP were linearly related to live aboveground biomass (AGB) enclosed by the chamber. The amount of GPP per unit ground area differed among the study periods, whereas GPP normalized by the amount of AGB did not differ significantly among the periods, suggesting that plant production per unit green biomass did not depend on the phenological stage. GPP/AGB fit well a rectangular hyperbolic light–response curve for all the study periods. When the air and soil were dry, considerable reduction in GPP was observed. The GPP/AGB ratio was also expressed as individual functions of air temperature, vapor pressure deficit, and volumetric soil water content. R_{eco} was exponentially related to the soil temperature and the relationship was modified by soil moisture. The amount of R_{eco} and its temperature sensitivity (Q_{10}) declined with decreasing soil moisture. Sharp increases of R_{eco} after rainfall events were observed. The values of R_{eco}, even including the rain-induced pulses, were expressed well as a bivariate function of soil temperature and soil moisture near the soil surface.

1. Introduction

In Mongolia, grassland covers approximately 80% of the country and comprises a major part of East Asian grasslands. The plants live in a semi-arid climate, and have often suffered from droughts. Global climate models predict that future increases in atmospheric carbon dioxide (CO_2) will cause significant drying in this region during summer, caused by increased temperature and potential evaporation (Intergovernmental Panel on Climate Change [IPCC], 2007). Studies have indicated that the grasslands respond sensitively to changes in climate, particularly to changes in precipitation (Kondoh and Kaihotsu, 2003; Ni, 2003; Miyazaki et al., 2004). However, few studies have been conducted to examine quantitative responses of vegetation to climate variability in semi-arid grasslands.

Exchange of CO_2 between terrestrial ecosystems and the atmosphere is controlled by the balance between CO_2 uptake during photosynthesis and CO_2 emission via plant and soil respiration. Photosynthetic uptake and respiratory release are

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separate processes, with different responses to environmental changes. Therefore, it is essential to investigate separately the dependence of plant photosynthesis and ecosystem respiration on environmental parameters.

Several recent studies examined the relationship between net ecosystem CO_2 exchange and environmental parameters in grasslands (e.g., Sims and Bradford, 2001; Suyker and Verma, 2001; Gu et al., 2003; Li et al., 2005; Fu et al., 2006). The majority of previous measurements were conducted using micrometeorological techniques, such as the Bowen ratio and eddy covariance methods. An advantage of these techniques is that they allow the collection of continuous, high-resolution data; however, fluxes measured using these techniques represent net values between photosynthesis and respiration, averaged over a widespread land surface. These recent studies constructed regression equations between nighttime eddy covariance and temperature, and they estimated daytime respiration rates by replacing nighttime temperature with daytime temperature in the regression equation. However, nighttime eddy covariance may underestimate ecosystem respiration, and there is uncertainty about the applicability of eddy covariance data for determining the carbon sink–source status of an ecosystem (Massman and Lee, 2002).

Another common approach to measuring CO_2 fluxes between the atmosphere and biosphere uses closed-chamber techniques (e.g., Dugas et al., 1997; Bubier et al., 1998; Angell et al., 2001; Arnone and Obrist, 2003; Patrick et al., 2007). These techniques usually result in noncontinuous data, and the environment in the chamber may be modified relative to ambient conditions (Hutchinson and Livingston, 1993). Despite these limitations, studies have reported good agreement between micrometeorological and chamber techniques (Held et al., 1990; Angell et al., 2001). In addition, chamber techniques are appropriate for measuring photosynthetic production and ecosystem respiration separately, because net CO_2 exchange and respiratory release can be measured using transparent and opaque chambers, respectively (Bubier et al., 1998). Furthermore, the closed-chamber method allows the amount of plant biomass that performs photosynthesis to be determined.

The objective of this study was to evaluate the quantitative dependence of photosynthetic production and ecosystem respiration on temperature, moisture, radiation, and plant biomass in a semi-arid grassland. Toward this aim, we measured CO_2 fluxes using a closed-chamber technique during the growing seasons of 2004–2006 in a grassland in central Mongolia.

2. Materials and methods

2.1. Site description

CO_2 flux measurements were conducted in a semi-arid grassland near Bayan-Unjuul village (lat. 47°02.6′N, long. 105°57.1′E, 1200 masl), located 130 km southwest of Ulaanbaatar, Mongolia. The climate at the site is typically continental and semi-arid, with low precipitation and large diurnal and annual temperature variations. Mean annual precipitation is 163.0 mm, concentrated on the summer months of May–August, and annual precipitation for 2004, 2005, and 2006 was 169.2, 96.9, and 94.4 mm, respectively. The climatological annual mean air temperature (1995–2005) is 0.1 °C. Soils are classified as Kastanozems with a calcic horizon from 15 to 110 cm below the surface. Soil texture is silty loam to sand. Bulk density within the surface horizon (0–5 cm) is approximately 1.5 g cm^{-3}. The plant community at the study site is dominated by graminaceous perennial grasses (*Agropyron cristatum*, *Cleistogenes squarrosa*, *Stipa krylovii*), forbs (*Artemisia adamsii*, *Chenopodium* spp.), and small shrubs (*Caragana* spp.). *Cleistogenes squarrosa* is a C_4 grass; the other dominant grasses are C_3 species. During our study, the plants started to grow in May, and live aboveground biomass (AGB) reached its yearly maximum in late August. Annual maximum values of AGB in the study area were 93.0, 87.1, and 44.9 g dry weight (dw) m^{-2} in 2004, 2005, and 2006, respectively (Shinoda et al., unpublished manuscript).

The study area has been enclosed by a fence (300 m × 300 m) since June 2004 to prevent livestock from grazing. While aiming to investigate the response of the CO_2 exchanges to extreme drought conditions, we conducted an experimental manipulation to exclude natural precipitation. A rainout shelter was placed at the southwestern part of the fenced study site from 23 May 2005 to 3 August 2005. The shelter was open-sided, 30 m wide × 30 m long, and was covered by a clear polyethylene film whose transmittance of short radiation was about 92%. We set up two sampling plots in the no-grazing area (NG plots) and the no-grazing and drought experiment area (D plots). Individual measurement points were randomly allocated within each plot, which included eight graminaceous grass-covered points (four in NG plots, four in D plots) and four bare-soil points (two in NG plots, two in D plots). Both C_3 and C_4 species grew at each grass-covered point.

2.2. CO_2 flux measurements

We measured CO_2 fluxes using a closed-chamber method during five periods: 20–25 July 2004, 7–12 May 2005, 27–31 July 2005, 18–22 September 2005, and 26–30 June 2006. Among these periods, the experimental exclusion of natural precipitation was conducted only in July 2005. Each closed chamber was a cube, 0.4 m on a side and open on the bottom. All sides of the chamber were clear and made of transparent acrylic plates. The chamber was equipped with a quantum sensor (LI-190SA, Li-Cor Inc., Lincoln, NE, USA) and a temperature and humidity sensor (model 1400-104, Li-Cor Inc.). The chamber was also equipped with a fan operated by a 12-V battery, which produced air velocities within the chamber ranging from 0.2 to 0.6 m s^{-1}.

Stainless-steel collars were embedded in the soil at the sampling points to depths of 5 cm on the first day of each study period and remained in the same locations throughout the period. To create an airtight seal during measurements, the chamber was fitted with a soft rubber strip in the groove of the collar. The chamber was connected to a LI-7000 CO_2/H_2O analyzer (Li-Cor Inc.) in a closed circuit. During 3 min the chamber was placed on the collar and the CO_2 concentration was recorded at 5-s intervals using a datalogger (LI-1400, Li-Cor Inc.). Inside the chamber, photosynthetically active