Spatial variability of photosynthetic production and ecosystem respiration on a hundred-kilometer scale within a Mongolian semiarid grassland

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Abstract

Grassland ecosystems cover a large area of the land surface and play an important role in the global carbon cycle. The objectives of this study were to examine the spatial variability of gross primary production (GPP) and ecosystem respiration (R_{eco}) within a semiarid grassland ecosystem and to evaluate the environmental factors that control the spatial patterns of carbon exchanges. We determined GPP and R_{eco} using transparent and opaque closed chambers at nine grassland sites in central Mongolia during the summers from 2009 through 2011. To remove effects of temporal changes in radiation and temperature, GPP and R_{eco} were fitted to light- and temperature-response curves. The fitting parameters (light-saturated GPP [P_{max}], apparent quantum yield [α], standardized R_{eco} at 20 °C [R_{20}], and the temperature sensitivity [Q_{10}] of R_{eco}) were compared among the sites. The GPP and R_{eco} parameters differed significantly among the sites. Spatial patterns of P_{max} and R_{20} were highly correlated with plant aboveground green biomass (AGB) and number of plant species. The Q_{10} of R_{eco} was significantly related to soil moisture. The light-saturated GPP normalized to the amount of AGB did not differ significantly among the sites, whereas the R_{20} residuals of the linear biomass model were correlated with soil water content and carbon/nitrogen ratios. The results suggest that, within this semiarid grassland, spatial variations of GPP are strongly controlled by AGB and that variations in R_{eco} are associated mainly with AGB and secondarily with soil water content and soil nutrient condition.

Key words: Ecosystem respiration, Gross primary production, Mongolia, Semiarid grassland, Spatial variability.

1. Introduction

The exchange of CO_2 between terrestrial ecosystems and the atmosphere is controlled by the balance between CO_2 uptake during photosynthesis and CO_2 emissions associated with plant and soil respiration. Physical and biological factors cause the spatial variability of these exchanges to be high. Several studies have used eddy covariance measurement networks to examine global and regional spatial variability of CO_2

exchanges. Kato and Tang (2008) compiled data collected from 49 flux towers in East Asia and assessed the spatial variability of ecosystem CO_2 exchange for a variety of ecosystem types, including tundra, wetlands, grasslands, and forests. Yuan *et al.* (2009) used the AmeriFlux and EuroFlux datasets to characterize spatial patterns, relative to latitude, of the variations of mean annual carbon budgets between sites. Yu *et al.* (2013) analyzed spatial variation and environmental drivers of the carbon fluxes in different terrestrial ecosystems in China. These studies have demonstrated that annual rates of gross primary production (GPP), ecosystem respiration (R_{eco}), and net ecosystem CO_2 exchange (NEE) are significantly correlated with mean annual temperature and annual precipitation.

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However, recent studies have reported that smaller-scale (from tens of meters to hundreds of kilometers) spatial variation of CO₂ fluxes is very large, even within ecosystems in which climate and vegetation are similar. Maestre and Cortina (2003) reported a large variability in soil respiration when comparing patches with different soil surface features and different plant cover in a Mediterranean semiarid steppe in Spain. Risch and Frank (2006) measured CO₂ fluxes at seven grassland sites in the northern winter range of Yellowstone National Park, USA, and found that there was a large amount of spatial variability in CO₂ fluxes related to aboveground biomass and shoot nitrogen content. Ngao *et al.* (2012) determined soil respiration in seven plots in a European beech forest and discovered that the spatial variability was explained by soil bulk density, carbon/nitrogen ratio, and leaf area index. Accurate estimates of regional and global carbon budgets therefore require knowledge of the amplitude and understanding of the underlying causes of small-scale spatial variation in atmosphere–ecosystem CO₂ exchanges.

In Mongolia, grasslands cover approximately 80 % of the country. Grasslands are characterized by large spatial heterogeneity in soil texture and moisture, carbon and nitrogen content, and plant composition and production (Risch and Frank, 2006). However, spatial variability of CO₂ fluxes within the Mongolian grassland ecosystem is still poorly understood. We have conducted CO₂ flux observations in a semiarid grassland of Mongolia since 2004 and have reported the

temporal changes in photosynthetic productivity and respiratory CO₂ release (Nakano *et al.*, 2008; Nakano and Shinoda, 2010). An important next step is examination of the spatial variability of CO₂ exchanges in this grassland ecosystem. The objective of this study was to assess the spatial variability of ecosystem CO₂ exchanges within a semiarid grassland in central Mongolia and to evaluate the dependence of plant photosynthesis and ecosystem respiration on the spatial variations of environmental parameters.

2. Materials and Methods

2.1 Site description

The measurements were conducted at nine sites in central Mongolia (46.3–47.5°N, 105.9–108.1°E; elevation ranges from ca. 1000 to 1500 m above sea level) in the summers of 2009, 2010, and 2011 (Fig. 1, Table 1). Sites BU-NG, BU-G1, and BU-G2 were located in Bayan Unjuul (BU) county and were within 1 km of each other. A 300 m × 300 m area has been enclosed by a fence since June 2004 to prevent livestock from grazing (Shinoda *et al.*, 2010). Site BU-NG was located inside that fence, and sites BU-G1 and BU-G2 were located outside the fence. Sites NB, SB1, and SB2 were located approximately 50 km north, 25 km south, and 40 km south of BU, respectively. Sites DT, BT, and BJ were located in grasslands near the villages of Delgertsogt (ca. 90 km south of BU), Bayantsagaan (ca. 100 km east of BU), and Bayanjargalan (ca. 170 km east of BU), respectively.

Fig. 1. Aridity indices and locations of the study sites in Mongolia.

Table 1. Locations and climate statistics of the measurement sites.

Site	2009 August			2010 August		
	BU-NG	BU-G1	SB1	NB	BU-G2	SB2
Sampling date	Aug. 15–16	Aug. 17–18	Aug. 19–20	Aug. 15–16	Aug. 17–18	Aug. 19–20
Latitude	47°02'4"N	47°02'39"N	46°50'01"N	47°27'02"N	47°02'33"N	46°42'09"N
Longitude	105°57'02"E	105°56'51"E	105°51'31"E	106°15'09"E	105°56'43"E	106°00'46"E
Elevation (m)	1200	1200	1296	1507	1200	1351
Aridity index [†]	0.24	0.24	0.23	0.34	0.24	0.24
Mean air temperature during the warmest quarter (°C) ^{††}	17.2	17.2	17.2	15.2	17.2	16.8
Precipitation during the warmest quarter (mm) ^{††}	139	139	141	172	139	140
Annual maximum NDVI ^{†††}	0.34	0.34	0.34	0.45	0.34	0.35

Site	2011 July-August		
	DT	BT	BJ
Sampling date	Jul. 30–31	Aug. 1–2	Aug. 3–4
Latitude	46°17'29"N	46°49'56"N	47°17'56"N
Longitude	106°16'20"E	107°12'19"E	108°07'55"E
Elevation (m)	1391	1363	1464
Aridity index [†]	0.22	0.27	0.36
Mean air temperature during the warmest quarter (°C) ^{††}	17.3	16.2	15.5
Precipitation during the warmest quarter (mm) ^{††}	129	157	200
Annual maximum NDVI ^{†††}	0.25	0.30	0.43

[†] Data were acquired from Global Aridity and PET database by CGIAR-CSI (see footnote 1).

^{††} Data were acquired from the WorldClim Global Climate Data (Hijmans *et al.*, 2005; see footnote 2).

^{†††} Data are average values for the period 2001–2010 (see footnote 3).

Fig. 2. Vegetation classification in Mongolia. Circles denote the study sites (same as Fig. 1).

The aridity index¹, which is calculated from mean annual precipitation and mean annual potential evapotranspiration (PET), is generally used for climate classification and is a measure of the deficit of precipitation compared to atmospheric water demand (UNEP, 1997). Figure 1 indicates that all of the nine sites were located in a “semi-arid” climate according to the aridity index. Climatic values of mean air temperature and precipitation during the warmest quarter (June–August)² are listed in Table 1. The temperature and precipitation ranged from 15.2 °C at NB to 17.3 °C at DT and from 129 mm at DT to 200 mm at BJ, respectively. Table 1 also shows the annual maximum normalized difference vegetation index (NDVI)³ averaged over the period 2001–2010. The data indicate that the NDVI was high at places where the precipitation was high, such as sites NB and BJ, and low where the precipitation was low.

The vegetation⁴ in the area is classified as “temper-

ate grassland” (Fig. 2) and is grazed by livestock. The plant community is dominated by graminaceous perennial grasses (*Agropyron cristatum*, *Cleistogenes squarrosa*, and *Stipa krylovii*), annual forbs (*Artemisia* spp. and *Chenopodium* spp.), and small shrubs (*Caragana* spp.). Soils at the study sites are classified as Kastanozems (IUSS Working Group WRB, 2006), a type of soil that is widely distributed in the Mongolian grasslands.

2.2 CO₂ flux measurements

We used a closed-chamber method to measure CO₂ fluxes. The 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, which transmit about 94 % of photosynthetically active radiation (*PAR*). For each site, three or four stainless-steel collars were inserted 5 cm into the soil before the measurements were started. They remained in place for the duration of the measurements to allow repeated measurements to be made at the same location. The chamber was fitted with a soft rubber strip in the groove of the collar to create an airtight seal during measurements. A closed circuit connected the chamber to a CO₂ analyzer (LI-7000, Li-Cor, Lincoln, NE, USA, in 2009; GMP343, Vaisala, Helsinki, Finland, in 2010 and 2011). The chamber was placed on the collar for 3 min, and the CO₂ concentration was recorded at 5-s intervals using a datalogger (Thermic 2300A, Eto Denki, Tokyo, Japan). Net ecosystem CO₂ exchange (*NEE*) was calculated from the rate of change of the chamber CO₂ concentration during the first 1 min of chamber closure. Positive and negative *NEE* values correspond to CO₂ emission and uptake, respectively,

¹ Data were downloaded from the Global Aridity and PET database by the Consultative Group on International Agricultural Research, Consortium for Spatial Information (CGIAR-CSI). URL: <http://www.cgiar-csi.org/data/global-aridity-and-pet-database>.

² Data were downloaded from the WorldClim Global Climate Data (Hijmans *et al.*, 2005). URL: <http://worldclim.org/>. The data are average values for the years 1950–2000.

³ NDVI was calculated from the MODIS land surface reflectance dataset (MOD09A1) downloaded from the Land Processes Distributed Active Archive Center (LP DAAC), U.S. Geological Survey. URL: <http://lpdaac.usgs.gov>. For details, refer to Nakano *et al.* (2013).

⁴ Data were downloaded from the Global Mapping Home Page of the International Steering Committee for Global Mapping (ISCGM). URL: <http://www.iscgm.org/>.

by the ecosystem. To measure daytime ecosystem respiration (R_{eco}), an aluminum shroud was placed over the chamber to eliminate all light immediately after measurements were taken in the light. Gross primary production was calculated by subtracting NEE from R_{eco} .

The CO₂ fluxes were measured for 2 days at each site. The measurements started at noon of the first day and continued for 24 h, every 2 h during the daytime and every 4 h during the nighttime, when there was no rainfall at the site.

2.3 Auxiliary measurements

Along with CO₂ flux measurements, measurements inside the chamber of photosynthetically active radiation (PAR_c), air temperature (T_c), and relative humidity (RH_c) were simultaneously measured by a quantum sensor (LI-190SL, Li-Cor) and a temperature-and-humidity sensor (2119A, Eto Denki), respectively.

The soil temperature (T_s) and soil volumetric water content (VWC) at a depth of 5 cm were measured at each site by soil-moisture-and-temperature sensors (5TM, Decagon Devices Inc., Pullman, WA, USA) and recorded at 5-min intervals by dataloggers (Em50, Decagon Devices).

Plant species composition within each collar was recorded. The number of plant species that covered more than 1 % of each area enclosed by collars was counted. Live aboveground green biomass (AGB) was measured by clipping green parts of the vegetation in each collar at the end of each observation period. Clipped plant samples were oven dried at 80 °C for 48 h and then weighed.

Soil samples were collected at each site after CO₂ flux measurements and were air dried and sieved to 2 mm and 0.5 mm for chemical analyses. Soil organic carbon (SOC) content was measured with the Tyurin titrimetric method by digestion with a mixture of K₂Cr₂O₇ and H₂SO₄ (Committee of Soil Standard Methods for Analyses and Measurements, 1986). Total nitrogen (TN) content was determined by dry combustion with an elemental analyzer (FLASH2000, Thermo Fisher Scientific Inc., Waltham, MA, USA). Particle size distribution was determined by the pipette method after oxidation of organic matter with H₂O₂ and elimination of carbonates with HCl (Committee of Soil Environment Analysis, 1997).

2.4 Data analysis

To remove the effects of temporal changes in radiation and temperature, GPP and R_{eco} were fitted to light- and temperature-response curves. The relationship between GPP and PAR was described by a rectangular hyperbola light-response function forced through zero (Michaelis and Menten, 1913):

$$GPP = \frac{P_{\text{max}} \alpha Q_p}{\alpha Q_p + P_{\text{max}}}, \quad (1)$$

where Q_p is incident PAR , P_{max} is maximum GPP at infinite light, and α is the initial slope of the light-response curve (also called the apparent quantum yield). Ecosystem respiration data from each set of measurements were fitted to the following equation (van't Hoff-type model):

$$R_{\text{eco}} = R_{20} Q_{10}^{(T_s - T_{\text{ref}})/10}, \quad (2)$$

where R_{20} is the standardized rate of respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$) at the reference temperature ($= 20$ °C), Q_{10} is the factor by which respiration rate increases for a 10 °C increment of temperature (dimensionless), T_s is soil temperature (°C) at a depth of 5 cm, and T_{ref} is the reference temperature of 20 °C. In our measurements, the soil temperature varied from approximately 10 °C to 30 °C, indicating that 20 °C was the center of the temperature range. To compare sites, the P_{max} , α , R_{20} , and Q_{10} values were calculated for each collar and averaged for each site.

We used the coefficient of variation (CV) of each variable to characterize the magnitude of its spatial variation. The CV is given by

$$CV = \frac{\sigma}{\bar{x}} 100, \quad (3)$$

where σ and $\bar{x}$ are the standard deviation and mean, respectively, of the variable.

The relationships between environmental parameters and GPP and R_{eco} values were analyzed using nonparametric correlations and linear and nonlinear regressions. Relationships were judged to be significant if the type I error rate was 5 % or less. All statistical and regression analyses were performed with ORIGINPRO 8.1 (OriginLab, Northampton, MA, USA).

3. Results

3.1 Parameters that characterize GPP and R_{eco} and environmental properties

Table 2. Soil and plant properties at the measurement sites.

Site	BU-NG	BU-G1	SB1	NB	BU-G2	SB2	DT	BT	BJ
Soil texture									
Sand (%)	85.4	93.1	69.5	54.8	87.5	83.1	70.5	75.9	76.8
Silt (%)	9.1	2.6	14.8	24.8	5.8	8.7	11.2	11.3	11.6
Clay (%)	5.5	4.3	15.7	20.4	6.8	8.3	18.3	12.9	11.7
SOC (g kg ⁻¹)	8.84	7.10	11.88	23.25	6.67	7.69	7.91	8.13	13.19
TN (g kg ⁻¹)	0.95	0.85	1.10	2.32	0.75	0.86	0.98	0.98	1.31
C/N ratio	9.30	8.35	10.80	10.04	8.89	8.93	8.04	8.30	10.08
VWC (m ³ m ⁻³)	0.055	0.184	0.162	0.205	0.140	0.067	0.079	0.045	0.117
AGB [†] (g dw m ⁻²)	59.7	78.4	55.5	105.2	94.4	49.5	78.1	119.9	182.5
PSN [†]	2.50	2.75	2.25	4.25	3.00	2.25	1.67	2.67	4.33
Plant species composition ^{††}	a, f, g, l	a, f, g, h, k	a, e, f	a, e, f, h, i, j, l	a, d, f, g, h, k	a, b, g, h, l	c, f, h	c, d, f, h, l	a, f, g, h, j

SOC, soil organic carbon; TN, total nitrogen; C/N, carbon-nitrogen ratio; VWC, soil volumetric water content; AGB, aboveground green biomass; PSN, plant species number.

[†] AGB and PSN are the average values of the three or four collars for each site.

^{††} a, *Artemisia* spp.; b, *Agropyron cristatum*; c, *Allium tenuissimum*; d, *Caragana* spp.; e, *Carex* spp.; f, *Chenopodium* spp.; g, *Cleistogenes squarrosa*; h, *Elymus chinensis*; i, *Heteropappus hispidus*; j, *Potentilla acaulis*; k, *Salsola ruthenica*; l, *Stipa krylovii*.

The average values of the parameters that characterize GPP and R_{eco} (P_{max} , α , R_{20} , and Q_{10}) for each site are shown in Figure 3. The values of P_{max} and α varied from 8.6 to 29.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ ($CV = 46.9\%$) and from 0.014 to 0.046 $\mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{photons}$ ($CV = 46.3\%$), respectively. The R_{20} and Q_{10} values varied from 1.7 to 6.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ ($CV = 44.3\%$) and from 1.5 to 2.5 ($CV = 18.0\%$), respectively. All the parameters differed significantly among the sites (one-way ANOVA, $p < 0.001$ for P_{max} , R_{20} , and Q_{10} ; $p = 0.007$ for α). The fact that P_{max} and R_{20} values were strongly correlated with each other (Spearman's rank correlation coefficient, $r_s = 0.92$; Table 3) suggests that spatial patterns of ecosystem CO_2 uptake and respiratory release were quite similar.

The soil and plant parameters measured at the nine sites are summarized in Table 2. Whereas the sand fraction was high at all the sites, site NB was characterized by higher silt and clay fractions than the other sites. The fact that the levels of SOC and TN were positively correlated with the fractions of silt and clay (Table 3) resulted in higher SOC and TN values at site NB than at the other sites. The values of VWC and AGB differed greatly between the sites. In general, vegetation activity is strongly correlated with soil moisture in Mongolia (Iwasaki, 2006; Nandintsetseg et

al., 2010), but we found no significant correlation between VWC and AGB (Table 3). Long-term averages of summer precipitation (Table 1) were linearly correlated with AGB values (Pearson's correlation coefficient, $r = 0.87$), but there was no relationship between VWC values and summer precipitation. Because the measurements were conducted in a short time span (24 h at each site), our VWC data should reflect short-term temporal variations rather than long-term spatial characteristics.

3.2 Factors controlling the spatial variation of CO_2 exchanges

Rank correlation coefficients (r_s) among the GPP and R_{eco} parameters and the plant and soil properties that we used to characterize the spatial differences between the environments of the sites are listed in Table 3. Strong relationships were found between P_{max} and R_{20} and AGB and plant species number (PSN), indicating that the greater rates of CO_2 uptake and release were caused by enhanced plant growth and productivity. Apparent quantum yield (α) was also significantly related to AGB . In contrast, Q_{10} showed a significant relationship only with soil VWC .

Both P_{max} and R_{20} were well described as linear functions of AGB (Fig. 4). To separate the combined effects of AGB and other factors, we calculated P_{max}

Fig. 3. Site-averaged values of (a) PAR-saturated GPP ($P_{\max}$), (b) apparent quantum yield of GPP (α), (c) standardized rates of R_{eco} at 20 °C (R_{20}), and (d) temperature sensitivity of R_{eco} (Q_{10}). Bars indicate standard deviations.

normalized by the amount of AGB ($P_{\max}/\text{AGB}$ [$\mu\text{mol g dw}^{-1} \text{s}^{-1}$]) and the R_{20} residuals, which are the differences between the measured values and the values estimated by the linear model in Figure 4b. The R_{20} residuals differed significantly among the sites ($p = 0.002$), whereas the $P_{\max}/\text{AGB}$ ratio did not differ ($p = 0.58$) (Fig. 5). The relationships between $P_{\max}/\text{AGB}$ ratios and R_{20} residuals and soil properties are shown in Figure 6. The R_{20} residuals were significantly related to VWC ($r_s = 0.83$; $p = 0.005$) and C/N ratios ($r_s = 0.73$; $p = 0.025$), whereas $P_{\max}/\text{AGB}$ ratios were not significantly related to any soil parameters.

4. Discussion

In the present study, GPP and R_{eco} varied greatly ($CV = 46.9$ % for $P_{\max}$; $CV = 44.3$ % for R_{20}) among the nine Mongolian semiarid grassland sites, although all of the sites are located in the same climate (semiarid) and the same vegetation (temperate grassland) zone (Figs. 1 and 2). A few studies have reported within-grassland spatial variation in the rates of GPP and

R_{eco} and have demonstrated that both fluxes vary markedly among sites. Risch and Frank (2006) measured CO₂ fluxes at seven grassland sites in the northern winter range (100,000 ha) of Yellowstone National Park, USA. They indicated that the greatest fluxes among the sites were four to five times the lowest fluxes. The CV values that we calculated from their data were 50.2 % for GPP and 49.9 % for R_{eco} . Petrone *et al.* (2008) measured NEE , GPP, and R_{eco} at three grass-dominated sites within a small catchment (500 m $\times$ 500 m) in Ontario, Canada, and reported CV values for GPP and R_{eco} of 18 % and 20 %, respectively. Hirota *et al.* (2010) also measured NEE , GPP, and R_{eco} at 14 points in a small area (30 m $\times$ 40 m) in an alpine meadow on the Qinghai-Tibetan Plateau, China, and determined $P_{\max}$, α , R_{20} , and Q_{10} . They reported that CV values for $P_{\max}$ and R_{20} were 29.4 % and 27.3 %, respectively. Thus, because the spatial variability of GPP and R_{eco} are large, even within a grassland, it is essential to take their variability into account when estimating regional carbon budgets.

Our results demonstrated that spatial variations in *AGB* and *PSN* were the best predictors of the variability of photosynthetic uptake and respiratory release of CO_2 (Table 3). Other studies have reported similar spatial relationships between *GPP* and *AGB* (Risch and Frank, 2006; Petrone *et al.*, 2008), between P_{max} and *PSN* (Hirota *et al.*, 2010), and between R_{eco} and *AGB* (Risch and Frank, 2006; Petrone *et al.*, 2008). As for temporal variability, many studies have shown a strong relationship between *GPP* and the amount of growing plant tissue, represented by indices such as the leaf area index (*LAI*) or *AGB* (Frank and Dugas, 2001; Flanagan *et al.*, 2002; Byrne *et al.*, 2005; Aires *et al.*, 2008; Nakano *et al.*, 2008). Our results showed that *AGB* was related to not only *GPP*, but also R_{eco} . Several recent studies have indicated that plant productivity associated with either *AGB* or *LAI* is the dominant control on the magnitude of ecosystem and soil respiration in grasslands (Craine *et al.*, 1999; Xu and Baldocchi, 2004; Bahn *et al.*, 2008; Zhang *et al.*, 2009; Nakano and Shinoda, 2010). This relationship reflects the fact that photosynthetic productivity has a strong influence on the activity of roots and associated organisms (Moyano *et al.*, 2008) and the belowground supply of labile carbon (Sampson *et al.*, 2007). Hirota *et al.* (2010) reported that *PSN* correlated positively with *GPP*, but not with R_{eco} and explained that the relationship might be attributable to interspecies differences in photosynthetic light use efficiencies of leaves. In the present study, we found a significant correlation between *PSN* and both *GPP* and R_{eco} , and between *PSN* and *AGB* (Table 3). The relationship between *PSN* and the CO_2 exchanges could therefore be apparent, a result of the dependency of the number of species on *AGB*. To understand the effect of the number of species on CO_2 exchanges, further investigations will be

Table 3. Spearman's rank correlation coefficients (r_s) among parameters of gross primary production and ecosystem respiration and plant and soil properties. Only significant values ($p < 0.05$) are listed.

	P_{max}	α	R_{20}	Q_{10}	<i>AGB</i>	<i>PSN</i>	<i>VWC</i>	<i>SOC</i>	<i>TN</i>	<i>C/N</i>	<i>Sand</i>	<i>Silt</i>	<i>Clay</i>
P_{max}	1.0	0.75*	0.92**	ns	0.80**	0.80**	ns	ns	ns	ns	ns	ns	ns
α		1.0	0.87**	ns	0.92**	ns	ns	ns	ns	ns	ns	ns	ns
R_{20}			1.0	ns	0.87**	0.87**	ns	ns	ns	ns	ns	ns	ns
Q_{10}				1.0	ns	ns	0.77*	ns	ns	ns	ns	ns	ns
<i>AGB</i>					1.0	0.71*	ns	ns	ns	ns	ns	ns	ns
<i>PSN</i>						1.0	ns	ns	ns	ns	ns	ns	ns
<i>VWC</i>							1.0	ns	ns	ns	ns	ns	ns
<i>SOC</i>								1.0	0.93**	0.67*	-0.73*	0.92**	0.67*
<i>TN</i>									1.0	ns	-0.87**	0.95**	0.80**
<i>C/N</i>										1.0	ns	ns	ns
<i>Sand</i>											1.0	-0.91**	-0.96**
<i>Silt</i>												1.0	0.83**
<i>Clay</i>													1.0

P_{max} , PAR-saturated *GPP*; α , apparent quantum yield of *GPP*; R_{20} , standardized ecosystem respiration at 20°C; Q_{10} , temperature sensitivity of R_{eco} ; *AGB*, aboveground green biomass; *PSN*, plant species number; *VWC*, soil volumetric water content; *SOC*, soil organic carbon; *TN*, total nitrogen; *C/N*, carbon-nitrogen ratio; *, $P < 0.05$; **, $P < 0.01$; ns, not significant.

Fig. 4. The relationships between aboveground green biomass (AGB) and (a) PAR -saturated GPP (P_{max}), and (b) standardized rates of R_{eco} at $20\text{ }^{\circ}C$ (R_{20}).

needed.

The temperature sensitivity of R_{eco} (Q_{10}) was positively correlated with soil VWC in this study. This result is in agreement with several recent studies suggesting that Q_{10} declines with decreasing water availability (Reichstein *et al.*, 2002; Flanagan and Johnson, 2005; Aires *et al.*, 2008; Li *et al.*, 2008).

After removing the contribution of AGB to the spatial variability of GPP and R_{eco} , we examined the relationship between soil characteristics and P_{max}/AGB ratios and R_{20} residuals (Fig. 6). Our analysis indicated that there were significant positive correlations between R_{20} residuals and VWC and C/N ratios, although P_{max}/AGB ratios were unrelated to any soil parameters. Several studies have indicated that soil water is an important variable that controls the rate of ecosystem respiration in grasslands (Hunt *et al.*, 2002; Byrne *et al.*, 2005; Flanagan and Johnson, 2005; Kjelgaard *et al.*, 2008). Some studies have shown a positive linear or exponential relationship between standardized R_{eco} at a reference temperature and soil mois-

Fig. 5. Site-averaged values of (a) PAR -saturated GPP normalized to aboveground green biomass (P_{max}/AGB), and (b) R_{20} residuals of the linear biomass model. Bars indicate standard deviations.

ture (Hunt *et al.*, 2002; Flanagan and Johnson, 2005; Kjelgaard *et al.*, 2008; Jia *et al.*, 2012), and others have found that there is an optimum soil moisture content at which the rate of ecosystem and soil respiration peaks (Byrne *et al.*, 2005; Wen *et al.*, 2006; Jassal *et al.*, 2008).

Although very few studies have assessed the effect of soil nutrient levels on ecosystem respiration, there have been many studies of soil nutrient level effects on soil respiration (R_s). These studies have reported a positive relationship between R_s and soil organic carbon content (Tufekcioglu *et al.*, 2001; Bahn *et al.*, 2008), a positive relationship between R_s and nitrogen content (Petrone *et al.*, 2008), a negative relationship between R_s and the C/N ratio (Khomik *et al.*, 2006; Petrone *et al.*, 2008; Qi *et al.*, 2010), and a positive relationship between R_s and the C/N ratio (Ngao *et al.*, 2012). Peng *et al.* (2010) and Jia *et al.* (2012) carried out nitrogen-fertilization experiments in a temperate grassland and in a semiarid grassland of China, respectively. They found that nitrogen addition significantly

Fig. 6. The relationships between PAR -saturated GPP normalized to aboveground green biomass ($P_{\max}/AGB$) and (a) volumetric water content (VWC), (b) soil organic carbon content (SOC), (c) total nitrogen content (TN), (d) carbon/nitrogen (C/N) ratio, and (e) clay content, and between R_{20} residuals of the linear biomass model and (f) VWC , (g) SOC , (h) TN , (i) C/N ratio, and (j) clay content. r_s , Spearman's rank correlation coefficient; ns, not significant.

increased soil CO_2 emissions compared with a control plot. Studies conducted with forest soils have indicated that soil microorganisms prefer substrates that are high in nitrogen (or have a low C/N ratio). Thus, in areas where the litter C/N ratio is low, one would expect higher R_s as a result of increased decomposition activity (Khomik *et al.*, 2006; Vesterdal *et al.*, 2008). Contrary to those findings, we found a positive relationship between R_{20} residuals and C/N ratios in our study. Ngao *et al.* (2012) also showed a positive correlation between R_s values and C/N ratios in a temperate beech forest in France. They mentioned that the positive relationship they observed probably reflected better carbon consumption efficiency with increasing C/N ratios under nonlimiting nitrogen conditions. Although the exact reason for the positive relationship in our study is difficult to explain, it might imply that soil carbon content is more of a limiting factor than nitrogen content in semiarid grasslands.

5. Conclusion

The present study revealed large spatial variability of CO_2 fluxes within semiarid Mongolian grassland ecosystems, despite similarities of climate and vegeta-

tion. Spatial variations in plant photosynthetic production were closely associated with variations in vegetation properties such as plant aboveground green biomass and numbers of species. Spatial patterns of ecosystem respiration were primarily related to vegetation properties and secondarily to soil water content and C/N ratios. Thus, our study suggests that understanding the spatial heterogeneity of ecosystem CO_2 exchanges will be important if estimates of carbon budgets are to be improved at regional scales.

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