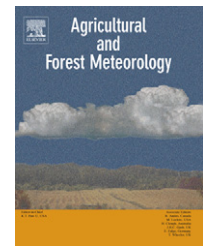


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Environmental controls on photosynthetic production and ecosystem respiration in semi-arid grasslands of Mongolia

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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.

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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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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

CO₂ 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 C₄ grass; the other dominant grasses are C₃ 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 CO₂ 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 C₃ and C₄ species grew at each grass-covered point.

2.2. CO₂ flux measurements

We measured CO₂ 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 CO₂/H₂O analyzer (Li-Cor Inc.) in a closed circuit. During 3 min the chamber was placed on the collar and the CO₂ concentration was recorded at 5-s intervals using a datalogger (LI-1400, Li-Cor Inc.). Inside the chamber, photosynthetically active

radiation (PAR_c), relative humidity (RH_c), and temperature (T_c) were simultaneously recorded by the datalogger. Vapor pressure deficit inside the chamber (VPD_c) was calculated from T_c and RH_c . Flux estimates were based on changes in chamber CO_2 concentration over time for the first 1 min of the chamber closure. To examine relationships between the CO_2 fluxes and the environmental parameters, mean values of PAR_c , T_c , and VPD_c were calculated for the same 1 min as the flux estimation. The 1-min-averaged T_c was 1.5–2.5 °C higher and 1–1.5 °C lower than the ambient temperature during the day and at nighttime, respectively. VPD_c was up to 10% lower than the ambient one by day, and was similar to the ambient at night. PAR_c was approximately 6% lower than the ambient one. To measure daytime ecosystem respiration (autotrophic plus heterotrophic), an aluminum shroud was placed over the chamber to eliminate all light immediately after measurements were taken in the light.

CO_2 fluxes were measured four times per day for each of the collars: night (02:00–04:00 local time [LT]), morning (07:00–10:00 LT), afternoon (14:00–16:00 LT), and evening (19:00–22:00 LT). In the study area, the sun culminates around 14:00 LT. The sunrise and sunset times are around 08:00 and 20:00 LT, respectively, in the spring and autumn equinoxes. They are around 06:00 and 22:00 LT, respectively, in the summer solstice.

2.3. Environmental parameters

Along with flux measurements, standard meteorological and soil parameters were measured continuously using automated weather and ground observing systems (AWS and AGS). The AWS was placed at the NG plots. The T_a and RH_a were measured at a height of 1.5 m using a shielded sensor (model HMP45A, Vaisala, Helsinki, Finland). Precipitation was collected using a tipping-bucket rain gauge (model 52203, Young Co., Traverse City, MI, USA). PAR_a was measured using a quantum sensor (LI-190SB, Li-Cor Inc.), and VPD_a was calculated from T_a and RH_a . The AGS was installed at both the NG and D plots. The soil temperature profile was measured at intervals of 5 cm between the surface and 95-cm depth using a temperature profile sensor (CHF-GP1, Climatec, Tokyo, Japan). For this study, we used only the soil temperature at a depth of 5 cm (T_s). Soil volumetric water content (VWC) at 10-cm depth was measured by time-domain reflectometry (TDR) probes (TRIME-EZ, IMKO Micromodultechnik GmbH, Ettlingen, Germany). All data were sampled every 1 s by dataloggers (CR10X and CR23X, Campbell Scientific Inc., Logan, UT, USA), and 30-min mean values were stored. In addition to the AGS, VWC at a 3-cm depth was manually measured by TDR probes (HydroSense, Campbell Scientific Inc.) concurrently with the CO_2 flux measurements in July 2004, May 2005, and July 2005. From July 2005 onward, VWC at a 3-cm depth was automatically measured at the NG and D plots by dielectric sensors (EC-10 in 2005 and EC-5 in 2006, Decagon Devices Inc., Pullman, WA, USA) and recorded at 5-min intervals by dataloggers (Em5, Decagon Devices Inc.).

Plant species composition within each collar was recorded. Live 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.

2.4. Data analysis

Net ecosystem CO_2 exchange (NEE) and ecosystem respiration (R_{eco}) were determined using the transparent (light) and opaque (dark) chambers, respectively. Because light and dark measurements were made within a few minutes of each other, the difference between NEE and R_{eco} was considered to represent gross primary production (GPP) at that light level for the vegetation within the chamber. Photorespiration, a metabolic process (O_2 consumption and CO_2 release) that is coupled with photosynthesis, takes place in the light in C_3 plant tissues (Larcher, 2003). Thus, gross photosynthesis should be distinguished from net photosynthesis (gross photosynthesis minus photorespiration). In this study, however, we considered net photosynthesis as GPP because photorespiration was difficult to measure separately from photosynthesis and did not occur in the dark.

The relationship between GPP and PAR was described by a rectangular hyperbola light–response function forced through zero (Michaelis and Menten, 1913):

$$GPP = \frac{F_{max}\alpha Q_p}{\alpha Q_p + F_{max}} \quad (1)$$

where Q_p is incident PAR, F_{max} is maximum GPP at infinite light, and α is the initial slope of the light–response curve (also called the apparent quantum yield).

Univariate and bivariate models were used to examine the relationship between R_{eco} and soil temperature and, optionally soil moisture (Xu and Qi, 2001a):

$$R_{eco} = \beta_0 e^{\beta_1 T} \quad (2)$$

and

$$R_{eco} = \beta_0 e^{\beta_1 T} W^{\beta_2}, \quad (3)$$

where T is soil temperature (°C) at 5 cm depth, W is volumetric soil water content (%) at 3 cm, and β_0 , β_1 , and β_2 are constants fitted with the least-squares technique. The Q_{10} value, the multiplier of the respiration rate for a temperature increase of 10 °C, was calculated as

$$Q_{10} = e^{10\beta_1}, \quad (4)$$

where β_1 is taken from Eq. (2).

3. Results and discussion

3.1. Micrometeorological conditions and aboveground plant biomass

Statistics for weather and soil conditions are summarized in Tables 1 and 2, respectively. Average air temperature (T_a) for the observation periods varied from 5.1 °C in September 2005 to 22.5 °C in July 2004. The maximum temperature reached 37.5 °C in July 2004 and the minimum temperature was –6.9 °C in September 2005. The period-average values of daily total PAR_a were more than 47 mol m^{–2} in July 2004, May 2005, and

Table 1 – Meteorological conditions for each observation period

		July 2004	May 2005	July 2005	Sep. 2005	June 2006
Air temperature (°C)	Mean	22.5	8.7	17.8	5.1	21.0
	Max	37.5	18.8	28.1	17.9	31.5
	Min	10.0	−5.3	11.2	−6.9	12.8
Daily photosynthetic active radiation (mol m ^{−2})	Mean	47.7	47.6	34.0	32.3	48.8
	Max	57.9	55.2	61.0	41.0	62.1
	Min	30.0	20.8	14.6	19.0	20.9
Vapor pressure deficit (kPa)	Mean	1.8	0.9	0.7	0.4	1.3
	Max	5.6	1.8	3.1	1.6	3.6
	Min	0.1	0.2	0.1	0.0	0.1
Precipitation (mm)	Total ^a	8.4	0.1	21.6	1.6	9.1
	Max ^b	6.5	0.1	17.2	1.5	4.6

Statistics were calculated from the data recorded at the site at 30-min intervals by an automated weather station.

^a Total precipitation over the whole-5 day observation period (mm 5-day^{−1}).

^b Maximum daily precipitation during the period (mm day^{−1}).

June 2006. In contrast, the site had high precipitation in July 2005 (maximum daily precipitation: 17.2 mm), resulting in low PAR_a during this period (mean PAR_a: 34.0 mol m^{−2}). Both the air and soil were very dry in the summer at the study site. The maximum VPD_a was over 3 kPa in July 2004, July 2005, and June 2006, with the value reaching 5.6 kPa in July 2004. The VWC at depths of 3 and 10 cm was mostly less than 0.1 m³ m^{−3}. In particular, the minimum VWC at 3-cm depth was less than 0.03 m³ m^{−3} in July 2005 (even in NG plots) and June 2006, suggesting that plants may have experienced water stress during those periods.

Temporal variations in precipitation and VWC from May to September 2005 are shown in Fig. 1. Natural rain of 60.3 mm was excluded at the D plots due to the rainout shelter being in place during June and July. VWC at depths of 3 and 10 cm at the D plots decreased to 0.019 and 0.042 m³ m^{−3}, respectively, at the end of the experiment. VWC at 3-cm depth was generally lower than that at 10-cm depth and showed a quick response

to precipitation: VWC increased immediately after every rain event and decreased exponentially to less than 0.03 m³ m^{−3} in a couple of days. In contrast, VWC at 10-cm depth increased slowly and only after a strong rain (>5 mm d^{−1}), and the higher VWC tended to be maintained longer.

The statistics of AGB within each collar are also listed in Table 2. The maximum mean AGB was 79.4 g dw m^{−2}, which was measured at the D plots in July 2004, and the minimum was 7.0 g dw m^{−2}, which was at the D plots in September 2005. The AGB differed significantly between NG and D plots (two-sample t-test, *p* < 0.05) in July 2005 (during the rainout shelter experiment) and September 2005 (after the experiment), whereas AGB showed no significant difference between the plots for the other periods. The amount of AGB was markedly low in June 2006, despite it being the middle of the growing season, because precipitation in May and June 2006 was extremely low (5.0 and 6.9 mm, respectively), and plants were subjected to water stress.

Table 2 – Soil conditions and plant above ground biomass for plots NG and D for each observation period

		July 2004		May 2005		July 2005		Sep. 2005		June 2006	
		NG	D	NG	D	NG	D	NG	D	NG	D
T _s at 5-cm deep (°C)	Mean	26.9	26.2	ND	12.3	21.5	26.0 ^a	9.2	10.6	24.3	21.3
	Max	35.9	35.3	ND	22.5	35.0	36.7 ^a	18.6	18.9	34.1	31.0
	Min	16.3	15.4	ND	3.8	15.6	20.3 ^a	1.8	2.8	16.9	12.9
VWC at 10-cm deep (10 ^{−2} m ³ m ^{−3})	Mean	7.1	9.7	ND	9.3	7.5	4.2 ^a	4.9	5.2	4.7	4.5
	Max	8.0	10.7	ND	9.8	11.7	4.4 ^a	5.2	5.3	5.1	4.6
	Min	6.7	8.5	ND	9.0	4.7	4.1 ^a	4.7	5.1	4.5	4.4
VWC at 3-cm deep (10 ^{−2} m ³ m ^{−3})	Mean	5.7 ^b	5.8 ^b	3.7 ^b	3.9 ^b	5.0	1.9 ^a	4.0	4.0	4.6	4.3
	Max	6.3 ^b	6.5 ^b	3.9 ^b	4.0 ^b	14.2	2.0 ^a	5.0	4.5	6.2	6.9
	Min	5.5 ^b	5.3 ^b	3.6 ^b	3.7 ^b	2.6	1.7 ^a	3.1	3.6	2.8	2.3
Aboveground biomass (g dry weight m ^{−2})	Mean	68.3	79.4	17.7	20.3	54.4	18.4 ^a	14.2	7.0	16.3	17.0
	Max	73.8	85.6	19.4	24.3	66.9	21.0 ^a	22.0	9.1	25.0	12.0
	Min	53.8	70.0	16.7	17.0	32.5	14.7 ^a	9.5	4.8	10.3	21.1

Mean, maximum and minimum values of soil temperature and moisture were calculated for the temporal variations and those of above ground biomass were calculated for the spatial variations. ND means “not determined”.

^a Measured under the rainout shelter.

^b Statistics from discontinuous data measured manually along with the CO₂ flux measurements.

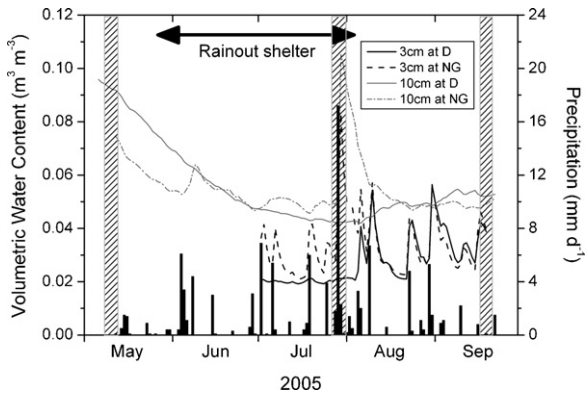


Fig. 1 – Time courses of volumetric soil water content (daily mean values; lines) and daily precipitation (bars) from May to September 2005. Shaded portions represent the periods when the CO₂ flux measurements were conducted.

3.2. Relationships between CO₂ exchanges and plant biomass

The magnitude of CO₂ flux is often related to the amount of growing plant tissue, represented by indices such as leaf area index (LAI) or AGB (Frank and Dugas, 2001; Sims and Bradford, 2001; Flanagan et al., 2002; Flanagan and Johnson, 2005). We determined the AGB for each collar during each observation period, and the relationships between GPP and AGB and between R_{eco} and AGB are plotted in Fig. 2a and b, respectively. The maximum values of GPP and the mean values of R_{eco} in each collar and each period were used. GPP was strongly related to the amount of AGB, and the coefficient of determination (r²) for the linear regression was 0.94 (Fig. 2a). Such a linear relationship between GPP and LAI was also reported in other grassland studies (Flanagan et al., 2002; Kato et al., 2004a; Xu and Baldocchi, 2004; Li et al., 2005). However, we found no significant relationship between R_{eco} and AGB, in contrast to some studies in which LAI or plant biomass was used as an index of R_{eco} (Suyker and Verma, 2001; Flanagan and Johnson, 2005). This difference in our findings is probably because the vegetation in our study site is very sparse and R_{eco} was regulated not by plant

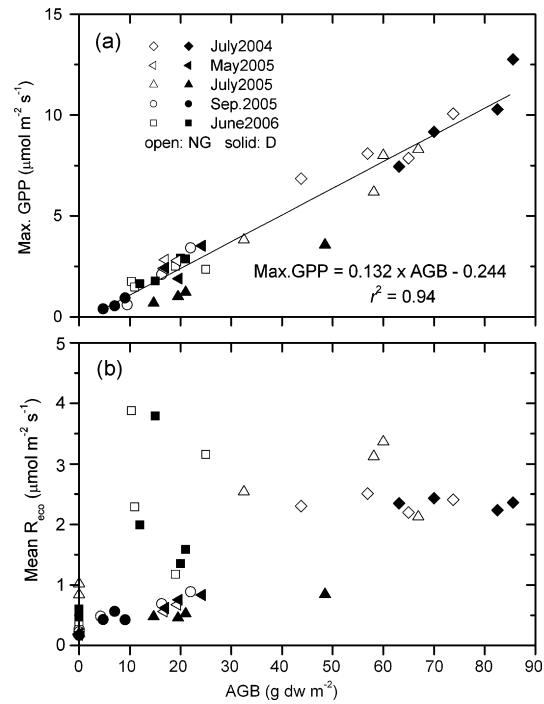


Fig. 2 – Relationships between aboveground live biomass (AGB) and (a) gross primary production (GPP) and (b) ecosystem respiration (R_{eco}). Individual data points represent the maximum values of GPP or the mean values of R_{eco} for each collar during each observation period.

respiration but by microbial decomposition of soil organic matter, which is not directly related to the amount of AGB.

3.3. Light-response curves

Because photosynthesis is primarily dependent on the availability of radiation, we first discuss the relationship between GPP and PAR inside the chamber (PAR_c). GPP per unit ground area was plotted against PAR_c for each study period (Fig. 3, top) and was fitted to a rectangular hyperbolic

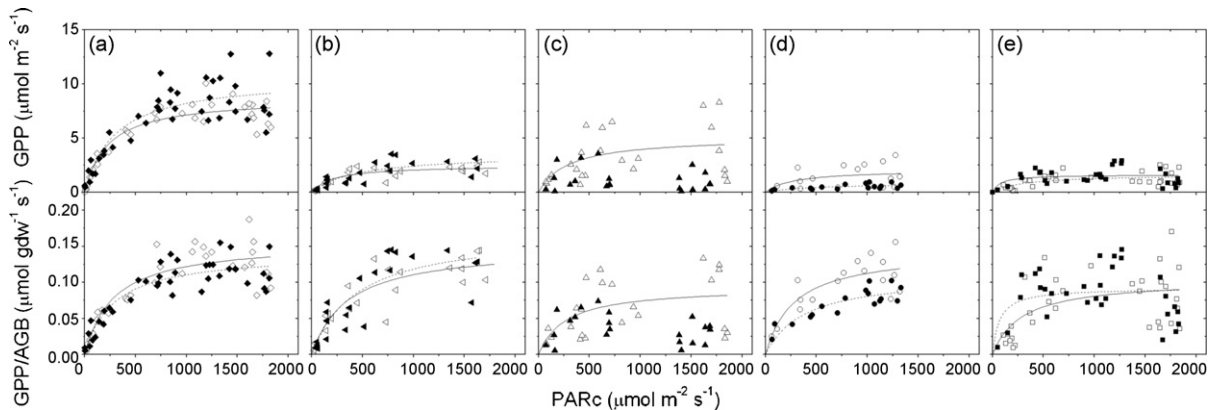


Fig. 3 – The relationship between photosynthetically active radiation inside the chamber (PAR_c) and gross primary production (GPP, top) and GPP normalized by aboveground biomass (AGB, bottom) in (a) July 2004, (b) May 2005, (c) July 2005, (d) September 2005, and (e) June 2006. Open and solid symbols denote the data at the NG and D plots, respectively. Solid and dashed lines indicate the fitted curve for the NG and D plots, respectively.

Table 3 – The coefficients of rectangular hyperbolic light–response functions fitted to the gross primary production (GPP) per ground area and the GPP normalized by aboveground biomass

Period	Plot	For GPP per ground area			For GPP per aboveground biomass		
		α	F_{\max}	r^2	α	F_{\max}	r^2
July 2004	NG	0.038	8.77	0.90	0.00055	0.156	0.82
	D	0.036	10.6	0.75	0.00051	0.141	0.82
May 2005	NG	0.011	2.49	0.71	0.00042	0.150	0.77
	D	0.008	3.53	0.66	0.00038	0.161	0.73
July 2005	NG	0.017	5.10	0.24	0.00035	0.094	0.27
	D	NS	NS	NS	NS	NS	NS
September 2005	NG	0.007	2.07	0.18	0.00051	0.144	0.66
	D	0.002	0.85	0.38	0.00029	0.111	0.74
June 2006	NG	0.005	1.64	0.31	0.00036	0.104	0.33
	D	0.020	1.62	0.20	0.00139	0.092	0.12

NS means “not significant”.

light–response curve (Eq. (1)); estimated coefficients of the function are listed in Table 3. Some other grassland studies have found a similar relationship between GPP and PAR (Valentini et al., 1995; Flanagan et al., 2002) or between NEE and PAR (Kim and Verma, 1990; Suyker and Verma, 2001; Kato et al., 2004a; Xu and Baldocchi, 2004; Gilmanov et al., 2007). Fig. 3(top) indicates that GPP–PAR relationships differed among the study periods. The GPP values measured in July 2004 and May 2005 fit the light–response function well ($r^2 > 0.65$ in Table 3), while the GPP values were fairly scattered during the other three periods, resulting in low coefficients of determination ($r^2 = 0.18–0.38$). GPP measured under the rain-out shelter at the D plots in July 2005 did not significantly fit the light–response curve, probably resulting from GPP depressions at high-radiation levels caused by high VPD (see Section 3.4.). The magnitude of GPP was relatively high in July 2004 and low in May 2005, September 2005, and June 2006.

Because GPP was strongly correlated with AGB, as mentioned above, we plotted the relationship between PAR_c and GPP normalized by the amount of AGB ($\mu\text{mol gdw}^{-1} \text{s}^{-1}$, Fig. 3, bottom). In contrast to GPP per unit ground area, there were no major differences for the relationships between GPP/AGB and PAR_c among the study periods, although the phenological stages of plants during these periods were different: germination (May), mid-growing season (June and July), and senescence (September). This result indicates that photosynthetic activity by plants per unit AGB did not differ among growth stages. The values of GPP/AGB were scattered widely in July 2005 and June 2006. The scatter in these relationships probably reflects the large variations in environmental parameters under which the measurements were made, in addition to the radiation. A relatively low GPP/AGB ratio at the D plots in September 2005 was presumably attributed to irreversible damage that plants suffered under the rainout shelter during June and July 2005.

The GPP/AGB ratios over all of the periods were plotted against PAR_c (Fig. 4), grouped by the conditions of soil VWC at 3-cm depth ($VWC_{3\text{ cm}}$) and VPD inside the chamber (VPD_c) when the measurement was made. The GPP data without drought-stress ($VWC_{3\text{ cm}} > 0.03 \text{ m}^3 \text{ m}^{-3}$ and $VPD_c < 3.0 \text{ kPa}$) were fitted by a rectangular hyperbolic function: $\alpha = 0.00044 \mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ photons gdw}^{-1} \text{ m}^2$, $F_{\max} = 0.148 \mu\text{mol gdw}^{-1} \text{ s}^{-1}$,

and $r^2 = 0.68$. Because this curve is independent of phenological stage at the study site, we can estimate the “unstressed” value of GPP throughout the growing season from PAR_c and AGB. For comparison with published data, the apparent quantum yield (α) and the maximum gross production (F_{\max}) per unit ground area were calculated using yearly maximum values of the AGB over the study area for 2004–2006 (93.0, 87.1, and 44.9 g dw m^{-2}). Estimated α values were 0.041, 0.038, and 0.020 $\mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ photons}$ for 2004, 2005, and 2006, respectively, and estimated F_{\max} values were 12.5, 11.7, and 6.03 $\mu\text{mol m}^{-2} \text{ s}^{-1}$, respectively. Our values of F_{\max} were similar to the dry-year values reported by Flanagan et al. (2002), but the values of α were slightly higher than those presented in their report.

3.4. Responses of GPP to temperature and moisture conditions

Photosynthesis is affected by abiotic, particularly climatic, parameters such as temperature, air dryness (VPD), soil

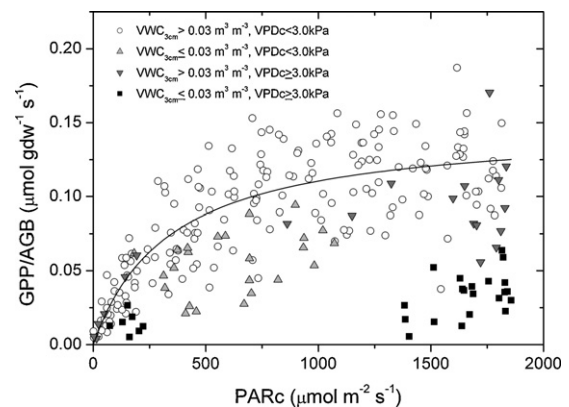


Fig. 4 – The relationship between gross primary production normalized by aboveground biomass (GPP/AGB) and photosynthetically active radiation (PAR_c) conditioned by volumetric soil water content at 3-cm depth ($VWC_{3\text{ cm}}$) and vapor pressure deficit inside the chamber (VPD_c). The solid line is a rectangular hyperbolic light–response curve fitted to the data without drought stress (open circles).

moisture, and radiation. Periods of excessively high or low temperature, depending on their intensity and duration, impair the metabolic activity of plants. Water deficiency also inhibits some cell functions and cellular processes and results, for instance, in decreased cell volume and increased stomatal closure (Larcher, 2003).

GPP tended to decline when either the air or the soil was dry ($VWC_{3\text{ cm}} \leq 0.03\text{ m}^3\text{ m}^{-3}$ or $VPD_c \geq 3.0\text{ kPa}$), and GPP decreased markedly when both the air and soil were dry (Fig. 4). Few studies have reported such a GPP reduction under dry conditions, although a reduction in NEE under dry conditions has been observed (Kim and Verma, 1990; Verhoef et al., 1996; Sims and Bradford, 2001; Suyker and Verma, 2001; Li et al., 2005; Fu et al., 2006). Sims and Bradford (2001) and Fu et al. (2006) found an afternoon depression in net CO_2 flux during midsummer in a mixed-grass prairie in the United States and in a semi-arid steppe in Inner Mongolia, respectively. Sims and Bradford (2001) suggested that this NEE reduction probably resulted from stomatal closure in leaf tissue due to high VPD. In addition to the stomatal limitation, Fu et al. (2006) inferred that high temperature at midday caused the NEE reduction through a decrease of photosynthesis and an increase of R_{eco} . Kim and Verma (1990) and Li et al. (2005) illustrated NEE–PAR curves grouped by values of soil moisture and VPD, which demonstrated that net CO_2 exchange was reduced when the soil moisture was low or the VPD was high. They suggested that a soil water shortage might aggravate VPD-induced decrease in carbon uptake, which was consistent with our result.

To further assess the individual quantitative effects of air temperature, VPD, and soil moisture on the photosynthetic production, we compiled GPP/AGB data under light-saturated conditions ($PAR_c \geq 800\ \mu\text{mol m}^{-2}\text{ s}^{-1}$) using different bins of T_c , VPD_c , and $VWC_{3\text{ cm}}$. Bin width was 2°C for T_c , 0.5 kPa for VPD_c , and $0.01\text{ m}^3\text{ m}^{-3}$ for $VWC_{3\text{ cm}}$. To avoid the confounding effect of each parameter, we defined the unstressed conditions as $15 < T_c < 35^\circ\text{C}$, $VPD_c < 3.0\text{ kPa}$, and $VWC_{3\text{ cm}} > 0.03\text{ m}^3\text{ m}^{-3}$. To examine the effect of a single parameter, we sampled the GPP/AGB data under the conditions in which the remaining two parameters were unstressed and averaged the data over each bin of the relevant parameter. This process allowed us to measure how photosynthesis responded to variations in air temperature, VPD, and soil moisture (Fig. 5a–c, respectively).

Photosynthesis responded to temperature changes in the form of a general bell-shaped curve (Fig. 5a; Farquhar et al., 1980; Kim et al., 1992; Chen and Coughenour, 2004), and GPP/

AGB reached the maximum around 27°C , which is consistent with the published data for most C_3 and desert plants (e.g., Larcher, 2003). However, CO_2 uptake was 90% of the maximum value at air temperatures from 14 to 38°C , suggesting that the photosynthetic reaction is not strongly affected by temperature within this range. Previous studies have shown that some grass species had a wide range of photosynthetic temperature optima (Knapp, 1985).

The amount of GPP/AGB showed a nearly linear decrease with increasing VPD (Fig. 5b), and it rapidly decreased when the soil VWC dropped to less than $0.04\text{ m}^3\text{ m}^{-3}$ (Fig. 5c). These findings suggest that a combination of high VPD and low soil moisture caused the considerable reduction of GPP, as shown in Fig. 4. Few studies have examined the quantitative dependence of GPP on changes in VPD and soil moisture based on field measurements in grasslands. However, numerous theoretical/empirical models of plant production have indicated that ecosystem carbon assimilation can be expressed as a function of LAI, PAR, and stomatal (or canopy, surface) conductance (g_s), and in turn g_s can be calculated as a function of VPD or soil moisture (Daly et al., 2004; Novick et al., 2004). Because GPP is proportional to g_s (Knapp, 1985; Kim and Verma, 1990), we can assume that the response of GPP to water stress is similar to that of g_s . Several studies reported that g_s declined with increasing VPD, although the relationships were expressed in different function forms (Collatz et al., 1991; Stewart and Verma, 1992; Leuning, 1995; Oren et al., 1999). The data presented in Fig. 5b agree with these previous findings.

Others have also reported that g_s increased with increasing soil moisture and reached a plateau under well-watered conditions (usually field capacity; Stewart and Verma, 1992; Daly et al., 2004). The form of the dependency of GPP on soil moisture in Fig. 5c is similar to that reported in these previous studies. However, the VWC at which GPP reached a plateau was near the wilting point and was much lower than in previous reports. Thus, the reduction of soil moisture due to low precipitation depressed plant photosynthesis, whereas moistening after precipitation did not strongly affect it. We infer that the slight response of photosynthetic activity to high soil moisture may be associated with the availability of soil nutrients, particularly nitrogen, which is one of the most important variables determining canopy photosynthesis rate (Larcher, 2003). An experimental study that added water and nutrients to a desert ecosystem indicated that instantaneous

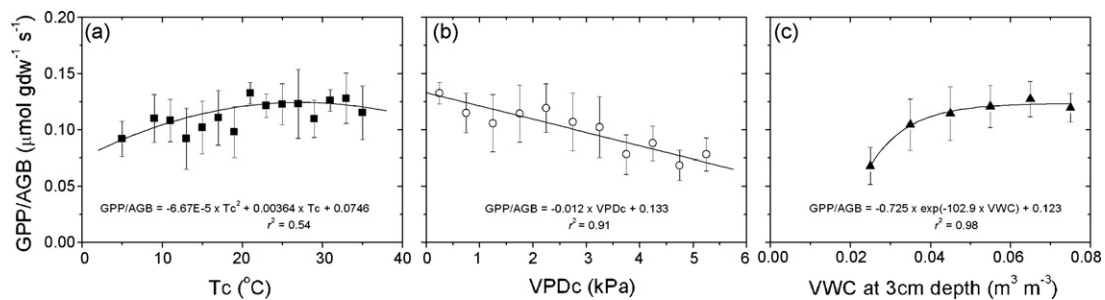


Fig. 5 – The responses of gross primary production per unit of aboveground biomass (GPP/AGB) to (a) air temperature inside the chamber (T_c), (b) vapor pressure deficit (VPD_c), and (c) volumetric soil water content (VWC) at 3-cm depth. Bin width was 2°C for T_c , 0.5 kPa for VPD_c , and $0.01\text{ m}^3\text{ m}^{-3}$ for $VWC_{3\text{ cm}}$. Bars indicate standard deviations.

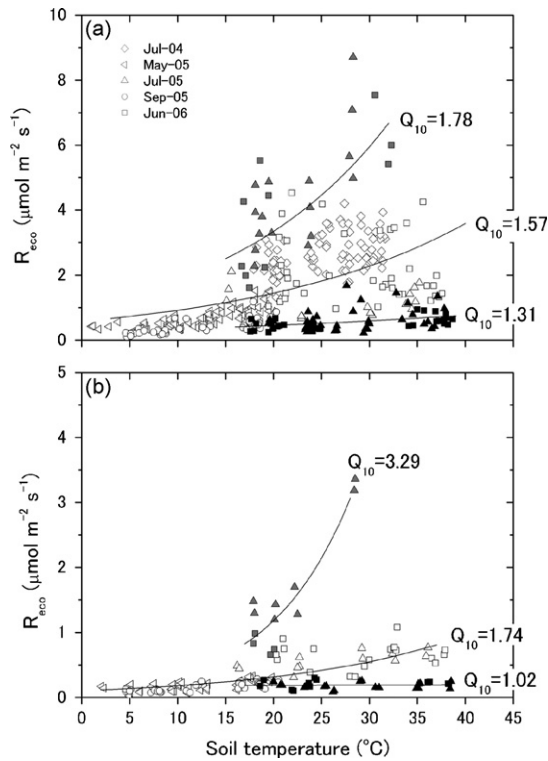


Fig. 6 – Response of ecosystem respiration (R_{eco}) to changes in soil temperature at the 5-cm depth at (a) grass-covered plots and (b) bare soil plots. Data over all study periods are plotted and are grouped by the soil moisture conditions. The shading of symbols represents the range of volumetric water content at 3-cm depth ($VWC_{3\text{ cm}}$): white: $0.03 < VWC_{3\text{ cm}} \leq 0.06\text{ m}^3\text{ m}^{-3}$; gray: $VWC_{3\text{ cm}} > 0.06\text{ m}^3\text{ m}^{-3}$ and black: $VWC_{3\text{ cm}} \leq 0.03\text{ m}^3\text{ m}^{-3}$.

photosynthesis and conductance were not significantly affected by water supply alone, whereas the combination of water and nutrients caused an increase in plant growth (James et al., 2005).

3.5. Magnitude and temperature sensitivity (Q_{10}) of R_{eco}

Ecosystem respiration consists of both autotrophic (plant) and heterotrophic respiration (i.e., microbial decomposition of soil organic matter). Although many environmental factors affect the biological and physical processes controlling respiration rates, previous studies indicated that respiration rates are mainly related to soil temperature and moisture (e.g., Davidson et al., 1998; Suyker and Verma, 2001; Xu and Qi, 2001a,b; Reichstein et al., 2002; Kato et al., 2004b; Xu and Baldocchi, 2004; Flanagan and Johnson, 2005). Therefore, for all study periods we plotted the values of R_{eco} against the soil temperature at 5-cm depth (T_s ; Fig. 6). The R_{eco} measurements were conducted at NG and D plots, but each plot included four grass-covered points and two bare-soil points. Thus, we sorted the data into grass-covered (Fig. 6a) and bare-soil plots (Fig. 6b) and grouped these data by the conditions of $VWC_{3\text{ cm}}$ when the measurements were made. The amount of R_{eco} at the plots with grass cover was significantly larger than at bare plots, as would be expected because R_{eco} at grass-covered plots reflects plant respiration in addition to soil microbial decomposition. The R_{eco} values at the grass-covered plots were highly variable compared with those at the bare plots, likely due to the difference of plant biomass within each collar, although there was no obvious relationship between the amount of AGB and R_{eco} (Fig. 2). The amount of R_{eco} also differed among the soil moisture conditions: R_{eco} declined with decreasing VWC. Consistent with these results, it has been reported that low soil moisture constrains soil CO_2 efflux, because water deficit decreases both microbial decomposition and living root respiration (Davidson et al., 1998; Xu and Qi, 2001a; Hunt et al., 2002; Flanagan and Johnson, 2005).

For the entire R_{eco} data set, with all soil moisture levels grouped together, no single temperature function was found to describe the variations in R_{eco} . By contrast, when data were grouped by degree of soil moisture, we found significant exponential relationships between R_{eco} and T_s (Eq. (2)) for both grass-covered and bare plots and for all soil moisture conditions. Temperature sensitivity (Q_{10}) was then calculated from Eq. (4) (Table 4), and the Q_{10} values varied from 1.02 to 3.29

Table 4 – Relationship of ecosystem respiration to soil temperature and soil moisture (Eqs. (2) and (3)) and the temperature sensitivity coefficient (Q_{10}).

Surface coverage	Moisture condition ^a	β_0	β_1	Q_{10}	r^2
For soil temperature (Eq. (2))					
Grass-covered plots	Normal	0.585	0.045	1.57	0.41
	Wet	1.059	0.058	1.78	0.44
	Dry	0.267	0.027	1.31	0.13
Bare soil plots	Normal	0.105	0.055	1.74	0.68
	Wet	0.109	0.119	3.29	0.87
	Dry	0.182	0.002	1.02	0.15
Surface coverage		β_0	β_1	β_2	r^2
For soil temperature and soil moisture (Eq. (3))					
Grass-covered plots		0.0322	0.0287	2.15	0.74
Bare soil plots		0.0032	0.0297	2.85	0.78

^a Soil moisture is grouped by volumetric water content at 3-cm deep ($VWC_{3\text{ cm}}$); normal: $0.03 < VWC_{3\text{ cm}} \leq 0.06\text{ m}^3\text{ m}^{-3}$, wet: $VWC_{3\text{ cm}} > 0.06\text{ m}^3\text{ m}^{-3}$, and dry: $VWC_{3\text{ cm}} \leq 0.03\text{ m}^3\text{ m}^{-3}$.

depending on the soil moisture and the existence of surface vegetation. Except for the Q_{10} value under wet and bare soil conditions (3.29), the Q_{10} values presented here (1.02–1.78) were at the lower end of the range reported in previous grassland studies: 4.6 in a Californian serpentine grassland (Valentini et al., 1995), 2.1–2.5 in a Mediterranean annual grassland in California (Xu and Baldocchi, 2004), and 1.3–2.5 in a semi-arid grassland in Canada (Flanagan and Johnson, 2005). Relationships between Q_{10} and environmental variables also have been examined for grasslands (Xu and Baldocchi, 2004; Flanagan and Johnson, 2005; Harper et al., 2005) and forests (Xu and Qi, 2001a,b; Reichstein et al., 2002). According to these studies, Q_{10} decreased as soil moisture was reduced, agreeing with our result. Reichstein et al. (2002) suggested that the dependence of Q_{10} on soil moisture was explained by substrate types which were available for decomposition. Q_{10} of decom-

position is higher for labile substrates than for stabile ones. Under dry conditions the main part of decomposition comes from more stabile material, resulting in the decrease in Q_{10} .

3.6. Respiration pulse after a rain event

Several studies have reported large pulses of R_{eco} immediately after a rain event based on field measurements (Hunt et al., 2002; Xu and Baldocchi, 2004; Zhao et al., 2006) and a rainfall manipulation experiment (Liu et al., 2002). Similarly, in this study the amount of R_{eco} was considerably large when soil moisture was high, which occurred after a rain event (Fig. 6). This rise in R_{eco} due to increasing soil moisture after rain was more noticeable at bare plots than at grass-covered plots. Xu and Baldocchi (2004) and Zhao et al. (2006) indicated that respiration pulses were especially notable during the dry season when the grass was dead, and these pulses were the consequence of quickly stimulated microbial activity.

Xu and Baldocchi (2004) and Zhao et al. (2006) also noted that R_{eco} suddenly increased even after a weak rain that did not cause any detectable increase of soil moisture. In our study site, VWC at 10-cm depth did not respond to weak rain (<5 mm d⁻¹), but that at 3-cm depth showed a quick increase after every rain event (Fig. 1). The R_{eco} data, even including those immediately after rain events, fit the bivariate function well (Eq. (3); Fig. 7) using soil temperature at 5-cm depth and VWC at 3 cm; coefficients of determination were 0.74 for grass-covered plots and 0.78 for bare soil plots (Table 4). Thus, it is possible to estimate the R_{eco} pulse after rain from soil temperature and soil moisture if VWC is determined at very shallow depth (e.g., 0–5 cm).

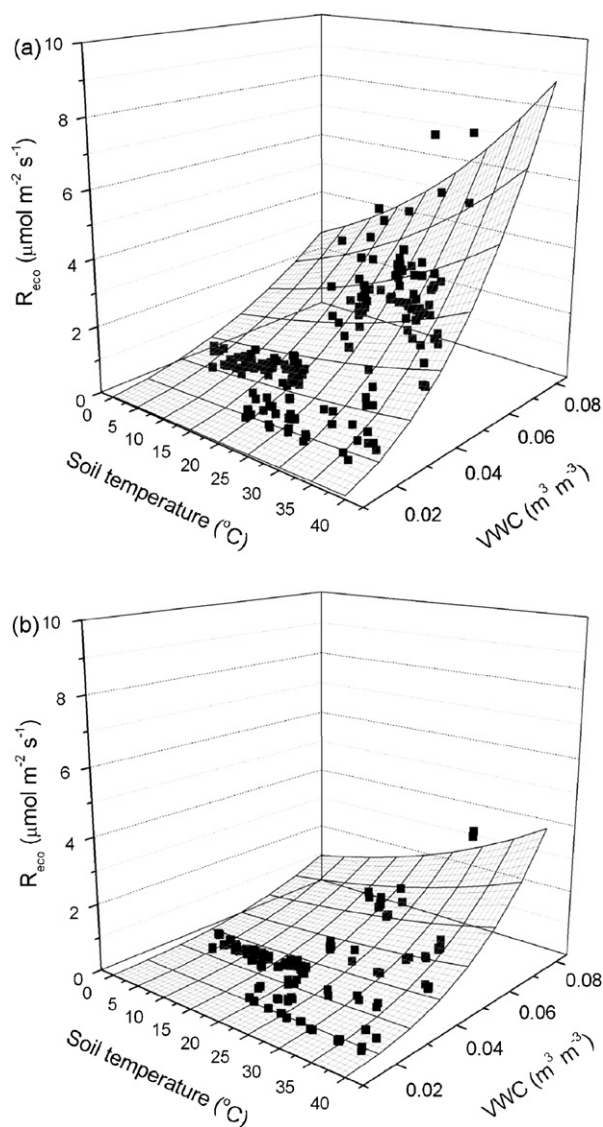


Fig. 7 – Response of ecosystem respiration (R_{eco}) as a bivariate function of soil temperature at a depth of 5 cm and volumetric soil water content (VWC) at 3-cm depth at (a) grass-covered plots and (b) bare soil plots. Dots and nets denote the measured and modeled data, respectively.

4. Concluding remarks

In this study of a semi-arid grassland in Mongolia, GPP and R_{eco} were separately determined using transparent and opaque closed chambers in five 1-week periods during the growing seasons of 2004–2006. Results showed that photosynthetic production was linearly related to the amount of AGB. The amount of GPP per unit ground area differed among the study periods (i.e., phenological stages of plants), whereas GPP normalized by AGB did not show significant differences among the growth stages. The values of GPP/AGB for all of the periods fit well the rectangular hyperbolic light–response curve, but the values declined considerably when the air and soil were dry. By expressing the GPP/AGB as separate functions of air temperature, VPD, and soil VWC, we found that photosynthetic activity was not strongly affected by temperature, that it declined almost linearly with increasing VPD, and that it rose with increasing soil moisture and reached a plateau at a much lower moisture level than that in previous reports. R_{eco} was exponentially related to soil temperature, but both the magnitude and temperature sensitivity (Q_{10}) of R_{eco} declined with decreasing soil moisture. Sharp increases in R_{eco} were observed after rainfall events. The values of R_{eco} , even including the rain-induced pulses, were expressed well as a bivariate function of soil temperature and VWC near the soil surface. Finally, it is noteworthy that the increase of soil moisture after rainfall caused an increase in the respiratory

release of CO₂, but not the photosynthetic uptake of CO₂, in this semi-arid grassland. This result suggests that the increase in soil moisture following a precipitation event during the growing season may change a grassland ecosystem from a carbon sink to a carbon source.

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