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## Original article

# CO<sub>2</sub>, H<sub>2</sub>O and energy exchange of an Inner Mongolia steppe ecosystem during a dry and wet year

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## ABSTRACT

We used an eddy covariance technique to measure evapotranspiration and carbon flux over two very different growing seasons for a typical steppe on the Inner Mongolia Plateau, China. The rainfall during the 2004 growing season (344.7 mm) was close to the annual average (350.43 mm). In contrast, precipitation during the 2005 growing season was significantly lower than average (only 126 mm). The wet 2004 growing season had a higher peak evapotranspiration (4 mm day<sup>-1</sup>) than did the dry 2005 growing season (3.3 mm day<sup>-1</sup>). In 2004, latent heat flux was mainly a consumption resource for net radiation, accounting for ~46% of net radiation. However, sensible heat flux dominated the energy budget over the whole growing season in 2005, accounting for 60% of net radiation. The evaporative rate (LE/R<sub>n</sub>) dropped by a factor of four from the non-soil stress to soil water limiting conditions. Maximum half-hourly CO<sub>2</sub> uptake was -0.68 mg m<sup>-2</sup> s<sup>-1</sup> and maximum ecosystem exchange was 4.3 g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> in 2004. The 2005 drought growing stage had a maximum CO<sub>2</sub> exchange value of only -0.22 mg m<sup>-2</sup> s<sup>-1</sup> and a continuous positive integrated-daily CO<sub>2</sub> flux over the entire growing season, i.e. the ecosystem became a net carbon source. Soil respiration was temperature dependent when the soil was under non-limiting soil moisture conditions, but this response declined with soil water stress. Water availability and a high vapor pressure deficit severely limited carbon fixing of this ecosystem; thus, during the growing season, the capacity to fix CO<sub>2</sub> was closely related to both timing and frequency of rainfall events.

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## 1. Introduction

On a global basis, climatic and environmental factors regulate water and carbon flux within terrestrial ecosystems,

especially in arid and semi-arid grasslands (Lawrence et al., 2002; Li et al., 2006). Improved understanding of these factors is required on because of their universality and agricultural importance and because of issues of sustainability

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(Hunt et al., 2002). Water availability is a limiting factor for plant growth in semi-arid environments and, over long time scales, the local water balance could play a significant role in determining the carbon uptake capacity of the terrestrial surface. An accumulation deficit in soil water can shift the positive absorption of carbon toward negative release into the atmosphere, which can then upset feedback relationships in the evaporative process. Drought also alters the seasonal development of leaf area and changes plant physiology, thus influencing both magnitude and time of maximal CO<sub>2</sub> fixation (Miranda et al., 1997; Meyers, 2001). Changes in seasonality, distribution, frequency of rainfall, and total magnitude of rainfall may greatly impact the net CO<sub>2</sub> flux of a given ecosystems, causing the system to alternate between net carbon sources and sinks. Consequently, long-term, continuous measurements of CO<sub>2</sub> flux are crucial to evaluate the impact of water deficits on the local surface energy balance and carbon budget over seasonal and annual time scales.

Previous studies have indicated that plant functional type, weather, seasonal drought, and soil physical properties can alter water and energy fluxes in grassland ecosystems (Baldocchi et al., 2004). Ham and Knapp (1998) reported that during wet periods, tallgrass prairie gained large daytime carbon accumulation, coupled with large nighttime carbon losses, from ecosystem respiration. Hunt et al. (2002) used an eddy covariance system to measure CO<sub>2</sub> and energy fluxes from tussock grassland during a 212-day summer drought with a 44-mm rainfall. They found that drought influenced both timing and magnitude of maximal CO<sub>2</sub> uptake by substantially modifying the seasonal development of leaf area and by altering plant physiology. At the ecosystem scale, grasslands can take up more carbon during wet years and less during drought year (Meyers, 2001; Suyker et al., 2003; Xu and Baldocchi, 2004). A study of tallgrass prairie suggested that carbon and water balances are significantly coupled; therefore, variations in precipitation or evapotranspiration can affect the carbon cycle (Verma et al., 1992; Ham and Knapp, 1998). However, studies that only qualitatively describe the effect of environmental factors on carbon exchange and do not involve quantitative calculations, do not to provide valid data for biophysical modeling (Pyles et al., 2003).

Eurasian grassland regions are the largest and most characteristic in the world, although their vegetation exhibits regional characteristics. The typical Eurasian steppe is widely distributed in the eastern Eurasian steppe zone, which has a total area of  $\sim 4.1 \times 10^7$  hm<sup>2</sup>, half of which is within China. Within China, typical steppes are distributed throughout the Northeastern Plain and eastern Inner Mongolia Plateau, with about 10.5% of the national grassland area under a temperate, semi-arid climate (Chinese Vegetation Committee, 1979). In this region, previous studies have indicated that primary production is strongly controlled by precipitation during the growing season and the relative balance of water and energy exchange, especially soil water content (Li and Ren, 1997). In addition, grasslands produce large asymmetric responses to yearly variations in rainfall, with consequent increases in productivity during wet years and decreases during drought years (Knapp and Smith, 2001; Hunt et al., 2002; Lawrence et al., 2002; Li et al., 2005). Chen et al. (2003) recently reported that the climate in this region has been displaying a warming

trend, accompanied by a clear increase in air temperature during winter and serious drought in spring. This pattern has potential serious consequences for primary production, carbon exchange, and water-energy balance under predicted warmer weather conditions.

In this paper, our aims were: (1) to compare carbon and energy exchange, measured by eddy covariance, between wet and drought years for a typical steppe on the Inner Mongolia Plateau, China; and (2) to determine and quantify the dependence of carbon and energy exchange on environment and soil water content during a wet and drought summer growing season.

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## 2. Materials and methods

### 2.1. Study site

The experimental site was the Inner Mongolia Grassland Ecosystem Research Station, which is located at Xilin River Watershed of the Inner Mongolia Autonomous Region (43°32'N, 116°40'E, 1200 m a.s.l.). The site has been fenced since 1979 and is located on a smooth wide plain with low hills on a second-level basalt platform. The low hills have a relative height of 20–30 m with a  $<5^\circ$  slope. The climate of this steppe is temperate and semi-arid with a dry spring and a moist summer. Annual temperature averages  $-0.4^\circ\text{C}$  with a growing season length of 150–180 days. The annual precipitation range is 350.43 mm, with 89% of the annual rainfall concentrated in April–September.

Soil type at the experimental site is dark chestnut (Mollisol) with a soil depth of 100–150 cm (Wang and Cai, 1988). Soil moisture is  $0.29\text{ m}^3\text{ m}^{-3}$  and  $0.12\text{ m}^3\text{ m}^{-3}$  at field capacity and wilting point, respectively. The A horizon reaches 20–30 cm deep and there is no obvious CaCO<sub>3</sub> layer in the soil profile. Mean soil composition is 21% clay, 60% sand, and 19% silt. Of the 86 species of flowering plants present (belonging to 28 families and 67 genera), 11 are grass species (Jiang, 1985). The xeric rhizomatous grass, *L. chinensis* (Trin.) Tzvelev (syn. *Aneurolepidium chinensis* (Trin.) Kitagawa), is the edicato species, and *S. grandis* Smirnov, *Koeleria pyramidara* (Lam.) P. Beauv (syn. *K. cristata* (L) Link), and *Agropyron cristatum* (L.) Gaertn. are dominant species. The height of the grass clusters is 50–60 cm; coverage averages 30–40% but can reach 60–70% in rainy years. Litter has been accumulating due to the enclosure since 1979.

### 2.2. Biomass and leaf area measurements

We measured above-ground biomass by cutting around the eddy covariance tower every 15 days during May–September. Twenty quadrats of  $1 \times 1\text{ m}^2$  were harvested at each sampling period. The above-ground parts of the vegetation were clipped to ground level and returned to the laboratory for dry-matter measurements. The clipped plant material was separated into live and standing dead parts, which were weighed as the fresh weight of live biomass and standing dead biomass, respectively. Plant materials were oven-dried at  $65^\circ\text{C}$ , and dry weights of live biomass and standing dead biomass were recorded (Xiao et al., 1996). Litter from the sampled quadrats also was collected. The leaf area index (LAI) was measured every 15 days during the growing season (May–September) in

2004 and 2005 using the leaf area-dry weight coefficient method (Du et al., 2001).

### 2.3. Eddy covariance measurements

We used an eddy covariance (EC) system to measure continuous carbon dioxide (CO<sub>2</sub>) fluxes over the grassland. The fetch area, calculated by the footprint model (Kljun et al., 2004), from all directions was more than 250 m. Sensible heat, latent heat, and CO<sub>2</sub> fluxes were measured at 2.3 m above ground level with a 3D sonic anemometer (model CSAT3, Campbell Scientific, MS, USA) with an adjacent open-path infrared CO<sub>2</sub>/H<sub>2</sub>O gas analyzer (model LI-7500, LI-COR, Lincoln, NE, USA). The eddy covariance measurements were taken at a frequency of 10 Hz and turbulent fluxes were recorded on a datalogger (CR5000, Campbell Scientific) as a half-hour average.

Other auxiliary micrometeorological variables were measured near the EC system. Wind speed was measured at 1.5 and 2.5 m above the ground with cup anemometers (034A-L and 014A; Traverse, MI, USA). Air temperature and humidity were measured at 1.5 and 2.5 m above ground level with a temperature and humidity probe, respectively (HMP45C, VAISALA Woburn, MA, USA). Net radiation and photosynthetically active radiation (PAR) were measured at 1.5 m above the ground with a net radiometer (CNR-1, Kipp & Zonen, NY, USA) and a quantum sensor (LI-190SB; LI-COR NE, USA), respectively. We used a tipping bucket rain-gauge set at 1.5 m above ground level (TE525MM, Campbell Scientific) to measure precipitation. Soil temperature was measured at 0.05, 0.10, 0.20, 0.50, and 1.0 m below the ground with copper-constantan thermocouples. Soil heat flux was attained by averaging the output of two heat flux plates (HFT-3, Campbell Scientific). We measured soil volumetric water content with a time-domain reflectometer probe at 0.05, 0.2, and 0.5 m. Profiles of soil moisture were also measured at a depth of 0–0.1, 0.1–0.2, 0.2–0.3, and 0.3–0.5 m every week with a soil auger. Data from these sensors were recorded below the canopy using a digital datalogger (CR23X; Campbell Scientific).

All flux and meteorological data collected were quality controlled. Roughly 20% of the data obtained from our EC system were discarded based on data screening criteria (Lee and Fuentes, 1999) and instrument malfunction. To fill in the gaps, we applied the MDV (Mean Diurnal Variation; Falge et al., 2001) and interpolation methods (Baldocchi, 2003; Xu and Baldocchi, 2004). Soil heat flux,  $G$ , was calculated as the average of the two soil heat flux plates and was corrected for heat storage above the plates. There is good agreement between half-hourly values of turbulent ( $H + LE$ ) and radiative ( $R_n + G$ ) fluxes. The slope of the regression line is 0.83 with an intercept of  $13.7 \text{ W m}^{-2}$  and a correlation coefficient,  $r^2$ , of 0.93.

## 3. Results and discussion

### 3.1. Precipitation and soil water content

To understand carbon and water exchange between the grassland ecosystem of the Inner Mongolia Plateau and the atmosphere, it is necessary to present background information about the local environmental variables. During the two

growing seasons of 2004 and 2005, daily average air temperature was variable, with a range from 0.2 to 25 °C. Maximum air temperature was observed in July in both years (Fig. 1c). Air temperatures during the 2005 growing season were slightly higher, however, than the 2004 values. Differences in soil temperatures between 2004 and 2005 were more obvious, with higher soil temperatures in 2005 (Fig. 1d). The 2004 growing season experienced 344.7 mm of rain over 73 rain days, with 28 days having rain >3 mm (Fig. 1a). In contrast, the 2005 growing season had precipitation of only 126 mm over 52 rain days, with 10 days of rainfall >3 mm (Fig. 1b). Fig. 1a,b also show seasonal trends in soil water content. Maximum daily average soil volumetric water content ( $\theta_v = 0.28 \text{ m}^3 \text{ m}^{-3}$ ) across the upper 0.20 m of the soil profile occurred in mid-July during the wet season in 2004, whereas the maximum value ( $\theta_v = 0.16 \text{ m}^3 \text{ m}^{-3}$ ) during the drought season in 2005 was observed in late-May (field capacity is  $0.29 \text{ m}^3 \text{ m}^{-3}$  and wilting point is  $0.12 \text{ m}^3 \text{ m}^{-3}$  (Du and Yang, 1988)). In particular, there was a significant increase in  $\theta_v$  during the peak of the growing season in 2004. However, the abrupt drop in soil moisture (DOY 150–180) in 2004 may be caused by the instrument malfunction. Examining Fig. 1b we note that the soil moisture was much lower in 2005 particularly during the summer months of June–September, closed to the wilting point: little rainfall and high evaporative demand caused this rapid depletion of soil moisture (Xu and Baldocchi, 2004). The vapor pressure deficit (VPD) also differed between the 2004 and 2005 growing seasons, with higher values from June to September in 2005 compared to 2004 (Fig. 1e).

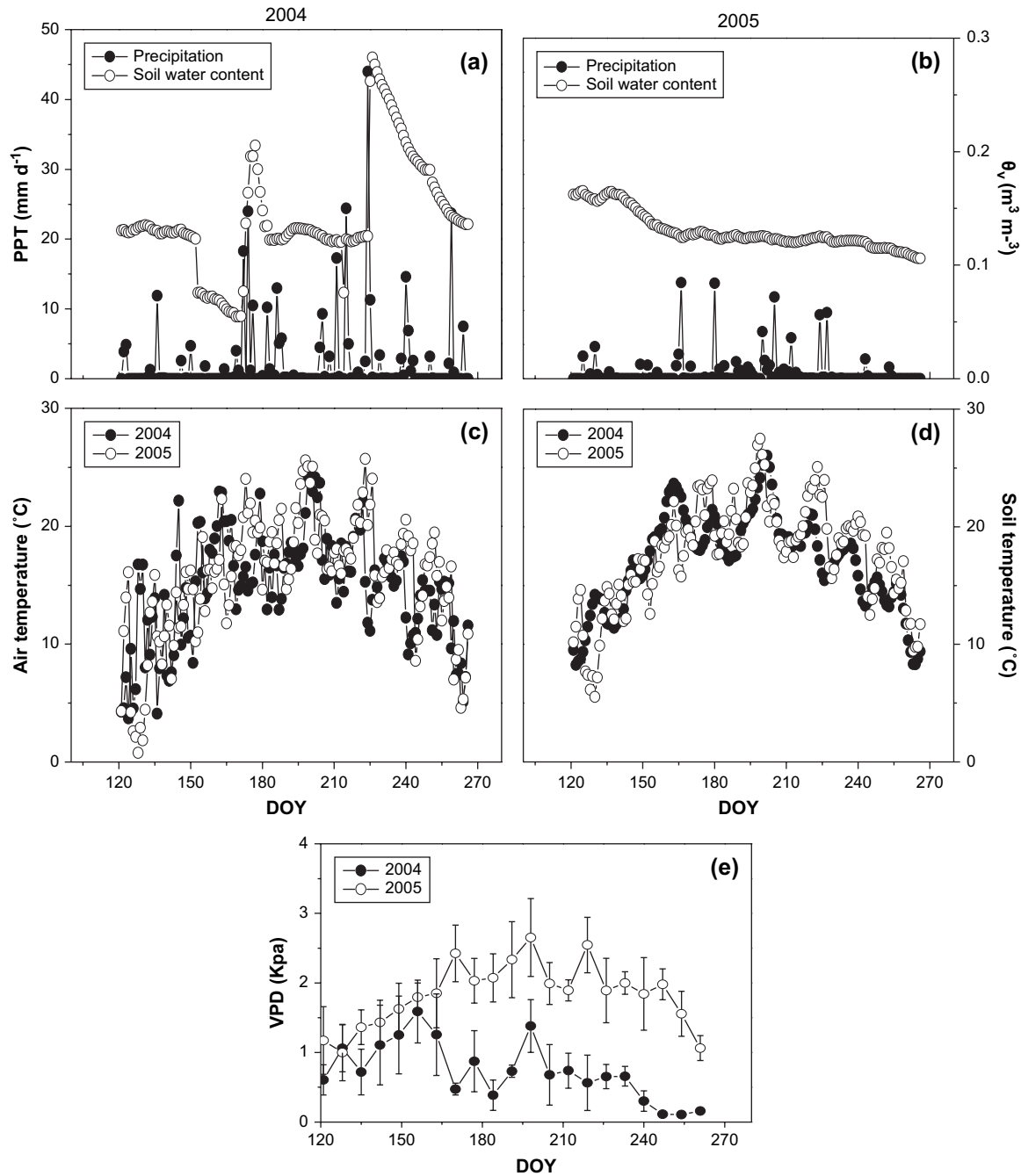
These large annual variations in climate and weather, accompanied by the wide scope of diel and seasonal temperature, provided us with a unique opportunity to better determine and quantify the impact of environmental factors on carbon and water exchange on a steppe of the Inner Mongolia Plateau.

### 3.2. Above-ground biomass and leaf growth

Fig. 2 shows the seasonal changes in above-ground biomass and LAI over the 2 years (2004–2005). The seasonal peak value of above-ground biomass for 2004 was  $188.13 \pm 23.82 \text{ gm}^{-2}$  and occurred in August, which had the maximum monthly precipitation (120.8 mm). However, in 2005, the maximal above-ground biomass was  $132.46 \pm 28.02 \text{ gm}^{-2}$  in August, which had only 24.7 mm of rainfall. The above-ground biomass for the whole 2004 growing season was distinctly higher than that of 2005. In 2004, LAI ranged from 0.23 to 0.48 in June, 0.62 to 1.15 in July, and 1.12 to 1.54 in August due to warmer temperatures, longer day length, and ample soil moisture (associated with ample rainfall in this wet year). Marked differences in LAI between 2004 and 2005 occurred for the whole growing season. The peak LAI in 2004 was approximately twice the value of LAI in 2005. The difference might be due to the differing contribution of various species and species groups to LAI between 2004 and 2005 (Du et al., 2001; Sims and Bradford, 2001).

### 3.3. Energy budget and evapotranspiration

Diurnal patterns of  $R_n$  (Net radiation),  $LE$  (Latent heat flux), and  $H$  (Sensible heat flux) during the wet and drought seasons are

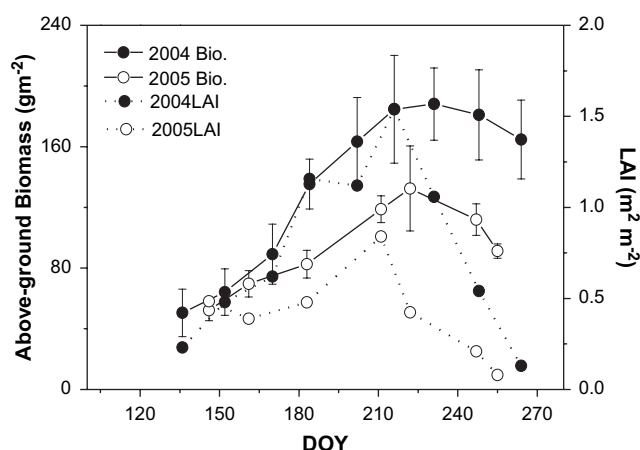


**Fig. 1 – (a)–(b) Seasonal and interannual variation of daily total precipitation (mm), daily average volumetric soil water content ( $\theta_v$ ) 0–0.2 m soil depth, (c)–(d) daily average air temperature ( $T_a$ ), daily average soil temperature ( $T_s$ ) 0–0.05 m soil depth and (e) daily average vapor pressure deficit (Values represent the mean ( $\pm$  S.E.) for two-week periods).**

presented as an ensemble mean diurnal cycles on selected 10 days average for various growing stages according to the variation in vegetation characteristics (Fig. 3). In the wet season, the daytime trends of LE and H followed a pattern similar to that of net radiation ( $R_n$ ). Maximum latent and sensible heat fluxes were similar over the entire growing season, with peak values of 200 W m<sup>-2</sup>. From the peak-to-senescence growth stages (days 202–263) in 2004, latent heat flux was the dominant consumption resource for net radiation, whereas sensible heat flux was the dominant component of energy

balance during the rapid growth stage. In contrast, sensible heat flux dominated the energy budget at midday during the entire 2005 growing season. Maximum sensible heat flux was higher than latent heat flux, with peak values of sensible heat flux of  $\sim 300$  W m<sup>-2</sup>. Soil heat flux was quite similar between the 2004 and 2005 seasons, with maximum values of 30–40 W m<sup>-2</sup> (Fig. 3).

Partitioning of  $R_n$  into LE and H during the wet and drought seasons was divided into three different growing stages. The average Bowen ratio ( $\beta = H/LE$ ) was 1.95–1.07 during the rapid



**Fig. 2 – Above ground biomass and LAI in wet 2004 and drought 2005.**

growth stage and ranged from 0.49 to 0.93 from peak to senescence growth stages in 2004. However, it exceeded 1 throughout the drought season in 2005 (Table 1). Albedo ( $\alpha_k$ ), which is defined as the ratio of reflected to incoming shortwave radiation (Xu and Baldocchi, 2004), decreased gradually with canopy development until the peak growth stage, from which point it increased again as the steppe senesced in 2004 and 2005. Seasonal distributions of energy fluxes were sinusoidal, but  $G$  exhibited a relatively stable change between the two growth seasons ( $G/R_n$ :  $\sim 0.04$ – $0.05$ ) and showed no relationship with soil moisture (Table 1). The evaporative fraction ( $LE/R_n$ ) had a positive correlation with soil moisture. When  $\theta_v \leq 0.12 \text{ m}^3 \text{ m}^{-3}$ , the evaporative fraction dropped by a factor of 4 from the non-soil stress state to the soil water limited state (Table 1). However, not all variations in  $LE/R_n$  were explained by  $\theta_v = 0.12 \text{ m}^3 \text{ m}^{-3}$ , as phenological changes also controlled the evaporative fraction. For instance,  $LE/R_n$  was 0.6 when  $\theta_v$  equaled the critical value in the peak stage during 2004 (Table 1). This may have been due to the fact that plants need sufficient evaporation to meet production and maintain growth. The dissipation of net radiation into sensible and latent heat flux is dramatically impacted by LAI and soil moisture (Wever et al., 2002). We found significant linear relationships between  $LE$  ( $LE$  in  $\text{Wm}^{-2}$ ) and  $LAI$  ( $LAI$  in  $\text{m}^2 \text{ m}^{-2}$ ):

$$LE = (129.36 \pm 2.3) + (29.41 \pm 2.4)LAI;$$

$$N = 138 \text{ adjusted } R^2 = 0.7, P < 0.0001, \text{ wet 2004}$$

$$LE = (87.5 \pm 3.5) + (55.37 \pm 7.1)LAI;$$

$$N = 136 \text{ adjusted } R^2 = 0.6, P < 0.0001, \text{ drought 2005}$$

and between  $LE$  and volumetric soil water content ( $\theta$ ) at 20 cm depth ( $\theta$  in %):

$$LE = (135.2 \pm 4.3) + (126.1 \pm 29.3)\theta;$$

$$N = 138 \text{ adjusted } R^2 = 0.4, P < 0.0001, \text{ wet 2004}$$

$$LE = (-12.6 \pm 11.7) + (393.6 \pm 89.3)\theta;$$

$$N = 136 \text{ adjusted } R^2 = 0.4, P < 0.0001, \text{ drought 2005}$$

Studies from different ecosystems, such as forestry, grassland, and tallgrass prairie, have shown that leaf emergence

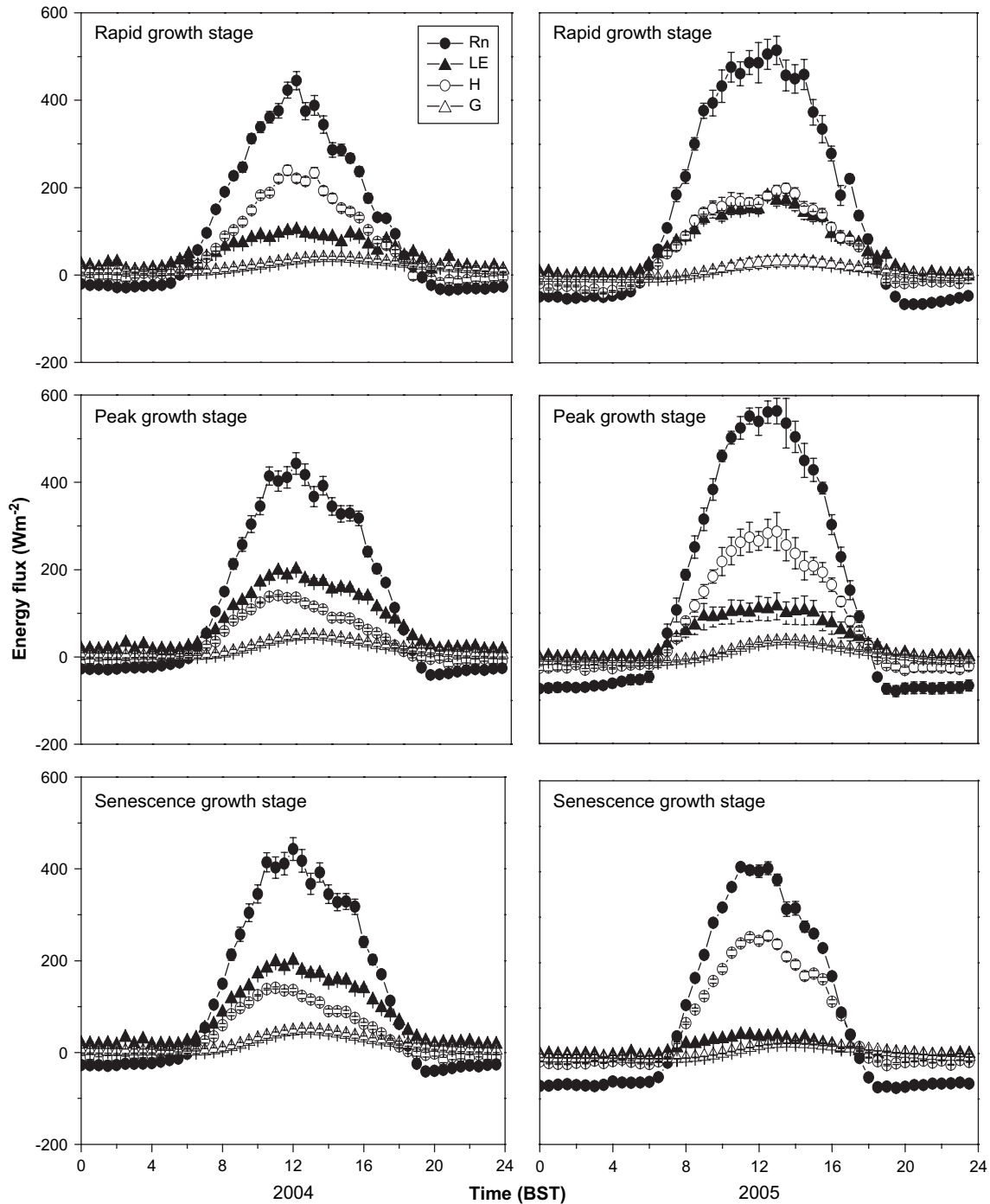
and senescence cause a switch in energy partitioning (Verma et al., 1992; Valentini et al., 1995; Blanken et al., 1997; Saigusa et al., 1998; Wever et al., 2002). In the steppe grassland studied herein, the distribution of available energy was controlled by soil moisture and phenological changes. This situation is different from that of the northern temperate grassland of Canada and tallgrass prairie, where drought stress was not a factor (Ham and Knapp, 1998; Wever et al., 2002).

In this study, evapotranspiration was an important component of water balance, as drainage was not significant during the study periods. The maximum value of evapotranspiration ( $E$ ) was  $4 \text{ mm day}^{-1}$  on 25 July in 2004. This value is similar to figures for a warm-temperate grassland in the southeastern USA ( $E_{\text{max}} = 4.7 \text{ mm day}^{-1}$ ) and grasslands throughout the world ( $E_{\text{max}} = 3$ – $5.5 \text{ mm day}^{-1}$ , derived from eddy covariance;  $E_{\text{max}} = 4.2$ – $6.2 \text{ mm day}^{-1}$ , derived from model estimations) and may be the result of direct transpiration of precipitation intercepted by vegetation and litterfall. A relatively lower maximum evaporation rate ( $E_{\text{max}} = 3.3 \text{ mm day}^{-1}$ ) occurred on 6 May in 2005. This value was less than that of a tussock grassland during a summer drought in New Zealand ( $3.8 \text{ mm day}^{-1}$ ; Hunt et al., 2002). For comparison, the equilibrium evaporation ( $E_{\text{eq}}$ ) was also calculated (for a detailed definition, see McNaughton and Jarvis, 1983). In the 2004 growth season,  $E$  and  $E_{\text{eq}}$  were 263 and 423 mm, respectively, and  $E$  was approximately 80% of precipitation (Fig. 4). In contrast, both  $E$  and  $E_{\text{eq}}$  were less than the 2004 values during the drought period of 2005. All rainfall was lost as evapotranspiration in 2005.

### 3.4. Carbon dioxide exchange

The marked difference in biotic and abiotic factors present in 2004 and 2005 offered a unique opportunity to assess and quantify their effects on carbon exchange. In the steppe, maximum net  $\text{CO}_2$  uptake was  $-0.68 \text{ mg m}^{-2} \text{ s}^{-1}$  in August 2004, compared to the maximum value of  $\text{CO}_2$  uptake of  $-0.22 \text{ mg m}^{-2} \text{ s}^{-1}$  in August 2005. Carbon fluxes declined by a factor of 3 from 2004 to 2005. The 2004 maximum value of  $\text{CO}_2$  uptake was similar to figures reported for mixed-grass prairie in the Southern Plain experimental range of Oklahoma and long-lived bunch grass ( $-0.68$  to  $-0.4 \text{ mg m}^{-2} \text{ s}^{-1}$ ; Sims and Bradford, 2001), and was less than that of native prairie tall grassland, with higher LAI and drought tolerant  $\text{C}_4$  species, in Texas ( $-1.5 \text{ mg m}^{-2} \text{ s}^{-1}$ ; Dugas et al., 1999). The maximum  $\text{CO}_2$  flux of the 2005 drought year was similar to values reported for the drought tussock grassland, with lower LAI, in New Zealand and the Brazilian cerrado grasslands during a dry season ( $-0.2$  to  $-0.18 \text{ mg m}^{-2} \text{ s}^{-1}$ ; Miranda et al., 1997; Hunt et al., 2002).

To examine carbon dioxide flux during the whole growing season,  $\text{CO}_2$  uptake was averaged at the same time of day over a period of 1 month during each year (Fig. 5). The timing and magnitude of maxima in 2005 decreased compared to the values measured in 2004. The shift towards the morning hours for the peak  $\text{CO}_2$  exchange occurred not only within a growth season but also between years (Fig. 5a,b).  $\text{CO}_2$  flux was suppressed drastically and the ecosystem began to release  $\text{CO}_2$  into the atmosphere at 12:00 h throughout the drought year and in June 2004. This may have been in response to the



**Fig. 3 – Seasonal and interannual variation in the averaged diurnal course of net radiation ( $R_n$ ), latent heat flux (LE), sensible heat flux (H) and soil heat flux (G) for three periods. The values represent the mean ( $\pm$ S.E.) for a 10 days periods.**

higher VPD, which was apparent in the higher values from June to September in 2005 compared to those observed in 2004, and also to soil stress (Fig. 1). Because a typical steppe in a semi-arid region is associated with relatively low rainfall, Du and Yang (1988), in a study within the same study field, suggested that the photosynthetic process in *L. chinensis* and *S. grandis* occurs during the midday depression when  $\theta_v \leq 0.12 \text{ m}^3 \text{ m}^{-3}$ . For *L. chinensis*, 76.8% of all-day photosynthetic production was lost by photosynthetic depression; the

value was 100% for *S. grandis*. Furthermore, higher respiration rate caused by high temperature and high solar radiation are the main reason for  $\text{CO}_2$  loss (Ripley and Saugier, 1978; Li et al., 2003; Fu et al., 2006).

In 2004, the integrated daily  $\text{CO}_2$  uptake was negative in August and reached a maximum during summer. This was consistent with the maximum above-ground biomass, LAI, and precipitation (Figs. 2 and 5c). Integrated daily  $\text{CO}_2$  fluxes, however, were near zero or positive in 2005 due to low levels

**Table 1 – Comparison of daily-means flux densities of global radiation (Q, MJ m<sup>-2</sup> per day), net radiation (R<sub>n</sub>, MJ m<sup>-2</sup> per day), sensible heat (H, MJ m<sup>-2</sup> per day), latent heat (LE, MJ m<sup>-2</sup> per day), soil heat (G, MJ m<sup>-2</sup> per day), available energy (R<sub>av</sub>, MJ m<sup>-2</sup> per day), Bowen ratio (β) and evapotranspiration (E, mm per day) over a typical steppe in Inner Mongolia Plateau, China**

Treatment	DOY	LAI	α <sub>k</sub>	α <sub>v</sub>	Q	R <sub>n</sub>	H + LE	G	H	LE	β	E	R <sub>a</sub>	G/R <sub>n</sub>	LE/R <sub>n</sub>	H/R <sub>n</sub>
2004	Rapid growth	157-163	0.23	0.17	30.1 ± 6.4	11.3 ± 2.93	9.52 ± 2.10	0.8 ± 0.27	6.29 ± 1.57	3.23 ± 0.71	1.95	1.3	10.5 ± 2.72	0.07	0.28	0.55
		198-203	1.12	0.15	30.5 ± 7.4	11.5 ± 3.48	9.53 ± 2.55	0.75 ± 0.30	4.93 ± 0.30	4.60 ± 1.26	1.07	1.9	10.80 ± 3.22	0.06	0.39	0.43
	Peak growth	217-222	1.54	0.15	31.2 ± 5.9	12.3 ± 2.69	11.04 ± 1.49	0.64 ± 0.2	3.65 ± 0.74	7.39 ± 0.80	0.49	3.0	11.69 ± 2.71	0.05	0.6	0.29
		230-237	1.48	0.14	29.2 ± 3.4	11.4 ± 2.36	9.36 ± 1.18	0.48 ± 0.19	3.13 ± 0.98	6.23 ± 0.60	0.50	2.5	10.93 ± 2.23	0.04	0.55	0.27
	Senescence	244-249	1.02	0.16	29.6 ± 2.8	11.3 ± 2.08	8.81 ± 0.74	0.42 ± 0.14	3.85 ± 0.65	4.96 ± 0.60	0.78	2.0	10.97 ± 2.13	0.04	0.44	0.34
251-257		0.51	0.16	27.7 ± 3.2	8.58 ± 2.02	7.90 ± 1.15	0.29 ± 0.17	3.81 ± 0.74	4.09 ± 0.45	0.93	1.7	8.29 ± 2.07	0.03	0.48	0.44	
Entire growth	121-273		0.17	27.9 ± 8.7	11.06 ± 2.72	9.33 ± 1.79	0.56 ± 0.27	4.26 ± 1.55	5.07 ± 1.56	0.84	2.1	10.50 ± 2.59	0.05	0.46	0.38	
2005	Rapid growth	154-164	0.38	0.18	34.1 ± 9.3	11.4 ± 3.7	11.0 ± 3.3	0.7 ± 0.2	6.1 ± 3.0	4.8 ± 1.4	1.3	1.9	10.6 ± 3.5	0.06	0.43	0.53
		172-188	0.40	0.17	30.9 ± 8.4	11.4 ± 3.2	11.3 ± 2.0	0.6 ± 0.2	6.7 ± 1.6	4.6 ± 1.1	1.5	1.8	10.8 ± 3.5	0.05	0.40	0.59
	Peak growth	218-224	0.84	0.15	26.2 ± 5.8	10.3 ± 1.9	7.8 ± 2.6	0.5 ± 0.3	6.2 ± 2.2	1.5 ± 0.4	4.3	0.6	9.8 ± 1.8	0.05	0.15	0.61
		234-242	0.21	0.15	29.7 ± 3.1	9.7 ± 1.5	8.3 ± 1.5	0.4 ± 0.1	6.7 ± 1.2	1.6 ± 0.3	4.2	0.7	9.3 ± 1.5	0.04	0.16	0.70
	Senescence	255-264	0.08	0.17	24.4 ± 5.8	7.2 ± 1.4	7.1 ± 1.7	0.1 ± 0.05	6.0 ± 1.5	1.2 ± 0.3	5.1	0.5	7.2 ± 1.4	0.013	0.17	0.83
121-273			0.17	28.3 ± 8.4	11.2 ± 3.3	9.6 ± 3.0	0.4 ± 0.2	6.1 ± 2.2	3.5 ± 1.7	1.7	1.4	9.8 ± 3.1	0.04	0.30	0.5	

of soil moisture. The diel and seasonal patterns of CO<sub>2</sub> fluxes in the wet year are similar to the results documented by Kim and Verma (1990) from a temperate grassland in Kansas, and those for the drought year are similar to those reported by Hunt et al. (2002) from a tussock grassland during a summer drought in New Zealand.

To examine the effect of VPD and soil moisture stress on CO<sub>2</sub> exchange, data from each growth stage were grouped into two VPD intervals (low: 0.0–1.0 kPa, high: >1.0 kPa). To eliminate the confounding effect of low soil moisture, we selected data under non-limiting soil water conditions ( $\theta_v > 0.12 \text{ m}^3 \text{ m}^{-3}$ ). Data were fitted with a rectangular hyperbola (for details, see Landsberg, 1977) of the form:

$$F_c = \frac{(F_{cm})(b)(PAR - PAR^*)}{F_{cm} + (b)(PAR - PAR^*)} \quad (1)$$

Table 2 presents results for the peak growth stage. CO<sub>2</sub> exchange declined when the VPD was high, a reduction in stomatal conductance may be responsible for this pattern (Kim and Verma, 1990). When VPD increased from low to high levels, for example, the maximum CO<sub>2</sub> flux decreased by 60–70%. Similar results were uncovered during other periods of the growing seasons. Using data derived from dry periods ( $\theta_v \leq 0.12 \text{ m}^3 \text{ m}^{-3}$ ), we attempted to examine the effect of low soil moisture on the CO<sub>2</sub> flux. The value of CO<sub>2</sub> flux under limiting soil water conditions was significantly lower than it was under non-limiting conditions (Table 2). In addition, the increase in VPD seems to have caused a much larger decline of CO<sub>2</sub> flux under non-limiting soil water conditions (Kim and Verma, 1990; Xu and Baldocchi, 2004). These responses to increased VPD and soil stress have been observed in a tussock and temperate grassland (Kim and Verma, 1990; Hunt et al., 2002).

Temperature and soil water availability are important environmental factors controlling ecosystem respiration (Flanagan and Johnson, 2005). In this study, we grouped data into three classes, namely  $\theta_v > 0.12$ ,  $\theta_v \leq 0.08$ , and  $0.08 < \theta_v < 0.12$ . Ecosystem respiration (R<sub>e</sub>) increased with increasing soil temperature (T<sub>soil</sub>) when the ecosystem had no soil water limit. A non-linear regression of the data, however, yielded a coefficient of determination (r<sup>2</sup>) of only 0.2 (Fig. 6). Q<sub>10</sub> was estimated to be 1.7 in wet conditions and declined to 0.2 in drought conditions. Following soil water stress, CO<sub>2</sub> emission declined with ascending T<sub>soil</sub>, soil water stress continued to build up, and the data became scattered. This pattern may have occurred because higher temperatures accelerate the passivation or inactivity of respiration enzymes.

Non-linear regression only accounted for 0.2 of the variation in soil respiration. Low Q<sub>10</sub> values from present study were mostly observed during the drought season. In addition to the abiotic factors controlling ecosystem respiration, a number of biotic factors also affect respiration rate, including the total quantity of ions absorbed, tissue chemistry, microbe activity, litter quantity and quality, and nitrogen content and availability. Our study area has been fenced since 1979 and has accumulated much above-ground litter. Microbial carbon in the surface soil increased 14.7–38.7%, and labile carbon increased 28.2–14.4%, although no variation in total soil organic carbon was apparent, compared to the vicinal-grazing steppe (Ma et al., 2005). This change has

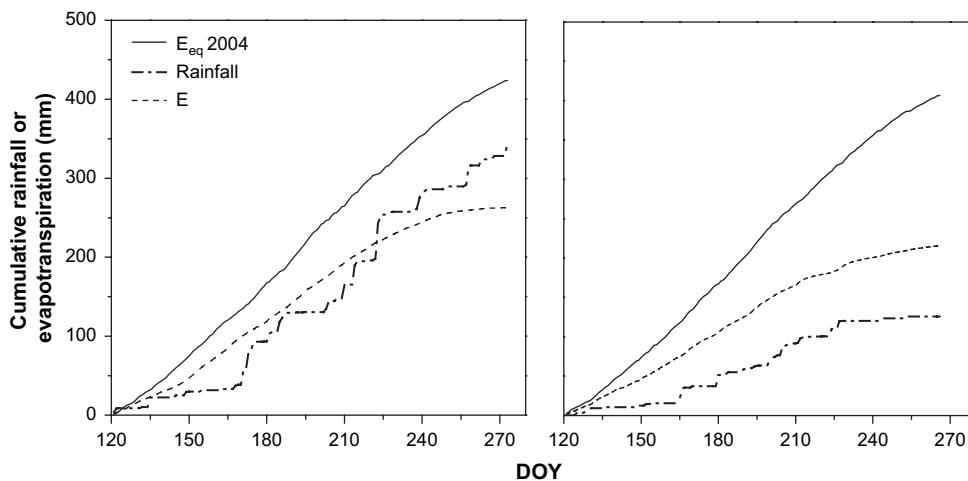


Fig. 4 - Cumulative rainfall (solid line), evapotranspiration (LE, dotted line) and equilibrium evapotranspiration ( $LE_{eq}$ , thin line) during two growing seasons in 2004 and 2005 at Inner Mongolia Plateau, China.

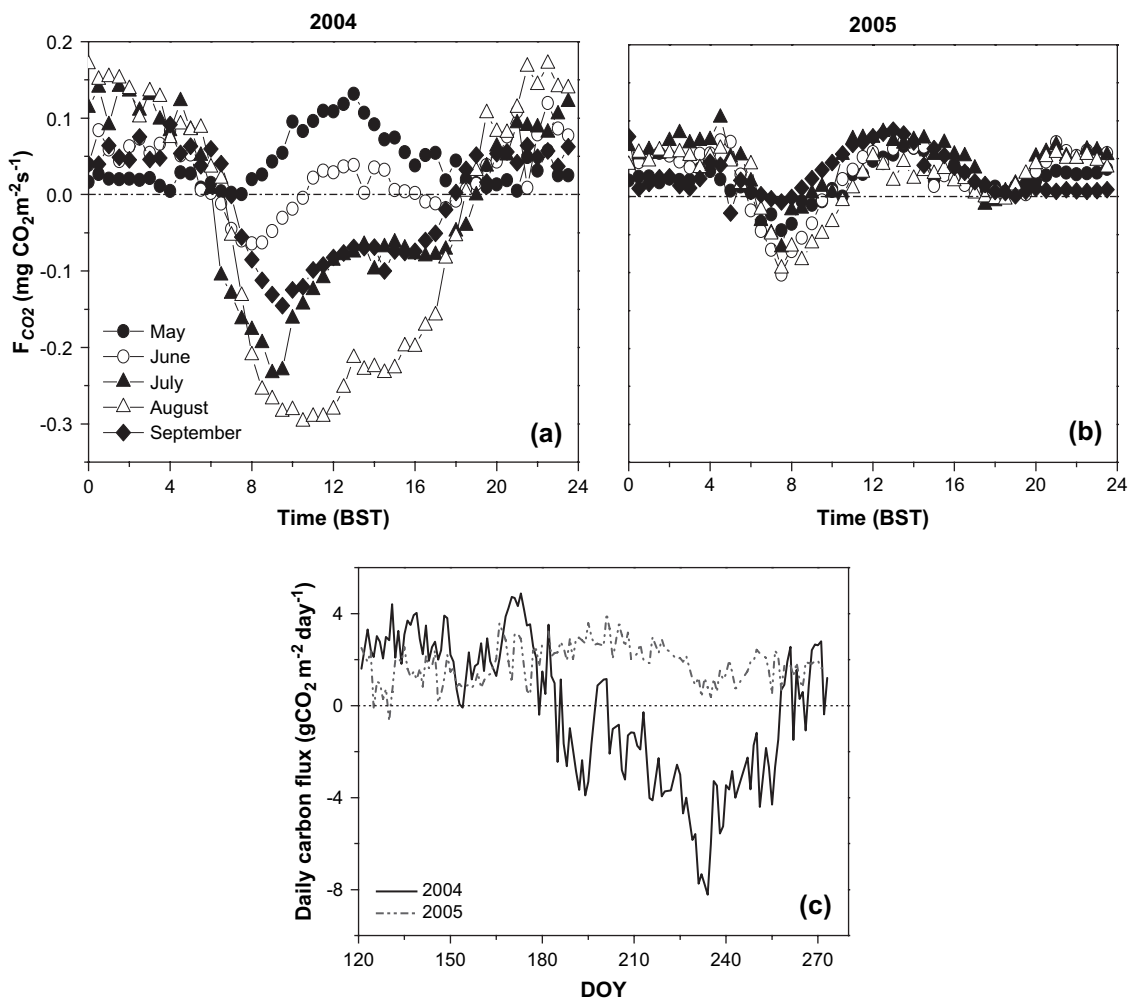


Fig. 5 - (a) Daily course of half-hourly mean  $CO_2$  exchange flux based on monthly processing in wet 2004 (left-hand side); (b) drought 2005 (right-hand side) in the typical steppe, Inner Mongolia Plateau, China; and (c) interannual variation in integrated daily carbon flux.



**Table 2 – Parameters estimated for the model describing the  $F_c$ -PAR relationship under different ranges of vapor pressure deficit (VPD, Kpa) during peak growth period (non-limiting soil water conditions ( $\theta > 0.12 \text{ m}^3 \text{ m}^{-3}$ ), limiting soil water conditions ( $\theta < 0.12 \text{ m}^3 \text{ m}^{-3}$ ))**

Soil water content	VPD	$F_{cm}$	B	PAR*	$R^2$
>0.12	0–1.0	$-0.41 \pm 0.05$	$-0.0007 \pm 0.0009$	$104.9 \pm 12.72$	0.6
	>1.0	$-0.09 \pm 0.008$	$-0.0009 \pm 0.00039$	$78.79 \pm 21.65$	0.2
<0.12	0–1.0	$-0.30 \pm 0.05$	$-0.0005 \pm 0.0001$	$60.2 \pm 16.83$	0.5
	>1.0	$0.10 \pm 0.02$	$-0.0006 \pm 0.0002$	$121.12 \pm 26.7$	0.3

been shown to increase soil respiration. Low temperature sensitivity may be attributed to the decomposition of accumulated litter, which releases more  $\text{CO}_2$  due to high temperatures, and serious drought effects ecosystem respiration. Lloyd and Taylor (1994) indicated that the correlation between drier soil and warmer soil temperatures may result in a decreasing  $Q_{10}$  of soil respiration. From their study of an annual Mediterranean grassland in California, Xu and Baldocchi (2004) suggested that severe drought can inhibit the temperature sensitivity of respiration.

### 3.5. Daily water use efficiency

We found pronounced differences in water use efficiency (WUE) between wet and drought seasons. We calculated daily WUE from daily  $\text{CO}_2$  exchange and water evapotranspiration from the land surface. Higher WUE occurred in 2004 compared to 2005. The higher above-ground biomass and LAI and lower VPD in 2004 may have contributed to the higher WUE in that year. Maximum daily WUE for this steppe was low, with a maximum value of  $\sim 1.2 \text{ mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$  in 2004 and  $0.4 \text{ mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$  in 2005 (Fig. 7a,b). These values are lower than those reported for a northern temperate grassland near Lethbridge, Canada ( $3.13 \text{ mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ ) but are similar to those of a tussock grassland during a summer drought in New Zealand ( $0.46 \text{ mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ ). WUE was well correlated with  $\theta_v$  (Fig. 7a,b).  $\theta_v = 0.12$  was a critical

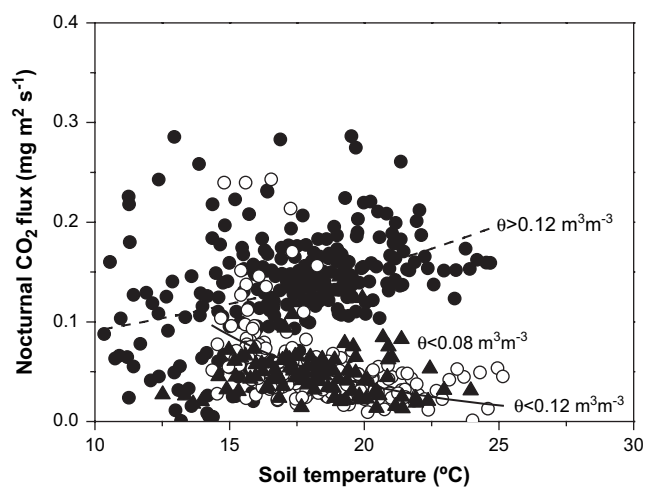
value, which corresponded to soil volume content during soil water stress. The  $\theta_v$  can account for 50% of the variation, whereas other factors, such as above-ground biomass, LAI, and VPD, also control WUE (Wever et al., 2002).

## 4. Conclusions

We observed and compared substantial interannual variation in evapotranspiration and carbon exchange in 2004 and 2005 for a typical steppe on the Inner Mongolia Plateau, China. The wet 2004 growing season had higher peak evapotranspiration rate ( $4 \text{ mm day}^{-1}$ ) than did the 2005 drought season ( $3.3 \text{ mm day}^{-1}$ ). During the wet growing season, high water soil moisture, associated with heavier rainfall, combined with relatively high LAI, above-ground biomass, and low VPD, resulted in a maximum half-hourly  $\text{CO}_2$  uptake of  $-0.68 \text{ mg m}^{-2} \text{ s}^{-1}$  and a maximum ecosystem exchange of  $4.3 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ . Consequently, the ecosystem acted as a carbon sink during the wet summer growing stage. In contrast, the 2005 drought growing stage had a maximum value of  $\text{CO}_2$  exchange of only  $-0.22 \text{ mg m}^{-2} \text{ s}^{-1}$  and had a lasting positive integrated daily  $\text{CO}_2$  flux over the entire growing season, which exceeded 120 days of drought. As a result, the ecosystem was a carbon source in the drought growing season.

Examination of our data under both non-limiting and limiting soil moisture conditions showed that the  $\text{CO}_2$  exchange was substantially controlled by high VPD. Soil respiration was temperature dependent when the soil was under non-limiting soil moisture conditions, but as soil endured water stress, this response became accumulatively decoupled from soil temperature and even decreased at higher temperatures.

Field data, measured with the eddy covariance system, demonstrated that soil moisture significantly affected respiration rate and the ability of a typical steppe to fix carbon. The  $\text{CO}_2$  uptake power of the ecosystem and the possibility of developing a carbon sink mainly depended on the magnitude and timing of rainfall events associated with the phenological stage.



**Fig. 6 – The nocturnal ecosystem respiration as a function of soil temperature.**

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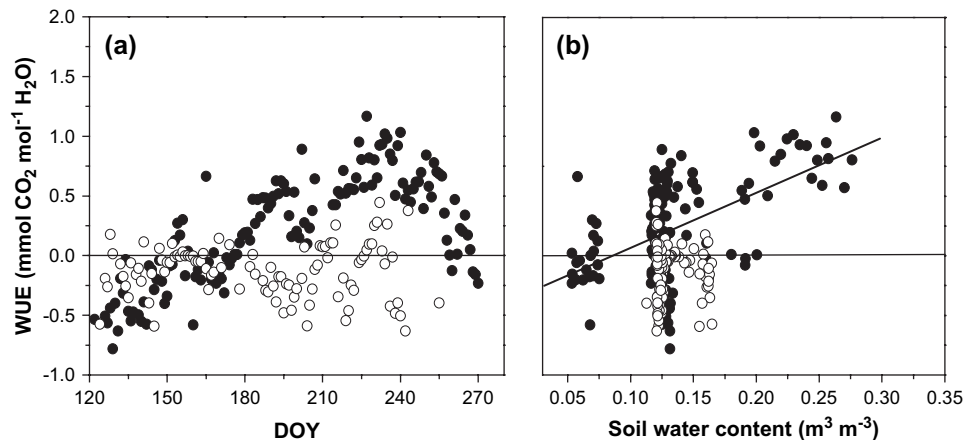


Fig. 7 – (a) Variation in the WUE of the ecosystem during two growing seasons (a) and (b) as a function  $\theta$  in wet 2004 and drought 2005.

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