

# Biophysical regulations of carbon fluxes of a steppe and a cultivated cropland in semiarid Inner Mongolia

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## Abstract

An increasing amount of grasslands in Inner Mongolia of Northern China has been converted to cropland. The conversions in this extensive semiarid region have produced adverse ecological consequences at local and regional scales (e.g., dust storms). An important research need is to understand the fundamental ecosystem processes, such as energy and material fluxes, associated with the land conversions. The carbon fluxes, including net ecosystem exchange (NEE), ecosystem respiration (RE), and gross primary production (GPP) in two contrasting land-use settings – a typical steppe and a crop field in Inner Mongolia – were measured in the growing season (May–September) of 2005 by deploying two eddy covariance flux towers. The diel amplitude of carbon fluxes varied substantially within the growing season, with the largest diel changes occurring in July. The daily maximum NEE of the two ecosystems occurred before noon, while maximum RE occurred around 16:00 pm. There was no difference in RE between the cropland and the steppe at night. Daytime RE in the steppe was higher than that in the cropland in July and August, but slightly lower in other months. GPP was similar between the two ecosystems, in June, but much higher in the cropland than in the steppe in July. The steppe was converted from a weak carbon sink in May to a weak source or carbon neutral in June because of the relatively low soil volumetric water content (VWC) and the relatively high temperature. With higher GPP and lower RE, the cropland ecosystem acted as a stronger sink in July than the steppe. Temperature and soil water content were the main factors controlling NEE in this semiarid agriculture-pasture transition region.

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## 1. Introduction

Grasslands cover 32% of the earth's land surface and are therefore important ecosystems for estimating the total carbon exchange between the land surface and the atmosphere. Unlike most forests, grasslands depend heavily on their responses to climate variability to act as

sinks or sources for atmospheric CO<sub>2</sub> (Parton et al., 1994; Scurlock and Hall, 1998). The Inner Mongolia steppe in Northern China belongs to arid and semiarid regions of the Eurasian continent, but the atmosphere-vegetation interactions are poorly understood. No direct measurements of carbon flux have been reported in the literature concerning net ecosystem CO<sub>2</sub> exchange (NEE) and its dependence on the biophysical environments. Filling this knowledge gap based on the biophysical regulations of carbon flux in semiarid grasslands is essential to address their importance in the global carbon cycle (Hunt et al., 2002).

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With the rapid increase in human population and its subsequent requirements for much more food production, ~40% of grasslands around the world have been managed as arable lands (Lal, 1998). In China, approximately 193 million ha of grasslands have been cultivated since 1949, accounting for 4.8% of the total existing grasslands. The agriculture-pasture transition region in southeast Inner Mongolia has been intensively cultivated for agriculture (Fan et al., 2002). Massive land conversion in the region has not only altered the regional carbon fluxes, but also has been responsible for some severe adverse effects, such as increased intensity and frequency of dust storms, lowered ground water table, and elevated surface run-off (Lu and Yang, 2001). Based on their studies in the southwestern United States, Schlesinger et al. (1990) warned that conversion of semiarid grasslands to row-crop agricultural land would add to small-scale heterogeneity and lead to permanent desertification during future periods of drought related to the climatic change. Among many emerging issues associated with these land conversions, understanding the functional changes and the underlying mechanisms of the grasslands are among the top research priorities for regional and global analysis of human influences (e.g., contribution to the global C cycle, Parton et al., 1993). Additionally, croplands are the most intensively and frequently managed land-use type and, hence, it is very difficult to predict their C sequestration strengths. Net ecosystem production (NEP) of cropland is near zero or slightly positive on an annual basis, but the system is one of the primary regulators for the seasonal fluctuation of global atmospheric CO<sub>2</sub> concentrations (i.e., lowered in summer months) (IPCC, 2001). Consequently, in this study we focused on how grassland conversion had altered the carbon fluxes in the growing season by comparing the carbon fluxes of a steppe and a neighboring cropland converted decades of years ago. Based on micrometeorological measurements, our specific objectives were to: (1) quantify the magnitude of the diel and monthly changes in net ecosystem exchange (NEE), ecosystem respiration (RE) and gross primary production (GPP) of two neighboring ecosystems during the growing season, (2) examine the dependence of carbon fluxes on abiotic and biotic factors, and (3) explore the effects of conversion of grassland to cropland on ecosystem C fluxes.

## 2. Material and methods

### 2.1. Site descriptions

Our study was carried out in Duolun (42°02'N; 116°17'E; 1350 m a.s.l.)—a semiarid agriculture-pasture

transition region in southeastern Inner Mongolia, China. The strong continental climate in this area is characterized with an average annual precipitation of 398.8 mm and mean annual temperature of 3.3 °C, mean monthly temperature of -15.9 °C in January and 19.9 °C in July (1990–2004). The growing season usually starts in late April and ends in early October, with more than 90% of precipitation falling in this period. The soils in the study area are chestnut soils (Yuan et al., 2005).

In April 2005, two eddy covariance flux towers were installed and instrumented for continuous measurements of micrometeorological variables (Section 2.2) and net exchange of CO<sub>2</sub>, H<sub>2</sub>O, and energy (Section 2.3) in two adjacent ecosystems: a steppe grassland and a cropland. Both study sites are flat and about 10 ha in size. The steppe grassland had been fenced since 2001 by Duolun Grassland Restoration Research Station as a long-term study plot, and was dominated by C<sub>3</sub> species (e.g., *Stipa kryroii*, *Agropyron cristatum*, *Artemisia frigida*, and *Leymus chinensis*) and a few C<sub>4</sub> species (e.g., *Cleistogenes squarrosa*). The cropland had been intensively managed by the conventional tillage cropping system for decades and was representative of common land-use types of this region. In general, the crops are planted in mid-May and harvested in mid-September with a mix of C<sub>3</sub> species (e.g., *Triticum aestivum*, *Avena nuda*, and *Fagopyrum esculentum* Moench) and C<sub>4</sub> species (e.g., *Zea mays* and *Setaria italica*).

### 2.2. Micrometeorological measurements

A complete micrometeorological system was installed on each of the eddy towers. Net radiation ( $R_n$ ) was measured above the canopy (4 m above the ground) by a ventilated net radiometer (Q7.1, REBS, Seattle, WA, USA). Three soil heat flux transducers (HFT3, REBS) were placed at a depth of 2–3 cm in the soil to measure soil heat flux ( $G$ ). Photosynthetically active radiation (PAR) was measured with a quantum sensor (LI-190SB, LI-COR, USA) at 4 m above the ground. Three 107 temperature probes (Campbell Scientific Inc. CSI, Logan, USA) were used to measure soil temperatures ( $T_s$ , °C) at 5, 10 and 20 cm in depth. A soil water content reflectometer (CS-616, CSI) was inserted into the soil at a 30° angle to measure volumetric soil water content (VWC, %) of the top 10 cm. Air temperature ( $T_a$ , °C) and relative humidity ( $H$ , %) were measured at heights of 1.5, 2.5 and 4 m above the ground by HMP45C temperature and relative humidity probes (CSI) with radiation shields. Wind speed and direction were measured by a propeller anemometer (05103, CSI) mounted at 3 m above the

ground. Precipitation was measured by a tipping-bucket rain gauge (TE525, CSI). All micrometeorological data were measured every 10 s and averaged over 30 min by a CR23X-TD datalogger (CSI).

### 2.3. Eddy covariance system

An open-path eddy covariance (EC) system was installed at each tower to record the net ecosystem exchange of CO<sub>2</sub> (mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>), latent heat (LE, W s<sup>-1</sup>), and sensible heat (H, W s<sup>-1</sup>) by a CR5000 datalogger (CSI). Each tower included a fast response 3D sonic anemometer (CSAT3, CSI) and an open-path gas analyzer (LI-7500, LICOR). The CSAT3 and LI7500 were mounted at heights of 3 m for the steppe and 4 m for the cropland. The half-hour NEE of CO<sub>2</sub> was calculated from the covariance between vertical wind velocity (m s<sup>-1</sup>) and CO<sub>2</sub> concentration (mg m<sup>-3</sup>) fluctuations using Reynolds decomposition rules (Baldocchi, 2003). CO<sub>2</sub> storage of the vegetation canopy was not measured or included in quantifying NEE in this study because of the relative short canopy height (Li et al., 2005). Positive values of NEE indicated fluxes leaving the surface and negative values indicated exchanges of CO<sub>2</sub> towards the surface.

### 2.4. Criteria for accepting or rejecting flux data

Spurious spikes and anomalous values of NEE were removed from the analysis data set. Half-hour NEE values were excluded from further analysis when: (1) calculated NEE was excessively high (>1 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>) or extremely low (<-1 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>); (2) rainfall events occurred; (3) insufficient sample points ( $N < 15,000$ ) were collected during a 30-min period; or (4) instruments malfunctioned. The data from stable nocturnal periods were also excluded when the friction velocity ( $u^*$ ) was less than 0.15 m s<sup>-1</sup>. In order to derive continuous time series of NEE, data gaps less than 2 h were filled by linear interpolation; larger gaps were filled by means of functional relationships between NEE and air temperature ( $T_a$ , °C) during the nighttime (Eq. (1)) and PAR during the daytime (Eq. (3)) (when  $PAR \geq 100 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) (Falge et al., 2001).

### 2.5. RE and GPP calculations

To separate net ecosystem CO<sub>2</sub> exchange into photosynthetic and respiration fluxes, we applied a conventional method in which GPP and RE are expressed as empirical functions of microclimatic variables. As is often done in long-term CO<sub>2</sub> flux

studies, we determined nighttime RE as an exponential function of air temperature. First, RE values were sorted by different VWC classes, including VWC < 10% and VWC > 10% (saturated soil volumetric water content in this region was about 18%); parameters  $A$  and  $B$  were then estimated under different VWC by fitting nocturnal NEE (i.e., RE) as an exponential function of  $T_a$  (Lloyd and Taylor, 1994):

$$NEE_{\text{nighttime}} = A e^{(BT_a)} \quad (1)$$

where  $A$  is the respiration rate at a temperature of 0 °C. This equation can be re-written as a  $Q_{10}$  relationship with  $B = \ln(Q_{10})/10$  (Lloyd and Taylor, 1994);  $Q_{10}$  is an index of temperature sensitivity of respiration. Based on the assumption that the daytime temperature response of RE is the same as the nighttime, we applied  $A$  and  $B$  to the daytime data to estimate daytime half-hourly RE for each water level. GPP was calculated as (Davis et al., 2003):

$$GPP = -NEE + RE \quad (2)$$

### 2.6. Biophysical regulations

In order to examine the dependence of the NEE–PAR response on abiotic variables, we selected NEE data of sunny days over the entire growing period (from May to August in steppe and from June to August in cropland) with respect to VWC levels (VWC ≤ 10%, 10% < VWC ≤ 14%, and VWC > 14%),  $T_a$  ( $T_a \leq 15$  °C,  $15$  °C <  $T_a \leq 25$  °C, and  $T_a > 25$  °C), and vapor pressure deficit (VPD ≤ 1 kPa, 1 kPa < VPD ≤ 2 kPa, and VPD > 2 kPa). In order to explore the independent effects of VPD and  $T_a$  on NEE–PAR, we analyzed the effects of VPD on NEE–PAR under different temperature level without soil moisture shortage (VWC > 10%). For each of the aforementioned microclimatic conditions, NEE data were further grouped by PAR at 100 μmol m<sup>-2</sup> s<sup>-1</sup> intervals ranging from 0 to 2200 μmol m<sup>-2</sup> s<sup>-1</sup>. NEE was then averaged for each PAR level. Statistically, this data compilation helped to reduce or offset the errors associated with the measurements (Falge et al., 2001; Li et al., 2005).

The Michaelis–Menten equation, referred to as the rectangular hyperbola model, was used to explore light regulation of NEE (Michaelis and Menten, 1913):

$$NEE = [\alpha \times PAR \times NEE_{\text{max}} / \alpha \times PAR + NEE_{\text{max}}] + R_{e,\text{day}} \quad (3)$$

where  $\alpha$  is the apparent quantum yield of the ecosystem,  $NEE_{\text{max}}$  (μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>) the saturation value

of NEE at an infinite light level, and  $R_{e,\text{day}}$  ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) is the bulk  $R_e$  during the daytime (Falge et al., 2001).

### 2.7. Vegetation and soil measurements

Aboveground and belowground biomass were measured in August 2005 by harvesting biomass of four 0.25 m<sup>2</sup> quadrats at the steppe and cropland, respectively. A metallic tube (10 cm in diameter) was driven 20 cm into the soil, with segments of 10 cm. Soil samples were rinsed with water before biomass determination. The biomass samples were dried in an oven at 65 °C for at least 2 days and then weighed. Soil bulk density over 20 cm depth was obtained by a metallic tube (5 cm in diameter). Soil samples of 0–20 cm depth in the two ecosystems were sampled, air-dried for 2 days, and then ground to pass through a 2-mm sieve. Soil organic carbon and total nitrogen contents were determined by an NC analyzer (KDY-9820, Tongrun Ltd., China).

### 2.8. Energy budget closure

We compared ( $R_n - G - S_{\text{soil}}$ ) and ( $LE + H$ ) over specified time periods to evaluate the energy balance ratio (EBR):

$$\text{EBR} = \frac{LE + H}{R_n - G - S_{\text{soil}}} \quad (4)$$

where LE is the latent heat,  $H$  the sensible heat, and  $S_{\text{soil}}$  is the heat storage in the soil layer above the heat flux plates for each 30-min period (Oliphant et al., 2004). The advantage of EBR is that it provides an overall evaluation of energy enclosure at larger temporal scales by averaging over random errors in the half-hour measurements (Mahrt, 1998; Gu et al., 1999; Wilson, 2002). Over the study period, EBR of the steppe was 0.84 ( $R^2 = 0.72$ ) and that of the croplands was 0.99 ( $R^2 = 0.60$ ); these values are within the range of mean imbalance of those reported at FLUXNET sites by Wilson (2002).

## 3. Results

### 3.1. Abiotic and biotic factors

Seasonal variation in PAR and precipitation (PPT) from 1 May 2005 to 30 September 2005 in the steppe and cropland sites were similar (Fig. 1A and B). Daily PAR reached its maximum in late June and then decreased gradually (Fig. 1B). Monthly

precipitation ranged from 22.3 to 92.7 mm, peaking in July. The maximum daily  $T_a$  and soil temperature ( $T_s$ ) occurred in July or August ( $\approx 25$  °C), and the minimums occurred in May ( $\approx 5$  °C) (Fig. 1D and E). Seasonal variation in soil volumetric water content (VWC) followed the PPT pattern closely, with low records (<10%) until July and August (Fig. 1C).

The aboveground biomass of the cropland (363.7 g m<sup>-2</sup>) was significantly higher than that of the steppe (115.8 g m<sup>-2</sup>) ( $P < 0.001$ ) (Table 1). However, the belowground biomass from 0 to 20 cm depth of the cropland (68.1 g m<sup>-2</sup>) was significantly lower than that of the steppe (151.1 g m<sup>-2</sup>) ( $P < 0.01$ ). No significant differences were found in the soil organic carbon content or the total nitrogen content of the two ecosystems. Soil bulk density of the steppe was significantly higher than that of the cropland ( $P < 0.05$ ) (Table 1).

### 3.2. Biophysical regulation of NEE

The Michaelis–Menten model (Eq. (3)) appeared to be an appropriate model for modeling daytime NEE at both ecosystems under different microclimates (Fig. 2). Net ecosystem exchange increased with PAR at low-to-intermediate levels of PAR, but as PAR exceeded the light saturation point (1000  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  at  $\text{VWC} \leq 10\%$  for both ecosystems;  $\sim 1200$  and  $1600 \mu\text{mol m}^{-2} \text{ s}^{-1}$  at  $\text{VWC} > 10\%$  for steppe and cropland, respectively), NEE began to decline (Fig. 2). Light saturated rates of net photosynthetic assimilation ( $\text{NEE}_{\text{max}}$ ) of the two ecosystems were greatly affected by VWC,  $T_a$ , and VPD.  $\text{NEE}_{\text{max}}$  increased with increasing VWC (Table 2). In the steppe,  $\text{NEE}_{\text{max}}$  when  $\text{VWC} > 14\%$  was twice that when  $\text{VWC} \leq 10\%$ . When VWC dropped to lower than 10% in the cropland,  $\text{NEE}_{\text{max}}$  was only 20–25% of that recorded when  $\text{VWC} > 10\%$ .  $T_a$  also had notable effects on  $\text{NEE}_{\text{max}}$ . The  $\text{NEE}_{\text{max}}$  in the two ecosystems was highest when  $T_a$  varied from 15 to 25 °C (Table 2). At these intermediate temperatures,  $\text{NEE}_{\text{max}}$  in the cropland was nearly 50% higher than in the steppe.  $\text{NEE}_{\text{max}}$  declined with increasing VPD.  $\text{NEE}_{\text{max}}$  of both ecosystems at the lowest VPD ( $\leq 1$  kPa) were more than twice those at the highest VPD ( $> 2$  kPa).  $\text{NEE}_{\text{max}}$  in the cropland was 38% higher than in the steppe under VPD less than 1 kPa.

Apparent quantum yield at the ecosystem level ( $\alpha$ ) showed clear differences in both ecosystems (Table 2). The  $\alpha$  of both ecosystems at low VPD ( $\leq 1$  kPa) was more than twice the  $\alpha$  at high VPD ( $> 2$  kPa). At the

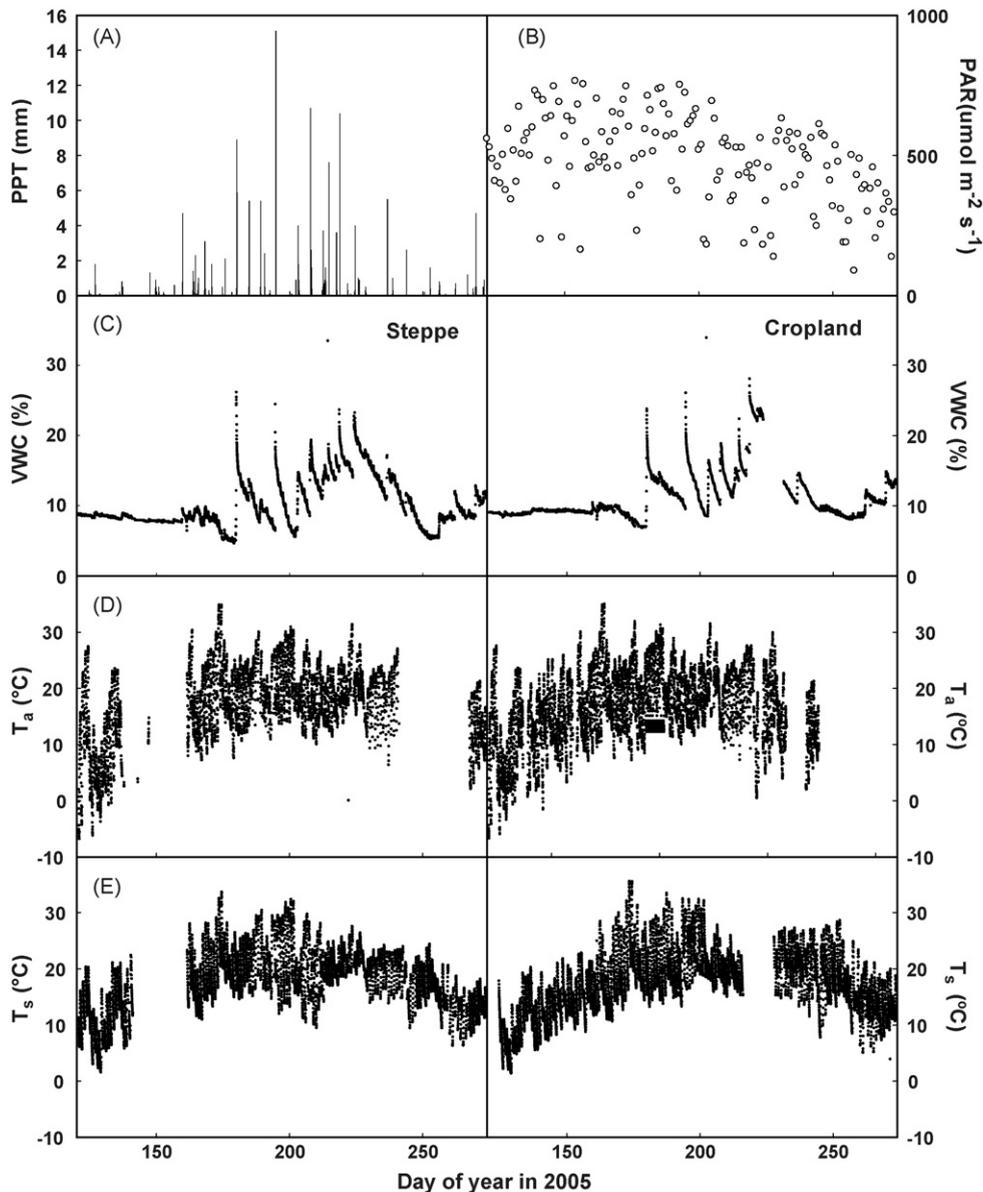


Fig. 1. Seasonal variations of (A) precipitation (PPT), (B) daily photosynthetic available radiation (PAR), (C) soil volume water content (VWC, 0–10 cm), (D) air temperature ( $T_a$ ) and (E) soil temperature ( $T_s$ ) in the steppe and cropland ecosystems from Julian days 121 to 274 of 2005 at Duolun, Inner Mongolia. Blank spaces in the figures indicate lost data due to power failure.

optimum temperature and VWC,  $NEE_{max}$  and  $\alpha$  of both ecosystems decreased with increasing VPD (Table 3). When VPD was less than 1 kPa and  $T_a$  was less than 15 °C,  $NEE_{max}$  in the steppe was higher than that in the cropland. And the changes of  $NEE_{max}$  in the steppe with temperature when  $VPD < 1$  kPa was much smaller than that in the cropland under the same VPD conditions. At  $1 \text{ kPa} < VPD \leq 2 \text{ kPa}$ ,  $NEE_{max}$  and  $\alpha$  of the steppe were depressed much while those of cropland changed little when  $T_a$  was over 25 °C. When VPD was over

2 kPa,  $NEE_{max}$  and  $\alpha$  of the two ecosystems were depressed (Table 3).

We determined RE as an exponential function of  $T_a$  (Eq. (1)) under different VWC levels (Table 4). With increasing VWC,  $R_0$  in cropland ecosystems also increased, but no changes occurred in the steppe.  $Q_{10}$  at low VWC ( $\leq 10\%$ ) was 2.64 and 2.87 in the steppe and cropland, respectively.  $Q_{10}$  in the steppe (3.31) was much higher than in the cropland (1.73) when VWC increased to more than 10%.

Table 1  
 Characteristics of the steppe and cropland sites at Duolun, Inner Mongolia

	Steppe	Cropland
Aboveground biomass (DW g m <sup>-2</sup> )	115.8 ± 15.1	363.6 ± 17.9 <sup>***</sup>
Belowground biomass (DW g m <sup>-2</sup> )	151.1 ± 19.9	68.1 ± 9.0 <sup>**</sup>
Soil organic carbon content (%)	1.14 ± 0.15	1.33 ± 0.06
Soil total nitrogen content (%)	0.14 ± 0.01	0.15 ± 0.01
Bulk density of soil (g cm <sup>-3</sup> )	1.4 ± 0.04	1.2 ± 0.03 <sup>*</sup>
Dominant species	<i>Stipa kryroii</i> <i>Agropyron cristatum</i> <i>Artemisia frigida</i>	<i>Triticum aestivum</i> <i>Avena nuda</i> <i>Fagopyrum esculentum</i>

Belowground biomass, organic carbon content, total nitrogen content, and bulk density were measured from soil samples taken over 0–20 cm depth.

<sup>\*</sup>  $P < 0.05$ .  
<sup>\*\*</sup>  $P < 0.01$ .  
<sup>\*\*\*</sup>  $P < 0.001$ .

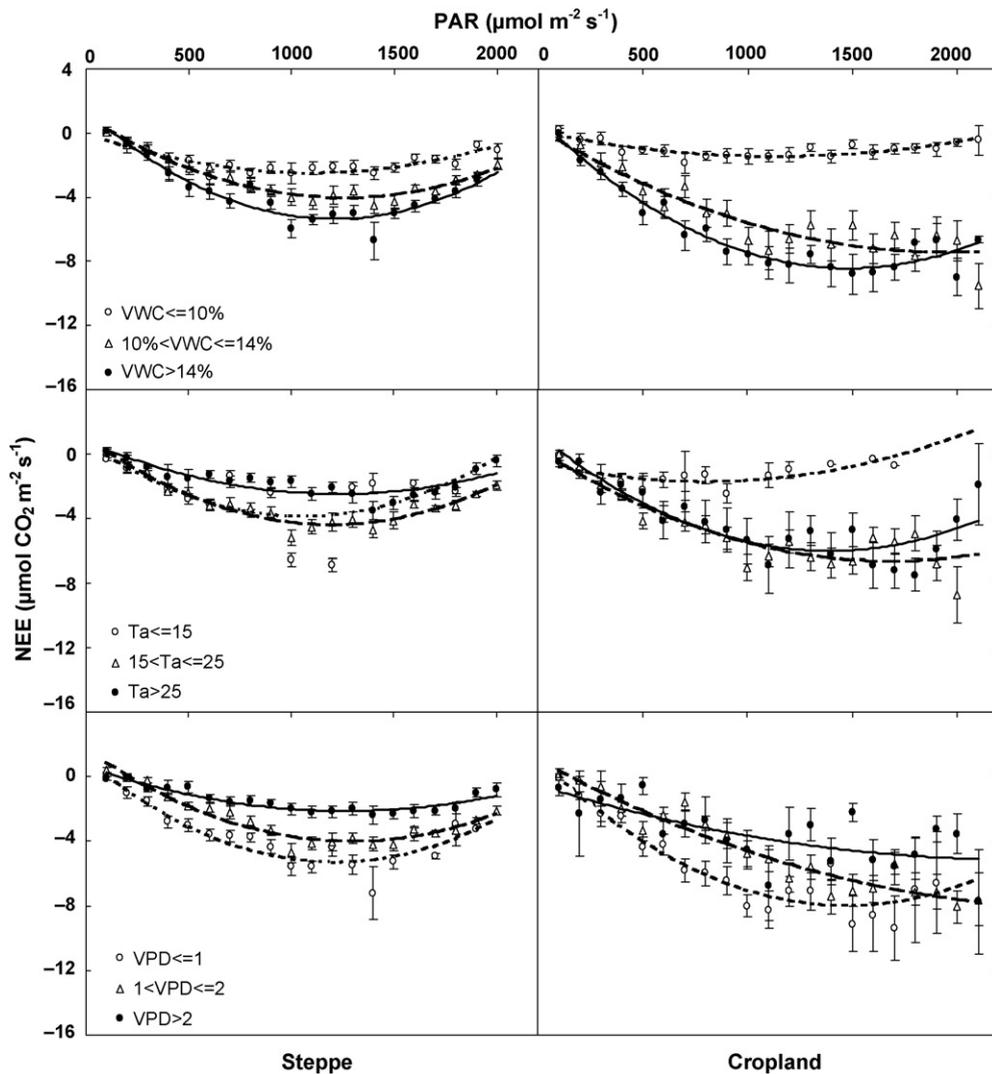


Fig. 2. Light response curves under different volumetric soil water content (VWC), air temperature ( $T_a$ ), and vapor pressure deficit (VPD) levels in the steppe and cropland ecosystems.

Table 2

Values of the parameters describing features of the rectangular hyperbolic responses of daytime NEE to incident PAR (Eq. (3)) under different VWC,  $T_a$  and VPD levels in the steppe and cropland ecosystems

	NEE <sub>max</sub> ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )		$R_{e,\text{day}}$ ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )		$\alpha$ ( $\text{mol mol}^{-1}$ )		$R^2$	
	Steppe	Cropland	Steppe	Cropland	Steppe	Cropland	Steppe	Cropland
VWC $\leq$ 10%	2.9 $\pm$ 0.4	1.8 $\pm$ 0.5	-0.9 $\pm$ 0.1	-0.7 $\pm$ 0.5	0.007 $\pm$ 0.001	0.004 $\pm$ 0.002	0.53	0.37
10% < VWC $\leq$ 14%	3.9 $\pm$ 0.5	9.5 $\pm$ 3.1	-0.3 $\pm$ 0.5	-0.9 $\pm$ 1.1	0.005 $\pm$ 0.001	0.01 $\pm$ 0.005	0.63	0.89
VWC > 14%	5.8 $\pm$ 1.2	8.3 $\pm$ 0.9	-1.0 $\pm$ 1.1	-0.3 $\pm$ 0.7	0.008 $\pm$ 0.004	0.009 $\pm$ 0.002	0.95	0.77
$T_a \leq 15^\circ\text{C}$	3.4 $\pm$ 0.7	1.5 $\pm$ 1.3	-0.2 $\pm$ 0.01	-0.3 $\pm$ 1.3	0.006 $\pm$ 0.003	0.007 $\pm$ 0.008	0.35	0.66
15 $^\circ\text{C} < T_a \leq 25^\circ\text{C}$	4.4 $\pm$ 0.04	8.2 $\pm$ 2.7	-0.8 $\pm$ 0.1	-1.0 $\pm$ 1.4	0.007 $\pm$ 0.0003	0.01 $\pm$ 0.007	0.81	0.92
$T_a > 25^\circ\text{C}$	2.8 $\pm$ 1.5	5.6 $\pm$ 1.0	-0.6 $\pm$ 1.3	-0.03 $\pm$ 0.9	0.005 $\pm$ 0.007	0.005 $\pm$ 0.001	0.74	0.36
VPD $\leq$ 1 kPa	4.9 $\pm$ 1.4	8.1 $\pm$ 0.8	-0.1 $\pm$ 1.4	-0.4 $\pm$ 0.7	0.006 $\pm$ 0.004	0.008 $\pm$ 0.001	0.41	0.45
1 kPa < VPD $\leq$ 2 kPa	4.5 $\pm$ 0.5	7.8 $\pm$ 0.5	-0.8 $\pm$ 0.4	-0.7 $\pm$ 0.4	0.005 $\pm$ 0.001	0.005 $\pm$ 0.001	0.61	0.79
VPD > 2 kPa	2.0 $\pm$ 0.3	4.0 $\pm$ 0.9	-0.1 $\pm$ 0.3	-0.3 $\pm$ 0.7	0.002 $\pm$ 0.001	0.004 $\pm$ 0.001	0.43	0.26

### 3.3. Diel and seasonal changes

The diel patterns of carbon fluxes (GPP, NEE and RE),  $T_a$ ,  $T_s$ , and PAR, averaged by month during the growing season, were presented in Fig. 3. Daily and monthly patterns in  $T_a$  were similar for the two ecosystems. Daytime  $T_s$  and nighttime  $T_s$  of the steppe were, respectively, 1.7  $^\circ\text{C}$  higher and 2  $^\circ\text{C}$  lower than those of the cropland in July, whereas no significant differences in  $T_s$  existed between the two ecosystems in other months (Fig. 3). Daytime average PAR exhibited a symmetrical distribution, peaking around noon; maximum PAR values occurred in June, while gradually decreasing from August. The diel amplitude of carbon fluxes varied substantially within the growing season. The largest diel changes in the two ecosystems were recorded in July. We also found that the variation of daily NEE in July was greater in the cropland (0.74  $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) than in the steppe (0.48  $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ). Overall, the daily NEE peaked before noon in both ecosystems, while the daily maximum RE occurred around 16:00 pm. The daily peak value of NEE in July was -0.29  $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in the steppe and -0.59  $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in the cropland, respectively. The daily peak value of RE in July of the steppe was 0.31  $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , while that of the cropland was 0.18  $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ . No significant difference in RE was found between the two ecosystems at night. Daytime RE in the steppe was higher than that in the cropland in July and August, but slightly lower in other months.

We detected no significant difference in GPP between the two ecosystems in June. GPP of the cropland in July was higher than that of the steppe ( $P < 0.01$ ) (Table 5). There were no differences in RE between the two ecosystems during May, June and

August. RE of the steppe was lower than that of the cropland in September, whereas it was much higher than that of the cropland in July ( $P < 0.05$ ) (Table 5). The ability of the two ecosystems to assimilate  $\text{CO}_2$  was the strongest in July ( $P < 0.05$ ). The net daily ecosystem exchange (NEP) for the cropland was 6.96  $\text{mg CO}_2 \text{ m}^{-2} \text{ day}^{-1}$  in July, much higher than that for the steppe (1.46  $\text{mg CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ ) ( $P < 0.01$ ) (Table 5).

## 4. Discussion

### 4.1. Dependence of NEE–PAR relationship on abiotic factors

Drought is the most critical environmental factor in semiarid grassland ecosystems (Seastedt et al., 1998; Li et al., 2005). It can substantially change plant physiology and therefore impact  $\text{CO}_2$  uptake (Hunt et al., 2002). Saturated NEE (NEE<sub>max</sub>) showed an increase with increasing VWC at our sites (Fig. 2 and Table 2), which was consistent with results from another study in the steppe in Mongolia (Li et al., 2005). Stomatal regulation of photosynthesis during periods of water shortage has been well documented (Chaves, 1991). At least under mild drought conditions, it has been shown that closure of the stomata causes a decline in net  $\text{CO}_2$  uptake and leads to decreases in leaf internal  $\text{CO}_2$  concentrations (Cornic, 2000). Moreover, the limitations to  $\text{CO}_2$  assimilation imposed by stomatal closure might promote an imbalance between photochemical activity and electron requirements for photosynthesis, leading to photoinhibition (Souza et al., 2004). That is, high light intensity is most likely to exceed the capacity for orderly dissipation of the energy absorbed by the photosynthetic systems of the leaves



Table 4

Values of the parameters describing the relationship between RE and  $T_a$  under different VWC in the steppe and cropland ecosystems ( $P < 0.05$ )

	$R_0$ (mg CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )		$Q_{10}$		$R^2$	
	Steppe	Cropland	Steppe	Cropland	Steppe	Cropland
VWC ≤ 10%	0.01	0.01	2.92	2.87	0.37	0.40
VWC > 10%	0.01	0.04	3.31	1.73	0.41	0.09

carbon uptake of a steppe in Mongolia increased linearly with temperature when water stress was removed. Temperature influences photosynthesis and respiration of plants primarily via temperature-dependent enzyme (Law et al., 2002). In our study, the optimum temperature for  $NEE_{max}$  appeared between 15 and 25 °C. Significant reduction in carbon assimilation was found when  $T_a$  was >25 °C in both ecosystems (similar to those reported by Li et al., 2005).  $NEE_{max}$  and  $\alpha$  of both ecosystems decreased with increasing in

VPD, because of the physical cohesiveness between temperature and VPD which influences photosynthesis and respiration of plants primarily via stomatal aperture (Farquhar et al., 1980) and due to the facts that high temperatures are often accompanied with low relative humidity in this region. The changes of  $NEE_{max}$  in the steppe with temperature when VPD < 1 kPa was much smaller than that in the cropland under the same VPD conditions, suggesting a stronger temperature dependence of the crops. At 1 kPa < VPD ≤ 2 kPa,  $NEE_{max}$

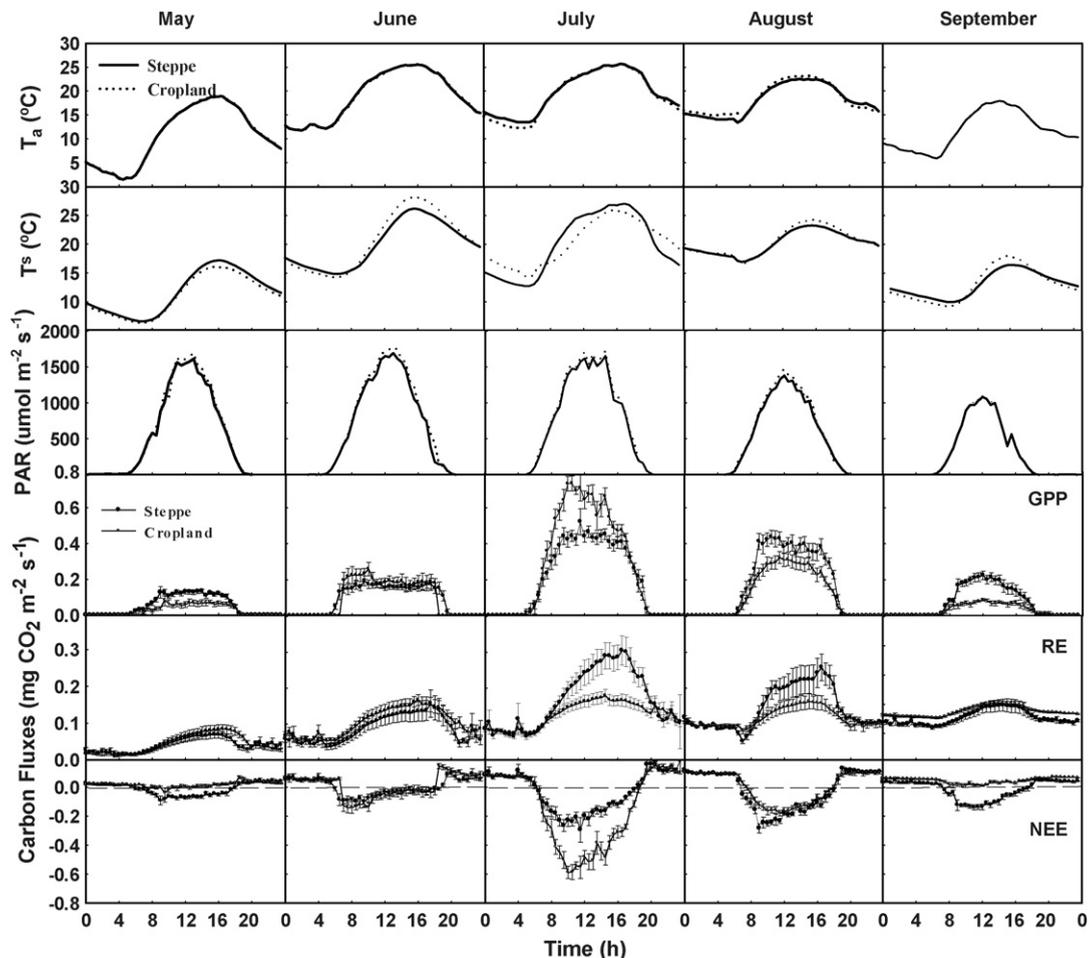


Fig. 3. Diel variations of monthly means of abiotic factors ( $T_a$ ,  $T_s$  and PAR) and carbon fluxes (GPP, RE and NEE) of the steppe and cropland ecosystems from May to September in 2005. GPP = gross primary production; NEE = net ecosystem exchange; RE = ecosystem respiration. The data shown are means of data from 7 to 10 typical sunny days selected in each month for two ecosystems.

Table 5

Monthly mean values of gross primary production (GPP), ecosystem respiration (RE), and net ecosystem production (NEP) in the steppe and cropland ecosystems during the growing season of 2005

	GPP (mg CO <sub>2</sub> m <sup>-2</sup> day <sup>-1</sup> )		RE (mg CO <sub>2</sub> m <sup>-2</sup> day <sup>-1</sup> )		NEP (mg CO <sub>2</sub> m <sup>-2</sup> day <sup>-1</sup> )	
	Steppe	Cropland	Steppe	Cropland	Steppe	Cropland
May	2.73 ± 0.24 a	1.30 ± 0.24 A **	-2.11 ± 0.31 a	-2.13 ± 0.32 A	0.62 ± 0.27 ab	-0.83 ± 0.21 B **
June	4.19 ± 0.44 b	4.53 ± 0.66 B	-4.15 ± 0.68 b	-5.01 ± 0.57 C	0.04 ± 0.41 a	-0.48 ± 0.47 B
July	9.57 ± 0.47 d	13.02 ± 0.55 C **	-8.11 ± 0.73 d	-6.09 ± 0.39 C *	1.46 ± 0.54 b	6.96 ± 0.58 C **
August	7.41 ± 0.47 c	5.53 ± 0.70 B **	-6.11 ± 0.45 c	-5.61 ± 0.47 C	1.31 ± 0.23 b	-0.08 ± 0.34 B **
September	3.34 ± 0.39 ab	1.40 ± 0.21 A **	-2.56 ± 0.41 ab	-3.63 ± 0.15 B *	0.78 ± 0.20 ab	-2.24 ± 0.10 A **

Positive values indicate CO<sub>2</sub> uptake and negative values indicate CO<sub>2</sub> release. Different letters indicate significant differences ( $P < 0.05$ , one-way ANOVA) among months in each ecosystem (small letters for steppe and capitals for cropland). Asterisks indicate differences in the means between the steppe and the cropland (\* $P < 0.05$ , \*\* $P < 0.01$ , *t*-test).

and  $\alpha$  of the steppe were more severely reduced than those of the crops when  $T_a$  was over 25 °C. These results suggested that the steppe performed better (i.e., higher NEE) at low temperatures while the crops do better under higher temperature. When VPD was greater than 2 kPa,  $NEE_{max}$  and  $\alpha$  of the two ecosystems showed similar reduction, suggesting a similar threshold on both ecosystems. Future research is needed to quantify the changes of  $T_a$ -VPD conditions in this region and assess their interactive influences (e.g., via modeling and multivariate analysis).

Our results clearly indicated that soil water content and temperature were the main factors controlling ecosystem carbon assimilation. The cropland ecosystem had a stronger ability to uptake carbon than the native steppe ecosystem under optimal soil water and temperature conditions due to species and management. The steppe showed relatively greater carbon uptake under drought stress and low air temperature conditions, which might be the result of evolutionary adaptations of steppe species to local stressful environments.

#### 4.2. Nighttime RE- $T_a$ relationships under different VWC levels

Temperature sensitivity of respiration is often expressed by  $Q_{10}$ , the factor by which respiration rate increases with every 10 °C increase in temperature. The  $Q_{10}$ -based formulation has been used commonly to calculate soil or ecosystem respiration at local to global scales (e.g., Cox et al., 2000; Fang and Moncrieff, 2001; Falge et al., 2002). However, the temperature response of respiration has been questioned recently. It has been documented that effects of temperature and moisture on  $Q_{10}$  are of critical importance in assessing the impacts of changing climate on ecosystem carbon fluxes (Betts, 2000; Wen et al., 2006). Therefore, we determined RE as an exponential function of  $T_a$  under different VWC

levels. Flanagan and Johnson (2005) reported that  $Q_{10}$  declined with reductions in soil moisture. However, there was an abnormal relationship between  $Q_{10}$  and VWC in our study. No difference in  $Q_{10}$  was seen between the two ecosystems in the early or late growing season when VWC was less than 10%. During the peak-growing season, VWC was higher than 10% most of the time due to frequent rain events, and  $Q_{10}$  values in the steppe increased to 3.77 while those in the cropland decreased to 1.73; these results might be caused by the contributions of different compositions to RE.

Ecosystem respiration (RE) is a composite flux, comprising aboveground respiration by foliage and stem tissues, and belowground respiration (soil respiration) by roots (autotrophic soil respiration,  $R_a$ ) and soil organisms (heterotrophic soil respiration,  $R_h$ ) (Janssens et al., 2001). Soil respiration is generally the largest flux contributing to RE. Dugas et al. (1999) demonstrated that up to 90% of soil CO<sub>2</sub> flux was due to root respiration in the prairie. At a given site, root respiration will increase with temperature because root biomass typically peaks in summer and specific root respiration rates increase with temperature (Zogg et al., 1996). Thus, in the absence of drought stress, temperature would exert dominant control over autotrophic soil respiration (Janssens et al., 2001), and root respiration should have a higher  $Q_{10}$  value than soil heterotrophic respiration. Boone et al. (1998) and Lavigne et al. (2003) demonstrated that root respiration had a higher  $Q_{10}$  value than soil heterotrophic respiration in both a temperate and a boreal forest. The belowground biomass of the steppe in August was much higher than that of the cropland ( $P < 0.01$ ) (Table 1), which could explain its higher  $Q_{10}$  value during the peak-growing season. Moreover, organic matter pools in the undisturbed soils of the steppe contributed less to soil respiration than organic matter in the cropland, where ploughing disturbed soil structure and accelerated

decomposition of soil organic matter (especially with moderate soil water level), increasing heterotrophic respiration rates (Lindroth et al., 1998) and resulting in a higher contribution to RE. Compared with Ra, Rh had a relatively lower  $Q_{10}$  value. Thus, the  $Q_{10}$  value of RE in the cropland was low during the peak-growing season without water stress. However, Tang et al. (2005) reported a lower  $Q_{10}$  for root respiration than soil heterotrophic respiration in a ponderosa pine plantation. Obviously, there is little agreement on temperature sensitivity of Ra and Rh. More empirical data are needed to confirm these patterns. It further indicated that the temperature sensitivity of RE depended not only on the soil water conditions but also on the biome type and the phenological stage of plant growth and development (DeForest et al., 2006).

#### 4.3. Diel and seasonal variation of NEE

Net ecosystem exchange (NEE) of CO<sub>2</sub> between the biosphere and the atmosphere is the balance between fluxes associated with photosynthetic assimilation by the foliage (i.e. GPP) and respiratory effluxes (RE). Multiple factors control NEE, including climate, nutrition, biome type, and physiological differences associated with the age of dominant vegetation and disturbance history (Schulze et al., 1999, 2000; Chen et al., 2002).

CO<sub>2</sub> uptake by plant species generally respond nonlinearly to increasing photosynthetically active radiation (PAR) with the absence of water stress while light intensity is low (Hanan et al., 2002). In our study, although highest PAR occurred at noon, CO<sub>2</sub> uptake by the canopies of the two ecosystems was stronger before noon during the growing season (Fig. 3). The asymmetrical distribution of NEE around noon was similar to the results from another study in a semiarid steppe in Mongolia by Li et al. (2005). Carbon assimilation was limited around noon and early afternoon because of low enzyme activity at high temperatures and stomatal closure at high VPD under higher PAR levels. The midday depression of photosynthesis is a common phenomenon for many plants in semiarid areas due to light stress and/or concomitant high temperature stress (e.g., Matos et al., 1998; Zhang and Gao, 1999; Fu et al., 2006) and is a survival strategy for plants (Chaves et al., 2002). The maximum daily NEE appeared earlier under low soil moisture conditions (in June), which also confirmed the dependence of the NEE–PAR response curve on VWC. However, RE, showing a different pattern than NEE, usually reached peak values in the afternoon (Fig. 3), indicating its greater dependence on changes in temperature.

At the beginning of the growing season (in May), low temperature and young vegetation limited carbon assimilation and respiration of ecosystems. Especially in the cropland ecosystem, there was almost no net carbon uptake prior to crop plantation. In addition, ploughing altered soil structure in croplands, which not only drove higher release rates of soil CO<sub>2</sub>, but also exposed previously physically protected soil organic carbon for consumption by micro-organisms (Watts et al., 2000). Therefore, the cropland released more CO<sub>2</sub> during spring than the steppe, becoming a weak carbon source.

With temperature increases and vegetation development, carbon assimilation and respiration were significantly elevated in June. However, carbon assimilation was limited greatly when temperature and PAR increased beyond certain levels and scarce precipitation induced drought stress in this period. As a result, the two ecosystems became weak carbon sinks, assimilating CO<sub>2</sub> only in the early morning and neither taking up nor releasing carbon for the remainder day, which was similar to another steppe site in Mongolia in May and June (Li et al., 2005). Yu et al. (2006) showed that water stress was the primary factor causing depression of net ecosystem CO<sub>2</sub> exchange in the semiarid steppe ecosystem in Inner Mongolia. Soil water moisture clearly played an important role in controlling net carbon exchange in this region.

During the peak-growing season, the maximum NEE of the steppe in July was  $-0.29 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , which was low compared with North American prairie grasslands and rangelands, where maximum CO<sub>2</sub> exchanges of  $-0.607$  (Meyers, 2001),  $-1.012$  (Ham and Knapp, 1998),  $-1.232$  (Dugas et al., 1999), and  $-1.496 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  (Verma et al., 1992) had been reported. However, maximum NEE of the steppe was close to nutrient-poor serpentine grasslands in California ( $-0.352 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , Valentini et al., 1995), but higher than the Brazilian Cerrado grasslands during the dry season ( $-0.176 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , Miranda et al., 1997), New Zealand grassland in summer ( $-0.216 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , Hunt et al., 2002), and the over-grazed steppe in central Mongolia in July ( $-0.158 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , Li et al., 2005). The maximum NEE ( $-0.59 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) of the cropland was very low compared with agricultural crops under more favorable conditions (e.g., from  $-1.98$  to  $-2.992 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  observed by Baldocchi (1994) for closed wheat crops). Parton et al. (1993) compared soil organic carbon content (SOC) of the surface layer (0–20 cm) of 12 typical grasslands worldwide and demonstrated that the values ranged

from 2 to 10 kg C m<sup>-2</sup>. The SOC of the surface layer (0–20 cm) in the two ecosystems at Duolun ( $\approx 3$  kg C m<sup>-2</sup>) were at the lower end of this range, indicating that low nutrient availability was probably one of the factors limiting NEE in this region.

In later part of the growing season, the magnitudes of the maximum NEE declined (Fig. 3). This suggested that phenological stage of plant growth and development was another major influence on NEE (see DeForest et al., 2006). This could be clearly seen from seasonal changes in NEE of the cropland. The cropland was a weak carbon source before plantation (in May). During the peak-growing season (i.e., summer), it became a strong carbon sink since the crops had much higher light use efficiency and stronger ability to uptake carbon than the native grasses. After maturity and harvest, the ecosystem quickly changed from a carbon sink to a carbon source (Table 4). Ham and Knapp (1998) showed that the rate of transition from sink to source was governed by the phenology of the canopy rather than abrupt environmental changes.

The structure of the vegetation in our study also influenced NEE (e.g., the cropland had greater vegetative cover and maximum NEE nearly twice that of the steppe). An increasing body of literature suggests that the structure and density of vegetation influences the amount of absorbed incoming short-wave radiation and the turbulent exchanges of momentum, heat, and moisture (Bounoua et al., 2002). In July, mean daytime  $T_s$  in the steppe were 1.7 °C higher than that in the cropland (Fig. 3). Bonan (1997) found that land-use change in the central United States, primarily conversion of grassland to cropland, had led to summertime surface temperature cooling up to 2 °C. This was because crops had a higher maximum photosynthetic rate than grassland at that time, resulting in greater canopy conductance to CO<sub>2</sub> and water. Accordingly, an increase in transpirational cooling with land cover conversion further cooled surface temperature (Bounoua et al., 2002). Conversely, at the beginning and the end of the growing season, the crops were low and their ability to uptake CO<sub>2</sub> was weak, thus no difference in  $T_s$  between the cropland and in the steppe during those times. Slightly higher  $T_s$  and higher sensitivity of RE to  $T_s$  in July made RE in the steppe much higher than in the cropland. With higher GPP and lower RE, the cropland ecosystem acted as a stronger sink at that time than the steppe. However, the growing period for the crops was short (from June to August) and nearly 76% of the biomass in the cropland was harvested at the end of the

growing season, leaving only 94.9 g m<sup>-2</sup> dry biomass in the system; thus, conversion of grassland to cropland reduced the ecosystem C sequestration ability.

## 5. Conclusion

We found a strong seasonality in NEE and its apparent dependence on environmental factors. Both the steppe and cropland ecosystems were water limited during most of the growing season. The flux measurements showed that the steppe was a weak carbon sink during the growing season, but drought and high temperature could switch it from a carbon sink to a neutral in C sequestration temporarily. The cropland had a stronger ability to uptake carbon and higher light use efficiency than native steppe. However, harvesting removed 76% of the cropland biomass, greatly reducing its sequestration strength. It is not enough for us to evaluate the actual effects of converting grassland to cropland based on the data only from one growing season. Longer term carbon fluxes data are needed to improve our knowledge on the effects of conversion of grassland to cropland on carbon fluxes in this region. At the same time, the variability of NEE as a function of environmental conditions suggested that the two ecosystems were very sensitive to environmental factors such as drought stress and high temperature.

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