

Effects of Spring Drought on Carbon Sequestration, Evapotranspiration and Water Use Efficiency in the Songnen Meadow Steppe in Northeast China

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ABSTRACT

Global climate change projections suggest an increasing frequency of droughts and extreme rain events in the steppes of the Eurasian region. Using the eddy covariance method, we measured carbon and water balances of a meadow steppe ecosystem in Northeast China during 2 years which had contrasting precipitation patterns in spring seasons in 2007 and 2008. The meadow steppe sequestered only 64.2 gC m⁻² year⁻¹ in 2007 compared to 160.5 gC m⁻² year⁻¹ in 2008, due to a severe spring drought in 2007. The 2007 spring drought resulted in a dramatic reduction of leaf area index (LAI) and aboveground net primary productivity (ANPP). However, the meadow steppe still acted as a carbon sink in 2007. The strength of the sink was much greater than that in the typical steppes in Central Mongolia and Inner Mongolia. Spring drought also caused a reduction of plant transpiration (Tr) and total ecosystem evapotranspiration (ET). However, the suppression of ET in 2007 was relatively small in comparison to gross ecosystem productivity (GEP) reduction. Thus, ecosystem water use efficiency (WEU) (GEP/ET) in 2007 was reduced to 5.0 gCO₂ kg⁻¹ H₂O or 75% of that of 2008. We concluded that spring drought detrimentally impacted meadow steppe ecosystem by reducing leaf areas, biomass, GEP, WUE and associated increases in soil evaporation (Es) that might aggravate soil salinization of the Songnen Plain. Copyright © 2011 John Wiley & Sons, Ltd.

KEY WORDS spring drought; net ecosystem CO₂ exchange; water use efficiency; meadow steppe; eddy covariance

Received 18 January 2010; Accepted 24 December 2010

INTRODUCTION

Current climatic changes induce not only increases in air temperature but also irregular distributions of rainfall, such as droughts and intense storms (Easterling *et al.*, 2000; NAST, 2000; Groisman *et al.*, 2005; IPCC, 2007). Seasonal variation and individual rain event size are more relevant than total rain quantity to plant and microbial processes (Schwinning and Sala, 2004), and affect C uptake and productivity (Knapp *et al.*, 2002; Fay *et al.*, 2003, 2008; Potts *et al.*, 2006). The number of drought-affected areas will likely increase in the coming decades (IPCC, 2007). Drought can result from decreases in annual precipitation, shifts in precipitation distribution over a region (Reichstein *et al.*, 2002a) and the timing of spring snowmelts (Barnett *et al.*, 2005). In addition, drought can substantially modify the seasonal development of leaf area and change plant physiology, thereby impacting both the timing and magnitude of CO₂ uptake. At the ecosystem scale, grasslands can capture more carbon during wet years than during dry years (Meyers, 2001; Suyker *et al.*, 2003; Xu and Baldocchi, 2004; Jaksic *et al.*, 2006).

The grassland ecosystems in China are classified into four major types: meadow steppe, typical steppe, desert

steppe and alpine steppe (Zhu, 1993). This paper focuses on meadow steppe in the Songnen Plain of Northeast China, which occurs on the most moist and fertile sites among the four grassland ecosystem types. Meadow steppe is a transitional type between steppe and forest. It lies at the east edge of the Eurasian steppes and extends westward to the eastern part of the typical steppe in Inner Mongolian Plateau. The total land area of this type of ecosystem is 1 290 000 ha. Compared with other steppe grasslands, the meadow steppe is located at a lower elevation, usually a plain rather than a plateau. The comprehensive weather conditions, i.e. heat and water were better. Vegetation in the meadow steppe is abundant and highly productive. In addition, a larger proportion of the area is affected by the accumulation of salts. The evaporative demands are extremely high, almost three times that of the annual precipitation, which tends to bring solutes dissolved in groundwater and deep soil up to the surface. The topographical features and climatic conditions of the area cause primary soil alkalization and salinization process. Human over-utilization of the grasslands, mainly through overgrazing and over-mowing, results in a faster deterioration of the secondary soil alkalization and salinization processes (Shang *et al.*, 2003).

Climate change scenarios for the Eurasian steppe, especially for the typical and meadow steppes in China, suggest an increase in mean air temperature and more

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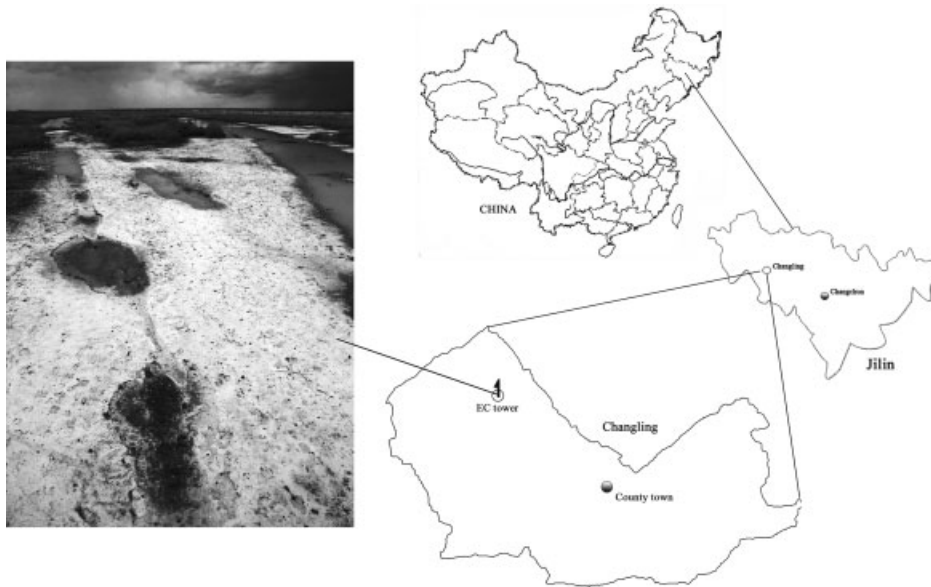


Figure 1. Site location and field photo.

frequent and prolonged droughts (McCarthy *et al.*, 2001). According to four global climate models (GCMs) outputs in reference to the Songnen meadow steppe, temperatures will rise 2.8–7.5 °C and precipitation will increase by 10% or so by the end of this century (Deng and Liu, 2000); however, this increased precipitation does not indicate an easing of drought. Since potential evapotranspiration (ET) will increase due to higher temperature, some areas will become even dryer (Zhou and Zhang, 1996). Evidence from previous studies indicate that soil water is a critical limiting factor for the vegetation production of the Songnen meadow steppe in such semi-arid environments (Guo and Zhu, 1994). Under an extreme drought condition, the impact of global change on net primary productivity (NPP) of this salinized meadow depends on the ground water table (Zhang, 2001). High underground water table could offset the soil drought due to rainfall shortage, thus avoiding the drastic weakening of plant photosynthetic capacity.

In China, eddy covariance (EC) tower-based flux observations and manipulative experiments for grasslands primarily focus on the typical and desert steppes, and little or no attention has been given to the meadow steppe ecosystem. Recent measurements and re-analysis of flux data confirm an uncertainty of the assessment of typical steppes as carbon sinks under a changing climate (Fu *et al.*, 2006; Wang *et al.*, 2008). Recently, Kwon *et al.* (2008) reported that spring drought substantially reduces net ecosystem CO₂ exchange (NEE) and changes its response to environmental drivers in a sagebrush-steppe ecosystem. According to their results, spring drought more substantially impacts the magnitude and pattern of NEE than does summer drought (Fay *et al.*, 2003; Gilmanov *et al.*, 2006); however, it is presumed that high salinity-induced water stress combined with spring drought could reduce NEE in the meadow steppe of northeast China, although the relation between soil salinization and spring drought requires further investigation.

Several studies have reported different responses of gross ecosystem productivity (GEP) and ET to vapour pressure deficit (VPD), soil water content (SWC), net radiation (Rn) and leaf area index (LAI) that have potentially been caused by disparities in grassland WUE (Hunt *et al.*, 2002; Hu *et al.*, 2008); however grassland resilience during and after a severe spring drought and grassland adaptability to stressful environments have not been adequately studied. For the majority of grasslands, especially for typical steppes in China (Li *et al.*, 2008), ecosystem WUE (WUE_{eco}) shows a tendency of increasing when exposed to water stress; hence, we have hypothesized that spring drought could also increase WUE_{eco} of the Songnen meadow steppe.

The objectives of this paper are (1) quantifying seasonal variation in NEE, ET and WUE and (2) assessing the inter-annual response in NEE, ET and WUE to an early growing season drought.

MATERIALS AND METHODS

Study site

The research site was on a northern meadow managed by the Songnen Grassland Ecology Field Station of the Northeast Normal University (NENU), in Changling, Jilin Province, China (123°30' E, 44°35' N, 171 m a s l) (Figure 1). Geographically, the study site was situated in the southern Songnen Plain. This site was representative of a temperate meadow steppe. Perennial grasses are the community dominants, in which *Leymus chinensis* (= *Aneurolepidium chinensis*) and *Phragmites communis* indicate local climax communities. For basic characteristics of the study site, see Table I.

The study area had a temperate, semi-arid continental monsoonal climate, characterized as cold and dry springs

Table I. Characteristics of the study site.

Ecosystem type	Temperate meadow steppe
Location	120°10'–124°10'E, 44°30'–44°45'N
Maximum leaf area index (LAI _{max})	2007: 2.9 (August) 2008: 3.1 (August)
Vegetation	<i>Leymus chinensis</i> , <i>Phragmites</i> <i>communis</i> , etc.
Vegetation cover	70–80%
Height	70–80 cm
Soil	Alkali-saline soil
Salinity layer	0–30 cm
PH	>9.0
Soil organic matter	1.5%
Exchangeable sodium percentage (ESP)	15.6%

and warm and wet summers. The mean annual temperature was 5 °C, with the maximum and minimum temperatures 39.2 °C and –33.9 °C, respectively. The frost-free period was about 130–165 days, and precipitation varied greatly within and between years. Annual long-term average rainfall was about 400 mm, 80% of which fell between June and August. The annual pan evaporation was as high as 1200–1600 mm, approximately 3–4 times the mean annual precipitation. Generally, the growing season was limited to late April to September.

Flux measurements

An open-path EC flux measurement system was deployed in 2007 for long-term measurements of CO₂, water vapour and energy fluxes at the study site. Footprint analysis using the flux source area model (FSAM) (Schmid, 1997) suggested a footprint in the prevalent wind direction (150–240°) extended to approximately 6.5–77.8 m during unstable conditions (Monin-Obukhov length (L) < 0), to about 11.3–229.9 m during stable conditions (L > 0) at night, representing 90% of the total flux. In order to have sufficient fetch (in all directions) that is representative of the meadow steppe being studied, a three-dimensional (3-D) ultrasonic anemometer (CSAT3, Campbell Scientific, Logan, UT, USA) and a CO₂/H₂O infrared gas analyzer (LI-7500, LI-COR, Inc., Lincoln, NE, USA) were mounted 2 m above the ground. Fluxes were calculated as the mean covariance of vertical wind speed fluctuation and the scalar fluctuation of interest. Downward fluxes are counted as negative and upward fluxes as positive. All raw data were sampled at 10 Hz and logged on a CR3000 data logger (Campbell Scientific, Inc., Logan, UT, USA).

Meteorological measurements

Meteorological measurements started from May 2007. Rn was measured using a four-component net radiometer (CNR-1, Kipp & Zonen BV, Delft, The Netherlands) 2 m above the ground. Photosynthetically active radiation (PAR), precipitation (P) and horizontal wind speed

(W) and direction were measured at a height of 6 m above the ground using a quantum sensor (LI190SB, LI-COR, Lincoln, NE, USA), a tipping-bucket rain gauge (TE525MM, Texas Electronics, Dallas, TX, USA) and a propeller anemometer (034B-L Met One Windset, Campbell Scientific, Inc., Logan, UT, USA), respectively. Air temperature (Ta) and relative humidity (RH) were measured at three levels (2, 4 and 6 m; HMP45C, Vaisala Inc., Helsinki, Finland).

Soil temperature profiles (Ts) were measured at depths of 5, 10 and 30 cm by a thermistor (107-L, Campbell Scientific, Inc., Edmonton, Alberta, Canada). Soil heat flux (G) was also measured at a depth of 5 cm using soil heat plates in three separate locations (HFT-3, Radiation and Energy Balance Systems, Seattle, WA, USA), and SWC was measured at a depth of 10 cm by time-domain reflectometry probe (CS616, Campbell Scientific, Inc., Edmonton, Alberta, Canada), which was buried horizontally in the soil. Additionally, soil water potential (SWP) was estimated using watermark probes at two levels (10 and 30 cm, 257-L, Campbell Scientific, Inc., Edmonton, Alberta, Canada). All micrometeorological data were recorded and averaged or summed over a 30-min interval by a separate data logger (CR3000, Campbell Scientific, Inc., Logan, UT, USA).

Vegetation

Biometric measurements of aboveground biomass (AGB), plant height (h) and LAI were conducted every month during the growing season (from May to October). Within a radius of 200 m around the EC system, there were 12 samples in 0.5 m² quadrats for measuring height and LAI by a plant canopy analyzer (LAI-2000, LI-COR, Lincoln, NE, USA), while AGB was measured by destructing another 12 sampling quadrats each time. After the canopy reached maximum vegetative development, plant heights were assumed to remain constant.

Quality control and gap-filling

Mean flux data on a half-hour time scale were calculated using the Edire software. Three-dimensional rotation was adopted before calculating CO₂ fluxes, sensible heat and latent heat (LE). The influence of water vapour on the measurement of sonic temperature, high frequency signal loss due to the inability of measurement and the effect of air density fluctuation on CO₂ and heat fluxes were corrected accordingly.

Stationary and integral turbulence tests were introduced to provide quality control of raw data by excluding data when there were rainfalls, dew formation, power failure or equipment failure. For the stationary test, we applied a method proposed by Foken and Wichura (1996) with a threshold of 30% to exclude poorly controlled data. During the integral turbulence test, we applied the σ_w/u^* protocol (Kaimal and Finnigan, 1994), where u^* is the friction velocity and σ_w is the half-hourly standard deviation of wind speed. Values that varied by more than 30% compared to the reference were rejected. Finally,

nighttime NEE that was less than zero was rejected. We also discarded some daily LE data when the values were abnormally higher than those of R_n .

In order to estimate annual carbon budget and compare with other ecosystems, data gaps were filled using the following procedures. For gaps of less than 1 h, simple linear interpolation was used by averaging the fluxes before and after the gaps. For large data gaps (<14 days), we used the mean diurnal variation (MDV) method proposed by Falge *et al.* (2001), using daytime 14-day independent windows and nighttime 7-day independent windows as the approximations.

Energy balance terms and closure

The accuracy of eddy flux was assessed by comparing turbulent heat fluxes to the available energy flux. The energy budget of the grassland surface can be written as

$$R_n - G - S = \lambda E + H \quad (1)$$

where R_n is the net radiation, λE is the LE flux, H is the sensible heat flux, G is the soil heat flux and the is the soil heat storage (Oliphant *et al.*, 2004). Considering the heights of plants, canopy heat storage only represents a small amount of heat exchange per day. Unlike the other three components (λE , H and G), S is not directly measured, but is calculated from a number of constituent components. Although an accurate measurement of S can be a challenge in any environment, measuring S in the steppe cannot be neglected, because S in the top soil layer not only influenced the magnitude of energy balance closure (EBC) but also adjusted soil heat flux to match the 'truth schedule' (i.e. effecting peak time) of residual of EBC (Shao *et al.*, 2008). The calculation of S in this study follows:

$$S = C_s \frac{\Delta T_s}{\Delta t} d \quad (2)$$

where T_s is the average soil temperature (K) above the heat flux plates (HFP), t is time (in this case $\Delta t = 1800$ s), d is depth between the HFP and soil surface and C_s is the soil heat capacity calculated from:

$$C_s = \rho_b C_d + \theta_v \rho_w C_w \quad (3)$$

where ρ_b is soil bulk density; ρ_w is the density of water; C_d and C_w are the specific heat capacities of dry mineral soil ($C_d = 890$ J kg⁻¹ K⁻¹) and soil water ($C_w = 4190$ J kg⁻¹ K⁻¹), respectively; and θ_v is SWC on a volume basis (%). The heat storage of air and organic matter in the soil were neglected due to their small quantities.

The energy balance ratio (EBR), defined as $(\lambda E + H)/(R_n - G - S)$, provides an overall evaluation of energy enclosure on a large temporal scale by averaging over random errors in the flux measurement (Mahrt, 1998; Gu *et al.*, 1999; Wilson *et al.*, 2002). Over the study period, EBR of the meadow steppe was 0.82 ($R^2 = 0.91$) on a half-hour scale and 0.94 ($R^2 = 0.83$) on a daily scale, suggesting that there was a daily cycle of

energy storage in the air, and particularly, in the biomass below the sensors (Blanken *et al.*, 1997; Gu *et al.*, 2007). The underestimation of the energy closure is a common feature in most eddy flux sites (Foken, 2008). Our results are generally within the range of mean imbalance of those reported at FLUXNET and ChinaFLUX sites (Wilson *et al.*, 2002; Li *et al.*, 2005).

Separating soil evaporation from total ET

We used the Shuttleworth–Wallace (S–W) model (Shuttleworth and Wallace, 1985) to estimate soil evaporation (E_s). As an extension of the Penman–Monteith (P–M) equation, the S–W model considers dual sources, namely transpiration (Tr) from vegetation and evaporation from the underlying soil substrate, wherein the total ET is given by

$$\lambda ET = C_c ET_c + C_s ET_s \quad (4)$$

where ET (mm day⁻¹) is the total ET, λ (MJ kg⁻¹) is the LE of water vaporization, ET_c and ET_s (MJ m⁻² day⁻¹) are respectively equivalent to the Tr and evaporation estimates given by applying the P–M equation to a 'closed' canopy and bare substrate, and C_c and C_s are weighting coefficients that are expressed as functions of resistances. The formulation of all of the terms in Equation (4) is given by Shuttleworth and Wallace (1985) as:

$$ET_c = \frac{\Delta(R_n - G) + [\rho_c p D - \Delta r_a^c (R_n^s - G)] / (r_a^a + r_a^c)}{\Delta + \gamma \{1 + [r_s^c / (r_a^a + r_a^c)]\}} \quad (5)$$

$$ET_s = \frac{\Delta(R_n - G) + [\rho_c p D - \Delta r_a^s (R_n - R_n^s)] / (r_a^a + r_a^s)}{\Delta + \gamma \{1 + [r_s^s / (r_a^a + r_a^s)]\}} \quad (6)$$

$$C_c = \frac{1}{1 + \{(R_c R_a) / [R_s (R_c + R_a)]\}} \quad (7)$$

$$C_s = \frac{1}{1 + \{(R_s R_a) / [R_c (R_s + R_a)]\}} \quad (8)$$

$$R_a = (\Delta + \gamma) r_a^a \quad (9)$$

$$R_c = (\Delta + \gamma) r_a^c + \gamma r_s^c \quad (10)$$

$$R_s = (\Delta + \gamma) r_a^s + \gamma r_s^s \quad (11)$$

where R_n^s (MJ m⁻² day⁻¹) is the R_n over the substrate soil surface, ρ (kg m⁻³) is the mean air density, c_p (MJ kg⁻¹ °C⁻¹) is the specific heat of moist air, r_s^c and r_a^c (s m⁻¹) are the respective bulk stomatal and boundary layer resistances of the canopy, r_a^s and r_a^a (s m⁻¹) are the respective aerodynamic resistances between soil and canopy and between canopy and reference height, and r_s^s (s m⁻¹) is the surface resistance of soil.

Water use efficiency (WUE)

In order to assess WUE, ecosystem CO₂ flux (F_c), and water vapour flux densities were considered potential surrogates of photosynthesis CO₂ uptake and ET, respectively. Similar approaches have been used in other studies

(Testi *et al.*, 2008; Jassal *et al.*, 2009; Mkhabela *et al.*, 2009). We then defined the ratio of GEP and the actual ET measured in the present study as the WUE_{eco} ($g\ CO_2\ kg^{-1}\ H_2O$) and the ratio of GEP and Tr as plant WUE ($g\ CO_2\ kg^{-1}\ H_2O$):

$$WUE_{eco} = \frac{GEP}{ET} \quad (12)$$

$$WUE_{plant} = \frac{GEP}{Tr} \quad (13)$$

where GEP equals the sum of measured NEE and estimated ecosystem respiration (R_e) ($GEP = NEE + R_e$), ET was derived by dividing the LE by the heat of vaporization (Sun *et al.*, 2008), and Tr was derived by separating the ET into E_s and Tr using the S–W model.

The R_e was obtained using a multiplicative model (Reichstein *et al.*, 2002b), which quantifies the coupled effect of temperature and soil moisture on R_e . In the multiplicative model, R_e is described by the product of functions $f(T_a)$ and $f(S_w)$. $f(T_a)$ is the temperature response function of Lloyd and Taylor (1994), and $f(S_w)$ is a quadratic function:

$$R_e = R_{10}f(T_a)f(S_w) \quad (14)$$

$$f(T_a) = \exp\left[308.56\left(\frac{1}{56.02} - \frac{1}{T_k - 227.13}\right)\right] \quad (15)$$

$$f(S_w) = \exp(aS_w^2 + bS_w + c) \quad (16)$$

where R_{10} denotes the R_e at reference temperature (T_{10}) and optimal SWC, T_k is the air temperature or soil temperature (K), S_w is SWC ($m^3\ m^{-3}$) and a, b, c are fitted site-specific parameters. The variables in the multiplicative model are generated under the time scales of growing season and non-growing season, respectively.

Canopy conductance

Environmental control of ET has been characterized in terms of the response of canopy conductance (G_c) to environmental factors. In this study, G_c was obtained by rearranging the P–M equation (Monteith and Unsworth, 1990):

$$G_c^{-1} = \left\{ \frac{\Delta}{\gamma} \frac{H}{\lambda E} - 1 \right\} r_a + \frac{\rho C_p D}{\gamma \lambda E} \quad (17)$$

where D is the VPD (kPa); C_p is the specific heat of air at constant pressure ($kJ\ kg^{-1}\ K^{-1}$); γ is the psychrometric constant ($kPa\ K^{-1}$); ρ is the air density ($kg\ m^{-3}$); β is the Bowen ratio, which is $H/\lambda E$; Δ is the slope of the saturation vapour pressure curve at the mean air temperature ($kPa\ K^{-1}$); and r_a is ($s\ m^{-1}$) the aerodynamic resistance calculated from the logarithmic wind profile for neutral conditions as

$$r_a = \frac{1}{k^2 u} \left[\ln \left\{ \frac{Z_h - d}{Z_0} \right\} \right]^2 \quad (18)$$

where Z_h (m) is the reference height above the canopy, Z_d (m) is the displacement height set as 2/3 of the

vegetation height, Z_0 (m) is the roughness length set as 1/10 of the vegetation height, k is Von Karman's constant and u ($m\ s^{-1}$) is wind speed at the reference height. An average daily G_c was calculated from data collected every 30 min between 11:30 and 15:30.

RESULTS

Microclimate

The daily mean air temperature (T_a) during 2007 and 2008 ranged from -15.9 to $30.4\ ^\circ C$ and -21.1 to $27.6\ ^\circ C$, respectively (Figure 2a). The maximum T_a occurred in July in both years. In 2007 the mean T_a was $8.2\ ^\circ C$, while it was $6.8\ ^\circ C$ in 2008. Soil temperature (T_s) exhibited a similar seasonal pattern with T_a , but was slightly decreased at deep soil depths (e.g. 30 cm from the soil surface).

Precipitation differed greatly between the 2 years, both in terms of amount and seasonal distribution (Figure 2e). The year 2007 was very dry with only 10 rain events that exceeded 3 mm and a total precipitation of 207.9 mm (46% below the 10-year average), whereas 2008 received 28 rain events that exceeded 3 mm and a total precipitation of 384.2 mm. Thus, in 2008, the meadow steppe received 85% more precipitation and experienced 18 individual rain pulses that exceeded 3 mm more than 2007. The driest episodes during 2007 were in the spring and the initial stage of the growing season. In 2007, the first rain (over 3 mm) fell on 30 June (DOY 181), while the last rain occurred on 6 October (DOY 279). There was hardly rainfall or snowfall throughout the initial 6 months. It should be noted that the first rainfall (over 3 mm) date in 2008 (22 March, DOY 81) was 3 months earlier than that in 2007, and the rainy season therein lasted longer and ended 15 November (DOY 320). It is worth mentioning that the monthly total precipitations of May and June in 2007 (9.1 mm) were only 11% of the 10-year average (86.5 mm), while in 2008 (89.2 mm), their total precipitations were above the 10-year average, indicating that the meadow steppe experienced a serious spring drought in 2007. A much higher VPD was observed in 2007 in comparison to that of 2008, especially in June (Figure 2b).

Seasonal variation of SWC was observed to closely follow the changes in precipitation. Clearly, the temporal distribution of SWC was asymmetrical in both years (Figure 2d). A long dry period in 2007 resulted in severe water deficits in the spring and early summer (before July) when the soil moisture content dropped below $0.2\ m^3\ m^{-3}$ in the upper 10 cm of the soil layer. The SWC recovered after a heavy rain in early July; however, the wet period did not last long, and there was a sharp decrease in SWC, followed by the summer drought. In contrast, frequent rain events during the next summer in 2008 resulted in a consistently higher SWC. Even during the summer drought in 2007, the soil moisture in the upper 10 cm of soil did not drop below $0.4\ m^3\ m^{-3}$ due to low soil drainage in the meadow. SWPs at

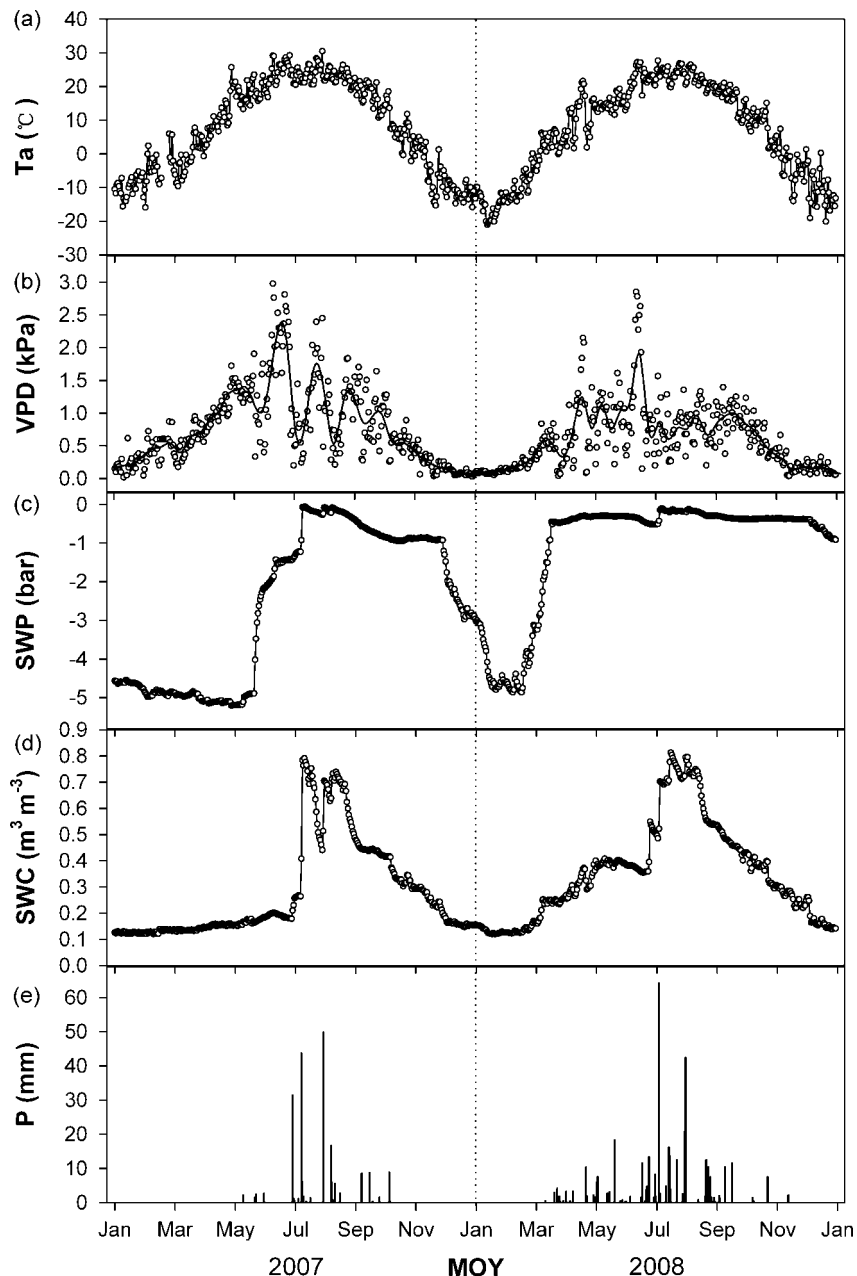


Figure 2. Mean daily micrometeorological conditions from 2007 to 2008: (a) air temperature (T_a), (b) vapour pressure deficit (VPD), (c) soil water potential (SWP) at a depth of 30 cm, (d) soil water content (SWC) at a depth of 10 cm and (e) precipitation (P).

different depths in the soil were analysed and found to be extremely different (not shown), probably due to the heterogeneity of the soil compositions.

Net ecosystem exchange of CO₂ (NEE)

We defined CO₂ uptake by vegetation as negative and net CO₂ release to the atmosphere as positive. Diurnal patterns of NEE demonstrated the sharp contrast in carbon sequestration between dry and wet years, especially in the initial periods of the growing season (Figure 3). The site was a carbon source ($NEE > 0$) in May 2007 while it was a carbon sink ($NEE < 0$) in May 2008. Moreover, NEE in both June and July 2007, had a relatively small magnitude of carbon uptake during the day and a small amount of carbon loss during the night, in comparison to 2008.

Maximum CO₂ uptake in 2007 was $-7.9 \mu\text{mol m}^{-2} \text{s}^{-1}$, which was approximately half of the maximum observed in 2008 ($-16.7 \mu\text{mol m}^{-2} \text{s}^{-1}$).

In both years, daily NEE became negative after the first large rain event that stimulated the germination of the *Leymus chinensis* community. Carbon sink/source switching occurred with the senescence of the meadow; however, daily NEE behaved differently during the spring drought period (Figure 4a). The ecosystem exhibited a relatively stable state of carbon emission until late May in 2007, whereas net carbon uptake occurred in early May of 2008. Variation of NEE was concomitant with the pattern of soil moisture and canopy growth. Daily NEE reached a maximum of $-6.3 \text{ gC m}^{-2} \text{ day}^{-1}$ in July 2008 and a maximum of $-3.2 \text{ gC m}^{-2} \text{ day}^{-1}$ in August 2007,

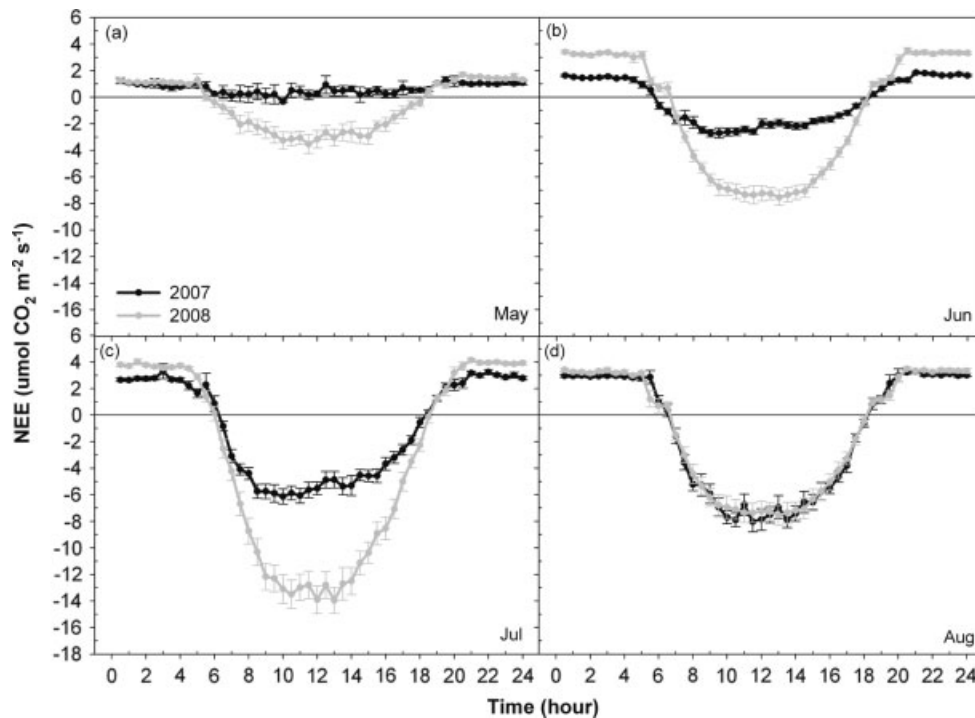


Figure 3. Average diurnal pattern of net ecosystem CO₂ exchange (NEE) with error bars (\pm SE) from May to August in 2007 and 2008.

indicating that 2008 exhibited a greater carbon capture ability compared to 2007.

Noted differences in annual NEE were also observed between dry and wet years (Figure 4b). The slope of cumulative NEE was indeed lower in 2007 than 2008 across the period between June and September; however, for 2008, the cumulative NEE dropped to its minimum was interrupted earlier in comparison to the drought year of 2007, wherein it leveled off in mid-August. Annual cumulative NEE over the entire 2 years varied from $64.2 \text{ gC m}^{-2} \text{ year}^{-1}$ in 2007– $160.5 \text{ gC m}^{-2} \text{ year}^{-1}$ in 2008, or approximately a 150% increase. Using the nighttime NEE temperature response function (Equation 6), we estimated the total R_e for the two respective growing seasons (May–September) of 2007 and 2008 was as 311.7 and 387.7 gC m^{-2} . The gross ecosystem productivity, $\text{GEP} = \text{NEE} + R_e$, was further calculated to be 400.6 gC m^{-2} for 2007 and 575.7 gC m^{-2} for 2008.

Water budget and balance

The average ET rate in 2007 (1.9 mm day^{-1}) was less than that in 2008 (2.2 mm day^{-1}) from May through September. An increasing trend of ET corresponds to large and frequent rain events, which also promote the emergence of meadow steppe due to seed germination. In 2007, daily ET increased starting late May, reaching the maximum of 5.2 mm day^{-1} on 1 August, and subsequently experienced a rapid decrease; however, daily ET in the wet 2008 rapidly increased starting late April, and reached the maximum of 5.6 mm day^{-1} on 6 July. Thereafter, daily ET remained relatively high until mid-August, wherein it declined until the end of the growing season.

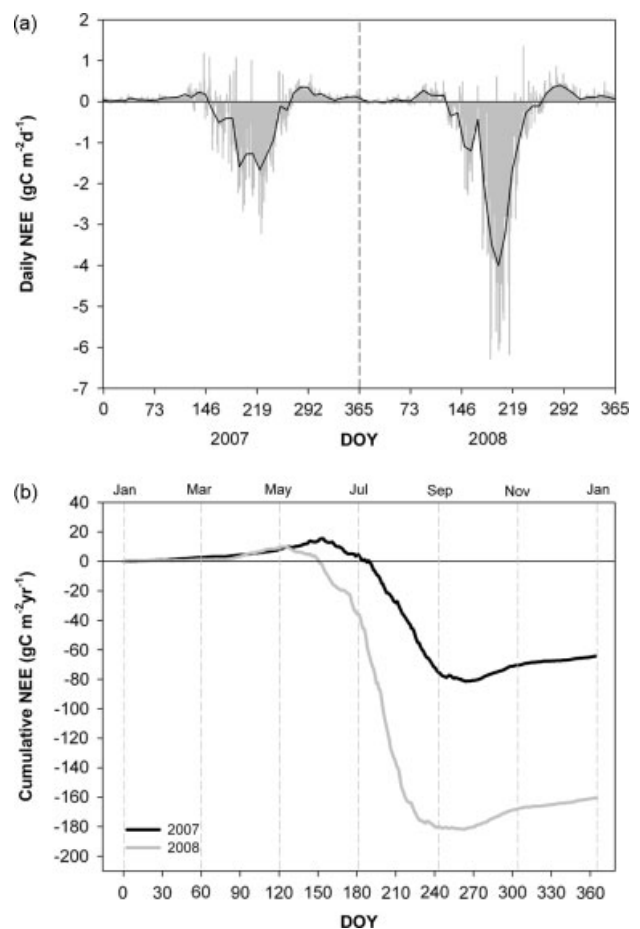


Figure 4. (a) Daily net ecosystem CO₂ exchange (NEE) from 2007 to 2008, the solid line is the running average sampled on the adjacent 10-day data; (b) cumulative NEE for 2007 (black) and 2008 (grey).

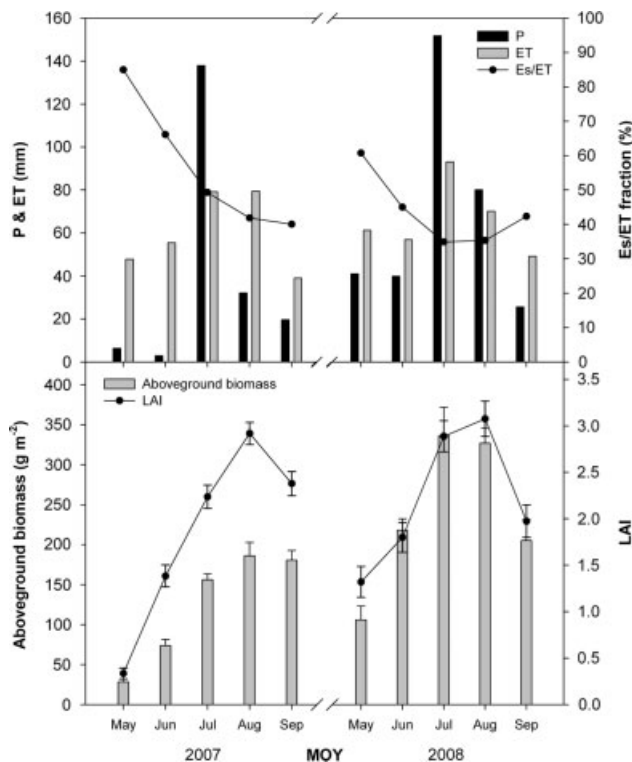


Figure 5. (a) Monthly total precipitation (P), evapotranspiration (ET) and the fraction of soil evaporation (Es)/ET; (b) aboveground biomass and mean leaf index area (LAI) with error bars (\pm SE) for each month of the growing season in 2007 and 2008.

The total ET during the growing season in 2007 was 300.9 mm, 9% lower than the 330.5 mm in 2008. ET in May was 21.9% lower than that in 2008 (Figure 5a). The overall monthly ET/P rates in the growing season of 2007 were much lower than those in 2008. The largest ET/P differences were observed in May and June. Except for July, every month of the 2007 growing season exhibited a ratio exceeding 1, wherein the greatest ratio (19.8) was attained in June (Table II). The ET of the entire growing season in 2007 possessed 151.4% of the total P; while in 2008, ET was 97.7% of the total P.

Es in May was much higher than Tr for both years as demonstrated by Es/ET ratios (Figure 5a), wherein up to 85% of the total available soil water was found to be lost by Es in the spring drought period of May,

2007. Furthermore, the duration of large Es was longer in 2007 than in 2008. The maximum LAI (LAI_{max}) occurred in August for both years; however, the beginning time for growth was approximately postponed for 1 month, and the LAI_{max} in August, 2007 was merely the value obtained in July, 2008 (Figure 5b). The low LAI in May, 2007 is regarded as the efficient cause of low Tr, i.e. high Es/ET rate during the spring drought period.

Aboveground biomass

Annually, the meadow steppe plants begin to rebirth in the early May, which is also the starting time of the dry matters accumulation. Specifically, the August of 2007 witnessed the AGB peak (185.9 gDW m⁻²), which was considered as the aboveground net primary productivity (ANPP) of that year. In contrast, the AGB peak of 2008 reached in July (336.3 gDW m⁻²), which was 1 month earlier than that in 2007. The carbon storage in vegetation can be estimated through the carbon proportion in the organic dry matters. Actually, the carbon concentration of different vegetation type was rarely measured directly, but generally assumed to be 45% of the dry weight biomass for steppes (Ma *et al.*, 2006). Therefore, carbon storage in the AGB of these two growing seasons was 83.7 gC m⁻² in 2007 and 151.3 gC m⁻² in 2008.

Canopy conductance

Gc values were much lower in 2007 than in 2008. The curve of Gc observed for the 2008 growing season exhibited an obvious 'single-peak' trend, i.e. it was very low during the spring, reached a maximum around early July (DOY 180–190) and fell suddenly in late summer. In contrast, a double-peak curve was observed for the 2007 growing season, which was followed by a sharp decrease in late July (DOY 200–210) (Figure 6a).

Comparing the Gc/LAI in drought and normal years, it showed that their changing trends were not in the same step. In the drought year, there existed an obvious disparity of the trends between Gc and LAI, which caused a fluctuation of Gc/LAI shown in Figure 6b. While in the normal year, the trend of Gc basically accorded with LAI, which was reflected by the little fluctuation of Gc/LAI

Table II. Total net ecosystem CO₂ exchange (NEE), gross primary productivity (GPP), precipitation (P), evapotranspiration (ET), transpiration (Tr), the ratio of ET/P, ecosystem-level water use efficiency (WUE_{eco}), and plant-level water use efficiency (WUE_{plant}) for each month and for the entire growing seasons (May–September) in 2007 and 2008.

	NEE (gC month ⁻¹)		GPP (gC month ⁻¹)		P (mm month ⁻¹)		ET (mm month ⁻¹)		Tr (mm month ⁻¹)		ET/P		WUE _{eco} (gCO ₂ kg ⁻¹ H ₂ O)		WUE _{plant} (gCO ₂ kg ⁻¹ H ₂ O)	
	2007	2008	2007	2008	2007	2008	2007	2008	2007	2008	2007	2008	2007	2008	2007	2008
May	6.0	-10.3	25.0	47.0	6.3	41.0	47.8	61.2	7.2	24.0	7.6	1.5	2.1	3.3	13.5	8.0
June	-9.6	-35.1	62.5	97.0	2.8	39.9	55.5	56.9	18.8	31.3	19.8	1.4	4.4	6.9	18.0	12.0
July	-31.1	-104.9	127.8	228.7	137.9	151.8	79.2	93.1	40.2	60.6	0.6	0.6	6.2	9.9	12.6	14.5
August	-44.3	-39.0	142.4	145.7	32.1	80.1	79.5	70.1	46.2	45.3	2.5	0.9	6.8	8.5	12.2	12.1
September	-5.9	1.2	56.7	56.2	19.6	25.6	38.9	49.1	23.3	28.3	2.0	1.9	5.3	4.5	8.7	7.4
	-84.9	-188.1	414.5	574.6	198.7	338.4	300.9	330.5	135.6	189.6	1.5	1.0	5.0	6.6	13.0	10.8

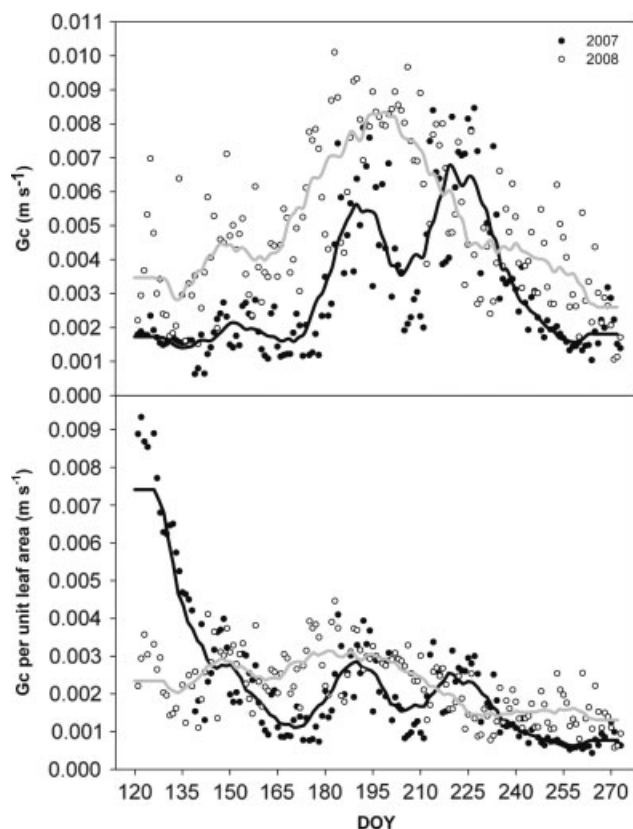


Figure 6. Daily values of (a) canopy conductance (G_c), and (b) G_c per unit leaf area (G_c/LAI) for the growing seasons in 2007 (closed circle) and 2008 (open circle). The solid line is the running average sampled on the adjacent 10% of data.

with high conductivity since the initial stage till the end of the growing season.

Water use efficiency

Daily values of WUE_{eco} during the aforementioned growing seasons had a large seasonal variability (Figure 7a). Daily average WUE_{eco} was $5.0 \text{ gCO}_2 \text{ kg}^{-1} \text{ H}_2\text{O}$ in 2007 and $6.6 \text{ gCO}_2 \text{ kg}^{-1} \text{ H}_2\text{O}$ in 2008. The maximum value was recorded in DOY 232 of 2007 ($10.1 \text{ gCO}_2 \text{ kg}^{-1} \text{ H}_2\text{O}$) and DOY 197 of 2008 ($14.8 \text{ gCO}_2 \text{ kg}^{-1} \text{ H}_2\text{O}$). WUE_{eco} in 2007 was much lower than that in 2008, especially during the spring drought period ($4.0 \text{ gCO}_2 \text{ kg}^{-1} \text{ H}_2\text{O}$). The peak WUE_{eco} value in 2007 came 1 month later than that in 2008. Throughout the 2007 drought, WUE_{eco} remained relatively unchanged and only observed rapid growth to relatively higher values in late summer. In contrast, WUE_{eco} in 2008 increased from the start of the growing season, wherein soil moisture was high due to large amounts of rainfall. In addition, plant water use (WUE_{plant}) was also restricted by spring drought (Figure 7b). The maximum value of WUE_{plant} was recorded in DOY 154 of 2007 ($38.6 \text{ gCO}_2 \text{ kg}^{-1} \text{ H}_2\text{O}$) and DOY 181 of 2008 ($23.1 \text{ gCO}_2 \text{ kg}^{-1} \text{ H}_2\text{O}$). Daily average WUE_{plant} was $13.0 \text{ gCO}_2 \text{ kg}^{-1} \text{ H}_2\text{O}$ in 2007 and $10.8 \text{ gCO}_2 \text{ kg}^{-1} \text{ H}_2\text{O}$ in 2008; however, the WUE_{plant} during the spring drought period in 2007 (before DOY 170) was $17.3 \text{ gCO}_2 \text{ kg}^{-1}$

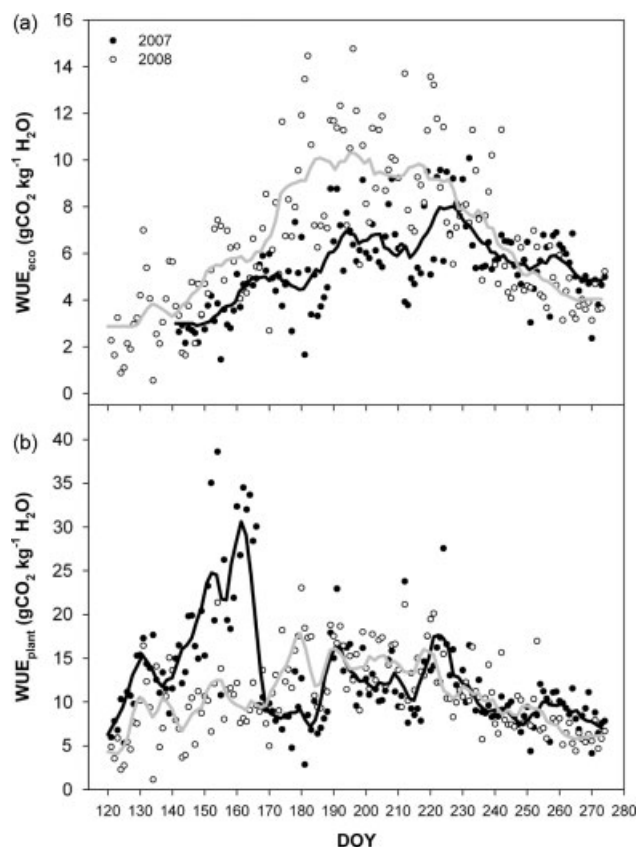


Figure 7. Seasonal and inter-annual variation in daily values of (a) eco-system water use efficiency (WUE_{eco}) and (b) plant water use efficiency (WUE_{plant}). The closed circles represent the observations in the growing season of 2007, the open circles refer to 2008, and black and grey lines are the running averages sampled on the adjacent 10% of data for 2 years, respectively.

H_2O , 1.9 times higher than the $8.9 \text{ gCO}_2 \text{ kg}^{-1} \text{ H}_2\text{O}$ in the corresponding period of 2008.

DISCUSSION

The influence of spring drought on carbon sequestration

The Songnen meadow steppe sequestered $64.2 \text{ gC m}^{-2} \text{ year}^{-1}$ in 2007 and $160.5 \text{ gC m}^{-2} \text{ year}^{-1}$ in 2008. For the typical steppe in China, a change from a wet to a dry season can switch the ecosystem from a carbon sink to a weak source (Zhang *et al.*, 2007; Wang *et al.*, 2008). It should be noted that even in the extreme drought year, the meadow steppe remained a carbon sink, wherein the strength of sink was much higher than that observed for typical steppes in Inner Mongolia and Central Mongolia. The difference in carbon sequestration between the 2 years was primarily caused by the spring and pre-summer GPP, whose variability was greater than ET in the meadow steppe of Songnen Plain. Less NEE in 2007 was believed to be caused by the low precipitation in the spring months in May and June.

Carbon dioxide fixation in aboveground plant biomass is the first step in the process of storing C. Many scholars claimed that there was a positive relation between the biomass and the carbon flux. Greater biomass means

stronger capability of carbon sequestration (Sims and Bradford, 2001; Hunt *et al.*, 2002). This was in agreement with our results. Specifically, even in the drought year, the maximum CO₂ fixation of meadow steppe still coincided with the LAI_{max} and biomass accumulation rate. The disparity of the AGB between 2007 and 2008 caused two different CO₂ flux patterns. The comparison between NPP from biomass and net ecosystem productivity (NEP) from flux measurement contributes to improve the accuracy of carbon stock in the meadow steppe ecosystem, and also offers a better understanding of the varying seasonality in CO₂ sequestration. In 2007, ANPP was very close to the NEP obtained from the eddy covariance measurement (Table II). But in 2008, there was still a difference (36.8 gC m⁻² or 81.7 gDW m⁻²) between ANPP and NEP. The disparity between ANPP and NEP implied that the belowground NPP (BNPP) might be particularly important to the meadow steppe, and the photosynthate allocation would be highly varied due to the sensitive response to the climate change. Therefore, it was assumed that the spring drought caused the low productivity and the change in belowground/aboveground C allocation. Many of the previous studies suggested that the plant adapted to the soil drought by means of increasing underground biomass and adjusting the root cap ratio (Li *et al.*, 2003). However, Wang *et al.* (2004) pointed out that the drought cast a promoting effect on the root distribution and root cap ratio in the early growing stage, but it restrained them in the later period of growth. This finding demonstrated that *Leymus chinensis*'s capability of increasing the root proportion to strengthen its drought tolerance was weakened because of the long-lasting drought. Owing to the imbalance between the plant's photosynthesis input and respiration output, the underground biomass kept being consumed. On average, the AGB reached the maximum in July and remained steady afterward. However, the photosynthetic rate this time was still high, and the majority of aboveground photosynthates were transported to the underground including the root and rhizome. This reflected that the good water condition contributed to both the accumulation of the underground biomass and the biomass transportation between the aboveground and underground.

In the meadow steppe ecosystem, phenological stage of plant growth and development had a major influence on determining the net carbon exchange. Later carbon capture in 2007 was a direct consequence of a later initiation of photosynthesis, which was due to slow grass rebirth after the dormancy and soil thaw. Symptoms of spring drought will vary widely depending on the stage of its ontogenetic development and duration of this stress factor (Svobodova and Misa, 2004). The year 2007 witnessed a serious drought in the Songnen Plain from spring to mid-summer, which negatively impacted grass growth and the development of different phenophases. The meadow steppe was dominated by perennial plants, the regeneration of aboveground shoots occurs principally by sprouting from buds located on rhizomes or

other types of perennial organs. The observation of *Leymus chinensis* indicated that the low soil moisture from spring drought significantly reduced the density of total buds, 291.7 ± 26.4 buds m⁻² in the growing season of 2007 compared to 633.1 ± 41.6 buds m⁻² in the growing season of 2008 (the May of 2007 had a zero budding rate), which finally influenced the aboveground shoot density. Besides, 111.7 ± 17.6 cm m⁻², as the average length of young rhizome, was shortened by 2007 spring drought (the normal is 676.6 ± 58.6 cm m⁻²). Zhang *et al.* (2009) reported that *Leymus chinensis* could allocate limited resources to each of the three main functions of parent shoot growth, young rhizome expansion and daughter shoot establishment. According to the theory of resource allocation, if resources were limited, increased investment in any one of these means could give rise to a compromise of the other two (Obeso, 2002). Thus, plants tended to adopt changing growth strategies during the growing season. During the 2007 spring drought, the appearance of many horizontal apical rhizome buds suggested the plants' expansion strategy to approach the necessary resources. After two significant rains in early July, the preformed horizontal apical rhizome buds rapidly developed into vertical buds, then began to initiate the aerial shoots. The performance of *Leymus chinensis* reflected the meadow steppe's resilience to drought under natural selection. Furthermore, water shortage at the developmental stage of plant stem elongation caused a withering of established tillers and a retardation of the shape of growing tillers.

Besides through clonal propagation, many perennial plants give rise to new individuals through sexual reproduction (Clark-Tapia *et al.*, 2005). Spring drought before anthesis induced a decrease in the number of florets per spike (47.2 ± 2.1 florets m⁻² in 2007 compared to 66.1 ± 3.4 florets m⁻² in 2008), as well as an increased floret sterility. On the basis of previous studies, AGB makes its most rapid progress in terms of development during the flowering stage of mid-June (Zhu, 2004). The water deficit in June critically influenced the structure and physiological construction of biomass by reproduction and phenotypic adaptation (Boutraa and Sanders, 2001; Parolin *et al.*, 2002). Meanwhile, the severe spring drought of 2007 inhibited the formation and development of plant assimilative organs, resulting in an inadequate assimilation capacity for the plant to effectively utilize plentiful rainfall in the coming period.

Change in P patterns combined with mid-summer drought could be considered causes for the difference in NEE between 2 years. Fewer and larger individual rainfall events, as well as longer intervals between events, potentially aggravated the severity of the drought in 2007. Inter-annual variation of carbon exchange in typical steppes has primarily been determined by the amount and patterns of precipitation (Wang *et al.*, 2008). The increase in the total numbers of rain pulse amount and frequency of rain pulses are likely to be the leading cause of the observed differences in the carbon budget for 2007 and 2008, since NEE is highly linked with rain pulses and

tightly coupled to water availability. Hunt *et al.* (2004) suggested that a net carbon sink mostly occurs in years with greater rainfall than the average. Our study supports this conclusion that rainfall distribution may determine not only the carbon sink strength but also the direction of net carbon flow in the meadow steppe.

The occurrence of mid-summer drought in July 2007 further shortened the length of time required to reach a biomass climax, thus enhancing the negative effect of less carbon sequestration by spring drought. Larger rainfall events with longer intervals were observed in July 2007, which followed the mid-summer drought (Figure 1). Under this water stress, the physiological processes of plants slowed and resulted in a thinning of the canopy and stunting. When feeder roots and root hairs dry up and die, the water absorbing capacity of the plant is reduced, creating a severe water deficit inside of the plant (Terrell, 2005). Low carbon uptake during this period confirms that drought stress relies on drought intensity and duration, wherein more severe drought stresses more seriously affect the meadow steppe. By estimation, during the mid-summer drought, approximately 25gC m^{-2} carbon was reduced compared to the normal amount. The results suggested that the following mid-summer drought further aggravated the severity of the spring drought; however, the negative consequence of mid-summer drought in reference to carbon storage in the meadow steppe was less than that of spring drought. Although two rain pulses at the beginning of July were large enough to recharge the soil profile sufficiently for plants to make additional investments in new growth, vegetation did not have the capacity to rapidly exploit available water, further indicating that the development of a root system was seriously curtailed because of spring drought. These data prove that carbon sequestration is far more sensitive to spring drought than to summer drought in the meadow steppe, which agrees with previous studies of the sagebrush-steppe ecosystem in North America (Fay *et al.*, 2003; Gilmanov *et al.*, 2006). In August 2007, NEE was stimulated by soil moisture recovery, which enabled root and leaf renewal, reflecting the strong ability of the meadow to respond to a step change from stressful to optimal water conditions. Although the indigenous plant species stayed green until the late summer, there was a limited period for the ecosystem to enlarge the canopy structure and recruit new individuals.

The influence of spring drought on water use efficiency

The spring drought affected the plant-level water use efficiency ($\text{WUE}_{\text{plant}}$) both through the process of photosynthesis and Tr from the leaves. During the spring drought period, the GEP was constrained due to the low AGB, the incomplete leafing and the weak photosynthesis. Also, the plants kept a low Tr rate through leaf stomatal regulation, which was the plant's adaptive strategy for the water stress. Referring to the meadow steppe, the suppression of Tr was even greater than that of photosynthesis during the spring drought period. Like spring

drought, increasing soil dryness progressively decreases SWP (Hasegawa *et al.*, 2000). The SWP reflects the tendency of soil water movement and condition of plant water absorption. It was observed that early in the 2007 growing season, SWP was five times lower than that of normal years, suggesting that the root hydraulic resistance was altered, resulting in poor water absorbability. Meanwhile, there appeared a sharp rise of SWP since mid-June (Figure 2c). This sharp increase of SWP was caused by the uplifting of underground water instead of the waterfall. In the month of June, the E_s was largely increased due to the high temperature and the enhanced ventilation. Strong evaporation condition, in combination with the high underground water level and the impeded drainage in the Songnen Plain, caused the underground water moving upward towards soil surface, thus alleviating the soil dryness.

In addition to precipitation, underground water is an essential resource for plants. As expected, rainfall shortage during the spring drought of 2007 greatly reduced the amount of available water; however, there was still a sharp decline of $\text{WUE}_{\text{plant}}$ in mid-June. The decline of $\text{WUE}_{\text{plant}}$ was caused directly by the Tr increase, but actually the Tr increase was a result of the underground water application. When the first rainfall came in July, $\text{WUE}_{\text{plant}}$ showed a decline and then a rise (Figure 7b), which suggested the plant's prior response to soil moisture change. To be specific, rainfalls could cause the increase of meadow steppe productivity and the decrease of $\text{WUE}_{\text{plant}}$, but the latter responded faster after the rain. Meanwhile, it suggested that if the rain intensity was comparatively high at optimal temperature and light for grass growth, regardless of the rain-free period, the rain received by the scarce steppe vegetation cover could still be fully biologically effective. Moreover, this recovery of the vegetation after drought-breaking rains further showed the meadow steppe's resilience to spring drought.

For a typical steppe (Li *et al.*, 2008), ecosystem-level water use efficiency (WUE_{eco}) usually increases when water stress occurs. According to the results of our study, the opposite is true for the Songnen meadow steppe. Spring drought undoubtedly contributed to a decrease in ET; however, the suppression of ET was relatively small compared to that of GEP. The small decrease in ET was due to the high water availability at the site that has a shallow groundwater table. Therefore, spring drought reduced the WUE_{eco} primarily by suppressing carbon sequestration. An important part of soil moisture available for Tr is evaporated directly from soil to the atmosphere without taking part in Tr . The variation of $\text{WUE}_{\text{plant}}$ did not correspond well with the WUE_{eco} . The difference between $\text{WUE}_{\text{plant}}$ and WUE_{eco} illustrated how the evaporation from the soil surface, not useful to grass production, decreased WUE_{eco} . The data obtained by separating ET confirmed that spring drought caused a larger proportion of E_s in the total ET, and a long-lasting low Tr during the growing season. Under the strong E_s condition, underground water moved upwards towards

the soil surface, and this capillary water flow carried some dissolved salts to the plant root zone. Therefore, high E_s would increase the tendency of mineralization, and accelerate topsoil salinization on the Songnen meadow steppe (Li *et al.*, 1997). The low T_r rate during the drought period could be attributed to the physiological activity of drought-tolerant perennial grasses (e.g. *Leymus chinensis*), which extends the roots deeply into the soil to enhance the utilization of underground water.

Moreover, the observed WUE_{eco} decrease under drought stress also correlated with an associated reduction in G_c (Figure 6a). The reduction in G_c cannot be presently explained due to the sensitivity of changes in meteorological conditions; however, it was shown that soil moisture could limit G_c in the growing season of 2007, especially during drought periods. A decrease of G_c would imply a loss of root and stem hydraulic conductivity to limit T_r , which was considered as the mechanism of self-protection and self-regulation of plants to extreme environments. In addition to G_c , G_c scaled to leaf-level (G_c/LAI) indicated that spring drought and mid-summer drought affected the meadow steppe by different means. The spring drought and mid-summer drought in 2007 gave rise to two declines of G_c/LAI . The first decline was caused by the gradual increase of LAI after water inputs from rainfall and underground water table; while the second decline was the result of the G_c decrease under mid-summer drought. In the spring drought period, the high G_c did not reflect the high carbon–water exchange rate but embodied the influence of the extremely low LAI. Therefore, the application of G_c/LAI before the leaf emergence period would cause an inevitable error.

Considering all of the above, the break of water balance revealed that the meadow steppe could be transport-limited for water use, and most of the water supply available from underground resources participated in E_s instead of T_r during the spring drought, thus reducing effective water availability for plant use.

CONCLUSIONS

This 2-year study reported measured NEE, ET and WUE for a meadow steppe in northeast China. The meadow steppe were found to be carbon sinks over 2 contrasting years, varying from $64.2 \text{ gC m}^{-2} \text{ year}^{-1}$ to $160.5 \text{ gC m}^{-2} \text{ year}^{-1}$ in dry year 2007 and a wet year 2008. Our study suggested that the meadow steppe was very sensitive to the altered precipitation patterns. Spring drought substantially reduced carbon uptake, but this ecosystem remained a carbon sink in the drought year and showed considerable recovery after drought-breaking rains. Spring drought slowed grass rebirth after the dormancy and soil thawing phases, postponed the phenophase and reduced NEE significantly in the growing seasons. BNPP might be particularly important to the meadow steppe, and aboveground and belowground C allocation would be highly changed due to spring drought. Spring drought reduced GEP due to reduction of

leaf areas and biomass, not water availability in the study region. For the meadow steppe in Songnen Plain, high salinity could further impede carbon sequestration and accelerate grassland degradation. Further study will focus on potential interactions between water use and soil salinization. In brief, the great capability of carbon capture and high sensitivity to water stress of Songnen meadow steppe may be vulnerable to future climate change.

ACKNOWLEDGEMENTS

This research was supported by the National Key Basic Research Program (2007CB106801), the National Natural Science Foundation of China (Nos. 30590382, 30870238), and the US-China Carbon Consortium (USCCC) through the USDA's Southern Global Change Program. Sincere thanks go to Dennis Baldocchi, Ray Desjardins, Kyaw Tha Paw U, Steve McNulty, Bin Zhao and Haiqiang Guo for their useful comments and valuable suggestions on previous versions of the manuscript. Many thanks to Shicheng Jiang and Hongmei Bi for their assistance with data collection and fieldwork. We also greatly appreciate the careful reviews by two anonymous reviewers.

REFERENCES

- Barnett TP, Adam JC, Lettenmaier DP. 2005. Potential impacts of a warming climate on water availability in snow-dominated regions. *Nature* **438**: 303–309.
- Blanken PD, Black TA, Yang PC, Neumann HH, Nesic Z, Staebler R, Den Hartog G, Novak MD, Lee X. 1997. Energy balance and canopy conductance of a boreal aspen forest: partitioning overstory and understory components. *Journal of Geophysical Research D: Atmospheres* **102**: 28915–28927.
- Boutraa T, Sanders FE. 2001. Influence of water stress on grain yield and vegetative growth of two cultivars of bean (*Phaseolus vulgaris* L.). *Journal of Agronomy and Crop Science* **187**: 251–257.
- Clark-Tapia R, Alfonso-Corralo C, Eguiarte LE, Molina-Freaner F. 2005. Clonal diversity and distribution in *Molnocereus eruca* (Cactaceae), a narrow endemic cactus of the Sonoran desert. *American Journal of Botany* **92**: 272–278.
- Deng HP, Liu HF. 2000. Impacts of global climate changes on the water and heat factors in the Songnen Steppe. *Acta Ecologica Sinica* **20**(6): 958–963.
- Easterling DR, Evans JL, Groisman PY, Karl TR, Kunkel KE, Ambenje P. 2000. Observed variability and trends in extreme climate events: a brief review. *Bulletin of the American Meteorological Society* **81**: 417–425.
- Falge E, Baldocchi D, Olson R, Anthoni P, Aubinet M, Bernhofer C, Burba G, Ceulemans R, Clement R, Dolman H, Granier A, Gross P, Grunwald T, Hollinger D, Jensen NO, Katul G, Keronen P, Kowalski A, Lai CT, Law BE, Meyers T, Moncrieff H, Moors E, Munger JW, Pilegaard K, Rannik U, Rebmann C, Suyker A, Tenhunen J, Tu K, Verma S, Vesala T, Wilson K, Wofsy S. 2001. Gap filling strategies for defensible annual sums of net ecosystem exchange. *Agricultural and Forest Meteorology* **107**: 43–69.
- Fay PA, Kaufman DM, Nippert JB, Carlisle JD, Harper CW. 2008. Changes in grassland ecosystem function due to extreme rainfall events: implications for responses to climate change. *Global Change Biology* **14**: 1600–1608.
- Fay PA, Knapp AK, Blair JM, Carlisle JD, Danner BT, McCarron JK. 2003. Rainfall timing, soil moisture dynamics, and plant responses in a mesic tallgrass prairie ecosystem. In *Changing Precipitation Regimes and Terrestrial Ecosystems*. Weltzin J and McPherson G. (eds.). University of Arizona Press: Tuscon, AZ, USA. 147–163.
- Foken T. 2008. The energy balance closure problem: an overview. *Ecological Applications: A Publication of the Ecological Society of America* **18**: 1351–1367.

- Foken T, Wichura B. 1996. Tools for quality assessment of surface based flux measurements. *Agricultural and Forest Meteorology* **78**: 83–105.
- Fu YL, Yu GR, Sun XM, Li YN, Wen XF, Zhang LM, Li ZQ, Zhao L, Hao YB. 2006. Depression of net ecosystem CO₂ exchange in semi-arid *Leymus chinensis* steppe and alpine shrub. *Agricultural and Forest Meteorology* **137**: 234–244.
- Gilmanov TG, Svecjar TJ, Johnson DA, Angell RE, Saliendra NZ, Wylie BK. 2006. Long-term dynamics of production, respiration, and net CO₂ exchange in two sagebrush-steppe ecosystems. *Rangeland Ecology & Management* **59**: 585–599.
- Groisman PY, Knight RW, Easterling DR, Karl TR, Hegerl GC, Razuvaev VN. 2005. Trends in intense precipitation in the climate record. *Journal of Climate* **18**: 1343–1367.
- Gu J, Smith EA, Merritt JD. 1999. Testing energy balance closure with GOES-retrieved net radiation and in situ measured eddy correlation fluxes in BOREAS. *Journal of Geophysical Research D: Atmospheres* **104**: 27881–27893.
- Gu L, Meyers T, Pallardy SG, Hanson PJ, Yang B, Heuer M, Hosman KP, Liu Q, Riggs J, Sluss D, Wullschlegel SD. 2007. Influences of biomass heat and biochemical energy storages on the land surface fluxes and radiative temperature. *Journal of Geophysical Research* **112**: D02107, 11 PP., doi:10.1029/2006JD007425.
- Guo JX, Zhu TC. 1994. Effect of climatic factors on the yield of a neurolepidium chinense (Trin.) community. *Acta Ecologica Sinica* **36**: 790–796.
- Hasegawa PM, Bressan RA, Zhu JK, Bohnert HJ. 2000. Plant cellular and molecular responses to high salinity. *Annual Review of Plant Physiology and Plant Molecular Biology* **51**: 463–499.
- Hu Z, Yu G, Fu Y, Sun X, Li Y, Shi P, Wang Y, Zheng Z. 2008. Effects of vegetation control on ecosystem water use efficiency within and amongst four grassland ecosystems in China. *Global Change Biology* **14**: 1609–1619.
- Hunt JE, Kelliher FM, McSeveny TM, Byers JN. 2002. Evaporation and carbon dioxide exchange between the atmosphere and a tussock grassland during a summer drought. *Agricultural and Forest Meteorology* **111**: 65–82.
- Hunt JE, Kelliher FM, McSeveny TM, Ross DJ, Whitehead D. 2004. Long-term carbon exchange in a sparse, seasonally dry tussock grassland. *Global Change Biology* **10**: 1785–1800.
- IPCC. 2007. *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press: Cambridge.
- Jaksic V, Kiely G, Albertson J, Oren R, Katul G, Leahy P, Byrne KA. 2006. Net ecosystem exchange of grassland in contrasting wet and dry years. *Agricultural and Forest Meteorology* **139**: 323–334.
- Jassal RS, Black TA, Spittlehouse DL, Brmer C, Nescic Z. 2009. Evapotranspiration and water use efficiency in different-aged Pacific Northwest Douglas-fir stands. *Agricultural and Forest Meteorology* **149**: 1168–1178.
- Kaimal JC, Finnigan JJ. 1994. *Atmospheric Boundary Layer Flows: Their Structure and Measurement*. Oxford press: New York.
- Knapp AK, Fay PA, Blair JM, Collins SL, Smith MD, Carlisle JD, Harper CW, Danner BT, Lett MS, McCarron JK. 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science* **298**: 2202–2205.
- Kwon H, Pendall E, Ewers BE, Cleary M, Naithani K. 2008. Spring drought regulates summer net ecosystem CO₂ exchange in a sagebrush-steppe ecosystem. *Agricultural and Forest Meteorology* **148**: 381–391.
- Li J, Zheng H, Yang Y, Zhang W, Lu J, Guo J, Gao Q, Yin L. 1997. *The Saline Grassland Restoration and the Biological Ecological Mechanisms on the Songnen Plains*. Science Press: Beijing.
- Li S, Xu X, Mi H, He J, Wei Y, Wang J. 2003. Effects of water stress on the growing and accumulation of osmolyte of *Cynanchum komarovii*. *Acta Botanica Boreali-occidentalia Sinica* **23**: 592–596.
- Li SG, Eugster W, Asanuma J, Kotani A, Davaa G, Oyunbaatar D, Sugita M. 2008. Response of gross ecosystem productivity, light use efficiency, and water use efficiency of Mongolian steppe to seasonal variations in soil moisture. *Journal of Geophysical Research* **113**: G01019, 13 PP., doi:10.1029/2006JG000349.
- Li ZQ, Yu GR, Wen XF, Zhang LM, Ren CY, Fu YL. 2005. Energy balance closure at ChinaFLUX sites. *Science in China Series D-Earth Sciences* **48**: 51–62.
- Lloyd J, Taylor JA. 1994. On the temperature dependence of soil respiration. *Functional Ecology* **8**: 315–323.
- Ma W, Han M, Lin X, Ren Y, Wang Z, Fang J. 2006. Carbon storage in vegetation of grasslands in inner Mongolia. *Journal of Arid Land Resources and Environment* **20**: 192–195.
- Mahrt L. 1998. Flux sampling errors for air craft and towers. *Journal of Atmospheric and ocean technology* **15**: 416–429.
- McCarthy J, Canziani O, Leary N, Dokken D, White K. 2001. *Climate Change 2001: Impacts, Adaptation, and Vulnerability*. Cambridge University Press: New York.
- Meyers TP. 2001. A comparison of summertime water and CO₂ fluxes over rangeland for well watered and drought conditions. *Agricultural and Forest Meteorology* **106**: 205–214.
- Mkhabela MS, Amiro BD, Barr AG, Black TA, Hawthorne I, Kidston J, McCaughey JH, Orchansky AL, Nescic Z, Sass A, Shashkov A, Zha T. 2009. Comparison of carbon dynamics and water use efficiency following fire and harvesting in Canadian boreal forests. *Agricultural and Forest Meteorology* **149**: 783–794.
- Monteith JL, Unsworth MH. 1990. *Principles of Environmental Physics*. 2nd edn, Edward Arnold: New York.
- NAST. 2000. *Climate Change Impacts on the United States: The Potential Consequences of Climate Variability and Change, Overview Report*. US Global Change Research Program: Washington DC: 68–73.
- Obeso JR. 2002. The costs of reproduction in plants. *New Phytologist* **155**: 321–348.
- Oliphant AJ, Grimmond CSB, Zutter HN, Schmid HP, Su HB, Scott SL, Offerle B, Randolph JC, Ehman J. 2004. Heat storage and energy balance fluxes for a temperate deciduous forest. *Agricultural and Forest Meteorology* **126**: 185–201.
- Parolin P, Oliveira AC, Piedade MTF, Wittmann F, Junk WJ. 2002. Pioneer trees in Amazonian floodplains: three key species form monospecific stands in different habitats. *Folia Geobotanica* **37**: 225–238.
- Potts DL, Huxman TE, Scott RL, Williams DG, Goodrich DC. 2006. The sensitivity of ecosystem carbon exchange to seasonal precipitation and woody plant encroachment. *Oecologia* **150**: 453–463.
- Reichstein M, Tenhunen JD, Rouspard O. 2002a. Severe drought effects on ecosystem CO₂ and H₂O fluxes at three Mediterranean evergreen sites: revision of current hypotheses. *Global Change Biology* **8**: 999–1017.
- Reichstein M, Tenhunen JD, Rouspard O, Ourcival JM, Rambal S, Dore S, Valentini R. 2002b. Ecosystem respiration in two mediterranean evergreen holm oak forests: drought effects and decomposition dynamics. *Functional Ecology* **16**: 27–39.
- Schmid HP. 1997. Experimental design for flux measurements: matching scales of observations and fluxes. *Agricultural and Forest Meteorology* **87**: 179–200.
- Schwinning S, Sala OE. 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. *Oecologia* **141**: 211–220.
- Shang Z, Gao Q, Dong M. 2003. Impacts of grazing on the alkalized–salinized meadow steppe ecosystem in the Songnen Plain, China—a simulation study. *Plant and Soil* **249**: 237–251.
- Shao C, Chen J, Li L, Xu W, Chen S, Gwen T, Xu J, Zhang W. 2008. Spatial variability in soil heat flux at three inner Mongolia steppe ecosystems. *Agricultural and Forest Meteorology* **148**: 1433–1443.
- Shuttleworth WJ, Wallace JS. 1985. Evaporation from sparse crops—an energy combination theory. *Quarterly Journal—Royal Meteorological Society* **111**: 839–855.
- Sims PL, Bradford JA. 2001. Carbon dioxide fluxes in a southern plains prairie. *Agricultural and Forest Meteorology* **109**: 117–134.
- Sun G, Noormets A, Chen J, McNulty SG. 2008. Evapotranspiration estimates from eddy covariance towers and hydrologic modeling in managed forests in Northern Wisconsin, USA. *Agricultural and Forest Meteorology* **148**: 257–267.
- Suyker AE, Verma SB, Burba GG. 2003. Interannual variability in net CO₂ exchange of a native tallgrass prairie. *Global Change Biology* **9**: 255–265.
- Svobodova I, Misa P. 2004. Effect of drought stress on the formation of yield elements in spring barley and the potential of stress expression reduction by foliar application of fertilizers and growth stimulator. *Plant, Soil and Environment* **50**: 439–446.
- Terrell C. 2005. *The Damaging Effects of Drought*. The Morton Arboretum: Lisle, IL, USA.
- Testi L, Orgaz F, Villalobos F. 2008. Carbon exchange and water use efficiency of a growing, irrigated olive orchard. *Environmental and Experimental Botany* **63**: 168–177.
- Wang Y, Xu Z, Zhou G. 2004. Changes in biomass allocation and gas exchange characteristics of *Leymus chinensis* in response to soil water stress. *Acta Phytocologica Sinica* **28**: 803–809.
- Wang Y, Zhou G, Wang Y. 2008. Environmental effects on net ecosystem CO₂ exchange at half-hour and month scales over Stipa krylovii steppe in northern China. *Agricultural and Forest Meteorology* **148**: 714–722.
- Wilson K, Goldstein A, Falge E, Aubinet M, Baldocchi D, Berbigier P, Bernhofer C, Ceulemans R, Dolman H, Field C, Grelle A, Ibrom A,

- Law BE, Kowalski A, Meyers T, Moncrieff J, Monson R, Oechel W, Tenhunen J, Valentini R, Verma S. 2002. Energy balance closure at FLUXNET sites. *Agricultural and Forest Meteorology* **113**: 223–243.
- Xu LK, Baldocchi DD. 2004. Seasonal variation in carbon dioxide exchange over a Mediterranean annual grassland in California. *Agricultural and Forest Meteorology* **123**: 79–96.
- Zhang H. 2001. Responses of NPP of salinized meadow in hyper-arid area to global change. *Journal of Natural Resources* **16**: 642–649.
- Zhang J, Mu C, Wang D, Wang J, Chen G. 2009. Shoot population recruitment from a bud bank over two seasons of undisturbed growth of *Leymus chinensis*. *Botany* **87**: 1242–1249.
- Zhang WL, Chen SP, Chen J, Wei L, Han XG, Lin GH. 2007. Biophysical regulations of carbon fluxes of a steppe and a cultivated cropland in semiarid Inner Mongolia. *Agricultural and Forest Meteorology* **146**: 216–229.
- Zhou GS, Zhang XH. 1996. Study on NPP of natural vegetation in China under global climate change. *Acta Phytoecologica Sinica* **20**: 11–19.
- Zhu TC. 1993. Grasslands of China. In *Natural Grasslands—Eastern Hemisphere and Resume*. Coupland RT (ed.). Ecosystems of the World, Elsevier: Amsterdam, The Netherlands. Volume 8B: 61–82.
- Zhu TC. 2004. *Leymus Chinensis Biological Ecology: Chapter 5*. Jilin Science and Technology Press: Changchun.