Soil moisture pulses drive the seasonal variability of steppe productivity in Mongolia

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1. Introduction

The Mongolian Plateau lies in a prominent transition belt (between latitudes 41.6–52. 2 ^{o}N and longitudes 87.6–119.9 ^{o}E) that borders the Gobi Desert of central Asia in the south and west, and the Siberian taiga forest in the north. Most of Mongolian territory experiences arid or semiarid climate. Steppe comprises over 80% (~1.3×10^6 km^2) of the territory in the country. Similar to other arid and semiarid ecosystems of the world, plant primary productivity of the steppe ecosystems in Mongolia is dramatically affected by water availability and is highly associated with inter- and/or intra-seasonal variability of precipitation. It is thus expected that the steppe ecosystem functioning is sensitive to interannual and decadal variability in climate and over-exploitation by human activities. Because of the vast area they cover, the Mongolian steppe ecosystems likely play a pronounced role in the global carbon and water cycles. However, relatively little attention has been paid by the global flux measurement community to the Mongolian grassland ecosystems over the past two decades (Sugita et al., 2006). To this end, measurements of energy, water vapor and CO_2 fluxes are being conducted over a steppe ecosystem in Kherlenbayan-Ulaan (KBU), Hentiy province, Mongolia, using the EC technique (Li et al., 2005; 2006).

Vegetation productivity can be evaluated in many ways including: (1) light use efficiency (LUE) that describes the ability of the vegetation to use incident photosynthetically active radiation (PAR), and (2) water use efficiency (WUE) that describes the ability of the vegetation to photosynthetically fix carbon in terms of water loss. The efficient use of available water and received sunshine is particularly important for the establishment and subsequent survival of vegetation in arid and semiarid environments. In this paper, the primary objectives are to: (1) describe diurnal and seasonal dynamics of LUE and WUE, (2) investigate the influences of environmental and ecophysiological variables on the performance of LUE and WUE, and (3) establish linkages between light use and water use by the steppe.

2. Materials and Methods

The study site is located at Kherlenbayan-Ulaan (KBU), the Hentiy province of Mongolia (lat. 47^{o}12.838'N, long. 108^{o}44.240'E, 1235 m a.s.l). The climate is continental in the temperate zone. Average annual air temperature is 1.2 ^{o}C and average annual precipitation is 196 mm. The soil is the typical Chestnut soil. The steppe vegetation is dominated by temperate C_3 plants.

We used an EC system to measure CO_2, water vapor and energy fluxes. It consisted of a 3-D ultrasonic anemometer-thermometer (SAT-550, Kaijo Sonic Co., Tokyo, Japan) and an open path infrared gas analyzer (Li7500, LICOR Inc., Lincoln, Nebraska). It monitored the fluctuations in 3-D wind components, sonic temperature, water vapor and CO_2 concentrations at 3.5 m above the ground at a rate of 10 Hz. Half-hourly flux data were online computed and recorded with a datalogger (CR23X, Campbell Scientific, Logan, Utah). This paper used the data obtained during the 2003 growing season (from 23 April to 21 October, 182 days). We also measured up and down long and short wave radiation by a net radiometer (CNR1, Kipp & Zonen BV, Delft, the Netherlands), air temperature and humidity at a height of 2.5 m by an air temperature/humidity sensor (HMP-45D, Vaisala Inc., Helsinki, Finland), soil moisture profile at depths of 10, 20, 30, 70, 100 and 150 cm by time domain reflectometry probes (CS616, Campbell Scientific, Logan, UT, USA), and PPT by a tipping bucket rain gauge (CYG-52202, RM Young Company, Traverse City, MI, USA). These variables were sampled at 0.1 Hz and their 30-min mean data were logged with a CR10X data logger (Campbell Scientific, Logan, UT, USA). In addition, leaf area index was measured monthly by the clipping method during the 2003 growing season. Details for flux data post-processing have been described in Li et al. (2005, 2006).

Gross ecosystem production (GEP) was indirectly estimated from:

$$\mathrm{GEP} = R_{\mathrm{eco}} - \mathrm{NEE}\,, \qquad (1)$$

where NEE is net ecosystem CO_2 exchange, and R_{eco} is total ecosystem respiration. NEE was measured by the EC method. Nighttime R_{eco} during low turbulence ($u_* < 0.2$ m s^{-1}) and daytime R_{eco} were estimated using exponential relationships between nighttime NEE obtained under high turbulence ($u_* \geq 0.2$ m s^{-1}) and ambient temperature (T_a) at 2.5 m (Li et al., 2005).

Incident photosynthetically active radiation (PAR) was estimated from the measured shortwave solar radiation (K_d). Ecosystem light use efficiency (LUE) (mmol CO_2 per mol PAR) can be directly defined as the ratio of GEP to incident PAR. Carbon and water fluxes are key aspects of ecosystem functions. Their relationship can be depicted by water use efficiency (WUE). We defined ecosystem WUE as photosynthetic carbon gain (GEP) per unit of evapotranspirative water loss from land surface (ET) (mmol CO_2 per mol H_2O). Only data obtained when PAR >500 μmol m^{-2} s^{-1} were used in our analysis of daily courses of LUE and WUE, to minimize the effect of low PAR on ET and WUE. Daily values of LUE and WUE were computed from daily sums of GEP, PAR and ET.

The surface reflectivity (albedo) for short-wave radiation (α_K) is defined as the ratio of reflected (K_u) to incoming (K_d) short-wave radiation ($\alpha_K = K_u/K_d$). The α_K values were averaged over daytime 30-min data when K_d >200 W m^{-2} to minimize the effect of low solar angles. The statistical analyses were employed by using the Data Desk (Data Description Inc., Ithaca, NY, USA).

3. Results and Discussion

Daytime amplitude of GEP varied substantially within the growing season with typical daytime peak GEP values ranging from 0.5 μmol CO_2 m^{-2} s^{-1} in May to 5.0 μmol CO_2 m^{-2} s^{-1} in July (Fig. 1a). GEP was larger in the morning than in the afternoon. Both lower T_a and lower vapor pressure deficit (VPD) in the morning stimulated carbon uptake, whereas in the afternoon higher T_a increased carbon loss by ecosystem respiration (Li et al., 2005). Simultaneously, the higher afternoon VPD values exceeding 1 kPa in all months are expected to result in partial closure of the stomata and thus to reduce carbon assimilation (Fig. 1f). Both LUE and WUE were higher in the early morning, declined with time until noon, and then increased slightly with the decrease of PAR, T_a and VPD in the late afternoon (Fig. 1 b-f). The higher LUE in early morning and in late afternoon is most likely related to solar elevation angle and thus to the increase of relative share of diffuse radiation. Both LUE (Fig. 1c) and WUE (Fig. 1e) were lowest in May and June when the vegetation was still in its early seasonal development stage. LUE was largest in July and in phase with highest GEP, whereas we did not find any significant difference in WUE between June, July, and August (Figs. 2c and 2e).

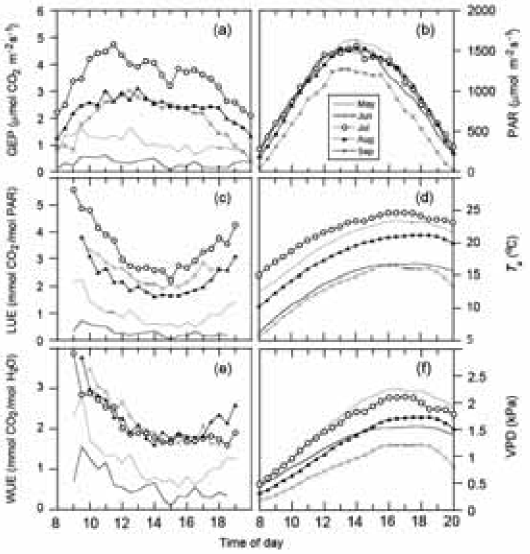

Fig. 1. Monthly-averaged daytime courses of (a) GEP, (b) PAR, (c) LUE, (d) T_a at 2.5 m, (e) WUE and (f) VPD.

Maximum PAR values were observed around the summer solstice, while T_a reached its maximums in mid July (Fig. 2a). Total PPT received during the growing season (from April to October) was 231 mm (Fig. 2b). There were twelve PPT events exceeding 5 mm that considerably affected soil water content (SWC) (Fig. 2b).

With the onset of the growing season, GEP began to increase from the lowest values in May to the highest values in July, which were usually over 100 mmol CO_2 m^{-2} d^{-1} (Fig. 2c). Water shortage in August (DOY 210–225, SWC <9% on average, Fig. 2b) caused GEP to decrease relative to July (Fig. 2c). GEP was again relatively high in September due to recovery growth after removal of water shortage by large PPT input in late August. In October, the steppe underwent rapid physiological changes, and photosynthesis further declined because of the combined negative effects of low PAR, low T_a, and low LAI.

On a daily basis, LUE values ranged from 0 to 7.0 mmol CO_2 mol^{-1} PAR with a mean of 2.1 mmol CO_2 mol^{-1} PAR during the entire growing season (Fig. 2d). The mean LUE for the steppe is similar to that (0.3-3.8 mmol CO_2 mol^{-1} PAR) of Serpentine grassland in California with LAI of 1-1.5 (Valentini et al., 1995), and lower than that of an alpine meadow (8-18 mmol CO_2 mol^{-1} PAR) on the Qinghai-Tibetan Plateau (Kato et al., 2004).

WUE was generally lower after than before the rain events (Fig. 2d), while GEP showed an opposite behavior (Fig. 2c). This means that although rain did increase productivity, bare soil evaporation and plant transpiration following rainfall events were comparatively large and reduced overall WUE. On a daily basis, WUE ranged from

0 to 8.1 (mean 2.2) mmol CO_2 mol^{-1} H_2O (Fig. 2d). The mean WUE of 2.2 mmol CO_2 mol^{-1} H_2O during the entire growing season was extremely low.

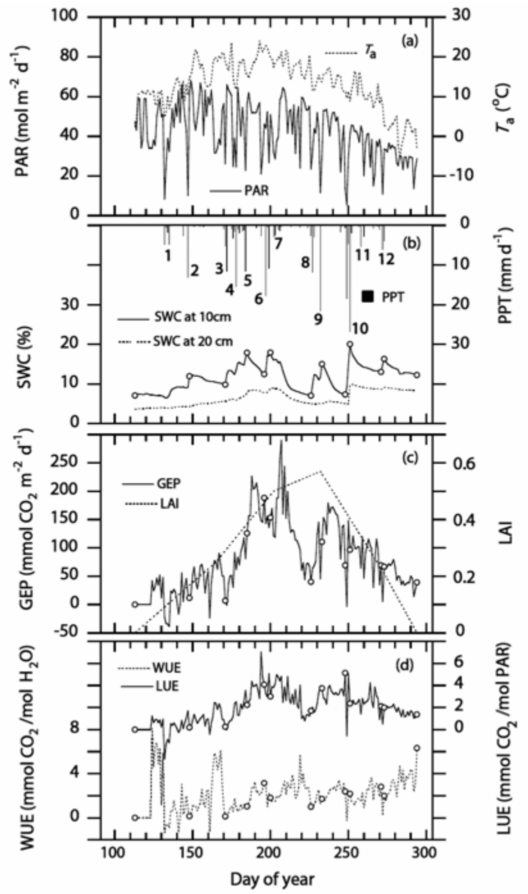

Fig. 2. The time series of (a) PAR and T_a at 2.5 m, (b) SWC at depths of 10 and 20 cm and PPT, (c) GEP and LAI, and (d) LUE and WUE during the growing season (DOY 113-294). Circles in (b)-(d) indicate major soil moisture pulses caused by recent rain events. Numbers in (b) indicate PPT pulse size over 5 mm.

In comparison, LUE is substantially higher for an alpine meadow on the Qinghai-Tibetan Plateau than for the steppe on the Mongolian Plateau. However, WUE compared well in both ecosystems (varying from 2 to 6 mmol CO_2 mol^{-1} H_2O for the alpine meadow, Gu et al., 2003; Kato et al., 2004). This is likely because alpine meadows have larger LAI (~3.8, Kato et al., 2004) than the steppe, and water losses directly from the soil surface are lower because of the denser vegetation cover.

The relationship between daily GEP and incident PAR is examined with respect to SWC at 10 cm depth by grouping the data into three SWC classes (SWC ≤10%, 10< SWC ≤15%, and SWC >15%) (Fig. 3). Although the data are scattered, on a daily basis, GEP appeared to respond to PAR in a linear way irrespective of soil moisture conditions ($P < 0.25$ for SWC ≤10%, $P < 0.025$ for 10< SWC ≤15%, and $P < 0.05$ for SWC >15%, respectively). Such a linear response of GEP to PAR has already been reported in literature for crops and grassland (Turner et al., 2003). The linear regression slope increased with increasing SWC, suggesting that the steppe used available light more efficiently under well-watered conditions (Fig. 3).

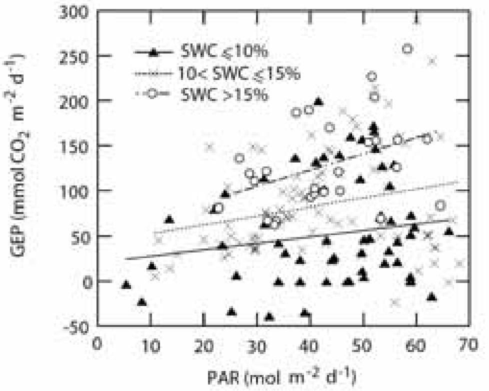

Fig. 3. The relationship between daily GEP and incident PAR.

GEP and ET were significantly correlated ($P < 0.001$ for SWC ≤10% and 10< SWC ≤15%, and $P < 0.005$ for SWC >15%, respectively) (Fig. 4). Regardless of soil moisture conditions, GEP increased with increasing ET. Similar linear relationships exist across various biome types (Law et al., 2002). Generally, the slope between changes in GEP and ET is also a measure of WUE (Law et al., 2002). Our observation shows that the slope, a surrogate of WUE, declined with increasing SWC (Fig. 4). For example, the slope at SWC >15 % was only half of that at SWC <10%, suggesting that a large increase in soil moisture, after a substantial rain event, could not be efficiently used for taking up carbon from the atmosphere, but rather returned rapidly to the atmosphere via soil evaporation.

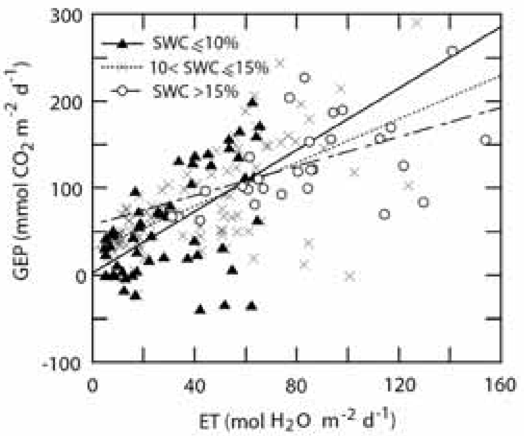

Fig. 4. The relationship between daily GEP and ET.

LAI had a significant effect on LUE (P <0.001, Fig. 5a). At lower LAI, LUE was low because of low GEP, and the canopy is expected to be light-saturated. Linear response of LUE to LAI compares well with observations from crops (Sinclair and Horie, 1989). On a daily basis, LUE increased significantly with increasing T_a (P <0.005, Fig. 5b), indicating that the steppe vegetation is generally below its photosynthetically optimal temperatures and in the temperature range with no signs of a combination of drought stress and heat stress. LUE shows a clear response to SWC, being significantly higher under well-water conditions (P <0.001, Fig. 5c). Other studies of LUE in grassland ecosystems have reported similar trends of drought induced decline in LUE (Hunt et al., 2002; Turner et al., 2003). We observed that LUE decreased considerably with the increase in α_K (P <0.001, Fig. 5d).

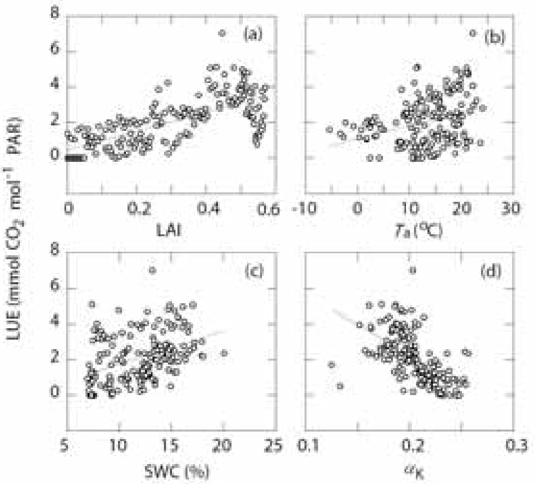

Fig. 5. The relationships of LUE vs. (a) LAI, (b) T_a, (c) SWC at 10 cm, and (d) α_K.

WUE differed from LUE in its response to above-mentioned biotic and abiotic factors. It appeared that LAI had only a small and insignificant effect on WUE (P >0.7, data not shown). WUE decreased slightly with increasing LAI. The insensitivity of WUE to LAI can be explained by physical evaporation from soil surface that overshadowed biological transpiration from plants at low LAI values during the whole growing season. In contrast, there was a decreasing trend of WUE with increasing T_a (P <0.05). WUE decreased with increasing SWC (P <0.05) and increased with increasing α_K (P <0.01). Obviously, the control of LAI, T_a, SWC, and α_K over LUE was much stronger than over WUE. On a daily basis, both LUE and WUE were not significantly correlated with VPD (P >0.5, data not shown).

4. Conclusions

In semi-arid environments such as the Mongolian Plateau, where water is often a limiting factor for vegetation productivity, an efficient use of water is essential for the steppe vegetation growth. At the same time, light conditions on the Plateau were not limiting photosynthesis, but light use efficiency clearly depended in a consistent way on SWC. LUE for this ecosystem was comparatively low because of low LAI. WUE was also low due to low LAI in combination with substantial evaporative water losses directly from the bare soil surface. In contrast to our expectations, we found that the steppe vegetation is active and ready to respond quickly to soil moisture pulses.

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