Response of gross ecosystem productivity, light use efficiency, and water use efficiency of Mongolian steppe to seasonal variations in soil moisture

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[1] The examination of vegetation productivity and use of light and water resources is important for understanding the carbon and water cycles in semiarid and arid environments. We made continuous measurements of carbon dioxide and water vapor fluxes over an arid steppe ecosystem in Mongolia by using the eddy covariance (EC) technique. These measurements allow an examination of EC-estimated gross ecosystem productivity (GEP), light use efficiency (LUE), and water use efficiency (WUE) of the steppe. Daily variations of GEP, LUE, and WUE were associated with daily variations of incident photosynthetically active radiation (PAR), ambient temperature (T_a), and vapor pressure deficit (VPD). The magnitudes of these variations were also dependent on canopy development. On the daily basis, GEP linearly correlated with evapotranspiration rate and PAR. LUE correlated positively with leaf area index, T_a, and soil moisture availability but negatively with the surface reflectivity for short-wave solar radiation. Throughout the growing season, both GEP and LUE responded strongly to precipitation-fed soil moisture in the top 20 cm of the soil. An examination of the responses of LUE and WUE to PAR under different soil moisture conditions shows that when soil water availability exceeded VPD, the steppe was most efficient in light use, whereas it was less efficient in water use. The multivariate analysis of variance also suggests that soil moisture availability, especially water status in the upper 20-cm soil layer with dense distribution of grass roots, is the most significant factor that governs GEP, WUE, and LUE. This study provides a preliminary assessment of the use of available water and light by the Mongolian arid steppe ecosystems under seasonally varying soil moisture conditions. A better understanding of these functional responses is required to predict how climate change may affect arid steppe ecosystems.

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1. Introduction

[2] Arid and semiarid regions of the world account for approximately one-third of the global land surface and play a significant role in global climate, biogeochemical, and hydrological processes [*Schlesinger et al.*, 1990]. Arid and semiarid environments are typically characterized by low precipitation, frequent droughts, high light availability, nutrient-poor soils, and low vegetation cover [*Schlesinger et al.*, 1990]. Under such environments, plant primary productivity is usually limited by deficiencies in soil moisture and nutrient availability [*Noy-Meir*, 1973; *Webb et al.*, 1983] and is largely dependent on short-term and/or long-term precipitation [*Fischer and Turner*, 1978; *Le Houérou et al.*, 1988; *Sala et al.*, 1988; *Lauenroth and Sala*, 1992; *McNaughton et al.*, 1993; *Breymeyer et al.*, 1996; *Nicholson et al.*, 1998; *Prince et al.*, 1998; *Knapp and Smith*, 2001; *Austin and Sala*, 2002; *Weltzin et al.*, 2003; *Austin et al.*, 2004; *Huxman et al.*, 2004; *Schwinning et al.*, 2004; *Schwinning and Sala*, 2004; *Potts et al.*, 2006].

[3] Resource use by vegetation 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 per unit of water transpired.

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It is noteworthy that when defined with eddy covariance measurements of CO_2 and water vapor fluxes, WUE encompasses the influences from bare soil evaporation and interception evaporation as well as heterotrophic respiration. Since LUE and WUE are tightly correlated, the effects of drought stress on water use are expected to be reflected in both variables. Understanding of LUE and WUE by vegetation and their biotic and abiotic controls is prerequisite in addressing carbon and water cycles in arid and semiarid environments [*Fowler*, 1986; *Walter*, 1979; *Schwinning and Ehleringer*, 2001; *Schwinning et al.*, 2002; *Schwinning and Sala*, 2004]. To date, LUE and WUE have been well studied at the individual leaf scale [e.g., *Collatz et al.*, 1991; *Jones*, 1992; *Salisbury and Ross*, 1992; *Jarvis*, 1995] but less at the canopy scale [e.g., *Baldocchi*, 1994; *Rochette et al.*, 1996; *Campbell et al.*, 2001; *Law et al.*, 2002; *Scanlon and Albertson*, 2004; *Williams and Albertson*, 2004]. At the canopy scale, research on LUE and WUE has been done primarily over crop fields [e.g., *Baldocchi*, 1994; *Rochette et al.*, 1996; *Moncrieff et al.*, 1997; *Campbell et al.*, 2001] and less over grassland and forest ecosystems [e.g., *Price and Black*, 1990; *Lamaud et al.*, 1996; *Verhoef et al.*, 1996; *Dewar*, 1997; *Moncrieff et al.*, 1997; *Berbigier et al.*, 2001; *Eamus et al.*, 2001; *Law et al.*, 2002; *Scanlon and Albertson*, 2004; *Williams and Albertson*, 2004]. Measurements of land surface fluxes of CO_2 and H_2O by micrometeorological techniques, especially the eddy covariance (EC) approach, provide a powerful tool for characterizing canopy-scale water and light use [*Ruimy et al.*, 1995; *Aubinet et al.*, 2000; *Valentini et al.*, 2000; *Baldocchi et al.*, 2001; *Falge et al.*, 2002a, 2002b; *Law et al.*, 2002].

[4] The Mongolian Plateau lies in a prominent transition belt (between latitudes 41.6–52.2°N and longitudes 87.6–119.9°E) that borders the Gobi Desert of central Asia in the south and west and the Siberian taiga forest in the north [*Batima and Dagvadorj*, 1998]. Most of Mongolian territory experiences arid or semiarid climate. Steppe composes over 80% ($\sim 1.3 \times 10^6$ km^2) of the territory in the country [*World Resources Institute*, 2003]. Mongolian steppe ecosystems can be characterized as follows: (1) low annual precipitation with large intraseasonal and interseasonal variability and frequent droughts that often constrain plant growth; (2) temperature limitation associated with very strong temperature seasonality and severe freezing; (3) sandy, nutrient-poor soils with a low–water holding capacity; and (4) low-statured vegetation cover with a low leaf area index even during the peak growing season. In these ecosystems, grazing is the major anthropogenic disturbance [*Batima and Dagvadorj*, 1998; *Sneath*, 1998; *Sugita et al.*, 2007]. Similar to other arid and semiarid ecosystems of the world, Mongolian steppe primary productivity is dramatically affected by water availability and is highly associated with interseasonal and/or intraseasonal variability of precipitation [*Schimel et al.*, 1990; *Galloway and Melillo*, 1998; *Ojima et al.*, 1998]. It is thus expected that steppe ecosystem function is sensitive to interannual and decadal variability in climate [*Galloway and Melillo*, 1998; *Chase et al.*, 2000]. Because of the vast area they cover, the Mongolian steppe ecosystems likely play a pronounced role in the global carbon and water cycles [*Schimel et al.*, 1990; *Galloway and Melillo*, 1998; *Intergovernmental Panel on Climate Change (IPCC)*, 2001]. Together with the Tibetan Plateau, the Mongolian Plateau also plays an important role in affecting the east Asia summer monsoon system [*Yasunari*, 2003].

[5] Flux measurements have been recently conducted over grassland ecosystems in the Tibetan Plateau [e.g., *Kim et al.*, 2000; *Gu et al.*, 2003; *Kato et al.*, 2004]. However, relatively little attention has been paid by the global flux measurement community to the Mongolian steppe ecosystems over the past two decades [*Sugita et al.*, 2007]. 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]. One of the major objectives of the measurements is to investigate and quantify the strength of the carbon sink or source of the Mongolian steppe and its sensitivity to seasonal and annual climate variability and anthropogenic disturbances. These measurements therefore have implications for relating ecosystem level dynamics of steppe vegetation properties such as productivity, water use, and light use capacity to climate change and potential anthropogenic disturbances (land use change) over both short and long temporal scales under global warming scenario [*IPCC*, 2001; *Sugita et al.*, 2007]. In addition, understanding the effects of environmental factors on ecosystem carbon and water exchanges is a major concern for politicians and economists in Mongolia to make policies that coordinate and harmonize interactive relations among land use, sustainable development, economic growth, and climate change.

[6] In an earlier paper, we discussed how biotic and abiotic factors affect net ecosystem CO_2 exchange above the steppe in KBU [*Li et al.*, 2005]. We observed that the steppe was a weak sink for atmospheric CO_2, and drought stress during the growing season could shift the steppe from a carbon sink to a carbon source, indicating the sensitivity of steppe functioning to water availability. In this paper, we extend our analyses to the patterns and processes that govern gross ecosystem productivity (GEP), light use, and water use of the steppe. The primary objectives are (1) to describe diurnal and seasonal dynamics of GEP, LUE, and WUE and (2) to investigate the influences of environmental and ecophysiological variables on GEP, LUE, and WUE.

2. Materials and Methods

2.1. Site Information

[7] The study was conducted at a steppe in KBU (latitude 47°12.838′N, longitude 108°44.240′E, and 1235 m above sea level). The climate is continental in the temperate zone with a mean annual air temperature (T_a) of 1.2°C and a mean annual precipitation (PPT) of 196 mm (1993–2002, the KBU Weather Station). The site receives most (88%) of PPT from June through September. In 2003, the mean annual T_a was 0.4°C, which is 0.9°C lower than the decadal mean, while the annual PPT was 244 mm, 24% above the decadal mean (Figure 1). The soil is classified as chestnut soil (Kastanozem), and is well drained with low–moisture holding capacity. Its bulk density, overall porosity, and hydraulic conductivity in the top 30-cm layer are 1.45 g cm^{-3}, 45%, and 0.01–0.08 mm s^{-1}, respectively. In terms of biomass and leaf area index (LAI), about 75% of the vegetation at the site is dominated by temperate perennial C3 plants, e.g.,

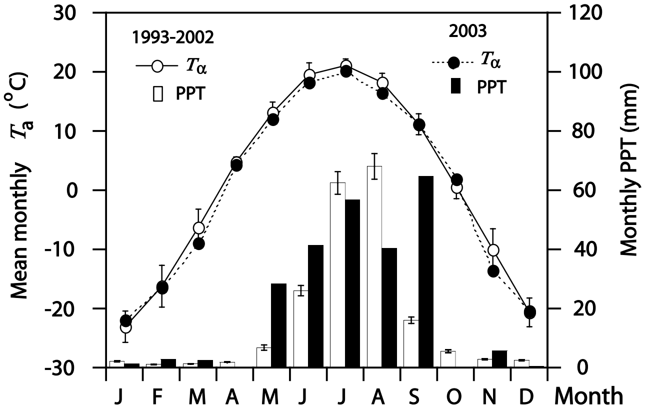

Figure 1. Mean monthly air temperature (T_a) and mean annual precipitation (PPT) at the Kherlenbayan-Ulaan Weather Station.

Stipa krylovii, *Carex duriuscula*, *Artemisia frigida*, *Allium mongolicum*, *Leymus chinensis*, and *Caragana microphylla*. Most common C4 plants include *Cleistogenes squarrosa* (perennial grass) and *Salsola collina* (annual forb). The steppe has experienced grazing over centuries, and the decadal mean stocking rate (1984–2003) was 0.3 animal unit equivalent (0.6 sheep equivalent). Since the onset of market economy in the early 1990s, the level of grazing intensity shows an increasing trend [*Sugita et al.*, 2007]. Additionally, the grazing intensity is strongly affected by dzud, a Mongolian term describing natural disaster including severe summer drought (black dzud) and heavy winter snowfall weather (white dzud) [*United Nations Disaster Management Team*, 2000]. For example, 3 consecutive years (1999–2001) of dzud resulted in 9% (1999–2000) and 14% (2000–2001) decrease in livestock population in Mongolia [*National Statistical Office of Mongolia*, 2003]. The steppe is grazed year-round primarily by domestic livestock (sheep, cattle, horses, camels, and goats). During the nongrowing season (November–April), the livestock relies mainly on standing, dried biomass for forage, and thus a dzud may considerably reduce livestock populations because of shortages of forage supply. The site was described in more detail by *Li et al.* [2005, 2006] and *Sugita et al.* [2007].

2.2. Measurements

[8] We used an eddy covariance 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) and an open path infrared gas analyzer (LI7500, LI-COR, 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 data logger (CR23X, Campbell Scientific, Logan, Utah). This paper used data obtained during the 2003 growing season (from 23 April to 21 October, 182 days). The growing season was defined according to phenological data from the Mongolian Institute of Meteorology and Hydrology [*Li et al.*, 2005].

[9] We also measured incoming and outgoing long- and short-wave radiation by a net radiometer (CNR 1, Kipp & Zonen BV, Delft, 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, Utah), and PPT by a tipping bucket rain gauge (CYG-52202, RM Young Co., Traverse City, Michigan). These variables were sampled at 0.1 Hz, and their 30-min mean data were logged with a CR10X data logger (Campbell Scientific, Logan, Utah).

[10] LAI was measured monthly by the clipping method during the 2003 growing season. Quadrate size was 0.25 m^2 with 12 replications. Live leaves were removed from the stems for determining green LAI by a scanner (CanoScan LiDE 40, Canon, Tokyo) and corresponding special software [*Yamamoto*, 2000]. On each LAI measuring date, mean canopy height (h_c) was also measured. The maximum LAI occurred around late August (day of year (DOY) 232) and reached a value near 0.6 m^2 leaf m^{-2} ground. The mean h_c was 12 ± 7.5 standard deviation cm measured in early July of 2003. The maximum h_c reached 45 cm (mean h_c, 20 ± 12 cm standard deviation) when *Stipa krylovii* was at its earing growth stage (late July to early August). LAI gaps were linearly interpolated to daily intervals.

2.3. Data Processing

[11] Flux data postprocessing includes the cospectral correction for CO_2 and water vapor fluxes [*Eugster and Senn*, 1995], the correction for the density flux effect [*Webb et al.*, 1980], and data gap filling [*Falge et al.*, 2001]. Details for flux calculation have been described by *Li et al.* [2005, 2006].

[12] 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 (friction velocity (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 T_a at 2.5 m [*Li et al.*, 2005].

[13] Ecosystem LUE (mmol CO_2 mol^{-1} PAR) can be directly defined as the ratio of GEP to absorbed PAR [*Turner et al.*, 2003]. Because we did not measure absorbed PAR, as a surrogate, we used incident PAR, which was computed directly from the measured short-wave solar radiation (K_d): PAR (μmol photons m^{-2} s^{-1}) = 2.16 × K_d (W m^{-2}) [*Weiss and Norman*, 1985]. This will underestimate LUE. Since the surface reflectivity (albedo) for short-wave radiation (α_K) varied roughly from 0.15 to 0.25, therefore this underestimation of LUE ranges from 15 to 25%. The α_K is defined as the ratio of reflected short-wave radiation (K_u) to K_d ($\alpha_K = K_u/K_d$). 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 [*Monteith and Unsworth*, 1990].

[14] Carbon and water fluxes are key aspects of ecosystem functions. Their relationship can be depicted by water use efficiency [*Jones*, 1992]. At the scale of the leaf, WUE is defined as the ratio of net assimilation of CO_2 by

photosynthesis to transpiration [*Rosenberg et al.*, 1983; *Jones*, 1992]. However, it is not possible to isolate canopy photosynthesis and transpiration from the aggregate ecosystem fluxes that are measured with the EC method. Therefore at the scale of the canopy, we defined ecosystem WUE as photosynthetic carbon gain (GEP) per unit of evapotranspirative water loss from land surface (ET) (mmol CO_2 mol^{-1} H_2O) [*Baldocchi*, 1994; *Law et al.*, 2002]. 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 [*Baldocchi et al.*, 1985a]. Daily values of LUE and WUE were computed from daily sums of GEP, PAR, and ET.

[15] Canopy surface conductance can be estimated by inverting the Penman-Monteith equation [*Priestley and Taylor*, 1972; *Stewart*, 1988] after having derived the aerodynamic conductance from wind data [*Thom*, 1972].

$$\frac{1}{g_c} = \frac{\rho C_P \mathrm{VPD}}{\gamma \lambda E} + \frac{\frac{s}{\gamma}\frac{H}{\lambda E} - 1}{g_a}, \qquad (2)$$

where g_c is the bulk canopy surface conductance (m s^{-1}), ρ is the air density (kg m^{-3}) at a given air temperature, C_P is the specific heat capacity of air at constant pressure (J kg^{-1} K^{-1}), VPD is the atmospheric vapor pressure deficit (kPa), H is the sensible heat flux (W m^{-2}), λE is the latent heat flux (W m^{-2}), s is the slope of the saturation water vapour pressure versus temperature curve (kPa K^{-1}), γ is the psychrometric constant (kPa K^{-1}), and g_a is the aerodynamic conductance (m s^{-1}). For more details on computing g_c, see *Li et al.* [2006].

[16] The statistical analyses were employed by using Data Desk (Data Description, Inc., Ithaca, New York). A standard simple linear regression technique was used to determine the linear relationship between two variables (e.g., GEP versus PAR) (sections 3.3, 3.4, and 3.5). Although each specific factor is important in influencing GEP, WUE, and LUE, our question was rather to find out which combination of factors explains most of the variance. To answer this question, we first compiled biotic (LAI and g_c) and abiotic (PAR, T_a, VPD, α_K, PPT, and SWC at 10 cm and SWC at 20 cm) factors as group variables by bin separation and then used a multivariate analysis of variance with daily resolution data (section 3.6).

3. Results and Discussion

3.1. Seasonal Variation of GEP, LUE, and WUE

[17] During the growing season (DOY 113–294), daily PAR ranged roughly between 5.4 MJ m^{-2} d^{-1} (DOY 249) and 68.1 MJ m^{-2} d^{-1} (DOY 249), and daily T_a varied from −5.4°C (DOY 283) to 24.1°C (DOY 193) (Figure 2a). The PPT total during the growing season was 231 mm (Figure 2b), 24% above the multiyear average (187 mm) for the same period. Above-average PPT was mainly observed in May, June, and September, while July and August totaled below-average PPT (Figure 2b) and thus can be considered to be affected by drought. In detail, there were twelve PPT events exceeding 5 mm that considerably affected soil water content (SWC) (Figure 2b). This effect was most pronounced in the top 10-cm soil layer, whereas the 20-cm and 30-cm layers only showed a quick response during event 10. SWC varied by 13.6% (6.4–20.0%) at 10 cm, 6.4% (3.6–10.0%) at 20 cm, and 5.7% (2.8–8.4%) at 30 cm, respectively. SWC below 30 cm depth (70–150 cm) varied by less than 1% over the growing season.

[18] The seasonal course of GEP does not perfectly follow the leaf area index (Figure 2c), demonstrating the important influence of drought periods in this steppe ecosystem. In the early growing season, GEP increased almost linearly with LAI from late April until July when the highest values (usually over 100 CO_2 mmol m^{-2} d^{-1}) were reached (Figure 2c). A drought period in August (DOY 210–225, SWC < 9% on average) (Figure 2b) caused GEP to decrease substantially as compared to July values (Figure 2c). Then GEP recovered quickly and yielded relatively high values again in September after drought conditions had ended thanks to a large PPT event (21.6 mm, DOY 232) in late August. This recovery of the steppe vegetation is noteworthy because the onset of senescence coincided with that period. In October (DOY 274–294), 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.

[19] On a daily basis, LUE values ranged from 0 to 7.0 (mean 2.1) mmol CO_2 mol^{-1} PAR (Figure 2d). The mean LUE for the steppe is similar to that (0.3–3.8 mmol CO_2 mol^{-1} PAR) for Serpentine grassland in California with LAI of 1–1.5 [*Valentini et al.*, 1995] and lower than that for an alpine meadow (8–18 mmol CO_2 mol^{-1} PAR) on the Qinghai-Tibetan Plateau [*Kato et al.*, 2004]. Low LUE values reflect the low vegetation cover and the relatively large fraction of uncovered bare soil [*Hunt et al.*, 2002]. However, broad ecosystem comparisons are difficult because various methods are used to express LUE in the literature.

[20] On a daily basis, WUE ranged from 0 to 8.1 (mean 2.2) mmol CO_2 mol^{-1} H_2O (Figure 2d). WUE for the Mongolian steppe agrees well with that (varying from 2 to 6 mmol CO_2 mol^{-1} H_2O) for the alpine meadow on the Qinghai-Tibetan Plateau [*Gu et al.*, 2003; *Kato et al.*, 2004] but is considerably higher than that (the maximum WUE of 1.7 mmol CO_2 mol^{-1} H_2O) for tussock grassland in New Zealand [*Hunt et al.*, 2002] and is lower than that for the C4-dominant grassland (3.0–6.0 mmol CO_2 mol^{-1} H_2O) [*Ham et al.*, 1995; *Colello et al.*, 1998]. Observations in tussock grassland in New Zealand demonstrate that lower WUE values were associated with a combination of a large soil surface area exposed to radiation, high soil temperatures, high mean wind speeds, and low LAI [*Hunt et al.*, 2002].

[21] In most occasions, rain increased productivity of the steppe (Figure 2c), but WUE otherwise decreased immediately after the rain (Figure 2d), showing a larger initial response of ET to wetting compared to the response of productivity. This is because of low–water holding capacity of the steppe soil with scarce vegetation cover that led to rapid depletion of SWC mainly through bare soil evaporation, which started immediately after the rain. It therefore suggests that if rain intensity is comparatively high or if rain-free periods are too short the rain received by the scarce steppe vegetation cover might not be fully biologically effective and partially only increase surface evaporation. It also suggests that a physiological interpretation of the canopy-scale WUE is misleading at least while bare soil

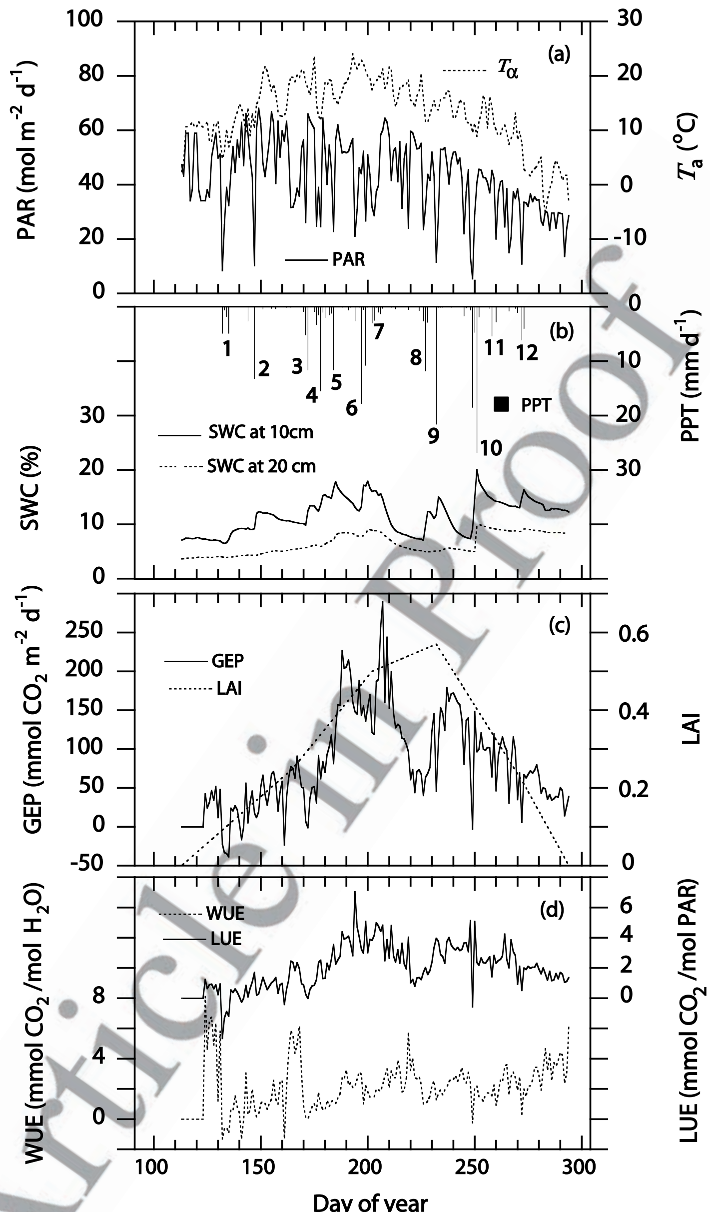

Figure 2. The time series of (a) photosynthetically active radiation (PAR) and T_a at 2.5 m, (b) soil water content (SWC) at depths of 10 and 20 cm and PPT, (c) gross ecosystem productivity (GEP) and leaf area index (LAI), and (d) light use efficiency (LUE) and water use efficiency (WUE) during the growing season (days of year 113–294). Circles in Figures 2b, 2c, and 2d indicate abrupt soil moisture change due to recent rain events. Numbers in Figure 2b indicate PPT size over 5 mm.

evaporation is a substantial contributor to ET. Confounding effect of the bare soil evaporation on WUE deserves further clarification in the future.

3.2. Diurnal Courses of GEP, LUE, and WUE

[22] Figure 3 illustrates monthly averaged daytime courses of GEP, LUE, WUE, PAR, T_a, and VPD. 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 (Figure 3a). GEP was larger in the morning than in the afternoon. Both lower T_a and lower 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 might result in partial closure of the stomata and thus reduce carbon assimilation (Figure 3f). 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 (Figures 3b, 3d, 3e, and 3f). The inverse relationship between WUE and VPD is theoretically based [*Tanner and Sinclair*, 1983; *Sinclair et al.*, 1984] and has been observed for other ecosystems (e.g., for crops [*Tanner and Sinclair*, 1983; *Monteith*, 1986; *Baldocchi*, 1994], for grasslands [*Verma et al.*, 1992; *Verhoef et al.*, 1996; *Moncrieff et*

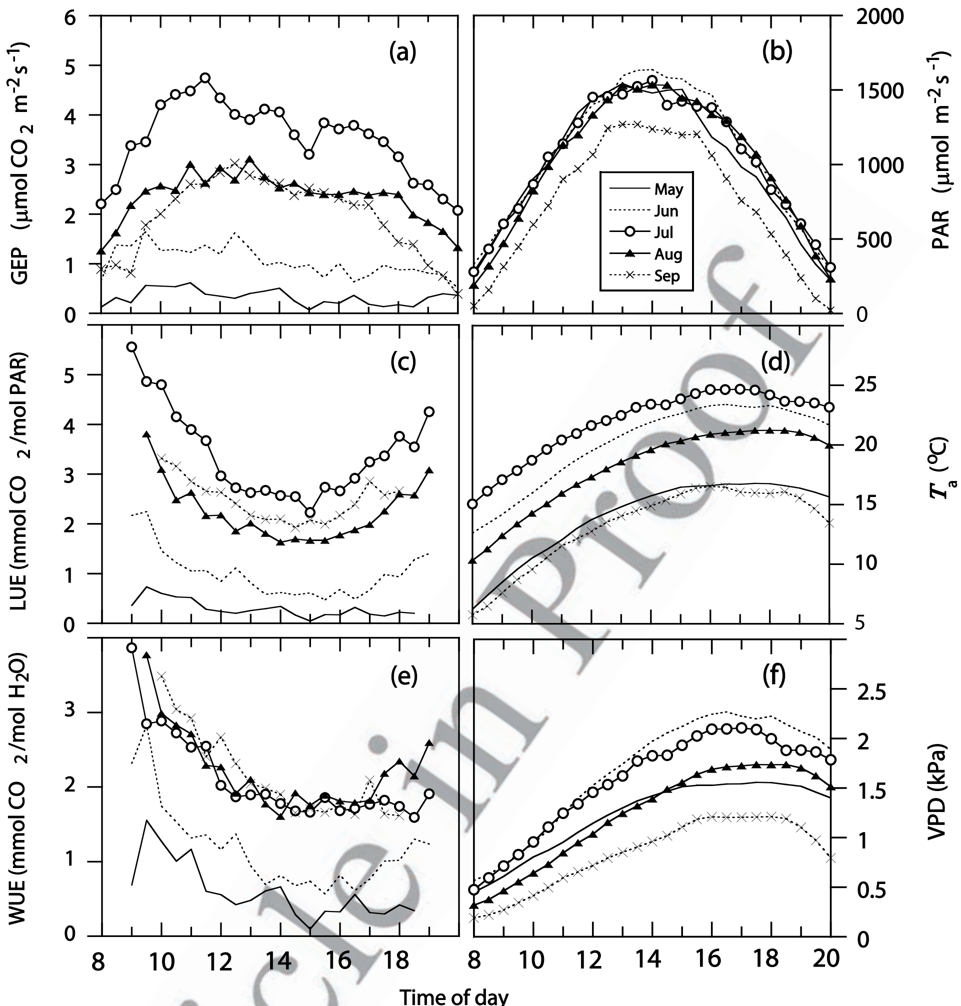

Figure 3. Monthly averaged daytime courses of (a) GEP, (b) PAR, (c) LUE, (d) T_a at 2.5 m, (e) WUE, and (f) vapor pressure deficit. Time of day is Mongolian Light-Saving Standard Time.

al., 1997], and for forests [*Baldocchi and Harley*, 1995; *Lindroth and Cienciala*, 1995]). WUE is also found to be sensitive to lower levels of PAR [*Baldocchi et al.*, 1985b; *Freedman et al.*, 2001; *Law et al.*, 2002]. 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 [*Jarvis et al.*, 1985; *Norman and Arkebauer*, 1991; *Rochette et al.*, 1996; *Anderson et al.*, 2000; *Freedman et al.*, 2001; *Roderick et al.*, 2001; *Gu et al.*, 2002; *Law et al.*, 2002]. Both LUE (Figure 3c) and WUE (Figure 3e) 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 July, August, and September (Figures 3c and 3e).

[23] The 30-min maximum GEP value for the steppe was 5.0 μmol CO_2 m^{-2} s^{-1} in July (LAI = 0.46, T_a = 19.4°C, and SWC = 14.7% at 10 cm depth on the monthly average), which was considerably lower than those (27.5 μmol CO_2 m^{-2} s^{-1} in 1 wet year and 8.6–12.9 μmol CO_2 m^{-2} s^{-1} in 2 dry years) for a moist mixed northern temperate grassland in Canada at the same latitude and with similar LAI (0.4–0.9) [*Flanagan et al.*, 2002]. Daytime 30-min mean values of LUE ranged from 0.3 (May) to 3.4 (July) mmol CO_2 mol^{-1} PAR with the midday (1200–1600) values varying from 0.2 (May) to 2.6 (July) mmol CO_2 mol^{-1} PAR. Daytime 30-min mean values of WUE ranged from 0.6 (May) to 2.2 (August) mmol CO_2 mol^{-1} H_2O with the midday (1200–1600) values of WUE varied from 0.4 (May) to 2.0 (September) mmol CO_2 mol^{-1} H_2O. Daytime WUE values are close to those of sandy millet (0.8–3.3 mmol CO_2 mol^{-1} H_2O) and savannah fallow bush (0.2–2.0 mmol CO_2 mol^{-1} H_2O) in Niger [*Moncrieff et al.*, 1997]. Midday WUE value (2.0 mmol CO_2 mol^{-1} H_2O) observed in the peak growth period compares well with values reported for a soybean crop [*Zur and Jones*, 1984] but is much lower than those (6.5 mmol CO_2 mol^{-1} H_2O) of a well-watered corn field [*Sinclair et al.*, 1975; *Reicosky*, 1990], of wheat and corn fields (2.0–6.1 mmol CO_2 mol^{-1} H_2O) [*Baldocchi*, 1994], and of Sahelian savanna (2.0–18.4 mmol CO_2 mol^{-1} H_2O) [*Verhoef et al.*, 1996]. The Mongolian steppe vegetation grows under dry and cold climate conditions. Therefore characteristics of the productivity and use of available water and light by the steppe might reflect climate impact to some extent.

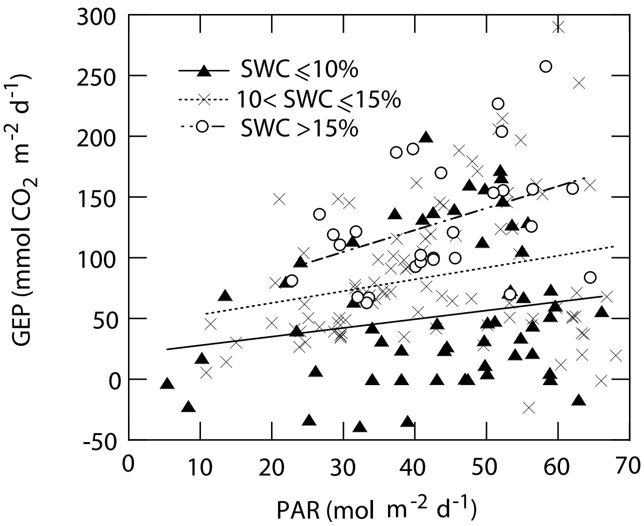

Figure 4. Relationship between daily GEP and incident PAR. Data are compiled with respect to SWC at 10 cm depth and linearly fitted (see Table S2a of the auxiliary material).

3.3. GEP-PAR and GEP-ET Relationships

[24] 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 $\leq$ 10%, 10 < SWC $\leq$ 15%, and SWC > 15%) (Figure 4). The group boundaries are not very firm and are primarily based on the experience that steppe productivity was water limited when SWC was below 10% and was not subject to any water stress when SWC was over 15% [*Ludlow*, 1989; *Bolger et al.*, 2005; *Li et al.*, 2005]. Variation in daily averaged PAR explained only a small fraction (~4%) of GEP variation over the course of the growing season; segregating by SWC level did little to improve this relation (Figure 4 and Table S2a of the auxiliary material).[1] GEP exhibited a much stronger correlation with LAI (Figure 2c) [*Li et al.*, 2005] and with air temperature than with daily light levels (Figure S1 of the auxiliary material), suggesting that seasonal phenology may be more important than light or water content at this timescale. We did not examine how PAR and SWC affect GEP at shorter timescales, but we hypothesize that if phenology were accounted for, GEP would show a stronger dependence on PAR and that the effects of changes in SWC on the slope of GEP with PAR might then be discernible (Figure 4). It has been reported in literature that there is a linear response of GEP to PAR for crops and grassland [*Ruimy et al.*, 1995; *Turner et al.*, 2003]. However, under cold and dry climate conditions in Mongolia, light alone may be a fairly good predictor of gross primary product up to about a monthly timescale, but unless phenology is accounted for, light is a poor predictor at longer timescales, and the effects of changes in SWC will be difficult to discern [*Turner et al.*, 2003; *Urbanski et al.*, 2007].

[25] GEP and ET were significantly correlated ($P < 0.001$ for SWC $\leq$ 10% and 10 < SWC $\leq$ 15%, and $P < 0.005$ for SWC > 15%, respectively) (Figure 5). 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 (Figure 5). 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 through soil evaporation. Hence the rain received might not always be biologically effective for a scarce vegetation cover such as the steppe in our study.

3.4. Biological and Environmental Constraints on LUE and WUE

[26] It is well known that GEP of any biome depends on LAI, length of the growing season, environmental conditions, and physiological performance in some way [*Ruimy et al.*, 1995; *Moncrieff et al.*, 1997; *Falge et al.*, 2002a, 2002b; *Law et al.*, 2002]. However, there is no universal function that relates LUE and WUE to these factors. To quantify these relationships for the steppe, we plotted daily LUE against daily values of LAI, T_a, SWC, and α_K in Figure 6.

[27] LAI had a significant effect on LUE ($P < 0.001$) (Figure 6a). At lower LAI, for the same PAR, GEP is low so LUE is low. Such a linear response of LUE to LAI is also reported for observations from crops [*Horie and Sakuratani*, 1985; *Sinclair and Horie*, 1989]. On a daily basis, LUE increased significantly with increasing T_a ($P < 0.005$) (Figure 6b), 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 ($P < 0.001$) (Figure 6c). Other studies of LUE in grassland ecosystems have reported similar trends of drought-induced decline in LUE [*Bremer and Ham*, 1999; *Nouvellon et al.*, 2000; *Hunt et al.*, 2002; *Turner et al.*, 2003]. We observed that LUE decreased considerably with the increase in α_K ($P < 0.001$) (Figure 6d). The strong dependence of LUE on T_a and SWC, especially in cold and dry climates like the Mongolian Plateau, has also been reported in literature [e.g., *Potter et al.*, 1999].

[28] WUE decreased with increasing T_a ($P < 0.05$) and SWC ($P < 0.05$) but increased with increasing α_K ($P < 0.01$). Obviously, the control of T_a, SWC, and α_K over LUE was much stronger than over WUE (Figure S2 and Table S3 of the auxiliary material). On a daily basis, both LUE and WUE were not significantly correlated with VPD ($P > 0.5$) (data not shown).

3.5. LUE and WUE and Canopy Conductance as a Function of PAR

[29] Both water vapor and carbon dioxide exchange between the atmosphere and the canopy are strongly dependent on canopy surface conductance (g_c) [*Jarvis and McNaughton*, 1986; *Baldocchi et al.*, 1991, 2004; *Collatz et*

[1] Auxiliary materials are available in the HTML. doi:10.1029/2006JG000349.

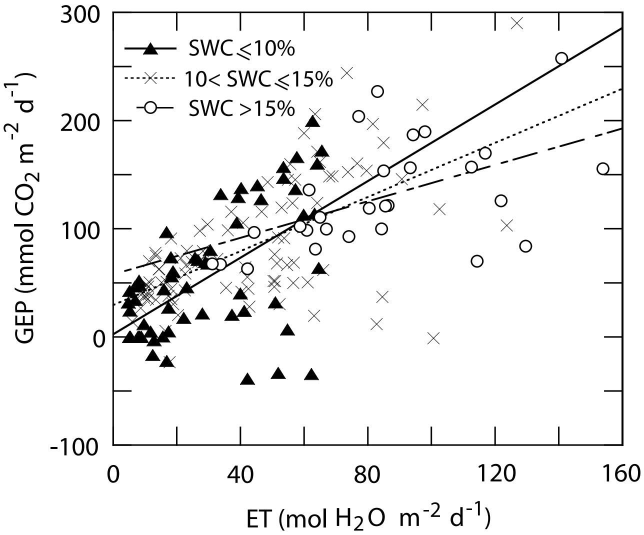

Figure 5. The relationship between daily GEP and ET. Data are compiled with respect to SWC at 10 cm depth and are linearly fitted (see Table S2b of the auxiliary material).

al., 1991; *McNaughton and Jarvis*, 1991; *Schulze et al.*, 1995]. Through stomata, plants have the ability to regulate the cost-benefit relationship between carbon gains and water losses. Hence understanding the nature of the LUE-g_c and WUE-g_c relationships is important for revealing biophysical controls over this relationship.

[30] Since both PAR and soil moisture availability affect g_c and thus water vapor and carbon dioxide exchange [*Jarvis*, 1976; *Baldocchi et al.*, 1991; *McNaughton and Jarvis*, 1991; *Sellers et al.*, 1997], stomatal control over LUE and WUE should be considered together with the effects from both PAR and SWC. For this purpose, we stratified the 30-min daytime data of LUE, WUE, and g_c (PAR > 500 μmol m^{-2} s^{-1}) again into three SWC groups (SWC $\leq$ 10%, 10% < SWC $\leq$ 15%, and SWC > 15%). Within each group, the 30-min data were further subdivided by PAR into 100 μmol m^{-2} s^{-1} increments ranging from 500 to 2200 μmol m^{-2} s^{-1}. The data were bin averaged for each PAR subgroup (Figure 7). Although this data stratification may decrease the precision and ability to mirror refined differences in the g_c effect on LUE and WUE, it is an appropriate approach for offsetting the errors in association with the flux measurements [*Falge et al.*, 2001].

[31] Regardless of soil moisture conditions, both LUE and WUE decreased with increasing PAR (Figures 7a and 7b), suggesting that the steppe used light and water more efficiently at lower levels of PAR when stomata were largely open (Figure 7c). This suggests that low levels of light are sufficient for maintaining high productivity. The response of g_c to PAR also strongly depended on soil moisture conditions (Figure 7c). When SWC was <15%, the dependence of g_c on PAR shows a negative relationship; whereas g_c appeared to be conservative with relatively higher values and showed a slight increase with increasing PAR when SWC was >15% (Figure 7c). It has been documented that LUE is conservative for a given vegetation type when there is no environmental stress [*Jones*, 1992; *Potter et al.*, 1993; *Baldocchi*, 1994; *Ruimy et al.*, 1994]. However, at our site, this is clearly not the case.

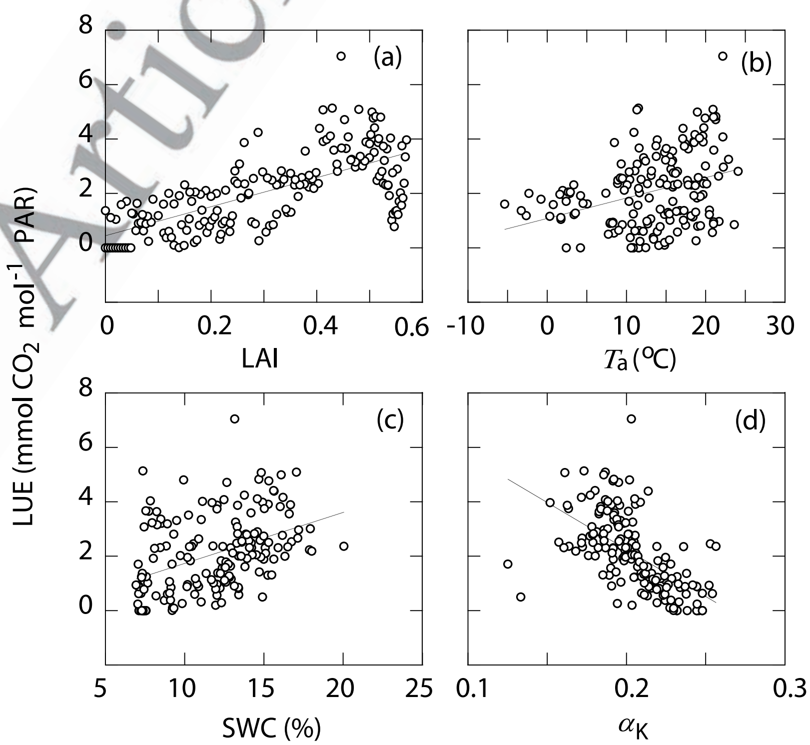

Figure 6. The relationships of LUE versus (a) LAI, (b) T_a, (c) SWC at 10 cm, and (d) surface reflectivity (albedo) for short-wave radiation (α_K). The data are daily average values and are linearly fitted (see Table S2c of the auxiliary material).

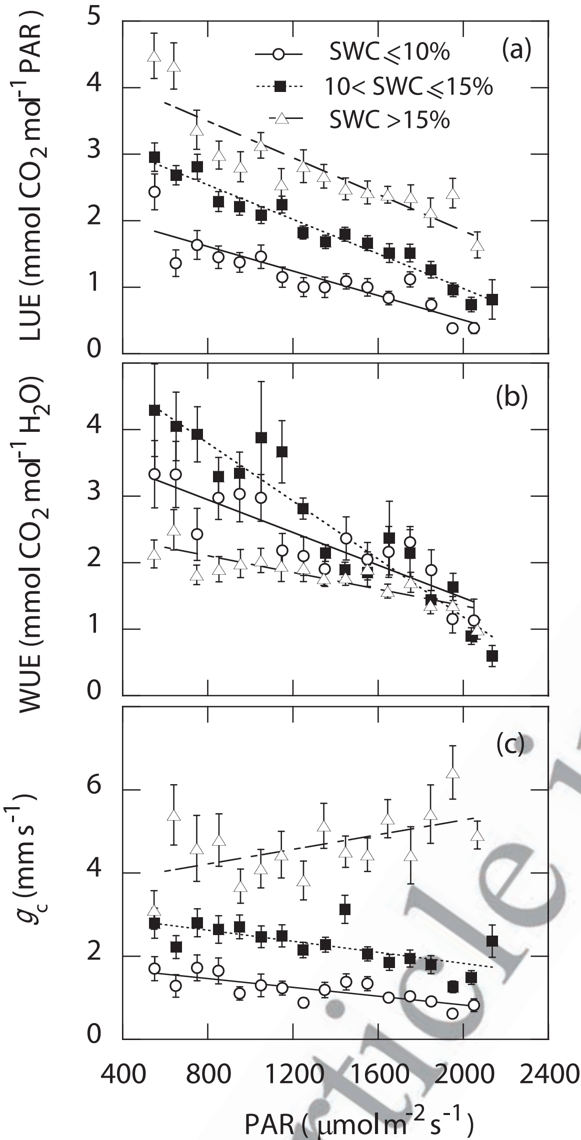

Figure 7. The responses of (a) LUE, (b) WUE, and (c) bulk canopy surface conductance (g_c) to incident PAR under various SWC conditions. The points are PAR bin averages of 30-min data with the bin size of 100 μmol m^{-2} s^{-1}. Vertical bars represent ±1 SE. The data are linearly fitted (see Table S2d of the auxiliary material).

[32] The LUE-g_c and WUE-g_c relationships were also affected by soil moisture conditions (Figure 8). When SWC was <15%, both LUE and WUE were positively related to g_c, whereas when SWC was >15%, their dependence on g_c shows a negative relationship. This suggests that when soil moisture is plentiful because of the influence of the bare soil evaporation on g_c, a higher g_c does not necessarily enhance LUE and WUE.

3.6. Primary Controlling Factors of GEP, LUE, and WUE

[33] Overall, our analyses suggest that GEP, WUE, and LUE respond differently to environmental factors. The scatter in these response models (Figures 4, 5, 6, and 7) illustrates the complication of or the interaction among various environmental factors. This analysis shows that the major factors affecting GEP include SWC at 20 cm (P < 0.001), SWC at 10 cm (P < 0.01), g_c (P < 0.05), and α_K (P < 0.05) (Table 1). There was only one highly significant factor (SWC at 20 cm) (P < 0.001), together with two marginally significant factors of PPT (P < 0.1) and α_K (P < 0.1), affecting WUE. This suggests that mechanisms that govern water use by the steppe vegetation are more complex than what bivariate analyses could assess. LUE was influenced mostly by SWC at 20 cm (P < 0.001), α_K (P < 0.001), SWC at 10 cm (P < 0.01), g_c (P < 0.05), and PPT (P < 0.05), very similar to what was found for GEP (Table 1). The multivariate analysis of variance provides further evidence that in terms of GEP, WUE and LUE the functioning of the Mongolian steppe ecosystem is mitigated by available water supply, especially from the top 20-cm layer soil.

4. Conclusions

[34] We explored gross ecosystem productivity and light and water use of an arid steppe in central Mongolia. Among other factors, soil moisture availability, especially at the top

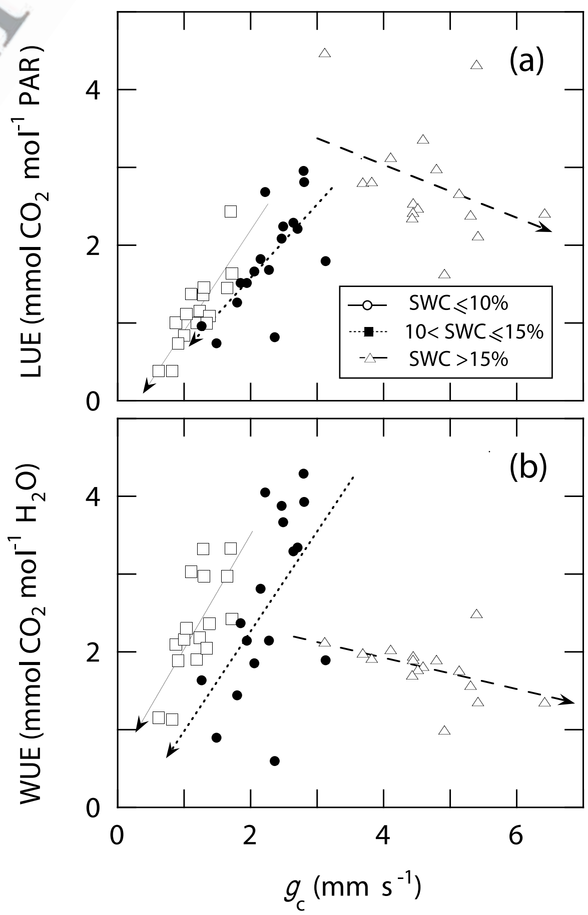

Figure 8. The responses of (a) LUE and (b) WUE to g_c under various SWC conditions. Data are PAR bin averaged with the bin size of 100 μmol m^{-2} s^{-1}. Vertical bars represent ±1 SE. The data are linearly fitted, and arrows indicate increasing trend of PAR (see Table S2e of the auxiliary material).

Table 1. Multivariate Analysis of Variance for GEP, WUE and LUE on the Daily Basis[a]

Source	DF	SS	MS	F	P
			GEP		
Constant[b]	1	1.1×10^6	1.1×10^6	1095.5	$\leq$0.0001
LAI	5	9207.63	1841.53	1.834	0.1138
PAR	5	1898.76	379.751	0.3782	0.8625
T_a	12	13207.6	1100.63	1.0961	0.3728
VPD[c]	5	13193	2638.6	2.6278	0.0287
PPT	4	4592.12	1148.03	1.1433	0.3411
SWC_{10}[d]	11	34233.2	3112.11	3.0994	0.0014
SWC_{20}[b]	6	63480.6	10580.1	10.537	$\leq$0.0001
α_K[c]	5	14606	2921.2	2.9093	0.0174
g_c[d]	4	17424.1	4356.02	4.3382	0.0029
Error	93	93381.7	1004.1		
Total	150	575474			
			WUE		
Constant[b]	1	844.596	844.596	479.85	$\leq$0.0001
LAI	5	3.80684	0.761367	0.43256	0.8248
PAR	5	9.93645	1.98729	1.1291	0.3505
T_a	12	28.2908	2.35756	1.3394	0.2101
VPD	5	3.55851	0.711702	0.40435	0.8447
PPT[e]	4	16.8607	4.21517	2.3948	0.0560
SWC_{10}	11	27.9137	2.53761	1.4417	0.1677
SWC_{20}[b]	6	44.9856	7.4976	4.2597	0.0008
α_K[e]	5	17.9501	3.59002	2.0396	0.0802
g_c	4	0.817799	0.20445	0.11616	0.9765
Error	93	163.692	1.76013		
Total	150	384.124			
			LUE		
Constant[b]	1	581.437	581.437	1210.3	$\leq$0.0001
LAI	5	3.29717	0.659435	1.3727	0.2417
PAR	5	1.41167	0.282334	0.58772	0.7093
T_a	12	9.29354	0.774462	1.6121	0.1015
VPD	5	3.50642	0.701283	1.4598	0.2105
PPT[c]	4	5.68382	1.42096	2.9579	0.0238
SWC_{10}[d]	11	15.9843	1.45311	3.0249	0.0017
SWC_{20}[b]	6	20.6757	3.44595	7.1732	$\leq$0.0001
α_K[b]	5	13.6846	2.73693	5.6973	0.0001
g_c[c]	4	5.75011	1.43753	2.9924	0.0226
Error	93	44.6764	0.480391		
Total	150	258.263			

[a]DF, degree of freedom; SS, sum of squares; MS, mean square; F, statistical test; P, probability; SWC_{10}, soil water content at 10 cm depth, %; SWC_{20}, soil water content at 20 cm depth, %. The biotic (LAI and g_c) and abiotic (PAR, T_a, VPD, α_K, PPT, SWC_{10} and SWC_{20}) factors are taken as group variables by bin separation. Bin width is 0.1 for LAI, 1 mm s^{-1} for g_c, 10 mol m^{-2} d^{-1} for PAR, 2°C for T_a, 0.25 kPa for VPD, 0.02 for α_K, and 1% for SWC, respectively. PPT was grouped into five classes (PPT < 0.1, 0.1 $\leq$ PPT $\leq$ 0.5, 0.5 < PPT $\leq$ 1, 1 < PPT $\leq$ 5, and PPT > 5 mm).
[b]$P < 0.001$.
[c]$P < 0.05$.
[d]$P < 0.01$.
[e]$P < 0.1$.

20 cm, which is strongly affected by recent rains, is important in controlling GEP, LUE, and WUE of the steppe. Irrespective of soil moisture conditions, both LUE and WUE decreased with the increase in PAR. In addition, LUE for this ecosystem was comparatively low because of low LAI. Interpretation of the variability of WUE is confounded by the bare surface evaporation, which might contribute greatly to ET since the steppe under study has low vegetation cover. However, with flux measurements from one growing season only, the statistical coverage of the effect of rain-fed soil moisture on GEP, WUE, and LUE is not yet perfectly satisfactory. It is known that grassland productivity is strongly affected by year-to-year variation of precipitation [*Sala et al.*, 1988; *Austin et al.*, 2004; *Huxman et al.*, 2004; *Schwinning and Sala*, 2004; *Potts et al.*, 2006]. Thus more and longer-term studies are needed to assess the degree of interannual variability in GEP, WUE, and LUE responding to this wide variation in environmental conditions.

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