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Seasonal variation in carbon exchange and its ecological analysis over *Leymus chinensis* steppe in Inner Mongolia

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Abstract Eddy covariance technique was used to measure carbon flux during two growing seasons in 2003 and 2004 over typical steppe in the Inner Mongolia Plateau, China. The results showed that there were two different CO₂ flux diurnal patterns at the grassland ecosystem. One had a dual peak in diurnal course of CO₂ fluxes with a depression of CO₂ flux after noon, and the other had a single peak. In 2003, the maximum diurnal uptake and emitting value of CO₂ were –7.4 and 5.4 g·m⁻²·d⁻¹ respectively and both occurred in July. While in 2004, the maximum diurnal uptake and release of CO₂ were –12.8 and 5.8 g·m⁻²·d⁻¹ and occurred both in August. The grassland fixed 294.66 and 467.46 g CO₂·m⁻² in 2003 and 2004, and released 333.14 and 437.17 g CO₂·m⁻² in 2003 and 2004, respectively from May to September. Water availability and photosynthetic active radiation (*PAR*) are two important factors of controlling CO₂ flux. Consecutive precipitation can cause reduction in the ability of ecosystem carbon exchange. Under favorable soil water conditions, daytime CO₂ flux is dependent on *PAR*. CO₂ flux, under soil water stress conditions, is obviously less than those under favorable soil water conditions, and there is a light saturation phenomena at *PAR*=1200 μmol·m⁻²·s⁻¹. Soil respiration was temperature dependent when there was no soil water stress; otherwise, this response became accumulatively decoupled from soil temperature.

Keywords: Leymus chinensis, CO₂ flux, photosynthetic active radiation, light saturation phenomena, eddy covariance technique.

Concerns about carbon and water/heat fluxes have incurred more attention with global environmental change^[1-5]. Recent researches suggest that the unbalance in global carbon budget have proved that there was a neutral C-sink in middle-latitude region of the Northern Atmosphere^[6]. This unbalance in global carbon budget is not influenced by a singular ecosys-

tem, but more little C-sink ecosystem^[7]. Grassland is a very important ecosystem among little C-sink ecosystems for approximately 32% of the worlds natural vegetation is covered by grassland. There is still great uncertainty in confirming whether grassland ecosystems act as C-sink or C-resource because grassland ecosystems show the interannual fluctuation in gross

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primary productivity^[8,9]. Concurrently, the responses of grassland ecosystems to environment and correlative biological dynamics have big dissymmetry, especially annual precipitation and distribution of precipitation^[10,11]. Therefore, the function of grassland ecosystems to future global climatic change should attach more importance.

Eddy covariance technique has been widely applied to measure carbon and water/heat exchange between atmosphere and land surface[10]. Currently, there are more than 180 groups to measure CO₂/H₂O fluxes with eddy covariance system^[2]. More recently, a few studies on CO2 exchange have been operated in grassland ecosystems across Savanna and the Great Central Plain and attained some results [8,12-16]. Dugas et al. [12] studied in a tall-grass grassland in Texas suggested that its carbon budget was nearly balanced, and leaf area index, photosynthetic active radiation and soil water content controlled carbon flux. Sims and Bradford[15] reported a mixed grassland in the northwest of Oklahoma has the potential of absorbing carbon, and vegetation structure affected the carbon flux. Nevertheless, little attention has been given to the carbon dioxide exchange in Eurasia grasslands regions.

Typical steppe ecosystems developed under semi-arid continental temperate climate condition cover approximately 4.1×10^7 hm² that is about 10.5% of the national grassland area. It is the most representative and typical grassland in temperate grasslands of China and much better reflects the vegetation characteristics and physiognomy of the temperate grassland regions. Some short-term studies have been operated with the static chamber means during the growing season. However, they only analyzed soil respiration and the diurnal variation of carbon exchange [17–20], and lack research for net ecosystem exchange (NEE). Therefore, there is a virtual need for long-term field measurements to quantify carbon dynamics under climatic changes condition and management practices.

The main objectives of this study are to deepen our understanding for the variation characteristics of CO₂ exchange in a typical steppe ecosystem during two years of growing season's measurements on Inner Mongolia Plateau. The specific objective is to analyze the effects of meteorological and biological factors on the fluxes exchanges.

1 Materials and methods

1.1 Study site description

The experimental site is located at Xilin River Watershed of Inner Mongolia Autonomous Region (43°32'N, 116°40'E, 1200 m a.s.l). The site has been fenced since 1979 and is located in a smooth wide plain with low hills on a second-level basalt platform^[21]. The low hills have a relative height of 20—30 m with slope of <5°. The climate is described as temperate, semi-arid continental climate with a dry spring and moist summer. Annual temperature averages -0.4°C with a growing season length of 150—180 d. Annual mean precipitation is 350 mm with 89% of the annual rainfall concentrated in April-September.

Soil type at the experimental site is dark chestnut (Mollisol) with a soil depth of 100-150 cm^[21]. The A horizon reaches 20-30 cm deep and there is no obvious CaCO3 layer in the soil profile. Mean soil texture is 21% clay, 60% sand and 19% silt. Of 86 species of flowering plants, belonging to 28 families and 67 genera in the site, there are 11 grass species (Jiang 1985). The xeric rhizomatous grass, L. chinensis (Trin.) Tzvelev (syn. Aneurolepidium chinensis (Trin.) Kitagava), is the constructive species, and S. grandis Smirnov, Koeleria pyramidara (Lam.) P. Beauv (syn. K. cristata (L) Link) and Agropyron cristatum (L.) Gaertn., are dominant species. The height of the grass clusters is 50-60 cm; coverage averages 30%-40% but can reach 60% - 70% in rainy years. Litter accumulated due to enclosure since 1979.

1.2 Eddy covariance measurements

An eddy covariance (EC) system was utilized to measure continuous carbon dioxide (CO₂) fluxes over the grassland. CO₂ fluxes were measured at 2.3 m above ground level with a 3D sonic anemometer (model CSAT3, Campbell Scientific, MS, USA) with an adjacent open-path infrared CO₂/H₂O gas analyzer (model LI-7500, LI-COR, Lincoln, NE, USA). The eddy covariance measurements were taken at a frequency of 10 Hz and turbulent fluxes were recorded on a datalogger (CR5000, Campbell Scientific) as a half-hour average.

Other auxiliary micrometeorological variables were

measured near the EC system. Wind speed was measured at 1.5 and 2.3 m above the ground with cup anemometers (034A-L and 014A; Traverse, MI, USA). Air temperature and humidity were measured at 1.5 and 2.3 m above ground level with a temperature and humidity probe, respectively (HMP45C, VAISALA, Woburn, MA, USA). Net radiation and photosynthetic active radiation (PAR) were measured at 1.5 m above the ground with a net radiometer (CNR-1, Kipp & Zonen, NY, USA) and a quantum sensor (LI-190SB; LI-COR), respectively. A tipping bucket rain-gauge at 1.5 m above ground level (TE525MM, Campbell Scientific) was used to measure precipitation. Soil temperature was measured at 0.05, 0.10, 0.20, 0.50 and 1.0 m below the ground with copper-constantan thermocouples. Soil heat flux was attained by averaging the output of three heat flux plates (HFT-3, Campbell Scientific). Soil volumetric water content was measured with a time-domain reflectometer probe at 0.05, 0.2 and 0.5 m. Profiles of soil moisture were also measured at a depth of 0-0.1, 0.1-0.2, 0.2-0.3 and 0.3-05 m every week with a soil auger. Data from these sensors were recorded below the canopy using a digital datalogger (CR23X; Campbell Scientific, Logan, UT, USA).

Post-processing of the data involved a two-axis rotation of the wind velocity components to align the coordinates with the mean wind directional component^[22]. A WPL density correction was applied to density changes resulting from fluctuations in heat and water vapor^[23]. To fill in missing data, resulting from data-screening criteria and instrument malfunction, we applied the MDV and interpolation methods^[24]. We designated fluxes toward the surface as negative and fluxes toward the atmosphere as positive.

1.3 Biomass, leaf area measurements

Above-ground biomass was investigated by cutting around the eddy covariance tower every 15 d during May-September. Twenty quadrates of 1×1 m² were harvested each time. The above-ground parts of the vegetation were clipped to ground level and returned to the laboratory for dry-matter measurements. The clipped plant material was separated into live and standing dead parts, which were weighed as the fresh weight of live biomass and standing dead, respectively.

Plant materials were oven-dried at 65°C, and dry weights of live biomass and standing dead recorded. Litter from the sampled quadrates was also collected. LAI was measured every 20 d during the growing season in 2004.

There are clear seasonal and interannual change of aboveground biomass, leaf area index and soil water content (Fig. 1). Precipitation was 354.3 mm during this study period in 2003, while 344.3 mm in 2004, which are both close to the long-term annual averaged precipitation (350.43 mm) (Fig. 1(a)). The community shooting production averaged (202.68±34.04) g dw·m⁻² and (188.13±23.82) g dw·m⁻² based on the peak standing crop of each sample in 2003 and 2004, respectively. The maximum value reached on August each year. The maximum LAI were 1.54 on August in 2004 (Fig. 1(b)). The correlation of LAI and above biomass was strong (LAI = $0.23 + 0.0057 \times above$ biomass, $r^2 = 0.97$). Due to the affect of precipitation frequency and precipitation distribution, the growth rhythm of vegetation is different. The magnitude of precipitation from May to July in 2003 accounted for 2/3 of total precipitation of the whole growing season while it was less than 1/2 in 2004. Soil water content across 0-20 cm depth (θ_{ν}) associated with rainfall exhibited the obvious seasonal and interannual fluctuation. Maximum daily average soil volumetric water content ($\theta_v = 0.23 \text{ m}^3 \cdot \text{m}^{-3}$) across the upper 20 cm of the soil profile occurred in middle-July in 2003, while the maximum value (only $\theta_v = 0.28 \text{ m}^3 \cdot \text{m}^{-3}$) was observed in middle-August during the growing season in 2004 (Fig. 1(c) and (d)).

2 Results and analysis

2.1 Diurnal variation in CO₂ flux

There were two different patterns in diurnal CO₂ flux course. One had dual uptake peaks (Fig. 2(a)). Several clear days were chosen to explain the first situation (Fig. 2 (a)). After sunrise (at 6:00-6:30 am, Beijing Standard Time), grassland began to take up CO₂ (F_c was negative) and F_c reached the daily maximum magnitude at 8:00-10:00 ($F_c = -0.14$ mg·m⁻²·s⁻¹). Then, F_c gradually decreased as *PAR* increased and the ecosystem started to release CO₂ at

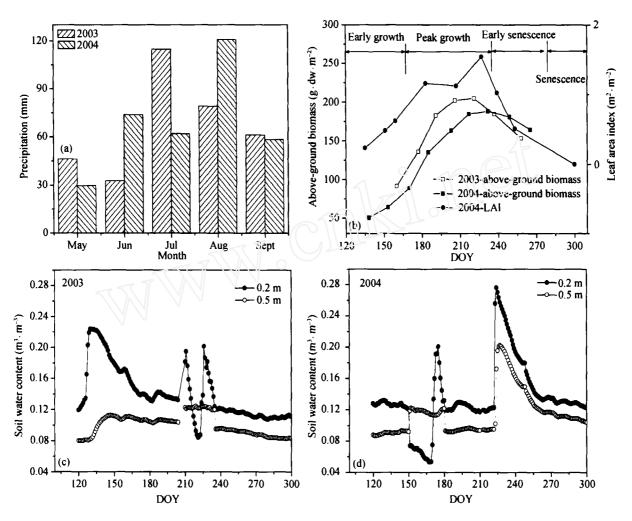


Fig. 1. The characteristics of precipitation (a), above-ground biomass (b), and soil water content ((c) and (d)) in 2003 - 2004's growing seasons.

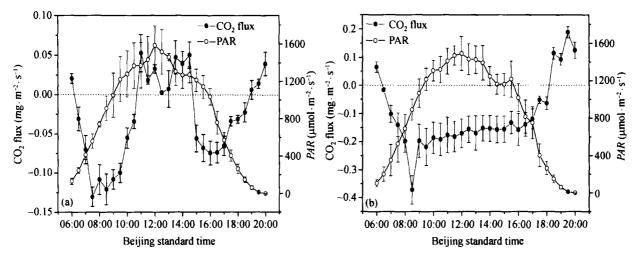


Fig. 2. The diurnal variation in CO₂ flux and photosynthetic active radiation (PAR) in 2003-2004's growing seasons.

12:00. The second peak of uptake occurred between 15:00 and 19:00. After that, the system kept the release

of CO₂ and became the net source of CO₂.

Another diurnal course of CO₂ flux has only a sin-

gle peak of uptake (Fig. 2(b)). The ecosystem started to take up CO_2 around 6:00~6:30. After reaching the maximum uptake around 8:00, F_c gradually decreased until the system became the net source of CO_2 around 19:00—20:00.

2.2 Seasonal variation in CO₂ flux

The sum of the half-hour carbon dioxide fluxes was calculated to represent the daytime and nighttime emission (Fig. 3). The daytime fluxes of CO₂ ranged from an uptake of -7.4 g·m⁻²·d⁻¹ for the month of July to an emission of about 5.4 g·m⁻²·d⁻¹ in July during this study period in 2003. The maximum uptake and release was -12.8 and 5.8 g·m⁻²·d⁻¹ in August respectively in 2004. By mid May in 2003, the grassland began to uptake CO₂.

The sum of diurnal and nocturnal F_c was calculated, and then the daily sum to one month was integrated (Fig. 4). The variation in monthly CO₂ fluxes was considerable distinction from May to September between 2003 and 2004. In 2003, the magnitude of maximum monthly CO₂ uptake -135.36 g·m⁻²·mon⁻¹ was observed in June. However, the maximum emission 95.2 g·m⁻²·mon⁻¹ exhibited in July (Fig. 4(a)). In contrast, both the maximum uptake (-244.26 $g \cdot m^{-2} \cdot mon^{-1}$) and emission (121.37 $g \cdot m^{-2} \cdot mon^{-1}$) occurred in August in 2004 (Fig. 4(b)). Grassland started to become a net sink of carbon dioxide in June and reached the maximum value during the growing season in 2003. However, in 2004, the date of the ecosystem's converse from source to sink is in July, which is almost one month delayed than that of 2003. The

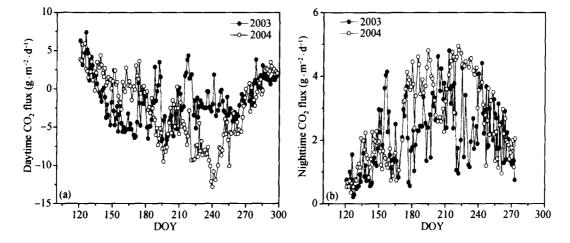


Fig. 3. The seasonal variation in daytime (a) and nighttime (b) CO₂ flux in 2003 – 2004's growing seasons.

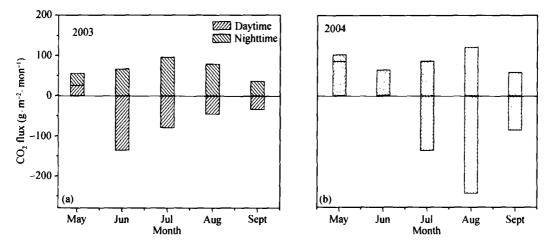


Fig. 4. The monthly variation in daytime (a) and nighttime (b) CO₂ flux in 2003 – 2004's growing seasons.

maximum monthly uptake appeared in August in 2004 while it appeared in June in 2003. The dates when grassland turned from net sink into net source of carbon dioxide were all in October in the two years.

The start point of the grassland growing season was tentatively defined in this study according to the measured F_c . The first three days when the ecosystem kept continuously taking up CO2 can be considered as the beginning of growth. On the contrary, it can be regarded as the end of growth when the ecosystem releases CO₂ continuously in three days. According to definition, the growing season lasted 128 d, from 17 May (the first day of negative F_c) to 22 September (the first day of positive F_c) in 2003, and 116 d, from 2 June to 26 September, in 2004. During the growing season in 2003, the ecosystem fixed 294.66 $g \cdot m^{-2} \cdot mon^{-1}$ and released 333.14 $g \cdot m^{-2} \cdot mon^{-1}$. The ecosystem, with a shorter growing season in 2004, fixed 467.46 g·m⁻²·mon⁻¹ and released 437.17 $g \cdot m^{-2} \cdot mon^{-1}$.

2.3 Effect of photosynthetic active radiation on CO₂ flux

In order to describe the relationship between F_c and PAR for peak-growth period of vegetation, data were selected when soil water condition was favorable ($\theta_v > 0.12 \text{ m}^3 \cdot \text{m}^{-3}$) and when vapor pressure deficit (VPD) was low (VPD < 0.5 kPa). As expected, a hyperbolic relationship existed between F_c and PAR during peak-growth stage. Data in Fig. 5 were fitted with a rectangular hyperbola of the following form:

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

where F_c is the CO₂ flux, F_{cm} is the maximum F_c , PAR^* is the value of PAR at the light compensation point (the value PAR at which $F_c = 0$) and b is the slope of the fitted curve at $F_c = 0$. These observations do not indicate light saturation of the steppe canopy up to PAR levels of 1200 μ mol·m⁻²·s⁻¹.

The light compensation point (canopy plus soil), derived from the F_c -PAR curves, ranged from 80 to 100 μ mol·m⁻²·s⁻¹, and depends on the growth stage of vegetation. Assuming soil respiration rate of about 0.018 mg·m⁻²·s⁻¹ (measured value with static chamber) would produce a canopy light compensation point of

approximately 20-50 µmol·m⁻²·s⁻¹.

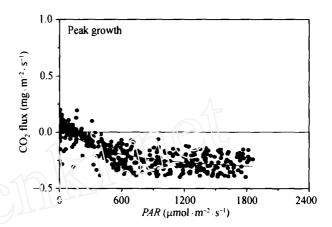


Fig. 5. Daytime CO₂ flux as a function of photosynthetic active radiation (PAR) during peak growth stage.

The magnitudes of F_c obtained by extrapolating the F_c -PAR curves while PAR=0 is close to those measured during nighttime (22:00-5:00), which shows that the F_c -PAR relationship derived from the daytime CO₂ flux under low VPD could be applied to attain reasonable estimates of the nocturnal CO₂ exchange of the ecosystem.

2.4 Effect of vapor pressure deficit and soil moisture

In order to check out the affect of vapor pressure deficit (VPD) on the CO_2 flux, data from each life cycle stage were grouped in three intervals of VPD (low: 0.0-0.5 kPa, moderate: 0.5-1.0 kPa, high: >1.0 kPa). To avoid the confounding effect of low soil moisture, data were excluded under soil water stress ($\theta_v < 0.12$ m³·m⁻³). Results for the peak-growth stage are presented in Fig. 6. It is clear that CO_2 exchange decreased when the VPD was high, probably through reduction in stomatal conductance. With an increase of VPD from low to high, for example, F_c (at PAR = 1000 µmol·m⁻²·s⁻¹) decreased by 20%. Similar affects of VPD on the Fc-PAR relationship were observed during the early growth stage and early senescence stages (Fig. 6(a)).

Data, selected under soil water limitation ($\theta_v < 0.12$ m³·m⁻³), were use to examine the affect of low soil moisture on CO₂ flux. Fig. 6(b) shows the F_c -PAR relationships under limiting soil moisture conditions. It is clear that the values of F_c under limiting soil water

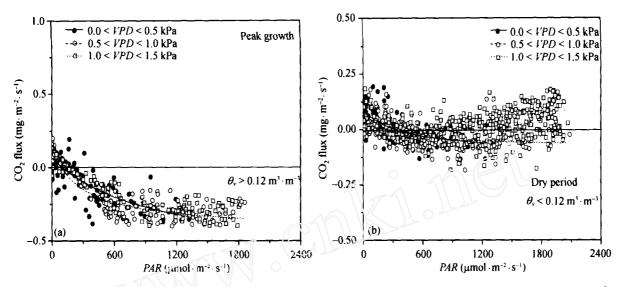


Fig. 6. Fc-PAR relationship under different ranges of vapor pressure deficit (VPD). (a) Under nonlimiting soil water conditions ($\theta_v > 0.12 \text{ m}^3 \cdot \text{m}^{-3}$); (b) under limiting soil water conditions ($\theta_v < 0.12 \text{ m}^3 \cdot \text{m}^{-3}$)).

conditions were marked lower than those under nonlimiting soil water conditions. Furthermore, an increase in VPD seems to have resulted in much larger reduction of F_c under soil water stress. The extent of reduction in F_c was 50%-60% when the increase of VPD went from low to high. In addition, the light saturation phenomenon occurred in the ecosystem at $PAR = 1200 \, \mu \text{mol·m}^{-2} \cdot \text{s}^{-1}$ under limiting soil water conditions.

2.5 Factors controlling nocturnal CO₂ flux

Temperature and soil water availability are the primary environmental factors which control nocturnal CO₂ release from grassland ecosystem. Data from 22:00 to 06:00 were chosen for average to minimize the confounding effect during the transition periods near sunrise and sunset, and U* < 0.2 m·s⁻¹ data were eliminated. The data are divided into two different intervals of soil moisture content ($\theta_{\nu} > 0.12 \text{ m}^3 \cdot \text{m}^{-3}$ and $\theta_{\nu} < 0.12 \text{ m}^3 \cdot \text{m}^{-3}$). The relationship between soil temperature and F_c is not notable under soil water stress conditions ($\theta_v < 0.12 \text{ m}^3 \cdot \text{m}^{-3}$). Although data are scatter and coefficient of determination (R^2) is only 0.2, nocturnal F_c appeared to increase with the increasing of soil temperature under the condition of no soil water stress (Fig. 7). It indicates that the response of the nocturnal CO2 flux to soil temperature (measured at 0-0.05 m depth) is controlled by soil water content.

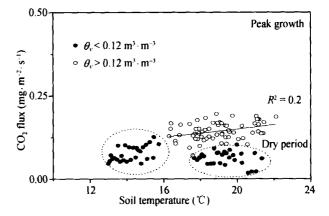


Fig. 7. The nocturnal CO₂ flux as a function of soil temperature.

3 Discussions

3.1 The ecosystem potential of CO_2 flux

As we analyzed the measurement data during the two growing seasons, we found the maximum CO₂ uptake was -0.68 mg·m⁻²·s⁻¹ at about 8:00 o'clock in July in 2003, but -0.54 mg·m⁻²·s⁻¹ at about 10:00 o'clock in August in 2004. The peak value of *PAR* trailed the maximum CO₂ uptake. Comparing with the other type of grassland ecosystems in the world, steppe in Inner Mongolia has a slightly higher capability in CO₂ uptake than tussock grassland in New Zealand (-0.26—-0.35 mg·m⁻²·s⁻¹)^[25], and similar to the mixed-grass prairie in Southern Plain Experimental Range (-0.68—-0.4 mg·m⁻²·s⁻¹)^[14], but less than na-

tive tall prairie in TX $(-1.5 \text{ mg} \cdot \text{m}^{-2} \cdot \text{s}^{-1})^{[12]}$. Although the diurnal CO₂ uptake values are similar, the release during the nocturnal is more than the mixed-grass prairie of Oklahoma^[14].

Xu et al. [26] and Sims et al. [15] measured the different growing stages during the growing season of the alpine shrub in Qinghai-Tibet Plateau and the mixedgrass prairie in Texas, respectively. The CO₂ flux of the two different grassland ecosystems has an obvious diurnal pattern. F_c increased gradually after 8:00 and reached the peak uptake value at 12:00. During nighttime, the value of CO₂ release is stately, and the mixed-grass prairie has the depression of CO2 flux in the afternoon. The diurnal pattern of CO2 flux in Leymus chinensis steppe ecosystem was entirely different with the two grassland ecosystems in two patterns; one is it has two uptake peak values and the other is the first peak uptake value occurred at 9:00, earlier than the alpine shrub in Qinghai-Tibet Plateau and the mixed-grass prairie in Texas.

3.2 Vegetation and CO₂ flux

The relationship between the measured daily net CO₂ flux and biomass and LAI was highly variable during two growing seasons. The maximum values of aboveground biomass were all observed in August in two years, but the peak CO₂ uptake was observed during mid-June to mid-July and there was no significant relationship between the CO₂ fluxes and the sum of aboveground biomass in 2003. Likely, one reason for this may be the contribution of the inorganic component (e.g. precipitation) to net CO₂ flux that was not related to plant biomass accumulation^[27]. For example, during mid-August (215-225 d) in 2003, when the biomass reached its peak value, the decrease of the precipitation and the soil water content (θ_{ν} < 0.12 m³·m⁻³) made the CO₂ flux of the ecosystem decrease, even in the daytime there was release of CO₂ (Figs. 1(c) and 3(a)). Therefore, the peak CO₂ uptake of the ecosystem was not consistent with the status of biomass. Mielnick et al. [9] had the similar report in desert grassland. However, in 2004, the maximum uptake and emission was observed when the maximum biomass and LAI appeared at the same period ($F_c = 3.68$ $-0.04 \times \text{biomass}, R^2 = 0.91$).

The second reason for this phenomenon may be

correlated with constitutes of CO₂ flux. There are two opposing processes which control CO₂ flux of the ecosystem between the surface of soil-vegetation and atmosphere, plant photosynthesis and the respiration. Photosynthesis process controls diurnal CO₂ flux while respiration plays the main role during nighttime. Generally, 40% of the fixed energy in herbage is used to maintain respiration of the live organisms^[28]. More living biomass and larger LAI can promote fixing more carbon and taking up more CO2 from the atmosphere. Therefore, there must be quite a positive correlation between CO2 flux and biomass of the ecosystem. However, soil respiration made CO₂ flux not only be affected by biomass, but also be related to the soil microbial activity and other environment factors. Our study plot has been fenced since 1979 and accumulated much litter above ground. Microbial carbon in the surface soil increased 14.7%-38.7%; labile carbon increased 28.2%-14.4%^[29], although no variation in total soil organic carbon was apparent compared to the vicinal-grazing steppe^[30]. This change has been shown to increase soil respiration.

3.3 The effects of water and PAR on CO_2 flux

A clear characteristic of CO_2 flux in *Leymus* chinensis steppe system is noon-release of CO_2 . The diurnal pattern of CO_2 flux does not follow that of *PAR*. The ecosystem began to emit CO_2 at PAR > 1200 μ mol·m⁻²·s⁻¹ under limiting soil water conditions.

The reason for that may be the affect of soil water stress, which mainly embodies two aspects. Soil water stress reduced partly leaf potential by reducing the turgor in the guard cell associated with stomata and by affecting enzymatic reactions associated with photosynthesis. This phenomenon was common in Leymus chinensis steppe system^[31], located at the typical grassland region in Inner Mongolia. Low precipitation and drier soil are its main traits. Du et al. [31] suggested that the diurnal course of photosynthesis of Leymus chinensis appeared the dual peak type (i.e. midday photosynthesis depression). The portion of 76.8% of all-day photosynthetic production was lost by midday photosynthesis depression. Light saturation phenomenon of the whole ecosystem was found to occur during soil water stress period. Soil water not only affects plant growth, but also affects ecosystem respiration.

Ecosystems also emit CO₂ even at daytime during growing season under soil water stress conditions^[32]. Kim and Verma^[11] studied over temperate grassland in Kansa, and found midday depression of CO₂ flux in the ecosystem happened when the soil suffered from serious drought.

4 Conclusions

We observed and compared substantial interannual variation in carbon exchange with eddy covariance technique in 2003 and 2004. Growing season in 2003 had the maximum diurnal uptake and emining value of CO_2 -7.4 and 5.4 g·m⁻²·d⁻¹ respectively occurred in July. Comparably, growing season in 2004 had the maximum diurnal uptake and release of CO_2 -12.8 and 5.8 g·m⁻²·d⁻¹ that both occurred in August.

The magnitude and distribution of rainfall affect on the occurring time of peak production and the value of CO₂ flux of grassland ecosystem. Consecutive precipitation can cause the reduction in the ability of ecosystem carbon exchange. The daytime CO₂ flux is controlled by photosynthetic active radiation under favorable soil water conditions. Examination of our data under both nonlimiting and limiting soil moisture conditions showed that the CO₂ exchange was substantially controlled by high *VPD*. Soil respiration was temperature-dependent when soil was under nonlimiting soil moisture conditions but, as soil endured water stress, this response became accumulatively decoupled from soil temperature, and even decreased at higher temperature.

Field data, measured with the eddy covariance system, demonstrated that soil moisture significantly affected the ability of a typical steppe to fix carbon and respiration rate. The CO₂ uptake power of the ecosystem and the possibility of developing a carbon sink mainly depended on the magnitude and timing of rainfall events associated with the phonological stage.

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