

Diurnal and Seasonal Dynamics of Soil Respiration at Temperate *Leymus Chinensis* Meadow Steppes in Western Songnen Plain, China

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Abstract: To evaluate the diurnal and seasonal variations in soil respiration (Rs) and understand the controlling factors, we measured carbon dioxide (CO₂) fluxes and their environmental variables using a LI-6400 soil CO₂ flux system at a temperate *Leymus chinensis* meadow steppe in the western Songnen Plain of China in the growing season (May–October) in 2011 and 2012. The diurnal patterns of soil respiration could be expressed as single peak curves, reaching to the maximum at 11:00–15:00 and falling to the minimum at 21:00–23:00 (or before dawn). The time-window between 7:00 and 9:00 could be used as the optimal measuring time to represent the daily mean soil CO₂ efflux. In the growing season, the daily value of soil CO₂ efflux was moderate in late spring (1.06–2.51 μmol/(m²·s) in May), increased sharply and presented a peak in summer (2.95–3.94 μmol/(m²·s) in July), and then decreased in autumn (0.74–0.97 μmol/(m²·s) in October). Soil temperature (Ts) exerted dominant control on the diurnal and seasonal variations of soil respiration. The temperature sensitivity of soil respiration (Q_{10}) exhibited a large seasonal variation, ranging from 1.35 to 3.32, and decreased with an increasing soil temperature. Rs gradually increased with increasing soil water content (Ws) and tended to decrease when Ws exceeded the optimum water content (27%) of Rs. The Ts and Ws had a confounding effect on Rs, and the two-variable equations could account for 72% of the variation in soil respiration ($p < 0.01$).

Keywords: soil respiration; *Leymus chinensis*; temperature sensitivity of soil respiration (Q_{10}); soil temperature; soil water content

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1 Introduction

The carbon dioxide (CO₂) emission from soils (or soil respiration (Rs)) is recognized as one of the largest fluxes in the global carbon cycle (Schlesinger and Andrews, 2000). The results of previous studies indicate that global soil CO₂ emissions are in the range of 98 ± 12 Pg/yr, with an annual increases of 0.1 Pg that have been suggested to be temperature-associated (Bond-Lamberty and Thomson, 2010). Even a small

change in soil respiration could thus equal or exceed the annual input of CO₂ to the atmosphere via land-use changes and/or fossil fuel combustion, and could significantly exacerbate or mitigate atmospheric increases of CO₂, with consequent feedbacks to climate change (Rustad *et al.*, 2000). Therefore, quantifying soil CO₂ efflux and understanding the controlling factors would be helpful for determining the behavior of the terrestrial ecosystem and predicting their response to climate change (Raich and Schlesinger, 1992).

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Soil temperature (Ts) and soil water content (Ws) have been identified as the most important environmental factors influencing soil CO₂ emissions (Singh and Gupta, 1977). These two factors affect the productivity of terrestrial ecosystems and the decomposition rate of soil organic matter, thereby driving the temporal variation of soil respiration (Wan *et al.*, 2007). Generally, Ts effect is commonly described as an exponential equation (Raich and Schlesinger, 1992), while the Ws effect is not always consistent (Davidson *et al.*, 2000). Meanwhile, the influences of these two factors on Rs may be different, depending on the geographical location and the vegetation types (Raich and Schlesinger, 1992). As an important indicator of temperature sensitivity of soil respiration, Q_{10} receives more attention to predict respiratory-induced CO₂ emission by temperature increasing (Xu and Qi, 2001). The results of previous studies showed that a small deviation in Q_{10} may cause a significant bias in the estimate of Rs (Xu and Qi, 2001). The Q_{10} was commonly used as a constant in many ecosystem models (Potter *et al.*, 1993). However, more evidences proved that the Q_{10} value varied with Ws, Ts and plant phenology (Janssens and Pilegaard, 2003; Wang *et al.*, 2010). Thus, better understanding of the influence of environmental factors on CO₂ fluxes and the Q_{10} variations may improve the estimation accuracy of carbon balance in terrestrial ecosystems by modeling.

Grasslands are one of the most widespread vegetation types in the world, taking up nearly 32% of the earth's natural vegetation (Suyker *et al.*, 2003) and covering approximately 40% of the earth's land area (excluding areas of permanent ice cover) (White *et al.*, 2000). Tropical and temperate natural grasslands store at least 10% of the global soil carbon (Eswaran *et al.*, 1993) and play a significant role in the global carbon cycle (Wang and Fang, 2009). Thereby, more attention should be paid to the CO₂ exchange in these grasslands. However, previous studies have shown that there are still large uncertainties in the magnitude and in the different driving mechanism of soil CO₂ emission among grasslands under various climatic conditions, management practices and vegetation types (Schlesinger and Andrews, 2000; Wang and Fang, 2009). In the past two decades, considerable efforts have been made to quantify the soil respiration in different grassland types of the world, especially in temperate tallgrass prairies, mixed-grass

prairies, tropical remnant grasslands and semi-arid grasslands (Suyker *et al.*, 2003; Wan and Luo, 2003; McCulley *et al.*, 2004; Kucharik *et al.*, 2006; Chen *et al.*, 2010; Carol Adair *et al.*, 2011). However, soil respiration from these grasslands has great variation, with the annual soil CO₂ efflux varying from 128.7 g C/(m²·yr) to 1004.0 g C/(m²·yr). Recently, reports on soil respiration of grasslands in China are mainly focused upon temperate grassland in Inner Mongolia (Chen *et al.*, 2010; Yan *et al.*, 2011; Chen *et al.*, 2013), and alpine grasslands in the Qinghai-Tibet Plateau (Cao *et al.*, 2004; Fang *et al.*, 2012), where the magnitude of CO₂ emission and mechanisms are well represented. However, the studies regarding soil respiration from meadow steppes in the western Songnen Plain, especially the field detection on soil respiration are still scarce.

As one of the most important meadow steppes in China, the vast steppe in the western Songnen Plain is characterized by its alkaline-saline soils. Large amounts of inorganic carbon are typically stored in the semiarid meadow steppe, but the organic carbon pool is small (Ren *et al.*, 2008), implying that Rs is the main process of organic carbon loss from this area. Moreover, because of the relatively small organic carbon pool in this area, Rs is one of the ecosystem properties most sensitive to climate change (West *et al.*, 1994). *Leymus chinensis* (Trin.) Tzvel, with a total area of 1.29×10^6 ha, is the typical vegetation type in the meadow steppe of the western Songnen Plain (Li *et al.*, 1988). Given the enormous area of the temperate *L. chinensis* meadow steppe occurring in the northeastern China, the in-situ measurements are indispensable for extrapolating our estimates of soil respiration to the regional scale. In this study, we investigated CO₂ fluxes from the *L. chinensis* steppe in the western Songnen Plain during the two growing seasons of 2011 and 2012. The objectives are to: 1) characterize the diurnal and seasonal variations in Rs; and 2) determine the relationships between Rs and Ts, Ws at the meadow steppe.

2 Materials and Methods

2.1 Study area

This study was conducted at a typical *L. chinensis* meadow steppe ecosystem in Da'an Sodic Land Experiment Station of China (DSLES, 45°35'58"–45°36'28"N, 123°50'27"–123°51'31"E) in the western Songnen Plain.

The study area is characterized by a temperate, semi-humid and semi-arid continental monsoon climate, with seasons alternating between dry and windy spring, humid and warm summer, windy and dry autumn and long, cold and dry winter. Its mean annual temperature is 4°C. Mean annual precipitation is 413.7 mm, of which 70%–80% occurs in July–September. In this region, the growing season is usually from early May to late September. The mean temperature and precipitation in the growing season are 17.4°C and 384 mm, respectively. The mean evaporation is 1791.6 mm, 4–5 times higher than the annual precipitation (Deng *et al.*, 2006). The main soil type is sodic meadow soil, and further characteristics of the soil in the study area are summarized in Table 1.

2.2 Measurement of soil respiration and environmental factors

Soil respiration was measured with a portable CO₂ infrared gas analyzer (Li-6400) equipped with a Li-6400-09 chamber (Li-Cor Inc, Lincoln, NE, USA). To minimize soil surface disturbances, the chamber was mounted on a PVC collar (10.2 cm in diameter and 5 cm in height) sharpened at the bottom and inserted into the soil about 3 cm deep one day before the measurements. At the study area, three or four PVC collars were placed at random locations where the aboveground vegetation and the litter were removed before measurements were started. The mean CO₂ efflux for each collar is the average of three values generated from three continuous measurements.

Soil respiration rates were measured mostly in the first week and the third week of each month from May to October in 2011 and 2012, and 23 times in total, including 11 times of daytime measurements and 12 times of diurnal measurements. The daytime measurements were done at the relatively uniform time, normally at 7:00–9:00 in the morning because CO₂ efflux measured during this time is regarded to be basically representative for the daily mean efflux (Jia *et al.*, 2006). Diurnal variations of soil CO₂ efflux were examined once every hour from 7:00 on the first day to 7:00 on the second day.

Data of daily precipitation and temperature were obtained from the meteorological station at DSLES. During the experimental periods, soil temperature at 10 cm depth (°C, T_s) was monitored with a digital thermometer (LI-6400-09 TC, LI-Cor). Soil water content (% v/v, W_s) at 10 cm depth was measured by gravimetric method (Jackson *et al.*, 2000). Soil bulk density (BD) at each site was determined using the volumetric core method (ISSCAS, 1978). Three soil pits with depths of 20 cm were randomly dug in the buffer area near each site in July 2011 and 2012. A 500-g soil sample from 0–5 cm, 5–10 cm, and 10–20 cm was taken to measure the concentration of soil organic carbon (SOC) and other soil properties. The soil samples were naturally dried and passed through a 2-mm sieve. Soil organic carbon (SOC) was measured by dichromate oxidation methods (Kalembasa and Jenkinson, 1973), total N was measured using the semimicro-Kjedahl method (Nelson and Sommers, 1982), pH and electrical conductivity (EC) were determined with a glass electrode using a 1 : 5 soil-water ratio (ISSCAS, 1978), field capacity (FC) was measured by Wilcox method (ISSCAS, 1978).

2.3 Data analysis

All statistical procedures were performed using the software packages SPSS 11.5 (SPSS Inc., Chicago, USA) and SigmaPlot 10.0 (SPSS Inc., Chicago, USA). Diurnal soil respiration rate in the growing season in 2011 and 2012 was integrated to obtain the diurnal and seasonal variations of Q_{10} values. Diurnal dynamics of soil respiration (R_s) could be described as Van't Hoff's function (Van't Hoff, 1899):

$$R_s = R_{\text{ref}} \exp(\beta(T - T_{\text{ref}})) \quad (1)$$

where T is soil temperature; T_{ref} is reference temperature; β is fitted data-specific parameter; and R_{ref} is the soil respiration rate at a reference temperature (T_{ref}).

In this study, the reference temperature for R_{ref} was 10°C. The coefficients R_{10} and β in Van't Hoff's equation were calculated by using the exponential model in curve regression for each measurement date. The pa-

Table 1 Characteristics of soil in study area

Plant community	SOC (g/kg)	Total N (g/kg)	pH	EC (mS/cm)	BD (g/cm ³)	FC (%)
<i>Leymus chinensis</i>	15.2±0.1	0.69±0.03	9.4±0.31	0.53±0.03	1.4±0.005	30.2±1.8

Notes: SOC, soil organic carbon; EC, electric conductivity; BD, bulk density; FC, field capacity. Given data represent the mean±standard error for three replicates

parameter β is the slope of the exponential function and commonly expressed as the respiration quotient Q_{10} ($Q_{10} = \exp(10\beta)$). One-way ANOVA was used to compare differences in mean soil CO_2 efflux between two measured years. Linear regression analysis was used to assess the relationships between R_s and W_s . The combined effects of T_s and W_s on R_s were evaluated using multivariate non-linear regression analysis.

3 Results and Analyses

3.1 Environmental variables

Measurements were conducted over a wide range of environmental conditions in the growing season (Fig. 1). The mean air temperature from May to October was 18.36°C and 19.44°C for 2011 and 2012, respectively. The dynamics of precipitation were different for the two measured years, with the total precipitation being 370.0 mm and 498.4 mm, respectively. The temporal variations of air temperature (T_a), ground temperature (T_g) and soil temperature (10 cm) (T_s) showed similar patterns, with the low values observed in October and May, and the maximal values occurred mostly in summer

months (Fig. 2a). Compared with the temporal trend of T_s , the W_s at 0–10 cm depth fluctuated markedly over the season depending on weather conditions (Fig. 2b).

3.2 Diurnal and seasonal dynamics of soil respiration rate

The diurnal patterns of soil respiration were similar in different measuring days, and could be expressed as single peak curves (Fig. 3). In general, soil respiration

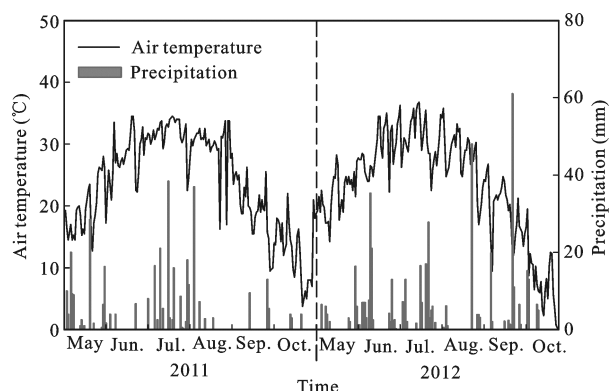


Fig. 1 Mean air temperature and precipitation in growing season in 2011 and 2012

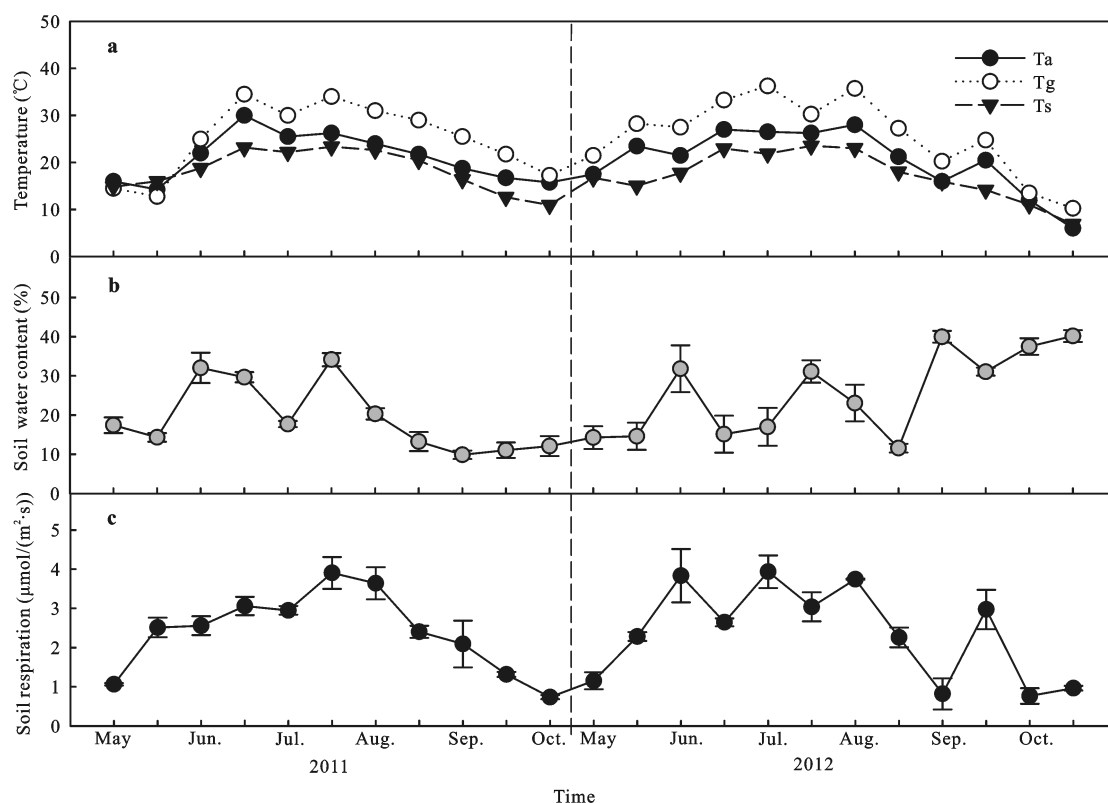


Fig. 2 Seasonal variations of soil respiration rates, air temperature, ground temperature, soil temperature at 10 cm depth and soil water content in growing season in 2011 and 2012. T_a , air temperature; T_g , ground temperature; T_s , soil temperature at 10 cm depth. Soil water content and respiration data are the mean of three or four replicates with standard error bars

rates reached to the maximum ($1.4\text{--}4.8\ \mu\text{mol}/(\text{m}^2\cdot\text{s})$) at 11:00–15:00 and fell to the minimum ($0.4\text{--}3.1\ \mu\text{mol}/(\text{m}^2\cdot\text{s})$) at 21:00–23:00 or before dawn, coinciding with the highest and the lowest temperature. During the whole observation period, soil CO_2 efflux intersected the mean daily Rs at 7:00–9:00 and 17:00–19:00 for each 24 h measurement (Fig. 3).

In the two years of measurement, soil CO_2 efflux exhibited a significant seasonal variation and overall corresponded to seasonal changes in T_s (Fig. 2a, Fig. 2c). The soil CO_2 efflux was moderate in late spring ($1.06\text{--}2.51\ \mu\text{mol}/(\text{m}^2\cdot\text{s})$ in May), increased sharply to a peak in summer ($2.95\text{--}3.94\ \mu\text{mol}/(\text{m}^2\cdot\text{s})$ in July), and then decreased in autumn ($0.74\text{--}0.97\ \mu\text{mol}/(\text{m}^2\cdot\text{s})$ in

October). Mean values of CO_2 efflux between 2011 and 2012 showed no significant difference ($p > 0.05$), and the mean Rs rates were $2.38\pm 0.3\ \mu\text{mol}/(\text{m}^2\cdot\text{s})$ and $2.37\pm 0.4\ \mu\text{mol}/(\text{m}^2\cdot\text{s})$ (Mean \pm SE), respectively.

3.3 Effects of temperature and soil water content on soil respiration

There were significantly positive correlations between Rs rate (R_s , $\mu\text{mol}/(\text{m}^2\cdot\text{s})$) and soil temperature at 10 cm depth (T_s , $^{\circ}\text{C}$) ($p < 0.01$) (Table 2). The T_s explained 54%–80% (mean of 65%) of the diurnal variations of Rs and 67% of the seasonal variation. The Q_{10} exhibited a large seasonal variation with minimum values of 1.35 occurring in warm months (June, July and August) and

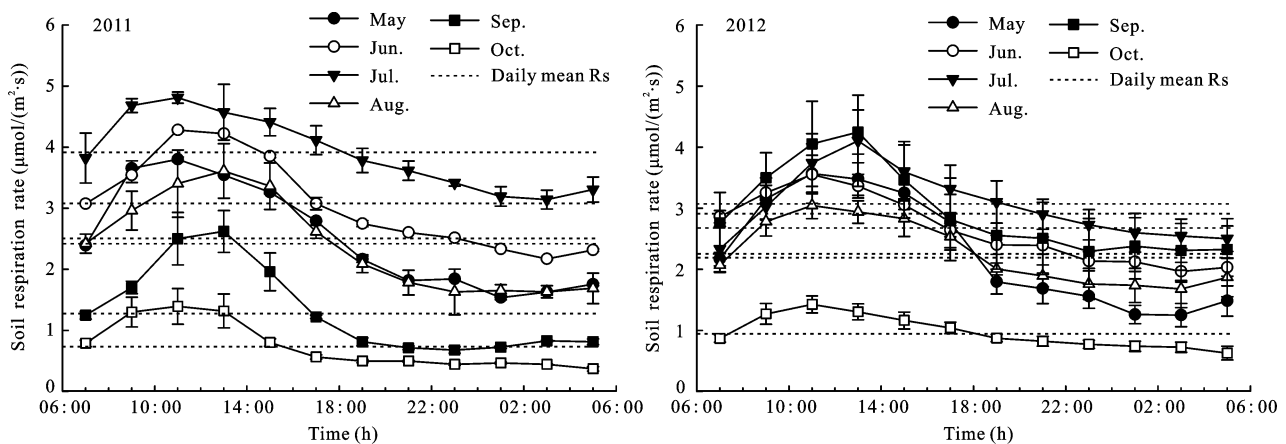


Fig. 3 Diurnal dynamics of soil respiration rates in growing season in 2011 and 2012. Flux data are the mean of three or four replicates with standard error bars

Table 2 Van't Hoff's equation between soil respiration rate and soil temperature during measuring period for each measured day in 2011 and 2012

Sampling data	$R_s = R_{10}\exp(\beta(T_s - 10))$	Number of data	R^2	Q_{10}^a	R_{10}^b	p -value
2011-05-14	$R_s = 0.67\exp(0.12(T_s - 10))$	36	0.602	3.32	0.67	< 0.01
2011-06-20	$R_s = 0.84\exp(0.08(T_s - 10))$	36	0.538	2.23	0.84	< 0.05
2011-07-22	$R_s = 1.44\exp(0.06(T_s - 10))$	48	0.560	1.82	1.44	< 0.01
2011-08-23	$R_s = 0.81\exp(0.09(T_s - 10))$	48	0.632	2.46	0.81	< 0.01
2011-09-22	$R_s = 0.73\exp(0.09(T_s - 10))$	48	0.549	2.46	0.73	< 0.05
2011-10-14	$R_s = 0.55\exp(0.12(T_s - 10))$	48	0.664	3.32	0.55	< 0.01
2012-05-21	$R_s = 0.77\exp(0.06(T_s - 10))$	36	0.801	1.82	0.77	< 0.01
2012-06-26	$R_s = 1.70\exp(0.03(T_s - 10))$	48	0.756	1.35	1.70	< 0.01
2012-07-27	$R_s = 1.92\exp(0.03(T_s - 10))$	36	0.596	1.35	1.92	< 0.01
2012-08-22	$R_s = 1.67\exp(0.03(T_s - 10))$	48	0.704	1.35	1.67	< 0.01
2012-09-20	$R_s = 1.78\exp(0.04(T_s - 10))$	48	0.683	1.49	1.78	< 0.01
2012-10-15	$R_s = 1.17\exp(0.07(T_s - 10))$	48	0.760	2.01	1.17	< 0.01
All seasons (2011–2012)	$R_s = 0.83\exp(0.06(T_s - 10))$	594	0.667	1.82	0.83	< 0.01

Notes: a, Q_{10} ($Q_{10} = e^{10\beta}$) represents the exponential change in CO_2 fluxes resulting from a change in temperature by 10°C ; b, R_{10} represents the soil respiration rate at 10°C

maximum values of 3.32 occurring in cold months (May and October). The Q_{10} value calculated based on all datasets of the two growing seasons across the two studied years was 1.82, a little lower than the mean daily Q_{10} (2.08) of all the measured days.

There was no significant correlation between mean daily Rs and Ws over the two growing seasons ($p > 0.05$), which suggested that Ws was not the main controlling factor to the seasonal dynamics of soil respiration. However, due to the large variations of precipitation in 2011 and 2012, the Ws had different impacts on Rs for the two measured years (Fig. 4). The Rs in-

creased in association with increased Ws in 2011. In 2012, however, the Rs increased gradually with Ws, and reached its highest value when Ws was 27%, and then decreased consistently toward higher Ws. The Rs and Ws were significantly correlated through quadratic models ($p < 0.05$), and Ws explained 42% and 57% variance of Rs for 2011 and 2012, respectively.

The Ws and Ts have an interactive effect on the seasonal variations of Rs. Combined changes in Ts and Ws explained 72% of the observed changes in the Rs ($R_s = -1.49 + 0.11T_s + 0.09W_s + 0.002T_s^2 - 0.001W_s^2$, $p < 0.01$) (Fig. 5).

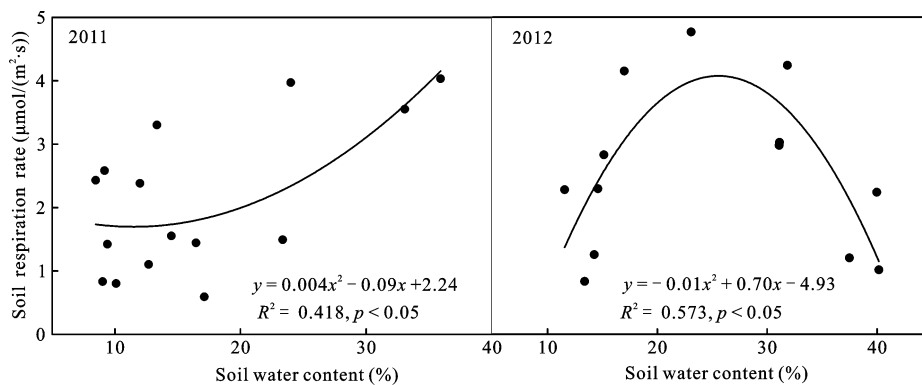


Fig. 4 Relationship between soil respiration rate and soil water content in growing season in 2011 and 2012. Each flux datum is the mean of three or four replicates

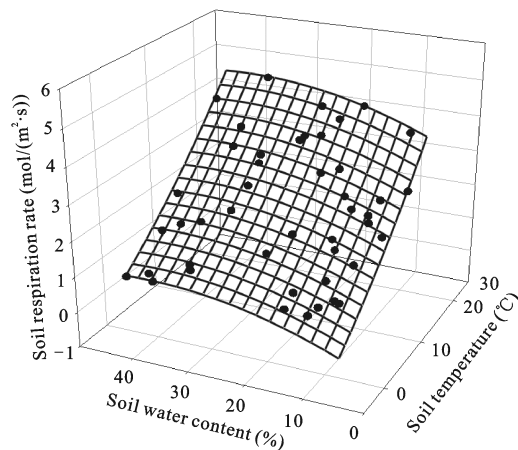


Fig. 5 Relationship of soil respiration rate with soil water content and soil temperature in growing season in 2011 and 2012. Each flux datum is the mean of three or four replicates

4 Discussion

4.1 Mean daily CO₂ efflux and its optimal measuring time

Mean CO₂ fluxes during the growing season from mea-

dow steppes in this study were 2.45–2.47 g C/(m²·d), and were within the range reported for global grasslands (0.41–4.55 g C/(m²·d)) (Raich and Tufekciogul, 2000), for a semiarid steppe in Inner Mongolia (1.40–2.84 g C/(m²·d)) (Yan *et al.*, 2011), and for two different grazing intensity conditions in an alpine meadow in the Qinghai-Tibet Plateau (0.48–2.09 g C/(m²·d)) (Cao *et al.*, 2004).

The mean daily soil CO₂ efflux, calculated from 12 individual measurements over each 24 h measurement campaign, were close to those at 7:00–9:00 and 17:00–19:00 at the study area. These two time-windows (7:00–9:00 and 17:00–19:00) represented the optimal time period to make soil CO₂ efflux measurements for the estimation of mean daily CO₂ efflux. Our result was inconsistent with the general measured time in forest, agriculture, and wetland ecosystem, in which the mean daily CO₂ efflux mostly occurred between 9:00 and 13:00 (Jiang *et al.*, 2010; Shi *et al.*, 2012; Wang *et al.*, 2012). If the Rs rate from 9:00–11:00 was used to represent the mean daily value, the mean daily CO₂ efflux would be

overestimated by 10%–76% in the study area. It indicated that this time window could be a poor representation of the mean daily soil CO₂ efflux for *L. chinensis* meadow steppe. Although the measurements conducted at approximately 17:00–19:00 at night may represent mean daily soil CO₂ efflux equally well as measurements in the morning (7:00–9:00), it is generally not practical to carry out measurements at night using manual chambers. The results of this study showed that the time-window between 7:00 and 9:00 could be used as the optimal measuring time to represent the mean daily soil CO₂ efflux. This optimal time for Rs measurement (7:00–9:00) was also found in the study from Jia *et al.* (2006) on *L. chinensis* steppes, Inner Mongolia, China.

4.2 Effects of soil temperature and soil water content on soil respiration

The Ts could influence Rs mainly by affecting root activities, decomposition of plant litter, soil organic matter and plant biomass production, leading to changes in carbon substrate availability for plant roots and soil microbes (Wan and Luo, 2003; Chen *et al.*, 2010). Our findings indicated that the change in Ts could account for most of the seasonal and diurnal variations in soil CO₂ efflux at *L. chinensis* meadow steppe in the western Songnen Plain. The exponential dependence of diurnal and seasonal dynamics of Rs upon Ts observed in this study (Table 2) was consistent with the relationships in other grassland ecosystems (Singh and Gupta, 1977; Wan *et al.*, 2007; Chen *et al.*, 2010).

The Q_{10} values (1.35–3.32) in the growing season from *L. chinensis* meadow steppe in the study area were comparable with previous studies on a steppe in Inner Mongolia (1.60–1.81), alpine steppe (2.75–3.32) and tallgrass prairie (1.93–2.90) (Chen *et al.*, 2003; Wan and Luo, 2003; Cao *et al.*, 2004; Kucharik *et al.*, 2006). Generally, the Q_{10} value was expected to be identical within a season, but the diurnal Q_{10} in this study showed large seasonal changes in the growing season. It is probable that Q_{10} value, at a diurnal scale, is no longer a reflection of temperature sensitivity, but a combined response to the seasonal changes in soil water content, root biomass, litter inputs, microbial populations and other seasonally fluctuating conditions and processes (Davidson *et al.*, 1998). Soil water content and plant growth, for example, were significantly different between sampling days; hence an irregular Q_{10} value would

be obtained. Xu and Qi (2001) found that W_s and Q_{10} values were positively correlated and that W_s explained more seasonal variance of Q_{10} values than T_s did. The variations in plant phenological process could significantly contribute to the variations in calculating seasonal Q_{10} values (Chen and Tian, 2005). The results of Wang *et al.* (2010) indicated that the variations of seasonal vegetation activity exerted dominant control over the seasonal variations of the apparent Q_{10} of Rs, highlighting the ecological linkage between plant physiological processes and soil processes.

Previous studies also suggested that Q_{10} changed with temperature range (Janssens and Pilegaard, 2003). The results of this study indicated that the diurnal Q_{10} value was higher at low temperature than at high temperature. Similar results also were obtained by other studies (Raich and Schlesinger, 1992; Chen and Tian, 2005). The reduction in Q_{10} value with increasing temperature may be associated with the transition from acclimation of enzymatic activity at low temperature to limitation by substrate supply at high temperature (Davidson *et al.*, 2006). Lower temperature might make active microbes become dormant, thus decrease the richness of microbial species, and potentially result in higher Q_{10} values than expected (Chen *et al.*, 2010). Moreover, temperature can affect microbial populations more strongly at lower temperature than at higher temperature, which leads to a higher Q_{10} value with decreasing temperature (Andrews *et al.*, 2000). Furthermore, substrate availability can become limiting at high temperature, either through the temperature sensitivity of the enzyme or through the effect of temperature and water content on substrate supply. These interactions tended to result in higher combined temperature sensitivities at the low end of the temperature spectrum for biological activity (Davidson *et al.*, 2006).

Soil water availability can directly influence soil respiration by altering activities of plant roots and soil microbes and indirectly by affecting plant growth, below-ground carbon allocation and substrate availability (Wan *et al.*, 2007). In the present study, the influence of W_s on seasonal dynamics of Rs was closely dependent upon the overall soil water regimes. The positive correlation between W_s and Rs existed only when W_s was relatively low and the Rs decreased as W_s exceeded a threshold (27%, v/v), which would be the optimum water content for Rs in the *L. chinensis* steppe. Our results

were in accordance with those in grassland ecosystems (Byrne *et al.*, 2005; Zhou *et al.*, 2009) and other terrestrial ecosystems (Jiang *et al.*, 2005; Saiz *et al.*, 2007). In general, metabolic activity increases with the increasing soil water availability in arid and semiarid environments (Jia *et al.*, 2006). However, extremely high soil water conditions would significantly affect the soil CO₂ emission (Davidson *et al.*, 1998). When the Ws exceeds the optimum water content for Rs, high soil water content could impede O₂ diffusion through pore spaces, thereby reducing rates of decomposition and microbial production of CO₂ (Linn and Doran, 1984). Moreover, both the diffusion of soluble substrates in soil water films (Yan *et al.*, 2011) and diffusion of CO₂ within the soil profile (Davidson and Trumbore, 1995) would also be constrained by high soil water conditions. As the Rs has different responses to the wet and dry soil water conditions, the specific soil water regime should be taken into account for identifying the relationship between Rs and Ws.

The optimum Ws for Rs was the Ws at which Rs was the highest. It represents the moisture threshold below which Rs increases with the increasing Ws and above which Rs decreases with the increasing Ws (Wan *et al.*, 2007). The optimum Ws for Rs (27% v/v) in this study was at intermediate water contents and near the field capacity of the study area (Table 1), which was in agreement with the results of Wang *et al.* (2003) and Wan *et al.* (2007). Davidson *et al.* (2000) also reported that the optimum water content of Rs was usually somewhere near field capacity, where the macropore spaces were mostly air-filled, thus facilitating O₂ diffusion, and the micropore spaces were mostly water-filled, thus facilitating diffusion of soluble substrates.

The results of previous studies showed that the effects of Ws and Ts are often confounded, especially in the case of field-based Rs measurements (Davidson *et al.*, 1998; Gao *et al.*, 2011). The results from this study showed that Rs at the *L. chinensis* steppe was closely related to both Ts and Ws (Fig. 5). The changes in Ts and Ws in the growing season explained a considerable fraction (72%) of the soil CO₂ efflux variation. Previous studies have suggested that Ts was the dominating factor of the Rs at < 15°C, while Ws would override or interact with Ts effects during the other periods at semiarid steppes (Jia *et al.*, 2006; Chen *et al.*, 2013). In the present study, stronger relationships between Rs and Ts

($R^2 = 0.602\text{--}0.801$) were also observed during the periods of low soil temperature (< 15°C) with less living biomass (at the beginning and the end of the growing season, i.e., May and October). The decomposition of soil carbon matter by soil microorganisms could account for a greater amount of the soil CO₂ emission at low temperature (< 15°C). Since temperature affected microbial populations more strongly at lower temperature than at higher temperature (Andrews *et al.*, 2000; Janssens and Pilegaard, 2003), the temporal variation of soil CO₂ efflux at low temperature was highly dependent on the change of temperature. However, when temperature was above 15°C, root respiration contributed most of the total Rs, and Ws and Ts may have interacted to influence soil respiration through their effects on carbon availability (Carol Adair *et al.*, 2011). Additionally, previous studies have reported that the temporal variations of Rs were influenced not only by Ts and Ws, but also by biotic factors, such as plant and microbial biomass, net primary productivity, and litter inputs (Wan and Luo, 2003; Chen *et al.*, 2010). Moreover, human activities are significantly modifying the carbon cycles of the grassland ecosystem in many ways, i.e., grazing, land-use changes, fertilization and fire (Cao *et al.*, 2004; Chen *et al.*, 2013). Therefore, it is necessary to take biotic and abiotic factors into account for evaluating future soil CO₂ emission.

5 Conclusions

This paper studied the diurnal and seasonal variations of soil respiration and its associated environmental factors at *L. chinensis* steppe in the western Songnen Plain. The main conclusions are as follows.

(1) The diurnal patterns of soil respiration display single peak curves, with lower values in the early mornings and late evenings and the peak CO₂ flux occurring around midday or mid afternoon. The soil respiration rate from 7:00 to 9:00 in the morning can be used as the daily mean soil CO₂ efflux.

(2) Soil CO₂ effluxes show significant seasonal variations corresponding to soil temperature changes. Soil temperature at 10 cm depth presents the dominant control on the diurnal and seasonal variations of soil respiration. The Q_{10} values exhibit a large seasonal variation and decreased with increasing soil temperature.

(3) The Rs tends to increase with increasing Ws and

can be limited when W_s exceeds the optimum water content (27% v/v). In the growing season, the interactions of soil temperature and soil water content can influence the soil respiration rate significantly and explain 72% of the variation in soil respiration.

In this study, we conduct the R_s measurements from May to October when temperature is above 0°C, but are unable to measure the R_s in the non-growing season because of instrument failure at low temperature. Therefore, further study at the annual scale might be more valuable for better understanding of soil CO₂ emission at the meadow steppe.

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