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Effect of water stress on ecosystem photosynthesis and respiration of a *Leymus chinensis* steppe in Inner Mongolia

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Abstract Many studies on global climate have forecast major changes in the amounts and spatial patterns of precipitation that may significantly affect temperate grasslands in arid and semi-arid regions. As a part of ChinaFLUX, eddy covariance flux measurements were made at a semi-arid *Leymus chinensis* steppe in Inner Mongolia, China during 2003—2004 to quantify the response of carbon exchange to environmental changes. Results showed that gross ecosystem production (F_{GEP}) and ecosystem respiration (R_{eco}) of the steppe were significantly depressed by water stress due to lack of precipitation during the growing season. Temperature was the dominant factor affecting F_{GEP} and R_{eco} in 2003, whereas soil moisture imposed a significant influence on both R_{eco} and F_{GEP} in 2004. Under wet conditions, R_{eco} showed an exponentially increasing trend with temperature ($Q_{10} = 2.0$), but an apparent reduction in the value of R_{eco} and its temperature sensitivity were observed during the periods of water stress (Q_{10}=1.6). Both heat and water stress can cause decrease in F_{GEP}. The seasonality of ecosystem carbon exchange was strongly correlated with the variation of precipitation. With less precipitation in 2003, the steppe sequestrated carbon in June and July, and went into a senescence in early August due to water stress. As compared to 2003, the severe drought during the spring of 2004 delayed the growth of the steppe until late June, and the steppe became a CO_2 sink from early July until mid-September, with ample precipitation in August. The semi-arid steppe released a total of 9.7 g C·m^{-2} from May 16 to the end of September 2003, whereas the net carbon budget during the same period in 2004 was close to zero. Long-term measurements over various grasslands are needed to quantify carbon balance in temperate grasslands.

Keywords: *Leymus chinensis* steppe, water stress, ecosystem respiration, gross ecosystem production, net ecosystem CO_2 exchange.

The response of terrestrial ecosystems to environmental change is one of the key global change issues that scientists are investigating by means of measurements and models on both short- and long-time scales[1]. Grassland, which comprises 32% of the earth's natural vegetation, may contribute greatly to global carbon balance as large sinks or sources[2]. In the arid and semi-arid regions of China, temperate grassland is important natural vegetation with an area of about 3.13×10^8 hm^2 that plays an important role in maintaining and regulating the environment and climate, especially in the north. Grassland carbon balance is controlled by factors such as temperature, soil moisture, available nitrogen and management practices (e.g. burning, grazing and harvesting). Global climate changes such as atmospheric warming, CO_2 enrichment, and increased variability in rainfall, can greatly affect key carbon cycling processes and alter the carbon balance in grassland ecosystems[3,4]. Grasslands in particular have very large, asymmetric responses to yearly variation of precipitation; in wet years, productivity increases are much more pronounced than reductions in productivity during dry years[5]. In grassland ecosystems of continental Eurasia and North America, primary production is strongly controlled by variation in annual precipitation, especially during the growing season[6,7].

Many studies on global change have forecast a major change in rainfall with a globally higher frequency of extreme rainfall events, a lower frequency of rainfall days and longer intervening dry periods[8]. Recorded data also show decreasing trends in precipitation amounts in northern China since the 1960s, accompanied by increased intensity of storms and longer dry spells[9]. The growing uncertainty in rainfall forecasting will lead to a higher variability in soil moisture[10], which would directly affect the carbon uptake in grassland ecosystems that are sensitive to variation of precipitation. The temperate, semi-arid *Leymus chinensis* steppe in Inner Mongolia often suffers from drought stress due to low precipitation. In these regions, heat stress often accompanies drought stress[11].

Moisture deficits and high temperature stress can impact the physiological processes of plants in several ways. Soil moisture deficits can cause reductions of cell expansion, leaf area development, photosynthesis, stomatal conductance and transpiration, and high leaf-temperature can inhibit plant growth by inactivating photosystem II and promoting respiration[12,13]. However, the effects of environmental stress on key carbon cycling processes in grassland ecosystems reported in previous studies have been inconsistent[14,15]. Such studies have been impeded by complex environmental conditions and difficulties with the limitation of measurement techniques. So far, few studies have been conducted to investigate CO_2 exchange in the semi-arid grasslands and their sensitivities to environmental stress at an ecosystem scale.

In recent years the eddy covariance technique has emerged as an alternative way to assess ecosystem carbon exchange[16,17]. The wide diversity of vegetation and climatic variability of grassland ecosystems offer special opportunities for the study of ecosystem physiology and environmental change[5,18]. The objectives of this study were to compare the responses of net ecosystem CO_2 exchange (F_{NEE}), ecosystem respiration (R_{eco}) and gross ecosystem productivity (F_{GEP}) to changes in temperature and soil moisture during the growing season (May to September) in 2003 and 2004, and to illustrate the effect of water stress on plant phenology and ecosystem carbon budget in the semi-arid *Leymus chinensis* steppe.

1 Materials and methods

1.1 Study site description

Measurements were taken at a semi-arid *Leymus chinensis* steppe site (43°33′11″N, 116°40′31″E, 1189 m above sea level, with a slope about 3%—6%) of ChinaFLUX, located in the Xilin River Basin. The site's vegetation is dominated by warm-season grasses such as *Leymus chinensis*, *Stipa grandis*, *Koeleria cristata and Agropyron cristatum*, etc. The canopy height is about 0.4—0.6 m, with a canopy coverage of 80%. The grasses germinate in late April and enter their senescence phase in mid-October, with a growth period of 150 d. The site has not been grazed since 1979 and there is a substantial amount of dead plant material (litter) on the ground surface. The soil is dark chestnut, with 21% silt and 60% sand on average. The dominant temperate, continental, semi- arid climate has an annual temperature around −1.1—0.2℃; mean daily temperatures for January and July are −22.3 and 18.8, respectively. The mean annual precipitation for the area is 313 mm (182—645.6 mm), mostly during the warm season (May to September). The annual evapotranspiration is about 1665 mm[19,20].

1.2 Experimental measurements

Fluxes of CO_2, sensible heat, latent heat and momentum were measured at a height of 2.2 m above the ground with an open-path eddy covariance system during the growing seasons of 2003 and 2004. Three-dimensional wind speed and temperature fluctuations were measured with a sonic anemometer (Model CSAT-3, Campbell Scientific, Logan, Utah, USA). Measurements of CO_2 and water-vapor densities were made with an open-path CO_2/H_2O infrared analyzer (Model LI-7500, Li-cor Inc., Nebraska, USA). All signals were recorded at a frequency of 10 Hz and the fluxes were calculated at half-hour intervals by a CR5000 data logger (Model CR5000, Campbell Scientific).

Profiles of mean air temperature (T_a), humidity (RH) and horizontal wind speed were measured at 1.2 and 2.2 m heights above ground. Incident and reflected solar radiation, net radiation (R_n), photosynthetically active radiation (Q_{PPFD}) and soil heat flux were also measured. Soil temperatures were recorded at five depths (−5, −10, −20, −40, and −80 cm) with thermometers (107-L, Campbell Scientific) and soil moisture was monitored at three depths (−5, −20 and −40 cm, respectively) with TDR probes (Model CS615-L, Campbell Scientific). Precipitation was measured hourly with a rain gauge (Model 52203, RM Young Inc., Traverse City, Michigan, USA). All meteorological data were averaged at 30 min intervals and recorded by a CR23X datalogger (Model CR23XTD, Campbell Scientific). The measurements were made continuously, beginning in late April 2003 and the data collected during both growing seasons (May to September, 2003 and 2004) were analyzed.

1.3 Data processing

To correct the effects of sensor tilt and sloping fields on flux calculation, measurements were corrected by rotating wind velocity axes using a traditional triple-rotation method to compute flux covariances aligned normally to the mean streamlines[21,22]. Correction was made on carbon dioxide and latent heat fluxes for variations in air density caused by heat and water-vapor transfer[23]. The data were screened to remove anomalous values caused by malfunction of sensors due to interference from dew, hoarfrost, rain or birds. Negative nighttime data were also excluded. Some breaks in data collection occurred due to system maintenance and power outages.

The eddy covariance technique is apt to underestimate net ecosystem CO_2 exchange at night, when air becomes stably stratified[24]. A common practice is to replace the flux during periods when friction velocity (u_*) is below its threshold (u_{*c}) with a flux that has been estimated using a temperature function established with data obtained during well-mixed, windy periods ($u_* > u_{*c}$). Many previous studies have shown that u_{*c} is dependent upon site-specific parameters. In this study, the u_{*c} was set at 0.15 according to the dependence of nighttime flux on friction velocity (u_*). Missing or rejected data comprised 19% of all possible 30-min time periods during the study.

Interpolated values were used to fill gaps that were 2 h or less. For large gaps (a few hours to several days), the daytime CO_2 flux was estimated as a function of Q_{PPFD} with the Michaelis–Menten equation[25],

$$F_{NEE}=\left(\frac{\alpha Q_{PPFD}F_{NEE,max}}{\alpha Q_{PPFD}+F_{NEE,max}}\right)+R_{eco,day}, \qquad (1)$$

where α is the ecosystem quantum yield (mg $CO_2 \cdot \mu mol^{-1}$ photon), and $F_{NEE,max}$ is the ecosystem gross primary productivity at "saturating" light (mg $CO_2 \cdot m^{-2} \cdot s^{-1}$). $R_{eco,day}$ is the ecosystem respiration during the daytime, and F_{NEE} the net ecosystem CO_2 exchange (both in mg $CO_2 \cdot m^{-2} \cdot s^{-1}$). Missing nighttime F_{NEE} was filled in from a Van't Hoff respiration model based on soil temperature[26]:

$$R_{eco}=R_{eco,T_{ref}}\,e^{BT_s}, \qquad (2)$$

where $R_{eco,T_{ref}}$ is the ecosystem respiration rate at reference temperature (T_{ref}, set as 0℃ in this study) and T_s is soil temperature (K) at a depth of 5 cm. A fitted, site-specific parameter is $B = \ln(Q_{10})/10$, where Q_{10} is temperature sensitivity of respiration, increasing at 10℃ increments. Thus eq. (2) can be rewritten as

$$R_{eco}=R_{eco,T_{ref}}\,e^{\ln(Q_{10})(T_s)/10}. \qquad (3)$$

It has been well proven in the literature that dry conditions impede ecosystem respiration[27]; however, traditional formulas may overestimate the response of ecosystem respiration to dry-season temperatures. The effects of temperature and soil moisture on the temperature sensitivity of ecosystem respiration, in arid and/or semi-arid ecosystems, could be illustrated as

$$Q_{10}=a-bT_s+cS_w, \qquad (4)$$

where S_w is soil water content in 0 to 5 m layer ($m^3 \cdot m^{-3}$) and a, b and c are fitted, site-specific parameters. Positive b and c mean that Q_{10} decreases with increasing temperature and decreasing soil moisture, respectively, over a limited range of soil water content[27−29].

The CO_2 flux measured by eddy covariance technique represents the net ecosystem CO_2 exchange (F_{NEE}), which is the balance between gross ecosystem production (F_{GEP}) and ecosystem respiration (R_{eco})[1]. Daytime ecosystem respiration ($R_{\text{eco,day}}$) could be estimated with eqs. (2)−(4) by establishing a function between R_{eco} and soil temperature and soil moisture. Gross ecosystem production (F_{GEP}) could then be derived by subtracting the estimated daytime respiration from the corresponding daytime F_{NEE}[25]:

$$F_{\text{GEP}} = F_{\text{NEE}} - R_{\text{eco,day}} . \qquad (5)$$

Daily ecosystem respiration is the sum of nighttime and daytime respiration. The above computations were done with MATLAB software (Math Works Inc., Natick, Massachusetts, USA).

2 Results

2.1 Environmental variables

The daily mean values of photosynthetically active radiation (Q_{PPFD}), air temperature (T_a) and vapor pressure deficit (VPD) from May to September in 2003 and 2004 were plotted in Fig. 1((a)-(c)). As compared to 2003, in 2004 the average daily Q_{PPFD} was higher from early May through mid-June and generally lower from mid-July through mid- August, with some cloudy days. There were two extremely cloudy periods in May and June 2003 (Fig. 1(a)). The average daily air temperature during the two growing seasons was comparable, 6.4 and 6.0℃ for 2003 and 2004 respectively, even though it was much warmer during early May, early June and mid-July in 2004 than in 2003. There were several evident cold snaps in 2003 (once each in early June, early July, and mid-July) in 2003. As compared to 2003, the mean daily vapor-pressure deficit in 2004 was much higher during May through mid-June and again in mid-July, but lower in late June and early August.

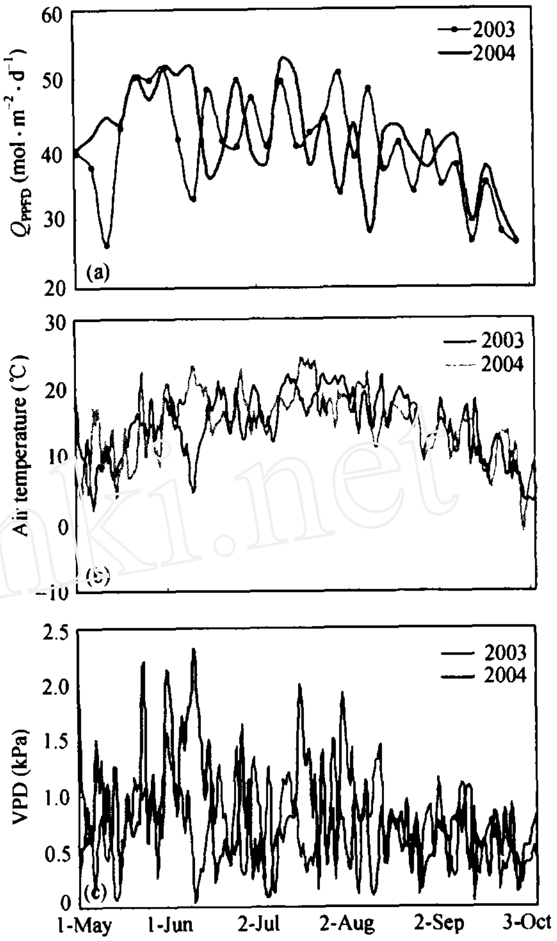

Fig. 1. Seasonal trends of (a) daily total photosynthetically active radiation (Q_{PPFD}, 5-day average), (b) daily mean air temperature (T_a, 2.2 m height) and (c) vapor pressure deficit (D_{ref}, 2.2 m) at the steppe during the growing seasons of 2003 and 2004.

Seasonal trends in volumetric soil moisture of the top 0.05 and 0.2 m layers and daily precipitation during the two growing seasons are included in Fig. 2. The precipitation in 2003 (211.5 mm), occurring mostly early and late in the season, is much less than that of 2004 (344.4 mm). Lack of precipitation after mid-June 2003 caused a serious drought stress on the steppe in July and August, with a continuous decrease in soil moisture in the deeper layer from early June until September (Fig. 2(a)). The variation of soil moisture in the upper layer significantly correlated with rainfall events. As compared to 2003, in 2004 much more precipitation occurred in July and August. Less precipitation during the early 2004 growing season resulted in extremely low root-zone soil moisture (S_w_20 cm) from May through mid-June, which imposed severe water stress on the steppe. Another dry period in 2004 appeared during mid-July, with little rainfall and high air temperature.

In summary, the major disparity in environmental conditions between the two growing seasons was the amount and timing of precipitation received (Fig. 2), which resulted in a dry warm spring and a appropriately moist period in late growing season (late July through August) of 2004. By comparison, the 2003 growing season had a relatively cool wet spring and a dry, hot summer. These variances explain much of the difference in net ecosystem carbon exchange during the two growing seasons.

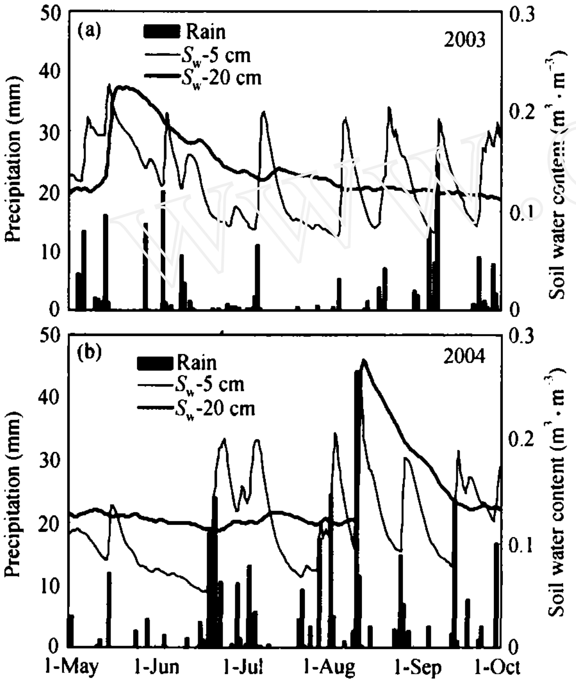

Fig. 2. Soil moisture (S_w, $m^3\ m^{-3}$) in the 0—0.05 m and 0—0.2 m layers and daily precipitation (mm) from May to September in 2003 and 2004.

2.2 *Response of F_{NEE} to temperature and moisture*

Fig. 3 shows the response of daily net ecosystem CO_2 exchange (F_{NEE}) in the *Leymus chinensis* steppe to the change of daily average air temperature and topsoil moisture. The measured data were averaged with a bin width of 1℃ of air temperature or 0.01 $m^3 \cdot m^{-3}$ of soil water content to reduce sampling error. In Fig. 3(a), the measured CO_2 flux data with topsoil moisture > 0.08 $m^3 \cdot m^{-3}$ were selected in order to reduce the strong confounding effects of severe moisture stress when analyzing the response of F_{NEE} to temperature. F_{NEE} reached the maximum when S_w >0.12 $m^3 \cdot m^{-3}$ and temperature around 15—17℃ and decreased when air temperature and/or soil moisture were above or below the optimum, shown as a quadratic function of temperature and/or soil moisture. F_{NEE} was significantly depressed when T_a>18℃ and S_w<0.1 $m^3 \cdot m^{-3}$. The decrease in F_{NEE} at low temperatures is likely due to the slow rate of plant growth in the early and late growing season, whereas the decrease in F_{NEE} at high temperatures could be ascribed to simultaneous water and heat stress.

Water stress is the most common limiting factor of vegetative growth in semi-arid grasslands. Fig. 3(b) indicates that excessive soil water could restrain ecosystem carbon uptake although the decrease of F_{NEE} under high soil moisture is not distinct. F_{NEE} is the

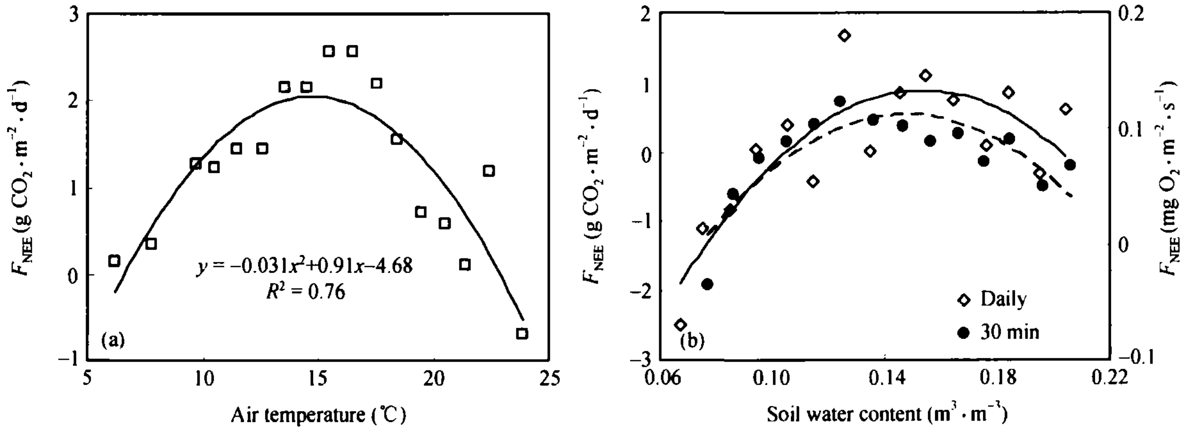

Fig. 3. (a) The response of daily net ecosystem CO_2 exchange (F_{NEE}) to mean daily air temperature; the data were averaged with a bin width of 1℃ air temperature. (b) The response of F_{NEE} to soil moisture at 5 cm depth; the data were averaged with a bin width of 0.01 $m^3 \cdot m^{-3}$ soil moisture. The hollow points are total daily F_{NEE}, the solid points represent measurements taken at half-hour intervals.

balance between photosynthesis uptake and respiration release, where F_{NEE} is determined by environmental factors that directly affect photosynthesis and respiration. Clearly, it is necessary to examine the effects of environmental factors on ecosystem photosynthesis and respiration separately, in order to better understand the underlying mechanisms of temperature and moisture on F_{NEE} in the *Leymus chinensis* steppe.

2.3 The effects of temperature and moisture on ecosystem respiration

The responses of ecosystem respiration (R_{eco}) to soil temperature and soil moisture during the two growing seasons are compared in Fig. 4. Although there is a difference in the response curves between the two years, R_{eco} shows an exponentially increasing trend with temperature in both growing seasons. The R_{eco} in 2003 has a faster increase rate and a better correlation with temperature than the case in 2004 (Fig. 4(a)). Soil moisture has significant influence on R_{eco} in 2004 ($R^2 = 0.37$) but R_{eco} is poorly correlated with soil moisture in 2003 ($R^2 < 0.1$). The results indicate that R_{eco} was primarily controlled by soil temperature during the growing season of 2003, whereas in 2004 the effect of temperature on R_{eco} was weakened by the enhanced effects of moisture on R_{eco}, resulting in part from a higher variability in soil moisture.

The relationships between R_{eco} and its primary controlling factors, soil temperature (T_s) and soil moisture, were further investigated based on the data collected in darkness during high turbulence ($u_* > 0.15$ m·s^{-1}) to examine the effect of soil moisture on the temperature sensitivity of R_{eco}. The valid data is separated into two groups, one with proper soil moisture ($S_w \geqslant 0.10$ m^3 m^{-3}) and the other under moisture stress ($S_w < 0.10$ m^3 m^{-3}). For each group, the data were averaged with a bin width of 1℃ soil temperature to reduce the sampling error of measured data. Then the Van't Hoff function (Eq. (2)) was used to describe the temperature sensitivity of R_{eco} under different moisture conditions.

As seen in Fig. 5, ecosystem respiration (R_{eco}) showed increasing trends with temperature under both soil moisture conditions, but differed in absolute value and rate of increase. R_{eco} was significantly restrained by moisture stress, and the temperature sensitivity parameter (Q_{10}) decreased from 2.0 under proper moisture conditions to 1.6 when the soil was under water stress. It could be inferred from the results of Fig. 4(b) and Fig. 5 that the direct effects of soil moisture on R_{eco} was relatively weak, but soil moisture could influence R_{eco} profoundly by regulating the temperature sensitivity of R_{eco}.

In order to understand the effects of spatial and environmental gradients on ecosystem F_{NEE} from eddy covariance data, it is essential to acquire estimates of its main components, R_{eco} and F_{GEP}. This task can easily introduce significant errors if the effect of confounding factors is ignored. Therefore, it is necessary to consider the effects of low soil water content on ecosystem respiration when using a temperature- R_{eco} relationship to estimate R_{eco}. In arid ecosystems, using a temperature – R_{eco} relationship based on a long-term data set can introduce a significant bias into R_{eco} and

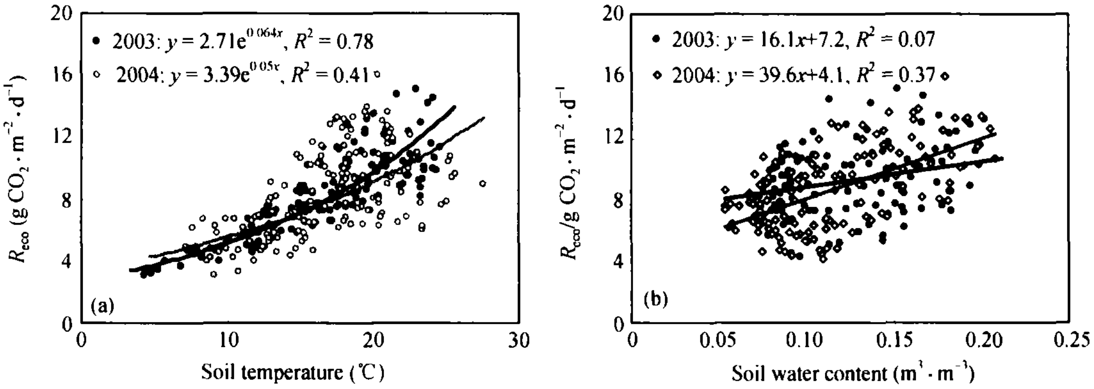

Fig. 4. The relationships between ecosystem respiration (R_{eco}) and (a) soil temperature and (b) soil moisture at 5cm depth during the 2003 and 2004 growing seasons. The curves were fitted with the data in the figures.

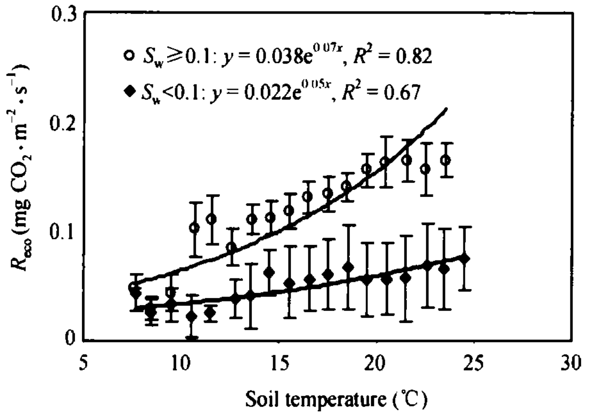

Fig. 5. Temperature response for nighttime ecosystem respiration (R_{eco}) under non-limiting soil moisture (circles, n=588) and soil moisture stressed (solid points, n=327) conditions. The R_{eco} data were classified with a bin width of 1℃ soil temperature from 7 to 22℃. Values represent the mean ±SE (0.05 confidence). The temperature sensitivity of ecosystem respiration was described with the Van't Hoff function (Eq. (2)).

F_{GEP} estimates due to the distinct seasonal variation in soil moisture. It is recommended that a short-term temperature sensitivity of ecosystem respiration be used, which largely avoids the bias introduced by confounding factors in seasonal data.

2.4 The effects of temperature and moisture on gross ecosystem production

Gross ecosystem production (F_{GEP}) was estimated with the method described in section 1.3. The relationship between daily F_{GEP} and air temperature and soil moisture during the two growing seasons were compared and are plotted in Fig. 6, after abnormal data from extremely cloudy and rainy days were screened out. Clearly, the effects of temperature and soil moisture on F_{GEP} were different in the two years. In 2003, temperature had an important effect on F_{GEP}, whereas F_{GEP} was weakly correlated with soil moisture ($R^2 = 0.1$, Fig. 6(a)).

As compared to 2003, soil moisture had a significant effect on F_{GEP} in 2004, with decreased effects of temperature on F_{GEP}. Therefore, it can be inferred that F_{GEP} is mostly controlled by the change of temperature during the growing season of 2003, whereas in 2004 soil moisture had more effect than air temperature did on F_{GEP}. In Fig. 6(b), F_{GEP} decreased markedly under soil water stress (S_w<0.1 $m^3 \cdot m^{-3}$), and the data were much scattered under ample soil moisture conditions (S_w>0.1 $m^3 \cdot m^{-3}$), which indicated that F_{GEP} was significantly restrained by water stress when the soil dried out, but also that other factors significantly influenced F_{GEP} when soil moisture was not limiting.

For determining the effects of a single factor (temperature or moisture) on F_{GEP}, we limited data, measured at half-hour intervals, to periods when light intensity (Q_{PPFD}) ranged between 1100 and 1400 μmol m^{-2} s^{-1}, to minimize the confounding effects of other factors. The selected light intensity is sufficient for plant photosynthesis and also avoids the depression of F_{NEE} under high radiation[30]. Fig. 7(a) shows the response of F_{GEP} to air temperature when soil moisture is non-limiting (S_w > 0.1 $m^3 \cdot m^{-3}$).

The optimal temperature range for the *Leymus chinensis* steppe to sequestrate carbon by photosynthesis is around 18—21℃, and F_{GEP} decreased from

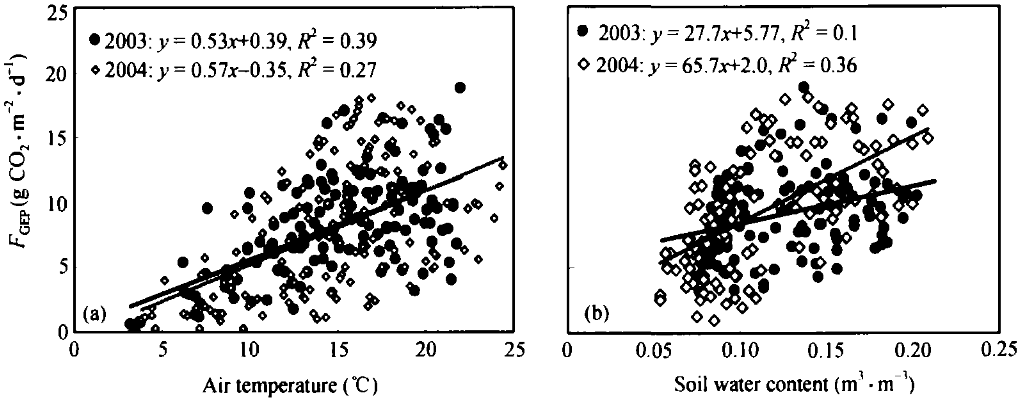

Fig. 6. The relationship between daily gross ecosystem production (F_{GEP}) and (a) air temperature and (b) soil moisture (5 cm depth) in the *Leymus chinensis* steppe during the growing seasons of 2003 and 2004.

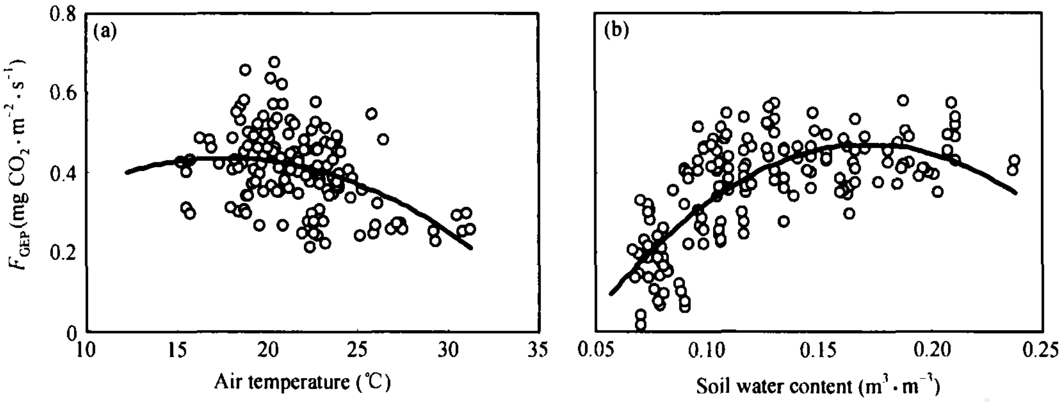

Fig. 7. The response of half-hour gross ecosystem production (F_{GEP}) to (a) air temperature and (b) soil moisture in a semi-arid steppe during July and August, 2004. The data were limited to 1100< Q_{PPFD} <1400 μmol m^{-2} s^{-1}. In (a), the data were also selected with S_w > 0.1 m^3 m^{-3} to reduce the confounding effect of water stress.

0.7 to near 0 mg CO_2 m^{-2} s^{-1} as air temperature increased from 20 to 30℃. F_{GEP} was significantly restrained by severe water stress in the steppe and showed a sharp decline when the soil dried out (S_w<0.1 m^3 m^{-3}), whereas Fig. 7(b) shows that F_{GEP} maintained a relative constant (around 0.4—0.5 mg $CO_2 m^{-2} \cdot s^{-1}$) in non-limiting soil (higher than 0.1 m^3 m^{-3}). These results suggest that the steppe has high gross productivity over a limited range of temperature and soil moisture, above and below which F_{GEP} decreased significantly.

In the field, heat stress often accompanies drought stress because the efficiency of leaf cooling by evapotranspiration decreases under moisture stress, which highlights the importance of soil water availability for stress relief in arid and semi-arid ecosystems[11]. Moisture deficits and high temperature stress can impact the physiological processes of plants in several ways. Soil moisture deficits can result in reductions of cell expansion, leaf area development, photosynthesis, stomatal conductance and transpiration, and high leaf-temperature can inhibit plant growth by inactivating photosystem II and promoting leaf respiration[12,13]. Net ecosystem production is determined by the coupling effects of temperature and moisture, and proper moisture stress can promote ecosystem carbon uptake; however, little precipitation at high temperatures under strong radiation during the summer often causes soil moisture deficit, and thus reduces the gross ecosystem production of the semi-arid *Leymus chinensis* steppe.

2.5 *Seasonal and interannual variation in ecosystem carbon budget*

The half-hour measurements of F_{NEE} and calculations of F_{GEP} and R_{eco} were integrated to provide daily values of ecosystem carbon budget and to investigate how F_{NEE} and its major components (F_{GEP} and R_{eco}) vary seasonally and interannually in response to variation in environmental conditions. In 2003, the grass germinated in early May and the steppe became a net sink of carbon during mid-May due to ample pre-rainfall (Fig. 2(a)), but net ecosystem CO_2 was still small due to active ecosystem respiration during the warm, wet spring. The first peak of F_{GEP} appeared in mid-June, followed by a decrease in both F_{NEE} and F_{GEP} due to moisture stress in late June. Brief relief from moisture stress occurred when topsoil was rewetted by rainfall events and uptake recovered temporarily in mid-July. F_{GEP} and F_{NEE} were significantly reduced by severe heat and moisture stress from mid-July through August, which caused the steppe to enter its senescence in early August 2003.

With 38% precipitation more than 2003, abundant rain in 2004 did not begin on the steppe until late June and mostly occurred in August (Fig. 2(b)), and there was very little precipitation during the normal period of plant germination and budding (May through late June). As compared to 2003, both F_{GEP} and R_{eco} during this period in 2004 were significantly depressed by drought stress, which also delayed the recovery of the steppe until late June, after some precipitation (Fig. 8(b)). The steppe became a sink of

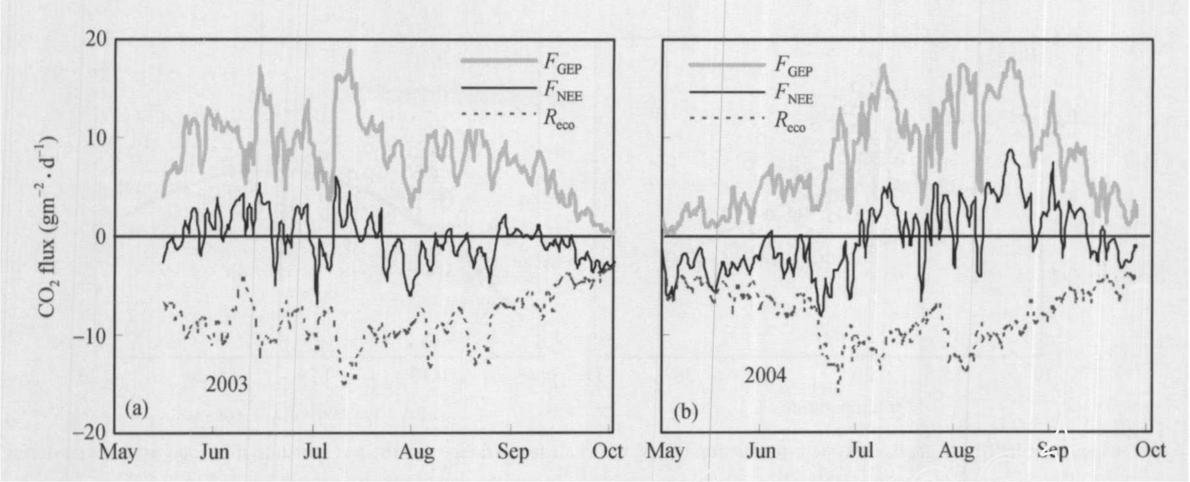

Fig. 8. Seasonal variation in daily net ecosystem CO_2 exchange (F_{NEE}) and its major components, gross ecosystem production (F_{GEP}) and ecosystem respiration (R_{eco}) of a semi-arid *Leymus chinensis* steppe during the growth seasons of year (a) 2003 and (b) 2004.

CO_2 until early July 2004, more than one month later than 2003.

It is worth noting that the abundant precipitation in August 2004 resulted in the two-year peak rate of F_{NEE}, which is the balance between the increased F_{GEP} with ample soil moisture and decreased R_{eco} at relatively low temperatures. In addition, the steppe remained a CO_2 sink before the senescence phase began in mid-September. Fig. 8 also shows that F_{GEP} has strong effect on R_{eco}, with a high agreement between the seasonal variation of F_{GEP} and R_{eco} since photosynthesis provides the substrate for ecosystem respiration. In 2004, R_{eco} was a significant contributor to the total ecosystem CO_2 budget of the steppe, accounting for about 60%−90% of daytime photosynthetic uptake. In summary, the semi-arid steppe released a total of 9.7 g C$\cdot$m^{-2} from May 16 to the end of September 2003, whereas the net carbon budget during the same period in 2004 was close to zero.

3 Discussion

Water stress, which has the largest interannual and seasonal variation among all environmental variables, is the most common limitation to growth of vegetation[1]. Annual site-water balance explains much of the interannual variation in the F_{GEP} of grasslands[5−7]. This study site often suffers heat and drought stress during the growing season due to low precipitation, which limits the steppe's carbon uptake. Net ecosystem CO_2 exchange (F_{NEE}) is determined by the processes of photosynthetic uptake and respiration release, which are directly affected by temperature and water balance. The results of this study show that temperature has important influence on ecosystem photosynthesis and respiration of the steppe, whereas the response of F_{GEP} and R_{eco} to temperature can be changed by variations in soil moisture (Figs. 4 and 6).

Correlation between F_{GEP} / R_{eco} and temperature of the steppe was reduced in 2004, when there was higher moisture variability compared to 2003. Further analysis shows that F_{GEP} decreased sharply when air temperature and soil moisture was above or below a limited range (Fig. 7), and reduction in R_{eco} and its temperature sensitivity (Q_{10}) during soil moisture stress was apparent (Fig. 5). It can be inferred by synthesizing the above results that the reduction in F_{NEE} during periods of severe moisture stress is mainly ascribed to the decrease of F_{GEP}, whereas the increased respiration with temperature is responsible for the decrease of F_{NEE} when soil moisture is non-limiting, since there is only a slight reduction in F_{GEP}.

It is has long been recognized that soil temperature is just one of a host of variables that influence ecosystem respiration; factors such as soil moisture, soil organic matter and microbes are also known to influence soil respiration[31,32]. Soil moisture deficit can restrain ecosystem autotrophic and heterotrophic respiration by limiting plant and microbial activity at low soil water content, particularly in arid or semi-arid ecosystems. Temperature-driven increases in respiration can also be impeded by low soil moisture[33,34].

In addition, gross ecosystem production is also a primary determinant of the rate of ecosystem respiration. In a Canadian temperate grassland, ecosystem respiration was mainly determined by above-ground productivity and soil moisture when temperatures changed very little[35]. This study of the semi-arid *Leymus chinensis* steppe demonstrates that water availablility is the second determining factor for net ecosystem CO_2 exchange.

Global carbon-budget studies from the 1980s and 1990s have shown that changes in climate and atmospheric CO_2 have enhanced primary production in global terrestrial ecosystems (F_{NEE})[36]. By contrast, F_{NEE} in China decreased during the 1980s and 1990s because of stronger warming than the global average in the arid north, which caused greater increases in R_{eco} than in F_{GEP}[37].

The recorded data shows that precipitation in northern China has declined since the 1960s; although it recovered in the late 1990s, it remained lower than the wet 1950s, with more extreme rainfall events that were punctuated by longer dry periods[9,38]. Continued increase in precipitation may reverse the F_{NEE} of the last two decades. However, if current warming trends are sustained, and if precipitation does not substantially increase, terrestrial ecosystem production in arid northern China may continue to decrease and have an important effect on net terrestrial ecosystem carbon budget of China.

4 Conclusions

Net ecosystem CO_2 exchange was measured in a semi-arid *Leymus chinensis* steppe, using an eddy covariance technique, during two consecutive growing seasons. In 2003, gross ecosystem production (F_{GEP}) and ecosystem respiration (R_{eco}) were strongly correlated with temperature rather than moisture, whereas in 2004 the effect of temperature on R_{eco} was weakened by effects of moisture on R_{eco}, with higher variability in soil moisture, and F_{GEP} was reduced by both heat and drought stress during the growing season. Overall, R_{eco} showed an exponentially increasing trend with temperature, but the reduction in the rate of R_{eco} and its temperature sensitivity were apparent under dry conditions. The combined effects of temperature and soil moisture on F_{GEP} and R_{eco} resulted in the depression of F_{NEE} when temperature or moisture was above or below a limited range. F_{GEP}, R_{eco} and F_{NEE} all decreased significantly during severe moisture stress.

The seasonality of ecosystem carbon exchange strongly correlated with variations in precipitation. With less rainfall in 2003, most of which happened either early or late in the growing season, due to moisture stress the steppe sequestrated carbon in June and July and went into senescence phase in August. The severe drought stress during spring in 2004 delayed the growth of the steppe, which became a sink of CO_2 in early July which was sustained until mid-September, with ample precipitation in August. In 2003, the semi-arid steppe released a total of 9.7 g $C \cdot m^{-2}$ from May 16 to the end of September; during the same period of 2004, the net carbon budget was close to zero.

Northern China's vast temperate grassland includes a wide diversity of vegetation due to distinct differences in precipitation. Most of this grassland has a long history of grazing, which could impose complex effects on vegetation structure and ecosystem productivity. The field site for this study has not been grazed in more than 20 years; therefore, its spatial representative is very limited. In order to estimate the terrestrial ecosystem carbon budget in northern China, forecast its response to future climate change and evaluate its role in global carbon balance, it is important to understand the responses of temperate grassland to environmental changes. To answer these questions, much more long-term measurement of various grassland vegetations is needed.

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