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Depression of net ecosystem CO_2 exchange in semi-arid *Leymus chinensis* steppe and alpine shrub

Yu-Ling Fu [a,c], Gui-Rui Yu [a,*], Xiao-Min Sun [a], Ying-Nian Li [b], Xue-Fa Wen [a], Lei-Ming Zhang [a,c], Zheng-Quan Li [a,c], Liang Zhao [b], Yan-Bin Hao [d]

[a] *Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, 11A Dtun Road, Anwai, Beijing 100101, China*
[b] *Northwest Plateau Institute of Biology, Chinese Academy of Sciences, 59 Xiguan Street, Xining 810001, China*
[c] *The Graduate School of Chinese Academy of Sciences, Beijing 100039, China*
[d] *Institute of Botany, Chinese Academy of Sciences, 20 Nanxincun Xiangshan, Beijing 100093, China*

Abstract

Uptake and release of carbon in grassland ecosystems is very critical to the global carbon balance and carbon storage. In this study, the dynamics of net ecosystem CO_2 exchange (F_{NEE}) of two grassland ecosystems were observed continuously using the eddy covariance technique during the growing season of 2003. One is the alpine shrub on the Tibet Plateau, and the other is the semi-arid *Leymus chinensis* steppe in Inner Mongolia of China. It was found that the F_{NEE} of both ecosystems was significantly depressed under high solar radiation. Comprehensive analysis indicates that the depression of F_{NEE} in the *L. chinensis* steppe was the results of decreased plant photosynthesis and increased ecosystem respiration (R_{eco}) under high temperature. Soil water stress in addition to the high atmospheric demand under the strong radiation was the primary factor limiting the stomatal conductance. In contrast, the depression of F_{NEE} in the alpine shrub was closely related to the effects of temperature on both photosynthesis and ecosystem respiration, coupled with the reduction of plant photosynthesis due to partial stomatal closure under high temperature at mid-day. The R_{eco} of the alpine shrub was sensitive to soil temperature during high turbulence ($u^* > 0.2$ m s^{-1}) but its F_{NEE} decreased markedly when the temperature was higher than the optimal value of about 12 °C. Such low optimal temperature contrasted the optimal value (about 20 °C) for the steppe, and was likely due to the acclimation of most alpine plants to the long-term low temperature on the Tibet Plateau. We inferred that water stress was the primary factor causing depression of the F_{NEE} in the semi-arid steppe ecosystem, while relative high temperature under strong solar radiation was the main reason for the decrease of F_{NEE} in the alpine shrub. This study implies that different grassland ecosystems may respond differently to climate change in the future.
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Keywords: Net ecosystem CO_2 exchange (F_{NEE}); Depression; *Leymus chinensis* steppe; Alpine shrub; High radiation; Water stress

1. Introduction

The response of terrestrial vegetation to the natural environments is a critical issue for global change which has been addressed in numerous studies (Law et al., 2002). Grasslands comprise 32% of the earth's natural vegetation (Adams et al., 1990) and are one of the most widespread vegetation types. The temperate semi-arid steppe and alpine grassland are two major natural ecosystems in Northern China. The alpine grassland ecosystems on the Qinghai-Tibet Plateau may have played a significant role in balancing the global carbon budget because of the high carbon storage in these

ecosystems, especially in the soil, over a large area of about 128 million ha (Xie et al., 2003; Wang and Zhou, 1999). The *Leymus chinensis* steppe is an important component of the temperate grassland in Eurasia, with half of its total area (about 84 million ha) located in China (Li et al., 1998). These temperate grasslands may contribute significantly to global carbon balance as large sinks or sources. Studies have shown that alpine grassland may have great potential in releasing carbon under global warming because of the sensitivity of frigid soil to increase of temperature (Wang et al., 2002), and the temperate steppe may be very sensitive and show large asymmetric response to variation of precipitation (Wever et al., 2002). The large vegetation diversity and climatic variability present in grasslands ecosystems offer special opportunities for the study of ecosystem physiology in respect to environmental change (Wever et al., 2002; Frank and Dugas, 2001).

Environmental stresses resulting from climate change can substantially reduce plant production in temperate grasslands (Parton et al., 1994). Solar radiation on both the Tibet Plateau and Inner Mongolia Plateau is very strong, and exposure of plants to excessive light energy generally induces photosynthetic depression (Cui et al., 2003; Long et al., 1994). The steppe in Inner Mongolia of China often suffers from drought causing this ecosystem to experience water stress frequently. In the field, heat stress often accompanies drought stress; this increases the importance of soil water availability for stress relief (Salvucci and Steven, 2004).

However, inconsistent effects of these environmental stresses on photosynthetic depression have been reported in previous studies (Lu and Zhang, 1999; Manuel et al., 1999) and little is understood on the controlling mechanisms of the patterns and processes of grassland ecosystems at high elevation. Previous leaf-level photosynthesis studies have shown that alpine species seemed to acclimate well to strong irradiation and low temperature (Manuel et al., 1999; Germino and Smith, 2000). However, much less attention has been given to net ecosystem CO_2 exchange (F_{NEE}) in grasslands and their sensitivities to climate conditions (Suyker et al., 2003). Moreover, few studies have been conducted to examine depression of F_{NEE} at ecosystem level for environmentally stressed grassland ecosystems. Therefore, the objectives of this study were to examine the depression of F_{NEE} under high solar radiation based on two contrasting ecosystems, the semi-arid *L. chinensis* steppe in Inner Mongolia and the alpine frigid shrub on the Tibet Plateau of China. The mechanism of mid-day depression of F_{NEE} under high radiation is discussed by comparing the distinctive response of F_{NEE} of the two ecosystems to various environmental stresses.

2. Materials and methods

2.1. Site description

Observations were performed at two grassland ecosystems belonging to the Chinese Terrestrial Ecosystem Flux Observational Network (ChinaFLUX) (for details see Yu et al., 2006). One is semi-arid *L. chinensis* steppe, located in the Xilin River Basin, close to the Inner Mongolia Grassland Ecosystem Research Station of the Chinese Ecosystem Research Network (CERN). The other is the alpine frigid *Potentilla fruticosa* shrub, located in the north of the Qinghai-Tibet Plateau, near to the Haibei Research Station of CERN. The alpine shrub is significantly distinct from the semi-arid steppe in its unique climate and high elevation, where the frigid soil is rich in organic matter due to the slow decomposition of litter under low-temperature conditions. Table 1 presents some basic climatic and environmental conditions of the two sites.

Table 1
Conditions of the observation sites

Ecosystem type	Semi-arid steppe	Alpine frigid shrub
Location	43°53′N, 117°27′E	37°29′N, 101°20′E
Elevation (m)	1189	3300
Mean air temperature (°C)	−0.4 (−18.8 to 22.3)	−1.7 (−14.8 to 9.8)
Precipitation (mm)	350.9 (180–500)	600 (426–800)
Vegetations	Warm season grasses, such as Chinese Leymus (*Leymus Chinensis*), Siberian Speargrass (*Achnatherum sibiricum*), Giant Feathergrass (*Stipa gigantea*) and Rhizome Wheatgrass (*Agropyron michnoi*)	Bush cinquefoil (*Potentilla fruticisa* L.), Drawf kobresia (*Kobresia humilis*), Annual bluegrass (*Poa Annua*), and Red Fescuegrass (*Festuca rubra*)
Soils	Chesnut soil (3% organic matter)	Alpine meadow soil (7% organic matter)
Observation period	From April 23, 2003	From October 16, 2002

The steppe has not been grazed for 20 years and there is a substantial amount of dead plant material (litter) on the ground surface. Since the alpine shrub was grazed by yaks and sheep only during wintertime, the vegetation height and LAI were same within and outside the fence (40 m × 40 m), which was built to prevent the herd from disturbing the measurement system. The terrain at the two site terrains is flat with sufficient fetch to meet the basic assumption (horizontally homogeneous surface for sufficiently long upwind area) for proper application of the eddy covariance technique.

2.2. Experimental measurements

The fluxes of CO_2, sensible heat, latent heat and momentum were measured at a height of 2.2 m from the ground with an open-path eddy covariance system at both sites, and recorded by a CR5000 datalogger (Model CR5000, Campbell Scientific, Logan, UT, USA). The canopy height was 0.6 m and 0.45 m for the alpine shrub and the steppe, respectively. The eddy covariance sensor array included a three-dimensional sonic anemometer (Model CSAT3, Campbell Scientific) and a CO_2/H_2O analyzer (Model LI-7500, Li-cor Inc., NE, USA).

Additional meteorological conditions, such as solar radiation, net radiation (R_n) and photosynthetic photon flux density (Q_{PPFD}), were observed at 1.2 m height above the ground using a four-component net radiometer (Model CNR-1, Kipp & Zonen, Netherlands) and a quantum sensor (LI190SB, Li-cor Inc.). Air temperature (T_a) and relative humidity (RH) were measured at two heights (1.1 and 2.2 m; Model HMP45C, Vaisala Inc., Helsinki, Finland), and horizontal wind speeds were measured at the same heights (Model A100R, Vector Instrument, North Wales, UK). The canopy infrared temperature was measured with a infrared thermocouple sensor (IRTS-P, Apogee Instruments Inc., Logan, UT) at 1.5 m height. Soil temperatures were recorded at five depths (0.01, 0.05, 0.2, 0.4 and 0.8 m) with thermometers (107-L, Campbell Scientific), and soil water contents were monitored at 0.2 and 0.4 m depths with TDR probes (Model CS615-L, Campbell Scientific). The above fluxes and meteorological data were calculated over half-hour intervals, except precipitation, which was measured hourly with a rain gauge (Model 52203, RM Young Inc., Traverse City, MI, USA). All meteorological data were recorded using a CR23X datalogger (Model CR23XTD, Campbell Scientific) with a 25-channel solid-state multiplexer (Model AM25T, Campbell Scientific).

Replicate samples ($n = 9$ for the shrub, $n = 20$ for the steppe) for aboveground biomass were collected during May–October in 2003 (intervals: 2 weeks for the shrub and 1 month for the steppe) by clipping vegetation of 0.5-m^2 quadrates within a radius of 250 m around the observation tower. Leaf area was not measured in 2003 at both sites, but investigated once at the alpine shrub (August 13) and four times at the steppe during the growing season in 2004. The leaf area index (LAI) was derived from the ratio of leaf area and aboveground biomass, expressed as total leaf area per ground area ($m^2\ m^{-2}$).

2.3. Data processing

The analyses for both sites were based on the half-hour mean values of CO_2 and water vapor fluxes collected from June to August and the relevant environmental factors from May to September of 2003. The flux data were corrected for the variation of air density caused by the fluxes of heat and water vapor (Webb et al., 1980). The data were screened to remove anomalous values caused by malfunction of sensors due to interference from dew, hoarfrost or birds. The data collected on rainy and extremely cloudy days were also excluded from the analysis. Some breaks in data collection occurred due to system maintenance and power outages. Missing or rejected data of all possible 30 min time period during the study occurred for a total of 3% and 14% for the steppe and alpine shrub, respectively.

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 respiration (R_{eco}) (Law et al., 2002). Positive values of F_{NEE} indicate net carbon sequestration by the ecosystem. The daytime F_{NEE} were assumed to be valid for the analysis when Q_{PPFD} was larger than 1 μmol $m^{-2}\ s^{-1}$. However, nighttime F_{NEE} ($Q_{PPFD} < 1$ μmol $m^{-2}\ s^{-1}$) with friction velocity $u^* < 0.2$ m s^{-1} were screened from the analysis, and negative nighttime F_{NEE} were also excluded. The response of ecosystem respiration (R_{eco}) to change in temperature was fitted with nighttime fluxes at high friction velocity ($u^* > 0.2$ m s^{-1} in this study) and soil temperature using Eq. (1) (Lloyd and Taylor, 1994):

$$R_{eco} = R_{eco,T_{ref}}\ e^{E_0[1/(T_{ref}-T_0)-1/(T_s-T_0)]} \tag{1}$$

where the parameter E_0 and the reference temperature T_{ref} were set to 309 and 283.16 K, respectively (Law et al., 2002), whereas the parameters T_0 and $R_{eco,T_{ref}}$, ecosystem respiration rate at T_{ref}, were fitted to the

respective data subset of the two ecosystems. T_s is soil temperature (K) at a depth of 5 cm.

The Michaelis–Menten equation (Michaelis and Menten, 1913) was used to describe the ecosystem light response:

$$F_{NEE} = \frac{\alpha Q_{PPFD} P_{max}}{\alpha Q_{PPFD} + P_{max}} - R_{eco} \qquad (2)$$

where Q_{PPFD} is the photosynthetic photon flux density (μmol m^{-2} s^{-1}), α the ecosystem quantum yield (μmol CO$_2$ μmol quantum^{-1}), and P_{max} is the gross primary productivity at "saturating" light (μmol CO$_2$ m^{-2} s^{-1}). $R_{eco,day}$ is the ecosystem respiration during the daytime and F_{NEE} is the net ecosystem CO$_2$ exchange (both in μmol CO$_2$ m^{-2} s^{-1}).

The stomatal conductance or canopy conductance was generally used to assess stomatal control on photosynthesis and evapotranspiration. With no independent measurements of transpiration or soil evaporation available in this study, a clean separation of the two sources is not possible with the eddy covariance measurements. Therefore, the surface conductance (g_s) rather than the canopy conductance (g_c) was calculated based on an inverted Penman–Monteith equation (Yu, 2001):

$$\frac{1}{g_s} = \left(\frac{\Delta}{\gamma} \frac{H}{\lambda E} - 1 \right) r_a + \frac{\rho C_p}{\gamma} \frac{D_{ref}}{\lambda E} \qquad (3)$$

where H and λE are sensible heat and latent heat fluxes, respectively, measured by the eddy covariance technique. D_{ref} is the vapor pressure deficit at reference height and ρ is the air density. C_p, Δ and γ are thermodynamic constants. r_a is the aerodynamic resistance derived from the following equation (Yu, 2001):

$$r_a = \frac{1}{ku^*} \ln \left(\frac{Z_r - d}{Z_0} \right) \qquad (4)$$

where u^* is the friction velocity, Z_r the reference height and k is the Von Karman's constant (0.41). For most grassland and crop ecosystems, Z_0 and d are defined approximately as: $d = 0.63h$, $Z_0 = 0.13h$, where h is the height of a canopy (0.45 and 0.5 m for the steppe and alpine shrub, respectively).

3. Results

3.1. Dynamics of environmental variables

Fig. 1 shows the daily mean values of various climatic variables during the observation period from May to September. The average daily air temperature observed at the steppe was much higher than that at the shrub despite the average annual temperatures at the two sites being comparable (Table 1). The maximum air temperature at the steppe ($\sim$30 °C) was $\sim$10 °C higher than that at the alpine shrub. Both air temperature and soil temperature experienced their highest from late July through early August at the two sites, although there was a cold snap in early June at the steppe. The vapor pressure deficit was much higher at the steppe than the shrub due to the higher air temperatures and lower absolute humidity at the steppe. There was a serious drought in the steppe after middle June with little precipitation, which resulted in a continuous decrease of moisture in the deep soil layer from early June until September (Fig. 1e). Comparatively, it was a humid year for the alpine shrub with abundant precipitation throughout the whole growing season (total 469.6 mm from May to September), which led to sufficient soil moisture and hence no evident water stress for the alpine shrub. The average daily total radiation at the alpine shrub was lower than that at steppe because of more cloudy conditions during daytime on the plateau. The Q_{PPFD} at the steppe site was generally <2000 μmol m^{-2} s^{-1} with more clear days during the growing season. However, the Q_{PPFD} at the alpine shrub site on Tibet Plateau was very high, frequently exceeding 2000 μmol m^{-2} s^{-1} at noon.

3.2. Dynamics of biomass and leaf area index (LAI)

Both ecosystems achieved their maximum aboveground biomass during mid-August in 2003, followed by a steady decline as the community senesced (Fig. 2). The measured maximum aboveground biomass was 278 and 218 g m^{-2} for the alpine shrub and the semi-arid steppe, respectively. The biomass at the shrub decreased sharply in late August and accumulated again in early September, probably due to the cold snap and heavy precipitation during late August and the warming up later. Although the LAI was not measured in 2003, the seasonal dynamics of biomass could partly indicate the variation of LAI in 2003. The measured LAI at the alpine shrub on August 13, 2004 was 2.78 ± 0.69 m^2 m^{-2} (mean $\pm$ standard deviation), which was averaged on 48 quadrats when maximum aboveground biomass occurred. The LAI of the semi-arid steppe changed rapidly during the growing season in 2004 and the measured maximum LAI was 1.54 (August 16, 2004).

3.3. Response of F_{NEE} to light intensity

According to Yu et al. (2002), F_{NEE} can be depressed if leaves are frequently exposed to high radiation for
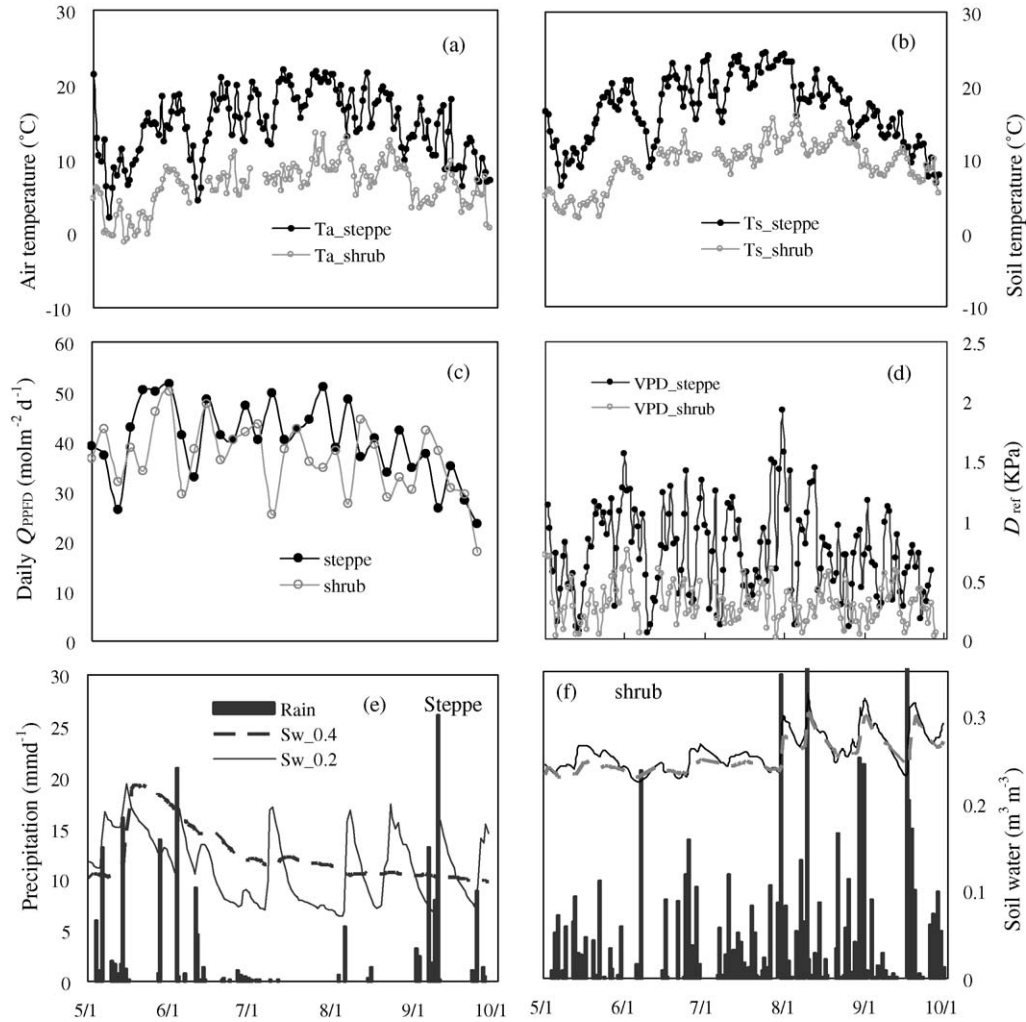
Fig. 1. Daily averages of (a) air temperature (T_a) at 2.2 m height, (b) soil temperature (T_s: 5 cm depth), (c) daily total photosynthetic photon flux density (Q_{PPFD}) runs on 5-day average, and (d) vapor pressure deficit (D_{ref}) in steppe and shrub ecosystems from May to September 2003. The daily precipitation (mm) and soil water content (S_w, $m^3 m^{-3}$) at two depths (0.2 and 0.4 m) are also shown for the steppe ecosystem (e) and the shrub ecosystem (f).
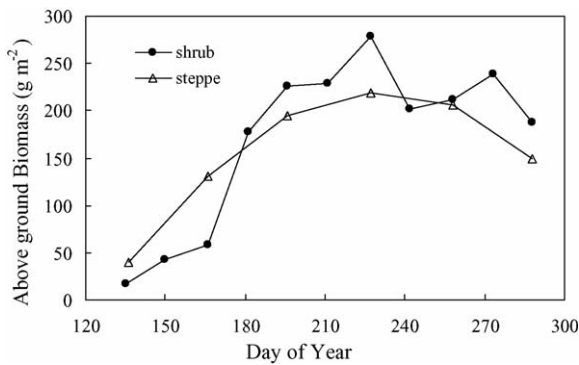

Fig. 2. The seasonal dynamics of aboveground biomass (g dry biomass m^{-2}) for the alpine shrub and semi-arid steppe in 2003.

long periods. The solar radiation at two sites was very strong, with $Q_{PPFD} > 1000$ µmol $m^{-2} s^{-1}$ lasting for about 6 h and mostly exceeding 2000 µmol $m^{-2} s^{-1}$ at noon on clear days. Such strong radiation exceeded the light saturation point for most plants there, which was about 850 µmol $m^{-2} s^{-1}$ measured with a portable photosynthesis system (Model LI-6400, Li-cor Inc.). Fig. 3 illustrates the typical light responses of F_{NEE} in the steppe and alpine shrub in July and August 2003. It can be seen that F_{NEE} in the steppe increased with light intensity and reached its maximum around 1200 µmol $m^{-2} s^{-1}$ of Q_{PPFD} (open circles). When the radiation further increased, the F_{NEE} dropped pronouncedly (closed circles). A similar trend was found for the
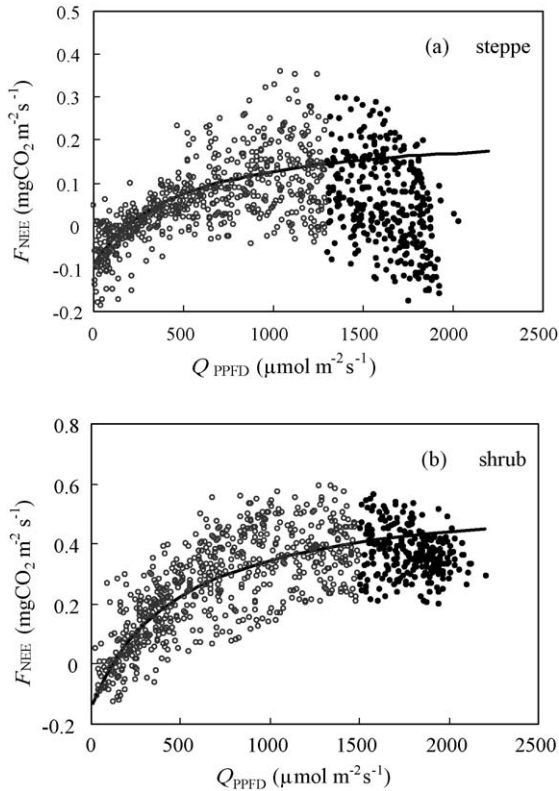
Fig. 3. Relationship between net ecosystem CO_2 exchange (F_{NEE}) and light intensity at (a) the semi-arid steppe and (b) the alpine shrub in July and August 2003. The observed F_{NEE} were separated into two sections with thresholds Q_{PPFD} of 1200 and 1500 μmol m^{-2} s^{-1} for the steppe and the shrub, respectively. The curves are fitted results using Eq. (2) based on the observed data with Q_{PPFD} smaller than the threshold values.

shrubs, except that the biggest F_{NEE} occurred at about 1500 μmol m^{-2} s^{-1} (Fig. 3b).

To understand the effect of high radiation on the depression of F_{NEE}, we separated the observed F_{NEE} into two sections, with and without photosynthetic depression, simply by using threshold values of Q_{PPFD} (1200 and 1500 μmol m^{-2} s^{-1} for the steppe and the shrub, respectively). Once the radiation exceeded the threshold, F_{NEE} began to decrease with increasing light intensity. The subset data of F_{NEE} with Q_{PPFD} lower than the thresholds (Fig. 3) was fitted with Eq. (2). The results showed that the magnitude of α and P_{max} for the semi-arid steppe (0.0154 and 7.3 μmol CO_2 m^{-2} s^{-1}, respectively) were much lower than those for the alpine shrub (0.034 and 16.6 μmol CO_2 m^{-2} s^{-1}, respectively), indicating larger capacity for carbon uptake in the alpine shrub than in the steppe.

It is worth noting the large scatter of the data points in Fig. 3, which apparently illustrates the dependence of F_{NEE}–Q_{PPFD} relationship on other environmental

factors, if measurement errors are not the sole reason for the scattering. As reported, for a given Q_{PPFD} ecosystem gross photosynthesis and respiration are certainly related to temperature, soil water availability and vapor pressure deficit. Interactions between various biotic and abiotic factors in influencing F_{NEE} may thus result in different light response of leaves at varying levels of light intensity (Law et al., 2002). Therefore, it is necessary to examine the response of F_{NEE} to other factors for understanding the underlying mechanism of depression of F_{NEE} under high radiation.

3.4. Relationship between F_{NEE} and temperature

The response of F_{NEE} to temperature is ascribed to its effects on ecosystem photosynthesis and respiration (Dewar et al., 1999). Temperatures on the Tibet Plateau are quite low even during the growing season, varying widely in a day with the highest air temperature mostly <20 °C. These low temperatures contrast with those at the steppe where air temperature usually varied from 10 to 30 °C. To examine the role of temperature on F_{NEE}, we grouped the measured F_{NEE} into three conditions of low, medium and high solar radiation when soil water was non-limiting. Plots of F_{NEE} against temperature for the steppe (Fig. 4a) and for the shrub (Fig. 4b) show a marked optimal temperature for F_{NEE} in both ecosystems. In abundant radiation, F_{NEE} reached its maximum around 20 °C at the steppe, while the maximal F_{NEE} appeared around 12 °C at the shrub. However, in low radiation F_{NEE} of both ecosystems was depressed with the optimal temperatures around 17 °C at the steppe and 9 °C at the shrub.

F_{NEE} is the balance of photosynthesis and respiration, which are two fluxes of approximately the same magnitude and opposite direction (Moncrieff et al., 1996); so F_{NEE} could also be regarded as the net flux of CO_2 from the atmosphere to the vegetation. Variation in the temperature optimum for F_{NEE} with Q_{PPFD} can be explained by changes in the relative amounts of CO_2 taken up by leaves photosynthesis and released from soil respiration. At any given temperature with the same soil respiration, relatively less CO_2 is taken up by photosynthesis at low light levels compared to that at high light, which causes less CO_2 transfer from the atmosphere to the vegetation. Whereas as temperature increases at a given light level, photosynthesis increases quicker than soil respiration in low-temperature environment, resulting in an increased F_{NEE} with temperature. As photosynthesis saturates gradually, soil respiration increases more rapidly than photosynthesis, thereby decreasing F_{NEE} with increasing temperature
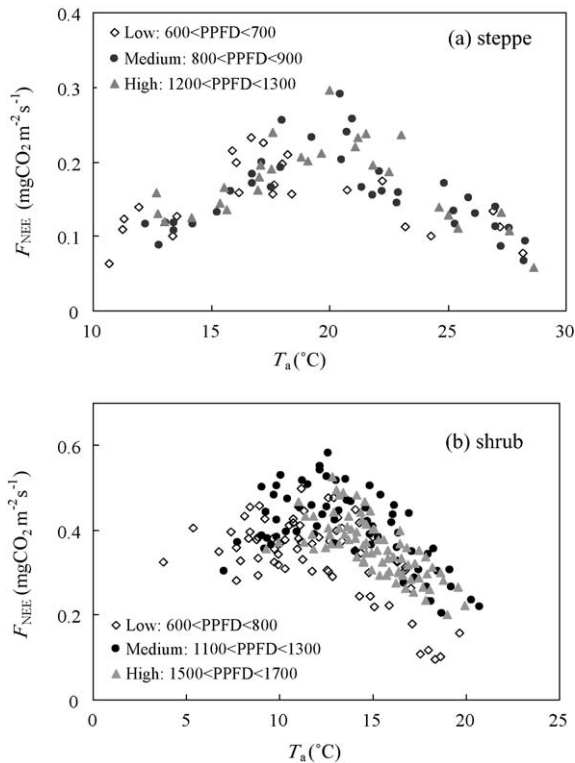
Fig. 4. The relationships between net ecosystem CO_2 exchange (F_{NEE}) and air temperature (T_a) under different light intensities in (a) the steppe and (b) the alpine shrub during the growing season of 2003 when soil water was non-limiting.

Fig. 5. Relationship between nighttime ecosystem respiration (R_{eco}) and soil temperature (T_s: 5 cm depth) at (a) the steppe and (b) the alpine shrub. The dataset includes measured F_{NEE} at nighttime from March to August for the shrub ($n = 644$) and from May to September for the steppe ($n = 692$) during high turbulence ($u^* > 0.2$ m s^{-1}). The non-linear regression curves were fitted with Eq. (1) based on the observed data.

as observed by the eddy covariance technique. Earlier studies have suggested that alpine plants would suffer photosynthetic depression under high temperature (Zhang et al., 1995; Guo et al., 1995). The above results imply that plants are likely to suffer photosynthetic depression if temperature and light intensity do not match appropriately.

The relationships between ecosystem respiration (R_{eco}) and soil temperature (T_s) were examined for the two ecosystems based on the data collected in darkness during high turbulence ($u^* > 0.2$ m s^{-1}). As shown in Fig. 5, the R_{eco} of both the steppe and the shrub followed an exponential relationship with soil temperature, consistent with previous studies (Lloyd and Taylor, 1994; Fang and Moncrieff, 2001). Comparison of the two ecosystems suggests that the alpine shrub was more sensitive to the change of temperature than the steppe probably because of the high sensitivity of frigid soil to increase of temperature (Wang et al., 2002). Ecosystem respiration by roots and soil microbial requires adequate moisture as well as temperature and the reduced soil moisture in the semi-arid steppe will also decrease the temperature sensitivity of R_{eco} (Qi et al., 2002). Besides,
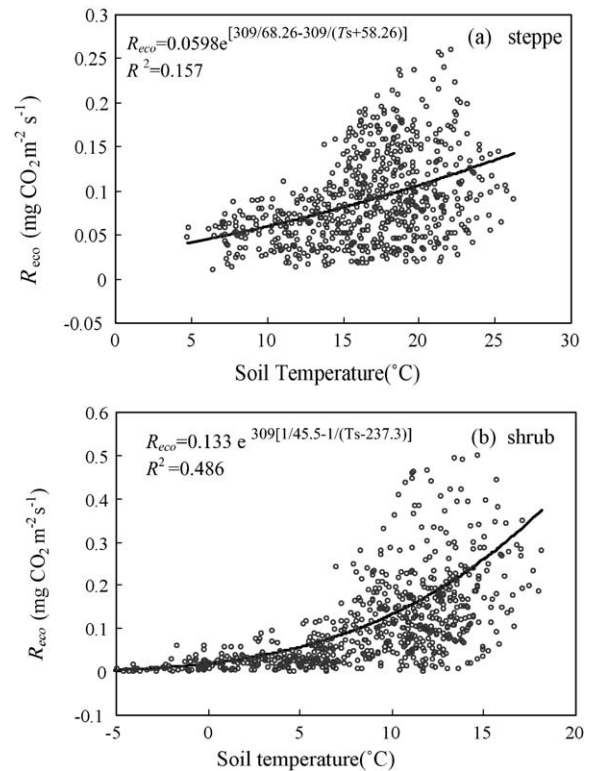
the profound differences in the capacity of photosynthesis between the two ecosystems also lead to the different response of R_{eco} to temperature since respiration is also effectively limited by the supply of carbohydrates fixed through photosynthesis. The rich organic matter in alpine meadow soil could potentially promote the release of carbon through enhanced soil respiration under elevated temperature.

3.5. Effect of water availability on F_{NEE}

The steppe in Inner Mongolia suffered a serious drought from mid-June to August in 2003 (Fig. 1e) and this allowed us to identify how soil water content affected F_{NEE}. In Fig. 6, the F_{NEE} measured in the steppe under dry conditions (with $S_w < 0.1$ m^3 m^{-3} and $D_{ref} > 2$ kPa) is compared with the results under relatively wet conditions (with $S_w > 0.1$ m^3 m^{-3} and $D_{ref} < 2$ kPa). Under wet conditions, daytime F_{NEE} increased with Q_{PPFD} to a maximum around 1200 μmol m^{-2} s^{-1} and
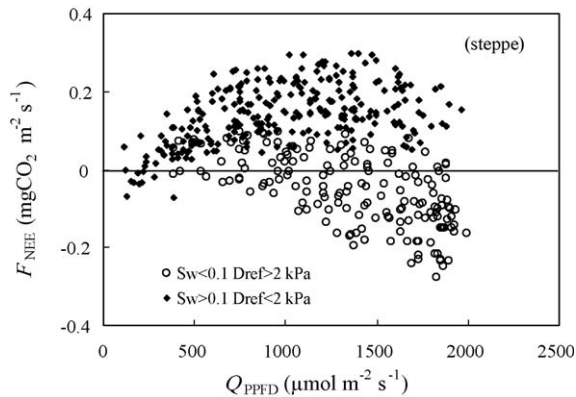
Fig. 6. Variation of daytime F_{NEE} under different soil water content and atmospheric humidity in the steppe from mid-June to mid-July 2003. The closed circles represent the observations under wet conditions with soil water content (S_w) > 0.1 $m^3 m^{-3}$ and vapor pressure deficit (D_{ref}) < 2.0 kPa, the open circles refer to dry conditions when S_w < 0.1 $m^3 m^{-3}$ and D_{ref} > 2.0 kPa.

also showed a slightly decreasing trend with increasing light intensity (closed circles). In contrast, under dry conditions F_{NEE} was depressed so much that the F_{NEE} values turned negative, indicating release of CO_2 outstripped uptake by photosynthesis (open circles). It is also found that rainfall events often caused change of the signs of the daily F_{NEE} values during the growing season in the steppe, and the steppe changed into a state of CO_2 emission during the dry period in August (data omitted). This suggests that frequent recovery of the ecosystem from water stress by rainfall is very critical to the ecosystem CO_2 exchange process. Similar phenomena have been observed in tallgrass prairie by Suyker et al. (2003).

In contrast to the steppe, the shrub on the Tibet Plateau had relatively stable and sufficient soil water due to the abundant precipitation during the entire growing season (Fig. 1f). As a result, F_{NEE} of the shrub varied little with soil moisture, indicating that moisture was not a limiting factor the alpine shrub growth in 2003.

4. Discussion

4.1. Depression of F_{NEE} in the steppe

The above results have shown that water stress seemed to be the dominant factor limiting the growth of the semi-arid steppe during the growing season (Fig. 6). To illustrate the underlying physiological mechanism of depression of F_{NEE}, we investigated the diurnal courses of F_{NEE}, ecosystem evapotranspiration (ET), surface conductance (g_s) and relevant environmental factors on clear days.

Fig. 7a shows the typical diurnal cycles of Q_{PPFD}, canopy temperature (T_c) and D_{ref} of the steppe on a clear day in summer. Similar variation trends were observed for T_a and D_{ref}, except there was a time lag for them to reach the maximum of the day. The diurnal variation of F_{NEE} on clear days in the steppe was characteristic of pronounced mid-day depression and a rapid recovery in the afternoon (Fig. 7b). The lower peak in the afternoon than in the morning might be due to the higher vapor pressure deficit and the reduced water flow from the soil to plant roots in the afternoon. The surface conductance (g_s) calculated with Eq. (3) was usually high in the early morning but declined rapidly as solar radiation and vapor pressure deficit increased (Fig. 7b). In the afternoon the decreasing rate of g_s slowed down and the recovery of g_s was very slight because of the reduced plant transpiration and soil evaporation, which were both limited by the low soil water content. The measurements of leaf photosynthesis (Model LI-6400) at the steppe in August 2004 also showed a marked down-regulation in both photosynthesis and stomatal conductance at mid-day. The mid-day drop of ET was less remarkable compared to F_{NEE} because the humidity deficit increased steadily with rising temperature from morning to mid-afternoon (Fig. 7a), which partly counteracted the decreasing of stomatal conductance. The above results were consistent with the studies by Tuzet et al. (2003) regarding the effect of soil water on the role of stomata in regulating photosynthesis and transpiration during a drying cycle.

Photosynthesis and transpiration are coordinated processes since the same opening–closing movement of the stomata controls both (Yu et al., 2001). Photosynthesis depends on stomatal behavior and the reduction of leaf photosynthesis is usually caused by either stomatal or non-stomatal limitation. The former could be partially attributed to stomatal closure, while the latter could be the decrease of leaf photosynthetic activity which can lead to irreversible reduction of plant photosynthesis (Farquhar and Sharkey, 1982; Xu, 1997). Du and Yang (1988, 1990) have also made many leaf-level studies on the photosynthesis of the major species in the *L. chinensis* steppe. They found that the decrease of leaf water content and stomatal conductance under drought condition is the major factors that cause the mid-day photosynthetic reduction in *L. chinensis* and *Stipa grandis*, coupled with the enhanced respiration due to high leaf temperature, which could reach as high as 40 °C (referring to canopy infrared temperature, Fig. 7a). According to results from this and earlier studies, we infer that the mid-day depression of F_{NEE} in the steppe was mainly due to
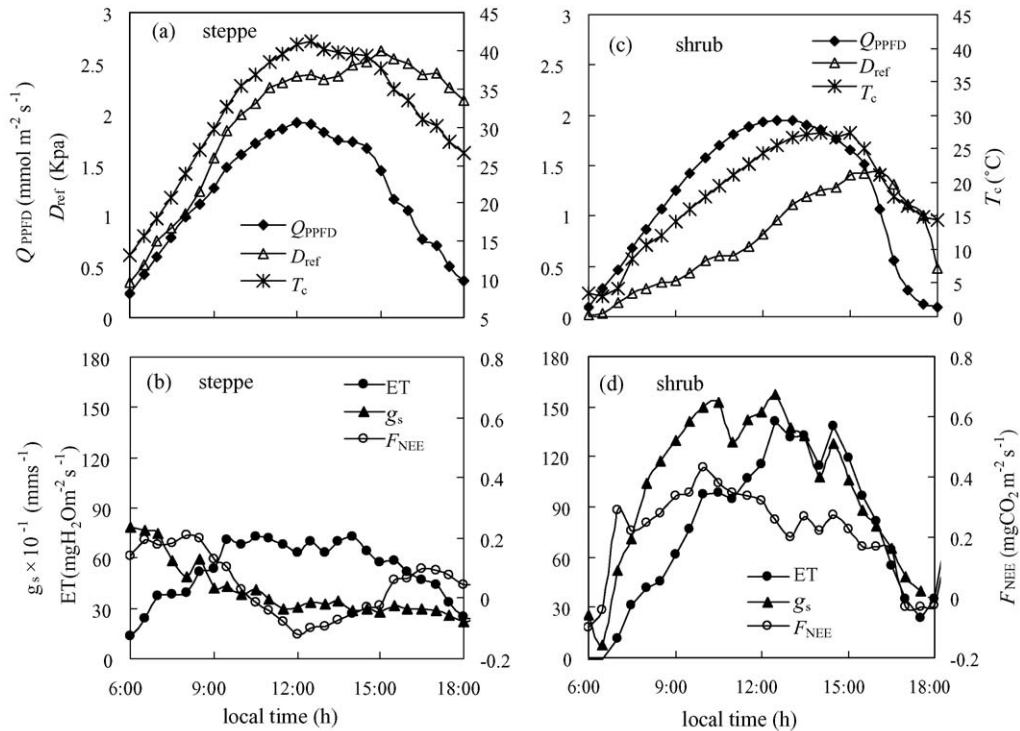
Fig. 7. Diurnal variations of net ecosystem CO_2 exchange (F_{NEE}), ecosystem evapotranspiration (ET), surface conductance (g_s) and correspondingly environmental factors of solar radiation (Q_{PPFD}), vapor pressure deficit (D_{ref}) and canopy temperature (T_c) in the *Leymus chinensis* steppe (a and b, July 1, 2003) and the alpine shrub (c and d, July 25, 2003) were plotted, respectively.

stomatal limitation caused by inadequacy of water moisture, coupled with the high temperature effects on both ecosystem photosynthesis and respiration.

4.2. Depression of F_{NEE} in the alpine shrub

The depression of F_{NEE} in the alpine shrub on the Tibet Plateau was not as significant as that in the steppe, in spite of the comparable light intensities at the two ecosystems. The diurnal courses of Q_{PPFD} and T_c at the alpine shrub were similar to those at the steppe, but D_{ref} at the shrub was much lower than the steppe (Fig. 7c). F_{NEE} in the alpine shrub (Fig. 7d) was a little depressed at mid-day and recovered slightly in the afternoon. The g_s also decreased a little but it could not fully account for the depression of F_{NEE}, since the recovered g_s at 13:00 h did not cause the recovery of F_{NEE}. Moreover, the increase of ET with rising temperature and humidity deficit from morning to mid-afternoon indicates that soil water was not a limiting factor of the alpine shrub.

Shi et al. (2001) studied the mid-day down-regulation of photosynthesis at leaf level in *Saussurea superba* and *Gentiana straminea*, which are two main accompanying species in the alpine shrub. Their results showed that under high radiation the stomata on the adaxial surface of leaves were partially closed, while most stomata on the abaxial surface were still open and could regulate leaf temperature by transpiration. They concluded that the partial stomatal closure could not directly result in the mid-day down-regulation of photosynthesis in the two alpine species. It was more likely due to insufficient thermal dissipation and enhanced photorespiration under high solar radiation that resulted in the down-regulation of photosynthesis (Shi et al., 2001; Cui et al., 2003). The results of this study indicated that the depressed F_{NEE} in the shrub were mostly accompanied by temperature much higher than the optimal temperature for F_{NEE} in shrub (Fig. 3b), and the R_{eco} in the alpine shrub increased sharply with rising temperature (Fig. 4b). Earlier studies also showed that the alpine plants living on the Tibet Plateau may have been acclimated to the long-term low temperature conditions, and that photosynthesis is depressed at relatively high temperature (Guo et al., 1995; Cui et al., 2003). Therefore, we inferred that the depression of F_{NEE} in alpine shrub could mainly be ascribed to enhanced respiration and depressed plant

photosynthesis by high temperature under high radiation, coupled by the reduction of plant photosynthesis due to partly stomatal closure probably resulted from the decrease of leaf water content under high radiation at mid-day.

5. Conclusions

This study presented the dynamics of net ecosystem CO_2 exchange (F_{NEE}) in two ecosystems (a semi-arid *L. chinensis* steppe and an alpine shrub in China) and their responses to various environmental stresses during the growing season of 2003. As observed, F_{NEE} was depressed under high solar radiation in both ecosystems. Comprehensive analyses show that the depression of F_{NEE} in the semi-arid steppe is mainly attributed to the decrease of ecosystem photosynthesis, coupled with the effects of high temperature at mid-day on photosynthesis and respiration. The stomatal limitation caused by soil water insufficiency was responsible for the reduced photosynthesis activity of leaves under high radiation. In contrast, the depression of F_{NEE} in the alpine shrub was mainly caused by the effects of relatively high temperature there on both respiration and photosynthesis, coupled with reduction in plant photosynthesis due to partial stomatal closure under high radiation at mid-day. The respiration of alpine shrub ecosystem increased rapidly with temperature; while the temperature-sensitivity of respiration at the steppe was suppressed by soil water stress. This study indicates that the patterns and mechanisms of responses of F_{NEE} to environmental changes vary with ecosystem conditions. The high sensitivity of grassland ecosystems to temperature and precipitation implies that the vast temperate grassland and alpine ecosystems may be critical to regulating future climate change. Systematic and mechanistic studies in these ecosystems are needed for developing and improving relevant prediction models.

Acknowledgements

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