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Net ecosystem CO_2 exchange and controlling factors in a steppe——*Kobresia* meadow on the Tibetan Plateau

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Abstract Knowledge of seasonal variation of net ecosystem CO_2 exchange (NEE) and its biotic and abiotic controllers will further our understanding of carbon cycling process, mechanism and large-scale modelling. Eddy covariance technique was used to measure NEE, biotic and abiotic factors for nearly 3 years in the hinterland alpine steppe——*Korbresia* meadow grassland on the Tibetan Plateau, the present highest fluxnet station in the world. The main objectives are to investigate dynamics of NEE and its components and to determine the major controlling factors. Maximum carbon assimilation took place in August and maximum carbon loss occurred in November. In June, rainfall amount due to monsoon climate played a great role in grass greening and consequently influenced interannual variation of ecosystem carbon gain. From July through September, monthly NEE presented net carbon assimilation. In other months, ecosystem exhibited carbon loss. In growing season, daytime NEE was mainly controlled by photosynthetically active radiation (PAR). In addition, leaf area index (LAI) interacted with PAR and together modulated NEE rates. Ecosystem respiration was controlled mainly by soil temperature and simultaneously by soil moisture. Q_{10} was negatively correlated with soil temperature but positively correlated with soil moisture. Large daily range of air temperature is not necessary to enhance carbon gain. Standard respiration rate at referenced 10°C (R_{10}) was positively correlated with soil moisture, soil temperature, LAI and aboveground biomass. Rainfall patterns in growing season markedly influenced soil moisture and therefore soil moisture controlled seasonal change of ecosystem respiration. Pulse rainfall in the beginning and at the end of growing season induced great ecosystem respiration and consequently a great amount of carbon was lost. Short growing season and relative low temperature restrained alpine grass vegetation development. The results suggested that LAI be usually in a low level and carbon uptake be relatively low. Rainfall patterns in the growing season and pulse rainfall in the beginning and at end of growing season control ecosystem respiration and consequently influence carbon balance of ecosystem.

Keywords: Tibetan Plateau, alpine steppe——*Kobresia* meadow, NEE, ecosystem respiration, PAR, soil moisture, temperature response, LAI, eddy covariance.

Grassland, accounting for 30% of total terrestrial ecosystem, occupies about 25% of global organic carbon[1]. The grassland ecosystems, especially those in the high elevated and high latitudinal areas, are characterized by low temperature and high root/shoot ratio of vegetation. Therefore, the litter and underground dead root are hard to decompose, and the assimilated organic carbon can exist in the underground root or soil for a long time. The natural grassland ecosystems located in the high latitudes or high elevations play an important role as carbon sink[2]. The net ecosystem CO_2 exchange (NEE) of grassland ecosystem is determined by carbon uptake and carbon release with the processes of photosynthesis and respiration, which are controlled by many biotic and abiotic factors[3]. It is of great significance to study ecosystem carbon budget through the analysis of seasonal and annual variation patterns of NEE and environmental factors, and to analyze the carbon exchange processes by using eddy covariance technique. It is also valuable to understand how the variation of vegetation structure influences carbon exchange as well as further modeling at large scale.

Present reports on carbon flux in grassland ecosystems show that the complex processes of photosynthesis and respiration are influenced by many biotic and abiotic factors. The photosynthetically active radiation (PAR), temperature, rainfall distribution, soil moisture and leaf area index (LAI) are among the key factors, and the interactions of these factors also play important roles on the ecological processes of ecosystem carbon cycle[3]. The major controlling factor for photosynthesis is PAR[4,5], while the case for respiration was more complicated. The key factor for respiration is temperature[4,6]. Ecosystem respiration (including soil respiration) is usually in an exponential function with temperature[7,8]. However, some studies showed that soil respiration decreased with the increasing of temperature. The reason might be that respiration coefficient Q_{10} declined with the increasing of temperature, which resulted in the decrease of respiration sensitivity to temperature[4,7,9]. Ecosystem respiration is also modulated by soil moisture, which is in positive correlation with Q_{10}[3,4]. It was reported that Q_{10} declined when a drought prevailed[3]. Moreover, ecosystem respiration is also closely related to net primary productivity and LAI[3,4,10,11]. This indicates that biotic factors and plant growth stages are also important factors controlling respiration. It is favorable to enhance NEE accumulation and carbon sink under relatively dry and cold climate conditions[12,13]. However, most studies have been conducted only in the grassland ecosystems at elevation below 1500 m. Little has been done in the high altitudinal areas in spite of its carbon sink function and more sensitive to future climate changes[2].

Grassland, accounting for about 1.2×10^6 km^2, occupies some 48% of the total land area on the Qinghai-Tibetan Plateau[14,15]. The plateau possesses highest grassland ecosystems with mean elevation above 4000 m. The plateau climate is characterized by intensive radiation, low air temperature, large diurnal variation of temperature. Temperature is in phase with monsoon and rainfall is in great variability in annual distribution, concentrating most in the growing season[16]. Soil moisture is influenced by rainfall events to a great extent. All these unique environmental conditions provide us natural experimental conditions to study carbon exchange processes including carbon uptake and respiration. The objectives of this paper are to: (i) examine the influence of PAR on NEE in different growing stages; (ii) analyze temperature dependence of ecosystem respiration R_{eco}; (iii) clarify whether the daily temperature variation is favorable for carbon gain or not; and (iv) study the impact of soil moisture on the ecosystem respiration, and how rainfall patterns influence R_{eco} through altering soil moisture.

1 Materials and methods

1.1 Study area

The study area is located at the Damxung grassland station (91°05E, 30°25N), north of Lhasa City, Tibet with an elevation of 4333 m. It is known as the highest carbon flux station of grassland ecosystem over the world. The terrain within one kilometer surrounding the station is flat with the slope less than 2%. The experimental site is categorized as plateau monsoon climate. Annual mean air temperature is 1.3℃, with minimal mean of −10.4℃ in January and maximal mean of 10.7℃ in July. Mean daily variation temperature is 18.0℃, while the annual one is 21.0℃. The average surface soil temperature is 6.5℃. Soil frozen duration is 3 months lasting from November to next January. Growing season duration is in May through September. Annual mean rainfall is 476.8 mm, with 80% in June to August. Annual evaporation is 1725.7 mm and average wetness coefficient is 0.28. The climate is in semiarid and semi-humid one. The annual average sunlight is 2880.9 h. And the amount of sun radiation is 7527.6 $\text{MJ}\cdot\text{m}^{-2}$, of which PAR is 3213.3 $\text{MJ}\cdot\text{m}^{-2}$[5]. The soil is classified as meadow soil with sandy loam. The soil has a depth of 0.3—0.5 m, with 30% of gravel content and 0.9%—2.97% of organic matter content. The vegetation is alpine steppe—*Korbresia* meadow which is typical on the northern Tibetan Plateau with three dominant species, *Stipa capillacea*, *Carex montis-everestii* and *Kobresia pygmaea*[17]. The coverage is about 50%—80%. And the highest LAI during the growing season is 1.88.

1.2 Observation items of eddy covariance system

Fluxes of CO_2, sensible heat, latent heat and momentum between atmosphere and vegetation were measured at a height of 2.1 m using the eddy covariance technique. The eddy covariance array sensors included a 3D sonic anemometer (CSAT3, Campbell Scientific Inc. USA) and an open-path CO_2 analyzer (Model LI7500, LI-COR Inc. Lincoln, Nebraska, USA). The data was collected with the frequency of 10 Hz, and the averaged values were calculated every 30 min, which would be stored in the data logger CR5000. Profiles of environmental factors, such as air temperature, relative humidity, rainfall, PAR, net radiation, soil temperature and soil moisture at different depth and soil heat flux were also measured. These data were collected by CR23XTD. Measurement began from July, 2003 to December, 2005.

The variation patterns of PAR, air temperature (T_a), daily maximum air temperature ($T_{\max}$) and minimum air temperature ($T_{\min}$), soil temperature at 5 cm depth (T_s), daily precipitation (PPT) and soil moisture at 5 cm depth (S_w) were illustrated in Fig. 1. From 2003 to 2005, the maximal PAR was 66.44 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, and it appeared on June 25, 2005. The maximum of PAR usually appeared in the late June, then decreased with the increasing of rainfall or the decline of solar altitude, and reached the minimum in late December or early January (Fig. 1(a)). The PAR was usually high, similar to that in alpine meadow area located in eastern Tibetan Plateau and higher than other grassland ecosystems[2]. The amplitudes of T_a, T_s were −17.1—14.8℃ and −10.0—19.1℃ respectively, with the maximum usually in early August and minimum in late January (Fig. 1(b), (d)). The highest $T_{\max}$ was 22.8℃, appearing in early August and lowest $T_{\min}$ was −27℃, appearing in January (Fig. 1(c)). This indicated that temperature at study site is fairly low. The maximum of daily range of air temperature, above 20℃, appeared in January, while the minimum, about 10℃, occurred in early June or July. Even in summer, the days with daily range more than 10℃ were prevalent. The rainfall was in phase with temperature, mainly concentrating from June to August. In 2004 and 2005, the rainfall from June to August was 78% and 79% of the yearly total, which was 550.4 mm and 489.9 mm respectively. The rain in September and October was little, with few days of PPT reaching 10 $\text{mm}\cdot\text{d}^{-1}$ (Fig. 1(e)). The S_w could reach above 0.2 from middle June to late August, while it decreased dramatically from late August as a result of the rainfall declination, low vegetation coverage and great evaporation induced by strong radiation. During non-growing season, the S_w was all below 0.1, and it was only 0.05 in January. The rainfall in 2004 was plentiful, concentrated and lasting, S_w was above 0.2 in the growing season. However, in 2005, there was an one-month-drought from mid-June to mid-July. Consequently S_w was low for nearly a month. Besides, S_w from January to May in 2005 was also low compared with that in 2004 (Fig. 1(f)). The influence of S_w change, induced by rainfall, on ecosystem primary productivity and R_{eco} will be discussed later.

1.3 Measurement of biomass and leaf area index

The aboveground biomass (B_a) and LAI were measured with harvest method[18]. In 2004 and 2005, the measurement was carried out every half month in the growing seasons. The sample plot was 50 cm × 50 cm, and 5 replicates were used. The green leaf area was measured with Area Meter AM200-001 (ACD BioScientific Ltd. UK). The leaf was dried for 24 h under 80℃ in oven, and then was weighed. The B_a and

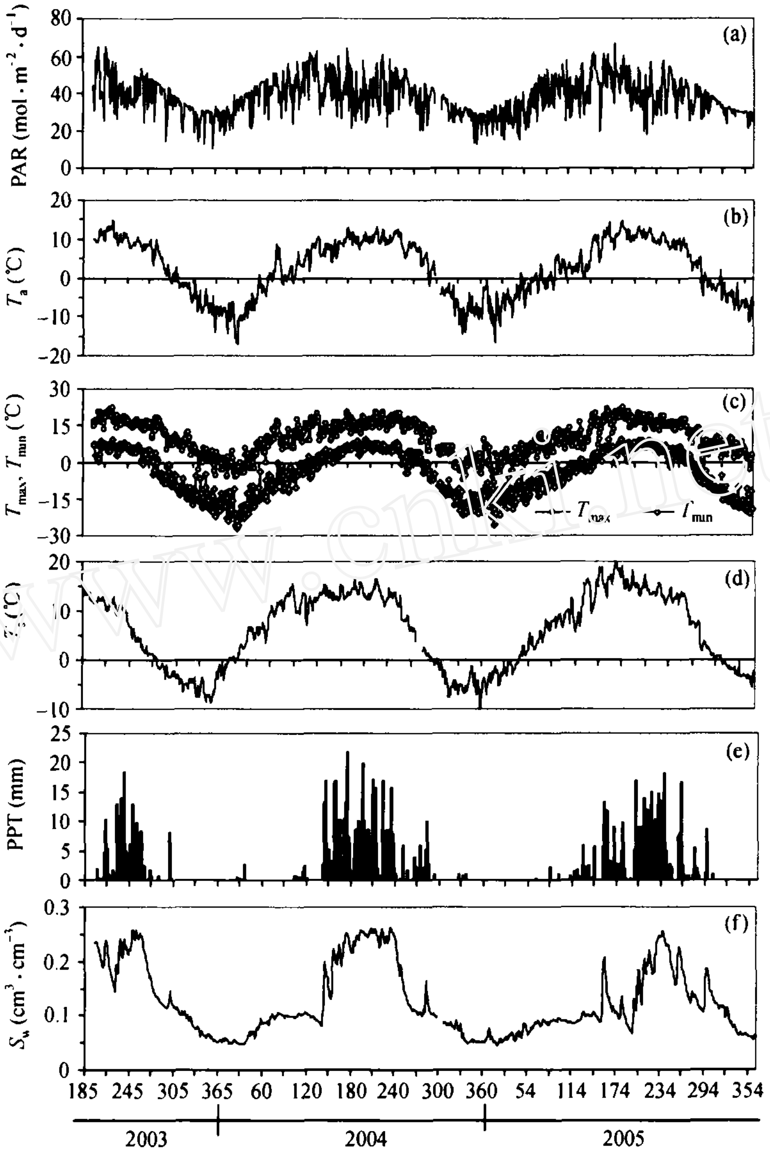

Fig. 1. Daily average climatic parameters in Damxung grassland station, Tibet. (a) PAR; (b) air temperature; (c) maximum air temperature and minimum air temperature; (d) soil temperature at 5 cm depth; (e) daily rainfall; (f) soil moisture at 5 cm depth.

LAI were calculated by average dry weight in the plots.

The change of biomass and LAI coincided with logistic curves in the growing season. The B_a and LAI in 2004 were higher than those in 2005 due to favorable soil moisture conditions (Fig. 2). The B_a and LAI started to increase from late May, and rose dramatically in July and August, then reached the maximum in late August or early September. In late September, the B_a and LAI dropped sharply as a result of plant senescence. The maximum of B_a and LAI in 2004 was 150.9 g · m^{-2} (on September 7, DOY 231) and 1.86 (on August 18, DOY 251), and those in 2005 were 106.2

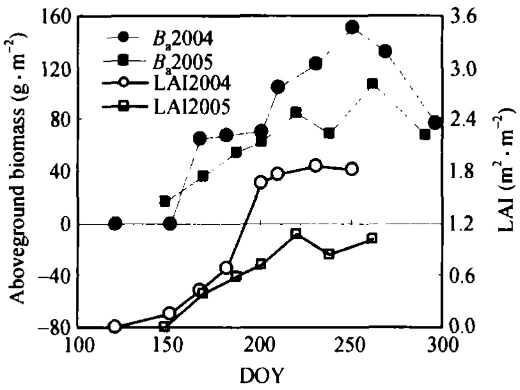

Fig. 2. Aboveground biomass and leaf area index of steppe —— *Kobresia* meadow in year 2004 and 2005.

$g \cdot m^{-2}$ and 1.01 (on September 11, DOY 262). Compared with in 2004, the time of maximum B_a and LAI in 2005 was delayed.

1.4 Data process

Data pretreatment was needed in order to adjust the flux data caused by sensor malfunction, which included spike removal ($\pm 3\sigma$), coordinate rotation and Webb-Pearman-Leuning revisal[19] etc. The data in rainy days and the data during nighttime (PAR < 1 $\mu mol \cdot m^{-2} \cdot s^{-1}$) with $u^* < 0.15$ were also discarded[20]. The missing data could be filled by the nonlinear relationship established between carbon flux and the environmental factors[5,20].

The carbon fluxes (F_c) were filled by the exponential function with T_s[21] in the non-growing season (from November to next April) and the nighttime (PAR < 1 $\mu mol \cdot m^{-2} \cdot s^{-1}$) in the growing season from May to October.

$$F_c = R_{10} Q_{10}^{((T_s - T_{ref})/10)}, \tag{1}$$

in which, F_c was carbon fluxes of $u^* > 0.15\ m \cdot s^{-1}$ during nighttime; T_{ref}, referenced temperature (10℃); R_{10}, standardized respiration coefficient (mg $CO_2 \cdot m^{-2} \cdot s^{-1}$), i.e. the respiration rate at the referenced temperature (10℃); Q_{10}, the sensitivity coefficient of respiration, i.e. the increasing multiple of respiration rate while the respiration was increased by 10℃. The missing NEE during nighttime and the daytime respiration R_{eco} was filled with eq. (1).

The missing daytime carbon fluxes were filled by the rectangular hyperbolic function between NEE and PAR[21].

$$F_c = \frac{F_{max} \cdot \alpha \cdot PAR}{\alpha \cdot PAR + F_{max}} + R_{eco}, \tag{2}$$

in which, F_{max} ($\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$) was the maximal ecosystem assimilation; α, apparent quantum yield; R_{eco}, daytime ecosystem respiration.

2 Results

2.1 Daily and seasonal variation of net ecosystem CO_2 exchange

Daily NEE presented single peak (Fig. 3). NEE changed to be negative (carbon uptake) at 6:00 1), rose with increase of PAR, reached maximum in middle noon at 10:00—12:00 and then decreased afterward. At nearly 18:00 NEE changed to be positive and ecosystem became carbon source. For instance in year 2004, maximum NEE in August reached −8.3 $\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$ at 11:00, and maximum carbon loss was 2.4 $\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$, occurring at 20:00. Carbon uptake in terms of monthly NEE in turn was August > July > June > September > October > May (Fig. 3(a)). In the non-growing season, NEE values indicated carbon loss. The carbon loss was fairly low in January through April, almost presenting straight lines. While there were obvious peaks in November and December. The peak of carbon loss in November reached 1.1 $\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$ and decreased to 0.7 $\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$ in mid-December (Fig. 3(b)). The daily and seasonal variations of NEE in steppe-*Kobresia* meadow in Damxung is similar to those of alpine

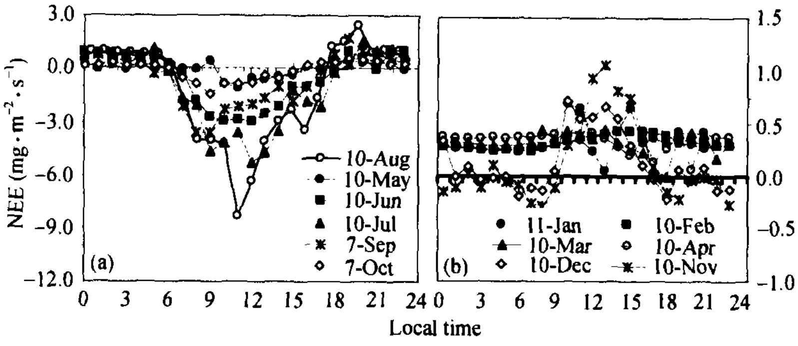

Fig. 3. Average hourly net ecosystem CO_2 exchange in middle months in 2004. (a) In growing season; (b) in non-growing season.

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1) It is local time except stated otherwise.

Kobresia meadow in eastern Qinghai-Tibetan Plateau[2,22,23].

Fig. 4 illustrates daily NEE and monthly amounts of steppe——*Korbresia* meadow in year 2004 and 2005. From daily NEE, the NEE of January through May presented carbon loss and from June to end of September or early October the ecosystem presented carbon uptake. After early October, the ecosystem started to be carbon source (Fig. 4(a), (c)). From month amounts, the NEE of July through September in 2004 and 2005 presented net carbon uptake. In June, the early growing season, whether ecosystem was carbon source or carbon sink was determined by rainfall and its distribution in this season. In other months of the non-growing season, the ecosystem was carbon source. In 2005, annual rainfall was relatively low and reached lately, monthly NEE presented carbon source. In the whole year, peak carbon loss occurred in May and November; peak carbon uptake took place in July and August. Carbon uptake or carbon loss was closely related to annual rainfall and its seasonal distribution. The annual rainfall in 2005 was lower than that of 2004, peak carbon uptake delayed to August (Fig. 4(b), (d)). Annual amount was −34.9 g $CO_2 \cdot m^{-2}$ and 54.4 g $CO_2 \cdot m^{-2}$ in year 2004 and 2005 respectively. The ecosystem presented as small carbon sink in 2004 and a small carbon source in 2005.

2.2 *Daytime NEE and its relation to PAR and LAI*

NEE is closely related to grass growing stages. The relation between NEE and PAR coincides with rectangular hyperbolic equation. For instance, in year 2004, in the four phonological stages of dominant grasses, the parameters of rectangular hyperbolic function between NEE and PAR are illustrated in Table 1. Change of PAR can explain 70% of NEE variation in daytime. This indicates that PAR is a key controller of daytime photosynthesis. From Table 1 we can see that the apparent quantum yield (α) and maximum photosynthetic rate (F_{max}) change with LAI in different phonological stages. From tillering, elongation to early heading stage, LAI increased from 0.7, 1.6 to 1.9, α increased from 0.012, 0.015 to 0.016, and F_{max} increased from −4.6, −6.4 to −8.7 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$. Dark respiration of ecosystem also increased simultaneously. At maturing stage, green leaves were dead and LAI decreased due to decrease of temperature. Photosynthetic rate significantly decreased. α and F_{max} decreased by 0.013 and −4.9 μmol $\cdot m^{-2} \cdot s^{-1}$ respectively. This suggested that PAR be major control-

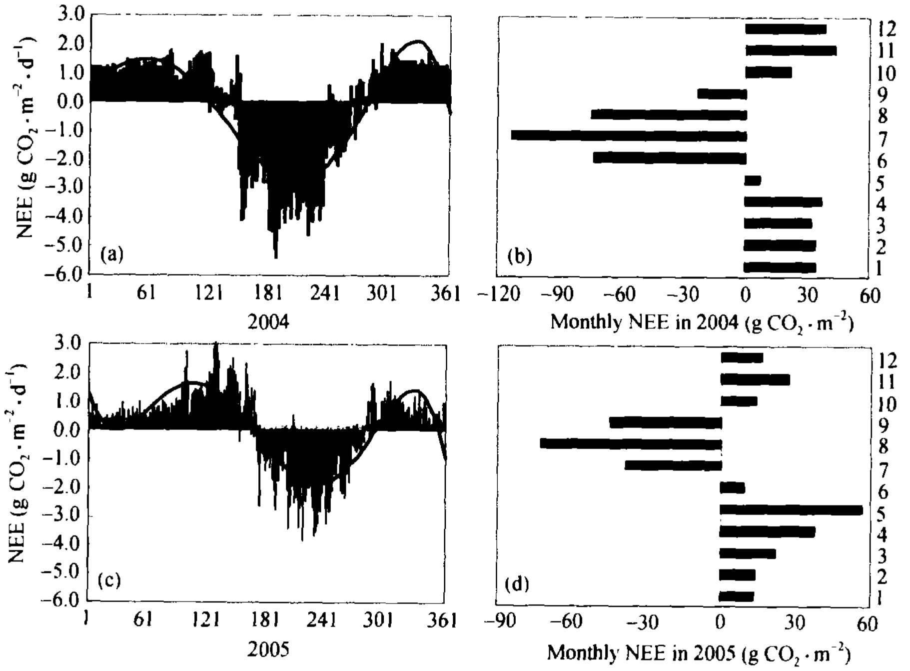

Fig. 4. Seasonal variation of net ecosystem CO_2 exchange in 2004 and 2005. (a) Daily NEE in 2004; (b) monthly NEE change in 2004; (c) daily NEE in 2005; (d) monthly NEE change in 2005.

Table 1 Parameters of light response curves of NEE in growing season in 2004

Month	Phonological stages	Day of year	LAI ($m^2 \cdot m^{-2}$)	α	F_{max}($\mu mol \cdot m^{-2} \cdot s^{-1}$)	R_{eco}($\mu mol \cdot m^{-2} \cdot s^{-1}$)	r^2
June	tillering	DOY177—187	0.7	−0.0119	−4.635	0.914	0.71
July	elongation	DOY197—204	1.6	−0.0147	−6.389	1.017	0.79
August	heading	DOY228—234	1.9	−0.0159	−8.675	1.235	0.85
September	maturing	DOY264—274	0.6	−0.0133	−4.918	0.732	0.74

ler of ecosystem photosynthesis. However, the phonological stage of grass plants could modulate ecosystem photosynthesis through LAI. Ecosystem respiration had similar trends with LAI and F_{max} and the later two parameters presented positive correlation. It implied that ecosystem respiration had positive correlation with photosynthesis.

2.3 Nighttime ecosystem respiration and its relation to T_s and S_w

We used nighttime NEE, with $u^* > 0.15\ m \cdot s^{-1}$, to establish the response of R_{eco} to T_s. Considering the impact of soil moistures in different phonological stages on R_{eco}[3], we used the R_{eco} under similar S_w regime to model its response to T_s in order to avoid the impact of fluctuation of LAI and S_w as low as possible. The R_{10} and Q_{10} in eq. (1) were parameterized.

The parameters of R_{eco} R_{10}, Q_{10} and corresponding T_s and S_w were shown in Table 2. We also listed aboveground biomass and LAI. In growing season, R_{10} was significantly correlated with T_s (r^2 = 0.34, p = 0.007), S_w(r^2 = 0.42, p = 0.002), LAI (r^2 = 0.77, p = 0.004) and aboveground biomass (r^2 = 0.55, p = 0.04). In the growing season, R_{10} increased with T_s and reached maximum in mid-August, and then decreased from late August on. Q_{10} decreased with the increase of T_s (r^2 = 0.01, p = 0.71, not significant), but significantly correlated with S_w (r^2 = 0.28, p = 0.02). The average Q_{10} values were 3.2 ± 0.6 and 3.4 ± 0.8 respectively in year 2003 and 2004, with average 3.3 ± 0.7 in the two years.

2.4 Influence of daily range of temperature on NEE

Daily range of air temperature ($T_{max} - T_{min}$) was also one of the important factors to control NEE. Fig. 5 illustrated NEE response to daily range of air tem-

Table 2 Parameters of ecosystem respiration R_{10} and Q_{10} and their relation to biotic and abiotic factors in growing season of year 2003 and 2004

Year	Date duration	LAI ($m^2 \cdot m^{-2}$)	B_a ($g \cdot m^{-2}$)	T_s (℃)	S_w ($cm^3 \cdot cm^{-3}$)	R_{10} ($mg \cdot m^{-2} \cdot s^{-1}$)	Q_{10}	r^2
2003	19—31, Jul	—	—	13.5	0.20	0.046	3.02	0.34
	1—4, Aug	—	—	12.1	0.23	0.034	3.85	0.63
	5—16, Aug	—	—	14.0	0.17	0.033	2.52	0.66
	16—20, Aug	—	—	12.2	0.19	0.041	2.61	0.37
	21—23, Aug	—	—	11.1	0.24	0.032	3.46	0.82
	23—25, Aug	—	—	11.9	0.21	0.034	2.96	0.49
	26—30, Aug	—	—	12.3	0.23	0.035	3.72	0.69
	30—31, Aug	—	—	12.2	0.21	0.037	3.04	0.84
	1—4, Sept	—	—	11.2	0.22	0.043	2.48	0.35
	5—21, Sept	—	—	13.5	0.25	0.037	4.32	0.41
2004	1—20, May	0	0	11.6	0.09	0.008	2.82	0.28
	21—31, May	0.15	0	9.2	0.15	0.015	3.08	0.41
	1—10, Jun	0.44	65.3	10.8	0.13	0.012	3.49	0.35
	11—30, Jun	0.69	70.6	11.2	0.21	0.021	4.92	0.69
	1—5, Jul	1.66	80.2	12.5	0.23	0.022	3.04	0.31
	6—31, Jul	1.77	104.1	11.9	0.25	0.035	3.69	0.34
	1—28, Aug	1.86	121.6	12.1	0.25	0.038	4.81	0.25
	29—31, Aug	—	—	13.3	0.22	0.045	3.06	0.38
	1—12, Sept	1.82	150.9	12.7	0.17	0.041	2.55	0.36
	13—30, Sept	0.652	131.5	11.9	0.11	0.021	2.28	0.27

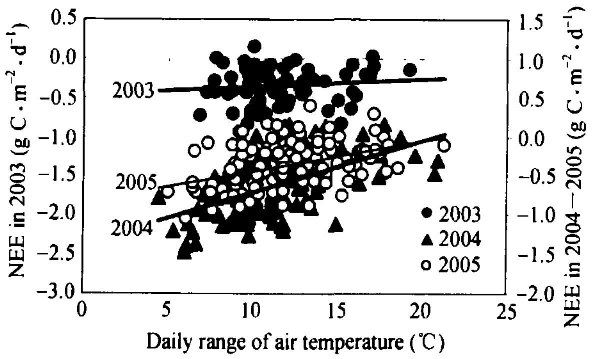

Fig. 5. Response of daily net ecosystem CO_2 exchange to daily range of air temperature in growing seasons of year 2003 to 2005.

perature in 3 growing seasons (July to September in 2003, June to September in 2004 and 2005). NEE decreased with increase of daily range of air temperature, i.e., large daily range is not necessary to enhance ecosystem carbon uptake and photo-assimilation. The phenomena were significant in year 2004 ($r^2 = 0.29$, $p < 0.001$) and 2005 ($r^2 = 0.17$, $p < 0.001$) except in 2003 ($r^2 = 0.02$, $p > 0.35$). It is contradictory to result observed in alpine *Korbresia* meadow in Haibei, northeastern Qinghai-Tibetan Plateau. In Haibei, higher daily range air temperature was beneficial to carbon uptake[22].

2.5 *Influence of pulse rainfall on R_{eco} in the beginning and at the end of growing seasons*

At the end of growing season, i.e., from October to early November, there were usually pulse rainfall events with 1—10 mm after a period of no rain. These pulse rainfall events could increase soil moisture to some degree and enhance R_{eco}. Fig. 6 indicates two cases of impact of pulse rainfall on R_{eco} in year 2003 and 2004. After 17 days of no rain, a daily rainfall of 8.1 mm occurred on October 10, 2003. Soil moisture increased from 0.1 $m^3 \cdot m^{-3}$ to 0.15 $m^3 \cdot m^{-3}$ (Fig. 6(c)). Q_{10} of R_{eco} changed with S_w in the process of pulse rainfall. It increased sharply from 2.1 before rainfall to 7.7 two days after rainfall, and then decreased to 3.8 (Fig. 6(a)). R_{eco} increased from 0.36 mg $CO_2 \cdot m^{-2} \cdot d^{-1}$ one day before rainfall to 0.80 mg $CO_2 \cdot m^{-2} \cdot d^{-1}$ in the raining day and reached maximum of 0.89 mg $CO_2 \cdot m^{-2} \cdot d^{-1}$ at the next day of raining (Fig. 6(e)). The rainfall in October in 2004 was more than that in 2003. A rainfall event of 10.0 mm took place on October 9, and also several days of lower than 5 mm rainfall events beforehand. S_w increased from 0.12 $m^3 \cdot m^{-3}$ to 0.16 $m^3 \cdot m^{-3}$ before and

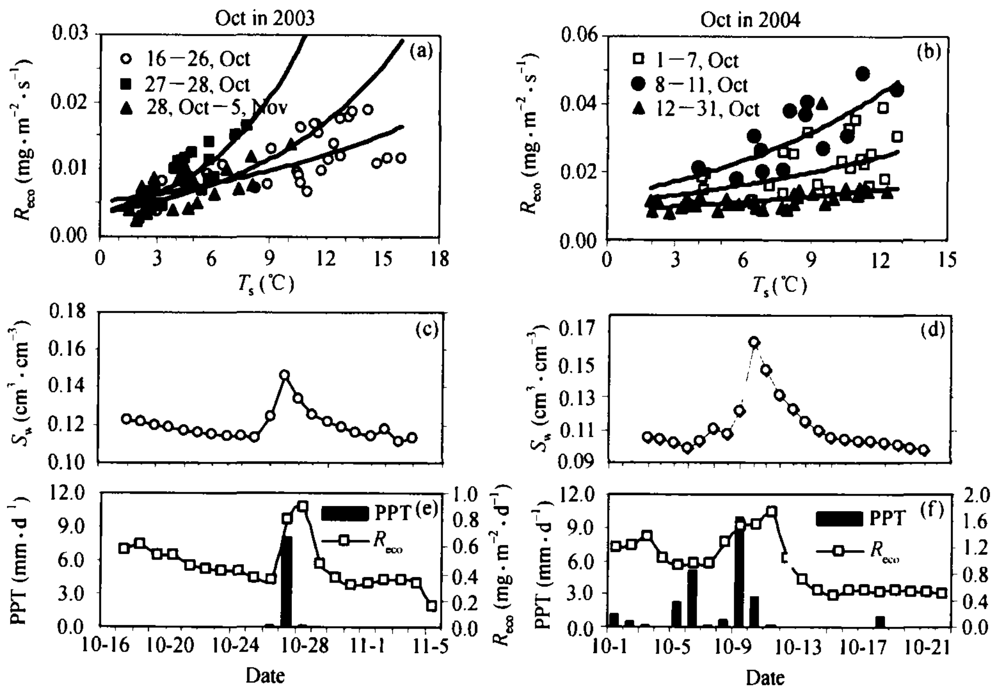

Fig. 6. Influence of pulse rainfall at the end of growing season (October) on soil moisture and ecosystem respiration in year 2003 and 2004. (a) and (b) ecosystem respiration; (c) and (d) soil moisture at 5 cm depth; (e) and (f) dynamics of daily rainfall and ecosystem respiration.

two days after the heavy rainfall event (Fig. 6(d)). In comparison with October in 2003, R_{eco} increased slowly because of lower rainfall before heavy pulse rainfall event. However the amount of ecosystem respiration is relatively high in 2004. It increased from 1.27 to 1.51 mg $CO_2 \cdot m^{-2} \cdot d^{-1}$ at the raining day, and reached maximum value of 1.74 mg $CO_2 \cdot m^{-2} \cdot d^{-1}$ two days later. Afterward, it decreased sharply with depress of soil moisture (Fig. 6(f)). Q_{10} changed slowly, from 2.0 to 2.8 before and after the heavy rainfall event, and then decreased to 1.6 (Fig. 6(b)). In 2005, there were also pulse rainfall events enhancing S_w and R_{eco} in the beginning (May to June) and end (late October) of growing season. This indicated that pulse rainfall events could enhance R_{eco} whenever it occurred in the beginning and at the end of growing season. The enhanced ecosystem respiration as a consequence of pulse rainfall events can influence ecosystem carbon budget to a great extent.

3 Discussion

The daily maximal uptake rate of CO_2 of the present study reached $-8.3\ \mu mol \cdot m^{-2} \cdot s^{-1}$, and the maximal value of R_{eco} was 2.4 $\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$. Compared with other grassland ecosystems in the world, it was apparently small. Taking the northern American prairie for example, the daily maximal uptake rates of CO_2 of the ecosystem are much higher, prevalently above 20 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The highest values can reach to a rate of $-23\ \mu mol \cdot m^{-2} \cdot s^{-1}$[24], $-27\ \mu mol \cdot m^{-2} \cdot s^{-1}$ [25], $-30\ \mu mol \cdot m^{-2} \cdot s^{-1}$ [26] and $-34\ \mu mol \cdot m^{-2} \cdot s^{-1}$[27]. The LAI values of these temperate grasslands are also higher with an average of 4—5 $m^2 \cdot m^{-2}$, with C_4 plant found in these grasslands. The maximum NEE at Damxung steppe-*Korbresia* meadow had a somewhat similar value compared with the $-8.0\ \mu mol \cdot m^{-2} \cdot s^{-1}$ [28] in Californian infertile grasslands and the $-10.8\ \mu mol \cdot m^{-2} \cdot s^{-1}$ [2] in northeastern alpine meadow on the Tibetan Plateau. It was $-5\ \mu mol \cdot m^{-2} \cdot s^{-1}$ higher than New Zealand tussock grassland[29]. The time of maximal uptake and CO_2 release was also in the period of maximum aboveground biomass and LAI in mid-August. After August, with the decline of the PAR, S_w, aboveground biomass and LAI, daily ecosystem CO_2 uptake and R_{eco} decreased to some extent, which indicated that ecosystem photosynthesis held a positive relation with the PAR and LAI. This was also found in American temperate grasslands[3] and Mediterranean annual grasslands[4]. The photosynthetic capacity of the ecosystem was controlled by PAR, presenting a nonlinear rectangular hyperbola relation. But the photosynthesis potentials, F_{max} and α of the ecosystem, were modulated by LAI. The level of LAI determined the photosynthesis potential (Fig. 1). The ecosystems with higher LAI, just like the Northern American grasslands, had higher CO_2 uptake rates. The alpine meadow on the northeastern Tibetan Plateau also had a higher LAI and photosynthesis rate than the present study[2]. In conclusion, the seasonal variability of the daily uptake rate was controlled by the interaction of PAR and LAI, and showed a obvious seasonal variation.

R_{eco} was influenced by many environmental factors and biotic factors, mainly by soil temperature and soil moisture[29]. R_{eco} and the soil respiration represented a exponential function with increasing temperature[7,8,30]. But from the whole growing season or longer time period, the relationship between R_{eco} and T_s indicated a tendency to scatter in the distributing chart[4]. So the relationship between R_{eco} and T_s should be established separately by different soil moisture regimes because the rainfall will alter soil moisture and influence the seasonal variability of the R_{eco}[3,4]. In addition, R_{eco} held a positive relationship with the B_a and LAI, judged from the positive relation between R_{10} and the factors mentioned above (Fig. 2). It went to the conclusion that a higher photosynthetic productivity induced a higher R_{eco}. But the photosynthetic productivity often weakened the influence of temperature on R_{eco}[11]. So R_{eco} was mainly controlled by the temperate, but in different growing stages, the variability of the soil temperature and LAI had a strong modulation on the R_{eco}, which created the pattern of the seasonal variability of R_{eco}.

The Q_{10} of R_{eco} in the 2003 and 2004 growing seasons were 3.2 and 3.4 with an average of 3.3, which is near to the upper limit of the extent of the Q_{10} in the world ecosystem[30,31], and higher than those in the lower altitudinal grassland ecosystems. It is close to the value of 3.7 in the alpine meadow on the northeastern Tibetan Plateau, and higher than the value of 1.83 in Northern Canadian temperate grassland, lower than the value of 4.6 in California serpentine grassland[28]. It was reported that Q_{10} of R_{eco} declined with the increasing temperate[4,9], and increased with the increasing soil moisture[3]. The higher Q_{10} was possibly caused by the lower temperature on the Tibetan Plateau. In a lower temperature condition, R_{eco} was more sensitive to the increasing temperature, leading to a higher value of Q_{10}. The Q_{10} of 2004 is possibly caused by higher rainfall during the growing season which led to higher soil moisture. The positive relation between R_{10} and S_w, B_a and LAI indicated that increasing temperature and moisture will not only enhance R_{eco}, but also promote the respiration of plants. This result indicated that net primary productivity and LAI were nice surrogate of the autotrophic respiration in the ecosystem. The combination analysis of the Q_{10}, R_{10}, and the environmental and biotic factors indicated that R_{eco} arrived at highest value in the peak period of plant physiological activities. Furthermore, because of rainfall in phase with temperature on the Tibetan Plateau, the maximal values of Q_{10} and R_{10} also appear in August during higher levels of soil moisture and temperature.

The daily range of air temperature is recognized as an important factor influencing photo-assimilates. Many studies indicated that acute daily range of temperature was beneficial to not only accumulating photo-assimilates[15], but also enhancing carbon sequestration in ecosystems[22]. But on the contrary in the present study, we found that this was not likely to exist. The main reasons might be as follows: (1) R_{eco} held an exponential relation with the temperature and the T_{max}, T_{min} (all higher than 5℃) of the growing season were both in the suitable range of R_{eco}. A higher daily range of air temperature meant a higher daily respiration. (2) In the growing season after August, although the daily ranges were enlarged, LAI and F_{max} of ecosystem declined gradually and so carbon uptake decreased. However, R_{eco} did not significantly decrease (see R_{10} in Table 2). As a result, carbon gain declined with the increasing daily range of air temperature. (3) Daily range of air temperature was also influenced by the rainfall. During raining season from June to August, the plateau usually had more rainfall in the night. Although night temperature and R_{eco} were both low, daytime rainfall reduction might promote temperature with the increasing of radiation. R_{eco} increased dramatically. As a consequence, large daily range of air temperature enhanced daily R_{eco} amount. (4) During the growth season, soil moisture often kept a higher level of above 0.15 due to its phase with temperature. R_{eco} was accelerated in higher soil moisture condition. For the above reasons, ecosystem carbon gain was not necessary to be accumulated because large daily range of air temperature induced higher R_{eco}.

The present study indicated that R_{eco} held a positive relation with soil moisture and pulse rainfall at the end of growing season markedly induced R_{eco}. It conformed to the observations in California annual grassland[4] and New Zealand tussock grassland[29]. After a relative long period of little rainfall in the beginning and at end of growing season, soil moisture usually decreases below 0.10 as a result of great transpiration induced by strong radiation on the plateau. Soil drought restricted plant autotrophic respiration and soil heterotrophic respiration. When pulse rainfall events happened, increase of soil moisture would enhance the activities of plant and microorganisms in soil and R_{eco} increased too. So pulse rainfall can enhance ecosystem carbon release and reduce the carbon gain. Under the semi-arid or arid climate of the alpine grassland ecosystem on the Tibetan Plateau, ecosystem respiration might be lowered down and carbon sequestration enhanced in the drought and cool years

4 Conclusions

The steppe-*Korbresia* meadow in Damxung is located at the ecotone between alpine meadow and alpine grassland on the Tibetan Plateau. It belongs to the semi-arid continental monsoon climate area. The rainfall is in phase with temperature. The climate is characterized by low temperature, concentrated rainfall in June through August and seasonal drought. Plant community is short and LAI is fairly low. Though much stronger radiation, the integrated modulation of LAI made photosynthetic capacity and efficiency somewhat low. So the carbon uptake of the present ecosystem is lower than most of the grasslands over the world. The larger daily range of air temperature is not necessary to benefit ecosystem carbon sink. The seasonal rainfall patterns play a great role in controlling soil moisture and net primary productivity. Soil moisture controls the intensity and amount of the ecosystem respiration. In the beginning and at the end of the growing season, pulse rainfall events usually enhance ecosystem carbon release and consume carbon gain. Therefore, it becomes the determinant factor of carbon budget. The sink/pool relationship of present ecosystem is to a large extent influenced by rainfall, its intensity and seasonal distribution.

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