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Effects of Temperature on CO₂ Exchange Between the Atmosphere and an Alpine Meadow

By

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Key words: Alpine grassland, ecosystem respiration, Qinghai-Tibetan plateau, photosynthesis, primary production.

Summary

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The alpine meadow ecosystem on the Qinghai-Tibetan Plateau is characterized by low temperatures because of its high elevation. The low-temperature environment may limit both ecosystem photosynthetic CO₂ uptake and ecosystem respiration, and thus affect the net ecosystem CO₂ exchange (NEE). We clarified the low-temperature constraint on photosynthesis and respiration in an alpine meadow ecosystem on the northern edge of the plateau using flux measurements obtained by the eddy covariance technique in two growing seasons. When we compared NEE during the two periods, during which the leaf area index and other environmental parameters were similar but the mean temperature differed, we found that NEE from 9 August to 10 September 2001, when the average temperature was low, was greater than that during the same period in 2002, when the average temperature was high, but the ecosystem gross primary production was similar during the two periods. Further analysis showed that ecosystem respiration was significantly higher in 2002 than in 2001 during the study period, as estimated from the relationship between temperature and nighttime ecosystem respiration. The results suggest that low temperature controlled the NEE mainly through its influence on ecosystem respiration. The annual NEE, estimated from 15 January 2002 to 14 January 2003, was about 290 g CO₂ m⁻² year⁻¹. The optimum temperature for ecosystem NEE under light-saturated conditions was estimated to be around 15 °C.

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Introduction

The concentration of atmospheric CO₂, one of the major greenhouse gases, has increased in recent decades because of changes in land use and the burning of fossil fuels (SIMS & BRADFORD 2001). Terrestrial ecosystems play an important role in reducing the rate of increase of CO₂ in the atmosphere. Among terrestrial ecosystems, grasslands not only cover a large proportion of the total land area, but also store a large amount of carbon, in particular in the soil (ADAMS & al. 1990, BATJES 1998, SUNDQUIST 1993, HUNT & al. 2002). Because of the extensive fibrous root system of grasses, grassland ecosystems have generally been considered to be an effective accumulator of carbon (FRANK & DUGAS 2001), and they may contribute to balancing the global carbon budget (RASTETTER & al. 1992, GIFFORD 1994, SCHIMEL 1995, KEELING & al. 1996, FAN & al. 1998). Clarifying the carbon dynamics of grasslands is thus essential for understanding the global carbon budget.

In most grassland ecosystems, water availability is often the major environmental control on ecosystem carbon dynamics (SUN 1999, KNAPP & SMITH 2001). Temperature is another important control on grassland carbon dynamics (RAICH & al. 1997), in particular in those ecosystems where water availability is not a major factor limiting productivity.

The Qinghai-Tibetan Plateau plays an important role in climate change because of its great geographic extent. Most of the plateau is covered with alpine meadow (ZHOU 2001), and precipitation and soil-water availability are usually sufficient for plant growth during the growing season, from May to September. Temperature, however, has been considered the major environmental constraint on ecosystem photosynthesis and respiration (KÖRNER 1999). As elevation increases, the temperature limitation may become greater. It is thus necessary to characterize the effect of temperature on the carbon dynamics of the alpine ecosystem to clarify and predict the carbon budget on this large plateau.

To better understand the influence of temperature on carbon uptake in an alpine meadow ecosystem, we focus in this study on the relationship between daytime net ecosystem CO₂ exchange (NEE) and photosynthetic photon flux density (PPFD) at different temperatures, using data obtained during the growing period with the eddy covariance method. We then determined the dependence of light-saturated NEE on temperature, and the effect of temperature on dark ecosystem respiration.

Material and Methods

Study site and meteorological conditions

The study site (lat 37°36'N, long 101°18'E, alt. 3250 m) is an alpine meadow on the Qinghai-Tibetan Plateau. The local climate is characterized by low temperatures; the annual mean air temperature is -1.7 °C, and the mean air temperature in January and July is -15.0 °C and 10.0 °C, respectively. The annual mean precipitation is 567 mm, of which more than 80% falls in the growing season, from May to September from the statistical data obtained from 1980 to 2000 at the local meteorological station. Soil water content is highest during the rainy season, from May to Septem-

ber.

We started our measurements in August 2001, and the data from 9 August 2001 to 14 January 2003 are presented in this study (for details see GU & al. 2003). The soil is classified as a Mat-Crylic Cambisol. Daily mean volumetric soil water at 5 cm depth ranged from about 0.20 to 0.56 $\text{m}^3 \text{m}^{-3}$ when the soil temperature at 5 cm depth was above 0 °C. The variation in soil water content depended strongly on precipitation (Fig. 1). Total annual precipitation in 2002 (555 mm) was similar to the average for the 21 years from 1980 to 2000. Other observed weather conditions during the measurement period were comparable to those during an average year (data not shown).

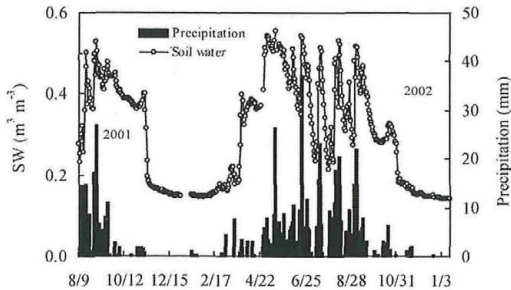


Fig. 1. Seasonal variation of precipitation and soil water at 5 cm depth (SW) from 9 August 2001 to 14 January 2003.

Daily mean air temperatures (T_a) and soil temperatures at 5 cm depth (T_s) increased gradually from January to July, and decreased from August (Fig. 2). Despite the strong incident radiation on the Tibetan Plateau, the alpine meadow ecosystem is still driven by the low air temperature, but with large annual variation. The annual range of the daily average air temperature was about 40 °C. The mean daily soil temperature at 5 cm depth was higher than the air temperature throughout the entire observation period. The largest value difference (disparity) between soil and air temperature appeared in winter.

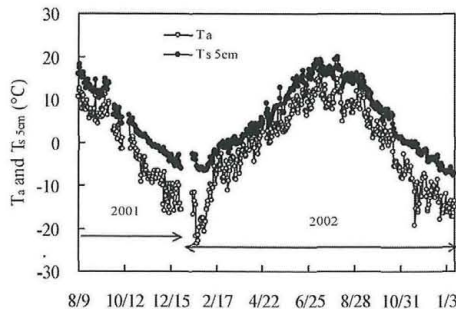


Fig. 2. Seasonal variation of mean daily air temperature (T_a) and soil temperature at 5 cm depth ($T_{s\ 5\text{cm}}$) from 9 August 2001 to 14 January 2003.

The alpine meadow is dominated by *Kobresia humilis*. The grassland around the study site usually was not grazed in summer. In August 2001 and 2002, the mean leaf area index (LAI) was 3.0 and 2.9, respectively, and the mean canopy height was about 30 cm both years.

Measurements

We placed the eddy covariance system on the flat *Kobresia* meadow where the fetch was more than 250 m. Other details of the study site are described elsewhere (GU & al. 2003).

The eddy covariance method was used to measure CO₂, sensible heat, and latent heat fluxes at 2.2 m above the ground. We used a CO₂/H₂O infrared analyzer (LI-7500; LI-COR, Inc., Lincoln, NE, USA) and a 3-dimensional supersonic anemometer (CSAT-3; Campbell Scientific, Inc., UT, USA) mounted on a horizontal bar extending from a tower at 2.2 m. Short-wave radiation from the sky and long-wave radiation from the land surface were measured with a net-radiometer (CNR-1; Kipp & Zonen B.V., The Netherlands) at 1.5 m above the ground. Air temperatures and humidity were measured with a temperature and relative humidity probe (HMP45C; CSI, USA). Soil water content was measured with TDR sensors (CS615; CSI, USA) at soil depths of 0.05, 0.2, and 0.5 m, and soil temperature was measured with thermocouples placed at 0.02, 0.05, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7 m depth under the ground surface. Soil surface temperature and soil heat flux (at 0.02 m below the surface) were measured with temperature probes (107; CSI, USA). Precipitation was measured with a tipping-bucket rain gauge (TE525MM; CSI, USA) 70 cm above the ground surface. Data were recorded with a data-logger (CR23X; CSI, USA) at 15-min intervals.

Gap filling

To fill gaps where the data were missing, we estimated nighttime ecosystem respiration by the Arrhenius equation (LLOYD & TAYLOR 1994), using the soil temperature at 5 cm depth from April to October 2002.

$$R_{E,night} = R_{E,T_{ref}} e^{(E_a/R)(1/T_{ref} - 1/T_k)} \quad (1)$$

where $R_{E,T_{ref}}$ is the ecosystem respiration rate at T_{ref} (283.16 K), E_a indicates the activation energy in J mol⁻¹, R is the gas constant (8.13 J K⁻¹ mol⁻¹), and T_k is the soil temperature at 5 cm depth. Details of the determination of parameters ($R_{E,T_{ref}} = 0.08$; $E_a = 88527$ J mol⁻¹) have been described by GU & al. 2003 and KATO & al. 2004a, b.

For daytime measurements, data gaps were filled by using the relationship between PPFD and NEE as shown by the following equation:

$$NEE = a_0 + a_1 * PPFD / (a_2 + PPFD) \quad (2)$$

The parameters a_0 , a_1 , and a_2 for a particular day were used for filling all of the gaps for that day. For nighttime measurements, on the other hand, data gaps of less than 3 h were filled by linear interpolation of the preceding and following data (LAFLEUR & al. 2001). If the gaps were longer than 3 h, they were filled by using Equation (1) and the soil temperature at 5 cm depth.

Results and Discussion

The seasonal pattern of NEE above the grassland canopy was estimated by the eddy covariance technique from 9 August 2001 to 14 January 2003 (Fig. 3). The start of the growing season was identified as the first week with a positive NEE after two or more consecutive weeks with negative NEE, and the end date as the beginning of the first of two or more consecutive weeks with negative NEE

(FALGE & al. 2002). The ecosystem absorbed CO₂ (NEE > 0) from early June to late September, and NEE reached its maximum value around the end of July in 2002. CO₂ was released from the soil in relatively large amounts in April and October. In winter, which were severe, NEE remained near zero.

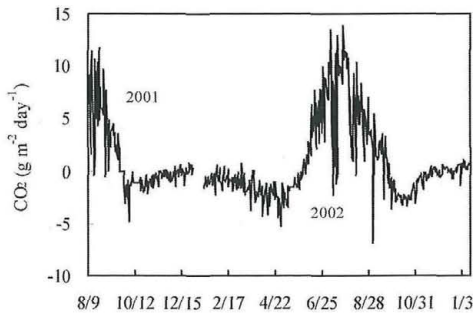


Fig. 3. Seasonal variation of net ecosystem CO₂ exchange from 9 August 2001 to 14 January 2003.

In this ecosystem, the biomass and LAI usually reached their maximum values in late July, and they maintained those values to early September (SHI & al. 2001). Generally, LAI is the major biological control on ecosystem carbon dynamics. However, environmental controls exert complicated influences on NEE. To examine these environmental controls, we compared the NEE and major meteorological variables during the growing period (from 9 August to 10 September) between 2001 and 2002 (Table 1).

Table 1. Comparison of NEE (g CO₂m⁻²) and major meteorological variables in late growing season from 9 September to 10 October for 2001 and 2002, respectively.

	Sum		Mean				
	NEE	Precipitation (mm)	R _n	T _a	T _{s(5cm)}	SW	LAI
2001	193	114.3	11.1	7.8	13.4	0.40	3.0
2002	132	107.9	11.1	8.9	14.7	0.40	2.8

Where R_n is net radiation (MJ m⁻²day⁻¹), T_a: air temperature, T_{s(5cm)}: soil temperature at 5 cm depth, SW: soil water content (m³ m⁻³) at 5 cm depth.

The results indicate that net radiation, precipitation, soil water, and LAI were similar during the same season between the two years. In contrast, NEE in 2001 was 47% greater than that in 2002, and the air and soil temperatures in 2002 was higher than that in 2001. We hypothesized that the difference in temperature between the two years caused the different NEE values.

To understand the effect of temperature on NEE, we further examined the

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relationship between PPFD and daytime NEE (equation (3)), using data from the late growth period (9 August to 10 September) for each of the two years, and calculated the NEE at light-saturation (NEE_{sat}) for different temperature ranges (4–6, 6–8, 8–10, 10–12, 12–14, 14–16, 16–18, 18–20, and >20 °C).

$$NEE = \frac{\alpha'_e * PPFD * NEE_{sat}}{NEE_{sat} + \alpha'_e PPFD} - R_e \quad (3)$$

where α'_e is the apparent quantum yield of the ecosystem.

There was a significant response of NEE_{sat} to the different temperature ranges in both years. NEE_{sat} increased with an increase of temperature in the low-temperature range, and reached its maximum value at around 15°C. When the temperature was higher than 15°C, however, NEE_{sat} decreased with further increases in temperature (Fig. 4, left).

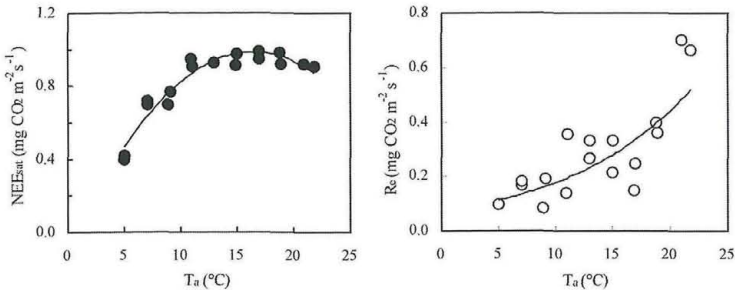


Fig. 4. Relationship between light-saturated net ecosystem exchange (NEE_{sat}) and air temperature (T_a) (left) and relationship between dark respiration (R_e) and air temperature (T_a) (right) in growth period for two years. Regression line is $NEE_{sat} = -0.004T_a^2 + 0.1308T_a - 0.0901$; $r^2 = 0.93$ and $R_e = 0.0706e^{0.0917T_a}$; $r^2 = 0.65$, respectively.

From equation (3), the ecosystem respiration in the dark can be considered to be R_e when the PPFD is equal to zero (the y-axis intercept). The dark respiration increased with an increase of temperature (Fig. 4, right), and, in particular, the increase was very fast when the temperature was higher than 15°C. The change in dark respiration with air temperature was similar to the relationship described by equation (1). The rapid increase in dark ecosystem respiration may be one of the reasons for the decrease in NEE_{sat} with increasing temperature at air temperatures higher than 15°C.

The daily integrated NEE and PPFD values for 9 August to 10 September were calculated for each of the two years. The average NEE in 2001 was signifi-

cantly higher than that in 2002 (Fig. 5, top; Table 1). In addition, we calculated the gross primary productivity (GPP) with following equation:

$$GPP = NEE - R_e \tag{4}$$

where ecosystem respiration (R_e) is computed from the relationship between nocturnal NEE and soil temperature at 5 cm depth ($T_{s(5\text{ cm})}$) in equation (1). The difference in GPP for the same PPFD is smaller than the difference in NEE between the two years (Fig. 6), we infer that the reason is the temperature influence.

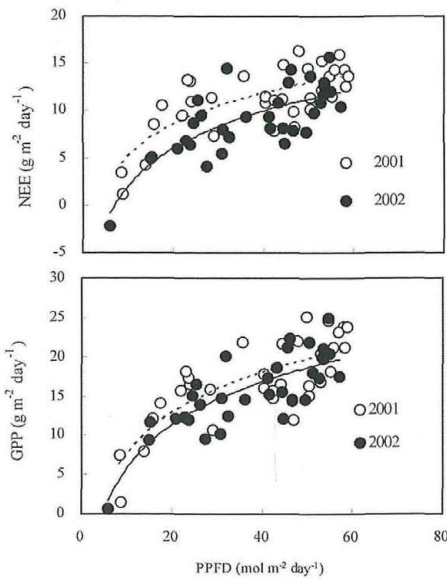


Fig. 5. Relationship of NEE/GPP and PPFD in late growth period for 2001 and 2002 respectively.

The difference in GPP between the two years (Fig. 5, bottom) may have resulted from differences in other environmental conditions (e.g., photorespiration or vegetation).

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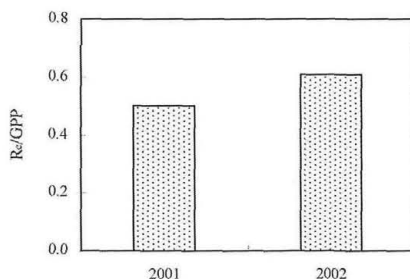


Fig. 6. Comparison of ratio of ecosystem respiration (R_e) to gross primary productivity (GPP) in late growth period from 9 Aug. to 10 Sep. for 2001 and 2002.

The influence of temperature on ecosystem respiration could further affect ecosystem GPP. We thus examined the ratio of ecosystem respiration (R_e) to GPP (R_e/GPP) for the two years (Fig. 6). The ratio for 2001 (0.50) was lower than that for 2002 (0.61), indicating that ecosystem respiration accounted for a higher proportion of GPP in 2002, perhaps partly because of the higher mean temperature in 2002, if we assume that the temperature dependence of respiration was the same between the two years. Therefore, the ecosystem respiration in 2002 may have been higher than that in 2001.

An alpine meadow ecosystem on the 3250-m-high Tibetan Plateau acted as a relatively large carbon sink, with a flux of about $290 \text{ g CO}_2 \text{ m}^{-2} \text{ year}^{-1}$ in 2002, despite the short growing season and low temperatures. The relatively high NEE at low temperatures suggests that the photosynthetic biochemistry of *Kobresia humilis* in the alpine meadow ecosystem is highly adapted to the alpine temperature environment.

By evaluating the response of NEE to PPFD at different temperatures during two years, we found that NEE was very sensitive to temperature variation in this alpine meadow ecosystem. Low temperature during the growing season restricts the NEE in subalpine forests (SMITH & KNAPP 1990, TESKEY & al. 1995). However, our study revealed that the optimum temperature for light-saturated NEE was around 15°C , and the light-saturated NEE decreased with an increase or decrease in the optimum temperature. The temperature optimum for photosynthesis has been reported for many high-altitude forest ecosystems (SMITH & KNAPP 1990, DELUCIA 1986, HUXMAN & al. 2003). The relationship between NEE and temperature in alpine meadow has been discussed by KATO & al. 2004b. GU & al. 2003 indicated that the NEE decreased as the air temperature increased when PPFD was higher than $1800 \mu\text{mol m}^{-2} \text{ s}^{-1}$. The decrease in the light-saturated NEE at high temperatures may have been caused by an increase in ecosystem respiration, which may have limited the carbon uptake during the growing season.

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