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Short communication

Strong temperature dependence and no moss photosynthesis in winter CO_2 flux for a *Kobresia* meadow on the Qinghai–Tibetan plateau

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Abstract

We examined the CO_2 exchange of a *Kobresia* meadow ecosystem on the Qinghai–Tibetan plateau using a chamber system. CO_2 efflux from the ecosystem was strongly dependence on soil surface temperature. The CO_2 efflux–temperature relationship was identical under both light and dark conditions, indicating that no photosynthesis could be detected under light conditions during the measurement period. The temperature sensitivity (Q_{10}) of the CO_2 efflux showed a marked transition around -1.0 °C; Q_{10} was 2.14 at soil surface temperatures above and equal to -1.0 °C but was 15.3 at temperatures below -1.0 °C. Our findings suggest that soil surface temperature was the major factor controlling winter CO_2 flux for the alpine meadow ecosystem and that freeze–thaw cycles at the soil surface layer play an important role in the temperature dependence of winter CO_2 flux.

Keywords: CO_2 gas diffusion; Freeze–thaw cycles; Microbial respiration; Moss photosynthesis; Spatial variability

The alpine meadow ecosystem on the Qinghai–Tibetan plateau experiences a very long and cold winter; these conditions limit biotic activities of the ecosystem, including respiration by plants and soil microorganisms. Eddy covariance measurements suggest that daytime ecosystem CO_2 exchange fluctuated greatly around zero in an alpine *Kobresia* meadow in winter (Kato et al., 2004a,b). It is unclear, however, whether photosynthesis plays a role in the ecosystem carbon budget and how the temperature environment affects daytime ecosystem respiration in winter. In other cold regions, such as arctic tundras and boreal bogs, ecosystem respiration has been observed even during winter (Fahnestock et al., 1998; Panikov and Dedysh, 2000). However, no data are available to clarify the contribution of photosynthetic uptake and ecosystem respiration in the alpine meadow ecosystem on the Qinghai–Tibetan plateau.

We expected that soil freeze–thaw cycles, which are an important characteristic of this cold region, might influence the CO_2 dynamics in the soil, as shown for tundra soil in laboratory experiments (Skogland et al., 1988; Larsen et al., 2002). In addition, we expect that moss on the plateau contributes to photosynthesis and thus to winter CO_2 flux. To characterize the winter CO_2 fluxes in this alpine meadow, we conducted field experiments to examine the ecosystem CO_2 exchange under different temperature and light conditions.

The experiments were done in a *Kobresia* meadow within a radius of 35 m from an eddy flux tower (for details, see Kato et al., 2004a,b). The climate at the study site is characterized by low temperatures and limited precipitation, with an annual average temperature of -1.7 °C and precipitation of 561 mm for 1981–2000. The aboveground parts of plants die in October (Li and Zhou, 1998). The soil surface under the plant canopies is partially covered by

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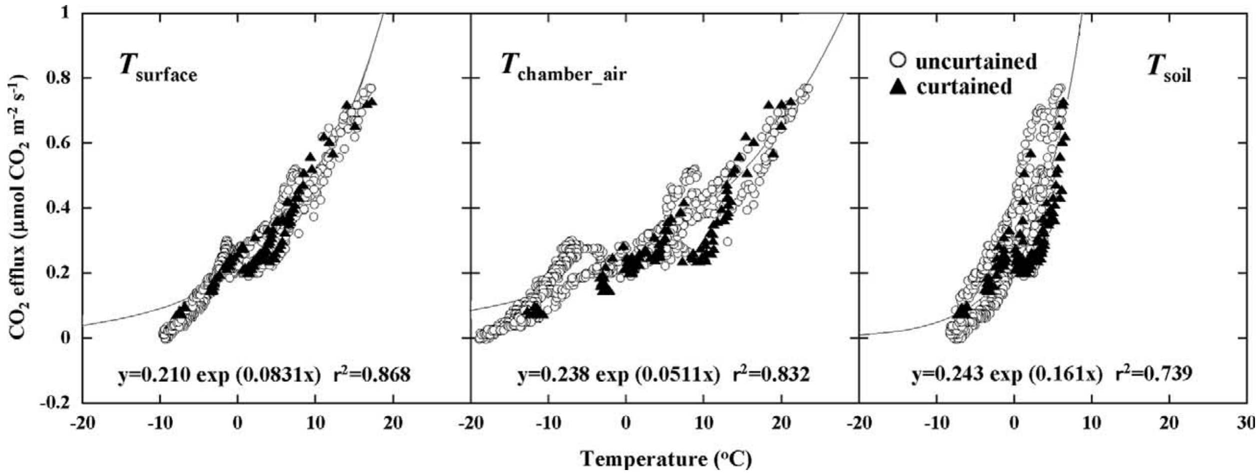

Fig. 1. Responses of the CO_2 efflux rate to the soil surface temperature ($T_{surface}$, left), the inner-chamber air temperature ($T_{chamber\_air}$, center), and temperature at 1 cm depth (T_{soil}, right) under uncurtained (open circle) and curtained (black triangle) conditions in the first experiment.

moss (*Distichium inclinatum (Hedw.) Bruch & Schimp.*, *Brachythecium* spp., and *Encalypta* spp.).

We conducted two field experiments to examine the CO_2 flux of the alpine meadow. In the first experiment, we measured the ecosystem CO_2 flux continuously from 1530 (Beijing Standard Time) on 21 February to 1600 on 22 February 2003 using an acrylic cylindrical chamber (150-mm diameter × 20-mm height). CO_2 moving into and out of the chamber was measured by a CO_2/H_2O analyzer (Li-6262, Li-Cor, Inc., Lincoln, NB, USA) contained in a heat-insulated box. The incident light was completely blocked with a light-proof curtain for nine 15 min intervals (beginning at 1600, 1700, 1800, 0830, 1000, 1100, 1200, 1300, and 1530).

In the second experiment, CO_2 flux was measured daily from 22 to 25 February 2003 for four 2 h intervals (2200–2400, 0930–1130, 1230–1430, and 1530–1730) in 15 plots (five plots in a day × 3 days; 22–23 Feb., 23–24 Feb., 24–25 Feb.) randomly selected around the same site used in the first experiment. The air stream moving into and out of the chamber (194-mm diameter × 88-mm height) was measured under both natural light and light-blocked conditions. The temperatures inside the chamber, at the soil surface, and at 1 cm depth were measured by copper–constantan manufactured thermocouples.

Moss chlorophylls were extracted in *N,N*-dimethylformamide and their concentrations were measured with a spectrophotometer (U-1000, Hitachi, Tokyo, Japan) at 663.8 and 646.8 nm. Litter samples were cut and collected, and soil samples were collected with a core sampler. Each sample was then weighed before and after oven drying at 65 °C for 48 h. The total carbon and nitrogen contents of the litter and of sieved soil samples were measured with an NC analyzer (Sumigraph NC-900, Sumika Chemical Analysis Service Ltd, Osaka, Japan). The depth of the thawed soil was measured by digging an ice pick into the top of the frozen layer at 1500 h.

To examine the relationships between the CO_2 effluxes and environmental factors, we fit an Arrhenius-type exponential function to the relationship between the flux and the temperatures inside the chamber, at the soil surface, and at 1 cm depth

$$F = R_0 \exp(kT) \qquad (1)$$

where F is the CO_2 emission rate (μmol CO_2 m^{-2} s^{-1}), R_0 is the CO_2 emission rate (μmol CO_2 m^{-2} s^{-1}) at 0 °C, k is the activation energy (°C^{-1}), and T is the temperature (°C). The Q_{10} value was calculated as follows:

$$Q_{10} = \exp(10k) \qquad (2)$$

The CO_2 efflux increased exponentially as temperature increased, and the exponential relationship was identical under the light and dark conditions, indicating that in the first experiment no significant photosynthetic activity could be detected using the current measuring system (Fig. 1).

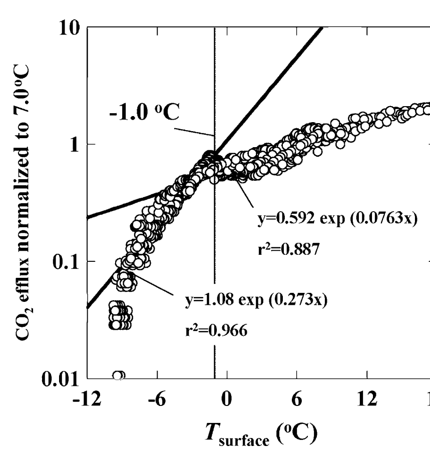

Fig. 2. Semilogarithmic graph of the CO_2 efflux versus the soil surface temperature in the first experiment. The CO_2 efflux data were normalized to the value of the regression curve at the surface temperature of the 7.0 °C in Fig. 1 (left); 0.376 μmol CO_2 m^{-2} s^{-1}. The exponential regression curves are fit to efflux data above and below −1.0 °C.

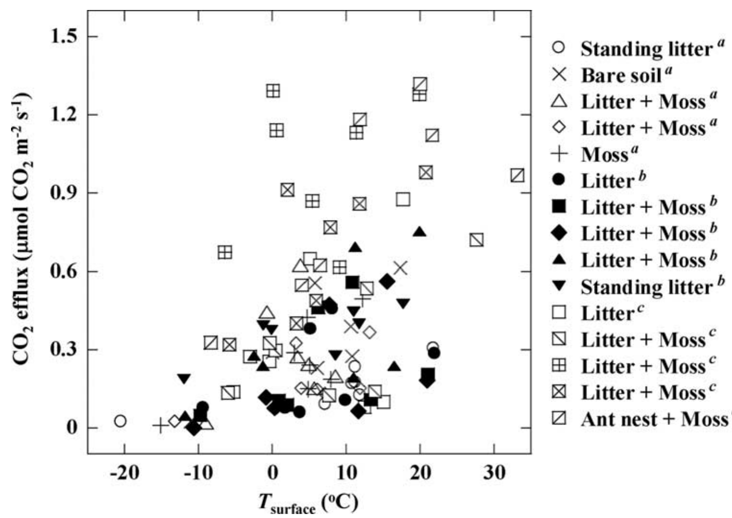

Fig. 3. Temperature response of the CO_2 efflux under various groundcover conditions in the second experiment. The CO_2 efflux was measured daily for four 2 h intervals (2200–2400, 0930–1130, 1230–1430, and 1530–1730) in 15 plots (5 plots × 3 days; 22–23 Feb. (a), 23–24 Feb. (b), 24–25 Feb. (c)). The daytime CO_2 efflux was measured under both natural light and light-blocked conditions.

The desiccation or freeze–thaw stress on moss could be the major reasons for the lack of (or extremely weak) photosynthetic activity, as suggested by Davey (1997) and Kennedy (1993). Moreover, the correlation coefficient between CO_2 flux and temperature was higher for the soil surface temperature than for air or soil temperatures. This suggests that soil surface temperature could play a more important role in the ecosystem carbon efflux than air or soil temperature.

The temperature sensitivity of the CO_2 efflux showed an abrupt change in temperature dependency around −1.0 °C (Fig. 2). Q_{10} was 2.14 ($r^2 = 0.887$) for temperatures above and equal to −1.0 °C and 15.3 ($r^2 = 0.966$) for temperatures below −1.0 °C. The abrupt change in the temperature dependency appears to be consistent with the laboratory observations of Elberling and Brandt (2003). Our evidence is not sufficient to elucidate the underlying mechanisms of the dramatic change, but we assume that both physical diffusion and biological controls may exhibit critical variations around the freezing temperature within soil. The soil freezing process also may play an important role in the rapid decrease of CO_2 efflux with the decline of temperature.

The CO_2 effluxes correlated positively with the soil surface temperature in the second experiment (Fig. 3).

Table 1
Partial correlation coefficients between temperature dependences of CO_2 efflux and environmental factors

	R_0	Q_{10}
Soil bulk density	−0.391	0.810
Soil water content	0.514	−0.495
Soil C	0.964	−0.496
Soil N	−0.953	0.315
Thawing depth	−0.413	−0.649
Litter dry weight	0.765	0.614
Litter water content	−0.169	−0.005
Litter C	−0.591	−0.419
Litter N	−0.834	0.100
Moss chlorophyll	−0.670	−0.492

Table 2
Regression models between temperature dependences of the CO_2 efflux and environmental factors

	Regression coefficients								Coefficient of determination
	Offset	Soil bulk density (g cm^{-3})	Soil C (g g^{-1})	Soil N (g g^{-1})	Thawing depth (m)	Litter dry weight (g m^{-2})	Litter N (g g^{-1})	Moss chlorophyll (mg m^{-2})	
R_0	0.273		69.1	−624		9.41×10^{-6}	−56.1	-2.35×10^{-3}	0.945***
Q_{10}	−0.754	4.20	−8.74		−8.30	2.83×10^{-5}		-6.43×10^{-3}	0.836*

Stepwise multi regression for the temperature dependence of the CO_2 efflux was conducted for 10 environmental factors presented in Table 1,but only five variables were selected for the R_0 and Q_{10}. *$P < 0.001$, **$P < 0.05$, ***$P < 0.01$.

The temperature dependency of CO_2 efflux derived from Eqs. (1) and (2) varied from 0.085 to 0.93 (mean = 0.30, CV = 0.76) for R_0 and from 1.12 to 2.23 (mean = 1.49, CV = 0.19) for Q_{10}. Linear regression analysis showed that R_0 was highly correlated to soil C and N, litter dry weight, litter N, and moss chlorophyll, whereas Q_{10} showed strong correlations with soil bulk density, thawing depth, and litter dry weight (Table 1). Using five parameters, a stepwise regression was used to construct the most parsimonious model of the soil respiration rate (Table 2). Nearly all the chosen parameters, including soil C, litter content, and moss chlorophyll content, were related to the organic matter content of the surface layer. The high correlations between Q_{10} and soil bulk density and between Q_{10} and thawing depth confirmed that the pore space of the surface soil was an important pathway for CO_2 gas diffusion (Table 1).

We, therefore, conclude that moss photosynthesis did not affect the ecosystem CO_2 flux significantly. By strongly suppressing the CO_2 gas diffusion, soil surface freezing was the major determinant of the ecosystem CO_2 efflux of this alpine meadow.

Acknowledgements

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References

Davey, M.C., 1997. Effects of short-term dehydration and rehydration on photosynthesis and respiration by Antarctic bryophytes. Environmental and Experimental Botany 37, 187–198.

Elberling, B., Brandt, K.K., 2003. Uncoupling of microbial CO_2 production and release in frozen soil and its implications for field studies of arctic C cycling. Soil Biology & Biochemistry 35, 263–272.

Fahnestock, J.T., Jones, M.H., Brooks, P.D., Walker, D.A., Welker, J.M., 1998. Winter and early spring CO_2 efflux from tundra communities of northern Alaska. Journal of Geophysical Research 103, 29023–29027.

Kato, T., Tang, Y., Gu, S., Cui, X., Hirota, M., Du, M., Li, Y., Zhao, X., Oikawa, T., 2004a. Carbon dioxide exchange between the atmosphere and an alpine meadow ecosystem on the Qinghai–Tibetan plateau, China. Agricultural Forest Meteorology 124, 121–134.

Kato, T., Tang, Y., Gu, S., Hirota, M., Cui, X., Du, M., Li, Y., Zhao, X., Oikawa, T., 2004b. Seasonal patterns of gross primary productivity and ecosystem respiration in an alpine meadow ecosystem on the Qinghai–Tibetan plateau, China. Journal of Geophysical Research Atmosphere 109, D12109.

Kennedy, A.D., 1993. Photosynthetic response of the Antarctic moss *Polytrichum alpestre* Hoppe to low temperatures and freeze–thaw stress. Polar Biology 13, 271–279.

Larsen, K.S., Jonasson, S., Michelson, A., 2002. Repeated freeze–thaw cycles and their effects on biological processes in two arctic ecosystem types. Applied Soil Ecology 21, 187–195.

Li, W., Zhou, X., 1998. Ecosystems of Qinghai-Xizang (Tibetan) Plateau and Approach for their Sustainable Management: A Series of Studies on Qinghai-Xizang (Tibetan) Plateau. Guangdong Science and Technology Press, Guangzhou, China (in Chinese).

Panikov, N.S., Dedysh, S.N., 2000. Cold season CH_4 and CO_2 emission from boreal peat bogs (west Siberia): winter fluxes and thaw activation dynamics. Global Biogeochemical Cycles 14, 1071–1080.

Skogland, T., Lomeland, S., Goksøyr, J., 1988. Respiratory burst after freezing and thawing of soil: experiments with soil bacteria. Soil Biology & Biochemistry 20, 851–856.