Altitudinal variation of ecosystem CO_2 fluxes in an alpine grassland from 3600 to 4200 m

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Abstract

Aims

Recent studies have recognized the alpine grasslands on the Qinghai–Tibetan plateau as a significant sink for atmospheric CO_2. The carbon-sink strength may differ among grassland ecosystems at various altitudes because of contrasting biotic and physical environments. This study aims (i) to clarify the altitudinal pattern of ecosystem CO_2 fluxes, including gross primary production (GPP), daytime ecosystem respiration ($Re_{daytime}$) and net ecosystem production (NEP), during the period with peak above-ground biomass; and (ii) to elucidate the effects of biotic and abiotic factors on the altitudinal variation of ecosystem CO_2 fluxes.

Methods

Ecosystem CO_2 fluxes and abiotic and biotic environmental factors were measured in an alpine grassland at four altitudes from 3600 to 4200 m along a slope of the Qilian Mountains on the northwestern Qinghai–Tibetan Plateau during the growing season of 2007. We used a closed-chamber method combined with shade screens and an opaque cloth to measure several carbon fluxes, GPP, $Re_{daytime}$ and NEP, and factors, light-response curve for GPP and temperature sensitivity of $Re_{daytime}$. Above- and below-ground biomasses and soil C and N contents at each measurement point were also measured.

Important Findings

(i) Altitudinal pattern of ecosystem CO_2 fluxes: The maximum net ecosystem CO_2 flux (NEP_{max}), i.e. the potential ecosystem CO_2 sink strength, was markedly different among the four altitudes. NEP_{max} was higher at the highest and lowest sites, approximately -7.4 ± 0.9 and -6.7 ± 0.6 µmol CO_2 m^{-2} s^{-1} (mean $\pm$ standard error), respectively, but smaller at the intermediate altitude sites (3800 and 4000 m). The altitudinal pattern of maximum gross primary production was similar to that of NEP_{max}. The $Re_{daytime}$, however, was significantly higher at the lowest altitude (3.4 ± 0.3 µmol CO_2 m^{-2} s^{-1}) than at the other three altitudes.

(ii) Altitudinal variation of vegetation biomass: The above-ground biomass was higher at the highest altitude (154 ± 27 g DW m^{-2}) than at the other altitudes, which we attribute mainly to the large biomass in cushion plants at the highest altitude. The small above-ground biomass at the lower altitudes was probably due to heavy grazing during the growing season.

(iii) Features of ecosystem CO_2 fluxes: $Re_{daytime}$ and GPP were positively correlated with above-ground biomass. The low ratio of $Re_{daytime}$ to GPP at either the measurement point or the site level suggests that CO_2 uptake efficiency tends to be higher at higher altitudes, which indicates a high potential sink strength for atmospheric CO_2 despite the low temperature at high altitudes. The results suggest that the effect of grazing intensity on ecosystem carbon dynamics, partly by decreasing vegetation biomass, should be clarified further.

Keywords: ecosystem respiration • grazing • gross primary production • net ecosystem production • Qinghai–Tibetan Plateau

INTRODUCTION

Alpine ecosystems, which cover ~3% of Earth's land area (Körner 2003), have received increasing attention in light of recent environmental changes for two main reasons. First, among terrestrial ecosystems, alpine ecosystems are predicted to be among the most sensitive and vulnerable to environmental changes, such as global warming and land-use change (e.g. Diaz *et al.* 2003, Körner 2003). Focusing on the effects of global warming, recent attention has been paid increasingly to the long-term monitoring of alpine environments, vegetation and ecosystem functions. For example, the Global Observation Research Initiative in Alpine Environments (GLORIA 2009) (http://www.gloria.ac.at/) has established a worldwide monitoring network to monitor alpine vegetation and environments to detect impacts of global climate change (e.g. Swerhun *et al.* 2009). The CARBOMONT (2009) project in Europe (http://www.uibk.ac.at/carbomont/) aims to quantify the sources, sinks and fluxes of carbon in non-forest mountain ecosystems and to examine effects of changes of climate and land use on carbon dynamics in mountain ecosystems (e.g. Wohlfahrt *et al.* 2008).

Second, alpine ecosystems contain extensive soil organic carbon (SOC) reserves (Körner 2003, Wang *et al.* 2002) because under low temperatures, rates of organic matter decomposition are moderate compared with primary productivity (Bowman *et al.* 1993, Kato *et al.* 2006). For example, Ni (2002) reported that an alpine meadow on the Tibetan plateau at ~3200 m above sea level contains an extensive SOC pool of 11.3 Pg C. Ohtsuka *et al.* (2008) reported a unique large SOC pool in a higher altitude zone (136.8 t-C ha^{-1} at 4950 m a.s.l.), even though this altitude is almost the edge of the habitat in which plants can survive on the Tibetan Plateau (hereinafter, we refer to this zone as the vegetation line).

For these reasons, clarifying the impacts of environmental changes on carbon dynamics in such alpine ecosystems is of great interest and crucial importance for predicting future global climate change (IPCC 2007). However, we still have no clear picture of carbon dynamics in alpine ecosystems in particular nor of the altitudinal changes of ecosystem CO_2 fluxes in such high mountain ecosystems. Without relevant knowledge, we will be able to foresee neither the changes in alpine ecosystems in response to future climate changes nor those of the global terrestrial ecosystem.

Carbon dynamics of a particular altitude have been observed in some alpine ecosystems, including the Alps, the Rocky Mountains and the Qinghai–Tibetan Plateau (Hirota *et al.* 2006, Kammer *et al.* 2009, Kato *et al.* 2006, Koch *et al.* 2008, Ohtsuka *et al.* 2008, Welker *et al.* 1999, 2004, Wohlfahrt *et al.* 2008). Almost all these studies have been conducted at altitudes lower than ~3500 m a.s.l. (but see Ohtsuka *et al.* 2008); little information is available about the carbon dynamics at higher altitudes. As high ecosystems seem to be more sensitive to environmental changes, any information about

them would provide important insights into not only alpine ecosystem carbon dynamics but also into the fundamentals of alpine ecosystem ecology.

To fill the gap in our knowledge about high-altitude ecosystems, we here report the ecosystem CO_2 flux and the characteristics of its altitudinal change across a gradient from an alpine meadow to the vegetation line in an extremely high alpine ecosystem on the Qinghai–Tibetan Plateau. The Plateau (~4000 m a.s.l.), 'the third pole of the Earth', is the largest geographical unit on the Eurasian continent and is a super site for carbon dynamics research (e.g. Gu *et al.* 2003; Hirota *et al.* 2006; Kato *et al.* 2006; Saito *et al.* 2009; Zhao *et al.* 2006). All the Qinghai–Tibetan Plateau super-site studies have pointed to the possibility that the large alpine ecosystem is very likely a huge sink for atmospheric CO_2, at least for now. We thus tried to quantify the major ecosystem CO_2 fluxes—gross primary production (GPP), daytime ecosystem respiration ($Re_{daytime}$) and net ecosystem production (NEP)—in relation to the vegetation and soil properties along an altitudinal gradient from 3600 to 4200 m a.s.l. The primary aims of our study were to clarify the altitudinal pattern of the ecosystem GPP, $Re_{daytime}$ and NEP and to elucidate the effects of biotic and abiotic factors on their altitudinal variations.

MATERIALS AND METHODS

Study site

We conducted our research in an alpine grassland along a southwest-facing slope on the Qilian Mountains in the Qinghai–Tibetan Plateau. The mountain slope is located ~12 km northeast of the Haibei Alpine Meadow Ecosystem Research Station, Northwest Plateau Institute of Biology, Chinese Academy of Sciences. We set four study sites on the slope along an altitudinal gradient, at 3600, 3800, 4000 and 4200 m (37°41′55″N, 101°21′35″E, 3600 m a.s.l., to 37°42′34″N, 101°22′37″E, 4200 m a.s.l.; Fig. 1). At each altitude, we decided the location of study site at a relatively gentle slope, so as to reduce possible noise from topographical heterogeneity, to make altitudinal comparison in a 'normalized' way in terms of topography and to set our observation system as well as to take a necessary number of sampling points at each altitude site because a steep slope usually has very sparse or even no vegetation. The highest site is on the vegetation limit, above which no substantial vegetation cover exists. The alpine grassland along the slope is often an important pasture for summer grazing of Tibetan sheep and yaks from June to October (Zhou *et al.* 2005). In this area, semi-nomadic herders set up a base camp at ~3400 to 3600 m, and almost all the alpine grasslands in this area are grazed by livestock every year. The annual average temperature and precipitation recorded at the Research Station in 1981–2000 were −1.7°C and 561 mm.

Meteorological measurements were made at each site every 30 min starting July 2007 from a meteorological tower at each altitude equipped with sensors and a data logger (HOBO
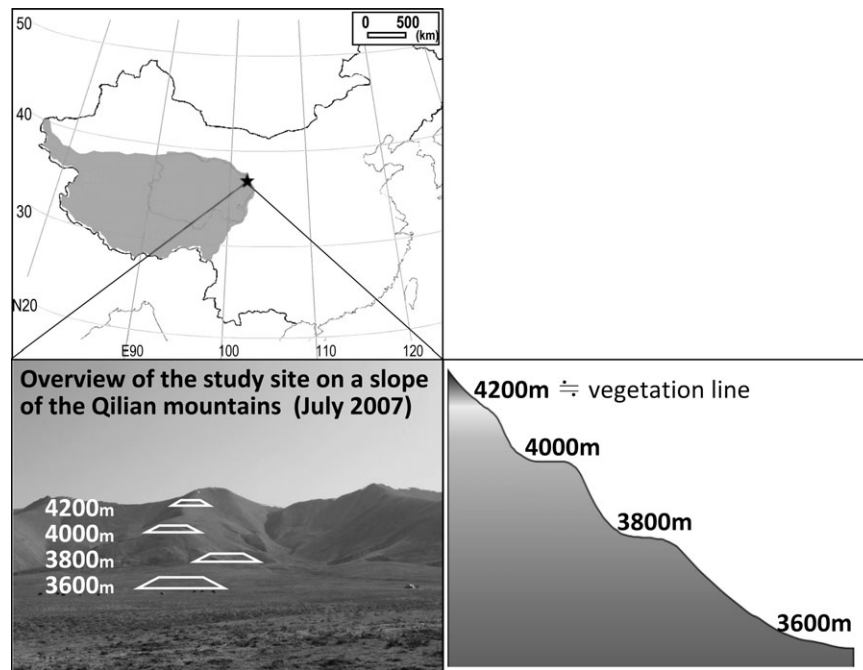
Figure 1: location of the study area and layout of the four measurement sites at altitudes of 3600, 3800, 4000 and 4200 m.

Weather Station, Onset Computer, Bourne, MA, USA). From one tower at each altitude, we monitored air temperature, relative humidity (RH), soil temperature at 5-cm depth and volumetric soil water content (SWC) (%) at 5-cm depth with permanently installed instruments (air temperature and RH, S-THA-M006; soil temperature, S-TMB-M006; volumetric SWC, S-SMA-M003, Onset Computer).

Net ecosystem CO_2 exchange

We randomly determined 16 measurement points at each of the four sites around the meteorological towers and then installed rigid pipe-shaped PVC basements (15-cm diameter × 5-cm height) on 20 July 2007, >1 week before the flux measurement, to reduce possible disturbance to vegetation and soil during the measurement of CO_2 flux. At the 16 measurement points at each altitude, we measured the net ecosystem CO_2 exchange (NEE), soil temperature and soil moisture between 10:00 and 18:00 (Beijing Standard Time) for 6 days, from 27 July to 1 August 2007, during the main growing season.

We measured NEE repeatedly by using four transparent chambers at each of two altitude sites in parallel every day. In total, NEE was measured at each site at least 3 days. The chamber (15-cm diameter × 15-cm height with a wall thickness of 2 mm) was equipped with a CO_2 probe (GMP343, Vaisala, Helsinki, Finland), a very small photosynthetically active radiation (PAR) sensor (SQ-410, Apogee Instruments, Inc., Logan, UT, USA), an air temperature/RH probe (HD9809T, Delta OHM S.R.L., Padua, Italy) and two thermocouples for soil temperature at 5-cm depth. The PAR sensor was attached to the top-inside surface on the chamber with glue. A micro-fan was set inside the chamber to mix the air

gently. The chamber was placed on the PVC basement and sealed with silicone tape during measurements. All the data were recorded in a data logger (Thermic 2300A, Etodenki, Tokyo, Japan) every 2 s during each 120-s closed-chamber period. During the closed-chamber periods, we were able to maintain the air temperature within the chamber at <1.3°C within the outside air temperature. We calculated the NEE (μmol CO_2 m^{-2} s^{-1}) from the temporal change of CO_2 concentration within the closed-chamber period according to the following formula:

$$\text{NEE} = d\text{CO}_2/dt \times (P/[R(273.15+T)]\,V)/A, \quad (1)$$

where $d\text{CO}_2/dt$ is the slope of chamber CO_2 concentration against time (μmol mol^{-1} s^{-1}), P is the atmospheric pressure (kPa), R is the gas constant (8.314 kPa m^3 K^{-1} mol^{-1}), T is the air temperature inside the chamber (°C), V is the chamber volume (m^3) and A is the surface area under the chamber (m^2). We used the data only for the period from 20 to 90 s after chamber closure. To measure the Re$_{\text{daytime}}$ and to obtain light-response curves for each measurement point, right after NEE measurement under 100% light we measured NEE under 65% light by using a shade screen and then 0% light by using an opaque cloth over the chamber. At each measurement point, it took ~8 min to measure NEE under all three light conditions. To compare NEE among the four altitudes under weather conditions as similar as possible, we used only the data obtained under clear skies. We did not use data collected under cloudy or rainy conditions, which accounted for 18% of the total data. Volumetric soil moisture content (m^3 m^{-3}) near each chamber was measured immediately after flux

measurement in the 0- to 12-cm soil depth layer by soil moisture probe (CD620, Campbell Scientific Inc., Orem, UT, USA).

Data analysis

CO_2 uptake by the ecosystem was treated as negative and CO_2 emission to the atmosphere as positive. We determined NEP as NEE under full light with the chamber uncovered. The relationship between NEP and PAR was described by a rectangular hyperbola using the curve-fitting technique of Thornley and Johnson (1990):

$$NEP = (\alpha NEP \times NEP_{max} \times PAR)/(\alpha NEP \times PAR + NEP_{max}) + R, \quad (2)$$

where αNEP is the initial slope of the rectangular hyperbola, also called the 'apparent quantum yield', NEP_{max} is the asymptotic approach to a maximum NEP at high light intensity and R is the y-axis intercept or apparent dark respiration. The observed $Re_{daytime}$ was regressed exponentially against soil temperature at a depth of 5 cm (ST5):

$$Re_{daytime} = a \times \exp(ST5 \times b), \quad (3)$$

where a and b are coefficients. The Q_{10} value, which is the rate of change of $Re_{daytime}$ over a change of 10°C in soil temperature (Raich and Schlesinger 1992), was expressed as

$$Q_{10} = \exp(10 \times b). \quad (4)$$

GPP was calculated as follows by using $Re_{daytime}$ and the NEP measured immediately beforehand under full light:

$$GPP = NEP + Re_{daytime}. \quad (5)$$

The relationship between GPP and PAR was described by a rectangular hyperbola:

$$GPP = (\alpha GPP \times GPP_{max} \times PAR)/(\alpha GPP \times PAR + GPP_{max}). \quad (6)$$

where αGPP is the initial slope of the rectangular hyperbola, also called the 'apparent quantum yield of GPP', and GPP_{max} is the asymptotic approach to a maximum GPP at high light intensity. We determined each parameter in equations (2, 3 and 6) for each measurement cycle by non-linear regression, minimizing the root-mean square error based on the Gauss–Newton method in SYSTAT (Systat Software, Inc., version 11).

To compare ecosystem CO_2 fluxes among the four altitudes, from equations (3 to 6), we calculated the three ecosystem CO_2 fluxes GPP_{max}, NEP_{max} and $Re_{daytime}$; αGPP, which indicates the initial slope of ecosystem photosynthesis in relation to radiation; and Q_{10}, which is the temperature sensitivity of $Re_{daytime}$.

Vegetation and soil properties

After the final flux measurement, we harvested the above-ground and below-ground biomass up to 5-cm soil depth at all sites on 2 August. We collected the green and live biomass of above-ground parts. The above-ground biomass was divided by species before being dried at 80°C for 2 days and weighed. The below-ground biomass was washed gently in running water and then dried at 80°C for 3 days and weighed. Species rich-

ness was measured as the total number of species within each measurement point. Diversity (Shannon index, H', Shannon and Weaver 1949) was calculated as

$$H = -\sum_{i=1}^{s} P_i \times \ln(P_i), \quad (7)$$

where s is the total number of species collected and P_i is the relative above-ground biomass of species i at the measurement site (Equation 7).

Soil samples in the surface 0- to 5-cm soil layer at each measurement point were collected with a soil sampler (DIK-1815, Daiki Rika Kogyo Co., Ltd., Saitama, Japan, 50 ml). After the roots were carefully removed, the soil samples were air-dried, triturated by pestle and passed through a 1-mm sieve. Total soil carbon and nitrogen content in the soil samples were measured with an NC analyzer (Sumigraph NC-900, Sumika Chemical Analysis Service, Ltd., Tokyo, Japan).

Statistical analyses

Statistical analysis was performed with version 11 of SYSTAT. All the data among the four altitudes were analyzed by one-way analysis of variance and then differences among means were analyzed using Tukey–Kramer multiple comparison tests, with the level of statistical significance taken as $P < 0.05$.

RESULTS

Environmental variables

Air temperature decreased with increasing altitude on the study slope; we estimated the lapse rate during the summer of 2007 to have been ~0.7°C per 100 m. The soil temperature at 5-cm depth, in contrast to air temperature, showed a different pattern (Table 1): soil temperature at 3600 m was markedly higher (9.9°C) than that at the three higher sites. RH at the two lower sites (3600 and 3800 m) was approximately double that at the 4200-m site. Altitudinal variation of SWC was similar to that of RH. SWC at 3600 m was highest (48.0%); SWC decreased with increasing altitude and was lowest (11.2%) at 4200 m.

Vegetation and soil properties

Vegetation biomass and species composition changed drastically with altitude among the four sites. The above-ground

Table 1: environmental variables along the altitudinal gradient from 3600 to 4200 m recorded at meteorological stations from July to August 2007

Altitude (m)	Air temperature (°C)	ST5 (°C)	RH (%)	SWC (%, m³ m⁻³)
4200	7.5 (0.3)[a]	5.6 (0.7)[a]	31.4 (5.2)[a]	11.2 (1.2)[a]
4000	8.9 (0.3)[b]	6.2 (0.2)[a]	no data	31.5 (2.5)[b]
3800	10.3 (0.2)[c]	6.2 (0.2)[a]	62.7 (2.0)[b]	33.6 (1.5)[b]
3600	12.0 (0.2)[d]	9.9 (0.5)[b]	63.5 (2.1)[b]	48.0 (1.0)[c]

RH at the 4000-m site could not be observed owing to a wiring disconnection. Differences between the altitudes at $P < 0.05$ are noted by different letters.

biomass and below-ground biomass up to 5-cm soil depth were highest at the highest altitude (154 and 1615 g DW m^{-2}, respectively, at 4200 m). The 4200-m site was dominated by one of the typical 'cushion' alpine species, *Androsace alaschanica*, which occupied 68.7% of the total above-ground biomass (Table 2). Although there was no significant difference in above-ground biomass among the other three altitudes, the lowest altitude (3600 m) showed the second-largest value, 121 g DW m^{-2}, and the 3800-m site showed the smallest value, 78 g DW m^{-2} (Table 3). As with above-ground biomass, below-ground biomass changed similarly with altitude from 3600 to 4000 m (1314, 907 and 1026 g DW m^{-2}). Species composition differed with altitude among the four sites (Table 2). *Kobresia pygmaea* dominated at 4000 m, while *Potentilla nivea* L. dominated at the 3800 and 3600 m. Species richness and diversity

(H') differed among the four altitudes, and we divided the sites into two groups on this basis (Table 3): at the lowest site (3600 m), species diversity was higher than at the other three sites. The ratio of above-ground biomass to below-ground biomass up to 5-cm soil depth increased gradually with increasing altitude: 0.07, 0.09, 0.11 and 0.12 (Table 3).

Contents of total carbon and total nitrogen in the surface soil also varied with altitude (Table 3). Contents decreased significantly with increase of altitude from 3600 to 4000 m, but those at 4200 m were somewhat larger than those at 4000 m. Differences between the C : N ratios among the four altitudes were not significant; the ratio was ~12 (Table 3).

Ecosystem CO_2 exchange

GPP_{max} and $Re_{daytime}$ at the site level differed significantly among the four sites and showed different altitudinal pattern between the two fluxes (Table 4). GPP_{max} was largest at 4200 m (-8.78 µmol CO_2 m^{-2} s^{-1}) and second largest at 3600 m (-7.25 µmol CO_2 m^{-2} s^{-1}) and at the two intermediate altitudes was approximately -5.4 µmol CO_2 m^{-2} s^{-1} (Table 4). $Re_{daytime}$ was significantly higher at the lowest altitude (3600 m: 3.36 µmol CO_2 m^{-2} s^{-1}) than at the three higher altitudes (1.54, 1.80 and 1.92 µmol CO_2 m^{-2} s^{-1} at 3800, 4000 and 4200 m, respectively, Table 4). NEP_{max} was largest at the highest altitude (4200 m: -7.35 µmol CO_2 m^{-2} s^{-1}) and second largest at the lowest altitude (3600 m: -6.66 µmol CO_2 m^{-2} s^{-1}).

At 4200 and 4000 m, the initial slope of GPP against light intensity (αGPP) was significantly higher than those at the lower two sites (Table 4). The temperature sensitivity of the $Re_{daytime}$ (Q_{10}) at the highest site (4200 m) was significantly smaller than at the other sites (Table 4).

The two ecosystem CO_2 fluxes, GPP_{max} and $Re_{daytime}$, were strongly positively correlated with the vegetation biomass. The above-ground biomass showed a higher non-linear correlation with GPP_{max}, while the total biomass showed a higher linear correlation with $Re_{daytime}$ (Fig. 2). For GPP_{max}, the relationship was best expressed by a hyperbolic regression; the estimated parameters of the regression differed among the four sites

Table 2: main dominant species along the altitudinal gradient from 3600 to 4200 m (relative biomass %)

Altitude (m)	Dominant species
4200	*Androsace alaschanica* (68.7), *Oxytropis kansuensis* Bunge (8.3), *Kobresia pygmaea* (8.0), *Leontopodium nanum* (3.5), *Poa* sp. (2.9)
4000	*Kobresia pygmaea* (35.7), *A.alaschanica* (22.6), *Potentilla nivea* L.(10.3), *Poa sp.* (8.5) *Kobresia humilis* (7.9)
3800	*Potentilla nivea* L. (32.9), *K.pygmaea* (21.9), *K.humilis* (21.4), *Thalictrum alpinum* Linn. (6.1), *Leontopodium leontopodioides* (5.3)
3600	*Potentilla nivea* L. (15.0), *Saussurea* sp. (14.9), *T.alpinum* Linn. (13.6), *Potentilla* var. *bifurca* Linn. (9.3), *Poa* sp. (8.2)

Table 3: vegetation and soil properties along the altitudinal gradient from 3600 to 4200 m (mean with standard error in parentheses, $n = 16$)

	Vegetation properties					Soil properties		
				Species richness per chamber		T-C content		
Altitude m	AGB g DW m^{-2}	BGB[#1]	AGB : BGB ratio[#2]	176.6 cm^{-2}	Diversity H'	%	T-N content	C : N ratio
4200	154.1 (26.8)[a]	1615.3 (243.7)[a]	0.12 (0.02)[a]	5.4 (0.7)[a]	1.3 (0.2)[a]	5.1 (0.7)[a]	0.42 (0.03)[a]	11.8 (0.7)[a]
4000	115.3 (27.5)[b]	1025.9 (276.3)[b]	0.11 (0.04)[ab]	5.2 (0.4)[a]	1.5 (0.1)[a]	4.7 (0.3)[a]	0.40 (0.02)[a]	11.7 (0.2)[a]
3800	78.2 (12.4)[b]	907.4 (102.7)[b]	0.09 (0.02)[b]	5.6 (0.5)[a]	1.9 (0.2)[b]	7.8 (0.3)[b]	0.65 (0.02)[b]	11.9 (0.1)[a]
3600	120.9 (26.7)[b]	1314.4 (109.4)[a]	0.07 (0.02)[b]	8.4 (0.6)[b]	2.4 (0.1)[c]	10.2 (0.6)[c]	0.85 (0.05)[c]	12.0 (0.1)[a]

Differences among the altitudes at $P < 0.01$ are noted by different letters.
[#1] BGB is root biomass up to 5 cm soil depth.
[#2] AGB : BGB is the ratio of above-ground biomass to below-ground biomass up to 5 cm soil depth.
AGB, above-ground biomass; BGB, below-ground biomass.

Table 4: ecosystem CO_2 flux at community level (NEP_{max}, GPP_{max}, $Re_{daytime}$) and characteristics of the responses of GPP to light intensity (αGPP) and $Re_{daytime}$ to soil temperature at 5-cm depth (Q_{10}) (mean with standard error in parentheses, $n = 16$)

Altitude m	Ecosystem CO_2 flux			Parameters of GPP and daytime Re	
	NEP_{max} $\mu mol\ CO_2\ m^{-2}\ s^{-1}$	GPP_{max}	$Re_{daytime}$	αGPP mol CO_2 mol photon^{-1}	Q_{10}
4200	−7.35 (0.90)[a]	−8.78 (1.14)[a]	1.54 (0.26)[a]	−0.038 (0.007)[a]	1.18 (0.33)[a]
4000	−5.10 (0.43)[b]	−5.45 (0.68)[b]	1.80 (0.26)[a]	−0.028 (0.004)[b]	1.99 (0.41)[b]
3800	−4.93 (0.67)[b]	−5.40 (0.68)[b]	1.92 (0.14)[a]	−0.017 (0.003)[c]	2.46 (0.40)[b]
3600	−6.66 (0.67)[a]	−7.25 (0.82)[c]	3.36 (0.28)[b]	−0.021 (0.003)[c]	1.79 (0.09)[b]

Differences among the altitudes at $P < 0.01$ are noted by different letters.

(Fig. 2a). The $Re_{daytime}$ showed a positive linear relationship with biomass, but the relationship between $Re_{daytime}$ and total biomass, i.e. gradient and *y*-intercept of the linear regression equation, differed among the four sites (Fig. 2b).

The ratio of d $Re_{daytime}$ to GPP_{max} significantly differed among the four altitudes and decreased with increasing altitude (Fig. 3).

DISCUSSION

Altitudinal changes of ecosystem CO_2 fluxes and vegetation biomass in a high alpine ecosystem

Little information is available about ecosystem CO_2 fluxes at high altitudes. This study is perhaps the first attempt to characterize the ecosystem CO_2 fluxes in relation to vegetation and soil properties along a high-altitudinal gradient that reaches the vegetation limit. We found a u-shaped pattern of vegetation biomass (Table 3) and ecosystem CO_2 fluxes along the gradient (Table 4), with higher values at the highest and lowest of the four altitudes sampled. This altitudinal pattern of vegetation biomass appears inconsistent with the widespread belief that alpine plant biomass at higher altitude decreases with increasing elevation (e.g. Körner 2003). One of the reasons for the pattern we observed is the impact of grazing during the growing season. Despite the lack of detailed information on grazing intensity at various altitudes in this study area, the grazing intensity of sheep and yaks must have been much higher at altitudes ~3800 m because almost all the tents of nomads were located ~3600 to 3800 m a.s.l. . Galen (1990) demonstrated a similar altitudinal pattern of herbivore (elk) impact on the perennial *Polemonium viscosum* near the Rocky Mountain treeline in Colorado. An investigation of the SOC pool in alpine to nival zones along an altitudinal gradient from 4400 to 5300 m on the Qinghai–Tibetan Plateau by Ohtsuka *et al.* (2008) showed the potential impact of grazing on the SOC pool: the SOC pool at the lower altitudes was much lower than that at the higher altitudes and reached its peak at ~5000 m a.s.l., around the vegetation limit. In this study, such the altitudinal change of ecosystem CO_2 fluxes and vegetation biomass from 3600 to 4200 m resulted from complex effects of biotic environmental factors (i.e. grazing) and abiotic environmental factors (such as temperature and soil moisture condi-
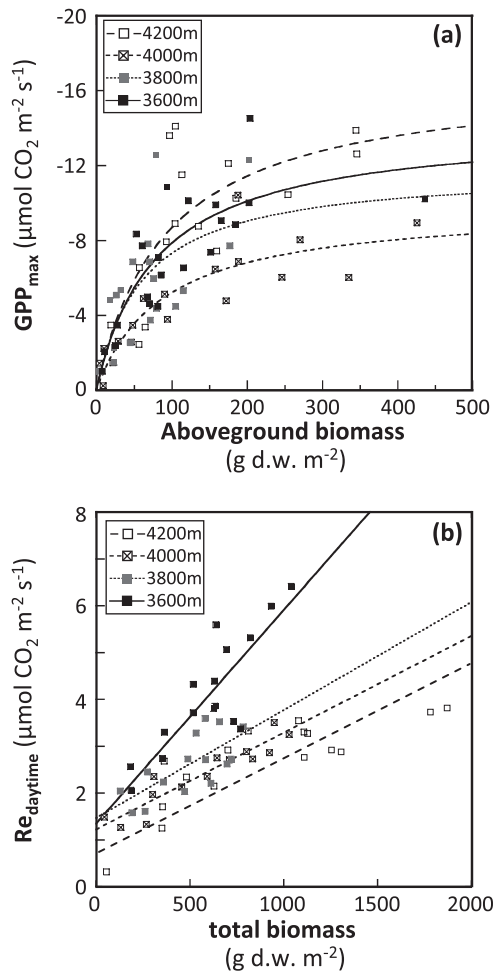
tion) that altered simultaneously along with altitude. We could not evaluate the biotic and abiotic environmental effects on ecosystem CO_2 fluxes and vegetation biomass individually. Hence, further studies focusing on grazing impact by conducting exclosure experiments in the alpine grassland are needed to clarify not only the grazing impact but also intrinsic eco-physiological features, which deeply related in ecosystem CO_2 fluxes in alpine grassland.

Importance of vegetation biomass and temperature as the major determinants of GPP and $Re_{daytime}$

Many previous studies of ecosystem CO_2 flux in grassland ecosystems have demonstrated that vegetation biomass and its relevant parameters, such as leaf area index, leaf nitrogen content and chlorophyll concentration, are key factors controlling ecosystem CO_2 fluxes, including GPP, Re and NEP (e.g. Arndal *et al.* 2009, Kato *et al.* 2004, Koch *et al.* 2008, Li *et al.* 2007, Street *et al.* 2007, Zhang *et al.* 2009). Our results that GPP_{max} increased with above-ground biomass (Fig. 2a) and that $Re_{daytime}$ increased with total biomass (Fig. 2b) are consistent with previous studies. This suggests that vegetation biomass is a good predictor of the main ecosystem CO_2 fluxes. Moreover, we also found that the relationships between vegetation biomass and GPP_{max} and $Re_{daytime}$ differed among the four altitudes sampled (Fig. 2a and b).
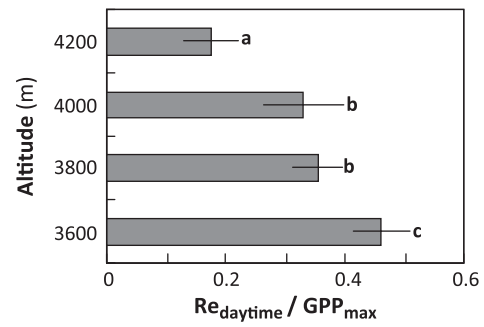
The ratio of GPP_{max} to above-ground biomass was highest at 4200 m and lowest at 4000 m (Fig. 2a). Such the difference in the ratio indicates differences in the photosynthetic capacity at the two altitudes, although the available evidence is insufficient to clarify the physiological differences among the vegetation at different altitudes. In the high Arctic ecosystems of northeast Greenland, Arndal *et al.* (2009) demonstrated that GPP correlated positively with leaf nitrogen content in five vegetation types, and the relation differed among vegetation types. Furthermore, the initial slope of the GPP to light intensity ratio (αGPP) may partly explain the difference in the ratio of GPP_{max} to above-ground biomass among the four altitudes (Table 4). The altitudinal variation of αGPP indicates that the alpine grassland dominated by cushion plants at the highest site (4200 m) had high light use efficiency than at the lower sites.

The $Re_{daytime}$ and soil temperature were all significantly higher at the lowest site (3600 m; Tables 1 and 4), which

Figure 3: variations in the ratio of $Re_{daytime}$ to GPP_{max} ($Re_{daytime}$: GPP_{max}) along the altitudinal gradient from 3600 to 4200 m. Differences among the altitudes at $P < 0.01$ are noted by different letters.

Figure 2: relationships between (a) GPP_{max} and above-ground biomass (AGB) and (b) $Re_{daytime}$ and total biomass (TB) at each altitude. Data points show (a) GPP_{max} calculated by equation (6) for each measurement point and (b) mean $Re_{daytime}$ calculated by using observed data for each measurement point. The regression lines in (a) indicate a hyperbolic relationship: $GPP_{max} = (a \times b \times AGB)/(a + b \times AGB)$. Parameters are as follows: altitude (a, b, r^2), 3600 m (−14.11, −0.17, 0.68), 3800 m (−11.80, −0.19, 0.48), 4000 m (−9.81, −0.11, 0.75), 4200 m (−16.76, −0.18, 0.55); $P < 0.0001$. The regression lines in (b) indicate a linear relationship: $Re_{daytime} = a \times TB + b$. Parameters are shown as follows: altitude (a, b, r^2), 3600 m (0.0023, 1.34, 0.64), 3800 m (0.0012, 1.46, 0.53), 4000 m (0.0010, 1.22, 0.85), 4200 m (0.0012, 0.75, 0.62); $P < 0.001$.

suggests that soil temperature is another important abiotic factor determining the $Re_{daytime}$. It is reasonable to assume that the difference in soil temperature across the altitudinal gradient would affect slope of the linear regressions between $Re_{daytime}$ and total biomass (Fig. 2b). In fact, when we calculated the $Re_{daytime}$ by equation (3) and the same soil temperature, e.g. 10°C, among the four altitudes and re-examined the relationship, the slope of the linear regressions was approximately the same (∼0.0023) at the four altitudes. Meanwhile, the sensitivity of $Re_{daytime}$ to soil temperature (Q_{10}) at lower sites (from 3600 to 4000 m) showed significant high value

compared with that at the highest site (Table 4). Considering that vegetation in the lower sites was grazed heavily compared with that in the highest 4200 m site, grazing intensity will affect the sensitivity of $Re_{daytime}$ to soil temperature.

The carbon-sink strength of the high alpine grassland ecosystem

The magnitude of NEP_{max} indicates that all four sites were weak sinks for atmospheric CO_2, at least daytime during the growing period, and the strength of the sink differed with altitude (Table 4). The NEP_{max} was highly correlated with above-ground biomass, which is because that most plants in the alpine grassland have a large leaf mass ratio (Körner 2003). Since grazing impact on the vegetation in the highest 4200-m site was the small compared with other lower three sites in this study, the highest site had large above-ground biomass and probably large leaf mass ratio, at least the study period. The current altitudinal pattern can be useful for remote-sensing data analysis for the corresponding period, but we should not consider it as a general pattern for the whole year. These results are consistent with the altitudinal variations in the SOC pool observed on the Tibetan Plateau (Ohtsuka *et al.* 2008). The GPP_{max} in our study was smaller than that in an alpine meadow at lower altitude (3200 m a.s.l.) in the same region in 2002: −5.4 to −8.8 μmol CO_2 m⁻² s⁻¹ here versus −10.5 μmol CO_2 m⁻² s⁻¹ in July and −20.4 μmol CO_2 m⁻² s⁻¹ in August in the alpine meadow (Kato *et al.* 2004). The difference is probably due to the larger above-ground biomass of the alpine meadow (maximum in 2002 = 370 g DW m⁻², Kato *et al.* 2006), which is used as a winter pasture. Meanwhile, our $Re_{daytime}$ values were comparable to those of the alpine meadow in 2002: 1.5–3.4 μmol CO_2 m⁻² s⁻¹ here versus ∼4 μmol CO_2 m⁻² s⁻¹ in July and ∼7 μmol CO_2 m⁻² s⁻¹ in August in the alpine meadow (Tables 1 and 3). Cao *et al.* (2004) demonstrated that grazing affects the magnitude of soil respiration in the alpine meadow on the Qinghai–Tibetan Plateau; soil respiration under light grazing intensity was quite large compared with that under heavy grazing intensity. Considering that $Re_{daytime}$ in the high alpine grasslands in this study was comparable with that in alpine meadow despite of small

biomass under low-temperature condition, $Re_{daytime}$ in lower altitudinal zone in this study will increase by moderate grazing intensity.

An interesting feature of the altitudinal variation in the ecosystem CO_2 fluxes observed here is that the alpine grasslands at the higher altitudes tended to have higher CO_2 uptake efficiency, which indicates a high potential of the carbon-sink strength at high altitudes during daytime in the growing season (Fig. 3). The ratio of $Re_{daytime}$ to GPP_{max} at the highest site (4200 m, around the vegetation line: 0.18 ± 0.05) was significantly smaller than those at lower altitudes (Fig. 3). Respiration in comparison to photosynthesis at the ecosystem level is primarily useful for evaluating the efficiency with which plants use photosynthate for growth and storage (e.g. Amthor and Baldocchi 2001). Alpine plant species will use photosynthates more efficiently than lowland plants under low-temperature and strong light intensity (Körner 2003) and thus, the $Re_{daytime} : GPP$ ratio in alpine ecosystems should be smaller, as shown here. Kato *et al.* (2004) also observed a very low Re : GPP ratio in the alpine meadow at 3250 m a.s.l. on the Qinghai–Tibetan Plateau during the growing season.

In this study, we demonstrate the magnitude and altitudinal pattern of ecosystem CO_2 fluxes in an extremely high alpine grassland, but uncertainties still exist about the long-term ecosystem carbon dynamics and their response to various disturbances. Furthermore, sampling design in sparse vegetation zone in higher alpine grassland, such as around vegetation line, will have to reconsider in further studies. Further observation is needed to enhance our understanding of alpine grassland ecosystems, including the effects of grazing on ecosystem CO_2 fluxes.

FUNDING

ACKNOWLEDGEMENTS

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