

Temperature and biomass influences on interannual changes in CO₂ exchange in an alpine meadow on the Qinghai-Tibetan Plateau

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Abstract

Three years of eddy covariance measurements were used to characterize the seasonal and interannual variability of the CO₂ fluxes above an alpine meadow (3250 m a.s.l.) on the Qinghai-Tibetan Plateau, China. This alpine meadow was a weak sink for atmospheric CO₂, with a net ecosystem production (NEP) of 78.5, 91.7, and 192.5 g C m⁻² yr⁻¹ in 2002, 2003, and 2004, respectively. The prominent, high NEP in 2004 resulted from the combination of high gross primary production (GPP) and low ecosystem respiration (R_e) during the growing season. The period of net absorption of CO₂ in 2004, 179 days, was 10 days longer than that in 2002 and 5 days longer than that in 2003. Moreover, the date on which the mean air temperature first exceeded 5.0 °C was 10 days earlier in 2004 (DOY110) than in 2002 or 2003. This date agrees well with that on which the green aboveground biomass (Green AGB) started to increase. The relationship between light-use efficiency and Green AGB was similar among the three years. In 2002, however, earlier senescence possibly caused low autumn GPP, and thus the annual NEP, to be lower. The low summertime R_e in 2004 was apparently caused by lower soil temperatures and the relatively lower temperature dependence of R_e in comparison with the other years. These results suggest that (1) the Qinghai-Tibetan Plateau plays a potentially significant role in global carbon sequestration, because alpine meadow covers about one-third of this vast plateau, and (2) the annual NEP in the alpine meadow was comprehensively controlled by the temperature environment, including its effect on biomass growth.

Key words: alpine ecosystem, carbon dynamics, eddy covariance, global warming, interannual variability

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Introduction

The Earth's climate system and the functioning of terrestrial ecosystems interact strongly through carbon (C) exchange (Roy *et al.*, 2001). Information on the C budgets of terrestrial ecosystems can improve our understanding of an ecosystem's functioning and its po-

tential response to the Earth's climate system, which is now at risk of disturbance by human activities carried out at an unprecedented scale with respect to both their intensity and their geographical extent (IPCC, 2001).

Recent studies have shown that grassland ecosystems sequester C, at least under normal climatic conditions (e.g. Suyker & Verma, 2001; Harazono *et al.*, 2003; Nieveen *et al.*, 2005). However, most grassland ecosystems also show large interannual variability in the annual net ecosystem exchange (NEE) of CO₂, and some even show a near-zero or negative annual uptake (Suyker *et al.*, 2003; Xu & Baldocchi, 2004). Long-term field measurements are needed to quantify C dynamics

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in a range of grassland environments under various climatic conditions. Eddy covariance technology provides a reliable way of measuring the net CO₂ exchange of an ecosystem. By applying this technology, we can use our knowledge of leaf and whole-plant physiology to interpret whole-system variability (e.g. Amthor *et al.*, 1994; Hollinger *et al.*, 1994). This micrometeorological approach has been used widely in various terrestrial ecosystems (Aubinet *et al.*, 2000; Baldocchi *et al.*, 2001; Yamamoto *et al.*, 2001).

Alpine grasslands, which are characterized by low temperatures and, potentially, plentiful sunlight owing to their high elevation, might be expected to be net C sinks because their decomposition rate of organic matter is lower and photosynthetic conditions are relatively favorable compared with high-latitude cold ecosystems such as tundra or taiga. However, most C-budget studies of grassland ecosystems have been conducted only at elevations below 1500 m. Much less attention has been given to CO₂ exchange in high-elevation alpine grassland ecosystems. Alpine meadow ecosystems in China cover approximately 6.37×10^5 km² and contain 11.3 Pg of C in biomass and soil (Ni, 2002). The soil C density of this ecosystem (18.2 kg m^{-2} ; Ni 2002) is much higher than that of savanna (5.4 kg m^{-2} ; Adams *et al.*, 1990) or of temperate grassland (13.0 kg m^{-2} ; Adams *et al.*, 1990) and similar to that of tundra (22.0 kg m^{-2} ; Adams *et al.*, 1990). Studies of alpine meadow ecosystems will further our understanding of terrestrial C dynamics and improve our predictions of their responses to climate change.

The IPCC (2001) reported that if the atmospheric CO₂ concentration rises at a rate of $1.0\% \text{ yr}^{-1}$, annual averaged temperatures during 2071–2100 on the Qinghai-Tibetan Plateau will increase by 3.3–8.4 °C during the summer months (June, July, and August) and by 3.2–10.9 °C during the winter months (December, January, and February) compared with those during 1961–1990. Little information is available by which we can assess how the plants and soil microbes on the plateau will react to this great warming or other climate changes, although Klein *et al.* (2004) performed a warming experiment in an alpine ecosystem and observed dramatic declines in plant species diversity.

To extend information from studies of global C dynamics and to project the influence of global warming on an alpine grassland for the near future, we measured the CO₂ exchange between the atmosphere and ecosystem from January 2002 to December 2004 in an alpine meadow on the Qinghai-Tibetan Plateau, China, by the eddy covariance method. The aims of this study were (1) to examine the interannual variation in annual C sequestration in an alpine meadow ecosystem and (2) to clarify the major environmental factors con-

straining the magnitude of annual and seasonal C sequestration.

Materials and methods

Site description

The research site is located in an alpine meadow that is part of the Haibei Alpine Meadow Ecosystem Research Station, Northwest Plateau Institute of Biology, Chinese Academy of Science (latitude 37°36'N, longitude 101°20'E; 3250 m a.s.l.). The annual average temperature and precipitation for 1981–2000 were -1.7°C and 561 mm, respectively. The soil is a clay loam, with an average thickness of 65 cm. The surface 5–10 cm of soil, which is classified as a Mat Cry-gelic Cambisol according to the classification system of the Chinese National Soil Survey (Institute of Soil Science and Chinese Academy of Sciences, 2001), is wet and high in organic matter. The study site is grazed by yaks and sheep every winter.

The plant community at the flux measurement site is dominated by three perennial sedges, *Kobresia humilis*, *K. pygmaea*, and *K. tibetica* (Cyperaceae; Li & Zhou, 1998). The plants start to grow in May, when the daily average air temperature exceeds the freezing point. The aboveground biomass reached its maximum, varying within $342 \pm 50 \text{ g d.w. m}^{-2}$ (average \pm SD), in early July to the middle of August between 1980 and 1993 (Li & Zhou, 1998). The foliage dies out almost completely in October (Li & Zhou, 1998).

Eddy covariance and micrometeorological measurements

Eddy covariance (EC) fluxes of CO₂, sensible heat, and latent heat flux were measured by the open-path eddy covariance method from 1 January 2002 to 31 December 2004. The flux observation site has a fetch of at least 1 km in all directions except the west, where a 100 m long clay fence about 1 m high is 250 m from the observation tower. Wind speed and sonic virtual temperature were measured at the height of 2.2 m above the ground with a sonic anemometer (CSAT-3, Campbell Scientific Inc., Logan, UT, USA). CO₂ and water vapor concentrations were also measured at 2.2 m with an open-path infrared gas analyzer (LI7500, Li-Cor Inc., Lincoln, NE, USA). Wind speed, sonic virtual temperature, and CO₂ and H₂O concentrations were sampled at a rate of 10 Hz. Their mean, variance, and covariance values were calculated and logged every 15 min. The cross spectrum between vertical wind, w' , and CO₂ concentration, c' , showed that the covariance of the two variables was close to zero when the sampling frequency was lower than 0.002 Hz (8.3 min cycle⁻¹).

An average period of 15 min was, thus, considered to be sufficient to include the necessary information for our analysis.

The effects of density fluctuations were accounted for following Webb *et al.* (1980). In this study, three common flux data corrections, that is, coordinate rotation, trend removal, and sonic velocity correlation against water vapor density, were not enforced on the collected data. However, the effect of not making these corrections on the calculated flux was examined for 10 days in July 2002 by using fluctuation data sampled at the frequency of 10 Hz, and the implicit estimation error in the flux data was evaluated by comparing corrected and uncorrected fluxes in latent heat and CO₂ flux calculations. The regression line slopes showed small differences, within 4%, between corrected and uncorrected fluxes. This result indicated that the small negative bias resulting from the omission of these corrections is likely to be negligible in the study. The closure of the 15 min averaged surface energy budget was examined by performing a linear regression between the sum of eddy fluxes ($H + \lambda E$) and the available energy ($R_n - G$) throughout the year: in 2002, $(H + \lambda E) = 0.70 \times (R_n - G) - 0.24$, $r^2 = 0.89$; in 2003, $(H + \lambda E) = 0.60 \times (R_n - G) - 7.50$, $r^2 = 0.91$; and in 2004, $(H + \lambda E) = 0.62 \times (R_n - G) - 8.94$, $r^2 = 0.89$, where H and λE are the sensible and latent heat fluxes, respectively, R_n is the net radiation, and G is soil heat flux, and where all the flux values are daily averages (MJ m^{-2}). We examined the energy imbalance using different approaches, including changing the average durations and using different methods of estimating soil heat flux. The slope of the energy balance equation, however, showed little significant change and varied between 0.6 and 0.7. The values fell in the median region of reported energy closure, the value of which ranges from 0.55 to 0.99 (Wilson *et al.*, 2002). Considering the long fetch over flat terrain of our study site, the low slope value could be caused by other factors, such as low temperature or low wind speed; these possibilities need to be further examined in the future. For the period from 29 April 2003 to 9 July 2003, when the λE derived by the eddy covariance method showed apparent lower values than in other periods owing to a wrong setting during H₂O sensor calibration, the CO₂ flux correction process for density fluctuations of water vapor (Webb *et al.*, 1980) was conducted using λE values calculated from the heat balance equation $\lambda E = 0.60 \times (R_n - G) - 7.50 - H$, as shown above for 2003.

Micrometeorological measurements were also made at the same site. Net radiation, photosynthetic photon flux density (PPFD), air temperature and humidity, wind speed, soil heat flux, soil temperature, soil water content, soil surface temperature, and rainfall were

logged every 15 min. Details are reported by Kato *et al.* (2004a).

Estimation of ecosystem respiration and gross primary production (GPP)

Ecosystem respiration, R_e , was assumed to be measured appropriately during night-time periods with strong turbulence (as the NEE at friction velocity $u^* > 0.2 \text{ m s}^{-1}$), and was extrapolated to other periods by exponential regression of measured R_e against soil temperature at 5 cm depth with the Arrhenius equation, as reported by Lloyd and Taylor (1994):

$$R_e = R_{e,T_{\text{ref}}} \exp \left[(E_a/R) \left(\frac{1}{T_{\text{ref}}} - \frac{1}{T_{\text{soil}}} \right) \right], \quad (1)$$

where R_e is the night-time ecosystem respiration rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), $R_{e,T_{\text{ref}}}$ the ecosystem respiration rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) at the reference temperature T_{ref} (K), and E_a the activation energy (J mol^{-1}). These latter two parameters are site-specific. R is the universal gas constant ($8.134 \text{ J K}^{-1} \text{ mol}^{-1}$), and T_{soil} the soil temperature at 5 cm depth. $R_{e,T_{\text{ref}}}$ was chosen as R_{10} , the respiration rate at T_{ref} equal to 283.16 K (10 °C), and evaluated for every month. E_a was evaluated from the regression of all R_e data points against T_{soil} as a constant value throughout each year (for 2002, 2003, and 2004, 81 519, 93 827, and 69 819 J mol^{-1} , respectively).

GPP was calculated as the sum of net ecosystem production (NEP) as CO₂ uptake (i.e. NEE) and R_e as follows:

$$\text{GPP} = \text{NEP} + R_e, \quad (2)$$

where all variables have units of $\mu\text{mol m}^{-2} \text{ s}^{-1}$.

Livestock grazed each winter at our study site. The livestock removed almost all of the aboveground biomass, and C from this biomass was released into the atmosphere again as CO₂ from the respiration of the livestock and the decomposition of their excrement. We ignored the C stored in the animals' bodies because, in general, livestock does not increase in weight during the winter in this grazing system. The CO₂ released either by livestock respiration or from excrement was considered to be included in R_e as determined by flux measurements. Other factors such as respiration from insects and mammals other than livestock were ignored in the data analysis.

Methodology for filling in missing data

The prime focus of C budget studies at a global or ecosystem scale is on the annual or seasonal balance of net ecosystem CO₂ exchange (Valentini *et al.*, 2000; Falge *et al.*, 2002). So that we could sum intervals of

consecutive C dynamics data points, we used a non-linear regression (Regr.) method, which is applicable to the EUROFLUX and AmeriFlux databases (Falge *et al.*, 2001), to fill in missing data resulting from system failures or data rejection.

Regression relationships were established with non-linear regression methods between the NEP components, that is, R_e and GPP, and associated controlling factors (temperature and light) for every month. Missing R_e values were extrapolated by using the exponential regression equation (Eq. (1)) between measured night-time R_e with strong turbulence ($u^* > 0.2 \text{ m s}^{-1}$) and soil temperature at 5 cm depth. Night-time eddy covariance flux data under low-turbulence conditions, that is, below the u^* threshold (Aubinet *et al.*, 2000; 0.2 m s^{-1} in this study), were also corrected with the same regression equation (Eq. (1)); this correction is called the ' u^* -correction.' GPP was extrapolated by rectangular hyperbolic regression of daytime GPP against PPFD with a Michaelis–Menten-type equation (Falge *et al.*, 2001) for every month:

$$\text{GPP} = \frac{\alpha \text{GPP}_{\text{SAT}} \text{PPFD}}{\text{GPP}_{\text{SAT}} + \alpha \text{PPFD}}, \quad (3)$$

where α is the initial slope of the light–GPP curve ($\mu\text{mol CO}_2 [\mu\text{mol photon}]^{-1}$) and is equivalent to the quantum yield, and GPP_{SAT} is GPP at light saturation ($\mu\text{mol m}^{-2} \text{s}^{-1}$). These two parameters are month-specific.

To examine the differences in annual NEP produced by different gap-filling methods, we used two additional gap-filling methods, mean diurnal variation (MDV) and look-up tables (LookUp; Falge *et al.*, 2001). In the MDV method, a missing datum is replaced by the mean for that time period (15 min) calculated from the values obtained on adjacent days. We chose data windows of 7 and 14 days using two different algorithms: (a) an independent window and (b) a gliding window. In (a), for each subsequent period of data, MDVs were established to fill gaps within that period. In (b), a window of prescribed size around each gap was used to construct MDVs for gap filling within that window. In the LookUp method, a missing datum is replaced by the prescribed NEP data from the look-up tables, which contain measured and averaged NEP values under the certain light and temperature conditions, and were created for six bimonthly periods or for four seasonal periods (1 April to 30 May, 1 June to 30 September, 1 October to 30 November, and 1 December to 31 March). For the look-up table, average NEP values were compiled for 27 PPFD classes \times 35 T_a (air temperature) classes. PPFD classes consisted of intervals of $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ between 0 and $2600 \mu\text{mol m}^{-2} \text{s}^{-1}$, with a separate class for PPFD = 0. Similarly, T_a classes

were defined as 2°C intervals between -35 and $+34^\circ\text{C}$.

Green aboveground biomass (Green AGB) estimation from normalized difference vegetation index (NDVI) data

To compare interannual growth of plants during measurement periods when no mowing was done, we used satellite NDVI data to estimate aboveground plant biomass. Nine pixels of the $250 \times 250 \text{ m}^2$ gridded NDVI data, in which the center pixel contains the flux tower location, were extracted from the NDVI data set of the MODIS/Terra satellite (data product name, MOD13Q1), downloaded from the USGS/EDC/DAAC web site (<http://edcimswww.cr.usgs.gov/pub/imswelcome/>). Those NDVI data were extrapolated by exponential regression of the Green AGB data, which were obtained by mowing near the flux tower site in 2003 and 2004 (Fig. 1), as follows:

$$\text{Green AGB} = 3.84 \exp(6.53 \times \text{NDVI}), \quad (4)$$

where Green AGB is the green aboveground biomass (g d.w. m^{-2}).

Results

Meteorological and biological factors

The daily averaged temperatures ranged from -23.9 to 15.7°C (air temperature) and from -7.9 to 19.8°C (soil temperature at 5 cm depth), with maximum temperatures recorded from the end of July to the beginning of

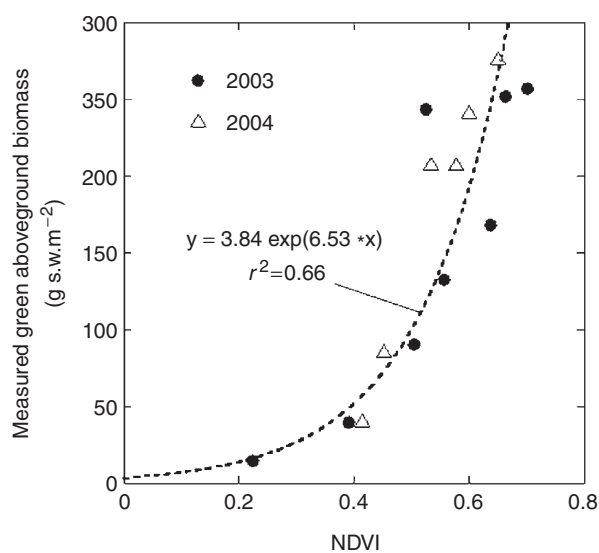


Fig. 1 Comparison of the normalized difference vegetation index (NDVI) to green aboveground biomass (Green AGB) measured in 2003 and 2004.

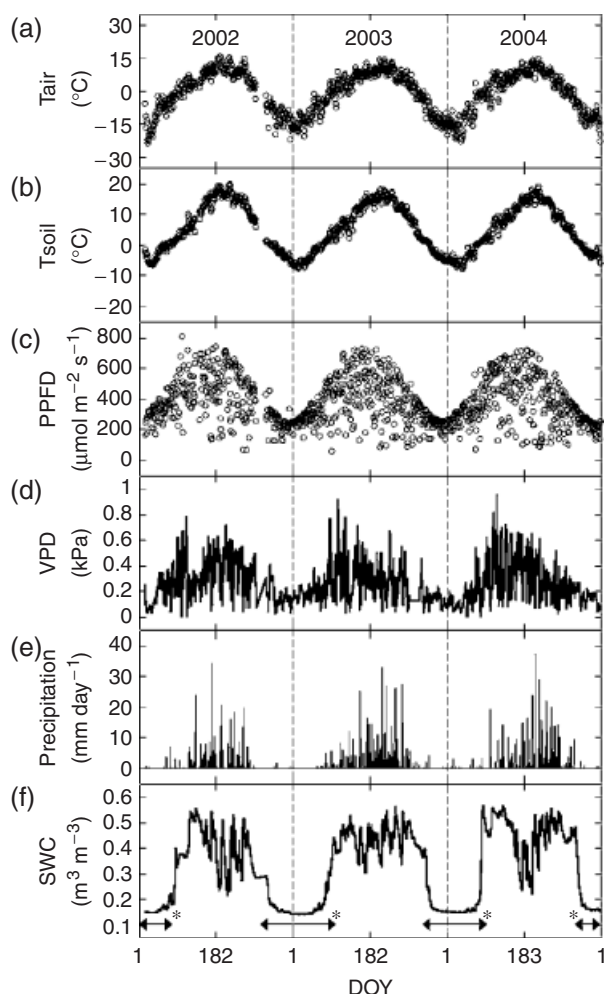


Fig. 2 Data for 2002–2004: (a) air temperature at 1.1 m height (T_{air}); (b) soil temperature at 5 cm depth (T_{soil}); (c) photosynthetic photon flux density (PPFD); (d) vapor pressure deficit (VPD) at 1.1 m height; (e) volumetric soil water content at 5 cm depth (soil water content, SWC); and (f) precipitation (Prec). *Data not reliable because of soil freezing at the depth at which the TDR sensor was installed.

August (Figs 2a, b). Summer, autumn, and annual averaged temperatures were all higher in 2002 than in the other 2 years (Table 1). PPFD reached its annual maximum in late June and then decreased gradually (Fig. 2c). The vapor pressure deficit (VPD) reached as high as around 1.0 kPa in spring and decreased to 0.6 kPa in summer even at the maximum state (Fig. 2d). Rainfall was concentrated in the period from May to August. Within this high-precipitation period, 7–14 consecutive dry days occasionally followed rainy days (Fig. 2e). During these short dry intervals, the soil water content (SWC) decreased gradually from about $0.5 \text{ m}^3 \text{ cm}^{-3}$ (saturation) to values close to $0.3 \text{ m}^3 \text{ cm}^{-3}$ (Fig. 2f).

Green AGB increased from mid-April (DOY100) each year and reached a maximum of $369.6 \text{ g d.w. m}^{-2}$ on 4

August (DOY216) in 2002, $266.2 \text{ g d.w. m}^{-2}$ on 14 August (DOY226) in 2003, and $284.7 \text{ g d.w. m}^{-2}$ on 15 August (DOY226) in 2004 (Fig. 3). The date estimated from NDVI data as that of the maximum Green AGB was earlier in 2002 than that determined from mowing data in 2003 and 2004, but the midsummer (DOY184–216) biomass was highest in 2002. The estimated Green AGB decreased earlier in the autumn in 2002 than in the other years.

Seasonal and interannual changes of C dynamics

On a 10-day moving-average basis, NEE between the atmosphere and the alpine meadow ecosystem increased gradually beginning on DOY1, and it started to decrease on DOY117 in 2002, on DOY120 in 2003, and on DOY114 in 2004. NEE became negative on DOY144 in 2002, on DOY149 in 2003, and on DOY143 in 2004 (Fig. 4). The annual minimum of 10-day moving-averaged NEE was $-3.17 \text{ g C m}^{-2} \text{ day}^{-1}$ on DOY203 in 2002, $-2.38 \text{ g C m}^{-2} \text{ day}^{-1}$ on DOY198 in 2003, and $-3.68 \text{ g C m}^{-2} \text{ day}^{-1}$ on DOY196 in 2004. Subsequently, the NEE started to increase gradually and became positive again on DOY265 in 2002, on DOY268 in 2003, and on DOY278 in 2004. The NEE began to decrease again on DOY286 in 2002, on DOY294 in 2003, and on DOY293 in 2004. Therefore, the growing period, defined as the period with negative NEE, when an ecosystem exhibits a net absorption of CO₂ from the atmosphere, was longer in 2004 (179 days, DOY114–292), than in 2002 (169 days, DOY117–285) or 2003 (174 days, DOY120–295). Over the 3 years, the ecosystem accumulated a total of 362.7 g C m^{-2} , half of which was gained in 2004 (Table 1).

When the diurnal variations in GPP, R_e , and NEE were compared by season (Fig. 5), there were no obvious differences among the C fluxes in winter, but GPP in spring was slightly higher and NEE was lower in 2004 than in the other 2 years. In summer, the diurnal courses of GPP were similar; a maximum value of about $13 \mu\text{mol C m}^{-2} \text{ s}^{-1}$ was reached at around 12:00 hours, Beijing time. However, both R_e and NEE showed lower afternoon values in 2004 than in the other years. In autumn, GPP varied among years; the largest values were observed in 2003, and the lowest in 2002. R_e was a little higher in 2003 than in the other years. However, the daytime NEE was lowest in 2002 and highest in 2003. Night-time NEE was also higher in 2003 than in the other years.

The annual courses of GPP, R_e , and NEE in 2003 and 2004 were compared with those in 2002 (Fig. 6). Cumulative GPP_{diff} and $R_{e\text{diff}}$ values for (2003–2002) (i.e., the value in 2003 minus that in 2002) were negative from May to early September (DOY120 to DOY250), but

Table 1 Annual and seasonal mfbudgets of ecosystem carbon dynamics (sums for each interval) and corresponding environmental factors (averages for each interval) in 2002–2004

Unit	Year	NEP (g C m ⁻²)	R _e (g C m ⁻²)	GPP (g C m ⁻²)	T _{air} (°C)	T _{soil} (°C)	VPD (kPa)	SWC (m ³ m ⁻³)	PPFD (μmol m ⁻² s ⁻¹)
Winter (January–March, November–December)	2002	−22.0	6.4	−15.6*	−10.5	−2.23	0.18	0.17 [†]	294.0
	2003	−17.6	15.6	−2.0*	−9.5	−2.07	0.19	0.19 [†]	283.9
	2004	−5.3	19.4	14.1*	−10.9	−2.51	0.16	0.20 [†]	284.7
Spring (April–May)	2002	−31.8	51.7	19.9	2.66	6.23	0.30	0.45	481.7
	2003	−36.0	43.8	7.8	2.80	6.21	0.36	0.44	449.3
	2004	−19.0	69.9	50.9	2.86	6.18	0.39	0.51	494.8
Summer (June–August)	2002	149.0	343.6	492.6	9.90	15.77	0.40	0.38	487.6
	2003	143.8	344.3	488.1	8.98	14.58	0.31	0.43	459.4
	2004	211.5	288.9	500.4	9.05	14.29	0.37	0.39	467.1
Autumn (September–October)	2002	−16.8	95.0	78.2	4.38	9.94	0.29	0.38	358.4
	2003	1.5	152.0	153.4	3.20	8.78	0.26	0.45	355.1
	2004	5.3	110.4	115.7	1.77	7.67	0.22	0.47	327.5
Annual	2002	78.5 [‡]	496.6 [‡]	575.1 [‡]	−0.65	5.86	0.28	0.40 [§]	388.1
	2003	91.7	555.6	647.3	−0.91	5.15	0.26	0.44 [§]	366.2
	2004	192.5	488.5	681.1	−1.53	4.86	0.26	0.45 [§]	377.4

*These winter GPP values were generated by the unavoidable methodological property resulting from the GPP being calculated automatically as a residual between NEE and R_e, which was estimated by the experimental relationship of soil temperature and nighttime respiration. If winter GPP is assumed to be zero, then annual GPP values are 590.7, 649.3, and 667.0 g C m⁻² yr⁻¹ for 2002, 2003, and 2004, respectively.

[†]Data not reliable because of soil freezing at the depth at which the TDR sensor was installed.

[‡]Reposted values from our previous report of identical flux measurements in 2002 (Kato *et al.*, 2004b).

[§]Average values for the growing season (spring, summer, and autumn), not including the winter data.

GPP, gross primary production; NEP, net ecosystem production; PPFD, photosynthetic photon flux density; SWC, soil water content.

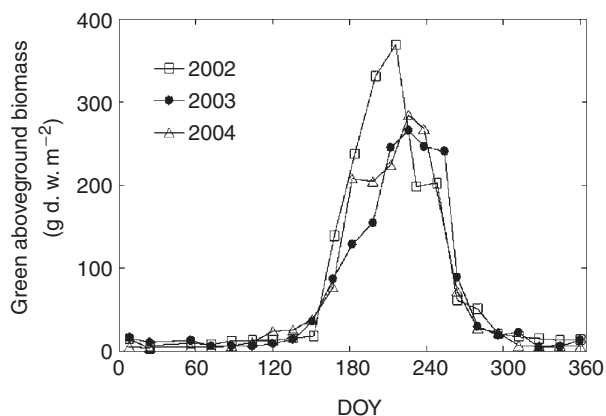


Fig. 3 Green aboveground biomass (Green AGB) estimated from the normalized difference vegetation index (NDVI) data for 2002, 2003, and 2004. During DOY136–254 in 2003 and DOY151–238 in 2004, the Green AGB values are measured data. For other dates, the Green AGB was estimated from the NDVI data using Eq. (4).

became positive after that period and increased rapidly until the end of autumn (around DOY300). In contrast, NEE_{diff} (2003–2002) showed relatively small variation (+26.6 to −14.5 g C m⁻²) throughout the year. GPP_{diff} between 2002 and 2004 (2004–2002), however, increased

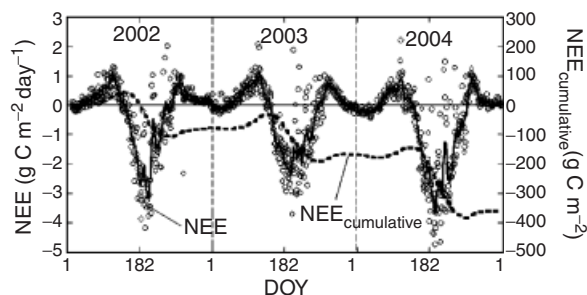


Fig. 4 Seasonal changes in the daily averaged net ecosystem exchange (NEE) and cumulative NEE data for 2002–2004. The solid line indicates the 10-day moving average of daily NEE.

gradually over the course of a year. R_{e diff} increased slightly in spring and then decreased, becoming negative in autumn, and approached zero (−8.1 g C m⁻²; Table 1) again by the year end. NEE_{diff} for 2004–2002 decreased continuously during the course of a year (Fig. 6c).

To examine ecosystem CO₂ uptake during the growing period, we examined the annual course of growing degree-days (GDD; cumulative air temperature above 5.0 °C for the days when the air temperature was greater

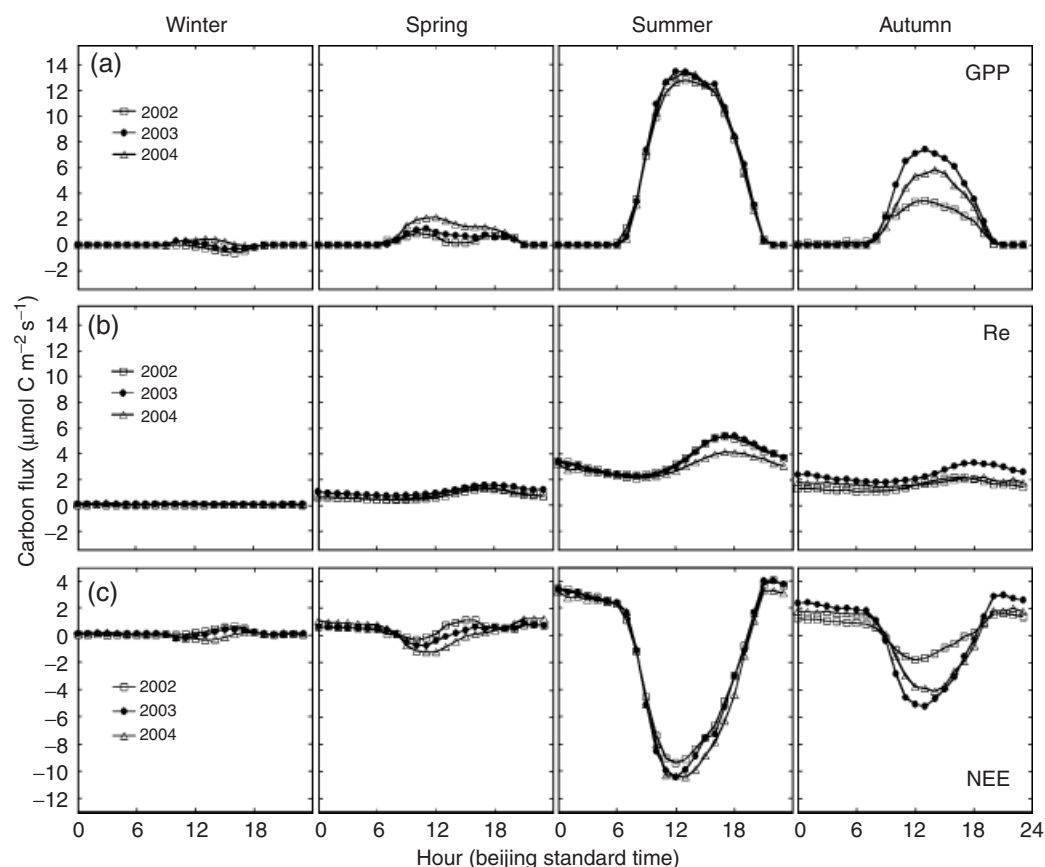


Fig. 5 Averaged diurnal changes of (a) gross primary production (GPP), (b) R_e , (c) net ecosystem exchange (NEE) for winter (January–March and November–December), spring (April–May), summer (June–August), and autumn (September–October). Each graph shows 1 h step changes of seasonal averaged value.

than 5.0 °C from DOY1), Green AGB, and the cumulative GPP from DOY100, in the spring (Fig. 7). The *GDD* started to increase earlier in 2004 (on DOY110) than in the other years (around DOY120 in 2002 and 2003), and it rose gradually as the year progressed. On average, the values were higher in the order 2004 > 2003 > 2002; in 2002 and 2003, the *GDD* reached the level of that of 2004 on DOY167 and DOY154, respectively. Green AGB increased gradually from DOY110 and was highest in the order 2004 > 2003 > 2002 until DOY150. $GPP_{\text{cumulative}}$ started to increase earlier in 2004 (around DOY110) than in 2002 or 2003 (around DOY120). The differences in $GPP_{\text{cumulative}}$ in 2004–2002 and 2004–2003 were 26.8 and 39.0 g C m⁻², respectively, by the end of spring (31 May, DOY151).

Relationship between night-time NEE and soil temperature and between GPP/PPFD and aboveground biomass

Night-time NEE (i.e. night-time ecosystem respiration) showed an exponential relationship with soil tempera-

ture in each of the 3 years (Fig. 8). The annual ecosystem respiration at 10 °C (R_{10}) was 1.60, 1.89, and 1.78 μmol C m⁻² s⁻¹ for 2002, 2003, and 2004, respectively, whereas the annual active energy (E_a) was 68 175, 87 204, and 60 671 J mol⁻¹, respectively. Thus, the temperature dependence was higher in 2003 than in the other years.

The relationship between the GPP/incident PPFD ratio, that is, the light-use efficiency, and the Green AGB increased logarithmically and did not differ greatly among the 3 years (Fig. 9).

Annual NEP and gap-filling methods

NEP (as negative values of NEE), gap-filled by the Regr., MDV, and LookUp methods, are shown in Table 2. The Regr. method, which with u^* -correction and a 1-month processing interval yielded the smallest NEP values among the methods, was the method generally applied in this study. This method resulted in large differences in annual NEP (–60.2 to –35.4 g C m⁻² yr⁻¹) between values without and those with

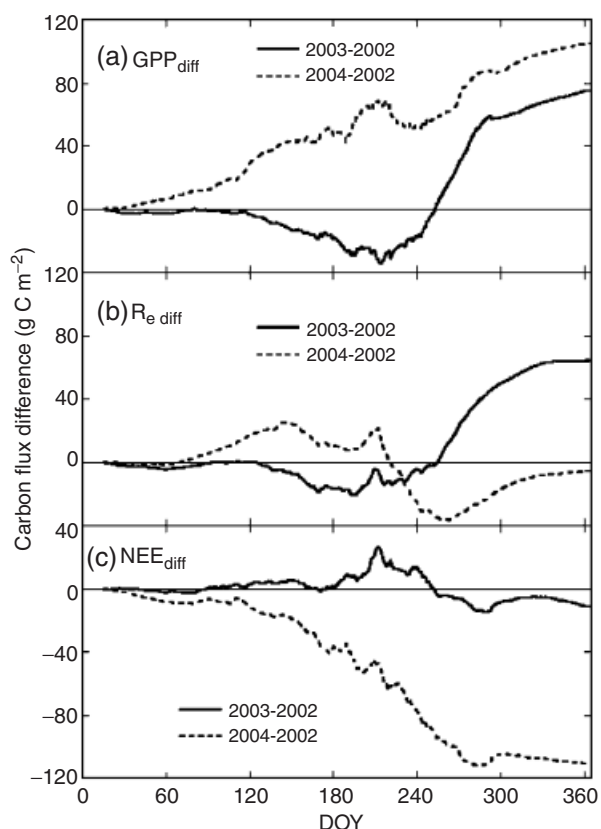


Fig. 6 (a) Seasonal changes in the gross primary production differences (GPP_{diff}), (b) ecosystem respiration ($R_{e,diff}$), and (c) net ecosystem exchange (NEE_{diff}) from 2002 to 2003 and from 2002 to 2004.

u^* -correction for each of the years. The MDV method resulted overall in higher NEP values than the other methods, and it showed very small differences for different window types and processing intervals in each year. The LookUp method resulted in intermediate NEP values, and it showed small differences between T_{soil} and T_{air} and for different processing intervals in each year, except in 2002. All gap-filled NEPs were positive.

Discussion

Factors influencing the annual variability of CO_2 exchange above the alpine meadow

The annual NEP in 2004 was about twice as high as that in the other 2 years (Table 1). A high NEP can result from either a high GPP or a low R_e . In the alpine meadow, the annual R_e in 2004 was lower than in the other 2 years. In particular, R_e was much lower in summer 2004 than in the other years (Table 1). The low summertime R_e can be attributed to low tempera-

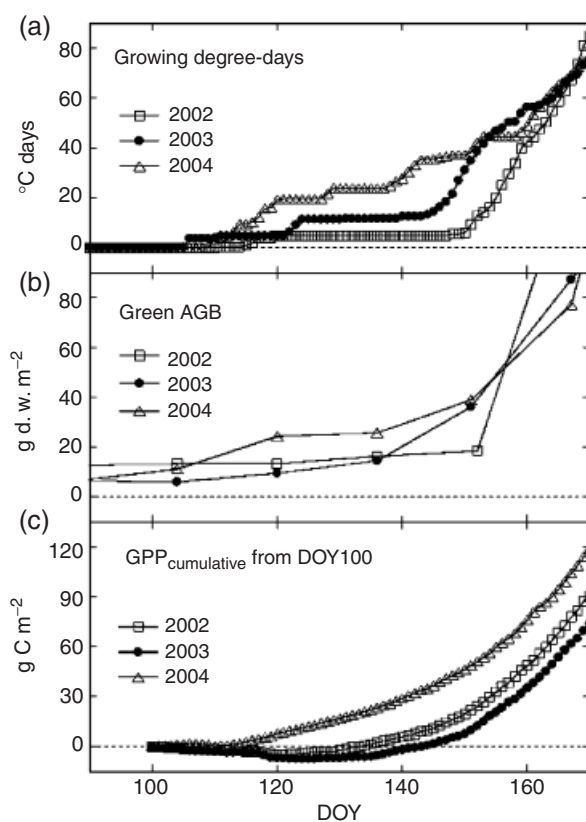


Fig. 7 (a) Growing degree-days (air temperature above 5 °C), (b) green aboveground biomass (Green AGB), and (c) cumulative gross primary production (GPP) from DOY100 in the photosynthetic onset period (DOY90–170) for 2002–2004. Growing degree-days were calculated as the sum of daily average air temperatures above the air temperature of 5 °C since DOY1.

ture or low R_e activity. Soil temperature skewed to the low side in 2004 as compared with the other 2 years, and this skew to small values was more prominent in summer (Fig. 10). Moreover, the ecosystem respiration activity indicated by the summertime R_{10} and E_a values in 2004 tended to be higher than those in 2002 but lower than those in 2003. We therefore conclude that both temperature and the ecosystem respiration activity contributed to the low ecosystem respiration during summer 2004, but that the low temperature might have played a more important role.

On the other hand, the annual GPP was the highest in 2004 among the 3 years. The high annual GPP was mainly contributed by the high GPP in late spring and early summer. A high GPP can result from a high Green AGB or a high ecosystem CO_2 uptake. In the current study, the high GPP in spring and summer 2004 can possibly be attributed to the high Green AGB in that year (Fig. 3 and Table 1), which in turn could have resulted from the high temperature and the

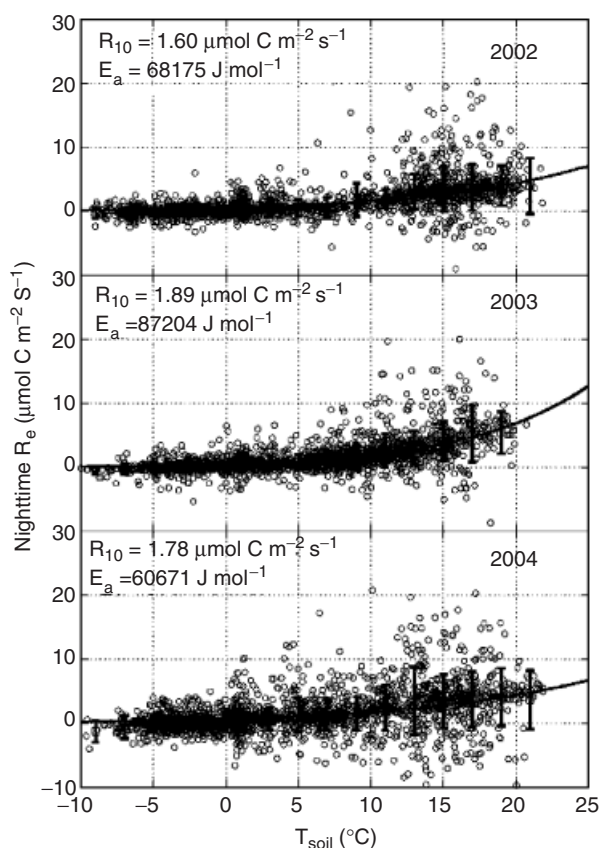


Fig. 8 Relationship between 15 min averaged night-time ecosystem respiration (R_e) and soil temperature (T_{soil}) at 5 cm depth for friction velocity $u^* > 0.2 \text{ m s}^{-1}$ in 2002 (upper), 2003 (middle), and 2004 (lower). The R_e values were bin-averaged for 2°C intervals \pm standard deviation. The regression fits to an Arrhenius-type exponential relationship for the bin-averaged R_e : $R_e = R_{10} \times \exp\{E_a/R \times [1/283.16 - 1/(T_{\text{soil}} + 273.16)]\}$, where R_{10} is the respiration rate at a soil temperature of 10°C ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), E_a is the active energy, and R is the universal gas constant ($= 8.134 \text{ J K}^{-1} \text{ mol}^{-1}$).

relatively early start of vegetation growth in early spring 2004. Moreover, to clarify whether GPP per unit aboveground biomass plays a role in the interannual variability of GPP, we examined the ratio GPP/Green AGB, which was similar during the summer, from June to August (DOY152–243; Fig. 11b). The result indicates that the CO₂ uptake per unit aboveground biomass cannot account for the GPP difference in summer among the 3 study years. However, the ratio of NEE/Green AGB tended to be higher in absolute terms in 2004 than in the other 2 years (Fig. 12a).

A great contribution of temperature to CO₂ flux dynamics often characterizes ecosystems that experience low winter temperatures, for example, relatively cold, humid ecosystems such as tundra (Harazono *et al.*, 2003) and subarctic fen (Griffis *et al.*, 2000). Not all

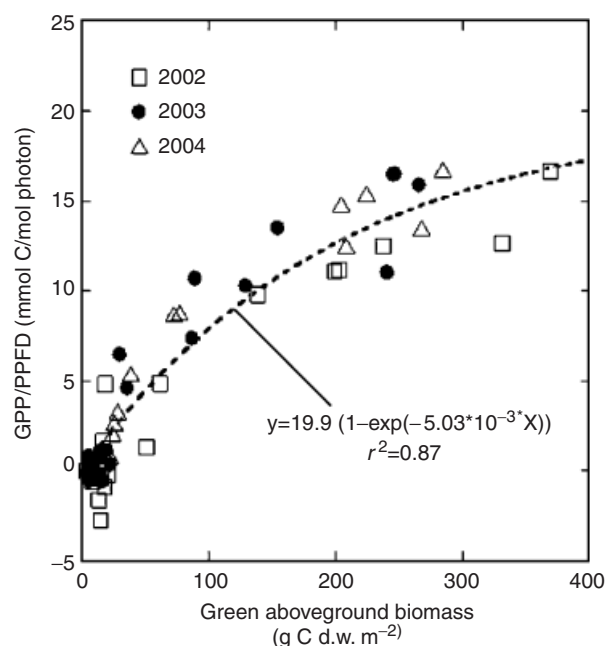


Fig. 9 Comparison of the light-use efficiency (the GPP/PPFD ratio) with the green aboveground biomass (Green AGB) for 2002–2004. PPFD, photosynthetic photon flux density; GPP, gross primary production.

annual and seasonal changes in NEP, however, can be explained directly by temperature variation. Law *et al.* (2002) showed that mean annual air temperature explained only 17% of variation in annual NEP across various FLUXNET sites in forest, grassland, cropland, and tundra ecosystems. Even at the current study site, we have found that diffuse light conditions and soil water content have been found to affect the short-term CO₂ flux (Gu *et al.*, 2003, 2005a,b; Kato *et al.*, 2004a). However, the annual and seasonal averages of CO₂ exchange were not significantly related to the moisture conditions (VPD and SWC; Table 1).

In the current study, it is notable that in autumn 2002, the aboveground biomass showed the largest decrease among the 3 years (Fig. 3), and the R_e and GPP values were correspondingly smallest in 2002, despite that year's having the highest observed soil and air temperatures (Table 1). Humphreys *et al.* (2005) reported that early senescence, induced by summer drought, reduced the annual R_e and GPP in a Douglas-fir forest on the eastern coast of Vancouver Island, Canada. These facts suggest that phenological changes in the ecosystem can strongly affect interannual changes in autumn R_e , and, thus, possibly the annual R_e , through autotrophic respiration induced by plant growth. We, therefore, suppose that the length of the growing season plays an important role in the interannual variability in the annual NEP.

Table 2 Comparison of the effects of different gap-filling methods on net ecosystem production (NEP) in 2002–2004

Method	Specification	Processing interval	NEP ($\text{g C m}^{-2} \text{yr}^{-1}$)			SD	Mean	CV
			2002*	2003	2004			
Regr.	With u^* -correction	1 month	78.5	91.7	192.5	62.4	120.9	0.516
Regr.	Without u^* -correction	1 month	113.9	151.9	230.2	59.3	165.3	0.359
MDV	Independent window	7 days	147.2	168.4	258.3	59.0	191.3	0.308
MDV	Independent window	14 days	145.2	171.5	256.6	58.2	191.1	0.305
MDV	Gliding window	7 days	149.5	169.1	260.1	59.0	192.9	0.306
MDV	Gliding window	14 days	141.8	170.2	256.3	59.6	189.4	0.315
LookUp	T_{soil}	2 month	122.3	140.1	221.1	52.7	161.2	0.327
LookUp	T_{soil}	Seasonal	96.9	143.4	224.1	64.4	154.8	0.416
LookUp	T_{air}	2 month	142.3	143.5	214.4	41.3	166.7	0.248
LookUp	T_{air}	Seasonal	113.8	146.2	225.7	57.6	161.9	0.356
SD of NEP for different methods			24.2	24.0	22.9			
Mean NEP for different methods			125.1	149.6	233.9			
CV for different methods			0.194	0.160	0.098			

*Reposted values from our previous report of identical flux measurements in 2002 (Kato *et al.*, 2004b). MDV, mean diurnal variation; NEP, net ecosystem production; Regr., regression.

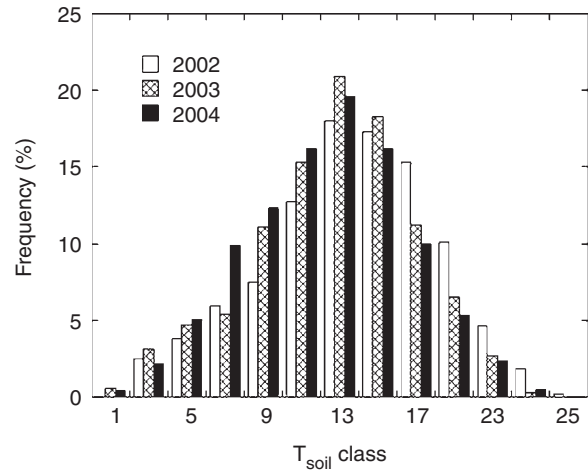


Fig. 10 Frequency of each 2.0°C interval class of the 15 min averaged soil temperature during the growing season (DOY121–273; May–September).

Magnitude of annual C sequestration and grazing effects

The 3 years of measurements suggest that at present the alpine meadow is a sink of atmospheric CO₂, with annual NEP ranging from 78.5 to 192.5 $\text{g C m}^{-2} \text{yr}^{-1}$ (average 120.9 $\text{g C m}^{-2} \text{yr}^{-1}$; Tables 1 and 2; Fig. 4). The strength of C sequestration in this alpine meadow ecosystem is similar to that observed in cold northern ecosystems. NEP in a Scots pine forest in Finland, with a similar growing period duration to the alpine meadow, ranged from 101 to 205 $\text{g C m}^{-2} \text{yr}^{-1}$ (Zha *et al.*, 2004). A subalpine forest in the Rocky Mountains (3250 m a.s.l. and lat 40°2'N) in the United States sequestered

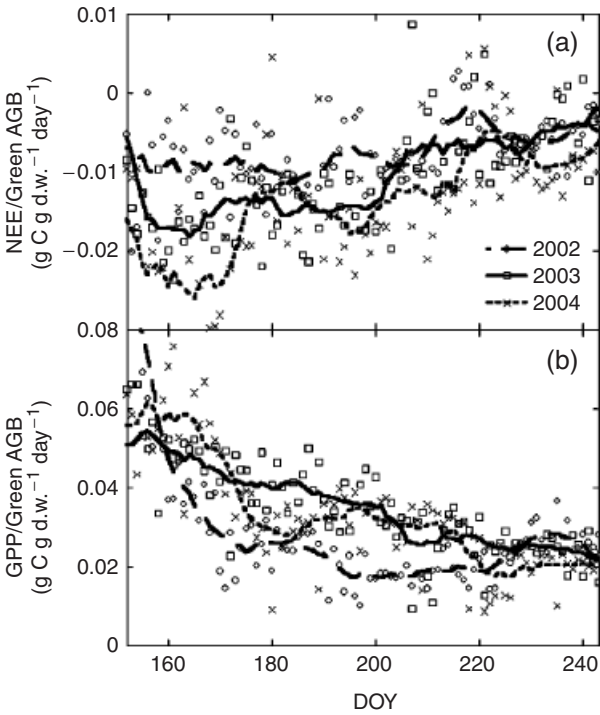


Fig. 11 Seasonal changes in the ratio of (a) net ecosystem exchange (NEE) and (b) gross primary production (GPP) to green aboveground biomass (Green AGB) during the middle of the growing season (DOY152–243; June to August). The corresponding lines show the 10-day moving average of daily NEE/Green AGB or GPP/Green AGB values.

57.6 to 80.5 $\text{g C m}^{-2} \text{yr}^{-1}$ (Monson *et al.*, 2002). NEP in boreal coniferous forests have been reported to range from –11 to 251 $\text{g C m}^{-2} \text{yr}^{-1}$, with an average of

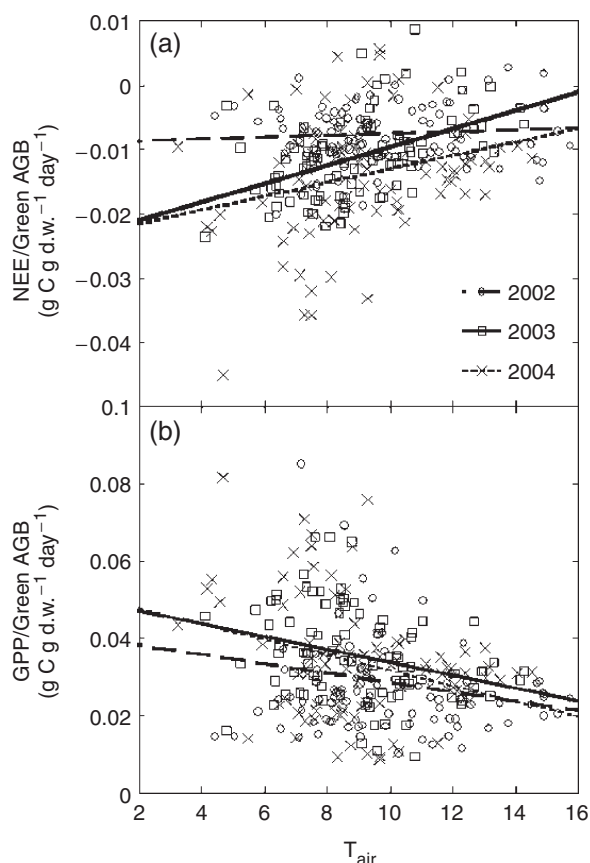


Fig. 12 Relationship between the ratio of (a) net ecosystem exchange (NEE) and (b) gross primary production (GPP) to Green aboveground biomass (Green AGB) to air temperature during the middle of the growing season (DOY152–243; June–August). The regression lines are (a) $y = 0.000140x - 0.00893$, $r^2 = 0.00605$ for 2002; $y = 0.00143x - 0.0238$, $r^2 = 0.225$ for 2003; and $y = 0.00106x - 0.0237$, $r^2 = 0.0751$ for 2004; and (b) $y = -0.00122x + 0.0407$, $r^2 = 0.0290$, for 2002; $y = -0.00168x + 0.0505$, $r^2 = 0.0876$, for 2003; and $y = -0.00201x + 0.0518$, $r^2 = 0.0914$, for 2004.

121.4 g C m⁻² yr⁻¹ (Falge *et al.*, 2002). Thus, C sequestration in alpine meadow ecosystems correlates more with climatic conditions than with the vegetation type of cold northern ecosystems.

Another remarkable characteristic of the alpine meadow, in comparison with tundra and grassland ecosystems, is the stability of the annual C sequestration, although the 3-year observation period was not long enough to analyze interannual variation in detail. Many grassland ecosystems often show large interannual fluctuations in C sequestration because of changes in moisture conditions. For example, drought or flooding events may result in a negative annual NEP (e.g. Alaskan tundra, Harazono *et al.*, 2003; Mediterranean-

type annual grassland in California, USA, Xu & Baldocchi, 2004; northern temperate grassland in Alberta, Canada, Flanagan *et al.*, 2002).

The grazing effect on CO₂ flux is complicated, with respect to not only grazing intensity but also grazing management practice and other factors (see Li *et al.*, 2005). The study site was grazed in winter. We assumed, therefore, that during the growing season, there was no direct effect of grazing on the CO₂ flux measurements. Grazing was allowed at the study site each year from December to the next April. The livestock removed almost all the aboveground biomass, and the contained C followed one of three major paths: (1) it contributed to the C stock in the animals' bodies; (2) it was returned to the ecosystem in excreta; or (3) it was released as CO₂ into the atmosphere by the livestock's respiration. Carbon following the latter two paths would have been included in the flux measurements, and C stored in the animals' bodies was extremely small, because the livestock shows little weight increase during the winter. Previous studies on the effect of grazing on the C cycle have yielded contradictory results (e.g. Derner *et al.*, 1997; Reeder & Schuman, 2002). Cao *et al.* (2004) suggested that high grazing intensity in a heavily grazed area near our study site reduced both the aboveground and belowground biomass, and decreased both the soil CO₂ efflux and the net ecosystem CO₂ fixation. Further studies are needed to clarify the effects of grazing on CO₂ assimilation in alpine meadow ecosystems.

Effect of gap-filling procedures on annual NEP estimates

We applied the nonlinear regression (Regr.) method with u^* -correction to fill the gaps in the flux data. However, we need to keep in mind that all current gap-filling methods involve bias, resulting in discrepancies between estimates and actual measurements (Table 2). The u^* -correction decreased the annual NEP greatly (by -60.2 to -35.4 g C m⁻² yr⁻¹). The largest difference (-60.2 g C m⁻² yr⁻¹) was seen in 2003, when R_e was the highest (Table 1). This effect is similar to those reported previously (Aubinet *et al.*, 2000; Falge *et al.*, 2001; Carrara *et al.*, 2003; Morgenstern *et al.*, 2004). The u^* -correction resulted in the largest annual variability in annual NEP among the gap-filling methods applied in this study, because stable atmospheric conditions often dominated at night in summer. However, the relative positions of the annual NEP values did not differ among the gap-filling methods; that is, NEP increased successively from 2002 to 2004 regardless of the method used. The differences in annual NEP, except as determined with the Regr. method with u^* -correction, were very small among the years compared with results reported by other studies (Table 2; Falge *et al.*, 2001;

Carrara *et al.*, 2003). We propose that the u^* -correction method combined with at least one other single or multiple gap-filling method should be applied to fill the measurement gaps to examine the potential NEP variation at this study site, because even a sign reversal could occur in annual NEPs when the u^* -correction method is used. In the future, if a more objective estimation of NEP is needed, new gap-filling methods or objective u^* -thresholds, such as were used by Hui *et al.* (2004) or Gu *et al.* (2005a,b), should be applied.

Implications for ecosystem modeling of global warming effects of the C dynamics in an alpine meadow ecosystem

In this alpine meadow, temperature is apparently the dominant factor controlling GPP and R_e dynamics, but the relationship between temperature and GPP or R_e changed, depending on seasonal variations; this dependence seemed to be related to the accumulated biological effects that resulted from previous temperatures, that is, cumulative temperature and consequent plant growth. The early onset and rapid increase in growing degree-days in the spring of 2004 induced an earlier onset of photosynthetic CO_2 uptake but resulted in a smaller increase in R_e , thus enhancing the spring NEP. In contrast, the earlier senescence in autumn 2002 might have been caused mainly by high air temperatures in the late summer of that year, resulting in a decrease in the autumn GPP and R_e and, thus, a low annual NEP in 2002. The 3 years of measurements suggest that climate warming would cause relatively small changes in R_e , and that an earlier onset of the growing season would cause an increase in GPP, but also that GPP might be decreased if excess warming caused an early cessation of photosynthetic activity. The early start of springtime net CO_2 uptake and the nonenhanced summertime vegetation activity seem to follow the global trends, as Angert *et al.* (2005) modeled on the basis of satellite measurements of the last two decades of the 20th century.

Wan *et al.* (2005) reported that global warming, simulated with infrared radiators, indirectly caused significant increases in biomass by extending the length of the growing season in a tallgrass prairie in the United States, which is at a similar latitude ($34^\circ 59' \text{N}$) to our study site. Their finding of positive effects of warming on plant growth is consistent with our results in this alpine meadow. However, focusing on a relatively dryer grassland, a montane meadow in the Rocky Mountains at a similar latitude and altitude ($38^\circ 53' \text{N}$, 2920 m a.s.l.), Saleska *et al.* (1999) showed that heating with infrared radiators caused a significant shift in the plant community composition from high- to low-productivity spe-

cies, the latter being more drought tolerant, and suggested that the changes in soil moisture caused by global warming might be as important in driving the ecosystem response as the direct effects of increased soil temperature. In contrast, in some wetter, northern ecosystems such as tundra or wet meadow ecosystems, which are often water saturated or flooded, productivity has been reported to increase under warming conditions simulated with open-top chambers (Hollister *et al.*, 2005). There is also a risk that an ecosystem will become a CO_2 source if the dominant effect of warming is to enhance respiration (Oechel *et al.*, 1993, 1998). However, Hollister *et al.* (2005) noted that predictions based on experimental warming studies differ, depending on both the duration of the study and the plant community studied in the experiments. Long-term studies focusing on both ecosystem-averaged fluxes and the LAI, as well as on plant community composition and productivities of individual species, are needed to clarify interannual variations in C dynamics.

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