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Authors: Koch, Oliver, Tscherko, Dagmar, Küppers, Manfred, and Kandeler, Ellen

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Interannual Ecosystem CO_2 Dynamics in the Alpine Zone of the Eastern Alps, Austria

*Oliver Koch**
*Dagmar Tscherko**
Manfred Küppers† and
Ellen Kandeler‡*

*Institute of Soil Science, University of Hohenheim, Emil-Wolff-Straße 27, D-70599 Stuttgart, Germany
†Institute of Botany, University of Hohenheim, Grabenstraße 30, D-70599 Stuttgart, Germany
‡Corresponding author: kandeler@uni-hohenheim.de

Abstract

Information about the annual carbon fluxes of fen and meadow ecosystems in alpine environments is rare. We studied the influence of photosynthetic active radiation (*PAR*), plant green area index (*GAI*), soil temperature, and water-filled pore space (*wfps*) on the net CO_2 emission at four alpine sites (one meadow and three fen sites) differing in water balance and plant community. Measurements over two years were made in the Eastern Alps, Austria, including two snow-free periods and two snow periods. During snow-free periods, net CO_2 gain during daylight periods (NEE_{light}, $PAR > 0$) depended on *PAR* and *GAI*. The net CO_2 emission rate at night (R_{tot}, $PAR = 0$) was positively related to soil temperature, while low *wfps* reduced the carbon loss via R_{tot} of the meadow and driest fen study site but reinforced carbon loss of the wetter fen sites. Daily average ecosystem net CO_2 gain (NEE_{day}) during snow-free periods (averaged over both years) at the meadow was 3.5 g CO_2 m^{-2} d^{-1} and ranged from 1.5 to 3.4 g CO_2 m^{-2} d^{-1} at the fen sites. Mean average daily wintertime CO_2 emission was low, being only -0.9 g CO_2 m^{-2} d^{-1} for meadow and between -0.2 and -0.7 g CO_2 m^{-2} d^{-1} for all fen sites. All sites function as significant annual net carbon sinks, with a net carbon gain from 50 to 121 g C m^{-2} a^{-1} (averaged over both years) irrespective of water balance. Our results indicate that these alpine fen sites that have built up a large carbon stock in the past do not gain a further carbon surplus compared with the meadow under the current climate.

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Introduction

Investigations dealing with the carbon balance of terrestrial ecosystems are important because changes in the global climate are expected to cause positive feedback mechanisms (Schlesinger and Andrews, 2000). Alpine tundra covers about 8% of the terrestrial global surface (Archibold, 1995) and alpine soils of major ecosystems are characterized by a high content of organic carbon (Körner, 1999). Therefore, investigations of CO_2 dynamics derived from alpine environments are necessary to further understand global carbon cycling.

The C cycle of quasi-stable ecosystems over long time scales and large areas must be balanced (Körner, 1999). In contrast, pristine peatlands are characterized by accumulation of atmospheric carbon because of the slow decomposition rate favored by water-logged and anoxic conditions. The formation of present peatlands in the Eastern Alps, Austria, started at the end of the last ice age (about 5000 years ago) (Bortenschlager, 1970). However, the future fate of these ecosystems under current climate conditions is unknown.

In general, net ecosystem CO_2 exchange (*NEE*) is the result of gross photosynthesis (P_g) derived by green plants minus the total respiration of the overall ecosystem (R_{tot}) consisting of plants, soil fauna, and soil microbes (e.g. Rustad et al., 2000). Atmospheric CO_2 is sequestered by vegetation via photosynthesis. Carbon is accumulated as organic carbon in the soil or respired again to the atmosphere. Photosynthesis in alpine plants is mainly influenced by irradiation, the phenological status of plants, the length of growing season, and to a lesser extent temperature (Körner, 1999). Although the standing above-ground plant biomass is much smaller compared to lowland plant communities, due to different C allocation, alpine plant species use photosynthetic CO_2 more efficiently than lowland plants (Körner, 1999).

Total ecosystem respiration (R_{tot}) in alpine environments depends on temperature, soil water content, and plant biomass (Cernusca and Decker, 1989). Moreover, R_{tot} is more sensitive to temperature than photosynthesis (Kirschbaum, 2000) and may be crucial for the present ecosystem carbon balance if global temperature increases due to climate change. Although the productivity of alpine meadows is reasonably well understood, the seasonal and annual net CO_2 balance of alpine wetland ecosystems has been investigated on only a few occasions.

We therefore (1) determined plant community properties by harvesting the above- and below-ground biomass, (2) empirically modeled the seasonal ecosystem CO_2 dynamics using meteorological data and the plant green area index (*GAI*), and (3) roughly estimated the annual C budget of four alpine sites in the Eastern Alps, Austria. Four study plots along a soil moisture gradient (one dry meadow and three sites in a fen) were selected, differing in vegetation community and water balance. Net CO_2 flux, plant biomass, and climatic properties (radiation, air temperature, precipitation, soil temperature, and water-filled pore space in 5 cm soil depth) were monitored over a two-year period.

Material and Methods

STUDY SITES

The study area is located in the Ötztal range (46°50′N, 11°03′E) in Tyrol, Austria. Sites are located in the Rotmoos valley

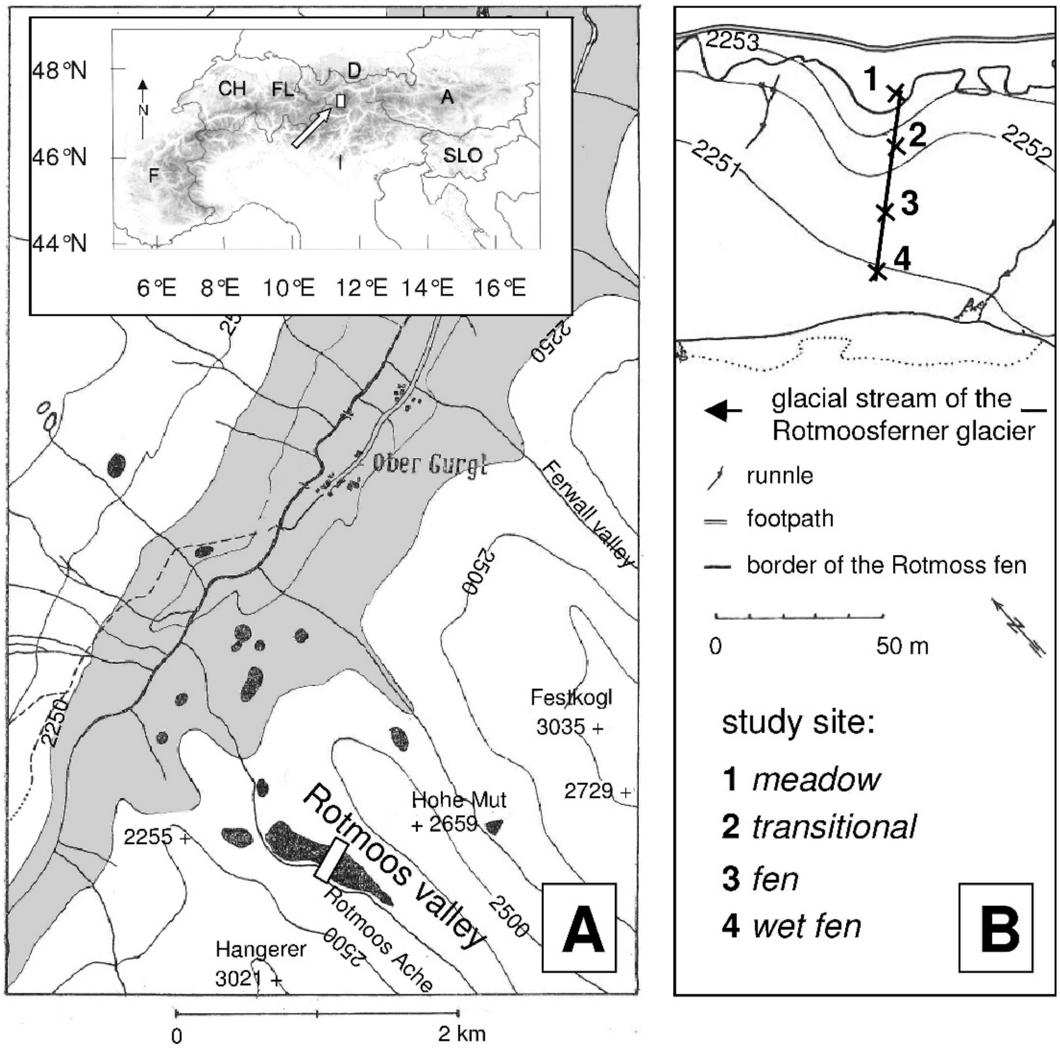

FIGURE 1. Map of the study area and study sites. (A) Overview of alpine fens in the study area (black areas) based on mapping by Rybníček and Rybníčková (1977); gray area in map represents the potential tree area (altitude below 2250 m a.s.l.). Legend of the overview of the Alps: A = Austria, D = Germany, CH = Switzerland, F = France, FL = Liechtenstein, I = Italy, SLO = Slovenia. (B) Map section of the Rotmoos valley with locations of study sites.

above the present tree line (2250 m a.s.l.) (Fig. 1). The valley is exposed SE to NW and flanked by the mountains Hohe Mut (2659 m a.s.l.) and Hangerer (3121 m a.s.l.). The climate is continental with cold, snowy winters and cool summers with a mean snow-free period of about 4.5 months (June to mid-October) (M. Strobel, University of Innsbruck, personal communication). Mean annual precipitation is 820 mm (1970–1996), and mean annual air temperature (1997–1998) is −1.3°C (Kaufmann, 2001).

Four study plots along a moisture gradient were chosen (one alpine dry meadow and three plots in the Rotmoos fen) having a SW exposure on a 1–3° slope; they differ in water balance and vegetation community. The dry study plot (*meadow*) was chosen in an alpine meadow site classified as a *Curvulo-Nardetum* (G.-H. Zeltner, University of Hohenheim, personal communication) (Table 1). The soil is classified as a Cambisol of loamy sandy silicates with a maximum observed soil depth of 50 cm. The meadow is well drained, and 90% of the soil surface is covered by vegetation (10% small boulders). The other three sites are located in the Rotmoos fen. The Rotmoos fen measures 8.5 ha, and the average peat thickness is 1.5 m (range 0.5–2.9 m) (Rybníček and Rybníčková, 1977). Its soils are classified as Rheic Histosols. According to Bortenschlager (1970), the fen was deposited periodically with 15 layers (1–27 cm) of silt or sand sediments (or both) mainly located in deeper than 2 m soil depth. One of the three fen sites (*transitional*) is located in the transition area between alpine dry meadow and the Rotmoos fen. According to Rybníček and Rybníčková (1977), the vegetation of the *transitional* site can be defined as a *Carici echinatae–Trichophoretum caespitosi* community. A relatively high cover of plant species also belongs to the *Curvulo–Nardetum* (Table 1). The second fen plot (*fen*) is located deeper in the Rotmoos fen and is characterized by a typical *Carici echinatae–Trichophoretum caespitosi* plant community (Rybníček and Rybníčková, 1977). The species richness of the *fen* site is lower than the *transitional* site (Table 1). The wettest fen site (*wet fen*) is located in the center of the Rotmoos fen and consists solely of *Carex nigra* L. (Table 1). The vegetation cover was only 30% and this site can be temporarily flooded.

CO_2 MEASUREMENTS

The net CO_2 flux was determined by measuring CO_2 concentration changes using the “closed chamber” technique

TABLE 1

Plant species and coverage (%) of the study sites.

	Meadow	Transitional	Fen	Wet fen
Herbs:				
Alchemilla vulgaris L.	<5			
Anthoxanthum odoratum L.	<5			
Anthyllis vulneraria L.	<5			
Bartsia alpina L.		<5		
Campanula cochlearifolia Lamk.	<5			
Campanula scheuchzeri Vill.	<5			
Dianthus carthusianorum L.	<5			
Euphrasia alpina Lamk.	<5			
Euphrasia minima Jacq. Ex. DC.	<5			
Gentiana ramosa L.	<5			
Geum montanum L.	<5			
Hippocrepis comosa L.	<5			
Homogyne alpina (L.) Cass.		<5		
Leonthodon helveticus Mérat	<5			
Ligusticum mutellina (L.) Crantz	<5	<5		
Phyteuma hemisphaericum L.	<5			
Potentilla aurea L.	<5	10		
Rhinantus angustifolius C.C. Gmelin	<5			
Silene vulgaris (Moench.) Garcke	<5			
Grasses:				
Carex curvula All.	<5			
Carex echinata Murray		5	<5	
Carex flava L.	<5			
Carex nig L.			<5	30
Carex sempervirens Vill.	<5			
Deschampsia cespitosa (L.) P.B.	<5			
Eriophorum angustifolium Honck.		20	40	
Luzula campestris (L.) DC.	<5			
Nardus stricta L.	10	10		
Poa alpina L.	<5			
Trichophorum caespitosum (L.) Hartman		30	60	
Shrubs:				
Calluna vulgaris (L.) Hull	<5	<5		
Salix herbacea L.	<5			
Vaccinium myrtillus L.	<5			

under depletion state. Plexiglas chambers with inserted septa in the lid (frame: 40 cm × 40 cm × 30 cm; lid: 40 cm × 40 cm) were used during the snow-free periods. On average, *PAR* was reduced by 11% due to the Plexiglas. Each chamber ($n = 12$) was equipped with a small battery-driven fan that ensured an adequate circulation of the enclosed air. Per study plot, three frames fitting to the lids were carefully inserted 3 cm into the soil at least 15 h before each measurement. Because of moderate grazing (sheep and horses) during the entire vegetation periods, the frames had to be removed between the sampling days; but the exact location of each chamber was discernible throughout the snow-free periods. On each plot, one chamber was provided with a common resistance thermometer 5 cm above the soil surface to estimate the temperature difference inside and outside the chambers. The maximum temperature in the chamber headspace during the time of measurements was on average 8.6°C (range 4.6 to 14.1°C depending on incident radiation) higher during daytime and 1.1°C (range 0.2 to 2.0°C) during nighttime compared to ambient conditions; these values were similar for all study sites. Vapor pressure deficit (*vpd*) of the enclosed air was reduced compared to the ambient conditions. Gas samples were collected for analysis approximately every 3 weeks within the snow-free season in 2003 ($n = 6$) and every 4 weeks during the snow-free season in 2004 ($n = 4$). Gas samples were taken with double needles connecting the chamber with butyl-rubber septa of evacuated flasks. The flasks were evacuated and washed with nitrogen 5 times in the laboratory prior to sampling. One sample drawing consists of four subsamples which were drawn 0, 6, 20, and 30 min after the chamber was closed. For the measurements during daylight, we additionally drew a subsample after 10 min. Since we simultaneously measured CH_4, the chambers had to be closed for a minimum of 30 min. The sampling procedure was repeated every 3 hours ($n = 8$); it started at noon and ended at 9:00 the following day. During snow periods, gas samples were collected every 1 to 3 months ($n = 11$ for each plot) using three stainless steel pots (diameter 15.5 cm; 25.0 cm height) per site. After the snow was removed from an area of about 2 m × 2 m at each study plot, the steel pots were gently placed on the soil surface and sealed with wet snow. After gas sampling and removal of pots, the area was recovered with snow. One sample drawing was made at noon and consisted of four subsamples, which were taken at 0, 30, 60, and 90 min.

In the laboratory, CO_2 concentrations of the collected air probes were measured using a flame ionization detector in a Perkin Elmer (PE Auto system and PE Headspace Sampler HS 40XL) gas chromatograph. Chromatographic separations were made using a 6 ft stainless steel column packed with Poropak Q (100/120 mesh). The oven of the column was maintained at 40°C and the detector was operated at 350°C. Nitrogen was used as a carrier gas (gas flow rate: 45 mL min^{-1}). Gas standards (200 ppm, 1000 ppm, and 3000 ppm) were used for calibration. CO_2 flux was calculated according to Livingston and Hutchinson (1995). The CO_2 release during nighttime and snow periods was calculated from linear regressions. During daytime, the measured net CO_2 flux followed a first-order exponential decrease caused by declining CO_2 concentrations in the chambers. The first derivative of simple first-order exponential curve fits ($f_{(x)} = ae^{bx}$) were used to calculate the CO_2 flux. At high *PAR* and high above-ground standing plant biomass, the first three subsamples of the sample drawings were used for calculations only, yielding better curve fittings. Regression coefficients of the curve fits lower than $R^2 = 0.90$ were rejected. All rates are expressed on a ground surface basis.

CLIMATE DATA

The climate data were provided by R. Kaufmann (University of Innsbruck, personal communication). The weather station (2270 m a.s.l.) is located 2 km away from the study sites. Air temperature (°C), global radiation (W m^{-2}), precipitation (mm), and relative humidity (%) were recorded 2 m above ground every 15 min. *PAR* (μmol m^{-2} s^{-1}) was monitored directly at our study location every minute during diurnal gas measurements using a *PAR* quantum sensor and data hog2 (Skye Instruments, United Kingdom). *PAR* and global radiation at the weather station were significantly correlated ($R^2 = 0.96$; $n = 326$; $p < 0.001$). This linear function was used to convert the global radiation data from the weather station to *PAR*; it was in the range of the conversion factors of the typical light situations (cloudy, sunny conditions) given by McCree (1972). Soil temperature and soil moisture were recorded hourly at every study site in 5 cm soil depth using temperature loggers (UTL-1, Geotest AG, Switzerland) and soil moisture sensors (SMS3; Cylobios, Austria). For calibration of the soil moisture sensors, soil cores (100 cm^3; $n = 3$) were taken from 0–5 cm soil depth at every sampling date and on every study site during the snow-free periods ($n = 10$). Volumetric water content (θ) was determined gravimetrically after drying at 105°C for 48 h. Water-filled pore space (*wfps*) (%) was calculated by the proportion of volumetric water content (θ) from the maximum saturation water content. Maximum saturation water content (g cm^{-3}) was determined in the laboratory. Soil cores (100 cm^3; $n = 5$) were saturated with degassed water over a 4-day period and weighed before and after drying at 105°C for 48 h. Our determined *wfps* sometimes exceeded 100% (maximum 107%), probably because desiccation and rewetting events were not congruously taken in the calibration curve; we set these values to 100%. Recorded moisture data of snow periods were rejected because values were not reliable due to frozen water conditions.

PLANT BIOMASS AND PLANT GREEN AREA INDEX (GAI)

Above-ground standing plant biomass (g m^{-2} ground area) and plant green area index (*GAI* [m^2 m^{-2}]) were determined for each study site during the snow-free periods in 2003 ($n = 6$) and 2004 ($n = 4$). Plant material was clipped from a 25 × 25 cm area ($n = 5$ for each site) inside a frame randomly positioned on the soil surface. Standing green biomass and non-green biomass were separated visually and oven dried at 70°C for 72 h before weighing. Specific projected leaf surface area (g m^{-2} leaf area) of the entire plant community was determined with an ordinary flatbed scanner and the software Rootedge (Version 2.3, Iowa State University, Inc.). *GAI* represents the projected area of green biomass per ground area (Wohlfahrt et al., 2001).

Below-ground plant biomass was estimated when peak above-ground standing biomass was observed in 2003 by sampling the fine roots (diameter < 2 mm) from 0 to 10 cm soil depth ($n = 5$ for each site). A bucket auger (diameter = 8 cm) was used. In the laboratory, live roots were visually separated from dead roots after being washed out with a sieve (mesh size 1 mm^2) according to Leuschner et al. (2004), and weighed after being dried at 70°C (72 h).

CALCULATIONS AND STATISTICS

Net CO_2 flux rate at daytime ($PAR > 0$) during the snow-free periods represents the net ecosystem CO_2 exchange rate at daytime (NEE_{light} [mg CO_2 m^{-2} h^{-1}]). NEE_{light} was described by a modified response function (Diemer and Körner, 1998; Küppers and Schulze, 1985) based on PAR (μmol m^{-2} s^{-1}) and GAI (Equation 1):

$$NEE_{light_{(PAR,\,GAI)}} = NEE_{\max} \cdot \left(1 - e^{-k \cdot (PAR - \Gamma)}\right) \cdot GAI, \quad (1)$$

where NEE_{max} is maximum NEE_{light} in full sunlight at a given GAI, Γ is the ecosystem light compensation point, and k a coefficient affecting the curvature of the function. PAR values were reduced by 11% to account for the reduction of PAR by the chambers. Temperature (soil, air) and *wfps* did not significantly contribute when additionally added to the model function. High leaf temperature had a negative affect on net photosynthesis, resulting in about 30% lower CO_2 assimilation when leaf temperature was 5°C higher than optimum temperature at full sunlight (Küppers and Schulze, 1985). The influence of the temperature difference of chambers compared to ambient temperature condition ($\Delta T°C_{cham\text{-}amb}$) on the function parameters used in Equation 1 was tested by dividing NEE_{light} values into $\Delta T°C_{(cham.\text{-}amb)}$ categories. No significant effect of $\Delta T°C_{(cham\text{-}amb)}$ was detected for any function parameter.

The CO_2 flux rates during nighttime ($PAR = 0$) of the snow-free period were used as an estimate for total ecosystem respiration (R_{tot} [mg CO_2 m^{-2} h^{-1}]). R_{tot} was described by a multiple linear regression model (Equation 2):

$$\ln R_{tot(st_5,wfps)} = b_1 + b_2 \cdot st_5 + b_3 \cdot wfps, \quad (2)$$

where st_5 (°C) represents soil temperature, and *wfps* (%) the water-filled pore space in 5 cm soil depth. *GAI* did not significantly contribute when additionally added to the model function. Wintertime CO_2 flux was not included in the model because measurements were made after removal of the snow cover. In Equations 1 and 2, we used the data of both snow-free periods to obtain better curve fittings. Here, R_{tot} (carbon loss) is presented as negative and NEE_{light} as positive values (if there was a positive net carbon gain for the ecosystem).

Calculations of the daily net ecosystem CO_2 flux during snow-free periods (NEE_{day} [g CO_2 m^{-2} d^{-1}]) were based on day-based integration on hourly data (t in hours) of NEE_{light} presented as $NEE_{daylight}$ (g CO_2 m^{-2} d^{-1}) and day-based integration on hourly data of R_{tot} presented as R_{night} (g CO_2 m^{-2} d^{-1}):

$$NEE_{daylight} = \int_{t1}^{t2} NEE_{light_{(t)}} \cdot dt, \quad PAR > 0 \quad (3)$$

$$R_{night} = \int_{t1}^{t2} R_{tot_{(t)}} \cdot dt, \quad PAR = 0 \quad (4)$$

$$NEE_{day} = NEE_{daylight} + R_{night}. \quad (5)$$

For seasonal ecosystem C fluxes, all day-based values (d in days) were summed over the snow-free periods, expressed as g C m^{-2} $season^{-1}$:

$$\sum NEE_{daylight} = \int_{d1}^{d2} NEE_{daylight} \cdot dt, \quad (6)$$

$$\sum NEE_{day} = \int_{d1}^{d2} NEE_{day} \cdot dt, \quad (7)$$

$$\sum R_{night} = \int_{d1}^{d2} R_{night} \cdot dt. \quad (8)$$

During snow periods we assumed that the measured CO_2 emission rate was constant over the entire day. Daily CO_2 flux during the snow period (R_w [g CO_2 m^{-2} d^{-1}]; d in days) was calculated taking the averaged hourly flux values for each site. Seasonal ecosystem C fluxes during winter [g C m^{-2} $season^{-1}$] are presented as:

$$\sum R_w = \int_{d1}^{d2} R_w \cdot dt. \quad (9)$$

Annual ecosystem C balance (NEE_{year} [g C m^{-2} a^{-1}]) was calculated:

$$NEE_{year} = \sum NEE_{day} + \sum R_w. \quad (10)$$

The lengths of snow periods were defined by the abrupt decrease and increase of topsoil temperatures (daily values). The *GAI* values of the sites were linearly interpolated between sampling dates. To fill the gaps of missing data from the beginning of the snow-free period until the first measurement, as well as between the last measurement during the snow-free period and the

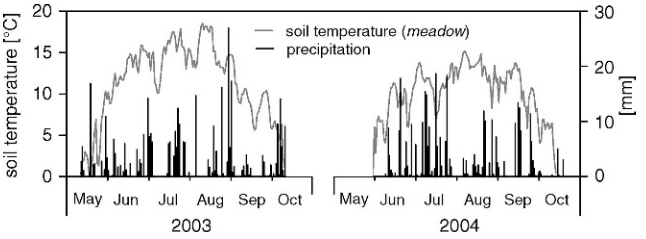

FIGURE 2. Time course of soil temperature at 5 cm soil depth (*meadow*) and precipitation during the snow-free periods.

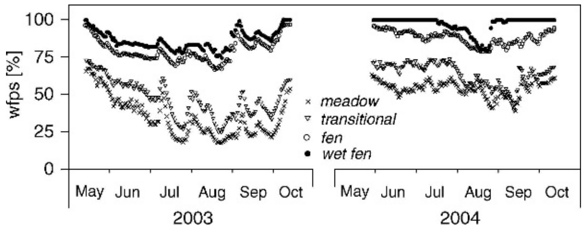

FIGURE 3. Time course of the water-filled pore space (*wfps*) at 5 cm soil depth during the snow-free periods.

onset of the snow period, we assumed a constant *GAI*, taking its value at the nearest sampling date.

Effects of the study site and study years on peak above-ground standing biomass (green, non-green) and below-ground biomass were tested by univariate analysis of variance followed by a Student-Newman-Keuls test. Additionally, a simple two-factorial analysis of variance (date and study site) was applied to quantify differences of the seasonal course of *GAI*. Both study years were treated separately. The Student-Newman-Keuls multiple range test was used to calculate maximum critical range (LSD) using time or site as the main factor.

Results

CLIMATIC PROPERTIES AND HYDROLOGY

The mean annual air temperature differed considerably between the two studied years, being −0.4°C (2003) and −1.3°C (2004), while mean annual soil temperatures (in 5 cm soil depth) at all study sites ranged between 3.5°C and 4.6°C for both years. The length of the snow-free period was 149 days and 123 days in 2003 and 2004, respectively. During snow-free periods, the mean soil temperature was on average 2.2°C higher in 2003 than in 2004. Diurnal soil temperature varied according to time of day (data not shown). The maximum temperature range was reached on a clear day at mid season (2003), ranging from 6.2°C to 29.4°C. During snow periods, soil temperature was almost constant, with no diurnal change because of the insulation effect of a deep snow cover (maximum 235 cm). On average it was between 0°C and 0.1°C. Total precipitation during snow-free period was lower in 2003 (276 mm) than in 2004 (326 mm) (Fig. 2). Average water-filled pore space (*wfps*) of both snow-free periods increased in the order *meadow* (46%) < *transitional* (59%) < *fen* (77%) < *wet fen* (81%) (Fig. 3). The year 2003 was much drier than 2004 at all sites. During snow-free periods, *wfps* decreased, reaching minimum values in August and early September; it increased again later in the season. In 2003, four distinctive desiccation periods were observed, whereas *wfps* was much more balanced during 2004. During the entire snow period, soils were water saturated for *fen* and *wet fen*. The soil of the *meadow* and the *transitional* site remained wet during snow periods.

VEGETATION PROPERTIES

The green above-ground standing plant biomass was similar at the *meadow*, *transitional*, and *fen* sites, but about three to four times lower at *wet fen* (Table 2). No significant differences between the study years were found at any study site. The ratio between green and non-green above-ground standing plant biomass (mainly necromass) was highest for *meadow* and lowest for *wet fen* (Table 2). In the wetter year 2004, this ratio increased for the fen sites. Highest root biomass (0–10 cm soil depth) was observed at *meadow* followed by *fen* and *transitional* (Table 2). Root biomass at *wet fen* was small, being three to four times lower than at the other sites. The plant green area index (*GAI*) peaked in July (2003) and August (2004) at all sites (Fig. 4). *Wet fen* had the lowest *GAI* throughout the snow-free periods, while all other sites had similar values. Maximum *GAI* for both study years were: *meadow* (4.3) > *transitional* (3.7) > *fen* (3.2) > *wet fen* (1.0).

CONTROLS OF NET ECOSYSTEM CO_2 EXCHANGE RATE DURING DAYTIME AND TOTAL ECOSYSTEM RESPIRATION RATE DURING NIGHTTIME

The net ecosystem CO_2 exchange rate during daytime (NEE_{light}) depended significantly on *PAR* and *GAI* (Table 3A). NEE_{max} derived from the models at a given *GAI* was highest at the *wet fen* site, and the ecosystem light compensation point (Γ) was highest for the *meadow*. A 1:1 dialog of the observed versus predicted values indicate a balanced distribution for NEE_{light} values smaller than about 800 mg CO_2 m^{-2} h^{-1}. A slight overestimation was found for higher NEE_{light} values (Fig. 5A). The average of the variation coefficients (absolute values) ranged between 23% (*meadow*) to 34% (*wet fen*). At all sites, significant linear relationships (R^2 = 0.54 to 0.69; $p < 0.001$) between measured NEE_{light} values and *GAI* were found at high *PAR* (>800 μmol m^{-2} s^{-1}). Total ecosystem respiration (R_{tot}) depended significantly on water-filled pore space (*wfps*) and soil temperature (st_5) (Table 3B). The influence of *wfps* was different for the sites (see b_2 in Table 3B). The total ecosystem respiration (R_{tot}) was positively related to *wfps* at the drier sites (*meadow*, *transitional*), whereas R_{tot} increased with decreasing *wfps* at the wetter sites (*fen*, *wet fen*). The observed versus predicted R_{tot} values were equally distributed about the 1:1 line of the dialog (Fig. 5B). The average variation coefficients of the observed values (not ln transformed) ranged between 18% (*fen*) and 27% (*transitional*). The response of R_{tot} to a temperature difference of 10°C (Q_{10}) was calculated using the multiple linear model. The derived Q_{10} values were 3.0 (*meadow*), 3.5 (*fen*), and 3.9 (*transitional*, *wet fen*).

SEASONAL DAILY CO_2 FLUXES

The calculated seasonal courses of NEE_{day} during snow-free periods increased until July (2003) or August (2004) and decreased towards the end of seasons (Fig. 6A). The pattern follows the trend of *GAI and PAR*, resulting in a sharper increase and decrease of NEE_{day} in 2003 versus 2004. *Wet fen* had the overall lowest NEE_{day} values during both snow-free seasons compared to all other sites. Average NEE_{day} of both study years were in the order: *meadow* (4.56 g CO_2 m^{-2} d^{-1}) > *transitional* (4.00 g CO_2 m^{-2} d^{-1}) > *fen* (3.45 g CO_2 m^{-2} d^{-1}) > *wet fen* (1.77 g CO_2 m^{-2} d^{-1}).

TABLE 2

Above- and below-ground plant biomass at peak standing plant biomass of the two investigated years 2003 and 2004. Different letters in the row indicate significant differences between study sites and years ($p < 0.05$).

Site	Meadow		Transitional		Fen		Wet fen	
Year	2003	2004	2003	2004	2003	2004	2003	2004
Above-ground:								
green biomass (g m^{-2})	242^{a}	237^{a}	239^{a}	280^{a}	204^{a}	222^{a}	64^{b}	71^{b}
green biomass/non-green biomass	0.98^{a}	0.89^{a}	0.71^{ab}	0.83^{a}	0.66^{b}	0.85^{a}	0.53^{b}	0.74^{ab}
Below-ground (0–10 cm):								
live biomass (g m^{-2})	349^{a}		273^{ab}		278^{ab}		95^{b}	

Daily nighttime ecosystem respiration (R_{night}) increased (became more negative) from the beginning of the snow-free periods and peaked at all study sites in August (both study years) (Fig. 6B). Towards the end of snow-free periods R_{night} decreased again. Average R_{night} values (both seasons) were *meadow* (−1.21 g CO_2 m^{-2} d^{-1}) > *transitional* (−0.89 g CO_2 m^{-2} d^{-1}) > *fen* (−0.74 g CO_2 m^{-2} d^{-1}) > *wet fen* (−0.36 g CO_2 m^{-2} d^{-1}).

On average, R_w (± standard error) during snow periods was highest at *meadow* (−0.87 ± 0.21 g CO_2 m^{-2} d^{-1}) followed by *transitional* (−0.65 ± 0.22 g CO_2 m^{-2} d^{-1}), *fen* (−0.21 ± 0.08 g CO_2 m^{-2} d^{-1}) and *wet fen* (−0.16 ± 0.06 mg CO_2 m^{-2} d^{-1}). Significant differences were calculated between sites ($F_{(\mathrm{site})} = 5.81$, $p < 0.009$) but not between sampling dates ($F_{(\mathrm{date})} = 1.73$, $p = 0.26$).

CUMULATIVE C FLUXES AND ANNUAL C BALANCE

All study sites function as net annual carbon sinks during snow-free seasons. The cumulative net ecosystem carbon exchange (ΣNEE_{day}) was highest at *meadow* for both study years (Table 4). However, ΣNEE_{day} at *transitional* and *fen* was almost as high as for *meadow*, while *wet fen* had the lowest values, being about two to almost three times lower than for all other sites. The cumulative total ecosystem respiration during snow periods (ΣR_w) was highest for *meadow*, while *transitional*, *fen*, and *wet fen* ΣR_w were about two to five times lower compared to *meadow*. The annual C balance (ΣNEE_{year}) is the sum of ΣNEE_{day} and ΣR_w. All sites were net annual carbon sinks, ranging from 96 to 125 g C m^{-2} $year^{-1}$ for *meadow*, *transitional*, and *fen* (average of both years). *Wet fen* had the lowest net annual carbon gain, about two times lower than all other sites.

Discussion

ENVIRONMENTAL CONTROLS OF NET ECOSYSTEM CO_2 EXCHANGE RATE AT DAYTIME

The ecosystem light compensation point (Γ) was higher for *meadow* (129 µmol m^{-2} s^{-1}) than for fen sites (109 to 103 µmol m^{-2} s^{-1}). Similar Γ values (70 to 130 µmol m^{-2} s^{-1}) were reported for ungrazed vegetation near the treeline in the central Caucasus (Tappeiner and Cernusca, 1996). Diemer and Körner (1998) found Γ values ranging between 80 and 110 µmol m^{-2} s^{-1} for mid-season, but increasing towards the end of vegetation period for an alpine grassland dominated by *Carex curvula* (Swiss Alps). In contrast, zero net ecosystem CO_2 exchange rates were found for a higher range of *PAR* (250 to 400 µmol m^{-2} s^{-1}) at an alpine meadow in the Tibetan plateau (Kato et al., 2004) with a similar amount of above-ground plant biomass as in our study. Taking the derived model from Hirota et al. (2006) yielded remarkably low Γ values (<1 µmol m^{-2} s^{-1}) for several wetlands in the Tibetan plateau. However, our calculated parameters include a considerably dry snow-free season. Γ values from a boreal nutrient-poor fen were generally higher than our data, but much lower for a wet vegetation period (147 µmol m^{-2} s^{-1}) than a dry vegetation period (281 µmol m^{-2} s^{-1}) (Bubier et al., 2003). In general, low ecosystem light compensation point favors the net carbon gain of an ecosystem. In our study, the lower *Γ* values of all fen sites compared to the *meadow* may be an adaptation of the occurring vegetation communities, which have built up a large pool of soil organic matter.

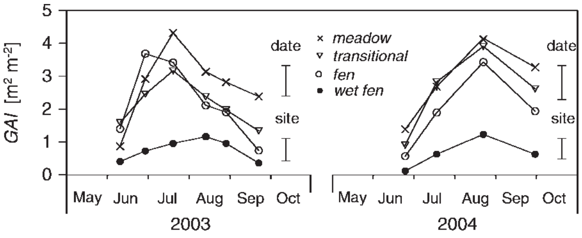

FIGURE 4. Time course of the plant green area index (*GAI*) during the snow-free periods. Error bars indicate the maximum critical range (LSD) for sampling date (date) and study site (site).

In this study, net CO_2 flux measured at high radiation (*PAR* > 800 µmol m^{-2} s^{-1}) was linearly related to *GAI*, confirming the importance of plant structure at different developmental stages. Similarly, a linearly interpolated leaf area index has been used in seasonal gross ecosystem CO_2 exchange models for boreal organic soils (Maljanen et al., 2004). The calculated NEE_{max} for maximum

TABLE 3

(A) Parameters of the model functions to calculate net ecosystem carbon exchange rate during daytime (*NEE_{light}* [mg CO_2 m^{-2} h^{-1}]) and (B) total respiration rate (*R_{tot}* [mg CO_2 m^{-2} h^{-1}]); *PAR*: photosynthetic active radiation (µmol m^{-2} s^{-1}), *GAI*: plant green area index (m^2 m^{-2}), *st_5*: soil temperature in 5 cm depth (°C), *wfps*: water-filled pore space (%). All model function parameters and correlation coefficients were highly significant ($p < 0.001$).

	Meadow	Transitional	Fen	Wet fen
A $NEE_{light(PAR,GAI)} = NEE_{\max} \cdot \left(1 - e^{-k(PAR-T)}\right) \cdot GAI$ ($n = 36$ for each study site)				
$NEE_{\max}$	233.72	250.78	228.04	324.44
k	0.0028	0.0027	0.0038	0.0044
T	128.91	109.13	106.86	93.03
R^2	0.71	0.67	0.60	0.59
B $(-1)\ln R_{TOT(st_5,wfps)} = b_0 + b_1 st_5 + b_2 wfps$ ($n = 30$ for each study site)				
b_0	4.05	3.52	4.94	6.94
b_1	0.17	0.14	0.12	0.14
b_2	0.007	0.005	−0.017	−0.045
R^2	0.80	0.81	0.88	0.86

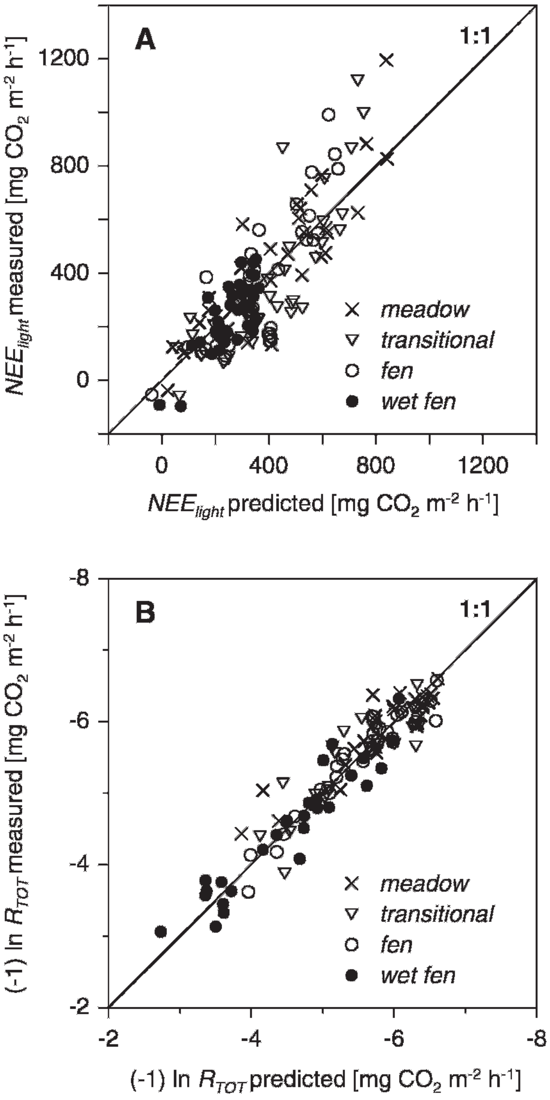

FIGURE 5. 1:1 dialog between the observed versus predicted values of NEE_{light} (A) and R_{tot} (B).

observed *GAI* was highest for *meadow* (1.01 g CO_2 m^{-2} h^{-1}) followed by *transitional* (0.93 g CO_2 m^{-2} h^{-1}), *fen* (0.75 g CO_2 m^{-2} h^{-1}), and *wet fen* (0.39 g CO_2 m^{-2} h^{-1}). Higher values were reported at mid-season for alpine meadows: 1.5 g CO_2 m^{-2} h^{-1} derived by single measurement in the Swiss Alps at full sunlight (Diemer, 1994) or for an alpine meadow in the Tibetan plateau (1.58 g CO_2 m^{-2} h^{-1}) (Kato et al., 2004). In contrast, a lower maximum NEE_{light} value (0.7 g CO_2 m^{-2} h^{-1}) over the entire growing season was found in a dry alpine tundra ecosystem, namely Niwot Ridge, Colorado (Welker et al., 1999). The seasonal NEE_{max} for the fen sites in our study (0.4 to 0.9 g CO_2 m^{-2} h^{-1}) were comparable with the range of seasonal NEE_{max} values (0.18 to 0.71 g CO_2 m^{-2} h^{-1}) of different wetlands in the Tibetan plateau (Hirota et al., 2006). Lower NEE_{max} values might be due to grazing. Remarkably reduced CO_2 uptake was observed for a grazed sub-alpine meadow (Rogiers et al., 2005) during the entire vegetation period and for alpine wetlands (Hirota et al., 2005) in comparison to control sites. Moreover, Gilmanov et al. (2007) reported reduced maximal net ecosystem carbon gain and reduced light-use efficiency (defined as the ratio of gross ecosystem carbon gain to incident *PAR*) after hay-mowing events or grazing for several European grassland sites (temperate to sub-alpine).

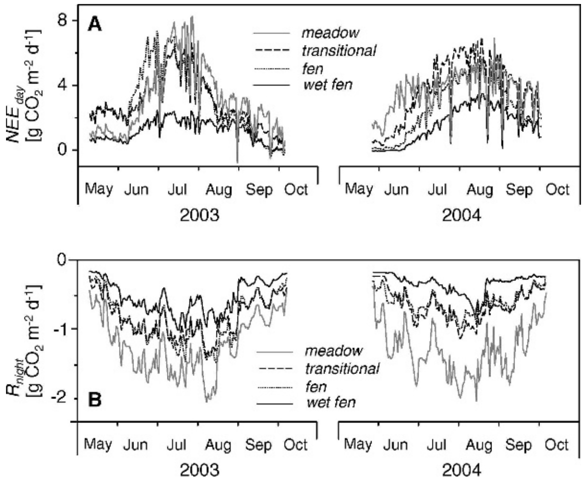

FIGURE 6. Time course of the seasonal NEE_{day} (A) and R_{night} (B) during the snow-free periods.

ENVIRONMENTAL CONTROLS OF ECOSYSTEM RESPIRATION RATE

During snow-free periods, the ecosystem respiration rate (R_{tot}) was related to soil temperature and *wfps* at 5 cm depth. Q_{10} values were lowest at *meadow* (3.0) compared to the fen sites (3.4 [*fen*] and 3.9 [*transitional*, *wet fen*]). Our Q_{10} values (corrected for soil moisture) fit to values calculated for other alpine ecosystems. Cao et al. (2004) found Q_{10} values based on soil temperature at 0–10 cm being 2.75 and 3.22 in a heavily grazed alpine meadow and lightly grazed alpine meadow, respectively. Q_{10} values for the entire snow-free season in alpine wetlands at the Tibetan plateau ranged from 2.7 to 5.1 (Hirota et al., 2006). An average Q_{10} of 3.5 was found for sub-alpine wetlands in the Rocky Mountains (Wickland et al., 2001). However, the wide range of temperature sensitivity of ecosystem respiration is difficult to compare and probably reflects several variables: Q_{10} values were found to be higher for a lower temperature range and/or for a higher ratio of root to soil respiration (Kirschbaum, 2000), but also highly depend on the quality of soil organic matter (Fierer et al.,2006). Moreover, soil respiration is exponentially related to temperature in contrast to respiration of above-ground plant biomass, which was linearly related to temperature in an alpine meadow (Cernusca et al., 1978). Beside soil temperature, *wfps* was the second important control of R_{tot}. Its influence, however, differed depending on study site. In the *meadow* and the driest fen (*transitional*), it was positively related to *wfps*. Since we used the sign convention of R_{tot} having negative values, this means that the absolute value of R_{tot} decreased with decreasing *wfps*, which is an indication of water stress. This is remarkable because most alpine environments are expected to be not water limited (Körner, 1999). Incubation experiments yielded an optimum of 40 to 50% water-holding capacity for soil respiration in forest and mineral soils (Bowden et al., 1998). In our experiments, however, *meadow* and *transitional* were exposed to very low *wfps* at 5 cm soil depth, especially during the snow-free period in 2003. These results identify topsoil as the major source for soil-derived CO_2 emission and explain the greater carbon loss via R_{tot} with decreasing *wfps* in topsoil even at one of the fen sites (*transitional*). The influence of *wfps* on R_{tot} was negative for the *fen* and *wet fen*. Accordingly, the absolute value of R_{tot} increases if *wfps* decreases. The positive influence of *wfps* can be explained by the shift of anoxic to oxic soil conditions at low *wfps* because aerobic respiration is the main source of CO_2 emission (e.g. Conrad, 1996). Also, water-logging

TABLE 4

Cumulative CO_2 fluxes (ΣNEE_{day} [g C m^{-2} period^{-1}], ΣR_w [g C m^{-2} period^{-1}]) and annual C balances [g C m^{-2} a^{-1}] of the two investigated study years 2003 and 2004.

Site	Meadow		Transitional		Fen		Wet fen	
Year	2003	2004	2003	2004	2003	2004	2003	2004
ΣNEE_{day}	171	167	141	155	146	110	67	64
ΣR_w	−51	−58	−27	−30	−12	−14	−9	−11
NEE_{year}	120	109	114	125	134	96	58	53

may prevent CO_2 diffusion in the soil matrix, resulting in lower soil CO_2 emission. Our results are in agreement with several studies for alpine (Hirota et al., 2006) or boreal wetland ecosystems (e.g. Alm et al., 1997; Bubier et al., 2003).

MAGNITUDE OF SEASONAL CO_2 FLUXES

In quasi-stable ecosystems, the gross annual primary production is positively correlated with total ecosystem respiration, while low annual temperatures negatively influence both processes (Gilmanov et al., 2007). The magnitude of NEE_{day} and the duration of snow-free periods are the main factors for the ecosystem net carbon gain; here, R_{night} is the carbon loss of NEE_{day} during nighttime. At *meadow*, the averages (both snow-free periods) of modeled NEE_{day} and R_{night} were 3.50 g CO_2 m^{-2} d^{-1} and −1.11 g CO_2 m^{-2} d^{-1}, respectively. In comparison with our meadow site, a high range of CO_2 fluxes have been reported from alpine meadow ecosystems. For example, Diemer and Körner (1998) found a higher average NEE_{day} (8.41 g CO_2 m^{-2} d^{-1}) and a similar average NEE_{night} (−1.18 g CO_2 m^{-2} d^{-1}) for a Swiss alpine meadow dominated by *Carex curvula*. A much lower average NEE_{day} (0.17 g CO_2 m^{-2} d^{-1}) was calculated for an alpine dry tundra ecosystem at Niwot Ridge, Colorado (Welker et al., 1999), even though maximum R_{tot} during nighttime was comparable with our data. Kato et al. (2004) reported an average NEE_{day} of 4.3 g CO_2 m^{-2} d^{-1}, yet the maximum R_{night} (−9.2 g CO_2 m^{-2} d^{-1}) was more than four times higher than our data. Lower R_{night} values are likely a result of grazing: Cao et al. (2004) found 30% lower total ecosystem respiration for heavily grazed than for lightly grazed meadows in the Tibetan plateau.

At our fen sites, average *NEE_{day} and R_{night}* values (both study years) were lower than at *meadow*, ranging from 1.58 to 3.38 g CO_2 m^{-2} d^{-1} and −0.26 to −0.66 g CO_2 m^{-2} d^{-1}, respectively. Similar NEE_{day} values (0.53 to 3.26 g CO_2 m^{-2} d^{-1}) were found for various wetlands in the Tibetan plateau (Hirota et al., 2006). Those authors reported day-based total ecosystem respiration for the entire day and found average values ranging from −1.43 to −4.00 g CO_2 m^{-2} d^{-1}. According to Atkin et al. (1997), however, artificial darkening (a common practice in many studies) of light-exposed leaves overestimates dark respiration compared to dark-acclimatized leaves and therefore overestimates total ecosystem respiration flux rates.

Average R_w at *meadow* (−0.87 g CO_2 m^{-2} d^{-1}) falls into the range of R_w (−0.32 g C m^{-2} d^{-1} to −1.16 g CO_2 m^{-2} d^{-1}; 0 to −5°C soil temperature) that was found at Niwot Ridge, Rocky Mountains, Colorado (Brooks et al., 1997). Similar R_w values (−0.93 mg CO_2 m^{-2} d^{-1} at 0°C) were found in an alpine meadow ecosystem in the Tibetan plateau (Kato et al., 2005) and in an alpine meadow in Austria (−1.06 g C m^{-2} d^{-1}; Cernusca et al., 1978). Other studies reported higher R_w values from alpine and sub-alpine meadows, like for Wyoming (−0.64 to −2.38 g CO_2 m^{-2} d^{-1}; Sommerfeld et al., 1993), Rocky Mountains National Park (−1.86 g CO_2 m^{-2} d^{-1}; Mast et al., 1998), and for a meadow in the Swiss Alps (−2.28 g CO_2 m^{-2} d^{-1}; Diemer and Körner, 1998). Average R_w at our fen sites were lower (−0.65 g CO_2 to −0.16 g CO_2 m^{-2} d^{-1}) than for the *meadow* site, following the mean water gradient of the study sites. In comparison, Mast et al. (1998) found higher R_w values: −1.86 g CO_2 m^{-2} d^{-1} and −0.64 g CO_2 m^{-2} d^{-1} for moist and saturated alpine soils, respectively. The wide variation of reported flux values for similar temperature may reflect site-specific biological activity. Moreover, differences between the snow gas gradient method and chamber method after snow removal were reported by Alm et al. (1999). Due to the long duration of snow periods in alpine regions, however, even small differences in R_w are significant for the ecosystem annual carbon budget. The ΣR_w correspond to 30–35% and 9–19% of ΣNEE_{day} for the *meadow* and fen sites, respectively (see Table 5). Sommerfeld et al. (1993) calculated a contribution of ΣR_w to yearly above-ground net primary production of 20–50% for alpine and sub-alpine meadows, and Brooks et al. (1996) reported 20% for an alpine meadow in the Rocky Mountains. Diemer and Körner (1998) found a much higher contribution of ΣR_w to ΣNEE_{day} (73%) for an alpine meadow; note, however, that ΣR_w was calculated taking a value more than twice as high and with a snow period about one month longer than in our study. Hence, assuming the same wintertime respiration for snow period duration, the ratio ΣR_w to ΣNEE_{day} for *meadow* would shift to values (about 85%) similar to those found by Diemer and Körner (1998). The fen sites appear to be more robust to severe changes in the length of annual snow cover because ΣR_w to ΣNEE_{day}

TABLE 5

Cumulative CO_2 fluxes ($\Sigma NEE_{daylight}$ [g C m^{-2} period^{-1}], ΣR_{night} [g C m^{-2} period^{-1}]) and selected ratios of cumulative CO_2 fluxes ($|\Sigma R_{night}/\Sigma NEE_{daylight}|$, $|\Sigma R_w/\Sigma NEE_{day}|$).

Site	Meadow		Transitional		Fen		Wet fen	
Year	2003	2004	2003	2004	2003	2004	2003	2004
Seasonal C fluxes:								
$\Sigma NEE_{daylight}$	218	210	176	186	180	131	84	74
ΣR_{night}	−47	−43	−35	−31	−34	−21	−17	−10
Ratio between C fluxes [%]:								
$\lvert\Sigma R_{night}/\Sigma NEE_{daylight}\rvert$	22	20	20	17	19	16	20	14
$\lvert\Sigma R_w/\Sigma NEE_{day}\rvert$	30	35	19	19	9	13	13	17

contribute less. Low ratios indicate that ecosystems are not in equilibrium and accumulate significant amounts of carbon (Diemer and Körner, 1998). However, dissolved organic carbon may be transported in the aquifer, leading to significant carbon loss from ecosystems; in our study, all fen sites are fed by water running down the hill slopes. Alm et al. (1997) also point to the role of leaching: they estimated an annual carbon loss of about 8 g C m^{-2} from dissolved organic matter leached from a boreal fen in Finland.

ANNUAL C BALANCE IN ALPINE ECOSYSTEMS AND GLOBAL ASPECTS

All of our sites proved to be significant annual carbon sinks (53–138 g C m^{-2} a^{-1}) for atmospheric CO_2. Beside *wet fen*, all other sites had similar values. Within the Rotmoos fen, *wet fen* cover was only roughly 5%. The cover of the *transitional* and *fen* site was estimated to be 10% and 85%, respectively. Thus, the Rotmoos fen has built up a huge amount of carbon per surface area in the past, but our results indicate no further carbon surplus compared to *meadow* under the current climate. Recent annual C balance data from alpine regions showed no consistent pattern. For example, Diemer and Körner (1998) found a lower annual carbon gain (20.4 g C m^{-2} a^{-1}) for a Swiss alpine meadow dominated by *Carex curvula*, while Welker et al. (1999) found a small carbon gain (7 g C m^{-2}) for the growing season in an alpine tundra ecosystem in Niwot Ridge, Colorado; because of the long annual winter period (7 months), the latter site is likely a net annual carbon source. Much greater differences in the annual C balance (-171 to 75 g C m^{-2} a^{-1}) derived from European sub-alpine meadows managed by grazing or cut herbage (no further manure application or mineral N input) were found by Gilmanov et al. (2007). For sub-alpine fen sites, Chimner and Cooper (2003) calculated an average ecosystem net carbon gain of 24 g C m^{-2} a^{-1} (range: -142 to 180 g C m^{-2} a^{-1}) in the southern Rocky Mountains, while Wickland et al. (2001) found, for a wetland in the same area, a net annual carbon loss (-106.8 to -115.2 g C m^{-2} a^{-1}). A global C model predicted an annual carbon gain of 0 to 10 g C m^{-2} a^{-1} for the European Alps (Zhuang et al., 2003), but the authors used only data from the North American continent. Great uncertainties still exist about net CO_2 fluxes from alpine ecosystems and the influence of management for those sites. These must be tackled before determining the role of alpine areas in the global C budget.

Conclusions

This study on the C balance of alpine ecosystems shows that net annual carbon gain was not related to the site's soil water properties under current climatic conditions. During snow periods, only a small part of the carbon gain during the vegetation period was respired. However, the high range of alpine wintertime CO_2 emission rates found in the literature is crucial for annual carbon loss during long snow periods. Due to the large variability of seasonal and annual net CO_2 fluxes from different alpine ecosystems, more investigations are necessary to evaluate the role of alpine areas in the global carbon budget under present und future climate conditions.

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