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## Seasonal and inter-annual variability of the net ecosystem CO<sub>2</sub> exchange of a temperate mountain grassland: effects of climate and management

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### Abstract

The role and relative importance of climate and cutting for the seasonal and inter-annual variability of the net ecosystem CO<sub>2</sub> (NEE) of a temperate mountain grassland was investigated. Eddy covariance CO<sub>2</sub> flux data and associated measurements of the green area index and the major environmental driving forces acquired during 2001-2006 at the study site Neustift (Austria) were analyzed. Driven by three cutting events per year which kept the investigated grassland in a stage of vigorous growth, the seasonal variability of NEE was primarily modulated by gross primary productivity (GPP). The role of environmental parameters in modulating the seasonal variability of NEE was obscured by the strong response of GPP to changes in the amount of green area, as well as the cutting-mediated decoupling of phenological development and the seasonal course of climate drivers. None of the climate and management metrics examined was able to explain the inter-annual variability of annual NEE. This is thought to result from (1) a high covariance between GPP and ecosystem respiration (R<sub>eco</sub>) at the annual time scale which results in a comparatively small inter-annual variation of NEE, (2) compensating effects between carbon exchange during and outside the management period, and (3) changes in the biotic response to rather than the climate variables per se. GPP was more important in modulating inter-annual variations in NEE in spring and before the first and second cut, while R<sub>eco</sub> explained a larger fraction of the inter-annual variability of NEE during the remaining, in particular the post-cut, periods.

### 1. Introduction

Atmospheric carbon dioxide (CO<sub>2</sub>) is responsible for around 60 % of anthropogenic global warming [Intergovernmental Panel on Climate Change, 2001]. Of the 7 Pg carbon (C) released on average each year to the atmosphere through fossil fuel burning, the terrestrial biosphere absorbs about one third (a similar share is absorbed by aquatic ecosystems; [Canadell et al., 2007]). Quantifying the spatial patterns of the net exchange of CO<sub>2</sub> (NEE) between land ecosystems and the atmosphere and projecting how NEE will be affected by likely future climate and land use is thus a critical issue in environmental science [Steffen et al., 1998; Running et al., 1999; Baldocchi et al., 2001] and requires understanding of the interactions and feedbacks within the carbon cycle and the way these are influenced by human interference [Pielke et al., 1998].

NEE varies on time scales ranging from seconds to decades [Stoy et al., 2005; Mahecha et al., 2007]: On the time scale of seconds, fluctuations in incident photosynthetically active

radiation (PAR) cause rapid changes in leaf photosynthesis [Kirschbaum et al., 1997] and turbulent eddies transfer CO<sub>2</sub> in and out of the plant canopy [Denmead and Bradley, 1987]. The diurnal cycle of sun light and associated changes in environmental drivers (air temperature, vapor pressure deficit, wind speed) govern the daily course of NEE. Seasonal changes in NEE reflect the vegetation phenological development and seasonal changes in environmental driving forces [Falge et al., 2002a,b]. Inter-annual variations in NEE have most frequently been attributed to environmental anomalies and the ecosystem's, sometimes lagged, response to these [e.g. Barford et al., 2001; Gu et al., 2003; Morgenstern et al., 2004; Saigusa et al., 2005; Barr et al., 2006; Dunn et al., 2006; Richardson et al., 2007]. Decadal variations in NEE have been shown to result from major disturbances (fire – [Goulden et al., 2006]; clear cutting and reforestation – [Kowalski et al., 2004; Fredeen et al., 2007; Humphreys et al., 2006; Schwalm et al., 2007] and relate to slow changes in the biogeochemical cycling of carbon, nutrients and water. Longer-term trends in successional changes in species composition [Urbanski et al., 2007], environmental conditions (e.g. warming – [Oechel et al., 2000; Dunn et al., 2006]) and low-frequency meteorological phenomena (e.g. El Nino/La Nina – [Baldocchi and Wilson, 2001; Morgenstern et al., 2004; Saigusa et al., 2005]; north-atlantic oscillation – [Piovesan and Adams, 2000]) may also cause variations in NEE at longer time scales. Our understanding of the variability in NEE across this wide range of time scales is higher for short (up to daily) and very long (decadal) time scales, less so for seasonal and inter-annual variability [Hui et al., 2003; Kucharik et al., 2006; Richardson et al., 2007; Urbanski et al., 2007].

For managed grasslands, as well as for croplands, an important source of seasonal and inter-annual variation in NEE is the frequency, timing and duration of management practices. Cutting and grazing turns grasslands temporarily into net sources of CO<sub>2</sub> [Maljanen et al., 2001; Barcza et al., 2003; Lohila et al., 2004; Novick et al., 2004; Wohlfahrt, 2004; Marcolla and Cescatti, 2005; Rogiers et al., 2005; Jaksic et al., 2006; Lawton et al., 2006; Ammann et al., 2007; Veenendaal et al., 2007]. The amount of CO<sub>2</sub> lost during and the duration of the recovery period after cutting vary from a few g C and several days [e.g. Barcza et al., 2003; Novick et al., 2004] up to 100 g C and one month [Ammann et al., 2007]. The causes for the observed variability in recovery from cutting/grazing and the implications for the seasonal and inter-annual variability in NEE have received little attention up to date. As shown by Wohlfahrt [2004], current soil-vegetation-atmosphere-transfer (SVAT) models have difficulties in accurately simulating the recovery of NEE after cutting. Such knowledge and respective modeling capabilities are required for assessing carbon mitigation options through altered grassland management practices, such as changes in the frequency and timing of cutting events or the length, frequency and intensity of grazing periods.

The objective of the present paper is to quantify the seasonal and inter-annual variability of NEE of a temperate managed grassland and to analyze the role and relative importance of climate and cutting in determining this variability. To this end we use six years of eddy covariance CO<sub>2</sub> flux measurements made above a mountain grassland in Austria, which is cut three times per year for hay production. We hypothesize that (1) cutting, through modifying the amount of photosynthetically active plant matter, will be the major control on the seasonal variability of NEE, and (2) that the inter-annual variability in NEE will be determined by inter-active effects of both climate and cutting.

## 2. Material and methods

### 2.1 Site description

The study site is located at a meadow in the vicinity of the village Neustift (47°07'N, 11° 19'E) in the Stubai Valley (Austria) at an elevation of 970 m a s l. in the middle of the flat valley bottom. The fetch is homogenous up to 300 m to the east and 900 m to the west of the

instrument tower, the dominant day and night time wind directions, respectively. The average annual temperature is 6.5 °C, average annual precipitation amounts to 852 mm. The vegetation has been classified as a Pastinaco-Arrhenatheretum and consists mainly of a few dominant graminoid (*Dactylis glomerata*, *Festuca pratensis*, *Phleum pratensis*, *Trisetum flavescens*) and forb (*Ranunculus acris*, *Taraxacum officinale*, *Trifolium repens*, *Trifolium pratense*, *Carum carvi*) species. The soil has been classified as a Fluvisol (FAO classification) and is approximately 1 m deep. Below a thin (0.001 m) organic layer, an A horizon, with an organic volume fraction of approximately 14%, extends down to 0.02 m, followed by the B horizon, which is best described as a (sandy) loam. Roots reach down to 0.5 m, but 80% of them are concentrated in the upper 0.13 m of the soil.

## 2.2 Eddy covariance (EC)

EC measurements at this site began in 2001 and measurements continue as of this writing - within this paper data from the period 2001-2006 are presented. The net ecosystem CO<sub>2</sub> exchange was measured using the eddy covariance method [Baldocchi et al., 1988] using the same instrumentation as and following the procedures of the EUROFLUX project [Aubinet et al., 2000]. The three wind components and the speed of sound were measured by a three-dimensional sonic anemometer (R3IA, Gill Instruments, Lymington, UK), CO<sub>2</sub> mole fractions by a closed-path infra-red gas analyzer (Li-6262, Li-Cor, Lincoln, NE, USA). Air was sucked from the inlet, a distance of 0.1 m from the centre of the sensor volume of the sonic anemometer mounted at 3 m above ground, through a 4 m Teflon tube of 0.004 m inner diameter through a filter (Acro 50, Gelman, Ann Arbor, MI, USA) to the infrared gas analyzer (IRGA) at a flow rate of 9 l min<sup>-1</sup> (N035ANE, KNF Neuberger, Freiburg, Germany). The infrared gas analyzer was operated in the absolute mode, flushing the reference cell with dry N<sub>2</sub> from a gas cylinder at 0.1 l min<sup>-1</sup>. Raw voltage signals of the CO<sub>2</sub> mole fractions were output at 10 Hz to the analogue input of the sonic, where they were synchronized with the sonic signals, which were measured at 20 Hz. All raw data were saved to a hard disc of a personal computer for post-processing using the *EdiSol* software (University of Edinburgh).

Half-hourly mean eddy fluxes were calculated as the covariance between the turbulent departures from the mean of the vertical wind speed and the CO<sub>2</sub> mixing ratio using the post-processing software *EdiRe* (University of Edinburgh). Means and turbulent departures there from were calculated by Reynolds (block) averaging. The tube induced time delay of the CO<sub>2</sub> signal was determined by optimizing the correlation coefficient with the vertical wind velocity [McMillen, 1988] within a given time window. A three-axis co-ordinate rotation was performed aligning the co-ordinate system's vector basis with the mean wind streamlines [Kaimal and Finnigan, 1994]. Finally, frequency response corrections were applied to raw eddy fluxes accounting for low-pass (sensor separation, dynamic frequency response, scalar and vector path averaging, frequency response mismatch and the attenuation of concentration fluctuations down the sampling tube) and high-pass filtering following Moore [1986] and Aubinet et al. [2000]. Experimentally derived frequency response correction factors, according to Aubinet et al. [2000, 2001], were used to calibrate and assess the validity of the theoretical low-pass filtering correction method, as described in detail in Wohlfahrt et al. [2005].

The net flux of CO<sub>2</sub> was calculated as the sum of the corrected vertical eddy term and the storage fluxes, the latter being estimated from the time-rate-of-change of the CO<sub>2</sub> concentration at the reference height, which in a previous comparison with a profiling system was found to be sufficiently accurate. Negative fluxes represent transport from the atmosphere towards the surface, positive ones the reverse.

### 2.3 Ancillary data

Supporting meteorological measurements of relevance to this study included photosynthetically active radiation (PAR) (BF3H, Delta-T, Cambridge, UK), air temperature ( $T_{\text{air}}$ ) and humidity at 3 m height and soil temperature ( $T_{\text{soil}}$ ) at 0.05 m depth, measured by the means of a combined temperature/humidity sensor (RFT-2, UMS, Munich, Germany) and a thermocouple (TCAV, Campbell Scientific, Logan, UT, USA), respectively, soil heat flux ( $G$ ) measured by the means of heat flux plates (3 replicates at 0.05 m depth, corrected for the change in heat storage above that depth; HFP01, Hukseflux, Delft, The Netherlands), volumetric soil water content (ML2x, Delta-T Devices, Cambridge, UK) and precipitation (52202, R. M. Young, Traverse City, MI, USA). Volumetric soil water content was converted to relative extractable soil water (REW) by normalizing between the water content at field capacity (100 % REW) and the wilting point (0 % REW), which were determined from water retention curve analysis [Hillel, 1980].

GAI was assessed (1) in a destructive fashion by clipping of square plots of 0.09 m<sup>2</sup> (3-5 replicates) and subsequent plant area determination (Li-3100, Li-Cor, Lincoln, NE, USA) and (2) from measurements of maximum canopy height which was related to destructively measured GAI using the following relationship:

$$GAI = \frac{11.07h}{0.64+h} \quad (r^2 = 0.89) \quad (1)$$

where  $h$  is the canopy height (m). Continuous time series of the GAI were derived by fitting sigmoid and quadratic functions to measured data separately for each growing phase before and after the third cut, respectively.

### 2.4 Quality control, gap-filling, uncertainty analysis, statistics

Half-hourly flux data were screened for validity by removal of time periods with (1) the CO<sub>2</sub> signal outside a specific range, (2) the coefficient of variation for CO<sub>2</sub> concentration and pressure within the IRGA outside a specific range, (3) the third rotation angle exceeding  $\pm 10^\circ$  [McMillen, 1988], (4) the stationarity test for the CO<sub>2</sub> flux exceeding 60% [Foken and Wichura, 1996], (5) the deviation of the integral similarity characteristics larger than 60% [Foken and Wichura, 1996], and (6) the maximum of the footprint function [Hsieh et al., 2000] outside the boundaries of the meadow [cf. Novick et al., 2004]. In order to avoid the potential underestimation of nighttime ecosystem respiration during calm and stable conditions [Gu et al., 2005], nighttime NEE data were excluded when friction velocity ( $u_*$ ) was below 0.2 m s<sup>-1</sup> [Wohlfahrt et al., 2005]. Together with gaps due to failure of the PC logging system, these quality control measures led to the exclusion of 59 (47) % of all possible (vegetation period only) data (Table 1).

In order to derive continuous time series of NEE, required for calculating the annual balance of NEE, the following gap filling procedure was employed at Neustift: Gaps less than two hours were filled by linear interpolation. Larger gaps were filled by means of functional relationships between NEE and  $T_{\text{soil}}$  and PAR during nighttime and daytime, respectively (G. Wohlfahrt, manuscript submitted, 2007). In the presence of snow-cover, CO<sub>2</sub> fluxes were noisy and the variability of soil temperature was too small for deriving defensible relationships with NEE and thus an average NEE value was used for gap-filling during winter. An uncertainty analysis, accounting for both random and systematic errors [Moncrieff et al., 1996], was conducted in order to obtain confidence intervals for the annual CO<sub>2</sub> balances. Details on the uncertainty analysis are provided in the Appendix.

$R_{\text{eco}}$  was estimated from nighttime NEE measurements and for daytime conditions by extrapolating these using the functional relationships with soil temperature also used for

gap-filling (see above). GPP was calculated as  $GPP = -NEE + R_{eco}$ . The inter-annual variance of NEE was decomposed into the variance of GPP,  $R_{eco}$  and the covariance between GPP and  $R_{eco}$  according to:

$$\text{var}(NEE) = \text{var}(GPP) + \text{var}(R_{eco}) - 2 \text{covar}(GPP, R_{eco}) \quad (2)$$

### 3. Results

#### 3.1 Environmental conditions and canopy development

The six-year study period was characterized by a wide range of environmental conditions (Fig. 1): The warmest years were 2002 and 2003 with annual averages of 7.7 and 7.1°C, respectively, the coldest year was 2005 with an annual average of 5.6°C. With average annual temperatures of 6.3-6.8°C, the remaining years were close to the long-term (1980-2000) average of 6.5°C. Precipitation ranged from 582 mm y<sup>-1</sup> in 2006 to 948 and 984 mm y<sup>-1</sup> in 2001 and 2002, and was somewhat below the long-term (1980-2000) average of 852 mm y<sup>-1</sup> during 2003-2005 (745-786 mm y<sup>-1</sup>). Monthly averages of relative extractable soil water ranged from above 100 % in spring and autumn down to values below 30 % in May, August and September 2003, June 2005 and July 2006 (Fig. 1). Following *Granier et al.* [1999] in assuming water stress to occur when REW drops below 40 %, 109 days with water stress were counted during the vegetation period April-September of 2003, for 2004-2006 this value ranged from 17-35 days, while not a single day with REW < 40 % occurred in 2001 and 2002. 2003 was also the year with the highest mean VPD of 0.43 kPa (2001-2006 average: 0.35 kPa; data not shown). Snow cover duration (Fig. 2) ranged from 93 days (2002) to 128 days (2001). Snow melting dates varied from 7 (2003) to 30 March (2005) and increased linearly by 0.2 days for each mm of winter precipitation ( $r^2 = 0.90$ ,  $p = 0.01$ ), the permanent winter snow cover established between 18 November (2005) and 20 December (2004). The amount of GAI ranged from close to nil after snow melt up to 7.6 m<sup>-2</sup> shortly before cutting (Fig. 2). The meadow was cut three times a year, the three cuts taking place between 2 and 16 June, 24 July and 12 August, and 21 September and 28 October. Cutting resulted in an immediate reduction of GAI down to 0.5-2.0 m<sup>-2</sup> (Fig. 2).

#### 3.2 Seasonal variability in NEE

The grassland acted as a net source of CO<sub>2</sub> as long as snow covered the ground (Figs. 2-3). After snow melt, the meadow continued to emit, on a daily basis, CO<sub>2</sub> until it eventually reached a reversal point (on average after 25 days), when GPP exceeded  $R_{eco}$  (Figs. 3-4), and the meadow became a net sink and remained so until the first cut (Fig. 3). The first cut turned the ecosystem into a net source of CO<sub>2</sub> and it took GPP on average 16 days to exceed  $R_{eco}$ , which varied comparably little with time, and thus the meadow to become (on a daily basis) a net sink for CO<sub>2</sub> again (Figs. 3-4). This pattern repeated itself after the second and third cut, although the meadow did not quite recover from the third cut (Figs. 3-4) - instead the grassland kept losing CO<sub>2</sub> until the continuous winter snow cover established and then further until the end of the year (Fig. 3). Daily average rates of net CO<sub>2</sub> uptake and loss before and after cutting, respectively, decreased from the first to the third cut (Fig. 3). Based on these seasonal patterns, which represent the combined effects of changes in phenology and anthropogenic interference, we divided the annual cycle of NEE into several periods:

1. Wintertime: delimited by the presence of snow cover;
2. Spring: starts after snow melt and ends at the reversal point when the meadow turns, on a daily basis, into a net sink;

3. Pre-cut periods: comprise the periods of daily net carbon gain preceding the three cutting events and are referred to as pre-cut1-3;
4. Post-cut periods: are assigned the periods between the cuts and the recovery of the (daily) net sink capacity and are referred to as post-cut1-3; the post-cut3 period ends with the establishment of the continuous winter snow cover.

During the later parts of the three pre-cut phases, NEE exhibited signs of saturation and even declined in some years (Figs. 2-3). As shown in Figure 5, this was due to GPP saturating (and sometimes decreasing) with increasing GAI. GPP saturated at values of 10.7 and 9.7  $\text{gC m}^2 \text{d}^{-1}$  once GAI exceed 3  $\text{m}^2 \text{m}^{-2}$  before the first and second cut, respectively, and at a value of 7.0  $\text{gC m}^2 \text{d}^{-1}$  before the third cut once GAI exceed 2  $\text{m}^2 \text{m}^{-2}$  (Fig. 5). The seasonal decrease in saturation GPP was related to day length, which decreased from around 18 to 13 hours between the first and third cut, respectively. After the third cut, the GAI did not exceed 4  $\text{m}^2 \text{m}^{-2}$  (Fig. 2) and no saturation was observed (Fig. 5).

The response of NEE, GPP and  $R_{\text{eco}}$  to the main environmental drivers changed with time during and varied substantially between the various periods - patterns were more conclusive for GPP and  $R_{\text{eco}}$ , as opposed to NEE, as well as for PAR as opposed to  $T_{\text{air}}$ , VPD and REW (Fig. 6): The correlation between GPP and PAR was poor shortly after snow melt and the cuts and then quickly increased with the developing GAI (Fig. 6). The correlation between NEE and PAR largely mirrored the one of GPP (Fig. 6).  $R_{\text{eco}}$  was significantly positively correlated with  $T_{\text{air}}$  except for spring, when the correlation was initially negative; no clear patterns were found for  $T_{\text{air}}$ -GPP and  $T_{\text{air}}$ -NEE (Fig. 6). VPD was strongly correlated with  $T_{\text{air}}$  (data not shown) and the response to VPD thus largely mirrored the one to  $T_{\text{air}}$  (Fig. 6). REW was most of the time negatively related to GPP and  $R_{\text{eco}}$  (Fig. 6), which reflected the inverse correlation to PAR,  $T_{\text{air}}$  and VPD (data not shown).

### 3.3 Inter-annual variability in NEE

Annual NEE varied from  $-42 \text{ gC m}^{-2} \text{y}^{-1}$  to  $+69 \text{ gC m}^{-2} \text{y}^{-1}$ , with a six-year average NEE of  $+18 \pm 49 \text{ gC m}^{-2} \text{y}^{-1}$  (Table 1, Fig. 3). The random and systematic uncertainties of these numbers varied between 6-7 and 11-35  $\text{gC m}^{-2} \text{y}^{-1}$ , respectively (Table 1). The annual NEEs of 2001-2003 and 2005 may thus be regarded significantly different from zero. Annual ecosystem respiration varied between 1455-1696  $\text{gC m}^{-2} \text{y}^{-1}$ , gross primary production between 1449-1687  $\text{gC m}^{-2} \text{y}^{-1}$  (Table 1).

The inter-annual variance of daily average NEE was in all periods but spring and post-cut1 dominated by the covariance between GPP and  $R_{\text{eco}}$  (Fig. 3) which was positive and thus acted to reduce the variance in NEE (Eq. 2). The variance of daily average GPP exceeded the one of  $R_{\text{eco}}$  in spring and pre-cut1-2, while the reverse was true for all post-cut phases and pre-cut3 (Fig. 3). The coefficient of variation of daily average NEE was smallest during winter (0.05), largest during pre-cut3 (0.52) and between 0.15-0.29 for all other phases (Fig. 3). On the annual time scale, the covariance term was about twice as large as the variance of GPP and  $R_{\text{eco}}$ , which were of almost equal magnitude (data not shown).

The most influential periods for annual NEE were post-cut1 and pre-cut3, which explained 45 % ( $p = 0.15$ ) and 47 % ( $p = 0.13$ ) of the variability in annual NEE, respectively - larger carbon losses in post-cut1 and larger carbon gains during pre-cut3 were associated with larger annual losses and gains, respectively. No significant lagged effects, i.e. correlations with NEE in antecedent periods or previous years, could be determined. Snow cover duration and cardinal dates, such as the timing of snow melt, the establishment of the continuous winter snow cover, the cuts, the duration of the inter-cut periods, and the duration between snow melt and first cut and the third cut and the establishment of the continuous winter snow cover explained all less than 30 % of the inter-annual variability of

NEE (data not shown). As shown in Figure 7, snow melting dates though explained significant fractions of the inter-annual variability in NEE before the first cut: While wintertime CO<sub>2</sub> losses were smaller for early snow melting dates, carbon losses were larger during spring and NEE was less negative during pre-cut1 in years with earlier snow melts (Fig. 7). Up to the first cut, the positive effect of early snow melts on wintertime carbon losses was thus outweighed by smaller carbon gains thereafter, leading to an increase (i.e. smaller net carbon gain) in cumulative NEE by 1.5 gC m<sup>-2</sup> for each day snow melt occurred earlier.

Environmental control on the inter-annual variability in NEE and its two component processes, GPP and R<sub>eco</sub> is explored in Table 2, which shows the results of a linear correlation analysis: On an annual time scale, the only significant correlation was found for R<sub>eco</sub>, which increased significantly with T<sub>air</sub>, but as GPP increased with T<sub>air</sub> as well, no significant effect on NEE was found (Table 2). No significant relationships could be found between annual NEE and environmental controls during the various periods (data not shown). Broken down to the time scale of the various periods, T<sub>air</sub> was the variable which most frequently yielded significant correlations, followed by PAR and REW, and VPD. The only significant correlation for NEE was found during post-cut1, when it increased with T<sub>air</sub> (Table 2). GPP was negatively correlated with T<sub>air</sub> during spring and positively before and after the third cut. During pre-cut3 T<sub>air</sub> was positively correlated with PAR (as well as VPD) and negatively with REW, resulting in a positive and negative correlation of these two environmental variables with GPP, respectively (Table 2). R<sub>eco</sub> was positively related to temperature during all post-cut periods as well as during pre-cut3 (Table 2), when the auto-correlation between T<sub>air</sub> and the other environmental variables resulted in the same correlation pattern observed for GPP. The same reasoning holds for the correlation between R<sub>eco</sub> and REW and PAR during post-cut2 and post-cut3, respectively (Table 2).

## 4. Discussion

The seasonal and inter-annual variability of NEE reflects the variability of the governing environmental forcing variables at these time scales, as well as changes in the ecosystem's response to these [Stoy *et al.*, 2005; Richardson *et al.*, 2007]. Through modifying the amount of photosynthetically active plant matter, cutting and grazing fundamentally alter how grassland ecosystems respond to environmental forcings [Wohlfahrt, 2004; Nieven *et al.*, 2005; Rogiers *et al.*, 2005] and thus have the potential to modulate the seasonal and inter-annual variability of NEE. The objective of the present paper is to examine the role and relative importance of climate and cutting for the seasonal and inter-annual variability of the NEE of a temperate mountain grassland in Austria. To this end we analyzed eddy covariance CO<sub>2</sub> flux data and associated measurements of the GAI and the major environmental driving forces acquired during 2001-2006 at the study site Neustift.

### 4.1 Seasonal variability in NEE

The seasonal variability of the NEE of the investigated mountain grassland combined features typical for natural ecosystems (which we define here as ecosystems not managed on an annual or finer time scale), but was also characterized by human-induced, step-change temporal patterns typical for agricultural ecosystems [Falge *et al.*, 2002a,b]:

No management activities occurred at the site between the establishment of the continuous snow cover in late autumn and the first cut in early summer (i.e. the wintertime, spring and pre-cut1 periods), except for the application of manure in autumn, which had no discernable influence on NEE though. During these periods, the seasonal course of NEE was modulated primarily by climate, such as the presence/absence of snow (Fig. 2) and the seasonal changes in environmental drivers (Fig. 1), and compared well with the progression from

dormancy and associated net CO<sub>2</sub> losses to active sink activity observed for natural temperate ecosystems during that same period [Falge et al., 2002a]. The period of snow cover was characterized by net losses of CO<sub>2</sub> to the atmosphere which were small in magnitude (Figs. 2-3), but due to the length of the snow cover period (3-4 months), accounted for an appreciable fraction of the annual NEE as found for other high-elevation or -latitude ecosystems [Aurela et al., 2002; Monson et al., 2002; Lafleur et al., 2003].

In between the first cut and the establishment of the continuous snow cover, the most obvious consequence of the three cuts the grassland is subject to each year, was the recurrent progression of NEE from CO<sub>2</sub> source to sink which resulted in a characteristic seasonal time course of NEE (Fig. 3) typical for repeatedly cut/grazed grasslands [Sousanna et al., 2007; Veenendaal et al., 2007]. Cutting thereby led to a decoupling of the phenological plant development, which is reinitiated by cutting [Wohlfahrt and Cernusca, 2002], and the seasonal progression of climatic conditions. As a consequence, the seasonal variability of NEE during the vegetation period was modulated primarily by changes in GPP rather than R<sub>eco</sub>, which was much less variable in time (Fig. 4). This was reflected also by the relationships between environmental drivers and NEE, which largely mirrored the response of GPP to these drivers (Fig. 6). As a further result of this decoupling, GPP and R<sub>eco</sub> were strongly out of phase between the first cut and the establishment of the continuous snow cover, which is again a typical feature of agricultural ecosystems [Falge et al., 2002a].

In contrast to many other grassland studies, where linear increases in GPP with GAI have been found [e.g. Suyker and Verma, 2001; Flanagan et al., 2002; Xu and Baldocchi, 2003; Li et al., 2005], GPP increased in a non-linear behavior with GAI at Neustift, saturating at values between 3-5 m<sup>2</sup> m<sup>-2</sup> GAI (Fig. 5). This saturation-type response is typical for crops [e.g. Suyker et al., 2004, 2005] and very productive grasslands [e.g. Veenendaal et al., 2007] and reflects trade-offs between increasing assimilatory area and associated self-shading [Wohlfahrt et al., 2003].

The response of NEE and its two component process, GPP and R<sub>eco</sub>, to the main environmental drivers changed rapidly with time, reflecting the active growth of the canopy (and associated changes in GAI) and thus changes in what Richardson et al. [2007] termed the ecosystem's "biotic response". The response of NEE, GPP and R<sub>eco</sub> to the main environmental drivers also varied substantially between the various periods, reflecting the above-mentioned decoupling of phenological development and the seasonal progression of climatic conditions. As in addition, the investigated environmental parameters were inter-correlated, it was very difficult to defensibly attribute seasonal changes in NEE, GPP and R<sub>eco</sub> to certain environmental parameters or combinations thereof.

#### 4.2 Inter-annual variability in NEE

None of the variables looked at in the present paper was able to explain, in a statistically significant fashion, the inter-annual variability of annual NEE. The investigated variables included metrics like the length of the vegetation period and the snow melting date (which varied by up to a month) for which Baldocchi and Wilson [2001], Baldocchi et al. [2001, 2005], Carrara et al. [2003], Aurela et al. [2004], amongst others, found clear correlations with NEE. Even environmental drivers such as PAR, temperature, soil moisture and vapor pressure deficit, for which the short-term response of NEE is well established [Stoy et al., 2005], did not yield significant relationships at the annual time scale. One reason for the failure of climate-based metrics in explaining the inter-annual variability of NEE may be that the variance in annual NEE is to be attributed to the biotic response to rather than the environmental drivers per se [Hui et al., 2003; Richardson et al., 2007]. In the present case, the response to climate forcings may have been obscured by inter-annual variations in the timing of the cutting events and thus the seasonal courses of GAI. Cutting dates varied by



2-5 weeks, so that for a given time of the year the ecosystem's response to climatic drivers may have greatly differed because of cutting-mediated differences in GAI. In addition, we observed a high covariance between GPP and  $R_{eco}$  at the annual time scale, resulting in a comparatively small inter-annual variation in NEE [Dunn et al., 2006; Jacobs et al., 2007; Richardson et al., 2007]. This covariance also held with regard to the controls by environmental drivers, causing annually averaged/integrated environmental parameters being better predictors of GPP and  $R_{eco}$  than NEE (Table 1). Very weak correlations between annual NEE and climatic indices, resulting from compensating influences of GPP and  $R_{eco}$ , have been reported also by Reichstein et al. [2007] in an analysis of 23 European flux tower sites. Generally, few studies have reported statistically significant relationships between annual NEE and single annually integrated/averaged environmental drivers, but rather multiple regression models had to be used for sufficient predictive power [Saigusa et al., 2005; Dunn et al., 2006; Barr et al., 2006]. Along this line, environmental conditions during certain cardinal periods, as opposed to annually integrated/averaged values, were generally more successful in predicting annual NEE [e.g. Hollinger et al., 2004; Zha et al., 2004], although this did not apply in the present case.

Contrary to our expectations, the timing of the cutting events, the time duration between cutting events, between snow melt and first cut, and third cut and the establishment of the continuous snow cover did not yield significant relationships with annual NEE. Even the amounts of carbon gained or lost during the various pre- and post-cut periods, which form part of the annual NEE, were not significantly correlated with annual NEE. The poor explanatory power of these management-related metrics may reflect that cutting, while significantly modulating the seasonal course of NEE, affects NEE only during approximately half of the year. Between the establishment of the continuous snow cover until the first cut, NEE is independent of management, resulting in compensating effects on annual NEE. For example year 2001, due to a late snow fall in April which resulted in sustained carbon losses during the spring period, had the lowest cumulative NEE up to the first cut, but compensated for this by comparatively large carbon gains after the first and second cut (Fig. 3), topping out with the highest annual net carbon gain observed during the six year study. Because the biotic response to environmental drivers changes abruptly with cutting [Wohlfahrt, 2004; Rogiers et al., 2005; G. Wohlfahrt, manuscript submitted, 2007] and because cutting acts as to decouple climate and phenology, any legacies from antecedent periods are quickly blurred after cutting. This became obvious in case of the significant correlation between snow melting dates and NEE cumulated up to the first cut (Fig. 7), which was completely lost when the integration period was extended beyond the first cut. In natural ecosystems, the effects of early/late snow melting often persist and sometimes even dominate annual NEE, as shown by Aurela et al. [2004] for a subarctic fen (even if the effect was of opposite sign in this study).

Several studies have ascribed inter-annual variability in NEE to variability in either GPP [Janssens et al., 2001; Griffis et al., 2003; Saigusa et al., 2005; Urbanski et al., 2007] or  $R_{eco}$  [Goulden et al., 1998; Valentini et al., 2000; Morgenstern et al., 2004]. While the strong covariance between GPP and  $R_{eco}$  prevented us from doing so at the annual time scale (see above), we found distinct differences in the control of inter-annual variability of NEE at sub-annual time scales (Fig. 3). Although the covariance between GPP and  $R_{eco}$  generally dominated also at these time scales, GPP was clearly more important in modulating inter-annual variance in NEE during spring and pre-cut1-2.  $R_{eco}$  explained a larger fraction of the variance in NEE during pre-cut3 and all post-cut periods, which is remarkable if we recall that the seasonal dynamics of NEE during the post-cut periods were driven by rapid changes in GPP (Fig. 4). Since  $R_{eco}$  increased significantly with temperature during all post-cut periods, it follows that high temperatures after cutting contribute to higher annual  $CO_2$  losses, even if this is supported by statistics only during post-cut1 (Table

2). NEE during pre-cut3 not only stood out by being characterized by the highest coefficient of variation, in contrast to the other pre-cut periods, its NEE was also modulated more by  $R_{eco}$  than GPP (Fig. 3). Because GPP and  $R_{eco}$  were driven in the same direction by the same environmental drivers during this period (Table 2), it is difficult to unambiguously assess what controlled the observed large variability in NEE. In any case, NEE during pre-cut3 explained 47 % of the variability in annual NEE ( $p = 0.13$ ), and thus constituted not only a climatologically very sensitive, but also the quantitatively most influential period for annual NEE.

## 5. Summary and Conclusions

The NEE of the investigated mountain grassland combined features typical for both natural and agricultural ecosystems resulting in characteristic temporal patterns and complex interactions between phenological development, cutting and climate. Our results show that the investigated mountain grassland, under present climate and management, exhibits a stable near-neutral NEE – the site is neither losing large amounts of carbon nor is there large potential for carbon storage.

Driven by three cutting events per year which kept the investigated mountain grassland in a stage of vigorous growth throughout most of the vegetation period, the seasonal variability of NEE was primarily modulated by GPP. The role of environmental parameters in modulating the seasonal variability of NEE was obscured by the strong response of GPP to changes in GAI, as well as the cutting-mediated decoupling of phenological development and the seasonal course of climate drivers.

None of the climate and management metrics examined in the present paper was able to explain, in a statistically significant fashion, the inter-annual variability of annual NEE. This is thought to result from (1) a high covariance between GPP and  $R_{eco}$  at the annual time scale which results in a comparatively small inter-annual variation of NEE, (2) compensating effects between carbon exchange during and outside the management period, and (3) changes in the biotic response to rather than the climate variables per se. GPP was more important in modulating inter-annual variations in NEE in spring and before the first and second cut, while  $R_{eco}$  explained a larger fraction of the inter-annual variability of NEE during the remaining, in particular the post-cut, periods. Inter-annual variations in temperature accounted for significant fractions of the variability in  $R_{eco}$  suggesting a potential sensitivity to predicted changes in climate.

## Acknowledgments

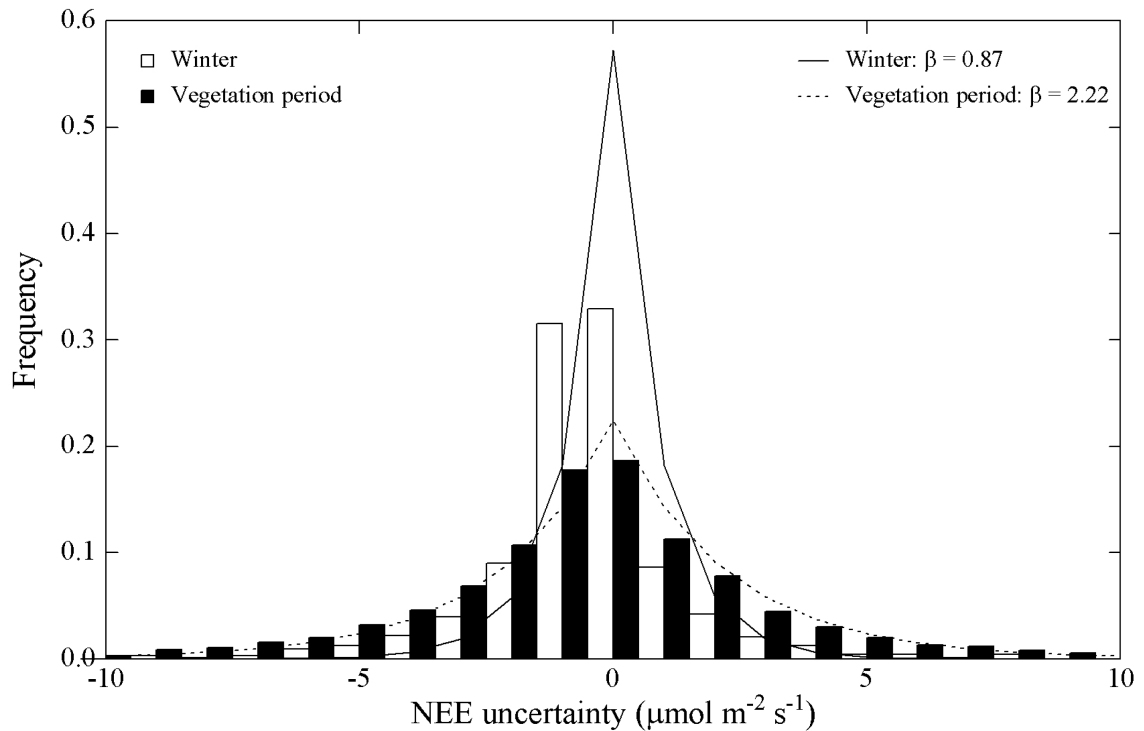
This study was financially supported by the EU FP 5 project CARBOMONT (EVK2-CT2001-00125), the Austrian National Science Fund (P17560), and the Tyrolean Science Fund (Uni-404/33). Family Hofer (Neustift, Austria) is thanked for granting us access to the study site. Long-term temperature and precipitation data have been generously provided by the Austrian Hydrographic Service.

## Appendix: Uncertainty analysis

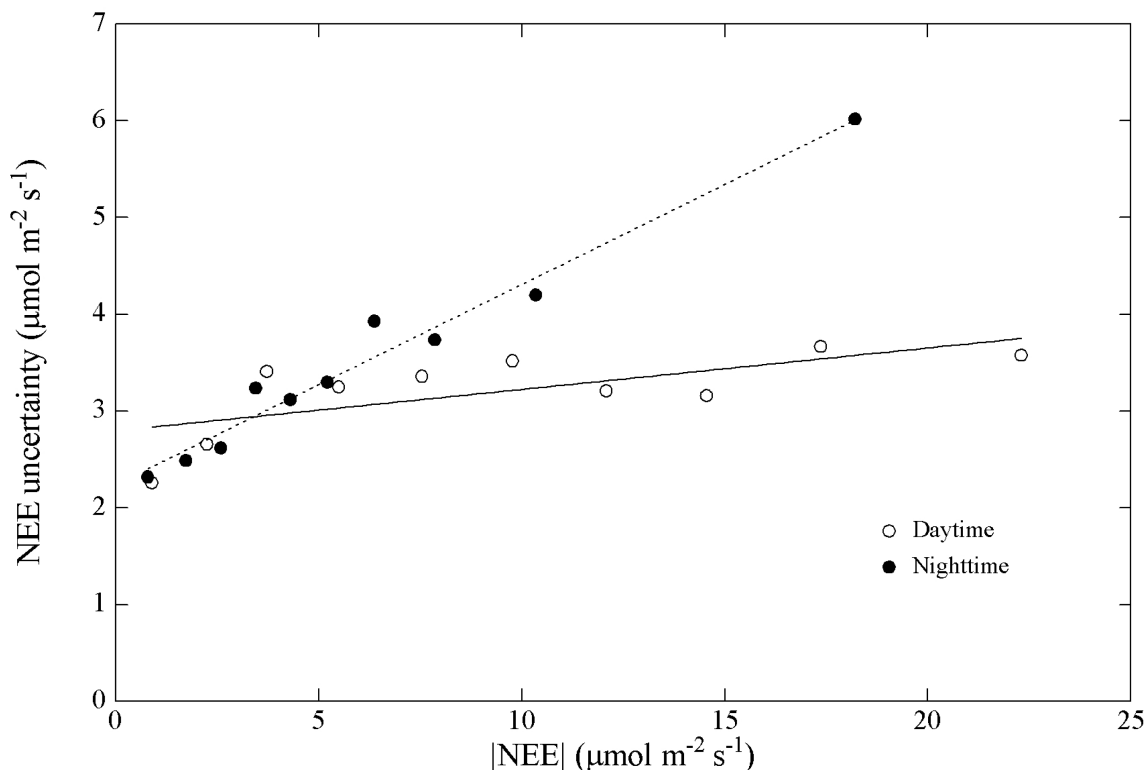
The random uncertainty of the half-hourly  $CO_2$  flux measurements was determined based on measurements under similar environmental conditions during adjacent days [Hollinger and Richardson, 2005]. The probability density distributions of the random  $CO_2$  flux uncertainty, which followed a Laplace rather than a normal distribution, are shown in Fig. A1 separately for wintertime and the vegetation period. In accordance with Richardson *et al.* [2006] a good linear correlation between the random uncertainty and the magnitude of NEE was found, which was used to estimate the random uncertainty of each valid half-hourly flux measurement (Fig. A2). The random uncertainty of the parameters of the functional

relationships between NEE and  $T_{\text{soil}}$  and PAR was then estimated with a Simulated Annealing algorithm nested within a bootstrapping loop with 1000 iterations using the absolute deviation criterion as the objective function [Hollinger and Richardson, 2005]. During wintertime the mean  $\text{CO}_2$  flux uncertainty (Fig. A1) was assigned to all measurements.

The largest systematic uncertainty in annual NEE is due to the potential underestimation of ecosystem respiration during calm nighttime conditions and the choice of the  $u_*$  threshold for excluding these. In order to assess the systematic uncertainty associated with rejecting nighttime ecosystem respiration measurements according to friction velocity, we calculated annual  $\text{CO}_2$  balances without filtering for  $u_*$  and with the default value of  $0.2 \text{ m s}^{-1}$  [Wohlfahrt et al., 2005] and estimated the systematic uncertainty as the difference between these two [cf. Morgenstern et al., 2004]. Following recommendations by Moncrieff et al. [1996], we report the annual NEE and its uncertainty as average  $\pm$  random uncertainty  $\pm$  systematic uncertainty.



**Figure A1.** >Probability density distribution of the random uncertainty of the net ecosystem  $\text{CO}_2$  exchange (NEE) calculated using the neighbouring days approach devised by Hollinger and Richardson [2005].



**Figure A2. Random uncertainty [see *Hollinger and Richardson, 2005*] of the net ecosystem CO<sub>2</sub> exchange (NEE) as a function of the absolute magnitude of NEE, separately for daytime (open symbols) and nighttime (closed symbols) hours of the vegetation period.**

Lines represent linear best fits with the following equations:  $y = 0.04x + 2.80$  (day, solid line,  $r^2 = 0.47$ ,  $p = 0.029$ ) and  $y = 0.21x + 2.24$  (night, dotted line,  $r^2 = 0.97$ ,  $p < 0.001$ ).

## 6. References

- Ammann C, Flechard CR, Leifeld J, Neftel A, Fuhrer J. The carbon budget of newly established temperature grassland depends on management intensity. *Agric. Ecosys. Environ.* 2007; 121:5–20.
- Aubinet M, et al. Estimates of the annual net carbon and water exchange of forest: the EUROFLUX methodology. *Adv. Ecol. Res.* 2000; 30:113–175.
- Aubinet M, Chermanne B, Vandenhoute M, Longdoz B, Yernaux M, Laitat E. Long term carbon dioxide exchange above a mixed forest in the Belgian Ardennes. *Agric. For. Meteorol.* 2001; 108:293–315.
- Aurela M, Laurila T, Tuovinen J-P. Annual CO<sub>2</sub> balance of a subarctic fen in northern Europe: Importance of wintertime efflux. *J. Geophys. Res.* 2002; 107(D21):4607. doi: 10.1029/2002JD002055.
- Aurela M, Laurila T, Tuovinen J-P. The timing of snow melt controls the annual CO<sub>2</sub> balance in a subarctic fen. *Geophys. Res. Lett.* 2004; 31:L16119. doi: 10.1029/2004GL020315.
- Baldocchi DD, Wilson KB. Modeling CO<sub>2</sub> and water vapor exchange of a temperate broadleaved forest across hourly to decadal time scales. *Ecol. Model.* 2001; 142:155–184.
- Baldocchi DD, Hicks BB, Meyers TP. Measuring biosphere-atmosphere exchanges of biologically related gases with micrometeorological methods. *Ecology.* 1988; 69:1331–1340.
- Baldocchi DD, et al. FLUXNET: A new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor and energy flux densities. *Bull. Am. Meteorol. Soc.* 2001; 82:2415–2435.

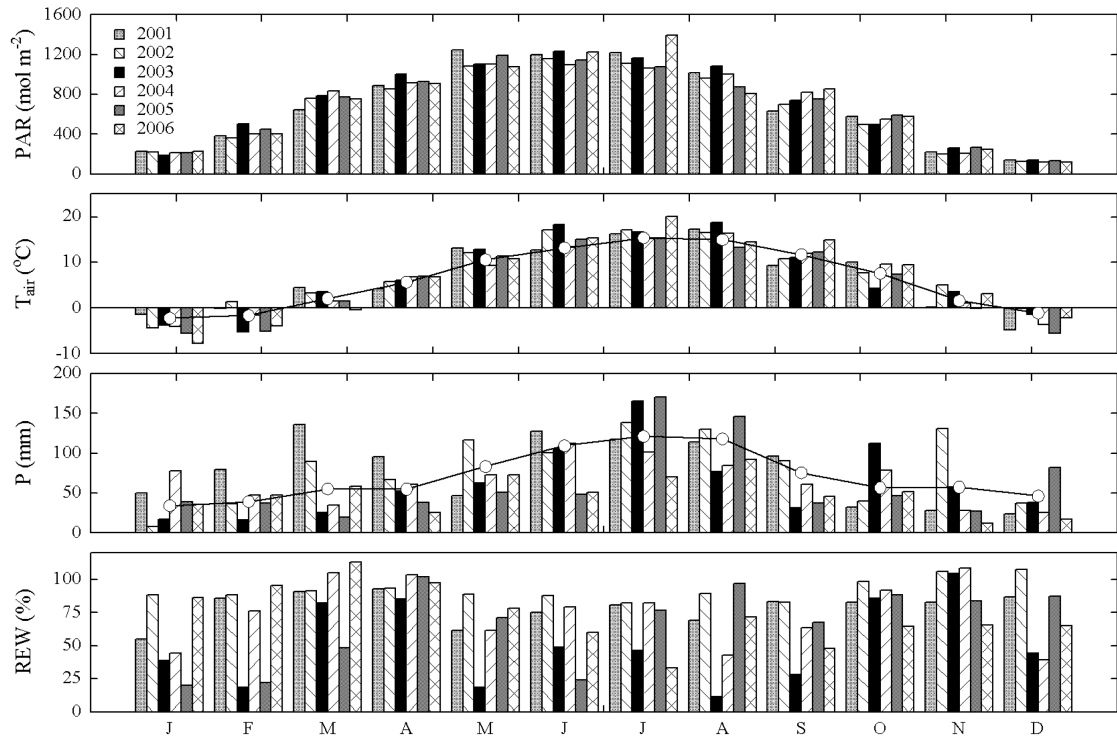
- Baldocchi DD, et al. Predicting the Onset of Carbon Uptake by Deciduous Forests with Soil Temperature and Climate Data: A Synthesis of FLUXNET Data. *Int. J. Biometeorol.* 2005; 49:377–387. [PubMed: 15688192]
- Barford CC, Wofsy SC, Goulden ML, Munger JW, Hammond-Pyle E, Urbanski SP, Hutrya L, Saleska SR, Fitzjarrald D, Moore K. Factors controlling long- and short-term sequestration of atmospheric CO<sub>2</sub> in a mid-latitude forest. *Science.* 2001; 294:1688–1691. [PubMed: 11721047]
- Barcza Z, Haszpra L, Kondo H, Saigusa N, Yamamoto S, Bartholy J. Carbon exchange of grass in Hungary. *Tellus.* 2003; 55B:187–196.
- Barr AG, Black TA, Hogg EH, Griffis TJ, Morgenstern K, Kljun N, Theede A, Nescic Z. Climatic controls on the carbon and water balances of a boreal aspen forest, 1994–2003. *Global Change Biol.* 2006; 13:561–576.
- Canadell, JG.; Pataki, DE.; Gifford, R.; Houghton, RA.; Luo, Y.; Raupach, MR.; Smith, P.; Steffen, W. Saturation of the terrestrial carbon sink. In: Canadell, JG.; Pataki, DE.; Pitelka, LF., editors. *Terrestrial ecosystems in a changing world.* Springer-Verlag; Berlin Heidelberg; 2007. p. 59–78.
- Carrara A, Kowalski AS, Neiryck J, Janssens IA, Yuste J., Curiel, Ceulemans R. Net ecosystem CO<sub>2</sub> exchange of mixed forest in Belgium over 5 years. *Agric. For. Meteorol.* 2003; 119:209–227.
- Denmead OT, Bradley EF. On scalar transport in plant canopies. *Irrigation Sci.* 1987; 8:131–149.
- Dunn AL, Barford CC, Wofsy SC, Goulden ML, Daube BC. A long-term record of carbon exchange in a boreal black spruce forest: means, responses to interannual variability, and decadal trends. *Global Change Biol.* 2006; 13:577–590.
- Falge E, et al. Phase and amplitude of ecosystem carbon release and uptake potential as derived from FLUXNET measurements. *Agric. For. Meteorol.* 2002a; 113:75–95.
- Falge E, et al. Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. *Agric. For. Meteorol.* 2002b; 113:53–74.
- Flanagan LB, Wever LA, Carlson PJ. Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland. *Global Change Biol.* 2002; 8:599–615.
- Foken, Th.; Wichura, B. Tools for quality assessment of surface-based flux measurements. *Agric. For. Meteorol.* 1996; 78:83–105.
- Fredeen AL, Waughtal JD, Pypker TG. When do replanted sub-boreal clearcuts become net sinks for CO<sub>2</sub> ? *For. Ecol. Management.* 2007; 239:210–216.
- Goulden ML, et al. Sensitivity of boreal forest carbon balance to soil thaw. *Science.* 1998; 279:214–217. [PubMed: 9422691]
- Goulden ML, Winston GC, McMillan AMS, Litvak ME, Read EL, Rocha AV, Elliot JR. An eddy covariance mesonet to measure the effect of forest age on land-atmosphere exchange. *Global Change Biol.* 2006; 12:2146–2162.
- Granier A, Breda N, Biron P, Villette S. A lumped water balance model to evaluate duration and intensity of drought constraints in forest stands. *Ecol. Model.* 1999; 116:269–283.
- Griffis TJ, Black TA, Morgenstern K, Barr AG, Nescic Z, Drewitt GB, Gaumont-Guay D, McCaughey JH. Ecophysiological controls on the carbon balances of three southern boreal forests. *Agric. For. Meteorol.* 2003; 117:53–71.
- Gu L, Baldocchi DD, Wofsy SC, Munger JW, Michalsky JJ, Urbanski SP, Boden TA. Response of a deciduous forest to the Mount Pinatubo eruption: enhanced photosynthesis. *Science.* 2003; 299:2035–2038. [PubMed: 12663919]
- Gu L, Falge E, Boden T, Baldocchi D, Black TA, Saleska S, Suni T, Verma S, Vesala T, Wofsy S, Xu L. Objective threshold determination for nighttime eddy flux filtering. *Agric. For. Meteorol.* 2005; 128:179–197.
- Hillel, D. *Fundamentals of soil physics.* Academic Press; New York: 1980.
- Hollinger DY, Richardson AD. Uncertainty in eddy covariance measurements and its application to physiological models. *Tree Physiol.* 2005; 25:873–885. [PubMed: 15870055]
- Hollinger DY, et al. Spatial and temporal variability in forest-atmosphere CO<sub>2</sub> exchange. *Global Change Biol.* 2004; 10:1689–1706.
- Hsieh CI, Katul G, Chi TW. An approximate analytical model for footprint estimation of scalar fluxes in thermally stratified atmospheric flows. *Adv. Water Resources.* 2000; 23:765–772.

- Hui D, Luo Y, Katul G. Partitioning interannual variability in net ecosystem exchange between climatic variability and functional change. *Tree Physiol.* 2003; 23:433–442. [PubMed: 12670797]
- Humphreys ER, Black TA, Morgenstern K, Cai T, Drewitt GB, Nestic Z, Trofymow JA. Carbon dioxide fluxes in coastal Douglas-fir stands at different stages of development after clearcut harvesting. *Agric. For. Meteorol.* 2006; 140:6–22.
- Intergovernmental Panel on Climate Change. *Climate Change 2001: The Scientific Basis, Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge Univ. Press; Cambridge: 2001. p. 881
- Jacobs AFG, Heusinkveld BG, Holtslag AAM. Seasonal and interannual variability of carbon dioxide and water balances of a grassland. *Clim. Change.* 2007; 82:163–177.
- Jaksic V, Kiely G, Albertson J, Oren R, Katul G, Leahy P, Byrne KA. Net ecosystem exchange of grassland in contrasting dry and wet years. *Agric. For. Meteorol.* 2006; 139:323–334.
- Janssens IA, et al. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biol.* 2001; 7:269–278.
- Kaimal, JC.; Finnigan, JJ. *Atmospheric Boundary Layer Flows.* Oxford Univ. Press; Oxford: 1994. p. 289
- Kirschbaum MUF, Küppers M, Schneider H, Giersch C, Noe S. Modelling photosynthesis in fluctuating light with inclusion of stomatal conductance, biochemical activation and pools of key photosynthetic intermediates. *Planta.* 1997; 204:16–26.
- Kowalski AS, et al. Paired comparisons of carbon exchange between undisturbed and regenerating stands in four managed forests in Europe. *Global Change Biol.* 2004; 10:1707–1723.
- Kucharik CJ, Barford CC, El Maayar M, Wofsy SC, Monson RK, Baldocchi DD. A multiyear evaluation of a Dynamic Global Vegetation Model at three AmeriFlux forest sites: Vegetation structure, phenology, soil temperature, and CO<sub>2</sub> and H<sub>2</sub>O vapor exchange. *Ecol. Model.* 2006; 196:1–31.
- Lafleur PM, Roulet NT, Bubier JL, Frolking S, Moore TR. Interannual variability in peatland-atmosphere carbon dioxide exchange at an ombrotrophic bog. *Global Biogeochem. Cycles.* 2003; 17(2):1036. doi: 10.1029/2002GB001983.
- Lawton D, Leahy P, Kiely G, Byrne KA, Calanca P. Modelling of net ecosystem exchange and its components for a humid grassland ecosystem. *J. Geophys. Res.* 2006; 111:G04013. doi: 10.1029/2006JG000160.
- Li S-G, Asanuma J, Eugster W, Kotani A, Liu J-J, Urano T, Oikawa T, Davaa G, Oyunbaatar D, Sugita M. Net ecosystem carbon dioxide exchange over grazed steppe in central Mongolia. *Global Change Biol.* 2005; 11:1941–1955.
- Lohila A, Aurela M, Tuovinen J-P, Laurila T. Annual CO<sub>2</sub> exchange of a peat field growing spring barley or perennial forage grass. *J. Geophys. Res.* 2004; 109:D18116. doi: 10.1029/2004JD004715.
- Mahecha MD, Reichstein M, Lange H, Carvalhais N, Bernhofer C, Grünwald T, Papale D, Seufert G. Characterizing ecosystem-atmosphere interactions from short to interannual time scales. *Biogeosci. Discuss.* 2007; 4:1405–1435.
- Maljanen M, Martikainen PJ, Walden J, Silvola J. CO<sub>2</sub> exchange in an organic field growing barley or grass in eastern Finland. *Global Change Biol.* 2001; 7:679–692.
- Marcolla B, Cescatti A. Experimental analysis of flux footprint for varying stability conditions in an alpine meadow. *Agric. For. Meteorol.* 2005; 135:291–301.
- McMillen RT. An eddy correlation system with extended applicability to non-simple terrain. *Boundary-Layer Meteorol.* 1988; 43:231–245.
- Moncrieff JB, Malhi Y, Leuning R. The propagation of errors in long-term measurements of land-atmosphere fluxes of carbon and water. *Global Change Biol.* 1996; 2:231–240.
- Monson RK, Turnipseed AA, Sparks JP, Harley PC, Scott-Denton LE, Sparks K, Huxman TE. Carbon sequestration in a high-elevation, subalpine forest. *Global Change Biol.* 2002; 8:459–478.
- Moore CJ. Frequency response corrections for eddy correlation systems. *Boundary-Layer Meteorol.* 1986; 37:17–35.

- Morgenstern K, Black TA, Humphreys ER, Griffis TJ, Drewitt GB, Cai T, Nesic Z, Spittlehouse DL, Livingston NJ. Sensitivity and uncertainty of the carbon balance of a Pacific Northwest Douglas-fir forest during an El Niño/La Niña cycle. *Agric. For. Meteorol.* 2004; 123:201–219.
- Nieven JP, Campbell DI, Schipper LA, Blair IJ. Carbon exchange of grazed pasture on a drained peat soil. *Global Change Biol.* 2005; 11:607–618.
- Novick KA, Stoy PC, Katul GG, Ellsworth DS, Siqueira MBS, Juang J, Oren R. Carbon dioxide and water vapor exchange in a warm temperate grassland. *Oecologia.* 2004; 138:259–274. [PubMed: 14628214]
- Oechel WC, Vourlitis GL, Hastings SJ, Zulueta RC, Hinzman L, Kane D. Acclimation of ecosystem CO<sub>2</sub> exchange in the Alaskan Arctic in response to decadal climate warming. *Nature.* 2000; 406:978–981. [PubMed: 10984048]
- Pielke RA, Avissar R, Raupach M, Dolman AJ, Zeng X, Denning AS. Interactions between the atmosphere and terrestrial ecosystems: influence on weather and climate. *Global Change Biol.* 1998; 4:461–475.
- Piovesan G, Adams JM. Carbon balance gradient in European forests: Interpreting EUROFLUX. *J. Veg. Sci.* 2000; 11:923–926.
- Reichstein M, et al. Determinants of terrestrial ecosystem carbon balance inferred from European eddy covariance flux sites. *Geophys. Res. Letters.* 2007; 34:L001402. doi: 10.1029/2006GL027880.
- Richardson AD, et al. A multi-site analysis of random error in tower-based measurements of carbon and energy fluxes. *Agric. For. Meteorol.* 2006; 136:1–18.
- Richardson AD, Hollinger DY, Aber JD, Ollinger SV, Braswell BH. Environmental variation is directly responsible for short-, but not long-term variation in forest-atmosphere carbon exchange. *Global Change Biol.* 2007; 13:788–803.
- Rogiers N, Eugster W, Furger M, Siegwolf R. Effect of land management on ecosystem carbon fluxes at a subalpine grassland sites in the Swiss Alps. *Theo. Appl. Clim.* 2005; 80:187–203.
- Running SW, Baldocchi DD, Turner DP, Gower ST, Bakwin PS, Hibbard KA. A global terrestrial monitoring network integrating tower fluxes, flask sampling, ecosystem modelling and EOS satellite data. *Remote Sens. Environ.* 1999; 70:108–127.
- Saigusa N, Yamamoto S, Ohtsuka T, Murayama S, Kondo H, Koizumi H. Inter-annual variability of carbon budget components in a cool-temperate deciduous forest in Japan (Takayama, Asiaflux). *Phyton.* 2005; 45:81–88.
- Schwalm CR, Black TA, Morgenstern K, Humphreys ER. A method for deriving net primary productivity and component respiratory fluxes from tower-based eddy covariance data: a case study using a 17-year data record from a Douglas-fir chronosequence. *Global Change Biol.* 2007; 13:370–385.
- Sousanna JF, et al. Full accounting of the greenhouse gas (CO<sub>2</sub>, N<sub>2</sub>O, CH<sub>4</sub>) budget of nine European grassland sites. *Agric. Ecosys. Environ.* 2007; 121:121–134.
- Steffen W, et al. The terrestrial carbon cycle: implications for the Kyoto protocol. *Science.* 1998; 280:1393–1394.
- Stoy PC, Katul GG, Siqueira MB, Juang J-Y, McCarthy HR, Kim H-S, Oishi AC, Oren R. Variability in net ecosystem exchange from hourly to inter-annual time scales at adjacent pine and hardwood forests: a wavelet analysis. *Tree Physiol.* 2005; 25:887–902. [PubMed: 15870056]
- Suyker AE, Verma SB. Year-round observations of the net ecosystem exchange of carbon dioxide in a native tallgrass prairie. *Global Change Biol.* 2001; 7:279–289.
- Suyker AE, Verma SB, Burba GG, Arkebauer TJ, Walters DT, Hubbard KG. Growing season carbon dioxide exchange in irrigated and rainfed maize. *Agric. For. Meteorol.* 2004; 124:1–13.
- Suyker AE, Verma SB, Burba GG, Arkebauer TJ. Gross primary production and ecosystem respiration of irrigated maize and irrigated soybean during a growing season. *Agric. For. Meteorol.* 2005; 131:180–190.
- Urbanski S, Barford C, Wofsy S, Kucharik C, Pyle E, Budney J, McKain K, Fitzjarrald D, Czirkowsky M, Munger JW. Factors controlling CO<sub>2</sub> exchange on timescales from hours to decadal at Harvard Forest. *J. Geophys. Res.* 2007; 112:G02020. doi: 10.1029/2006JG000293.
- Valentini R, et al. Respiration as the main determinant of carbon balance in European forests. *Nature.* 2000; 404:861–865. [PubMed: 10786790]

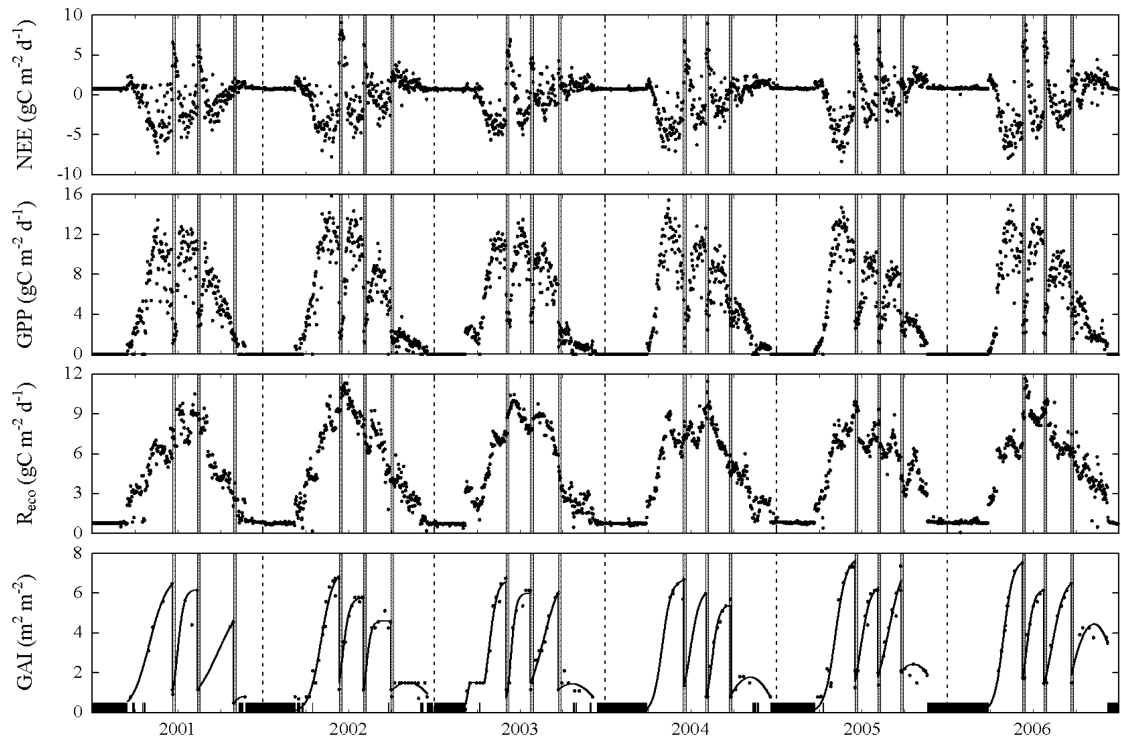
- Veenendaal EM, Kolle O, Leffelaar PA, Schrier-Uijl AP, Van Huissteden J, Van Walsem J, Möller F, Berendse F. CO<sub>2</sub> exchange and carbon balance in two grassland sites on eutrophic drained peat soils. *Biogeosci. Discuss.* 2007; 4:1633–1671.
- Wohlfahrt G. Modelling fluxes and scalar concentrations of CO<sub>2</sub>, H<sub>2</sub>O and sensible heat within and above a mountain meadow canopy: a comparison of three Lagrangian models and three parameterisation options for the Lagrangian time scale. *Boundary-Layer Meteorol.* 2004; 113:43–80.
- Wohlfahrt G, Cernusca A. Momentum transfer by a mountain meadow canopy: a simulation analysis based on Massman's (1997) model. *Boundary-Layer Meteorol.* 2002; 103:391–407.
- Wohlfahrt G, Bahn M, Newesely Ch, Sapinsky S, Tappeiner U, Cernusca A. Canopy structure versus physiology effects on net photosynthesis of mountain grasslands differing in land use. *Ecol. Model.* 2003; 170:407–426.
- Wohlfahrt G, Anfang Ch, Bahn M, Haslwanter A, Newesely Ch, Schmitt M, Drösler M, Pfadenhauer J, Cernusca A. Quantifying nighttime ecosystem respiration of a meadow using eddy covariance, chambers and modelling. *Agric. For. Meteorol.* 2005; 128:141–162.
- Xu L, Baldocchi DD. Seasonal variation in carbon dioxide exchange over a Mediterranean annual grassland in California. *Agric. For. Meteorol.* 2003; 123:79–96.
- Zha T, Kellomäki S, Wang K-Y, Rouvinen I. Carbon sequestration and ecosystem respiration for 4 years in a Scots pine forest. *Global Change Biol.* 2004; 10:1492–1503.



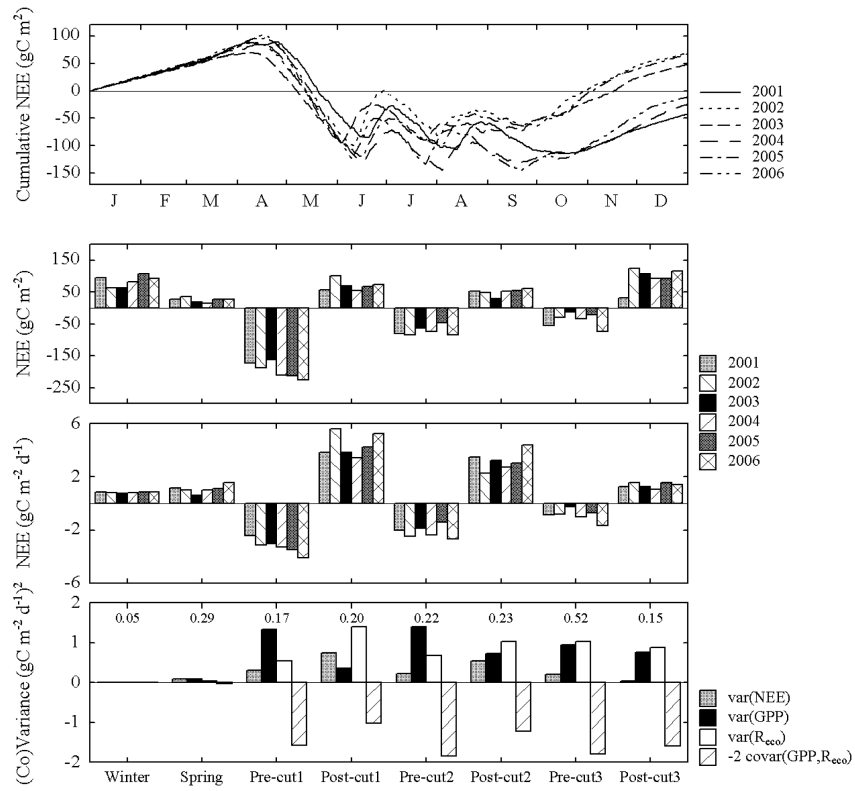


**Figure 1. Monthly sums of photosynthetically active radiation (PAR), monthly average air temperature ( $T_{\text{air}}$ ), monthly sums of precipitation (P) and monthly average relative extractable soil water (REW).**

Lines in the two middle panels refer to monthly long-term (1980-2000) data of air temperature and precipitation.

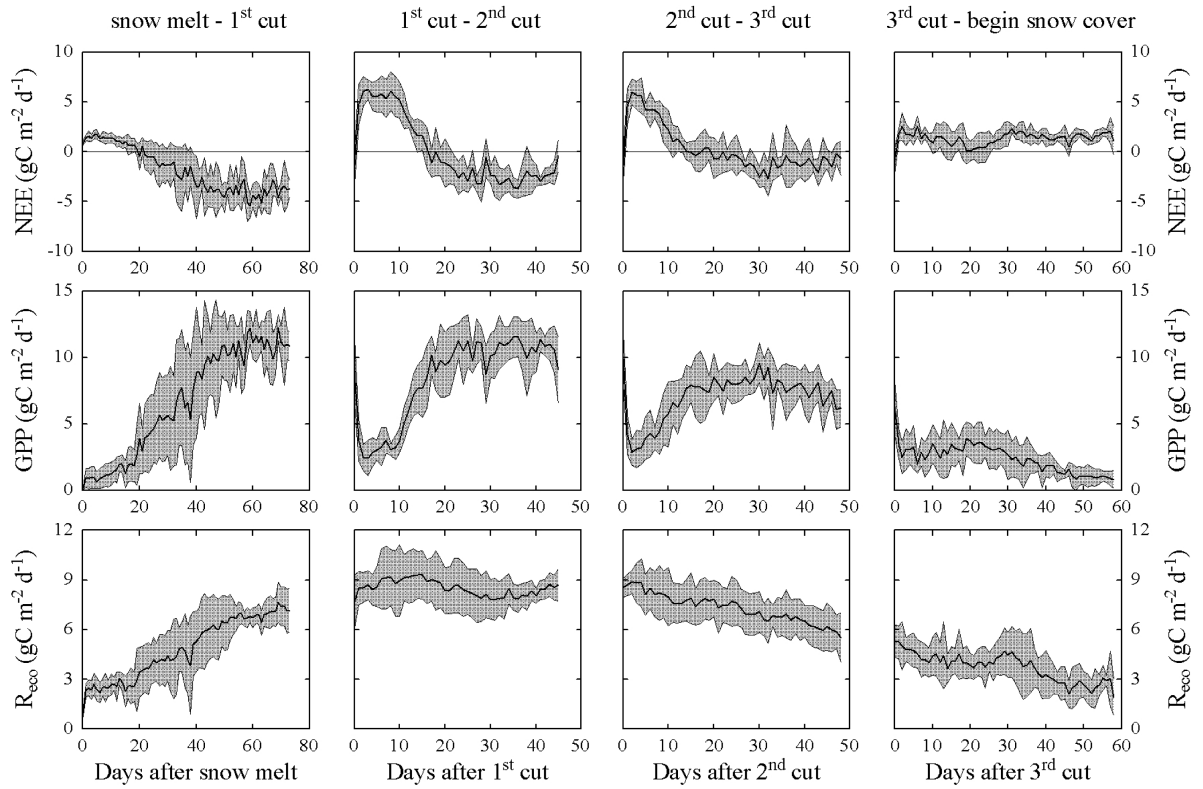


**Figure 2. Daily average net ecosystem  $\text{CO}_2$  exchange (NEE), gross primary production (GPP), ecosystem respiration ( $R_{\text{eco}}$ ) and green area index (GAI).** Vertical shaded areas indicate cutting dates. Black horizontal bars in the lowermost panel indicate snow cover duration, the solid line is a sigmoidal/quadratic fit to measured GAI (symbols).

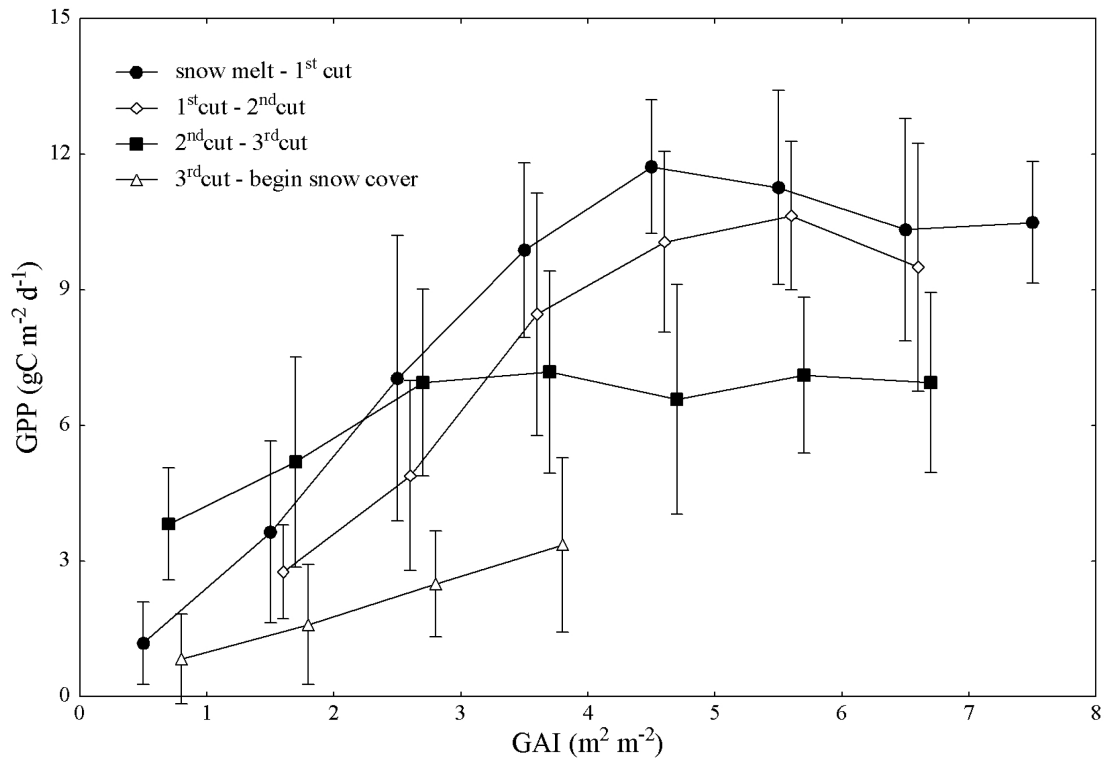


**Figure 3. Cumulative net ecosystem CO<sub>2</sub> exchange (NEE, uppermost panel), NEE and daily average NEE (middle panels), and (co)variance of daily average NEE and its components (lowermost panel) during various periods (refer to text).**

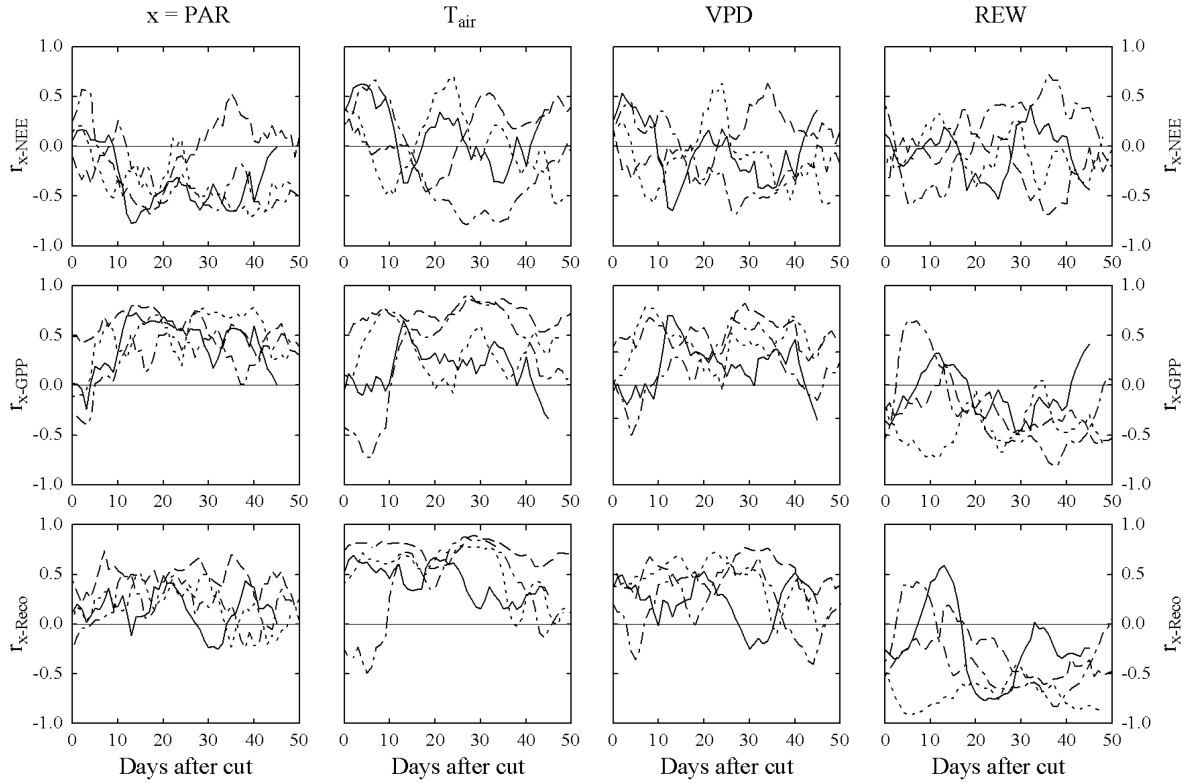
Numbers in lowermost panel indicate the coefficient of variation of NEE. For the decomposition of the variance of NEE into its components refer to Eq. (2).



**Figure 4.** Seasonal variation of daily average net ecosystem  $\text{CO}_2$  exchange (NEE, upper panels), gross primary production (GPP, middle panels) and ecosystem respiration ( $R_{\text{eco}}$ , lower panels). Solid lines represent six year means, grey areas  $\pm$  one standard deviation around the mean.

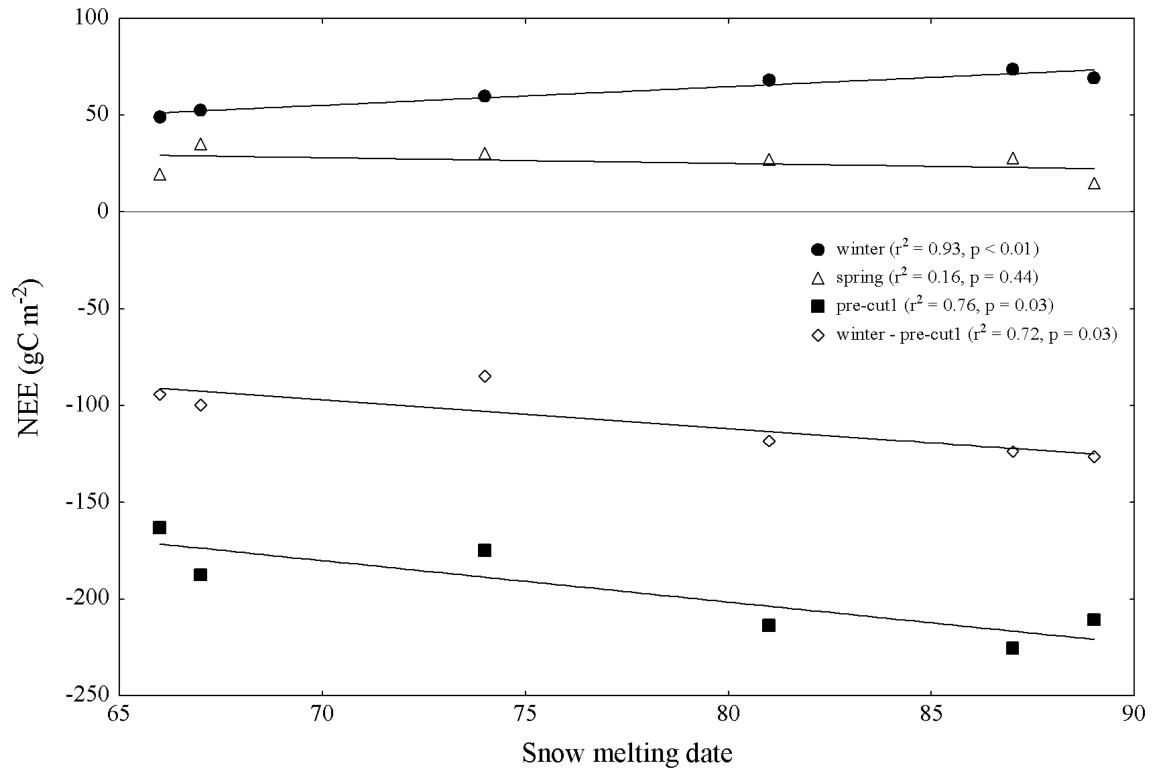


**Figure 5.** Daily average gross primary production (GPP) as a function of green area index (GAI). Symbols are bin-averages and have been shifted by  $0.1 \text{ m}^2 \text{ m}^{-2}$  GAI to the right in order to improve legibility. Error bars refer to  $\pm$  one standard deviation around the mean.



**Figure 6. Correlation coefficients ( $r$ ) between photosynthetically active radiation (PAR), air temperature ( $T_{\text{air}}$ ), vapour pressure deficit (VPD) and relative extractable soil water (REW) and daily average net ecosystem  $\text{CO}_2$  exchange (NEE, upper panels), gross primary production (GPP, middle panels) and ecosystem respiration ( $R_{\text{eco}}$ , lower panels).**

The periods shown are: snow melt to first cut (dash/dot line), first to second cut (solid line), second to third cut (dotted line) and third cut to beginning of snow cover (dashed line). Correlation coefficients were calculated using five-day moving windows (i.e.  $n = 20$ ) and are significant at  $p < 0.05$  when  $|r| > 0.44$ . Correlations with soil temperature are both quantitatively and qualitatively similar to  $T_{\text{air}}$  and are thus not shown.



**Figure 7.** The net ecosystem  $\text{CO}_2$  exchange (NEE) during wintertime, spring, pre-cut1 and the cumulative NEE up to the first cut as a function of the snow melting date.

**Table 1**  
**Annual net ecosystem CO<sub>2</sub> exchange (NEE), gross primary production (GPP), ecosystem respiration (R<sub>eco</sub>) and data coverage.**

Numbers in parenthesis refer to random and systematic uncertainty of annual net ecosystem CO<sub>2</sub> exchange, respectively. Average  $\pm$  one standard deviation over the six study years are given in lowermost line.

	NEE (gC m <sup>-2</sup> y <sup>-1</sup> )	GPP (gC m <sup>-2</sup> y <sup>-1</sup> )	R <sub>eco</sub> (gC m <sup>-2</sup> y <sup>-1</sup> )	Data coverage (%)
<b>2001</b>	-42 ( $\pm 6 \pm 35$ )	1497	1455	32
<b>2002</b>	69 ( $\pm 7 \pm 11$ )	1627	1696	45
<b>2003</b>	49 ( $\pm 7 \pm 13$ )	1551	1600	36
<b>2004</b>	-23 ( $\pm 7 \pm 28$ )	1595	1572	42
<b>2005</b>	67 ( $\pm 7 \pm 21$ )	1450	1517	39
<b>2006</b>	-11 ( $\pm 7 \pm 21$ )	1687	1676	40
<b>Average</b>	18 $\pm$ 49	1568 $\pm$ 87	1586 $\pm$ 92	39 $\pm$ 5



**Table 2**  
**Results (correlation coefficients) of linear regression analysis with daily average NEE, GPP and  $R_{eco}$  as independent and daily average PAR,  $T_{air}$ , VPD and REW as independent variables.**

Significant correlation coefficients are shown in bold letters for clarity. Correlations with soil temperature are both quantitatively and qualitatively similar to  $T_{air}$  and are thus not shown. (\* ...  $p < 0.05$ , \*\* ...  $p < 0.01$ , \*\*\* ...  $p < 0.001$ ;  $n = 6$ ).

	NEE				GPP				$R_{eco}$			
	PAR	$T_{air}$	VPD	REW	PAR	$T_{air}$	VPD	REW	PAR	$T_{air}$	VPD	REW
Winter	0.29	-0.64	-0.75	0.24	-	-	-	-	0.29	-0.64	-0.75	0.24
Spring	0.57	0.54	-0.35	0.21	-0.64	<b>-0.80*</b>	0.10	-0.58	-0.09	-0.41	-0.45	-0.62
Pre-cut1	0.54	0.04	0.26	0.13	-0.63	0.27	0.01	0.00	-0.61	0.45	0.21	0.10
Post-cut1	0.67	<b>0.76*</b>	<b>0.78*</b>	-0.07	0.16	0.53	0.19	-0.08	0.57	<b>0.83*</b>	0.67	-0.09
Pre-cut2	-0.57	-0.64	-0.22	0.24	0.58	0.70	0.33	-0.31	0.51	0.64	0.35	-0.31
Post-cut2	-0.16	0.36	0.25	-0.44	0.40	0.69	0.66	-0.61	0.21	<b>0.83*</b>	0.73	<b>-0.83*</b>
Pre-cut3	0.03	0.04	0.47	-0.34	<b>0.92**</b>	<b>0.97***</b>	0.62	<b>-0.78*</b>	<b>0.90**</b>	<b>0.95**</b>	<b>0.81*</b>	<b>-0.91*</b>
Post-cut3	0.44	0.56	0.17	0.09	0.72	<b>0.78*</b>	0.53	-0.58	<b>0.76*</b>	<b>0.84*</b>	0.53	-0.52
Annual	-0.18	0.32	0.17	-0.18	-0.05	0.69	0.07	-0.15	-0.15	<b>0.81*</b>	0.18	-0.23