Drivers of long-term variability in CO_2 net ecosystem exchange in a temperate peatland

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Abstract

Land-atmosphere exchange of carbon dioxide (CO_2) in peatlands exhibits marked seasonal and inter-annual variability, which subsequently affects the carbon (C) sink strength of catchments across multiple temporal scales. Long-term studies are needed to fully capture the natural variability and therefore identify the key hydrometeorological drivers in the net ecosystem exchange (NEE) of CO_2. Since 2002, NEE has been measured continuously by eddy-covariance at Auchencorth Moss, a temperate lowland peatland in central Scotland. Hence this is one of the longest peatland NEE studies to date. For 11 years, the site was a consistent, yet variable, atmospheric CO_2 sink ranging from -5.2 to -135.9 g CO_2-C m^{-2} yr^{-1} (mean of -64.1 ± 33.6 g CO_2-C m^{-2} yr^{-1}). Inter-annual variability in NEE was positively correlated to the length of the growing season. Mean winter air temperature explained 87% of the inter-annual variability in the sink strength of the following summer, indicating a phenological memory-effect. Plant productivity exhibited a marked hysteresis with respect to photosynthetically active radiation (PAR) over the growing season, indicative of two separate growth regimes. Ecosystem respiration (R_{eco}) and gross primary productivity (GPP) were closely correlated (ratio 0.74), suggesting that autotrophic processes were dominant. Whilst the site was wet most of the year (water table depth < 5 cm) there were indications that heterotrophic respiration was enhanced by drought, which also depressed GPP. NEE was compared to 5 other peatland sites which have published long-term NEE records. The CO_2 uptake rate during the growing season was comparable to 3 other European sites, however the emission rate during the dormant season was significantly higher.

1 Introduction

Northern peatlands are one of the most important global sinks of atmospheric CO_2; with their ability to sequester C controlled by hydrometeorological variables such as precipitation, temperature, length of growing season and period of snow cover, they also potentially represent an important climatic feedback mechanism (Aurela et al., 2001, Frolking et al., 2001, Lafleur et al., 2003). All these factors either directly or indirectly link to plant productivity. Peatland carbon models generally suggest a decline in net sink strength in a warming climate, although the magnitude of the decline predicted by individual models is variable (Clark et al., 2010). UK peatlands are predicted to become a net source of carbon in response to climate change (Worrall et al., 2007), with climate models predicting a rise in global temperature of ca. 3^{o} C between 1980-1999 and 2100 (IPCC, 2007; scenario A1B which considers a balanced distribution between fossil fuel intensive and non-fossil fuel energy sources). The McGill wetland model (St-Hilaire et al., 2010) predicted that a modest rise in temperature in a peatland in Ontario (Canada) would lead to it becoming a CO_2 source rather than a sink. A greater understanding of drivers and feedback mechanisms, across a range of temporal scales, is therefore a current research priority.

Eddy covariance measurements using fixed flux towers provide the best method for assessing year-on-year changes in catchment scale CO_2 exchange between the land surface and the atmosphere (Dinsmore et al., 2010, Nilsson et al., 2008, Roulet et al., 2007). Continuous measurements reveal strong inter-seasonal and inter-annual variation. In most years and in most peatlands net ecosystem exchange (NEE) is the largest and most variable of the C flux terms (Roulet et al., 2007). In combination with aquatic fluxes (downstream and evasive losses) and CH_4 emissions, it is a key component, if not the foremost, of C and greenhouse gas (GHG) budgets for peatland systems (Billett et al., 2010, Dinsmore et al., 2010). Understanding what is driving inter-seasonal and inter-annual changes is one of the most important uses of long-term data. Although more sites are now being established globally, there are still relatively few peatland sites (< 10) with published NEE measurements for periods of 3 years or more. This is partly because past flux measurements were often made on a short-term or campaign basis, focussing on site comparisons across land-use or vegetation types (Hargreaves et al., 2003). Small-scale chamber measurements or mesocosm studies are also widely used to study the effects of variables such as water table, soil temperature and plant species on GHG exchange between the land surface and the atmosphere (Dinsmore et al., 2009, Macdonald et al., 1998). Whilst chamber approaches provide useful methods for comparing sites/treatments, the scale of measurement and potential spatial heterogeneity, mean that upscaling chamber-derived fluxes to larger land surface areas can be problematic.

Including the Auchencorth Moss site, there are to our knowledge only 6 peatland sites in the Northern hemisphere for which long-term (≥ 3 years) datasets of NEE are now available and all show that peatlands continue to operate as a sink for CO_2 from the atmosphere, albeit with different annual sink strengths. The 6-year mean NEE for Mer Bleue peatland (Ontario, Canada) was -40.2 g C m^{-2} yr^{-1} (negative values signify uptake), varying year-to-year from a minor (-2) to a major (-112) CO_2 sink (Roulet et al., 2007). Similarly McVeigh et al. (2014) found that a blanket bog in SW Ireland had a mean 9-year NEE of -55.7 g C m^{-2} yr^{-1} and exhibited significant inter-annual variability (-32.1 to -79.2 g C m^{-2} yr^{-1}). Degerö Stormyr in Northern Sweden showed consistent yet variable CO_2 uptake over 12 consecutive years (12-year mean -58 ± 21 g C m^{-2} yr^{-1}, range -18 to -105 g C m^{-2} yr^{-1}) (Peichl et al., 2014). Eddy covariance measurements at Lompolojänkkä, a nutrient-rich fen in Northern Finland, again showed that the site operated as a weak (-3 g C m^{-2} yr^{-1}) to strong (-59 g C m^{-2} yr^{-1}) CO_2 sink over a 3 year period (Aurela et al., 2009). In contrast to the variability exhibited by these sites, Christensen et al. (Christensen et al., 2012) found that over the period 2001-08 annual CO_2 uptake in Stordalen, a sub-arctic permafrost mire in Northern Sweden, was relatively stable (-46 g C m^{-2} yr^{-1}).

Quantifying inter-annual variability in NEE is a prerequisite for detecting longer term trends or step changes in flux magnitude in response to climatic or anthropogenic influences. Furthermore, identifying the drivers of this variability is an essential step towards understanding and modelling the effects that long-term climatic changes will have on peatlands, as well as managing the impact of future climate change. For the UK as a whole there have been significant regional changes in precipitation and temperature since the beginning on the 20th century, with the most rapid changes occurring over the last 50 years (Jenkins et al., 2009). During the period 1961-2006 annual precipitation increased by 2.5-23.2% in different regions of the UK, with the largest increases occurring in the winter (particularly in Scotland and Northern England); summer months were typically characterised by a decrease in precipitation amount. Mean annual temperature during the same period (1961-2006) increased in parts of the UK by 1.05-1.64°C (Jenkins et al., 2009). Individual site-specific records show a similar picture. For example, an upland peatland site in Northern

England showed an increase in mean annual temperature of 0.53°C between the period 1931-1960 and 1991-2006, with the winter months (January-February) warming much faster than the other months of the year (Holden & Rose, 2011). These data therefore show that significant changes are taking place in seasonal climatic patterns, which are likely to have a major impact on annual net CO_2 uptake by peatland systems.

Meteorological conditions such as rainfall, temperature and levels of photosynthetic active radiation (PAR) control NEE and its components, total ecosystem respiration (R_{eco}) and gross primary productivity (GPP). R_{eco} is in turn composed of a plant respiration term (autotrophic respiration, R_A) which quantifies metabolic respiration from both above- and below-ground biomass (R_{AA} and R_{AB}, respectively), and a soil respiration term (heterotrophic respiration, R_H) resulting from microbial decomposition of organic matter. Autotrophic respiration can account for up to 60% or R_{eco} (van der Molen et al., 2011), whilst total below ground respiration ($R_{soil} = R_{AB} + R_H$) can account for up to 70%. R_{eco} and GPP have been shown to be tightly linked in a range of ecosystems on both short-term and annual timescales (Irvine et al., 2008, Law, 2005, Ryan & Law, 2005) and respond similarly, although not necessarily with the same magnitude, to extreme events such as drought. For example, short-term dynamics of R_{eco} have been shown to be more sensitive to the availability of labile C compounds produced by photosynthesis than to the effects of varying soil moisture on soil microbial activity (Irvine et al., 2008). On a global scale, drought has been identified as the main cause of decreased GPP alongside continent-specific secondary drivers such as cold spells and precipitation (Zscheischler et al., 2014a; Zscheischler et al., 2014b). Although less well understood and modelled than GPP, R_{eco} plays a major role in ecosystem C exchange dynamics and sink strength, and increases in R_{eco} have been shown to turn a sink of C into a source (Lund et al., 2012). In order to interpret inter-annual variability in NEE, it is therefore of paramount importance to partition fluxes of CO_2 into GPP and R_{eco} and study their dynamics with respect to meteorology. We have done this on Auchencorth Moss, an ombrotrophic peatland in SE Scotland. The first eddy covariance measurements of CO_2 exchange at Auchencorth Moss took place in 1995-96 (Hargreaves et al., 2003), with continuous measurements starting in 2002. Previous measurements of NEE have been published for specific 2-3 year time periods and suggest that year-on-year values are highly variable. Dinsmore et al. (Dinsmore et al., 2010) and Drewer et al. (Drewer et al., 2010) reported that over a 3 year period (2006-08) the peatland acted as a very strong CO_2 sink (-88 to -136 g C m^{-2} yr^{-1}), whereas Billett et al. (Billett et al., 2004) reported that between 1995-96 it was acting as a weaker CO_2 sink (-36 and -8 g C m^{-2} yr^{-1}). In comparison to NEE, CH_4 emissions at Auchencorth Moss are small (average of 0.32 g CH_4-C m^{-2} yr^{-1} in 2007 and 2008, (Dinsmore et al., 2010)). Although these individual studies highlight significant inter-annual variability at Auchencorth Moss, they are for relatively short periods of time and are insufficient to investigate the drivers of inter-annual variability in NEE. Here we present the first complete analysis of the 2002-2013 dataset in terms of monthly, seasonal and annual fluxes and explore the drivers of temporal variability in NEE. In addition, we compare the 11 year period 2002-2013 with the longer term (1960-2013) local meteorological record to place the recent 11 year period into a wider climatic context. We use our data to test the following hypotheses:

- Peatlands release more CO_2 to the atmosphere under drier and warmer conditions.
- The length of the growing season has a significant impact on annual NEE.
- Plant productivity during the growing season is affected by the preceding winter's meteorological conditions and can exhibit significant inter-annual variability.
- Autotrophic processes dominate heterotrophic processes at well-watered, vegetated sites.

2 Materials and methods

2.1 Site description

Auchencorth Moss (55°47'32 N, 3°14'35 W, 267 m a.s.l.) is a low-lying ombrotrophic peatland situated 17 km south-west of Edinburgh (Scotland, UK). Parent material comprises Upper Carboniferous/Lower Devonian sedimentary rocks overlain by fluvio-glacial till; peat depth range from < 0.5 m to > 5 m. Long-term research (e.g. Billett et al. 2004: Dinsmore et al. 2010) on C fluxes is focussed on the 3.4 km^2 upper part of the catchment (elevation range 249-300 m) where the soils comprise peats (85%), gleysols (9%), humic gleysols (3%) and cambisols (3%). The open moorland site has an extensive uniform fetch over blanket bog to the south, west and north with a dominant wind direction from the SW; winds from the NE are the second most important wind direction. The terrain is relatively flat with a complex micro-topography consisting of hummocks and hollows. Hummocks are relatively small in size (typically 40 cm in diameter and ~30 cm in height) and covered by either a mix of *Deschampsia flexuosa* and *Eriophorum vaginatum*, or *Juncus effusus*. In contrast, hollows are dominated by mosses (*Sphagnum papillosa* and *Polytrichum commune*) and a layer of grasses (Dinsmore et al., 2009).

The site was drained more than 100 years ago; the drains have become progressively less effective and re-vegetated over time, leading to slow and progressive rewetting of the site.

Over the last 20 years the site has been used for seasonal low intensity sheep grazing; areas of peat extraction occur at the margins of the catchment outside the footprint of the flux tower measurements.

2.2 Instrumentation and data processing

Fluxes of carbon dioxide (CO_2) have been measured continuously by eddy-covariance (EC) at Auchencorth Moss since May 2002. The principles of operation and flux calculation methods using the eddy-covariance technique have been extensively discussed elsewhere (Aubinet et al., 2000, Baldocchi et al., 2001). The EC system at Auchencorth Moss consists of a LI-COR 7000 closed-path infrared gas analyser operating at 10 Hz for the simultaneous measurement of carbon dioxide and water vapour. Turbulence measurements were made with an ultrasonic anemometer (initially model Solent R1012A R2 operating at 20.8 Hz; from 2009 Gill Windmaster Pro operating at 20 Hz; both Gill Instruments, Lymington, UK), mounted atop a 3 m mast. The effective measurement height is 3.5 m with a vertical separation of 20 cm between the anemometer and the inlet of the sampling line. Air is sampled at 20 lpm through a 40 m long Dekabon line (internal diameter 4 mm). In addition to eddy-covariance measurements, the site is equipped with a Campbell Scientific 23X datalogger for the automated acquisition of a comprehensive suite of meteorological parameters which include net radiation (Skye instruments SKS1110), PAR (Skye instruments SKP215), air temperature (fine wire type-E thermocouple), air pressure (Vaisala PTB101C), wind speed and direction (Gill Instruments WindSonic), soil water content (Campbell Scientific CS616 TDR probes), soil temperature (Campbell Scientific 107 thermistors at 10 cm, 20 cm, 30 cm, and 40 cm), rainfall (tipping bucket rain gauge) and, since April 2007, water table depth (Druck PDCR 1830).

High-frequency eddy-covariance data is acquired by in-house software written in LabView (National Instruments) and processed offline into half-hourly fluxes.

Half-hourly data points were excluded from further analysis if any of the criteria listed below was not met:

- The total number of “raw” (high-frequency) data points per notional half-hour period was less than 90% of the maximum possible number of points (36000), i.e. below a minimum averaging period of 27 minutes.

- The number of spikes in raw w (vertical wind velocity component), CO_2 (CO_2 mole fraction) and H_2O mole fraction exceeded 1% of the total number of points per half-hour period.
- The stationarity test devised by Foken et al. (Foken & Wichura, 1996), which compares half-hourly fluxes to the average of six 5-minute averaging periods within the half hour, did not fulfil the quality criterion.
- Turbulence was insufficient for reliable EC measurements ($u_* < 0.1$ m s^{-1}).
- CO_2 mole fractions < 330 ppm.
- Half-hourly CO_2 fluxes (F_{CO2}) fell outside the [-50 µmol m^{-2} s^{-1}, + 120 µmol m^{-2} s^{-1}] interval.
- Half-hourly latent fluxes (LE) fell outside the [-250 W m^{-2}, + 600 W m^{-2}] interval.

After quality control, the number of good data points ranged from 45% (in 2005) to 78% (in both 2004 and 2008), with an annual mean of 65% ± 11%.

Gapfilling of net ecosystem exchange (NEE) measured by eddy-covariance and partitioning of the gapfilled half-hourly fluxes into ecosystem respiration (R_{eco}) and gross primary production (GPP) were achieved using an online tool developed at the Max Planck Institute for Biogeochemistry, Jena, Germany[1] (Reichstein et al., 2005). In this flux partitioning approach, daytime ecosystem respiration is obtained by extrapolation of the night time parameterisation of NEE on air temperature (using an exponential relationship of the form given in equation (1)) and GPP is the difference between ecosystem respiration and NEE.

Due to technical difficulties with the sampling pump (gradual decline in pumping performance) which were not detected immediately, most of the flux data for the summer period of 2011 were discarded as a precautionary measure.

2.3 Calculations of ecosystem respiration, Q_{10} and GPP

Ecosystem respiration was determined from night-time CO_2 fluxes measured by EC and parameterised as a function of temperature using equation (1).

$$\mathbf{R_{eco} = a\,exp(bT)} \qquad (1)$$

Where T is either air or soil temperature and a and b are fitting coefficients.

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[1] http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/upload.php

The growth rate (Q_{10}) for ecosystem respiration for a change of 10 °C was determined using the relationship:

$$\mathbf{Q_{10}} = \left(\frac{\mathbf{R_2}}{\mathbf{R_1}}\right)^{\mathbf{10}/(\mathbf{T_2}-\mathbf{T_1})} \qquad (2)$$

T_1 and T_2 are reference temperatures, and R_1 and R_2 are the corresponding respiration rates.

GPP was parameterised with respect to PAR using the following rectangular hyperbolic regression function:

$$\mathrm{GPP} = \frac{\alpha.\mathrm{GPP_{sat}}.\mathrm{PAR}}{\mathrm{GPP_{sat}}+\alpha.\mathrm{PAR}} \qquad (3)$$

Where GPP_{sat} (GPP at light saturation) and α (quantum efficiency) are fitting parameters.

3 Results

3.1 Site meteorology

During the study period 2002-2013, the site received a mean annual precipitation of 1018 mm ± 166 mm (± values denote standard deviation). Autumn (September-November) was the wettest season with 96 mm ± 11 mm of rain per month, and spring (March-May) was the driest with 64 mm ± 17 mm per month. Rainfall is highly variable year on year but records from a weather station of the UK Met Office (UK Meteorological Office, 2013) located 3.5 km North of the study site indicate a slight upward trend since the early 1970s (average annual precipitation 899 mm ± 166 mm for the period 1961-2001).

Mean annual air temperatures were 8.3°C ± 4.6 °C for the study period 2002-2013 compared to 7.7 °C ± 4.5 °C for 1961-2001. Despite year-on-year variability there are indications of a steady increase of the order of 0.019 °C y^{-1} since records began in 1961 at the nearby Met Office station, which is consistent with UK and global trends (Jenkins et al., 2009). All seasons were warmer in 2002-2013 than in 1961-2001, albeit not significantly. Summer (June-August) was the warmest season with an average temperature of 13.6 °C ± 1.1 °C, and winter (December – February) the coldest with 3.7 °C ± 1.0 °C (Fig. 1).

Over the period April 2007 to December 2013, water table depth (WTD) was within 4 cm of the peat surface for 50 out of 81 months (62%). During dry periods, however, the water table could fall quickly to depths > 35 cm (Table 2).

3.2 Seasonal and inter-annual variability of R_{eco}, GPP and NEE

Ecosystem respiration typically peaked in July/August and was distributed asymmetrically around its peak value (Fig. 2), following the annual cycle of temperature. Plotting monthly GPP as a function of photosynthetically active radiation (PAR) reveals two separate plant productivity regimes culminating around mid-summer (Fig. 3). The hysteresis of GPP v. PAR is characterised by an exponential growth phase from March to June/July followed by a logarithmic decline in photosynthetic efficiency. The ratio of GPP to R_{eco} showed that on average carbon uptake by vegetative growth exceeded losses to the atmosphere through respiration for six months of the year, from April to September (Fig. 2, inset).

A negative correlation was established between mean annual values of GPP_{sat} (GPP at light saturation, eq. (3)) and WT (Spearman $\rho = -0.63$, $p < 0.05$, Table 1) indicating that the photosynthetic capacity of the plant community tended to decrease as WT deepened. Furthermore, GPP_{sat} was positively correlated to the average temperature during the preceding winter ($\rho = 0.73$, $p < 0.01$, Table 1).

Both GPP and R_{eco} exhibited significant inter-annual variability with peak summer time values ranging from 96 to 245 g CO_2 –C m^{-2} $month^{-1}$ for GPP and 76 to 198 g CO_2 –C m^{-2} $month^{-1}$ for R_{eco} (August 2010 and July 2006, for minima and maxima, respectively). The site was consistently a sink for CO_2, however inter-annual variability was large. NEE (mean -64.1 ± 33.6 g CO_2–C m^{-2}) ranged from -5.2 to -135.9 g CO_2-C m^{-2} yr^{-1} with minimum and maximum CO_2 uptake in 2013 and 2007, respectively (Fig. 4). As observed at other sites (Christensen et al., 2012), annual values of NEE were well-correlated to the length of the growing seasons (LGS from here onward; $R^2 = 0.64$; Fig. 5). Furthermore, whilst mean spring/summer (April to September) NEE (NEE_{SS}) at Auchencorth Moss was not significantly correlated to summer temperature, a strong negative correlation (i.e. net uptake increased with increasing winter T_{air}) was observed between mean NEE_{SS} and the mean air temperature of the preceding winter (January to March) ($R^2 = 0.87$, Fig. 6; $p << 0.01$). Comparable correlations to winter T_{air} were observed for GPP_{SS} and R_{ecoSS} ($\rho = 0.73$, $p < 0.01$; $\rho = 0.61$, $p = 0.02$, respectively, Table 1). Linear correlations between summer gross ecosystem production and ecosystem respiration and pre-growing season mean air temperature have also been observed over a 12-year period at a boreal fen in Northern Sweden (Peichl et al., 2014).

3.3 Effects of dry periods on CO_2 exchange

Throughout most years and most seasons Auchencorth Moss can be considered a wet site, with mean water table depth (WTD) 3.5 ± 6.8 cm and monthly range -3.8 cm (flooded; negative values denote water table levels above the peat surface) to +36 cm (April 2007 to December 2013; no WT measurements prior to April 2007). The site was generally waterlogged during the autumn and winter months. During dry spells, which we arbitrarily define as any period lasting 1 week or longer with WTD > 5 cm, the water table can drop quickly at rates up to 3 cm day^{-1} (Table 2).

Three notable dry spells occurred during the summer of 2010 and two during the summer of 2008, characterised by cycles of rapid fall and rise of the water table. Meanwhile, air temperatures exhibited little variation. Details of the drainage rates (water table drawdown) and maximum water table depths are given in Table 2. Under normal hydrological conditions (water table typically within 3-5 cm of the peat surface), R_{eco} at Auchencorth Moss did not exhibit a significant correlation with WTD. In contrast, during the dry spells of 2008 and 2010, daily R_{eco} was non-linearly correlated to WTD (Fig.7). The response of R_{eco} to changes in WTD occurred with time lags ranging from 0 to 5 days (Table 2). During the first two dry spells of 2010 the relationship between R_{eco} and WTD was of clear parabolic form, with R_{eco} reaching a minimum a few days after the onset of the dry period. Dry spell 1 and 2 were separated by a strong rainfall event on June 9 2010 which resulted in a rapid rise in WT; the ecosystem response to the second cycle of drought was quasi-instantaneous and the decrease in total respiration at the beginning of the second dry period was less pronounced than at the onset of the first dry period; minimum R_{eco} in the second dry period coincided with a WTD of 12.5 cm, compared to 15.6 cm for the first dry spell. The parabolic trend was weaker during the third dry spell ($R^2 = 0.65$), and minimum R_{eco} reached at a much shallower WTD (2.9 cm). Except for the second dry period of 2010, the residuals of the regressions between R_{eco} and WTD were not correlated with air or soil temperature. The 2 dry spells of 2008 exhibited similar parabolic relationships between R_{eco} and WTD but differed in magnitude. Of all 5 dry spells, R_{eco} was at the lowest in May 2008. However, at the end of that dry spell the trend in R_{eco} was consistent with the 2010 trends. The second dry spell of summer 2008 differed from all others both in terms of magnitude and rate of change of R_{eco} with respect to WTD: both parameters were largest in July 2008 which also saw the highest mean air temperature of the 5 dry spells. In contrast, T_{air} during the first dry spell of 2008 was the lowest. Such parabolic relationships between R_{eco} and WTD were however not observed during the summer of 2013, which was the second driest in the 2002-2013 study period (the driest was 2003 with 346 mm rain between April and September compared to 361 mm in 2013); 2013 also had the longest winter of the study period (start of the growing season at day 103 in 2013 compared to day 77 ± 21 for the entire study period) as well as the lowest soil temperatures. Soil temperature at –5 cm increased by 3°C in the 10 days prior to the start of the thermal growing season; T_{soil} rose steadily until mid-July and reached 15°C, the highest value of the 11-year study period, on July 26. The dry period began on May 25, culminating on July 22 (WTD = 48 cm), and WTD was ≥ 5 cm until early September. In 2013, the relationship between R_{eco} and WTD was linear across the 6 temperature classes considered (Fig. 8). Between 8°C and 16°C, the mean slope between R_{eco} and WTD (average of the 4 2°C temperature classes) was 0.016 ± 0.004 and the vertical offset increased with temperature. Above 16°C, the positive correlation between R_{eco} and WTD was less pronounced and was even found to be negative for the 16°C-18°C temperature class which could be due to spatial inhomogeneity as the wind direction alternated between prevailing SW and NE. Above 18 °C, the positive linear correlation was no longer statistically significant.

For all years for which WTD data was available, the sensitivity of R_{eco} to air temperature (Q_{10}) decreased with a drop in water table; in contrast, the theoretical values of R_{eco} at $T_{air} = 0$ °C (obtained by extrapolation to the origin of the temperature-dependent functions fitted to monthly R_{eco} and averaged to annual values) were found to increase with WTD. One-way analysis of variance (ANOVA) on GPP, NEE and R_{eco} with respect to 10 WTD classes (making the assumptions that a) the WTD classes constitute different treatments and b) that the plant community has reached a steady state in terms of growth; Table 3) demonstrates that the position of the WT does have a statistically significant impact on R_{eco} for all years between 2007 and 2013, except 2012. For GPP, the correlation with WTD was significant in 2008 and 2010, and for NEE in 2013 only.

4 Discussion

4.1 Seasonal and inter-annual variability of NEE and GPP

The relationship between GPP and PAR exhibited a marked hysteresis during the growing season (Fig.3), which we attribute to the degradation of the photosynthetic efficiency of the plant community as senescence sets in. A recent study on soybean crops revealed that the fraction of PAR absorbed by the plants during the green-up phase was three times larger than during senescence, despite LAI of senescing plants being 1.5 times greater than for growing plants (Gitelson et al., 2012). A marked hysteresis was also observed between GPP normalised by potential PAR (i.e. maximum PAR at a given time of year) and near-infrared reflectance over the life cycle of the crop. Senescing plants possess greater LAI (albeit due to a combination of photosynthetically active and inactive leaves) and increase light scattering but are less productive than the greening plants. We also expect the relationship between GPP and PAR to vary due to the relative contributions to total measured GPP of individual plant species, whose productivity can vary from year to year (Bates et al., 2005, Kreyling et al., 2010, Kreyling et al., 2008, Weltzin et al., 2000). Although spatial quantitative information regarding leaf area index (LAI) or aboveground biomass is not available at a sufficiently fine temporal scale at Auchencorth Moss, other studies have reported correlations between winter meteorological conditions and the development of plant populations later in the year. Weltzin (2000) reported increased total net primary productivity (TNPP) in shrubs, a decrease in graminoids and no effect on bryophytes exposed to a gradient of infrared loading (i.e. continuous heating by infrared lamps). Individual species of bryophytes at a temperate UK site have been shown to respond to winter warming and/or summer drought in opposite ways, but this was not reflected at the community level whose mean cover did not exhibit significant differences between treatments (Bates et al., 2005). Kreyling (2008) demonstrated enhancement of aboveground net primary productivity (ANPP) in grasses as a result of freeze-thaw cycles the preceding winter, whilst belowground net primary productivity (BNPP) was adversely affected.

At plant community level we observed a net positive feedback between winter time meteorology and productivity as GPP_{SS}, GPP_{sat} and α were significantly correlated to mean air temperature during the preceding winter (Table 1). Based on the knowledge that Sphagnum mosses are capable of photosynthesising as soon as the snow cover disappears and daily air temperature > 0 °C (Loisel et al., 2012) we speculate that the sensitivity of GPP and GPP_{sat} to winter air temperature is predominantly caused by graminoids and other non-moss species. WTD had a statistically significant negative feedback on GPP indicating a decrease in plant productivity caused by the onset of drought stress. This has previously been shown to be important at other sites, particularly in moss species (Aurela et al., 2009, Lafleur et al., 2003, van der Molen et al., 2011); furthermore, a negative linear relationship between leaf area index (LAI) and WTD has been reported for a grassland established on drained organic soil in Ireland (Renou-Wilson et al., 2014) which illustrates the effect of water availability on graminoid productivity. It must however be noted that the WTD range in the Renou-Wilson (2014) study was significantly deeper (typically 20 cm to 60 cm below peat surface) than at our study site. Wet-adapted moss species growing in hollows are known to have large variability in growth rate directly linked to WTD (faster growth than hummock and lawn species under wet conditions but susceptible to dessication under dry conditions; (Gunnarsson, 2005, Loisel et al., 2012)). Weltzin et al. (2000) showed that, along a gradient of decreasing WTD of range consistent with our study site, TNPP increased in bryophytes, decreased in shrubs and was unchanged in graminoids. Graminoids and bryophytes being the dominant species in the EC footprint, the sensitivity of GPP to WTD observed at our study site is likely to be mainly due to mosses.

We found that GPP and R_{eco} followed the same temporal pattern on a monthly and seasonal basis, with an average R_{eco}/GPP ratio of 0.74 for the study period. Whilst these two terms are not fully independent of one other due to the gapfilling and flux partitioning procedures, it is nevertheless interesting to compare their ratio to those obtained at other sites. A ratio of 1:3 between maximum ecosystem respiration and carbon uptake has been reported for a boreal peatland in northern Manitoba, Canada (Bubier et al., 1998), and ratios ranging from 0.46 to 0.76 were recorded at four Scandinavian mires (Lindroth et al., 2007). The constant ratio between R_{eco} and GPP points to common mechanistic controls, and suggests that autotrophic respiration was the dominant driver of the seasonal dynamics of total ecosystem respiration (see also Lindroth et al., 2007).

Mean winter T_{air} explained 87% of inter-annual variability in NEE during the following summer (NEE_{SS}) (Fig. 6). Based on this strong linear relationship and our observations that (a) GPP_{sat} (GPP at light saturation) of the ecosystem were linearly correlated to winter T_{air}, and (b) the ratio R_{eco}/ GPP was fairly constant over the years, we hypothesize that winter meteorological conditions (in particular mean T_{air}) mainly affect overall plant biomass, rather than species richness.

4.2 Importance of dry periods

The parabolic trend seen in the relationship between R_{eco} and WTD during dry spells (Fig. 7) is interesting as it may help understand the mechanistic drivers of R_{eco} at Auchencorth Moss. The parabolic trends were especially strong during the two first dry spells of 2010 (15/05-09/06/2010 and 10/06-10/07/2010) during which the prevailing wind direction was South. The WT measurements might not be representative of the entire flux footprint which could perhaps explain the markedly different trends observed in 2008 when wind was blowing from the East. We postulate that the initial decline in respiration was caused by a reduction in plant metabolic activity as water availability decreased (Lund, 2012). Meanwhile, the lowering of the WT also favoured aerobic processes and increasing microbial decomposition of organic matter within the peat profile (Hendriks et al., 2007). Minimum R_{eco} could then correspond to equilibrium between declining autotrophic and increasing heterotrophic respiration. The subsequent net increase in R_{eco} with deepening WTD could then be explained by a gradual increase in the ratio of heterotrophic to autotrophic respiration. The decrease of the sensitivity of R_{eco} with respect to T_{air} (Q_{10}) with deepening water table further supports the idea that the contribution of heterotrophic to total ecosystem respiration was enhanced under drier conditions.

Based on these observations, we attribute the differences in respiration patterns during the dry spells to water table dynamics, which differs from drier sites where temperature (not WT) was found to be the dominant control of R_{eco} (Lafleur et al., 2005, Updegraff et al., 2001). This is further supported by the result of a one-way ANOVA which demonstrates a statistically significant correlation between R_{eco} and WTD for all growing seasons (except for 2012 which had a wetter than average growing season with WT near or above the peat surface for the entire growing season). The linear (rather than parabolic) response of R_{eco} to WTD in 2013 could perhaps be linked to the long winter of 2013 (the thermal growing season began 69 days later than in 2008, and 10 days later than in 2010) and the fact that the dry spell which lasted most of the summer began less than a month after the start of the growing season; under these circumstances, the moss population could have switched from relatively low metabolic activity to dessication while active growth had just begun in the graminoid community.

Hence, the R_A/R_H ratio could have been smaller than in previous years. In contrast to other years, GPP during summer 2013 was positively correlated to WTD ($p << 0.001$) and $R_{eco}/GPP = 0.8 \pm 0.1$ (range 0.6 to 1.2); this suggests growth in species less susceptible to drought-stress than mosses.

Disentangling the effects of lower than average winter air temperature and summer dry spells on annual NEE is not straightforward, but the former seems to be the dominant driver based on our results (Table 1). The combined effects of a long, relatively cold winter and warm, dry summer which could have slowed plant growth, disturbed the normal phenological cycle and enhanced carbon losses from the peatland through enhanced heterotrophic respiration, were illustrated in 2013 when the sink strength of Auchencorth Moss was dramatically weakened (-5.2 g C-CO_2 m^{-2} yr^{-1}) compared to the long-term mean of -64.1 ± 33.6 g C-CO_2 m^{-2} yr^{-1} (2002-2011).

4.3 NEE in Northern Hemisphere Peatland C Budgets

Compared to other peatlands in the Northern Hemisphere annual values of NEE at Auchencorth Moss are at the high end of both the mean (-64.1 ± 33.6 g CO_2–C m^{-2} yr^{-1}) and inter-annual range (-5.2 to -135.9 g CO_2–C m^{-2} yr^{-1}). However, when the length of the growing season (LGS; the start of the growing season was defined as the first day of the year when mean diurnal air temperature exceeded 5 °C for 5 consecutive days. Conversely, the end of the growing season was defined as the first day of the year when mean diurnal air temperature fell below 5 °C for 5 consecutive days.) is accounted for, the mean daily growing season NEE (NEE_{GS}) at Auchencorth Moss (-0.57 g CO_2-C m^{-2} day^{-1}) is remarkably similar to that found at both Mer Bleue (cool temperate bog; -0.58 g CO_2-C m^{-2} day^{-1}; Roulet et al., 2007) and Degerö Stormyr (boreal mire; -0.48 g CO_2-C m^{-2} day^{-1}; Peichl et al., 2014). By contrast, mean daily NEE_{GS} at Glencar (maritime blanket bog; Koehler et al., 2011, McVeigh et al., 2014) is slightly lower (-0.39 g CO_2-C m^{-2} day^{-1}), whilst the two sub-arctic Scandinavian peatlands Lompolojänkä (nutrient-rich sedge fen; Aurela et al., 2009) and Stordalen (sub-arctic palsa mire; Christensen et al., 2012) stand out with mean daily growing season NEE rates 2 to 2.5 times higher than the values found for Auchencorth Moss, Degerö Stormyr and Mer Bleue, and over 3 times higher than the value found at Glencar (Table 4).

Auchencorth Moss had a mean daily NEE during the dormant season (NEE_{DS}) of 0.61 g CO_2–C m^{-2} day^{-1}, the highest amongst the aforementioned catchments (10-fold higher than that of Glencar, five times that of Degerö Stormyr, three times that of Stordalen and twice that of Mer Bleue). Mean daily NEE_{DS} at Lompolojänkä was only slightly lower than at Auchencorth Moss (0.52 g CO_2-C m^{-2} day^{-1}).

Despite the lower daily mean NEE, the long growing season at Auchencorth Moss made its total NEE_{GS} comparable to that of Lompolojänkä and Stordalen. The vigorous net uptake at Lompolojänkä during the growing season was offset by relatively high carbon losses during the rest of the year. Auchencorth Moss, Lompolojänkä and Stordalen therefore had comparable NEE but for very different reasons: Auchencorth Moss had long growing seasons but also relatively high carbon losses the rest of the year, which could be due to milder winters with minimal snow cover. Lompolojänkä and Stordalen had vigorous carbon uptake rates, their LGS were comparable to one another, but were half that of Auchencorth Moss, whilst Lompolojänkä had high carbon losses during the dormant season which strongly reduced the site's sink strength.

Carbon uptake rates at Degerö Stormyr and Mer Bleue were very similar to Auchencorth Moss but their carbon loss rates, which were comparable to Stordalen's, were half or less of Auchencorth Moss's. This could be explained by cooler climate and prolonged periods of snow cover compared to Auchencorth Moss.

Considering the differences in latitude, climate, hydrology and vegetation, these sites (with the exception of Stordalen and Lompolojänkä) are remarkably similar in terms of their daily mean NEE_{GS}.

NEE represents only one flux pathway within the full net ecosystem C budget (NECB). When terrestrial CH_4 emissions (2007-2008; Dinsmore et al., 2010), downstream aquatic flux losses and water surface evasion (2007-2011; Dinsmore et al., 2013) are accounted for, the total long-term sink strength of Auchencorth Moss is reduced to approximately 28 g C m^{-2} yr^{-1} (whilst recognising uncertainty as the fluxes are not measured over the same time period). Using literature values of CH_4 (Roulet et al., 2007) and aquatic C losses for Mer Bleue (Billett & Moore, 2008) results in an approximate total C sink strength of -17 g C m^{-2} yr^{-1}; for Degerö Stormyr the total C sink strength is 24 g C m^{-2} yr^{-1} (Nilsson et al., 2008), 30 g C m^{-2} yr^{-1} for Glencar (Koehler et al., 2011) and 34 g C m^{-2} yr^{-1} for Stordalen (Christensen et al., 2012, Lundin et al., 2013, Olefeldt et al., 2013); data for Lompolojänkä could not be found. Hence when all flux pathways are accounted for the C balances of the different peatlands appear to converge. Whilst further work is required to understand the processes and time-scales involved, the results suggest a potential internal feedback mechanism between different flux pathways.

5 Summary

Eleven years of continuous monitoring of net ecosystem exchange of carbon dioxide at a temperate Scottish peatland revealed highly variable inter-annual dynamics despite little or no change in land management. Variation in climate and especially winter time air temperature is thought to be the dominant control at the study site. The latter explained 87% of inter-annual changes in NEE and a modest rise of 1 °C above average winter air temperature for the 2002-2013 study period was accompanied by a 20% increase in CO_2 uptake. Colder winters appear to have an adverse effect on the peatland’s CO_2 sink strength possibly due to disturbances to the phenological cycle of the graminoid species at the site. Dry spells have been linked to enhanced ecosystem respiration and depressed GPP and it is thought that a) heterotrophic respiration can become the dominant term as water availability decreases, and b) mosses are more sensitive to WTD than other species at the site. Cold winters and dry summers both have negative effects on the CO_2 sink strength of the bog; these two factors converged in 2013 and led to a dramatic reduction in net CO_2 uptake (-90% compared to the 11-year mean). Auchencorth Moss, although always a sink of CO_2 during the study period, is highly sensitive to even modest changes in hydro-meteorological conditions at relatively short timescales. The large inter-annual variability of NEE observed to date makes future trends difficult to predict and quantify. Changes in seasonal hydro-meteorological conditions, especially changes in precipitation patterns and intensity, could however be pivotal for the CO_2 cycling of this peatland. Drier summers could lead to a reduction in net CO_2 uptake but this could be offset by milder temperatures, particularly in winter time, and longer growing seasons. Mean annual temperatures at the study site have risen by 0.019 °C yr^{-1} since 1961, which could, in theory, benefit C uptake by the peatland in the long-term since NEE was found to be closely linked to the length of the growing season.

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Table 1: Spearman's rank correlation coefficients (ρ) and associated p-values for all statistically significant inter-annual correlations between ecosystem response and hydro-meteorological parameters observed at Auchencorth Moss during the study period 2003-2013. The suffix SS denotes spring/summer means and LGS is the length of the growing season. GPP_{sat} and α are GPP at light saturation and quantum efficiency, respectively, obtained by non-linear regression between GPP and PAR using eq. (4).

Ecosystem response	Parameter	ρ	p-value
NEE_{SS}	Winter T_{air}	-0.96	$<< 0.01$
NEE (annual)	LGS	-0.80	< 0.01
GPP_{SS}	Winter T_{air}	0.73	< 0.01
R_{ecoSS}	Winter T_{air}	0.61	0.02
GPP_{sat}	Winter T_{air}	0.68	0.02
α	Winter T_{air}	0.68	0.02
GPP_{sat} (annual)	WT (annual)	-0.63	< 0.05

Table 2: Water table drainage rates and maximum water table depths (WTD) observed during the summer dry spells of 2008, 2010 and 2013. The time lag is the number of days elapsed between the start of the dry period and the onset of a response from the ecosystem respiration (R_{eco}); the time lag was determined by optimising the polynomial fit between R_{eco} and WTD. The minimum value of R_{eco} for each dry spell and the water table depth corresponding to each minimum value of R_{eco} were calculated using a second degree polynomial regression functions between R_{eco} and WTD. No parabolic relationship was observed in 2013 between R_{eco} and WTD; for this reason, time lag, minimum R_{eco} and WTD for minimum R_{eco} could not be calculated.

Period	Drainage rate [cm day^{-1}]	Maximum WTD [cm]	Time lag [days]	Minimum R_{eco} [μmol m^{-2} s^{-1}]	WTD for minimum R_{eco} [cm]	Mean T_{air} [°C]	Wind direction [°]
05-29/05/2008	1.2	20.4	2	0.03	1.5	10.1	70
22/07-01/08/2008	3.0	19.1	3	2.31	4.5	16.1	100
15-26/05/2010	1.6	30.7	2	1.05	15.6	12.9	181
09-24/06/2010	2.0	36.1	0	1.58	12.5	13.0	176
21/07-08/08/2010	2.0	22.1	5	2.01	2.9	11.4	191
26/05-06/09/2013	1.4	48.5	-	-	-	14.5	222

Table 3: results (p-value) of 1-way analysis of variance (ANOVA) on daily GPP, R_{eco} and NEE with respect to 10 water table depth (WTD) classes (< 0 cm to > 45 cm in increments of 5 cm). Missing values denote failure of the equal variance test.

Year	NEE	R_{eco}	GPP
2007	-	0.02	-
2008	0.14	< 0.01	0.02
2009	0.72	0.04	0.80
2010	0.93	< 0.01	< 0.01
2012	-	0.06	0.48
2013	0.03	< 0.01	0.05

Table 4: Annual minimum, maximum and mean values of NEE at several long-term peatland monitoring sites in the Northern hemisphere. LGS and LDS are the length of growing and dormant season respectively, and subscripts GS and DS denote growing and dormant season. The length of the growing season for the study site Auchencorth Moss was bounded by the first and last day for which mean daily air temperatures exceeded 5 °C for 5 consecutive days. For the other sites, LGS was estimated from data available in the respective articles. References: [1]Christensen et al. (2012); [2]Roulet et al. (2007); [3]McVeigh et al. (2014); [4]Aurela et al. (2009); [5]Peichl et al. (2014).

[a] Estimated from Lafleur et al. (2003): growing season from May to September (1998-2002)

[b] Mean growing season lengths 2002-2007 (Sottocornola & Kiely, 2010).

[c] Use of NEE and LGS for the years 2006-2008 only, as winter measurements of NEE during the other years of the study were deemed unreliable by the authors (Christensen et al., 2012).

Site	Auchencorth Moss (this study)	Stordalen[1]	Mer Bleue[2]	Glencar[3]	Lompolojänkkä[4]	Degerö Stormyr[5]
Latitude	55°47’	68°20’	45°23’	51°55’	68°0’	64°11’
Duration [years]	11	8	6	9	3	12
Minimum NEE [g CO_2–C m^{-2}]	-5.2	-20	-2	-32.1	-3.3	-18
Maximum NEE [g CO_2–C m^{-2}]	-135.9	-95	-112	-79.7	-58.9	-105
Mean NEE [g CO_2–C m^{-2}]	-64.1 ± 33.6	-66 ± 29.1	-40.2 ± 40.5	-55.7 ± 30.0	-31.9 ± 27.8	-58.0± 21.0
Mean NEE_{GS} [g CO_2–C m^{-2}]	-142 ± 55.0	-133 ± 28.0	-97.1 ± 38.7	-60 ± 15.0	-160 ± 13.0	-84.8 ± 23.6
Length of growing season (LGS) [days]	247	117	168[a]	153[b]	119	120
NEE_{GS}/LGS [g CO_2–C m^{-2} day^{-1}]	-0.57	-1.14	-0.58	-0.39	-1.34	-0.48
NEE_{DS}/LDS [g CO_2–C m^{-2} day^{-1}]	0.61	0.27	0.29	0.06	0.52	0.11

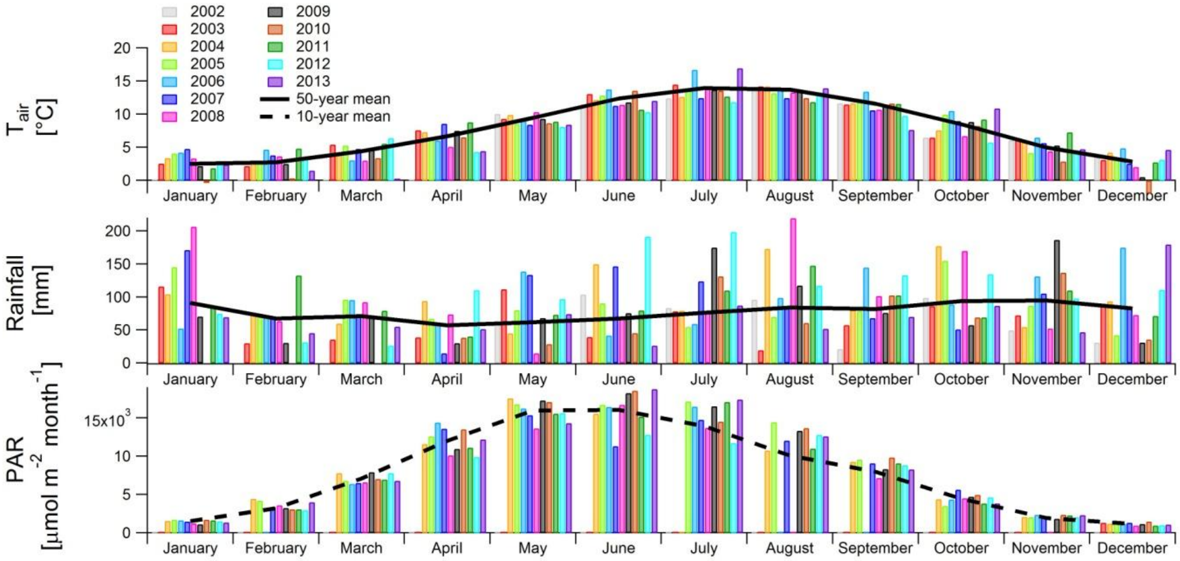

Figure 1: Monthly air temperature, rainfall and photosynthetically active radiation (PAR) for the study period 2002-2013.

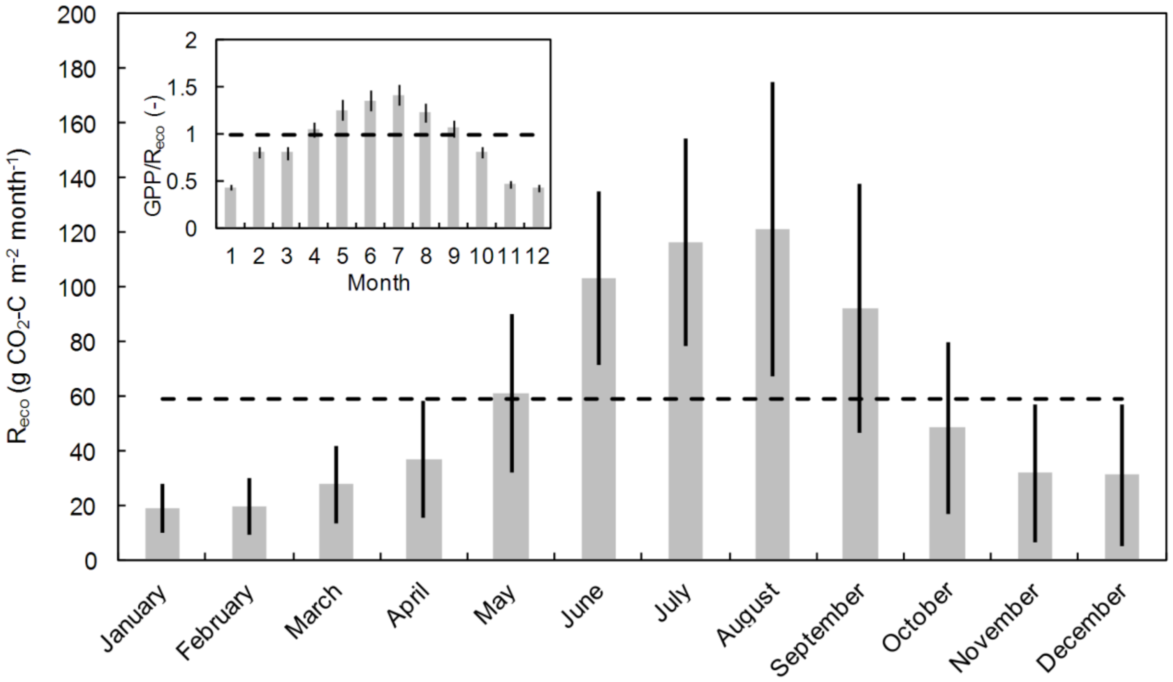

Figure 2: 10-year monthly averages of ecosystem respiration and, inset, ratio of gross primary production (GPP) to ecosystem respiration (horizontal dashed lines are 10-year annual mean, and error bars are the standard deviations).

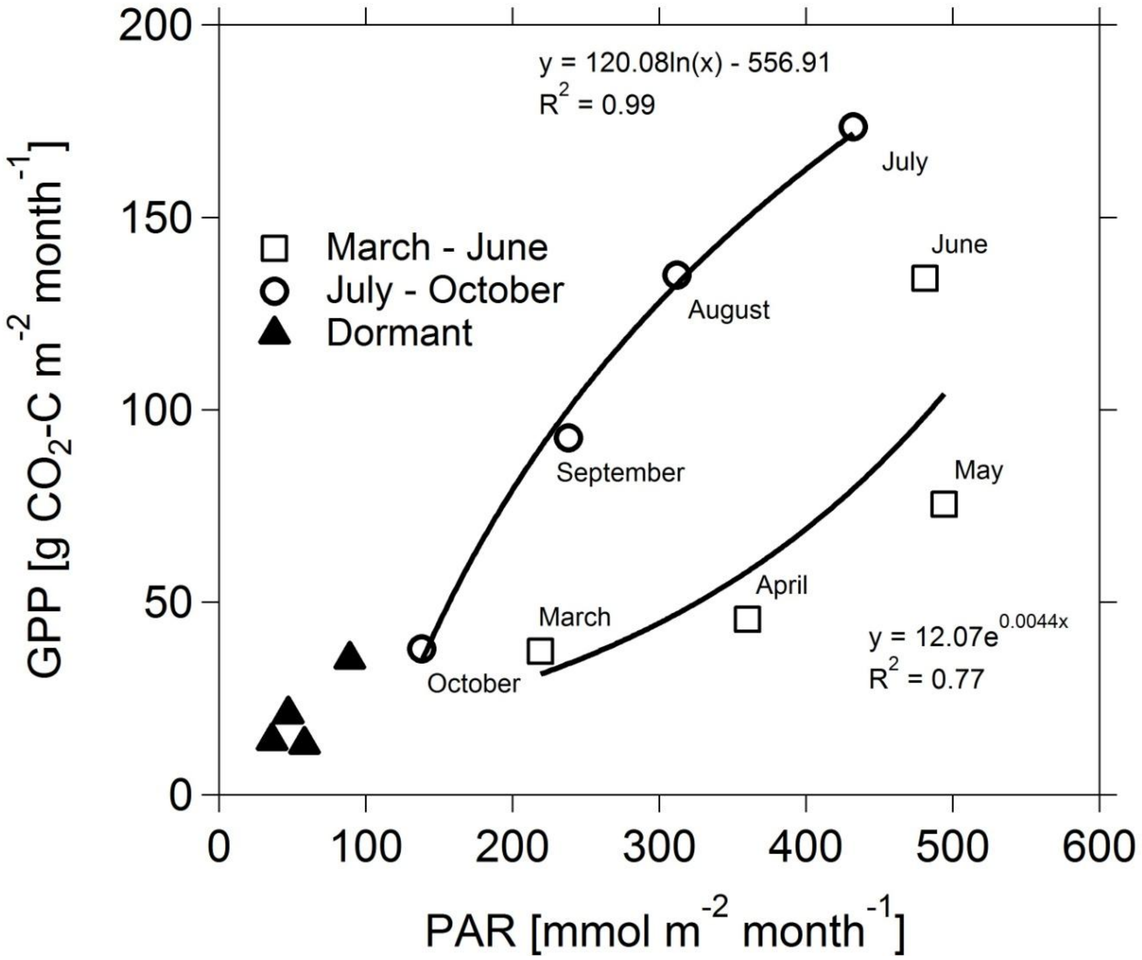

Figure 3: Hysteresis in gross primary production (GPP) as a function of photosynthetically active radiation (PAR) (10-year monthly means).

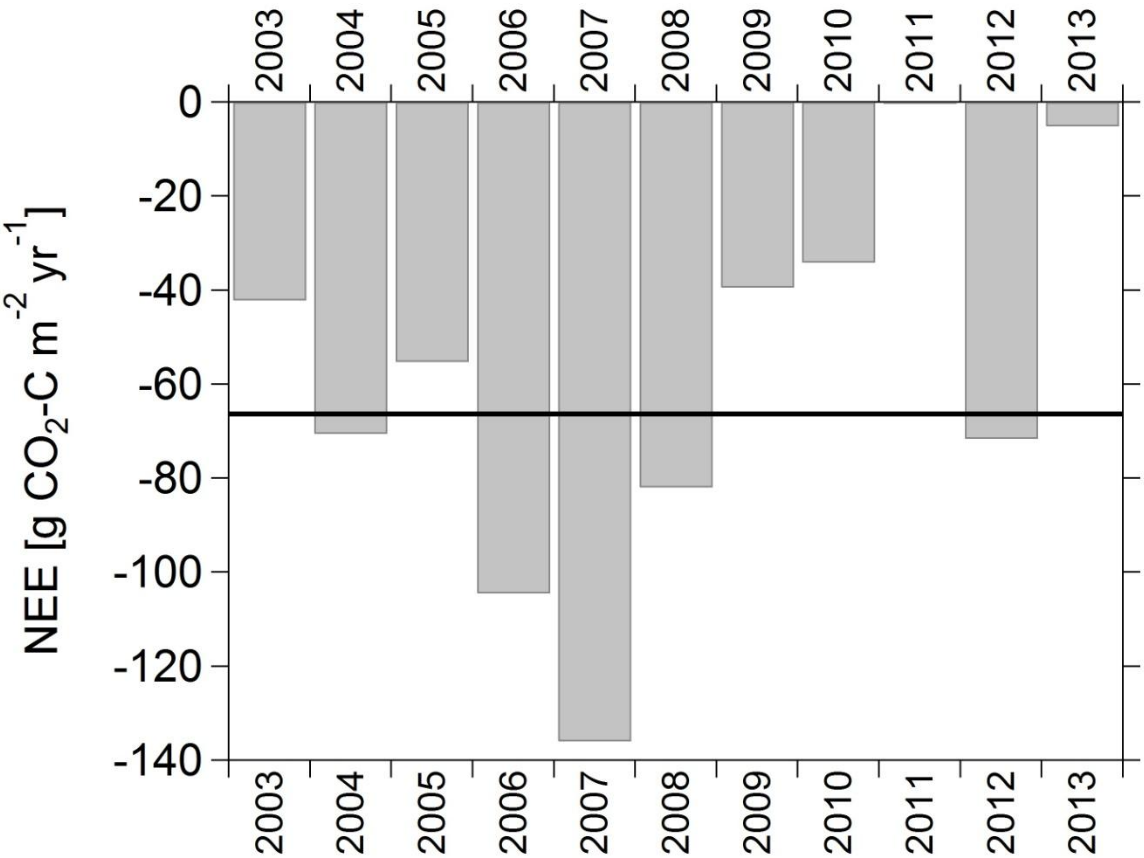

Figure 4: Annual NEE for 2003-2013 (no data for 2011 due to instrument failure during the growing season); the horizontal line is the mean NEE for the study period.

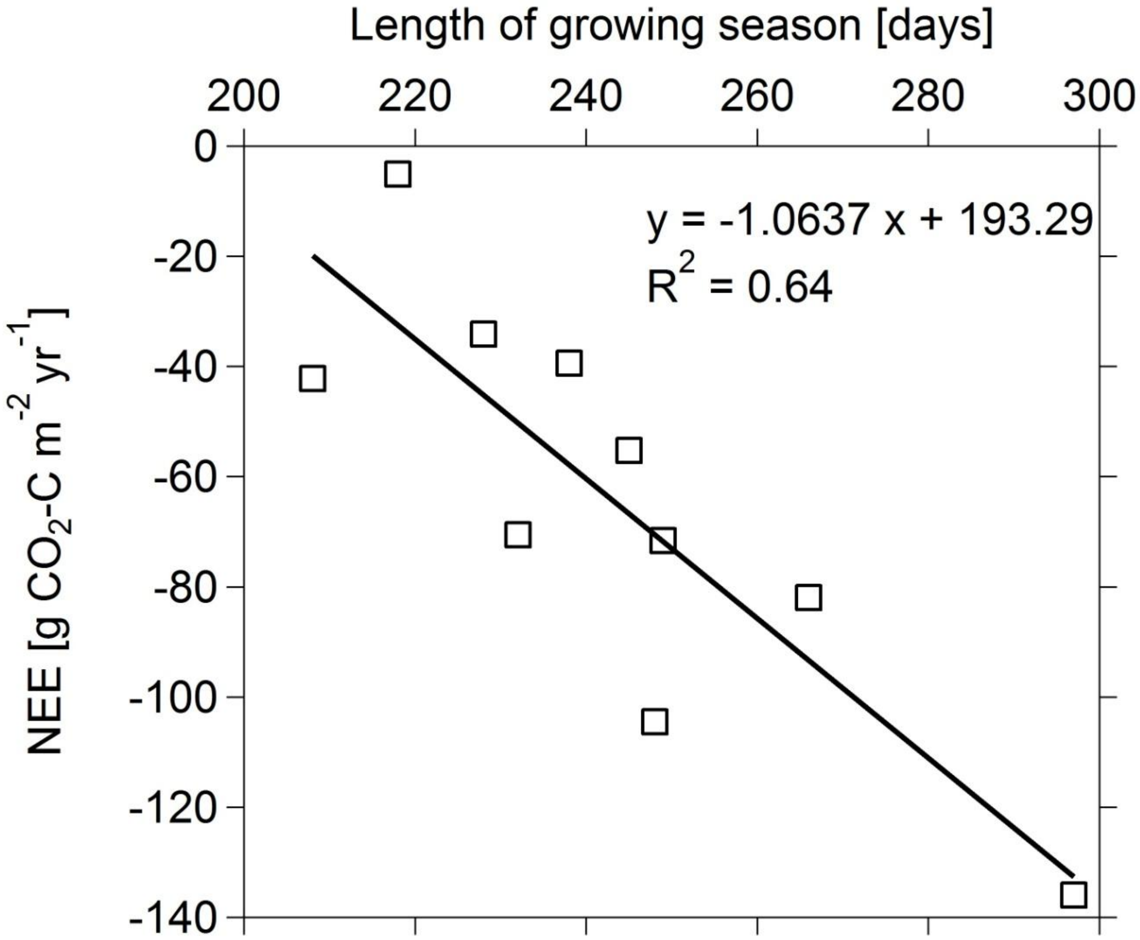

Figure 5: Annual NEE as a function of the length of the growing season.

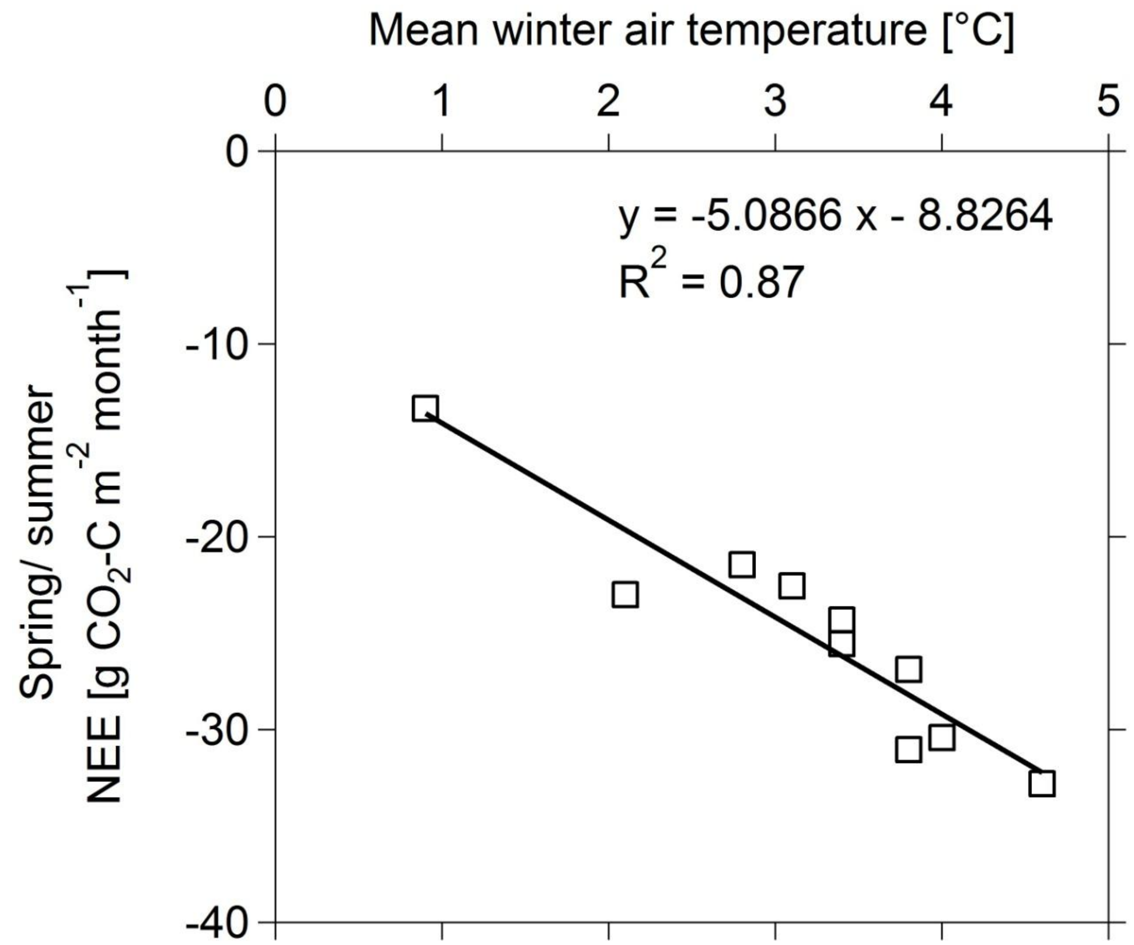

Figure 6: Spring/summer NEE (mean from April to September) as a function of the preceding winter's mean air temperature (mean from December to March).

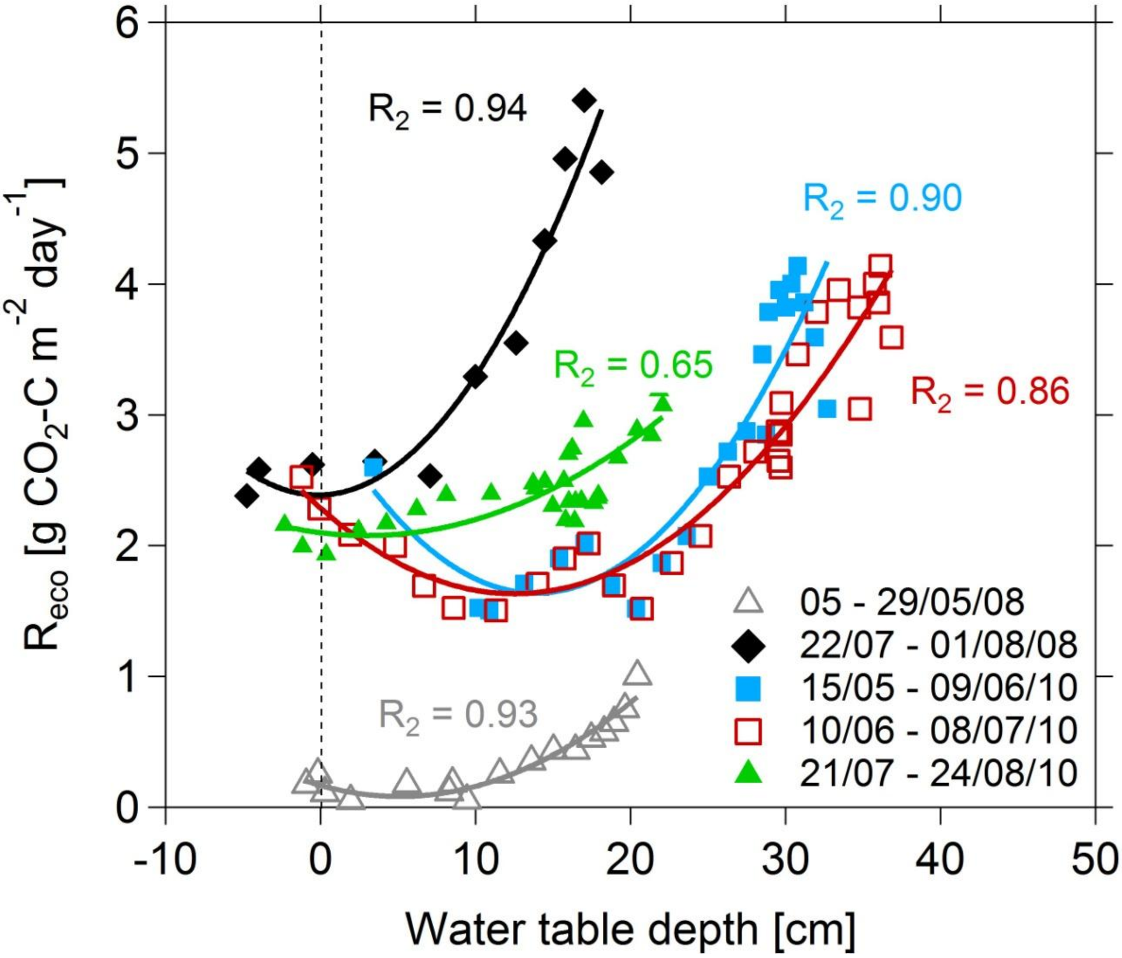

Figure 7: Daily ecosystem respiration as a function of water table depth during five dry spells (two in summer 2008 and three in 2010).

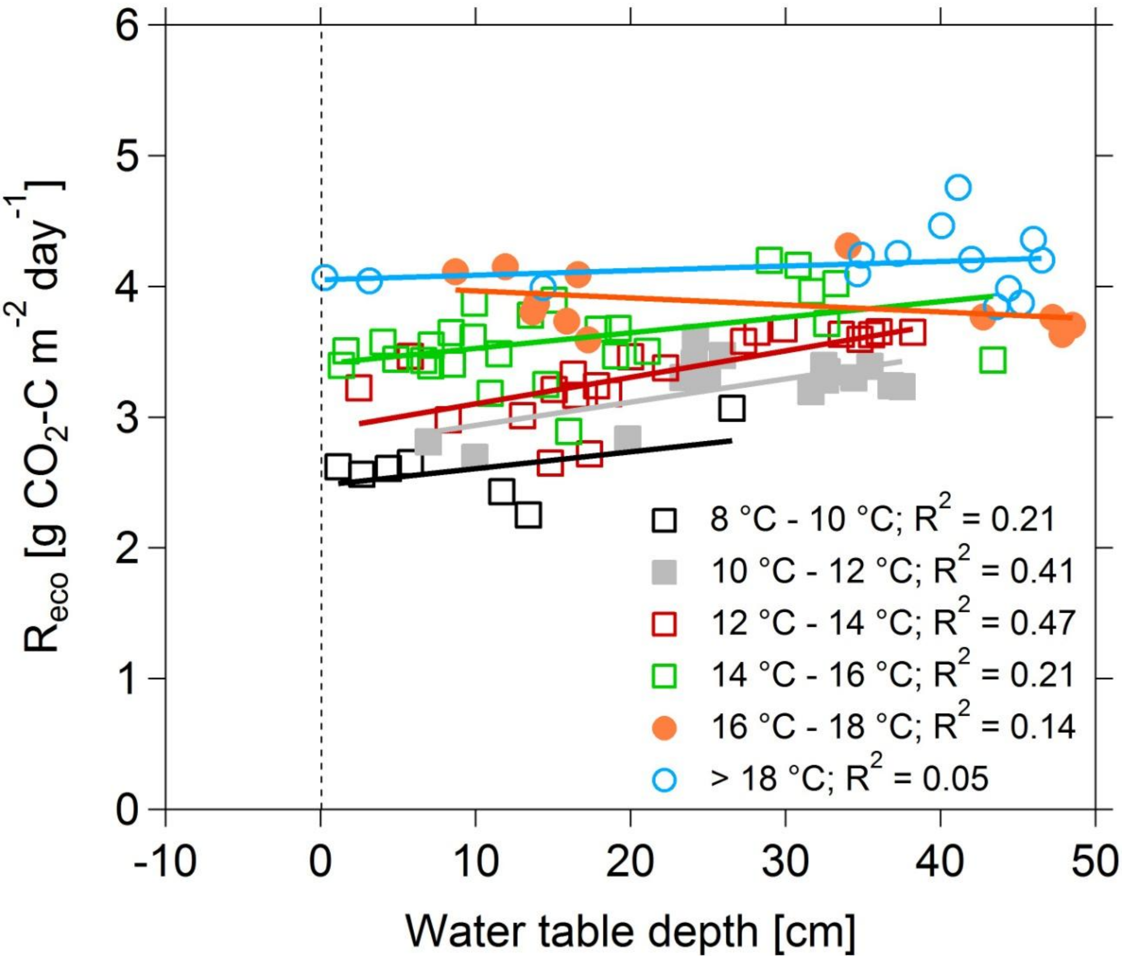

Figure 8: Ecosystem respiration as a function of water table depth and air temperature (daily means for May to September 2013).