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LETTER

Low impact of dry conditions on the CO_2 exchange of a Northern-Norwegian blanket bog

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Abstract

Northern peatlands hold large amounts of organic carbon (C) in their soils and are as such important in a climate change context. Blanket bogs, i.e. nutrient-poor peatlands restricted to maritime climates, may be extra vulnerable to global warming since they require a positive water balance to sustain their moss dominated vegetation and C sink functioning. This study presents a 4.5 year record of land–atmosphere carbon dioxide (CO_2) exchange from the Andøya blanket bog in northern Norway. Compared with other peatlands, the Andøya peatland exhibited low flux rates, related to the low productivity of the dominating moss and lichen communities and the maritime settings that attenuated seasonal temperature variations. It was observed that under periods of high vapour pressure deficit, net ecosystem exchange was reduced, which was mainly caused by a decrease in gross primary production. However, no persistent effects of dry conditions on the CO_2 exchange dynamics were observed, indicating that under present conditions and within the range of observed meteorological conditions the Andøya blanket bog retained its C uptake function. Continued monitoring of these ecosystem types is essential in order to detect possible effects of a changing climate.

1. Introduction

Northern peatlands are important ecosystem types in a climate change context, as they hold large amounts of organic carbon (C) in their soils, amounting to about half of the current atmospheric C pool (Gorham 1991). Peatlands are wetlands that during the last millennia have converted atmospheric carbon dioxide (CO_2) into soil organic material, i.e. peat, because of reduced decomposition rates due to anoxic soil conditions. Changes in temperature and soil wetness can modify the C sink functioning of peatlands, with potential feedback effects on the climate system (Ise *et al* 2008, Dorrepaal *et al* 2009).

For peatlands as well as for most other ecosystem types, net ecosystem exchange (NEE) of CO_2 is the main component of the C budget. However, due to prevalent wet conditions, CH_4 emissions and C loss through runoff can also be of importance for the peatland C budget (Roulet *et al* 2007, Nilsson *et al* 2008, Koehler *et al* 2011). Hydrological conditions exert a strong control on peatland NEE (Limpens *et al* 2008, Lafleur 2009, Lund *et al* 2012). Drier soils can lead to increased soil respiration as well as decreased plant photosynthesis (Lafleur 2009). Dependent on timing, severity and duration of a drought, the effects on NEE, gross primary production (GPP) and ecosystem respiration (R_{eco}) may differ (Lafleur 2009, Lund *et al* 2012). In addition, hydrological settings, primarily whether the peatland is connected to the groundwater system (fen) or not (bog), as well as

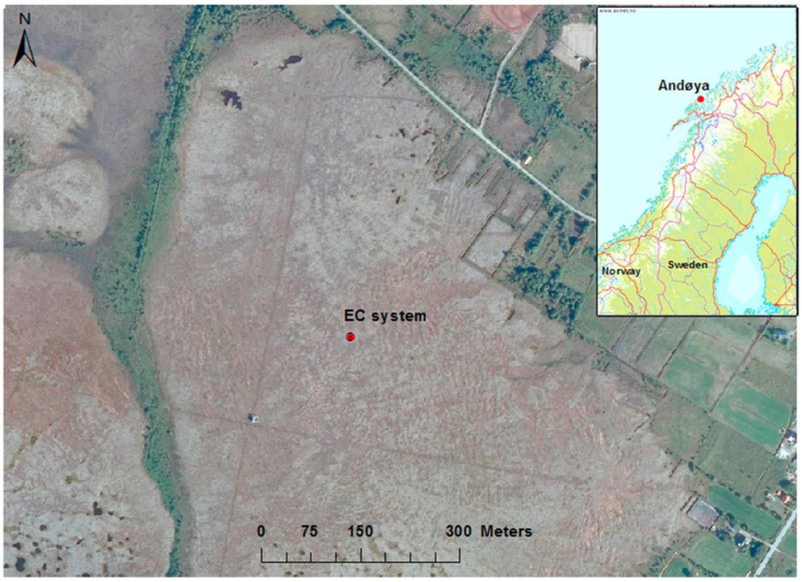

Figure 1. Google Earth imagery (Image © 2015 DigitalGlobe) of the Saura peatlands, Andøya, Norway. Inset map (© Kartverket) shows the location of the island Andøya in northern Norway.

vegetation composition, regulate peatland response to drought periods (Sulman *et al* 2010, Lund *et al* 2012).

Blanket bog is a distinctive peatland type restricted to maritime climates, where a positive water balance allows ombrotrophic vegetation to develop over extensive areas (Charman 2002). Palaeoecological records indicate that climatic variability, affecting soil wetness, has regulated the development of blanket bogs (Ellis and Tallis 2000). A recent modelling study showed that blanket bogs are endangered by climate change, because of marked shrinkage of their present bioclimatic space as a consequence of global warming, which may lead to peat erosion and vegetation change (Gallego-Sala and Prentice 2012).

Few studies exist on the contemporary C exchange in unmanaged blanket bogs, with the exception of a temperate Atlantic blanket bog in Ireland (Glencar) from which a host of work has been published on CO_2 fluxes (e.g. Sottocornola and Kiely 2005, Sottocornola and Kiely 2010, McVeigh *et al* 2014) as well as the exchange of CH_4 and DOC (Koehler *et al* 2011). In addition, Beverland *et al* (1996) studied the exchange of CO_2 and CH_4 in a blanket bog area in Scotland. To our knowledge, there has been no extensive study on land-atmosphere C exchange from more northerly situated blanket bogs.

In this study, we present 4.5 years of eddy covariance (EC) measurements of the land–atmosphere exchange of CO_2 in the Saura blanket bog area on the island of Andøya in northern Norway. The purpose of the study was to describe the multi-year CO_2 exchange in the bog, and to investigate impacts of dry conditions (i.e. low soil water content (SWC) and high vapour pressure deficit (VPD)) on NEE, GPP and R_{eco}.

2. Methods and materials

2.1. Site description

The site is located in the middle boreal vegetation zone (Moen 1999) at the Saura peatlands on the island of Andøya, Nordland County, northern Norway (69°08' N, 16°01' E, 17 m.a.s.l.; figure 1). Despite the high latitude, the site does not have permafrost due to the maritime influence of the nearby Atlantic Ocean. Long-term (1961–1990) mean annual air temperature is 3.6 °C, with February being the coldest month (−2.2 °C) and July and August the warmest (both 11.0 °C). Long-term mean precipitation is 1060 mm per year (data from station 87 110 operated by Norwegian Meteorological Institute, located approximately 17 km north of the Saura site).

The peatlands on northern Andøya are dominated by ombrotrophic bogs and poor fens (Buys 1992). The un-eroded concentric raised bogs of Andøya are the most northern within Europe (Vorren *et al* 2007), many assessed to be of national and international conservation value. Intermediate fens are scattered in areas influenced by former sea shore shell deposits. The Saura blanket bog is dominated by hummocks with a relatively dry surface. Peat depth is expected to be approximately 2–3 m, similar to the raised bog Sellevollmyra (Vorren *et al* 2007) located ca. 7 km southwest of Saura, underlain by late glacial and Holocene raised beaches. Hollows are present between the hummocks. Vegetation and microtopography surrounding the EC system was investigated in August 2009. Plots ($1\ m^2$) were established in a cross centered close to the EC system, and sites were selected at a distance of 50, 100 and 200 m from the centre. At each site two plots were established, one at a hummock and one in a

Table 1. Annual CO_2 flux data coverage (%) before and after post-processing steps. See descriptions in section 2.3 Data processing.

Year	Raw data	Out of range	RH	$(H_2O)_{mod}$	QC_{LE}	$u_* < 0.1$	QC_{CO2}
2008[a]	44	38	36	30	29	24	23
2009	77	63	59	47	45	37	35
2010	85	69	63	53	51	43	40
2011	94	80	73	62	59	51	48
2012	88	74	73[b]	69[b]	66	54	50

[a] First day of available data 27 June 2008.

[b] Post-processing steps RH and $(H_2O)_{mod}$ only possible until 23 July 2012 due to breakdown of T_a/RH sensor.

hollow. We recorded both the field (vascular plants) and bottom layer (mosses and lichens) at each plot.

2.2. Instrumentation

The EC system, consisting of a LI-7500 open-path gas analyzer (Li-Cor, USA) and a CSAT3 3D sonic anemometer (Campbell Sci., UK), was installed at a height of 2 m during the summer of 2008. Data from both sensors was collected at a frequency of 10 Hz on a CR3000 data logger (Campbell Sci., UK). Supporting half-hourly ancillary data includes air temperature (T_a) and relative humidity (RH; HMP45C, Vaisala, Finland), photosynthetic photon flux density (PPFD; LI-190, Li-Cor, USA), net radiation (R_n; Q*7, REBS, USA), soil temperature (T_s; TCAV-L, Campbell Sci., UK) and SWC (CS616, Campbell Sci., UK). The SWC probes were not calibrated to the local soil characteristics, but were considered to provide a good measure of relative differences.

2.3. Data processing

Raw data files were processed with the EdiRe software package (Robert Clement, University of Edinburgh) producing half-hourly fluxes and averages. Fluxes were calculated based on standard flux community methodology (see Aubinet *et al* 2000), including despiking (Højstrup 1993), 2D coordinate rotation, time lag removal by covariance optimization, block averaging, frequency response correction using model spectra and transfer functions (Moore 1986) and WPL correction (Webb *et al* 1980). It has recently been suggested that measurements using an open-path gas analyzer need an additional term in the WPL correction, to account for the local heat flux created by the instrument itself during cold conditions (Burba *et al* 2008). In this study, we have applied method 4 in Burba *et al* (2008) to correct measurements obtained during cold periods, here defined as days with mean $T_a < 5$ °C. Effects of the self-heating correction are taken into account in the uncertainty assessment (see below).

Data post processing in Matlab R2012a (The Mathworks, USA) included quality control, storage term calculation and gap-filling. When applicable for a given test, the growing season was defined as the period from the first three consecutive days with daily mean $T_a > 5$ °C until the first three consecutive days with daily mean $T_a < 5$ °C. Half-hourly flux values were excluded when (a) wind components and scalar concentrations were beyond preset ranges, (b) RH > 98%, (c) the difference between measured H_2O concentration and modelled H_2O concentration (based on T_a and RH) deviated by more than 1 mmol mol^{-1} from a two-week running median of the difference, (d) growing season fluxes of latent (LE) and sensible heath (H) were more than 3 standard deviations (SD) off from half-monthly quadratic fits with R_n, (e) friction velocity $u_* < 0.1$ m s^{-1} and (f) daytime growing season fluxes of CO_2 were more than 2 SD off from half-monthly light response curve fits (equation (1)) and nighttime and cold season fluxes were more than 2 μmol m^{-2} s^{-1} off from a two-week running median (table 1).

Gap-filling was performed using a look-up table methodology based on Reichstein *et al* (2005) with slight modifications: a missing value was replaced with the mean of at least four values obtained during similar meteorological conditions (PPFD ±20 μmol m^{-2} s^{-1}, T_a ±2.5 °C, VPD ±0.5 kPa) within periods of ±5 days or ±10 days. Long gaps (>7 days) during non-growing season (15 December 2008–16 February 2009, 12 March–15 April 2010) were filled with the median flux of the week before and after the gap. Long gaps during the growing season (4 June–2 July 2009, 26 June–3 July 2012) were filled with a light response curve approach (*Misterlich* function (Falge *et al* 2001)), parameterized on data one week before and after the gap with PPFD as independent variable:

$$\mathrm{NEE} = -\left(F_{\mathrm{csat}} + R_d\right)\left(1 - \mathrm{e}^{\frac{-\alpha\,(\mathrm{PPFD})}{F_{\mathrm{csat}}+R_d}}\right) + R_d, \quad (1)$$

where F_{csat} is CO_2 uptake rate at light saturation, R_d is dark respiration, and α is the initial slope of the light response curve. The light response curve (equation (1)) was parameterized for daytime periods using an eight day moving window (time step one day). The parameterization was only considered successful when based on more than 50 observations (half-hours) and when all parameters (F_{csat}, R_d, α) were significantly different from zero ($p < 0.05$).

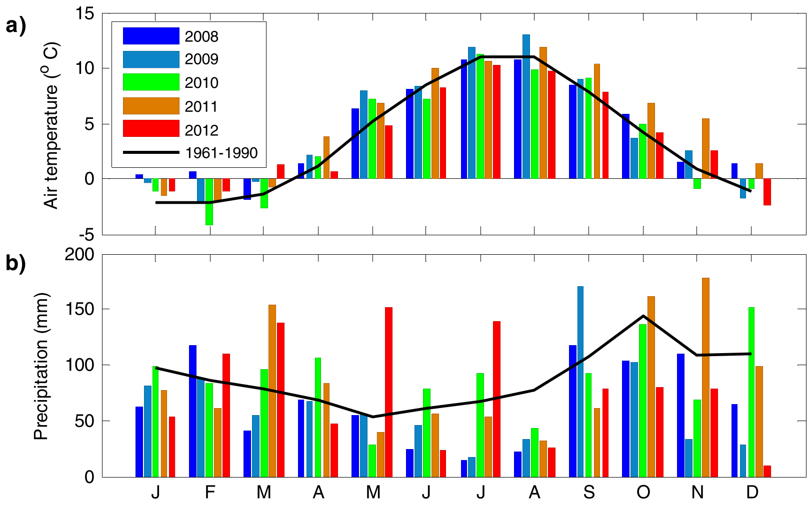

Figure 2. Monthly means (2008–2012) and long-term means (1961–1990) of air temperature (a) and precipitation (b) from station 87 110 operated by Norwegian Meteorological Institute. This station is situated approximately 17 km north of the Andøya EC site.

Growing season GPP was modelled by using equation (1) and subtracting R_d (Lindroth *et al* 2007). Daytime R_{eco} was calculated as the difference between gap-filled NEE and modelled GPP, while nighttime R_{eco} corresponded to gap-filled NEE.

The estimated uncertainty in annual NEE sums was based on Elbers *et al* (2011). Random error (E_{rand}) and frequency response correction uncertainty (E_{freq}) were assessed according to Aurela *et al* (2002) and u_* threshold selection uncertainty (E_{ustar}) according to Elbers *et al* (2011). Gap-filling uncertainty (E_{gap}) was assessed by varying the length of the period during which similar meteorological conditions was sought (3–6 days and 7–14 days). E_{gap} was calculated from the SD of the three NEE sums (gap-filling periods 3/6, 5/10 and 7/14 days, respectively). In addition, we assessed the self-heating correction (Burba *et al* 2008) uncertainty by using a deviation of ±5 °C around the default definition for cold periods (thus days with mean $T_{\mathrm{a}} < 0$, 5 and 10 °C, respectively), for which the self-heating correction was applied. The uncertainty, E_{burba}, was determined as the SD of the NEE sums in these three periods.

The flux footprint of the EC system was estimated using the parameterization by Kljun *et al* (2004), to assess whether other landscape elements surrounding the peatland would have any influence on the measured flux. The streamwise dimension of the footprint x_R, was calculated as

$$x_R = (2.4c - d)\, z_m \left(\frac{\sigma_w}{u_*}\right)^{-0.8} \tag{2}$$

where z_m is measurement height (2 m), σ_w is the SD of vertical wind speed and u_* is friction velocity. Parameters c and d were calculated from equations (15) and (16) in Kljun *et al* (2004), where roughness length (z_0) is used as parameter. Roughness length was calculated as

$$z_0 = \frac{z_m - d_h}{\left(\dfrac{\exp\,(0.4U)}{u_\star}\right)}, \tag{3}$$

where d_h is displacement height (2/3 of the mean height of obstacles, 0.1 m) and U is horizontal wind speed.

3. Results

3.1. Environmental characteristics

Based on the inventory of vegetation and microtopography performed in August 2009 at the Andøya peatland, the ratio of hummock to hollows surrounding the EC system was estimated to be approximately 70:30, with an estimated mean height difference of 0.15 m. Hummocks were characterized by dwarf shrubs (*Empetrum nigrum*, *Vaccinium uliginosum*, *Calluna vulgaris*, *Rubus chamaemorus*) with a mean height of less than 0.05 m, mosses (*Dicranum scoparium*, *Hylocomium splendens*, *Pleurozium schreberi*, *Racomitrium lanugionsum*, *Sphagnum* spp.) and lichens (*Cladonia* spp.). In hollows, *Sphagnum* mosses (*S. fuscum*, *S. warnstorfii*, *S. magellanicum*, *S. cuspidatum*) and sedges (*Carex rariflora*) dominated. The cover of cryptogams (lichens and bryophytes/mosses) was almost twice as high as the cover of vascular plants (76% versus 44%), where lichens covered on average 41% of the hummocks.

Mean annual T_{a} during the study period (2008–2012) was above long-term average (1961–1990: 3.6 °C) for all years except for 2010, which had a mean annual T_{a} of 3.5 °C (figure 2(a)). The extra warming during the study period was not equally distributed throughout the year. The winter months (December–February) were on average 2.2 °C warmer compared with the long-term average (−1.8 °C), while there was no significant difference

Table 2. Growing season periods start (GS_{start}), ending (GS_{end}) and length (GS_{length}) 2008–2012. GS_{start} was defined as first of three consecutive days with daily average $T_a > 5$ °C; GS_{end} was defined as first of three consecutive days with daily average $T_a < 5$ °C.

Year	GS_{start}	GS_{end}	GS_{length}
2008	—	302	—
2009	120	270	150
2010	131	283	152
2011	131	284	153
2012	135	290	155

($p > 0.05$) for the summer months. Growing season onset occurred on average (±1 SD) at DOY 129 ± 6 (table 2), whereas the growing season ended on average at DOY 286 ± 12. Precipitation sum was below average (1060 mm) in all years, except for 2010 (1075 mm). The seasonal patterns in precipitation during the study period did not show as pronounced differences compared with long-term mean as was the case for T_a. However, the spring period (March–May) was on average wetter than the long-term mean, whereas other seasons were generally drier (figure 2(b)).

Daily values of T_s and SWC at the Andøya peatland (figure 3) largely reflected meteorological data. The top-soil (upper 5 cm) thawed the earliest in 2011 (mid-April) while in 2010, it thawed in early May. In general, during spring and early summer, highest T_s was recorded in 2011 and lowest in 2010. This pattern was especially pronounced in June (DOY 152-181). The soil was water saturated for most of the time in 2010 and 2012. In contrast, 2008 and 2009 were characterized by a relatively steady decrease in SWC during the growing season with values stabilizing around 0.3 $m^3 m^{-3}$ during late summer. 2011 was more variable in terms of soil moisture; with decreasing SWC during early summer similar to 2008 and 2009 but with rapid increases around 25 July and 27–30 August due to heavy rainfall.

3.2. CO_2 fluxes

The mean 90% footprint length during the entire measurement period was 89.5 ± 12.1 m (figure 4). Since the blanket bog extends >200 m in all directions surrounding the EC system (figure 1), the whole data set is considered reliable in terms of flux footprint. It should be noted that for the non-growing season south-westerly winds dominate, while north-easterly winds dominate during the growing season.

The temporal variation in the period 2008–2012 of mean daily NEE, GPP and R_{eco} at the Andøya peatland is shown in figure 5. Mean July daily NEE means across all years was −1.40 ± 0.19 $\mu mol\ m^{-2} s^{-1}$, with highest uptake in 2009 (−1.65 $\mu mol\ m^{-2} s^{-1}$) and lowest in 2010 (−1.16 $\mu mol\ m^{-2} s^{-1}$). Mean July GPP and R_{eco} were −2.55 and 1.17 $\mu mol\ m^{-2} s^{-1}$, respectively. Mean July fluxes in the Andøya bog are compared with other wetland sites in table 3. Average wintertime flux (December–February) during the whole study period was 0.32 ± 0.10 $\mu mol\ m^{-2} s^{-1}$.

The mixed peatland Stordalen in northern Sweden (Christensen *et al* 2012) and the fen Kaamanen in northern Finland (Aurela *et al* 2004) are situated at similar latitudes as the Andøya peatland. These three sites are located along a gradient ranging from maritime (Andøya) towards more continental (Kaamanen) climates. Therefore, we have paid particular attention to a comparison among these sites, as well as the extensively studied temperate Atlantic blanket bog Glencar (see McVeigh *et al* 2014) located in Ireland, due to its presumed functional similarity to Andøya. Parameters of the light response curve (equation (1)) derived from each site are shown in figure 6. In general, all parameters are lower for the two blanket bogs, except for the latter part of the season. Also, the increase in early growing season and the decrease in late growing season for F_{csat} and R_d for both blanket bogs occur at a lower rate compared with Stordalen and Kaamanen.

The mean annual CO_2 budget of the Andøya blanket bog across all complete measurement years (2009–2012) amounted to −19.5 ± 18.3 $g\ C\ m^{-2}$ (table 4). However, these estimates should be interpreted with caution as the total uncertainty was estimated to be on average 75.1 ± 4.9 $g\ C\ m^{-2}$. Of the separate components in the uncertainty analysis, the uncertainty relating to the choice of temperature threshold for applying the self-heating correction (Burba *et al* 2008) was overriding all other components (table 4). For the period May–September, the CO_2 budget was −111.8 ± 10.3 $g\ C\ m^{-2}$, with an associated uncertainty of 51.9 ± 5.5 $g\ C\ m^{-2}$ (table 4).

Reduced SWC in the top-soil during summertime, as in 2008 and 2009 (figure 3), did not have an apparent effect on NEE, GPP and R_{eco}. Instead, the wettest year, 2010, had the lowest summertime values of net CO_2 uptake (thus lowest NEE), GPP and R_{eco} (figure 5). This year was characterized by low T_s (figure 3) and low PPFD during June–July (table 5), which may have slowed down vegetation growth. Light response curves based on data from July each year indicate that 2008 and 2010 had the lowest CO_2 uptake rates at PPFD > 1000 $\mu mol\ m^{-2} s^{-1}$ (figure 7).

To further investigate the role of dry conditions, measured July fluxes of NEE at light saturation (PPFD > 1000 $\mu mol\ m^{-2} s^{-1}$) were arranged into VPD bins (table 6). Significant differences ($p < 0.05$) in NEE across bins were observed in all years except for 2012. In 2012, there were not enough observations in the 0.4–0.5 kPa VPD bin to calculate statistics, thus indicating a less dry summer from a meteorological perspective. In general, the net CO_2 uptake was lower (i.e. less negative NEE) at high VPD than at low VPD. This was especially true for 2009 and 2011; years that were characterized by below average precipitation through

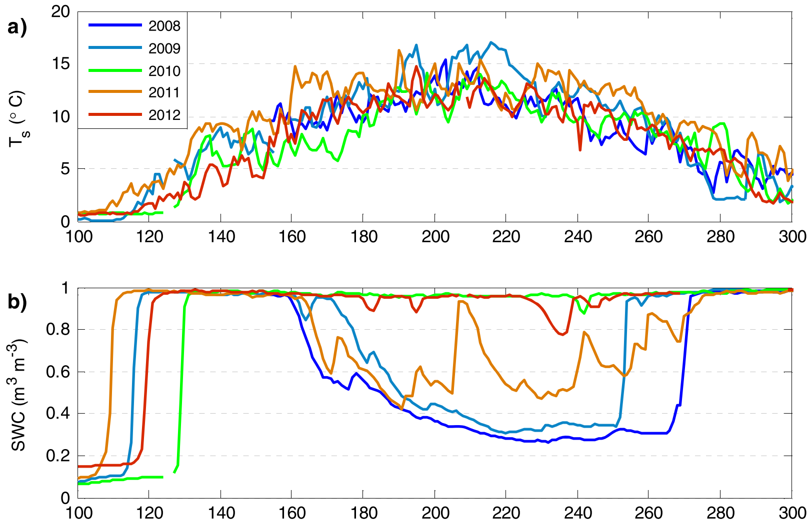

Figure 3. Daily means of soil temperature at 5 cm depth (a) and soil water content (b) 2008–2012 from the Andøya peatland.

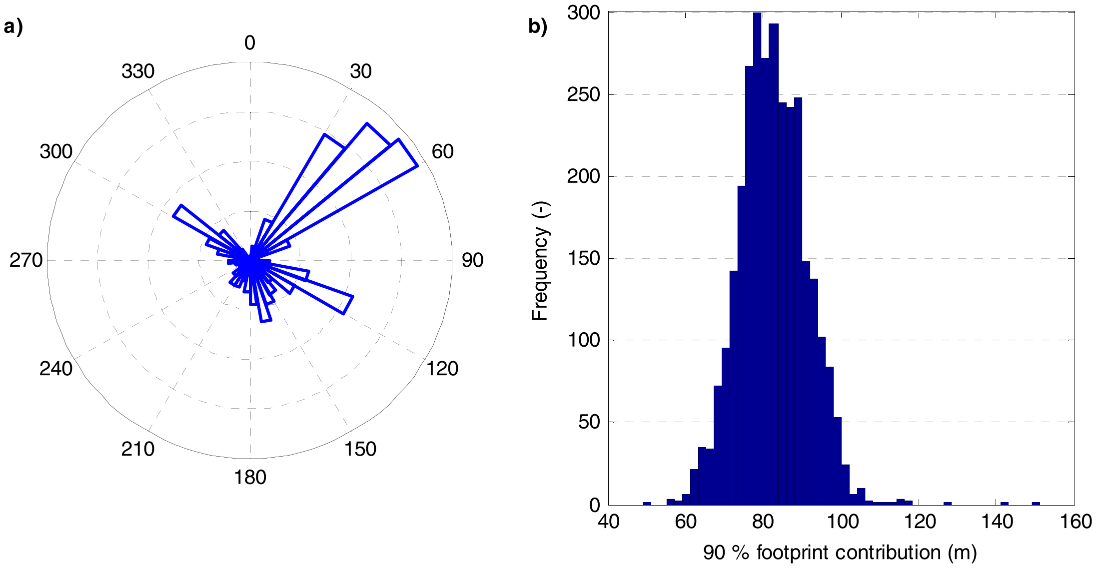

Figure 4. Wind rose (a) and histogram of streamwise dimension of the 90% footprint (b) during growing season 2011 (12 May–13 October).

June and July and low SWC. Since GPP and, subsequently, R_{eco} were modelled using an eight day moving window (equation (1)), the instantaneous effect of high VPD on those flux components cannot be assessed. Instead, we used a separate approach to model R_{eco} and GPP, hereafter denoted $R_{eco,2}$ and GPP_2: daily means of measured nighttime (PPFD < 20 μmol m^{-2} s^{-1}) NEE were plotted against T_s, and an exponential model was fitted to the data (figure 8). The obtained model for each year was then fed with the mean T_s from each VPD bin, providing estimates of $R_{eco,2}$ ($GPP_2 = NEE°–°R_{eco,2}$; table 6). These estimates indicate that the difference in NEE across VPD bins can primarily be explained by variations in GPP_2, whereas variations in $R_{eco,2}$ have a lower influence.

4. Discussion

The estimated annual CO_2 budget 2009–2012 of the Andøya blanket bog (−19.5 ± 18.3 g C m^{-2}) is higher (i.e. weaker CO_2 sink) than a 3-year mean from the Stordalen subarctic mixed peatland (−90.0 ± 5.6 g C m^{-2}; Christensen *et al* (2012)), a 12-year mean from the Degerö boreal fen (−58.0 ± 21.0 g C m^{-2}; Peichl *et al* (2014)) and a 9-year mean from the Glencar Atlantic (i.e. maritime) blanket bog (−55.7 ± 18.9 g C m^{-2}; McVeigh *et al* (2014)); but similar to a 6-year mean from the Kaamanen subarctic fen (−21.5 ± 19.8 g C m^{-2}; Aurela *et al* (2004)). However, as noted previously, annual budget estimates derived from EC measurements with an open-path sensor should be interpreted with

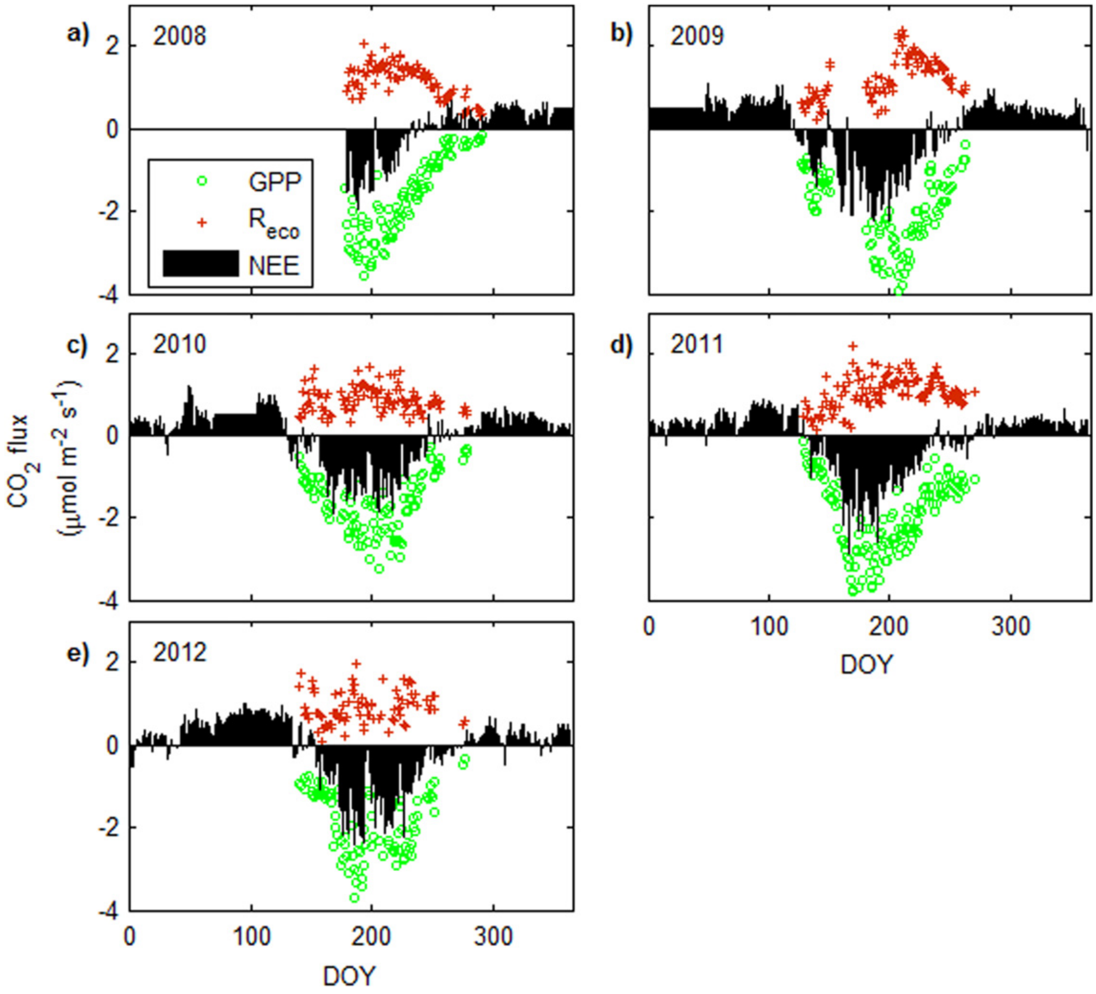

Figure 5. Daily means of measured and gap-filled NEE and modelled GPP and R_{eco} 2008–2012.

caution, due to uncertainties regarding the application of the self-heating correction (Burba *et al* 2008). This correction especially applies to measurements during wintertime in cold areas, and, therefore, several previous studies on northern peatlands using a similar sensor have not applied the self-heating correction to growing season data (see Kwon *et al* 2006, Lafleur and Humphreys 2007, Humphreys and Lafleur 2011, Parmentier *et al* 2011, Christensen *et al* 2012, McVeigh *et al* 2014). As such, our growing season fluxes are directly comparable with those studies. The seasonal (May–September) CO$_2$ sink at Andøya (-111.8 ± 10.3 g C m^{-2}) was slightly stronger compared with Glencar, where the corresponding budgets varied from −75 to −100 g C m^{-2} (McVeigh *et al* 2014), likely due to higher mid-summer radiation and higher plant cover.

In terms of mean fluxes during July, the Andøya blanket bog generally had low fluxes of GPP and R_{eco} compared with other northern wetland ecosystems (table 3). We attribute this to the low density of vascular plants at Andøya and the relatively high cover of mosses and lichens; these plant functional types are less productive than vascular plants. However, flux magnitudes in Glencar are even lower, indicating a lower productivity and respiration values in blanket bogs compared with other peatland types, due to high precipitation and thus high water table levels (Sottocornola and Kiely 2010, McVeigh *et al* 2014). Annual precipitation is high in Glencar (2467 mm; McVeigh *et al* 2014) and Andøya (1060 mm), compared with lower values in Kaamanen (470 mm; Aurela *et al* 2004) and Stordalen (340 mm; Christensen *et al* 2012). Also, the variation between years, i.e. the SD's in table 3, were low in Andøya and Glencar compared with other sites, likely related to less inter-annual variation in weather conditions in maritime sites. However, the sum of the counter-acting components of GPP and R_{eco}, i.e. NEE, is in the middle of the range of NEE values from other sites. Across all sites in table 3, there is no relationship between fluxes and latitude, nor is there any apparent grouping of fluxes between sites with and without permafrost. Previous studies have demonstrated that variables describing vegetation density, such as NDVI and LAI, can significantly explain spatial variation in CO$_2$ fluxes across northern peatland and tundra sites (Lund *et al* 2010, Mbufong *et al* 2014).

Table 3. Mean (±SD in case of more than one year of data) July fluxes of NEE, GPP and R_{eco} (μmol m^{-2} s^{-1}) in various northern wetland ecosystems.

Site	Latitude	Longitude	Ecosystem type	Permafrost	Time period	Gas analyzer	Self-heating correction	NEE	GPP	R_{eco}	Reference
Barrow	71°19′ N	156°36′ W	Wet sedge tundra	Yes	1998–2002	LI-7500	No	−1.00 ± 0.47	−1.58 ± 0.82	0.57 ± 0.39	Kwon *et al* (2006)
Kytalyk	70°49′ N	147°29′ E	Polygonal tundra	Yes	2003–2010	LI-7500	No	−1.52 ± 0.27	−2.85 ± 0.37	1.34 ± 0.44	Parmentier *et al* (2011)
Andøya	69°09′ N	16°01′ E	Blanket bog	No	2008–2012	LI-7500	No	−1.40 ± 0.20	−2.55 ± 0.27	1.17 ± 0.16	This study
Kaamanen	69°08′ N	27°17′ E	Fen	No	2000–2006	LI-6262	—	−1.19 ± 0.59	−3.16 ± 0.74	1.97 ± 0.26	Aurela *et al* (2002)
Stordalen	68°20′ N	19°03′ E	Mixed peatland	Yes	2001–2008	LI-7500	No	−1.95 ± 0.32	n/a	n/a	Christensen *et al* (2012)
Seida	67°03′N	62°56′ E	Mixed tundra	Yes	2008	LI-7500	Yes	−1.77	−5.14	3.38	Marushchak *et al* (2013)
Daring Lake	64°52′ N	111°34′ W	Mixed tundra	Yes	2004–2012	LI-7500	No	−1.00 ± 0.19	−2.99 ± 0.49	2.00 ± 0.42	Lafleur and Humphreys (2007)
Degerö Stormyr	64°11′ N	19°33′ E	Fen	No	2001–2005	LI-6262	—	−1.19 ± 0.17	−3.38 ± 0.68	2.20 ± 0.76	Sagerfors *et al* (2008)
Kobbefjord	64°07′ N	51°21′ W	Fen	No	2010	LI-7000	—	−1.49	−4.01	2.53	Westergaard-Nielsen *et al* (2013)
Glencar	51°55′ N	9°55′ W	Blanket bog	No	2003–2012	LI-7500	No	−0.71 ± 0.22	−1.68 ± 0.23	0.97 ± 0.06	McVeigh *et al* (2014)
Kinoje Lake	51°35′N	81°46′W	Low shrub bog	No	2011–2012	LI-7200	—	−0.64 ± 0.03	−2.41 ± 0.04	1.76 ± 0.01	Humphreys *et al* (2014)

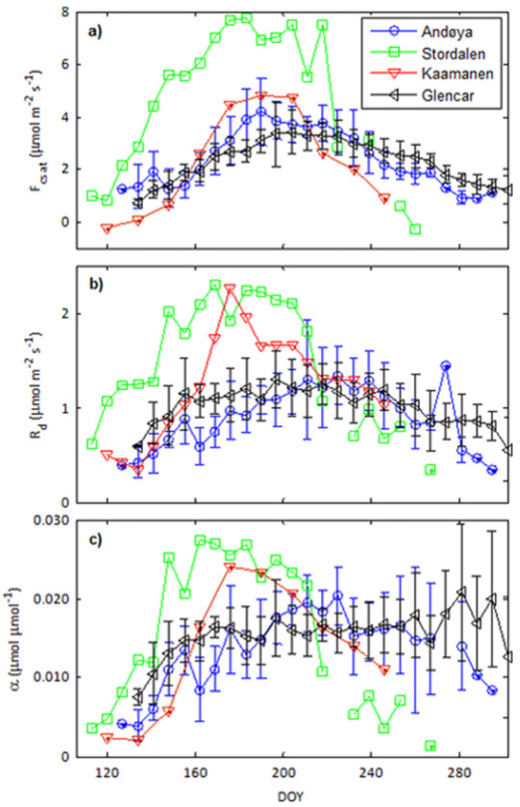

Figure 6. Comparison of light response curve parameters (F_{csat} (a), R_{d} (b), α (c)) between Andøya, Stordalen, Kaamanen and Glencar. Time series from Stordalen and Kaamanen are from Christensen *et al* (2012), while time series from Glencar are based on data from McVeigh *et al* (2014) that has been processed in the same way as for Andøya.

The temporal evolution of the light response curve (equation (1)) parameters (F_{csat}, R_d, α) for the peatlands Andøya, Stordalen, Kaamanen and Glencar (figure 6), illustrates the influence of site specific settings on the CO_2 exchange dynamics. The generally lower parameter values for Andøya can be attributed to the more open and less mesotrophic vegetation type compared with Stordalen and Kaamanen. Also, the slower start and ending of peak activity period, illustrated by the rate of change especially for F_{csat} and R_d, can be related to more maritime conditions on Andøya attenuating seasonal temperature variations. Despite being located in the temperate zone, the onset of peak activity period does not occur earlier in Glencar, which may be explained by lower cryptogam (lichen and bryophyte) cover in Glencar (25%; Sottocornola *et al* 2009) compared with Andøya (76%). Cryptogams may start photosynthesizing as soon as there is sufficient light and mild subfreezing temperatures (Larsen *et al* 2007). Relatively high values of F_{csat} in the late season (DOY 240 an onwards) for Andøya and Glencar can be attributed to on-going photosynthetic activity by evergreen shrubs, mosses and lichens during non-freezing conditions.

Within most years we found that the rate of CO_2 uptake decreased (i.e. NEE less negative) at high VPD (table 6). Most of the decrease could be associated with decreasing GPP. Dry near-surface conditions lead to reduced enzymatic capacity and to stomatal closure in vascular plants (van der Molen *et al* 2011), while

Table 4. Total and separate uncertainties for annual and seasonal (May–September) CO_2 sums in g C m^{-2} (percentage of annual sums in parenthesis).

Annual year	CO_2–C	E_{total}	E_{rand}	E_{freq}	E_{ustar}	E_{gap}	E_{burba}
2009	−7.2	78.6 (1091)	0.42 (5.8)	0.31 (4.3)	4.92 (68.5)	0.20 (2.8)	78.4 (1091)
2010	−0.5	72.7 (14 550)	0.01 (2.2)	0.02 (4.0)	4.19 (816)	1.30 (253)	72.6 (14 135)
2011	−34.5	69.4 (201)	0.66 (1.9)	1.41 (4.1)	1.74 (5.0)	0.30 (0.9)	69.4 (201)
2012	−35.7	79.8 (223)	0.91 (2.6)	1.49 (4.2)	1.88 (5.3)	0.11 (0.3)	79.8 (224)
Seasonal year	**CO_2–C**	**E_{total}**	**E_{rand}**	**E_{freq}**	**E_{ustar}**	**E_{gap}**	**E_{burba}**
2009	−118.0	53.3 (45.2)	1.42 (1.2)	4.38 (3.7)	3.79 (3.2)	0.55 (0.5)	53.0 (44.9)
2010	−96.4	55.1 (57.2)	1.04 (1.1)	3.54 (3.7)	3.61 (3.7)	0.76 (0.8)	54.9 (56.9)
2011	−117.6	43.7 (37.2)	1.17 (1.0)	4.30 (3.7)	2.58 (2.2)	0.33 (0.3)	43.4 (36.9)
2012	−115.1	55.4 (48.1)	1.47 (1.3)	4.27 (3.7)	1.48 (1.3)	0.56 (0.7)	55.2 (48.0)

Table 5. Mean PPFD (μmol m^{-2} s^{-1}), ±SD, during June–August 2008–2012.

	2008	2009	2010	2011	2012
June	513 ± 456	470 ± 432	362 ± 345	430 ± 420	446 ± 414
July	409 ± 405	434 ± 420	288 ± 322	375 ± 383	309 ± 347
August	316 ± 360	286 ± 333	288 ± 332	291 ± 342	238 ± 284

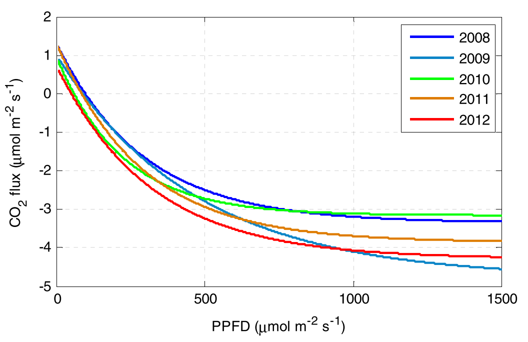

Figure 7. Light response curves (equation (1)) based on measurements during July 2008–2012 from Andøya.

Table 6. Mean measured fluxes of NEE (PPFD >1000 μmol m^{-2} s^{-1}), ±standard error of the mean, and T_s and modelled fluxes of $R_{eco,2}$ and GPP_2 during July 2008–2012, arranged into 0.1 kPa VPD (vapour pressure deficit) bins.

VPD bin	0.2–0.3	0.3–0.4	0.4–0.5	*p*
2008				
n	46	47	30	
NEE	−3.54 ± 0.09	−3.26 ± 0.07	−3.38 ± 0.08	0.041
T_s	10.31	11.52	11.57	<0.001
$R_{eco,2}$	1.19	1.40	1.41	n/a
GPP_2	−4.73	−4.66	−4.79	n/a
2009				
n	48	49	14	
NEE	−4.95 ± 0.12	−4.58 ± 0.09	−3.92 ± 0.23	<0.001
T_s	10.20	10.32	12.04	<0.001
$R_{eco,2}$	1.08	1.09	1.30	n/a
GPP_2	−6.03	−5.67	−5.22	n/a
2010				
n	18	25	13	
NEE	−3.70 ± 0.20	−2.99 ± 0.15	−2.98 ± 0.23	0.012
T_s	11.43	11.02	11.30	0.343
$R_{eco,2}$	0.91	0.87	0.90	n/a
GPP_2	−4.61	−3.86	−3.88	n/a
2011				
n	67	42	8	
NEE	−4.20 ± 0.10	−4.06 ± 0.15	−3.22 ± 0.24	0.013
T_s	11.85	11.38	12.32	0.032
$R_{eco,2}$	0.88	0.84	0.93	n/a
GPP_2	−5.08	−4.90	−4.15	n/a
2012				
n	23	27	2	
NEE	−4.37 ± 0.17	−4.70 ± 0.12	n/a	0.183
T_s	10.73	10.28	n/a	0.063
$R_{eco,2}$	0.93	0.88	n/a	n/a
GPP_2	−5.30	−5.58	n/a	n/a

Note: *n* values indicate number of observations within each bin (bins with less than eight observations were excluded from the analysis). *p* values denote the probability that all values are drawn from populations with same mean.

Sphagnum mosses and lichens dry out and may even be damaged by long-term desiccation (Schipperges and Rydin 1998). This finding, that lowered GPP explains a majority of the reduction in CO_2 uptake during dry conditions, is in line with previous studies (Shurpali *et al* 1995, Arneth *et al* 2002, Lafleur *et al* 2003, Sottocornola and Kiely 2010, Lund *et al* 2012). Earlier studies have indeed shown that dry soil conditions may not result in large changes in R_{eco} (Lafleur *et al* 2003, Parmentier *et al* 2009), which may be related to the recalcitrant litter in nutrient-poor peatlands (Aerts *et al* 1999) and also that autotrophic respiration generally dominates the R_{eco} signal (Kurbatova *et al* 2009, St-Hilaire *et al* 2010).

It is interesting to note that the warm and dry years from a meteorological perspective (2008, 2009, 2011), compared with long-term mean, had lower NEE and higher GPP (figure 5) and were stronger annual CO_2 sinks (table 4), compared with 2010 when both T_a and precipitation were close to normal. This effect was observed despite higher VPD in July that lead to weaker NEE on a half-hourly basis (table 5), which suggests that drier conditions did not have persistent effects on the CO_2 exchange dynamics on longer time scales (seasonal–annual). It can be argued that the maritime conditions at the site reduced the frequency, duration and intensity of dry conditions (i.e. high VPD), and that other environmental characteristics were more important for the inter-annual variation in CO_2 exchange. Low T_s in early growing season of 2010

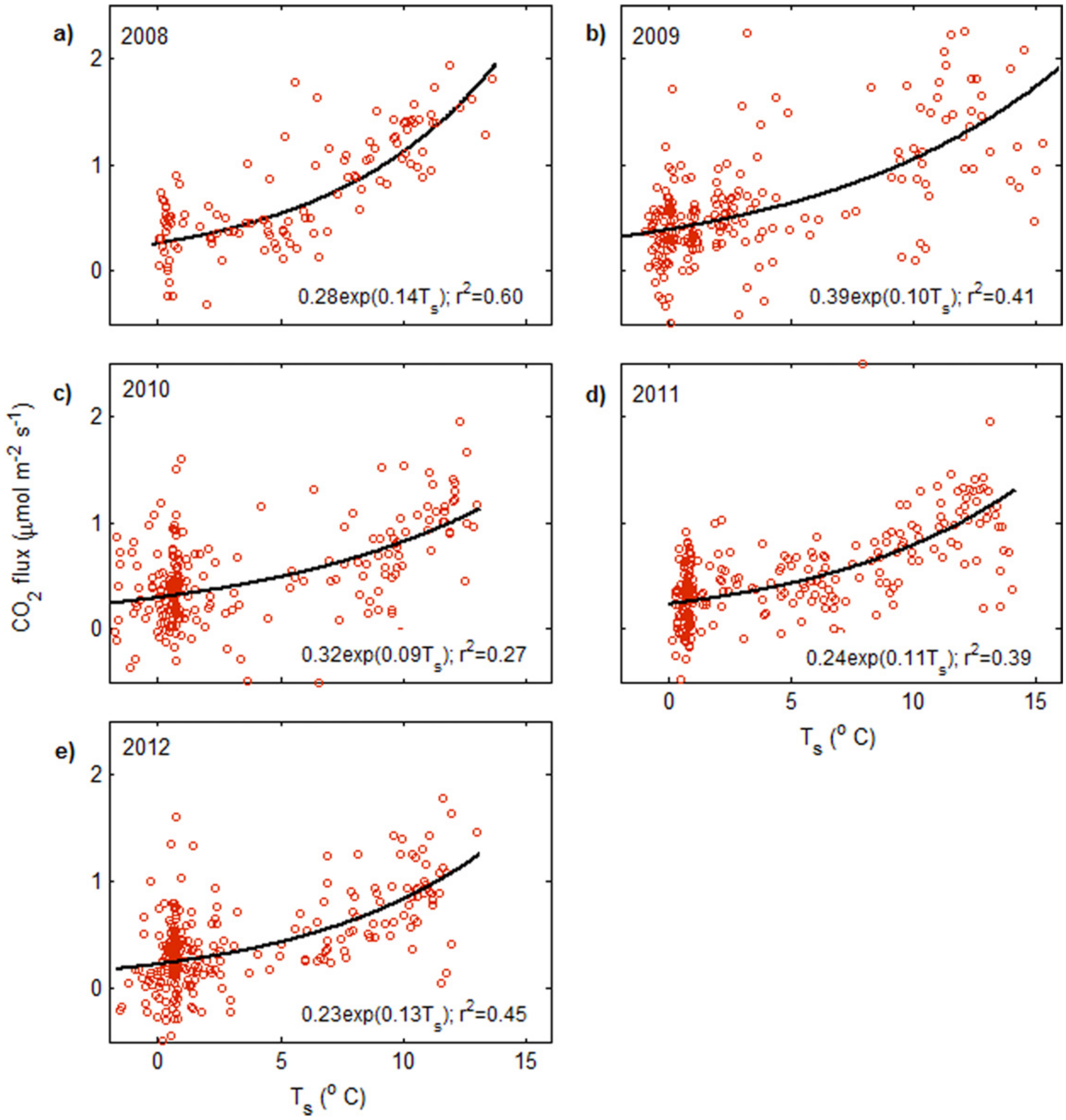

Figure 8. Scatter plots of T_s (5 cm) versus measured nighttime (PPFD < 20 μmol m^{-2} s^{-1}) NEE.

as well as low PPFD levels during June–July (table 5) likely resulted in low biomass build-up compared with other years, which can be illustrated by the low CO_2 uptake capacity at high PPFD levels in 2010 (figure 7). The reduced CO_2 uptake capacity in combination with low levels of incoming light during summer (table 5) likely explains lower fluxes in 2010.

Based on mean summer-time fluxes and annual budgets, there was no apparent long-lasting effect of dry conditions on the CO_2 exchange, indicating an inherent resistance of the Andøya peatland to dry conditions. However, for extended drought periods, increased heterotrophic respiration may become increasingly important for the R_{eco} signal (Ise *et al* 2008). As the summer months during our study period were not significantly warmer than the long-term average, although slightly drier, we may not yet have captured an extreme drought event in our measurement record. Ground surface wetness has been found to have a significant influence on NEE interannual variation in Glencar (Sottocornola and Kiely 2010, McVeigh *et al* 2014), with highest summer-time CO_2 uptake observed for years with intermediate (not too cold, not too dry) rather than extreme meteorological conditions (Sottocornola and Kiely 2010).

As stated previously by several authors (e.g. Limpens *et al* 2008, Lafleur 2009, Lund *et al* 2012), the effect of a changing climate on peatland C exchange is dependent on site specific characteristics, most importantly hydrological settings and vegetation composition. As such, it is not feasible to draw general conclusions valid for all types of peatlands. However, since a positive water balance is a prerequisite for blanket bogs, future higher temperature must be followed by an increase in precipitation to maintain the water balance for such peatland types. If not, it is likely that vegetation change will occur in blanket bogs (Gallego-

Sala and Prentice 2012), with uncertain consequences for the C budget.

5. Conclusions

We have used 4.5 years of EC measurements from the Andøya blanket bog in Norway to describe the multi-year CO_2 exchange and assess the impacts of dry conditions. Our main conclusions include;

- The bog acted as a small sink for atmospheric CO_2 (-19.5 ± 18.3 g C m^{-2}); however, uncertainties regarding self-heating correction of the open path analyzer were large.
- On a half-hourly scale, we observed reduced CO_2 uptake (i.e. higher NEE) during periods with high VPD, mainly caused by a decrease in GPP.
- On longer time scales, seasonal to annual, no persistent effects of dry conditions on the CO_2 exchange were observed. Instead, other variables such as growing season onset and amount of incoming light were important regulators for the between-year variation.

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