A 12-year record reveals pre-growing season temperature and water table level threshold effects on the net carbon dioxide exchange in a boreal fen

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Abstract
This study uses a 12-year time series (2001–2012) of eddy covariance measurements to investigate the long-term net ecosystem exchange (NEE) of carbon dioxide (CO₂) and inter-annual variations in relation to abiotic drivers in a boreal fen in northern Sweden. The peatland was a sink for atmospheric CO₂ in each of the twelve study years with a 12-year average (± standard deviation) NEE of −58 ± 21 g C m⁻² yr⁻¹. For ten out of twelve years, the cumulative annual NEE was within a range of −42 to −79 g C m⁻² yr⁻¹ suggesting a general state of resilience of NEE to moderate inter-annual climate variations. However, the annual NEE of −18 and −106 g C m⁻² yr⁻¹ in 2006 and 2008, respectively, diverged considerably from this common range. The lower annual CO₂ uptake in 2006 was mainly due to late summer emissions related to an exceptional drop in water table level (WTL). A positive relationship (R² = 0.65) between pre-growing season (January to April) air temperature (Ta) and summer (June to July) gross ecosystem production (GEP) was observed. We suggest that enhanced GEP due to mild pre-growing season air temperature in combination with air temperature constraints on ecosystem respiration (ER) during the following cooler summer explained most of the greater net CO₂ uptake in 2008. Differences in the annual and growing season means of other abiotic variables (e.g. radiation, vapor pressure deficit, precipitation) and growing season properties (i.e. start date, end date, length) were unable to explain the inter-annual variations of NEE. Overall, our findings suggest that this boreal fen acts as a persistent contemporary sink for atmospheric CO₂ that is, however, susceptible to severe anomalies in WTL and pre-growing season air temperature associated with predicted changes in climate patterns for the boreal region.

Keywords: boreal landscape, climate, eddy covariance, peatland, ecosystem production, respiration

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1. Introduction

Northern peatlands cover 3% of the Earth’s land area but contain with ~400–600 Gt C a quarter to a third of the global soil organic carbon (C) pool (Gorham 1991, Turunen et al 2002, Yu 2011, Charman et al 2013). Moreover, these ecosystems have provided a small but consistent sink for atmospheric carbon dioxide (CO2) throughout the Holocene with estimated accumulation rates of 0.075 to 0.096 Gt C yr⁻¹ (Gorham 1991, Turunen et al 2002, Yu 2011, Charman et al 2013). Recent studies also indicated that the contemporary peatland C balance represents a net C sink (Roulet et al 2007, Nilsson et al 2008, Koehler et al 2011). However, the strength of the future peatland C sink potential has been questioned given predicted changes in climatic patterns (Oechel et al 1993, Christensen et al (1999), IPCC 2007, Dise 2009). Since the vertical exchange of CO2 accounts for most of the magnitude and variability of the peatland C balance (Roulet et al 2007, Nilsson et al 2008, Koehler et al 2011), its sensitivity to abiotic controls and the implications for the future peatland C balance has become of great interest in recent years (Bu et al 2011, Dise 2009, Fenner and Freeman 2011).

While nutrient availability, hydrology and vegetation properties (e.g. leaf area) define a baseline for ecosystem biogeochemistry and functioning, the inter-annual variation of the net ecosystem exchange (NEE) of CO2 in peatlands is commonly related to anomalies of the abiotic controls (Humphreys et al 2006, Lafleur et al 2003, Lund et al 2010). Specifically, changes in photosynthetically active radiation (PAR), air temperature (Ta), and precipitation (PPT) may affect the C cycle of peatlands, e.g. due to alterations of the growing season length, water and energy input, vegetation composition and water table levels (WTLs) (Flanagan and Syed 2011, Humphreys and Lafleur 2011, Cai et al 2010, Lund et al 2010, Sulman et al 2010, Yurova et al 2007). To date, however, much uncertainty still exists in predicting abiotic effects on NEE and its individual component fluxes (i.e. gross ecosystem production (GEP) and ecosystem respiration (ER)) and consequently the net C balance in northern peatlands.

The two most important abiotic controls on peatland C cycling commonly reported are temperature (air and/or soil) and the depth of the WTL (Clymo 1984, Clymo et al 1998, Frolking et al 2001, 2010, Lindroth et al 2007). Since temperature is positively related to both photosynthesis and decomposition, the net effect of increasing temperature on NEE is mainly determined by the respective temperature sensitivities of GEP and ER (Cai et al 2010, Flanagan and Syed 2011, Lindroth et al 2007). However, these relationships of temperature with GEP and ER vary temporarily and in dependence of other controlling factors (e.g. WTL, leaf area). Thus, temperature changes may have contrasting effects on NEE depending on whether this change occurs during e.g. summer or winter. In addition to temperature, changes in WTL affect plant species composition and modify GEP through altered water supply to both moss and vascular plant communities (Robroek et al 2009, Rydin and McDonald 1985a, Williams and Flanagan 1996). At the same time, fluctuations in WTL also control ER by regulating the thickness of the acrotelm in which decomposition occurs at a faster rate than in the catotelm (Clymo 1984). Recent studies proposed that higher temperature and lower WTL in a future warmer and drier climate might enhance decomposition and consequently turn peatlands into C sources (Oechel et al 1993, Ise et al 2008, Dise 2009, Dorrepaal et al 2009, Cai et al 2010, Fenner and Freeman 2011). In contrast, other studies found that higher temperature and/or lower WTL may stimulate photosynthesis equally (Flanagan and Syed 2011, Sulman et al 2010) or more than decomposition and thus may potentially enhance the peatland CO2 sink strength (Charman et al 2013, Lindroth et al 2007). Nevertheless, due to similar responses of GEP and ER to abiotic controls, as well as the coupling of ER to GEP via autotrophic respiration, peatland NEE may be resilient to moderate changes in abiotic conditions (Belyea and Clymo 2001).

Given the inter-annual variations in abiotic conditions, multi-year eddy covariance (EC) measurements are required to obtain a robust long-term estimate of NEE and to fully understand the complex relationships between abiotic variables and NEE on the ecosystem scale. Despite extensive research in various peatland sites, such multi-year EC measurements are still scarce. To our knowledge, time series with five or more years of EC data are published only for few peatlands including the Mer Bleu bog in Ontario, Canada (Lafleur et al 2003, Roulet et al 2007, Teklemariam et al 2010), a treed fen in western Alberta, Canada (Flanagan and Syed 2011), an Atlantic blanket bog in Ireland (Koehler et al 2011, Sottocornola and Kiyeli 2010) and the palsmire Kaamanen (Aurela et al 2004) in northern Finland.

In this study we use twelve years (2001–2012) of EC measurements to explore the long-term CO2 land-atmosphere exchange dynamics and drivers in an oligotrophic minerogenic mire in northern Sweden. The main objectives were: (i) to identify the long-term CO2 sink-source strength of the mire ecosystem, (ii) to explore the seasonal and inter-annual variability of NEE and its main drivers and (iii) to assess the resilience of NEE against abiotic anomalies.

2. Materials and methods

2.1. Site description

The study was conducted at Degerö Stormyr, (64°11′N, 19°33′E; 270 m a.s.l.) an oligotrophic minerogenic mire located near the municipality of Vindeln, county of Västerbotten, northern Sweden. Degerö Stormyr is also a level one site in the national research infrastructure ICOS (Integrated Carbon Observation System) Sweden. The mire catchment is predominantly drained by the small creek Vargstugbäcken towards northwest. The depth of the peat is generally between 3–4 m, but depths up to 8 m have been measured. The 30-year (1961–1990) mean annual PPT and Ta are 523 mm and +1.2 °C, respectively (Alexandersson et al 1991). The snow cover normally lasts from early November until late April.
The micro-topography within the study area is characterized by mainly carpets and lawns, with only sparse occurrences of hummocks. The vascular plant community of the mire consists mainly of *Eriophorum vaginatum* L., *Tri-chothamnus cespitosum* L., Hartm., *Vaccinium oxycoccos* L., *Andromeda polifolia* L., and *Rubus chamaemorus* L. *Sphagnum majus* Russ. C. Jens is found on the bottom of the carpets while *Sphagnum balticum* Russ. C. Jens dominates the lawn. The hummocks are dominated by *Sphagnum fuscum* Schimp. Klinggr. (Laine *et al.* 2012, Nilsson *et al.* 2008). Total (moss + vascular plants) aboveground biomass is 141 ± 45 g m⁻² (Laine *et al.* 2012). Maximum leaf area index was estimated at 0.9 m² m⁻² in 2012 (unpublished data).

### 2.2. EC measurements

The EC technique was used to measure the NEE of CO₂ at a sampling frequency of 20 Hz. The system consisted of a three-dimensional sonic anemometer (1012R3 Solent, Gill Instruments, UK; heated during winter months) and a closed-path infrared gas analyzer (IRGA 6262, LI-COR, Lincoln, Nebraska USA) mounted on a tower at a height of 1.8 m. Fluxes were calculated by the EcoFlux software (*In Situ Flux AB*, Ockelbo, Sweden) according to the EUROFLUX methodology (Aubinet *et al.* 1999) and stored as 30 min averages. Raw data processing included a two fold coordinate rotation by sector fit and a frequency correction for the signal attenuation in the sampling path. The IRGA CO₂ measurements were calibrated against two reference gases approximately every two weeks. The annual energy balance closure was estimated at around 0.96 (Sagerfors *et al.* 2008, Peichl *et al.* 2013). Since no effect of low friction velocity (u₀) on NEE could be detected, u₀ threshold filtering was not applied to the NEE data (Sagerfors *et al.* 2008). More details regarding the instrumental set up, data processing and quality control were previously outlined by Sagerfors *et al.* (2008) and Nilsson *et al.* (2008). While the measurement height was adjusted with snow depth during the winter periods of 2001–2005, it was kept constant in the following years since no effect on the fluxes was apparent. No other alterations to the experimental set up or instrument replacement have occurred since 2005.

Missing half-hourly NEE data (due to instrument and power failure, etc.) were filled with the mean diurnal variation approach using a 14-day window during the winter season (described by Sagerfors *et al.* 2008). During the summer, NEE was filled using bi-weekly regression relationships of NEE with Ta during nighttime and of NEE with PAR and Ta during daytime. Filled data represented 35, 20, 31, 35, 35, 7, 11, 9, 8, 17, 22, and 9% of the annual time series for the years 2001–2012, respectively. Separate estimates of GEP and ER were derived with the procedure described by Barr *et al.* (2004). Negative NEE values indicate net CO₂ uptake while positive NEE values indicate emission of CO₂. To facilitate the direct comparison between the two component fluxes, both GEP (by definition a negative flux) and ER are presented as positive fluxes. Based on different estimates from three different footprint models (Schuepp *et al.* 1990, Hsieh *et al.* 2000, Kljun *et al.* 2004), the mean growing season peak source and the 90% fetch distances of the measured fluxes from the tower during daytime (nighttime) ranged between 15–21 m (22–26 m) and 82–215 m (117–375 m), respectively.

### 2.3. Abiotic measurements

Instruments for meteorological variables were mounted on the same tower as the EC sensors. PAR was measured by a Quantum sensor (SKP 215, Skye Instruments Ltd, Powys, UK). Net radiation (Rn) and global radiation (RG) were measured using a NR-Lite sensor (Kipp&Zonen, Delft, the Netherlands) and a Li200sz sensor (LI-COR, Lincoln, NE, USA), respectively. In addition, air temperature (Ta) and relative humidity (RH) were measured by a MP100 temperature and moisture sensor (Rotron AG, Bassersdorf, Switzerland) equipped with a ventilated radiation shield. The Ta and RH data were used to derive the atmospheric vapor pressure deficit (VPD). PPT was measured using a rainfall tipping-bucket (ARG 100, Campbell Scientific, Logan, UT, USA) from May to October. During the remaining period, PPT data were obtained from a nearby (1 km away) standard climate station which is part of a reference climate monitoring program at the Vindeln experimental forests. The 30-year long-term normal (1961–1990) of Ta and PPT were obtained from the national Swedish climate station Kalvbergsudden (5 km away). The snow depth at the study site was measured by a Sr-50 ultrasonic sensor (Campbell Scientific, Logan, UT, USA) nearby the flux-tower. Gaps in abiotic variables (due to instrument failure) were filled either directly (i.e., for PPT) or with seasonal regression relationships (i.e., for PAR, Ta, RN, and RH) with respective data from the nearby (13 km away) standard climate station at the Svarberget field station. Soil temperatures at 2, 10, 18, 26, 34, and 42 cm depths were measured by TO3R thermistors mounted in sealed, waterproof, stainless steel tubes (TOJO Skogsteknik, Djäkneboda, Sweden) in a lawn community 100 m northeast of the flux tower. At the same location, WTL below the peat surface was measured using a float and counterweight system attached to a potentiometer (Roulet *et al.* 1991). All abiotic data were collected at 10 s intervals and averaged to 30 min mean values. The growing season start and end dates were defined as the first day out of five consecutive days with daily mean Ta > 5 °C and < 5 °C, respectively.

### 2.4. Partial least square (PLS) regression analysis

PLS regression analysis (Geladi and Kowalski 1986, Wold *et al.* 2001) was conducted to investigate the model component structure among the abiotic variables (x-variables; listed and defined in supplementary table S1) explaining the annual sums of NEE, GEP and ER, respectively (y-variables). Due to the large number of abiotic variables (n = 29), a two-step analysis was conducted. First, a Jack–Knifing confidence interval of 0.90 was set for the first two component loadings as an initial threshold for removing variables without significant contribution in either one of the two components (see results in supplementary table S1). Then, a second PLS
analysis was conducted with the remaining variables using a confidence interval of 0.95. The analysis was carried out using the SIMCA software (SIMCA v.13.0, UMETRICS, Umeå, Sweden).

3. Results

3.1. Climatic conditions

Out of the twelve study years, ten years showed higher (0.7 to 2.2 °C) annual mean Ta and nine years received more (~25 to 300 mm) annual PPT compared to the 30-year long-term norm (figure 1(a)). Among the twelve study years, growing season Ta and PPT anomalies ranged from approximately −2 to +2 °C and −125 to 175 mm, respectively (figure 1(b)). Compared to other years on both the annual and the growing season scale, 2001 was the wettest year, 2002 the driest year, 2011 the warmest year, and 2004 was the coolest year. It is noteworthy that the years 2006 and 2008 were not characterized by exceptional Ta nor PPT conditions on either the growing season or annual scale, which is relevant in the context of further results on the CO2 exchange anomalies described below in section 3.2. The 12-year long-term average (±SD) NEE of −58 ± 21 g C m⁻² yr⁻¹ (figure 2; table 1). For ten out of twelve years (i.e. excluding 2006 and 2008), the cumulative annual NEE was within a range of −42 to −79 g C m⁻² yr⁻¹ with a mean of −57 ± 11 g C m⁻² yr⁻¹. In the years 2006 and 2008, however, the annual NEE diverged significantly from this range with lower annual CO2 uptake of −18 g C m⁻² yr⁻¹ occurring in 2006 and a greater uptake of −106 g C m⁻² yr⁻¹ measured in 2008. In 2006, the autumn switch from accumulating CO2 to becoming a source of CO2 occurred in early August, about one month earlier compared to other years (figure 2; see also figure 4(a)). In 2008, the net uptake rate of CO2 during June and July was considerably higher compared to other years (figure 2; see also figure 4(a)). The annual NEE was correlated to the June–July NEE (R² = 0.50) and June to August NEE (R² = 0.71). The 12-year averages (±SD) of GEP and ER were 336 ± 98 and 278 ± 92 g C m⁻² yr⁻¹ and the CVs of annual NEE, GEP and ER were 36, 29 and 33%, respectively (table 1). The ratio between growing season anomalies of GEP and ER was defined by a strong linear relationship (slope = 0.89; R² = 0.96) (figure 3). However, the years 2006 (reduced GEP and average ER) and 2008 (greater GEP with relatively less enhanced ER) deviated from this general relationship. Annual GEP and ER were also strongly correlated (R² = 0.94) with a linear slope of 0.92 (supplementary figure S2).
3.3. Abiotic controls on the peatland CO2 exchange

3.3.1. PLS analysis

PLS analysis resulted in two significant components which together explained 64, 90 and 92% of the variances in NEE, GEP and ER, respectively (figure 4). Annual NEE showed the strongest positive relationships with maximum (of the weekly means) summer Ta and VPD (figure 4(a)). In both cases, the relationship was mainly driven by the year of 2006 with its unusual dry and warm late summer. In contrast, annual NEE corresponded most negatively to GEP and growing season PPT. Growing season timing characteristics such as the start, end or length of the growing season or the timing of shallow soil thawing and freezing could not explain any of the variations in the annual NEE. In contrast to NEE, both annual GEP and ER were most strongly related to variables representing winter conditions and growing season timing characteristics, including pre-growing season mean, snow depth, and the dates of snowfall, snowmelt, spring soil thawing and growing season start (figures 4(b), (c)). The pre-growing season mean was the only variable that was significant in both components for GEP and ER. The PLS analyses also showed that growing season and annual means of most abiotic variables (see supplementary table S1) had little or no relation with the annual NEE, GEP or ER.

3.3.2. Seasonal patterns

The decrease of the net CO2 uptake and emission in August 2006 coincided with a drop in WTL below 30 cm depth (figures 5(a), (b)). The enhanced CO2 uptake during June and July of 2008 coincided with cooler Ta, compared to other years (figures 5(a), (c)).

Seasonal and inter-annual variations in PAR were limited and could not explain differences in NEE (figures 5(a), (d)). Bin-averaged responses of NEE to different WTL classes indicate that net CO2 uptake increased with decreasing WTL up to a threshold of about 30 cm, below which a shift in NEE towards lower uptake and even emissions occurred (figure 6(a)). This shift resulted primarily from a greater reduction of GEP compared to ER.

Table 1. Annual (A) and growing season (GS) sums of net ecosystem exchange (NEE), gross ecosystem production (GEP), ecosystem respiration (ER) and precipitation (PPT), and averages of photosynthetically active radiation (PAR), air temperature (Ta) and water table level (WTL); SD = standard deviation; CV = coefficient of variation in %; n.a. = not available.

| Year | NEE (g C m⁻²) | GEP (g C m⁻²) | ER (g C m⁻²) | PAR (μmol m⁻² s⁻¹) | Ta (°C) | PPT (mm) | WTL (cm) |
|------|---------------|--------------|--------------|----------------------|--------|---------|---------|
|      | A GS          | A GS         | A GS         | A GS                 | A GS   | A GS    | A GS    |
| 2001 | −58 −85       | 319 304      | 261 219      | 193 337              | 1.8    | 11.2    | 888 571 |
| 2002 | −60 −92       | 503 491      | 443 399      | 218 408              | 2.9    | 13.5    | 533 256 |
| 2003 | −59 −95       | 449 431      | 402 332      | 208 367              | 2.3    | 10.3    | 584 367 |
| 2004 | −58 −87       | 358 333      | 298 238      | 199 325              | 0.9    | 8.8     | 650 401 |
| 2005 | −58 −87       | 380 363      | 322 276      | 209 337              | 3.1    | 11.5    | 659 405 |
| 2006 | −48 −48       | 283 279      | 265 231      | 219 379              | 3.1    | 11.8    | 661 346 |
| 2007 | −48 −48       | 302 278      | 254 211      | 212 356              | 2.8    | 10.9    | 586 298 |
| 2008 | −105 −142     | 456 452      | 351 310      | 207 339              | 2.8    | 9.2     | 751 462 |
| 2009 | −41 −61       | 215 211      | 174 149      | 211 373              | 2.0    | 11.3    | 702 408 |
| 2010 | −66 −76       | 203 196      | 137 119      | 215 378              | 0.4    | 11.7    | 639 392 |
| 2011 | −79 −93       | 340 335      | 261 242      | 214 348              | 3.5    | 11.1    | 707 460 |
| 2012 | −57 −72       | 229 226      | 172 154      | 194 325              | 1.9    | 10.7    | 630 377 |
| Mean | −58 −85       | 336 325      | 278 240      | 208 356              | 2.3    | 11.0    | 666 395 |
| SD   | 21 23         | 98 95        | 92 82        | 9 17                 | 0.9    | 1.2     | 92 76   |
| CV   | 36 30         | 29 29        | 33 33        | 4 5                  | 40 9   | 14 17   | 46      |

a Defined as the period with daily mean Ta > 5 °C for five consecutive days.

b Growing season means of WTL are shown only since annual WTL differs little due to freezing outside the GS.

Figure 3. Growing season anomalies of gross ecosystem production (GEP) and ecosystem respiration (ER) during the study years 2001–2012 relative to their 12-year averages; red and blue symbols highlight the years 2006 and 2008, respectively. Dotted and dashed lines represent the linear fit for all years (slope = 0.82; $R^2 = 0.96$) and without the years 2006 and 2008 (slope = 0.89; $R^2 = 0.99$), respectively.

Figure 4. Growing season anomalies of gross ecosystem production (GEP) and ecosystem respiration (ER) during the study years 2001–2012 relative to their 12-year averages; red and blue symbols highlight the years 2006 and 2008, respectively. Dotted and dashed lines represent the linear fit for all years (slope = 0.82; $R^2 = 0.96$) and without the years 2006 and 2008 (slope = 0.89; $R^2 = 0.99$), respectively.
Meanwhile, NEE became negative at Ta above \(\sim 10 \degree C\) and the net uptake increased with increasing Ta until it leveled out beyond approximately 20 \degree C (figure 6(c)). This logistic regression relationship between NEE and Ta resulted from a greater sensitivity of GEP to Ta within the range of 10 to 20 \degree C, compared to that of ER (figure 6(d)). The light response curves of NEE and GEP leveled off beyond \(\sim 1500 \mu\text{mols m}^{-2}\text{s}^{-1}\) (figures 6(e), (f)).

The mean Ta of the pre-growing season period (January to April) was strongly correlated with the subsequent summer (June to July) GEP \((R^2 = 0.65)\) and ER \((R^2 = 0.66)\) with slopes of 0.44 and 0.36, respectively (figure 7(a)). Furthermore, mean summer Ta partly explained ER \((R^2 = 0.45)\) and to a lesser extent the GEP \((R^2 = 0.32)\) within the same period (figure 7(b)).

4. Discussion

4.1. Boreal fen acts as a persistent contemporary sink of atmospheric CO₂

Twelve years of EC measurements clearly demonstrated that the land-atmosphere exchange of CO₂ (i.e. NEE) at this boreal oligotrophic fen was characterized by a net uptake of atmospheric CO₂ despite different weather conditions during the past decade. Our long-term mean NEE of \(-58 \pm 21\)
g C m\(^{-2}\) yr\(^{-1}\) is similar to the six-year means reported for the ombrotrophic bog Mer Bleu in Canada with \(-40 \pm 41 \text{ g C m}^{-2}\text{ yr}^{-1}\) (Roulet et al. 2007) and the Atlantic blanket bog Glencar in Ireland with \(-48 \pm 30 \text{ g C m}^{-2}\text{ yr}^{-1}\) (Koehler et al. 2011), about twice that of the \(-22 \pm 20 \text{ g C m}^{-2}\text{ yr}^{-1}\) observed at the Kaamanen aapa fen in northern Finland (Aurela et al. 2004), but much lower compared to the six-year mean of \(189 \pm 47 \text{ g C m}^{-2}\text{ yr}^{-1}\) reported for a moderately rich treed fen in western Alberta (Flanagan and Syed 2011). The relatively small and confined range of inter-annual variability (in terms of SD) at our fen is in contrast to those other sites. A relatively shorter growing season length compared to the two bogs, as well as smaller variations in Ta and WTL during the summer and the absence of shrubs (i.e. lower vascular plant
LAI) compared to the Mer Bleu bog could explain this difference. Since moss GEP saturates at lower light level compared to that of vascular plants, its relatively greater contribution to ecosystem GEP (given the reduced presence of vascular plants) might constrain the variation in NEE at our site. Thus, the shorter growing season, low vascular plant LAI and smaller variations in Ta and WTL might limit the potential for inter-annual variations of production and decomposition processes which may explain the narrow range of annual NEE (i.e., for ten years out of twelve years) at our boreal fen.

Annual GEP and ER in this boreal fen were at the lower end of the respective ranges (~250–800 g C m^{-2} yr^{-1} and ~250–600 g C m^{-2} yr^{-1}, respectively) reported for seven contrasting peatlands by Lund et al (2010). These differences in GEP and ER capacities between our and other peatland sites are likely explained by nutrient availability, lower LAI and the lack of shrubs and woody plants at our oligotrophic fen (Laine et al 2012). Given the small amount of biomass, limited plant production and autotrophic respiration potentials and the strong coupling of both processes may further condition a general stability of the ecosystem functioning and resilience of NEE to moderate inter-annual weather variations in this fen.

4.2. WTL threshold effects on the sink potential for atmospheric CO2

Despite the generally narrow range of annual NEE, the severe WTL anomaly below a threshold of ~30 cm in the late summer of 2006 triggered a substantial deviation by considerably reducing the cumulative NEE. This highlights the potential risk of substantial shifts and imbalance of the NEE triggered by anomalies beyond threshold limits in our boreal fen. Similar negative impacts of severe WTL anomalies on NEE have also been noted at other sites (e.g. Arneth et al 2002, Lafleur et al 2003, Sonnentag et al 2010, Sulman et al 2010, Charman et al 2013) further supporting the existence of a threshold-type relationship between WTL and NEE in peatland ecosystems.

The observed threshold WTL depth of ~30 cm at our site is likely defined by both the maximum depth of the vascular plant root zone (based on visual field observations) and the maximum depth to support capillary forces required for maintaining sufficient water transport to the Sphagnum communities (Rydin and McDonald 1985a,b, Ketcheson and Price 2014). WTL drops below such threshold may therefore cause constraints on both vascular plant and moss photosynthesis which is in agreement with our observation that the reduction of the net CO2 uptake in August 2006 was primarily driven by a decrease of GEP. This is also in line with other studies in peatland ecosystems where reduced net CO2 uptake during dry periods was caused by reductions of GEP (e.g. Arneth et al 2002, Sonnentag et al 2010). In contrast, our results disagree with previous studies that suggested enhanced decomposition processes as the main explanatory mechanism for reduction in the net CO2 uptake during drought (Oechel et al 1993, Alm et al 1999, Aurela et al 2007, Ise et al 2008).

These contrasting results might be partly related to different timings of the drought events and their contrasting effects on GEP and ER (Lund et al 2012a). It is further noteworthy that impacts from short-term droughts with a subsequent recovery phase as observed in this study are likely to differ from those of long-term WTL drawdowns which may alter nutrient dynamics and vegetation composition (Laine et al 1995, Talbot et al 2010, Macrae et al 2013). Moreover, while the 2006 drought had no apparent effect on the CO2 exchange of subsequent years in our study, an increased re-occurrence frequency in WTL anomalies beyond such threshold might also trigger a memory effect causing a gradual shift in the peatland C balance and development. However, some uncertainty remains in our study since such WTL drop below the critical threshold occurred only once within the twelve study years while repeated occurrences of this phenomena would be required to further explore its implications and underlying mechanism.

4.3. Pre-growing season and summer temperature effects on the CO2 sink potential

Among all abiotic variables tested, the mean Ta during the pre-growing season period showed the strongest correlation with summer CO2 exchange processes. Although the observed correlation does not imply direct causality, we suggest that this positive relationship between pre-growing season Ta and GEP also explained most of the enhanced net CO2 uptake in summer 2008. Milder winter temperature prior to snowmelt in 2008 may have resulted in less deep soil frost and root damage (Cleavitt et al 2008, Templer 2012, Haei et al 2013). As a consequence, water and nutrient access and supply to plants were greater and thus plant development and productivity enhanced in the subsequent summer period. Further impacts on soil freezing could be expected from concurrent snow cover depth and timing (Dorrepaal et al 2004, Cleavitt et al 2008, Templer 2012). Warmer pre-growing season temperature in northern ecosystems may also result in earlier snowmelt and therefore in greater soil moisture availability and an earlier onset of both moss and vascular plant phenology (Aerts et al 2006, Kreyling 2010). While this strong correlation between pre-growing season Ta and CO2 exchange has not been reported previously for any other peatland ecosystem, Lund et al (2012b) found that winter snow cover dynamics were important for the subsequent seasonal CO2 exchange patterns at an arctic tundra heath. In our boreal fen, however, correlations of snow depth or length of snow cover (and their interaction terms with Ta) with NEE or GEP were not observed. Thus, details on the underlying processes and mechanism causing this statistical relationship remain unclear.

Moreover, cooler summer Ta may have favored higher net CO2 uptake by limiting ER during the summer of 2008. This is supported by our observation that Ta was a greater constraint on ER than on GEP during the summer period. Thus, the sequence of mild pre-growing season Ta and cool summer Ta may have caused enhanced GEP with concurrent relatively lower ER during the summer period which may
explain the unusually high net CO2 uptake observed in 2008. Thus, while the NEE anomaly in 2008 was likely the result from a combination of various causes and periodic events, the combined effects from relationships of pre-growing season and summer Ta with GEP and ER, respectively, might be the dominant control on inter-annual variations of NEE in this boreal fen.

Given the observed correlation between pre-growing season Ta and inter-annual variations of NEE, the recent trend towards warmer and wetter conditions on the annual scale might have less impact on the CO2 sink strength compared to changes in the preceding winter temperature and snow cover conditions. Since current climate projections suggest temperature increases in the high latitudes region primarily during winter time (IPCC2007), our findings may entail important implications for the ecosystem CO2 exchange and sink potential in northern peatlands.

5. Conclusions

We used twelve years of EC measurements to explore the long-term CO2 exchange and its abiotic drivers in an oligotrophic minerogenic mire in northern Sweden. Based on our findings we conclude that:

- The land-atmosphere CO2 exchange of this boreal peatland provided a persistent long-term sink of atmospheric CO2 under various weather conditions.
- The observed narrow range of CO2 uptake for most years suggests a general stability and resilience of NEE to moderate inter-annual climate variations in this boreal fen.
- Negative anomalies of the WTL below a threshold (i.e. ~30 cm in this study), however, may lead to a considerable reduction of the net uptake of atmospheric CO2 highlighting the risk that frequent occurrences of such anomaly events could trigger a shift in the peatland C balance.
- Based on statistical correlation analysis, pre-growing season played a major role in determining summer GEP and was, in combination with summer control on ER, the dominant control on the annual net ecosystem CO2 exchange in this boreal fen.

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