Effects of drought conditions on the carbon dioxide dynamics in a temperate peatland

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Abstract
Drought is arguably the most important regulator of inter-annual variation in net ecosystem CO\textsubscript{2} exchange (NEE) in peatlands. This study investigates effects of drought periods on NEE and its components, gross primary production (GPP) and ecosystem respiration ($R_{\text{eco}}$), on the basis of eddy covariance measurements of land–atmosphere exchange of CO\textsubscript{2} in 2006–2009 in a south Swedish nutrient-poor peatland. Two drought periods had dissimilar effects on the CO\textsubscript{2} exchange. In 2006, there was a short but severe drought period in the middle of the growing season resulting in increased $R_{\text{eco}}$ rates, but no detectable effect on GPP rates. In contrast, in 2008 the drought period began early in the growing season and lasted for a longer period of time, resulting in reduced GPP rates, suggesting that GPP is most sensitive to drought during leaf out and canopy development compared with the full canopy stage. Both in 2006 and in 2008 the peatland acted as an annual source of atmospheric CO\textsubscript{2}, while in 2007 and 2009, when there were no drought periods, the peatland constituted a CO\textsubscript{2} sink. It was concluded that the timing, severity and duration of drought periods regulate the effects on peatland GPP, $R_{\text{eco}}$ and NEE.

Keywords: peatland, drought, carbon dioxide, eddy covariance, net ecosystem exchange, gross primary production, ecosystem respiration

1. Introduction
Northern peatlands are important in the context of biospheric feedback effects on the climate system, as they store vast amounts of organic carbon (C) in their soils. Estimates of the amount of C stored in peatlands range 270–450 Pg C (Gorham 1991, Tolonen and Turunen 1996, Turunen \textit{et al} 2002), which equals about one-half of the current atmospheric C pool. Hydrological conditions exert a strong control on both peatland formation and functioning; and there is a growing consensus that drought is the most important controller of inter-annual variation in net ecosystem CO\textsubscript{2} exchange (NEE) in peatlands (Limpens \textit{et al} 2008, Lafleur 2009). Drought implies a lowering of the ground water table which potentially enhances soil respiration and decreases photosynthesis, which may turn the ecosystem into a source of CO\textsubscript{2} to the atmosphere (Lafleur 2009). Earlier studies have found that dry conditions affect CO\textsubscript{2} fluxes in peatlands (Shurpali \textit{et al} 1995, Lafleur \textit{et al} 1997, Alm \textit{et al} 1999, Arneth \textit{et al} 2002, Lafleur \textit{et al} 2003, Aurela \textit{et al} 2007, Lund \textit{et al} 2007, Riutta \textit{et al} 2007); however, the underlying causes and dynamics affecting ecosystem respiration ($R_{\text{eco}}$) and gross primary production (GPP) are not fully understood.

During a drought period, vascular plants respond physiologically and structurally to prevent excessive water loss. Physiological responses include reduced enzymatic
activity and stomatal closure, while structural responses include reductions in leaf area due to leaf senescence and leaf shed (van der Molen et al. 2011). Sphagnum mosses, which are an integral part of most peatlands due to their ability to intercept airborne nutrients (Malmer and Wallén 2005) and their recalcitrant litter (Aerts et al. 1999), lack xylem to transport water but do absorb water through leaves and stems. During drought conditions, Sphagnum mosses suffer from various degrees of desiccation resulting in reduced photosynthetic rates (Schipperges and Rydin 1998).

Ecosystem respiration includes both autotrophic and heterotrophic respiration. Autotrophic respiration, which has been reported to account for 30–90% of $R_{eco}$ in peatlands (Froling et al. 2002, Riutta et al. 2007, Kurbatova et al. 2009, St-Hilaire et al. 2010), is related to plant biomass and activity (Flanagan and Johnson 2005). Heterotrophic respiration is also related to vegetation processes through its dependency on supply and quality of substrates provided by plants (Giardina and Ryan 2000). In peatlands, drought conditions will decrease soil wetness and lower water tables, resulting in thicker aerobic layers and increased potential for aerobic respiration (Lafleur 2009).

In this study we present land–atmosphere exchange measurements of CO$_2$ between 2006 and 2009 from a temperate, nutrient-poor peatland (bog) in southern Sweden. The main objective was to investigate the effects of drought conditions, identified through water table depth (WTD) measurements, on the CO$_2$ dynamics and CO$_2$ balance of the peatland. Measurements of NEE were conducted using the eddy covariance technique, allowing for landscape scale interpretation of whole ecosystem response to droughts.

2. Methods and materials

2.1. Site description

The study site, Fäjemyr, is a temperate, ombrotrophic peatland (raised bog) located in southern Sweden (56° 15′N, 13° 33′E). The long-term (1961–90) mean annual temperature is 6.2°C with July being warmest month (15.1°C) and January coldest (−2.4°C). Long-term mean annual precipitation is 700 mm. The water table fluctuates 0–20 cm below the surface, and the topographical pattern is dominated by hummocks, lawns and carpets, while hollows and open pools are scarce. The vegetation is dominated by dwarf shrubs (Calluna vulgaris, Erica tetralix), sedges (Eriophorum vaginatum) and Sphagnum mosses (S. magellanicum, S. rubellum). The depth of accumulated peat is approximately 5 m. More detailed site descriptions can be found in Lund et al. (2007, 2009).

2.2. Measurements

Measurements of the land–atmosphere net ecosystem exchange (NEE) of CO$_2$ were performed using an eddy covariance system, consisting of a closed-path infrared gas analyser (Li-Cor 6262, Li-Cor Inc., USA) and a three-dimensional sonic anemometer (Gill R3, Gill Instruments, UK). The anemometer was mounted on a mast at a height of 3.4 m above ground. In all directions surrounding the mast, there were at least 290 m of homogeneous surface properties. According to previous footprint modelling, more than 90% of the flux emanated from this area for atmospheric conditions ranging from weakly stable to unstable (Lund et al. 2007). Additional environmental variables such as air (EMS 33, EMS Brno, Czech Republic) and soil temperatures (Type T thermocouples), precipitation (ARG100, Skye Instruments, UK), water table depth (WT; SKPS 1830, Skye Instruments, UK) and photosynthetic photon flux density (PPFD; JYP 1000, SDEC, France) were monitored continuously at the site. Water table depth was measured in a lawn community type, i.e. the zero datum was set at an intermediate topographical level.

Normalized difference vegetation index (NDVI) data was acquired from the Terra/MODIS vegetation index product MOD13Q1 (16 day temporal resolution, 250 m spatial resolution). The selected single grid cell subset included the eddy covariance mast and covered only peatland area, excluding surrounding forest. Due to the prevailing south-westerly winds at Fäjemyr, a cell where the eddy covariance tower was situated in the eastern part was found to largely overlap the flux footprint (Schubert et al. 2010).

2.3. Data handling

Raw data from the eddy covariance system was collected at a frequency of 20 Hz and processed using the Ecoflux software, producing half-hourly fluxes according to Fluxnet methodology (Aubinet et al. 1999). The software corrects for sensor separation by covariance optimization, air density fluctuations and frequency response losses. The storage term was calculated based on the single-point CO$_2$ concentration measurements and added to the flux. Data was screened for periods of low atmospheric mixing (defined as friction velocity $< 0.1$ m s$^{-1}$). The system setup and data processing are described in more detail in Lund et al. (2007).

Gaps in CO$_2$ flux data were filled using the following approaches. Firstly, small gaps ($<2$ h) were filled using linear interpolation. Secondly, the $Misterlich$ function (Falge et al. 2001) was parameterized for daytime periods (PPFD $> 10$ µmol m$^{-2}$ s$^{-1}$) using an 8 day moving window (time step 1 day) with PPFD as independent variable;

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

where $F_{\text{csat}}$ is CO$_2$ exchange at light saturation (mg CO$_2$ m$^{-2}$ s$^{-1}$), $R_d$ is dark respiration (mg CO$_2$ m$^{-2}$ s$^{-1}$) and $\alpha$ is initial slope of the light response curve (mg CO$_2$ µmol$^{-1}$ PPFD).

The parameterization of the light response curve was only considered significant when all parameters ($F_{\text{csat}}, R_d, \alpha$) were significantly different from zero ($p < 0.05$). Gaps in PPFD were filled using data from STRÅNG (http://strang.smhi.se/), an operational mesoscale radiation model from SMHI (Swedish Meteorological and Hydrological Institute) that produces radiation data covering Scandinavia at a resolution of about 11 km. The obtained light response curve parameters and PPFD data were subsequently used to fill gaps.
in CO₂ flux data. Remaining CO₂ flux gaps, smaller than 7 days, were filled with mean diurnal variation using an 8 day window (Falge et al. 2001). Remaining longer gaps (DOY 208–255 and 300–327 in 2006; DOY 97–108 in 2007; DOY 225–235 in 2008; DOY 161–169, 221–231 and 233–240 in 2009) were filled using artificial neural networks (Papale and Valentini 2003).

The total uncertainty in annual CO₂ sums was estimated based on the procedure described in Elbers et al. (2011) and Lund et al. (2012). In addition, the effect of the long gaps (>7 days) was evaluated by using alternative gap-filling methods. The parameters of the light response curve (Fcsat, Rsat, α) were estimated based on available PPFD and NEE data 4 and 8 days prior to and following the gap, respectively. In case the parameterization of the light response curve was not significant, the gap was filled using average NEE 4 and 8 days prior to and following the gap, respectively. The uncertainty related to long data gap-filling was determined from the standard deviation of the three resulting NEE sums (calculated from artificial neural network and alternative gap-filling method based on 4 and 8 days, respectively).

Gross primary production (GPP) was subsequently modelled using the light response curve (equation (1)) by subtracting Rsat (Lindroth et al. 2007). Daytime ecosystem respiration (Reco) was calculated as the difference between measured and gap-filled NEE and modelled GPP, while night-time Reco equalled measured and gap-filled NEE.

To extract seasonality and reduce random noise, time series of original MODIS NDVI were smoothed using local Savitzky–Golay curve fits in the TIMESAT software (Jönsson and Eklundh 2004). Based on the quality information of the MODI3Q1 data, higher weights were assigned to data points with higher quality and lower weights to those with lower quality (Schubert et al. 2010).

3. Results and discussion

3.1. Meteorological conditions

The annual temperature during the study period was on average 1.6 °C above the long-term (1961–90) average (figure 1). Most of the excess heating occurred during the winter months; the period DJF was on average 2.1 °C warmer while MAM, JJA and SON ranged from 1.0 to 1.5 °C warmer. The annual precipitation was on average slightly above the long-term average (+88 mm); however, there were large variations within and between years. For example, in 2006 the months of June and July only received 31% of normal (1961–90) precipitation, while in 2007 the same months will therefore be referred to as drought periods. The inter-annual variation in net ecosystem exchange (NEE) during the growing season between late May (DOY 150) and early September (DOY 250). In 2008 the summer-time

DOY 213. In 2007 and 2009 the water table generally varied between 0 and −10 cm, while in 2008 the water table was below −10 cm from DOY 126 until DOY 217 (WTN data is missing from DOY 211 but there was low precipitation until DOY 217). Outside of the time period shown in figure 2, water table was above −10 cm in all years. Using WTD = −10 cm as a threshold for dry soil conditions in Fäjemyr, two long time periods with dry conditions can be identified: DOY 164–213 in 2006 and DOY 126–217 in 2008. These two periods in 2006 and 2008 will therefore be referred to as drought periods. The mean WTN (±1 standard deviation) for DOY 100–300 was −3.0 ± 7.3, −0.2 ± 3.9, −7.3 ± 6.7 and −5.0 ± 3.1 cm for 2006, 2007, 2008 and 2009, respectively.

3.2. Net ecosystem exchange of CO₂

The inter-annual variation in net ecosystem exchange (NEE) was large with a range of −108 to 87 g CO₂ m⁻² yr⁻¹ (figure 3). Most of this variability was caused by differences in NEE during the growing season between late May (DOY 150) and early September (DOY 250). In 2008, the summer-time
CO₂ net uptake rate was lower compared with other years, which coincided with the drought period (figure 2). The summer-time net CO₂ uptake during 2008 barely balanced the emissions during previous winter and spring, and after taking the net CO₂ emissions during late part of the year into account the peatland acted as an annual source of 86.4 g CO₂ m⁻², with an associated uncertainty of ±29.1 g CO₂ m⁻². In 2006, the net uptake rates during early summer were similar to the wetter years (2007 and 2009); however, around DOY 201 the peatland no longer acted as a sink of CO₂ on a daily basis. Again, this event corresponded to drought conditions with low water table (figure 2). In 2006, the peatland was an annual source of 52.4 ± 26.0 g CO₂ m⁻² while for 2007 and 2009, when water tables were close to the surface throughout the growing season, the annual CO₂ balances were −107.7 ± 28.1 and −106.1 ± 16.3 g CO₂ m⁻², respectively.

The four year CO₂ balance of this temperate bog (−18.8 ± 102.7 g CO₂ m⁻² or −5.1 ± 28.0 g C m⁻²) was close to neutral, i.e., zero net CO₂ exchange. Other studies on comparable peatland sites have generally reported stronger CO₂ sinks: in a boreal poor fen in Sweden, the annual CO₂–C balance ranged between −48 and −61 g C m⁻² (Sagerfors et al 2008) based on three years of measurements. Roulet et al (2007) reported six years of annual CO₂–C balances for a temperate Canadian bog ranging −2 to −112 g C m⁻². The annual CO₂–C balance of an Irish blanket bog based on six years of measurements ranged −13 to −84 g C m⁻² (Koehler et al 2011). Although being multi-year averages, these budgets may still not reflect the true contemporary CO₂ exchange in northern peatlands, as extreme events such as droughts may occur on timescales longer than 3–6 yr. Similarly, the CO₂ balance at Fäjemyr may be biased by the fact that summer-time droughts occurred during two out of the four years in this study.

3.3. CO₂ flux components

In 2008, ecosystem respiration (Reco) rates were similar compared with other years (figure 4), while gross primary production (GPP) rates were generally lower (i.e. less negative GPP rates) during the drought period (DOY 126–217). In 2006, when the drought period began DOY 164, GPP rates were comparable to or even higher than the wet years of 2007 and 2009; however, Reco rates during the drought period of 2006 were also higher compared with other years.

Daytime NEE and GPP are largely regulated by the amount of incoming photosynthetic photon flux density (PPFD). To be able to assess how the drought periods affected the Fäjemyr peatland ecosystem independent from variations in PPFD, daily GPP rates at PPFD > 1000 µmol m⁻² s⁻¹ were calculated, which represent GPP at or close to light saturation (figure 5). Such GPP rates were not lower (i.e. less negative) during the drought period in 2006, while in 2008 GPP rates were consistently lower during DOY 140–220.

3.4. Effects of drought conditions on peatland vegetation and CO₂ exchange

3.4.1. Short-term effects (days to years). The effects of drought and low water tables at Fäjemyr on the land–atmosphere exchange of CO₂ and its components were regulated by the timing of the drought event. In 2008, when water tables were low during early growing season (figure 2), the vascular vegetation of the peatland was likely affected by water stress during its developing phase. It was also
observed in the field that Sphagnum mosses suffered from desiccation during this period. This resulted in decreased biomass build-up (figure 6) and lowered photosynthetic rates throughout large parts of the growing season (figure 5), and the peatland acted as a source of CO₂ on an annual basis. In 2006, the drought period occurred later when vascular plants were already established. Therefore, GPP at light saturation was not affected (figure 5); however, the unusually low water table exposed a thicker layer of peat for aerobic decomposition, and the ecosystem turned into a source of C at an earlier moment in time compared with the wet years. This argument is further supported by TIMESAT-smoothed NDVI data (figure 6). Summer-time NDVI were similar in 2006, 2007 and 2009, with average NDVI values during summer (DOY 152–243) being 0.68, 0.71 and 0.69, respectively. In 2008, the average NDVI was 0.63 during the same period, indicating less dense vegetation and greenness during this year. During a prolonged drought litterfall may decline due to reduced GPP (van der Molen et al. 2011); such carry-over effect from the drought period in 2008 may be an explanation for the low CO₂ emissions during early 2009 (figure 3), caused by the reduced supply of labile C.

Previous studies have suggested that droughts in peatlands primarily affect GPP (Shurpali et al. 1995, Armeth et al. 2002, Lafleur et al. 2003), while others have argued that $R_{ecm}$ is more affected (Alm et al. 1999, Aurela et al. 2007). The results in this study indicates that the timing, severity and duration of the drought periods regulate the effects on GPP, $R_{ecm}$ and NEE in a temperate bog. A short but severe drought period during the peak growing season may not significantly affect GPP, but can increase $R_{ecm}$ due to increased heterotrophic respiration. On the other hand, a long drought period during the vegetation developing phase may significantly decrease GPP and to a lesser extent also $R_{ecm}$. Furthermore, it is likely that various peatland types will show dissimilar responses to dry conditions (Lafleur 2009, Sulman et al. 2010). Aurela et al. (2004) argue that peatlands characterized by hydrological buffers, such as fens (minerotrophic peatlands) with a dynamic connection to the catchment scale water system, will increase their C uptake in a warmer climate. Bogs (ombrotrophic peatlands) on the other hand, which are decoupled from the groundwater of surrounding watershed, are dependent on precipitation inputs to maintain their water balance. A possible generalization may thus be that bogs are more sensitive to dry conditions in terms of their CO₂ balance as compared with fens, since the former are rainwater-fed while the latter is fed by rain and groundwater. The relative contribution of vascular plants and mosses will act to regulate peatland ecosystem resilience to drought, due to differences in water uptake and evapotranspiration processes (Sulman et al. 2010).

3.4.2. Long-term effects (years to centuries). If dry summer conditions become more abundant in the future, the C sink functioning of peatlands that are sensitive to variations in water balance may cease. Summer-time (JJA) temperature and precipitation in northern Europe are predicted to increase with on average 2.7°C and 2%, respectively, for the period 2080–99 compared with 1980–99, according to 21 global climate models for the A1B scenario (Christensen et al. 2007). According to our data the summer period (JJA) in 2006 was 2.6°C warmer and received 7% more precipitation compared with long-term average 1961–90. The precipitation was, however, not equally distributed with 80% of the rainfall occurring in August. Still, the mid-summer drought period in 2006 was associated with the lowest water table and highest $R_{ecm}$ rates during the study period. Modelling studies assessing the impact of water level variations on peatland CO₂ exchange have shown that heterotrophic respiration is most sensitive to changes in WTD (Yurova et al. 2007, St-Hilaire et al. 2010), due to increases in soil temperature and increased potential for aerobic decomposition. But, as heterotrophic respiration may contribute as little as 10% to peatland $R_{ecm}$, the relative impact of decreased GPP and autotrophic respiration through effects on vascular plant conductance and moss water content may be more important for the contemporary net CO₂ exchange (St-Hilaire et al. 2010). However, on a longer timescale, an increased frequency and extent of drought conditions are likely to have important effects on peat soil decomposition, due to the feedback effect between water table and decomposition rates, known as the paludification (pond-making) process (Clymo 1984, Ise et al. 2008). Lowered WTD reduces peat soil water retention capacity and the summer-time temperature insulation by peat, increasing the sensitivity of peat decomposition to temperature. Ise et al. (2008) found that a long-term simulation with experimental warming of 4°C caused a loss of 40 and 86% of shallow and deep peat soil organic C, respectively. However, their study did not include vegetation dynamics. Peatland plants will respond to changes in temperature, hydrology and nutrient status, and changes in vegetation structure and composition will act to regulate CO₂ dynamics. Drier and warmer conditions will stimulate vascular plant growth at the cost of Sphagnum mosses (Riutta et al. 2007, Limpens et al. 2008), resulting in increased litter decomposability. Trees may invade peatlands with sufficiently lowered water tables, however, nutrient-poor bogs can support only limited tree growth (Alm et al. 1999). An increased
amount of vascular plants, especially shrubs, will increase peatland above-ground biomass, and given increased soil decomposition rates there may thus be a transfer of C from the soil pool to standing biomass, although such C reallocation should be transient in time. By taking these factors into account, it is likely that if increased evapotranspiration rates are not balanced by increased precipitation rates in a warmer future, peatlands, especially bogs, will weaken their sink strength or even become persistent sources of atmospheric CO₂.

4. Conclusions

This study underlines the importance of drought periods as regulators of inter-annual variation in CO₂ exchange in peatlands. Based on four years of eddy covariance CO₂ flux measurements, we found that timing, severity and duration of drought regulated the effect on the CO₂ dynamics. A short but severe drought period during mid-summer 2006 increased Rₚₑₑₒ rates, while GPP was not affected; while an early and prolonged drought period in 2008 decreased GPP rates. Data presented in this study can be useful to study the effects of droughts on the biophysical processes responsible for the net CO₂ exchange in more detail, using process-based peatland models with high temporal resolution such as McGill wetland model (St-Hilaire et al 2010) and the modified GUESS-ROMUL model (Yurova et al 2007).

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