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Responses of carbon dioxide flux and plant biomass to drought in a treed peatland in northern Alberta: a climate change perspective

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Abstract

Northern peatland ecosystems represent large carbon stocks that are susceptible to changes such as accelerated mineralization due to water table lowering expected under a climate change scenario. During the growing seasons of 2011 and 2012 we monitored CO₂ fluxes and plant biomass along a microtopographic gradient (hummocks-hollows) in an undisturbed dry continental boreal treed bog (control) and a nearby site that was drained (drained) in 2001. Ten years of drainage in the bog significantly increased coverage of shrubs at hummocks and lichens at hollows. Considering measured hummock coverage and including tree incremental growth, we estimate that the control site was a larger sink in 2011 of -40 than that of -13 g C m⁻² in 2012 while the drained site was a source of 144 and 140 g C m⁻² over the same years. We infer that, drainage induced changes in vegetation growth led to increased biomass to counteract a portion of soil carbon losses. These results suggest that spatial variability (microtopography) and changes in vegetation community in boreal peatlands will affect how these ecosystems respond to lowered water table potentially induced by climate change.

1 Introduction

Northern peatlands, functioning as carbon (C) sink ecosystems of the boreal forest over millennia, have stored approximately one third of global soil carbon (Tarnocai, 2006; Tarnocai et al., 2009; Turunen et al., 2002). These peatlands dominate the Canadian and Albertan landscape with coverage of 12% and 16.3% respectively and contain almost twice as much C per unit area (115 kg m⁻²) as tropical forests (Carlson et al., 2010; Vitt et al., 2009). Bogs in Western Canada (e.g. Alberta) are often covered by trees in contrast to open bogs in Eastern Canada (Turetsky et al., 2002). In Canada, the large peatland coverage (1.136 million km²) combined with high carbon density results in a store of approximately 147 Gt of soil organic C (Tarnocai, 2006). The large C pools

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formed as a result of net uptake of carbon dioxide (CO₂) from the atmosphere over millennia, if destabilized through a change in climate (e.g. atmospheric warming and subsequent drought), would lead to accelerated emission of greenhouse gases (GHGs) to the atmosphere (Gruber et al., 2004; IPCC, 2007; Limpens et al., 2008).

5 The formation and stability of peatland C stock is sensitive to changes in climatic conditions (e.g. atmospheric temperature and precipitation) (Vitt et al., 2009). Ongoing climate change is predicted to be most severe at northern latitudes where most of the peatlands are situated (Tarnocai, 2006; IPCC, 2007). The Canadian Global Climate Model (CGCM1, 2000) predicted 3–4 °C increase in mean annual air temperature
10 by 2020, with the greatest potential temperature increase (> 20 °C) occurring in winter months under extreme climate warming scenarios (Hengeveld, 2000). The increase of air temperature, combined with altered precipitation patterns, could lead to overall decrease in soil moisture across the high latitude region (IPCC, 2007). Drought/warming induced water table drawdown could have a significant impact on the sustainability and
15 ecosystem functions of boreal peatlands (Tarnocai, 2006; Adkinson et al., 2011; Blo-dau and Siems, 2012; Chivers et al., 2009; Ise et al., 2008; Riutta, 2008; Robroek et al., 2009; Roulet, 2000; Waddington and Price, 2000; Limpens et al., 2008). The increased atmospheric temperature and lowered water table can cause enhanced rates of organic matter decomposition and CO₂ emission, consequently resulting in the gradual
20 depletion of peat C pool (Turetsky and Louis, 2006).

Carbon fluxes in peatlands occur in the forms of the uptake of C from the atmosphere via gross ecosystem photosynthesis (GEP) and the release of C to the atmosphere by plant (autotrophic) respiration and respiration by heterotrophic microorganisms (R_{tot}). The sum of GEP and R_{tot} is defined as the net ecosystem exchange (NEE) of CO₂.
25 Net uptake of CO₂ causes the accumulation of carbon in the form of plant biomass and soil organic matter.

Photosynthesis and autotrophic respiration may vary independently with changing temperature (Ryan, 1995; Ow et al., 2008). Warm and dry conditions in peatlands can either stimulate CO₂ uptake by enhanced GEP (e.g. Moore and Dalva, 1993; Upde-

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graff et al., 2001; Syed et al., 2006; Ise et al., 2008; Cai et al., 2010) or reduce C uptake by limiting moisture (Alm et al., 1999; Roulet et al., 2007; Ise et al., 2008). Lowered water table in a treed bog increased black spruce productivity and fine root biomass significantly in a Canadian (Lieffers and Rothwell, 1987) and a Finnish peatland (Heikurainen and Pakarinen, 1982). Cool temperatures and near surface water
5 table conditions which typically occur in northern peatland ecosystems suppress respiration (Gorham, 1991; Hanson et al., 2000; Davidson and Janssens, 2006; Chapman and Thurlow, 1998). Predicted warming and subsequent lowered water table will result in enhanced CO₂ emissions from northern peatland soils (Moore, 2002; Roulet et al.,
10 1992) where fine tree root biomass may contribute to soil total respiration (Lieffers and Rothwell, 1987). However, while the variation in respiration may not always be linked to fluctuation in water table, it is related to changes in moisture. Thus water table is an important control on respiration in peatlands in which soil peat moisture is sensitive to lowering of water table (Parmentier et al., 2009). Therefore, depending on the balance
15 of GEP and R_{tot} changes as a consequence of warming and/or drought, there may be a net increase or decrease in thickness of peat (Moore et al., 2006).

Autotrophic respiration by tree/shrub roots may contribute a significant amount to R_{tot} when lowered water table stimulates root growth and promotes overall shrub/tree growth in dried peatlands (Lohila et al., 2011). Separating tree root respiration (R_r)
20 from R_{tot} is critical in order to attribute the C losses to various sources of soil respiration and to better understand C source/sink dynamics (Hanson et al., 2000; Valentini et al., 2000; Janssens et al., 2001) of boreal treed peatlands in the face of global climate change. Isolating R_r from R_{tot} can make possible the comparison of CO₂ fluxes and plant biomass of a treed bog with those of an open bog provided all controlling
25 variables are similar. The contribution of R_r to R_{tot} has been quantified using closed chamber technique in various forest ecosystems. Hermle et al. (2010) separated black spruce root respiration from soil total respiration by measuring the difference between control and trenched plots. They found that the R_r was 24 % of the soil total respiration. The contribution of R_r to soil total respiration was higher (37 %) in a subtropical forest

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(Wang et al., 2008) in a similar trenching experiment. An even higher contribution of rhizomicrobial respiration was quantified by Hanson et al. (2000) in forest vegetation in Florida.

As peatlands become drier under warming climate, it has been suggested that vegetation communities could shift towards a shrub/tree dominated system (Weltzin et al., 2000; Camill, 1999; Lohila et al., 2011), which in turn can alter the above (Lohila et al., 2011) and belowground C dynamics (Blodau and Siems, 2012).

The shift in vegetation coverage and C dynamics vary with microtopographic features (e.g. hummocks (H) and hollows (W)) in peatlands (e.g. Strack et al., 2006, Waddington and Roulet, 2000). Also, the relationships between peatland CO₂ fluxes and water table may vary spatially between different microtopographic features in peatlands (Charman and Chichester, 2002; Joosten and Clarke, 2002). For example Strack et al. (2006) reported reduced GEP at hummocks and enhanced GEP at hollows and lawns in a water table drawdown experiment in an open poor fen peatland. Bubier et al. (2003) reported a significant increase in respiration at a bog hollow during a dry summer and no change in the rate of respiration at the hummock.

Drought response experiments have been conducted in Eastern Canada: for example, Strack et al. (2006) and Whittington and Price (2006) where most of the peatlands generally receive high precipitation, have high surface humidity and are characterized by their open nature often lacking tree cover. Climatic and environmental (temperature, precipitation and water table position) response experiments have been conducted in Western Canada (Adkinson et al., 2011; Syed et al., 2006) where in contrast to Eastern Canada, most of the peatlands are generally drier and warmer and are characterized by their tree cover (Vitt et al., 1998; Price, 2010). However, these are short-term responses to drought studies and differences in microtopographic response were not considered. Therefore, the Western Canadian continental treed bogs are expected to respond to predicted climate change differently for CO₂ fluxes and plant biomass than those of Eastern Canadian open peatlands with the potential for vegetation succession when water tables are persistently lowered. Moreover, we are unaware of any drought

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response CO₂ flux and biomass change experiments in treed peatland that has measured contribution of R_r to R_{tot} using the closed chamber technique.

Therefore, our research aimed: (1) to compare CO₂ fluxes along a microtopographic gradient (hummock vs. hollow) between a natural (control) and a drained bog, (2) to quantify changes in tree biomass and ground layer biomass along microtopographic gradient in response to drainage, and (3) to determine the contribution of tree root respiration to soil total respiration as affected by drainage.

2 Methods

2.1 Study sites

Two sections of a dry continental ombrotrophic bog were selected: one undisturbed section (CONTROL) (55.21° N, 112.31° W) and one section that was drained in 2001 (DRAINED) (55.16° N, 112.28° W). The two sections were approximately 8 km apart and located in north central Alberta, approximately 100 km northeast of Athabasca, Alberta, Canada. Both sites are underlain by sandy clay substrate and have peat depth exceeding 4 m. Climate in this region is sub-humid continental with mean annual and growing season (May to October) temperatures at 2.1° C and 11.7° C (Environment Canada, 2013). Mean annual precipitation at Athabasca is 504 mm, with 382 mm falling as rain. The research was conducted over two growing seasons (2011–2012). Mean growing season rainfall and air temperatures measured on site were 402.7 mm and 281.6 mm and 13.06° C and 13.08° C for 2011 and 2012, respectively.

These bogs are classified as treed low shrub bogs with typical mosaic of hummock and hollow microforms (Riley, 2003). The hummocks and hollows at the control site are dominated by *Sphagnum* mosses with sparse shrubs. The drained site has higher coverage of shrubs on the hummocks and higher lichen coverage in the hollows. Common mosses include *Sphagnum fuscum*, *Sphagnum magellanicum*, *Sphagnum capillifolium* and *Pleurozium schreberi* while common shrubs include Labrador Tea (*Ledum*

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groenlandicum), Lingonberry (*Vaccinium vitis-idaea*), small bog cranberry (*Oxycoccus microcarpus*) and cloudberry (*Rubus chamaemorus*). Black spruce (*Picea mariana*) is the most common tree in these bogs.

2.2 CO₂ exchange

5 At each site, three hummocks and three hollows were chosen as the study plots. A 60 × 60 cm steel collar was permanently installed in each plot. The CO₂ fluxes were measured weekly during the growing seasons using a closed chamber having dimensions of 60 × 60 × 30 cm (L × D × H), made of clear acrylic glass and corrected for transmittance (88 %). Two small battery operated fans were installed inside the chamber to circulate the air and achieve equilibrium CO₂ concentration between measurements. 10 The instantaneous CO₂ concentration in the chamber was monitored with a portable infrared gas analyser (PP systems, USA, EGM-4). Photosynthetically active radiation (PAR) was measured with a quantum sensor (PP systems, USA) placed at the top of the chamber. The temperature inside the chamber was measured with a thermocouple thermometer (VWR Int., USA). All measurements were made at 15 s intervals for up to 15 1.75 min. At the time of flux measurements, soil temperatures at the depths of 2, 5, 10, 15, 20 cm were measured with a thermocouple thermometer at all plots. Water table relative to moss surface was measured from a permanently installed well associated with each plot.

20 Net ecosystem CO₂ exchange (NEE) was calculated using exponential change (Kutzbach et al., 2007) instead of linear change in CO₂ concentration in the chamber headspace with time, as a function of volume, air temperature and pressure inside the chamber, according to ideal gas law. The exponential regression was used because covering soil and/or vegetation essentially manipulates the spontaneous CO₂ fluxes by 25 altering the concentration gradients between the soil, the vegetation and the air inside the chamber. Due to the constantly changing controls on CO₂ flux within the chamber, no linear decrease or increase of CO₂ concentration inside the chamber can be expected. Kutzbach et al. (2007) found that the linear CO₂ fluxes compared with exponen-

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tial fluxes were up to 40 % lower, over CO₂ chamber closure time of only two minutes. CO₂ flux measurements in the dark when the chamber was covered with an opaque tarp, represented R_{tot} . We recognize that this R_{tot} represents only understory above-ground biomass respiration, heterotrophic soil respiration and tree root respiration and 5 ignores respiration of the overstory aboveground tree biomass. GEP was determined as the difference between NEE and R_{tot} . We used the convention that negative values indicate an uptake of CO₂ by the ecosystem. Maximum rates of GEP (GEP_{max}) and NEE (NEE_{max}) were calculated when PAR level was > 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ following Bubier et al. (2003).

10 2.2.1 Seasonal CO₂ exchange model

The growing season GEP was estimated using an empirical model following Riutta et al. (2007) parameterized separately for each sampling plot for the seasons 2011 and 2012. The seasonal GEP was estimated by:

$$\text{GEP} = \frac{\text{PAR} \times P_{\text{max}}}{\text{PAR} + k} \times e^{\left[-0.5 \times \left(\frac{\text{WT} - \text{WT}_{\text{opt}}}{\text{WT}_{\text{tol}}}\right)^2\right]} \times e^{\left[-0.5 \times \left(\frac{T - T_{\text{opt}}}{T_{\text{tol}}}\right)^2\right]} \quad (1)$$

15 where, P_{max} denotes the potential maximum rate of GEP ($\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) if water table and temperature are not limiting and the parameter k denotes the level of PAR at which half of the GEP_{max} occurs. WT is the water table position (cm), WT_{opt} and WT_{tol} are parameters in a Gaussian response of GEP to water table when GEP is optimized and width of the curve respectively, T is the soil temperature ($^{\circ}\text{C}$) at 5 cm below moss surface and T_{opt} and T_{tol} are parameters in a Gaussian response of GEP to the soil 20 temperature when GEP is optimized and width of the curve.

Model parameters for seasonal GEP, r^2 values, standard errors (\pm) and standard errors of the estimates at control and drained microforms are presented in Table 1. Two-thirds of the data were used for model construction, whereas one-thirds of the 25 data were used for independent testing of the models following Tuittila et al. (2004).

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The growing season R_{tot} was estimated using multiple linear regressions with soil temperature at 5 cm depth and water table position by:

$$R_{\text{tot}} = a \times T + b \times \text{WT} + c \quad (2)$$

where, a , b and c are regression coefficients (Table 2).

5 Seasonal GEP and R_{tot} were estimated based on Eqs. (1) and (2) for each twenty minute period between 1 May and 31 October, averaged daily and summed for a growing season total based on measurements made on site for PAR (LI-190, LI-COR, Nevada, USA), WT (Levellogger Junior, Solinst, USA) and temperature (Onset HOBOWare Pro, MA, USA). Growing season ground layer NEE was determined by
10 adding seasonal GEP to seasonal R_{tot} estimates.

2.2.2 Model validation

The GEP and R_{tot} models were validated by correlating the measured data (not used for model construction) and modeled values. Model validation showed excellent agreement between predicted and measured values (Fig. 1a and b).

15 2.2.3 Tree root respiration

To explain the contribution of tree root respiration (R_r) to total soil respiration (R_{tot}), a trenching method (Wang et al., 2008) was used. A total of 32 plots (eight hummocks and eight hollows at each site, (in addition to the CO₂ flux plots) were chosen. At each site, four hummocks and four hollows were trenched to 30 cm depth (approximately
20 the bottom of the root zone) around 60 × 60 cm plots in May 2012. The trenched plots were lined with a thick polyethylene sheet to prevent root ingrowths. The trenches were backfilled in reverse order of removal while minimizing disturbances as much as possible. It was assumed that the trenching cut down most of the live root ingrowth. The remaining four hummocks and four hollows were left intact to measure the difference
25 in CO₂ emission between trenched (having minimal tree roots) and intact (with all tree

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roots) plots. All plots were clipped every two weeks, using shears, to ensure that soil surface was free of live mosses, shrubs and herbs during July to September 2012. The CO₂ emissions from all plots were measured using the same instruments and chamber used for the measurement of GEP and R_{tot} . We had a methodological challenge that
5 while the trenching separates R_r from R_{tot} , it also adds fresh litter to the soil that can add to the existing heterotrophic soil respiration.

Trenching experiments have been performed to separate root autotrophic respiration from R_{tot} (e.g. Hermle et al., 2010; Hanson et al., 2000; Wang et al., 2008; Díaz Pinés et al., 2010; Kuzyakov, 2006; Brant et al., 2006). In all cases the assumption
10 has been made that the trenched roots die off within a short time and that afterwards the measured R_{tot} can solely be attributed to heterotrophic soil respiration. Trenching immediately disrupts the supply of recent photosynthates to the roots and mycorrhiza. The mycorrhizal fungi and associated bacteria will suffer from the lack of labile C. Bowden et al. (1993), Boone et al. (1998) and Rey et al. (2002) in trenching experiments
15 showed that C content of decomposing fine roots in trenched plots contribute little to R_r and become stable in the four months after trenching. Therefore, no correction for extra CO₂ from decaying fine roots is necessary. However, the root exclusion experiment may not be useful if extended through a complete annual cycle, as over such a long period there is the possibility of reinvasion of roots into the previously root free trenched
20 plot (Edwards and Norby, 1999). While it is clear that findings from such trenching measurements should be interpreted carefully, the primary focus of this paper is to quantify R_{tot} while investigating R_r to better understand the contribution of various processes to shifts in R_{tot} following drainage.

2.3 Biomass and tree productivity

25 Aboveground biomass was measured by clipping 18 (9 H and 9 W), 25 × 25 cm quadrats at each of control and drained sites, in mid July 2011. The biomass was clipped at the base of the capitulum at 1.0 cm below moss surface following Clymo (1970) and Loisel et al. (2012). From the microforms at each site, soil cores of only

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20 cm depth were collected due to frozen peat beyond this depth. The soil cores were sectioned into two depths (0–10 and 10–20 cm) and roots were sorted into coarse (> 2 mm) and fine (< 2 mm) fractions. For tree biomass, we selected three 10 × 10 m quadrats at each site. Trees were divided into tall (> 137 cm height) and short (< 137 cm height) for biomass estimation. All trees were measured for their height, diameter at breast height (DBH, when tall enough) and basal diameter (DB). Tall tree biomass was calculated by using an allometric equation from Grigal and Kernik (1984) while short tree biomass was determined by using an allometric equation generated by regressing height with oven-dried weight as (Dry biomass = 0.0085 (tree height)^{2.2088}, $R^2 = 0.93$, $p < 0.001$).

The incremental biomass growth of tall trees for 2011 and 2012 was calculated based on tree ring widths using DendroScan (Varem-Sanders et al., 1996). The incremental biomass of short trees for 2011 and 2012 was calculated by regressing leader length with height following Mullin et al. (1992) and Macdonald and Lieffers (1990).

2.4 CO₂-C balance calculations

The C balance of the treed control and drained sites was calculated separately for 2011 and 2012. To calculate the seasonal C balance of the sites, two components of the C budget were added: the seasonal CO₂ fluxes of the ground-layer (understory, aboveground and belowground) biomass and the incremental biomass growth of the tree cover during the study years.

The seasonal CO₂ fluxes at hummocks and hollows were upscaled by multiplying mean estimated growing season CO₂ exchange by their respective coverage of 56 and 44 % and 52 and 48 % at the control and drained sites, respectively (Table 4). The incremental growth of the tree cover was added to the ground-layer CO₂ exchange assuming that biomass had a carbon content of 50 %.

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2.5 Statistical analysis

Differences in GEP_{max}, R_{tot} , NEE_{max}, and aboveground biomass between sites and microforms were tested by two-way ANOVA, using Minitab 16.0 (Minitab Inc., PA, USA). Differences in R_r between sites, microforms and trenched and intact plots were tested for significance using a three-way ANOVA using SPSS 20.1. The nonlinear and linear regression models (Eqs. 1 and 2) were used to construct GEP and R_{tot} models (SPSS 20.1) and to estimate seasonal CO₂ balance.

3 Results

3.1 Site conditions

Ten years after initial drainage, the water table at the drained site was as much as 80 cm lower than that at the control site (Fig. 1). The growing seasons of 2011 and 2012 were warmer by 1.36 °C and 1.38 °C respectively, and wetter by 41.9 mm in 2011 and drier by 79.2 mm in 2012 than 30-yr average at Athabasca. The combination of lower rainfall and higher temperature in 2012 led to a decrease in water level at control and drained hollows by 4.5 and 4.3 cm and at control and drained hummocks by 8.0 and 7.2 cm respectively (Fig. 2).

The drained site was trenched around in 2001 and the data on pre-drawdown hydrology was not available. However, the control and premises of drained sites being part of the same peatland complex and having similar vegetation layers, air temperature and peat depth are considered to be statistically similar before start of this study in 2001. As a result of 10 yr drainage, *Sphagnum* coverage at the drained site was reduced significantly ($F(3, 32) = 33.40$, $p < 0.001$) compared to the control site, but no significant difference in *Sphagnum* coverage was observed between microforms at either site. *Sphagnum* at drained site was replaced by shrubs at hummocks and lichens at hollows (field observation, data not presented here).

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3.2 Biomass

Vascular plant biomass at the drained hummock was significantly higher than that at the control hummock ($F(1, 32) = 17.07, p < 0.001$) and there was a significant interaction between drainage and microform ($F(1, 32) = 35.74, p < 0.001$), while there was no difference between control and drained hollows (Table 3, Fig. 3). Conversely, moss biomass at drained hummocks was significantly lowest of all plots ($F(1, 32) = 26.28, p < 0.001$). In fact, moss biomass at the drained site was overall much lower than those in the control site regardless of microform type, indicating a strong decline of moss cover with drainage. Lichen biomass on the other hand showed an increase following drainage, but it was the drained hollow that had the highest lichen biomass (over 30 times higher than that in the control hollows) ($F(1, 32) = 7.9, p = 0.008$) and the interaction between drainage and microform was statistically significant. As a whole, aboveground biomass was highest at drained hummocks ($F(1, 32) = 14.24, p = 0.003$) while lowest at control hollows. Neither total belowground root biomass nor tree biomass were significantly different between microforms and/or sites. However, total root biomass was higher in the drained site than that in the control (Table 3).

Although tree biomass was higher in the control site by 178 g m^{-2} , yet the annual increment during the study years (2011 and 2012) was significantly higher in the drained site (66 and 60 g C m^{-2}) than that in the control (38 and 33 g C m^{-2}) ($F(1, 3) = 3025, p = 0.012$).

3.3 CO₂ fluxes

3.3.1 Measured CO₂ fluxes

Drainage did not change GEP_{max} significantly both in 2011 and 2012 (Fig. 4; two-way ANOVA, 2011; $F = 0.06, p = 0.813$, 2012; $F = 4.13, p = 0.08$). However, GEP_{max} was significantly higher at hummocks than hollows (2011; $F = 7.84, p < 0.027$, 2012; $F = 8.99, p < 0.017$). Drainage had a significant interaction with microtopography in

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2012 leading to significantly different GEP_{max} at drained microforms. Drainage resulted in significantly higher R_{tot} (2011; $F = 6.85, p < 0.037$, 2012; $F = 8.52, p < 0.019$), but remained statistically similar between microforms at both sites in both years. The drained hollows were the largest sources of CO₂ emission largely due to the significantly higher contribution of R_r ($5.03 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) to R_{tot} ($18.02 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) than that of the R_r contribution of $1.51 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ to R_{tot} ($11.84 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) at control hollows (see 2012 in Fig. 3). NEE_{max} was positive in 2011 but became negative (net sink of CO₂) in 2012 at control microforms. Subtracting R_r from NEE_{max} switched the drained hummocks to a moderate sink and the control microforms to larger sinks of CO₂, while considerably reduced emissions at the drained hollows (Fig. 4).

3.3.2 Modeled CO₂ fluxes

Based on empirical models (Eqs. 1 and 2), the ground layer at the control site was a small sink of CO₂ taking up an estimated $6.9 \text{ g CO}_2 \text{ m}^{-2}$ largely due to the significantly higher GEP at its hollows than that of its hummocks, whereas the ground layer at the drained site was a substantial source of CO₂ losing an estimated $770 \text{ g CO}_2 \text{ m}^{-2}$ largely due to significantly higher R_{tot} at its hollows than that of its hummocks, during the 2011 growing season (Table 4). In 2012, a shift in the functions of hollows and hummocks at the control site was noticed, where hummocks became a moderate sink of CO₂, and the hollows became a substantial source. However, the drained microforms and site remained consistently sources of CO₂ (Table 4).

3.4 C balance

In the growing season of 2011, the ground-layer of control and drained sites were a small sink (2 g C m^{-2}) and substantial source (210 g C m^{-2}), respectively. In the growing season of 2012, the control site became a moderate source (20 g C m^{-2}) while the drained site remained a substantial source (200 g C m^{-2}). To calculate the final C balance, we included estimated tree incremental growth during study years, and estimated

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that the control site was a larger sink of 40 g C m^{-2} in 2011 than that of 13 g C m^{-2} in 2012. However, the drained site remained a source through both study seasons, losing 144 g C m^{-2} in 2011 and 140 g C m^{-2} in 2012 growing season.

4 Discussion

5 Previous research has shown that warm and dry summer conditions can reduce net CO_2 uptake in peatlands by enhancing respiration greater than productivity (Alm et al., 1999; Arneeth et al., 2002; Bubier et al., 2003; Aurela et al., 2007). Similarly, in our experiment warmer and drier weather in 2012 reduced net uptake of CO_2 and reduced the growing season C sink at the control site. The shift was due to the substantially
10 increased R_{tot} at the hollows greater than that of combined increase in GEP at the microforms (Table 4). The enhanced R_{tot} at hollows might be due to stressed vegetation growth observed at the drier hollows (Fig. 2). In contrast there was a little change in GEP or R_{tot} at the drained site in 2012 and thus no real change in net CO_2 emission. Similar to our findings on response of warmer and drier weather, Aurela et al. (2004)
15 and Lafleur and Humphreys (2008) also found increased GEP with warmer growing season temperature but reduced GEP and enhanced R_{tot} at extreme temperature in a sub-arctic fen. Our findings together with others (e.g. Griffis et al., 2000; Bubier et al., 2003; Aurela et al., 2007) demonstrate the important interaction between temperature and water availability for GEP and R_{tot} response, as either factor alone could not
20 determine the overall growth response of peatland vegetation under changing climatic conditions. Persistently deep water table at the drained site likely limited any response to the short term drying in 2012 as this did little to further lower the water table.

Ten years of drainage in a dry continental boreal bog had a significant impact on the plant community, plant biomass and carbon fluxes, and the responses of the peat-
25 land to drainage varied between microforms and over time. Drainage replaced mosses with shrubs at hummocks and lichens at hollows significantly such that the ground layer aboveground biomass increased significantly (Fig. 3). The aboveground biomass

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appears to be within a range of previous reports for similar types of peatlands. Published data for aboveground tree biomass across 20 bogs and ground layer shrubs biomass across 16 bogs varied quite broadly with means of 2177 g m^{-2} ($\pm 2259 \text{ g m}^{-2}$) and 478 g m^{-2} ($\pm 224 \text{ g m}^{-2}$) respectively (Moore et al., 2002). Our data for average total
5 of the ground layer and aboveground tree biomass ($3490 \pm 263 \text{ g m}^{-2}$) fall within the range of the published values. The drainage induced increase in ground layer biomass including aboveground and belowground biomass observed was also reported by Moore et al. (2002). We could measure belowground biomass to only 20 cm depth due to frozen lower layers of soil and therefore it is likely that we may have underestimated the root biomass particularly at the drained site with large oxic zone. However,
10 this still likely captured the majority of below ground biomass as Lieffers and Rothwell (1987) found only 6% of root biomass occurred below 20 cm deep in a drained bog.

Although aboveground tree biomass was slightly higher at control site due to denser but smaller diameter trees, yet we found higher total biomass at the drained site due to
15 its significantly higher ground layer biomass than that at the control site. In both of the study years, the tree productivity was significantly higher at the drained site than that at control. The higher belowground biomass supported with higher R_r at the drained site, is a strong indication that lowered water table enhanced tree growth as concluded by (Hanson et al., 2000), Hermle et al. (2010) and Lieffers and Rothwell (1987). Although we briefly consider explaining the contribution of R_r to R_{tot} in our treed peatland
20 study, our main aim was to quantify and include R_{tot} in seasonal model construction. The drainage induced significantly higher coverage of vascular plants and ground layer aboveground biomass offsets some of the loss of CO_2 due to deeper oxic zone and higher decomposition rates as the water table drops (Ise et al., 2008). However, our
25 carbon balance estimates suggest that drainage has led to a shift from CO_2 sink to a substantial CO_2 source as the drainage induced increase in R_{tot} (supported by R_r in 2012) was substantially higher than that of increase in GEP in both study seasons of 2011 and 2012. Similarly, Chivers et al. (2009) conducted a water table drawdown response experiment in an Alaskan moderately rich treeless fen and found after two

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years of drainage similar to our finding that the drainage shifted the peatland from a sink of CO₂ to a source, although this change was much smaller than that of the change observed in our study of effects of drainage after 10 yr.

Peatland microforms have been shown to have different rates of CO₂ exchange and respond differently to changes in environmental conditions. For example, Waddington and Roulet (2000) found significantly higher uptake of CO₂ at a wetter microform (lawn) than that at the drier one (ridge) in over two growing seasons. Strack et al. (2006) studied CO₂ exchange following water table drawdown along a microtopographic gradient in a cool temperate poor fen and compared results to a natural microtopographic gradient over two growing seasons. They also reported higher uptake of CO₂ at the wetter microform (hollow). They found that drained hummocks had lower GEP_{max} than drained hollows in contrast to control microforms and suggested that lower water tables would result in flattening of the peatland microtopography (i.e. hummocks shrink while hollows accumulate peat). In contrast, in the present study in a dry continental boreal treed bog we found that after a decade of drainage, the GEP_{max} was in fact the highest at drained hummocks in both growing seasons. The increase in GEP_{max} at drained hummocks was probably due to enhanced growth and greater coverage of shrubs. Conversely, replacement of *Sphagnum* by lichens at drained hollows (over 30 times higher biomass than at control hollows) probably led to the observed reduction in GEP_{max} (Table 4). Moreover, the drained hollows were the largest net source of CO₂ in both years. Therefore we expect an increase in relative equilibrium peat depth at the hummocks and decrease in equilibrium peat depth at the hollows as an effect of drainage over the long run. These findings are not consistent with Strack et al. (2006) and are likely due to contrasting climate conditions of the two studies. For example, the earlier study was conducted in an open poor fen where average growing season precipitation recorded during the two study years were 433 and 358 mm in contrast to 402 and 281 mm recorded at our treed continental bog. Also the water table in the earlier study was much shallower and linked to regional hydrology whereas the much deeper water table in this study was controlled by the precipitation and the

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local elevation. On the other hand, these results together are consistent with a general “humpbacked” relationship between peat accumulation and water table depth (e.g. Belyea and Clymo 2001). Given the initially dry conditions at this continental bog, further drying is expected to shift both hummocks and hollows to lower rates of peat accumulation whereas a flattening of the curve at deep water tables would reduce this effect at already dry site (e.g. hummocks).

To sum up, the drained continental bog compared with a natural one simulated the potential climate induced lowered water table and revealed spatial and temporal heterogeneity in CO₂ fluxes and plant biomass in the treed peatland complex. Drainage affected vegetation coverage, plant biomass and CO₂ fluxes differently at the microforms after a decade. Significant replacement of mosses with shrubs at hummocks and lichens at hollows increased ground layer aboveground biomass significantly at the hummocks and generally at the hollows. This drainage induced change in vegetation coverage and biomass shifted the bog from a sink of CO₂ to a source. Net emission of CO₂ can decelerate the rate of vertical growth of microform whereas net uptake of CO₂ can accelerate the rate of vertical growth (Belyea, 2009). In this study we noticed significant increase in net CO₂ uptake at hummocks and net release at hollows as a result of 10 yr of drainage (Table 4) in contrast to previous studies in wetter climates. This illustrates the importance of initial climatic conditions for predicting peatland response (e.g. Hilbert et al., 2000). Continued low water tables could lead to further shifts in vegetation in the future and thus a different C balance than determined following 10 yr of water table drawdown.

5 Conclusions

Ten years of drainage in an ombrotrophic treed bog induced ecological succession: mosses were replaced by shrubs at hummocks and lichens at hollows. The overall greater coverage of vascular plants and higher total biomass at the drained site increased the uptake of CO₂ but the loss via respiration was even higher due to peat

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oxidation and increased contribution of tree root respiration. The research strongly suggests that the deepening of unsaturated zone affected C sequestration rates differently at hummocks and hollows potentially resulting in steepened microtopographic gradient over time. Overall, drainage promoted CO₂ emissions but offset a portion of these losses by increasing total biomass in a dry continental boreal treed bog.

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Table 1. Parameters Estimates, SEE and Goodness of Fit (r^2) for the Gross Ecosystem Photosynthesis Model (Eq. 1).

	GEP vs. PAR		GEP vs. WT		GEP vs. T		SEE (g CO ₂ m ⁻² d ⁻¹)	r^2
	P_{\max} (g CO ₂ m ⁻² d ⁻¹)	k (μmol m ⁻² s ⁻¹)	WT _{opt} (cm)	WT _{tol} (cm)	T_{opt} (°C)	T_{tol} (°C)		
Control Hummock	-28.90 ± 12.2	831 ± 120	-34.9 ± 6.3	21.1 ± 14.2	16.2 ± 9.4	14.2 ± 6.0	2.32	0.83
Control Hollow	-30.20 ± 6.0	767 ± 152	-31.6 ± 4.5	14.5 ± 7.6	15.4 ± 8.1	9.5 ± 6.2	2.72	0.76
Drained Hummock	-42.86 ± 20.0	758 ± 130	-114.4 ± 14.6	29.2 ± 1.4	13.6 ± 7.4	15.7 ± 6.8	2.88	0.76
Drained Hollow	-24.37 ± 21.6	871 ± 636	-113.0 ± 48.5	21.3 ± 4.6	16.7 ± 2.7	12.6 ± 11.6	1.29	0.68

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Table 2. Regression Constants and Goodness of Fit (r^2) for Total Respiration (R_{tot}) Model (Eq. 2).

	a	b	c	SEE ($\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$)	r^2
Control Hummock	0.51 ± 0.80	-0.12 ± 0.53	-6.66 ± 18.71	0.22	0.82
Control Hollow	1.58 ± 0.82	-0.38 ± 0.61	-24.52 ± 15.88	0.46	0.73
Drained Hummock	0.50 ± 0.25	0.09 ± 0.13	13.90 ± 18.67	0.17	0.87
Drained Hollow	0.63 ± 0.61	0.05 ± 0.26	8.43 ± 14.98	0.48	0.81

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Table 3. Aboveground, Belowground, Tree, and Total Site Biomass (g m^{-2})*.

	Mosses	ABOVEGROUND			Fine (< 2 mm)	BELOWGROUND		TREES (Site)	TOTAL (Site)
		Vascular	Lichens	Total		Coarse (> 2 mm)	Total		
Control Hummocks	$215 \pm 68^{\text{A}}$	$218 \pm 84^{\text{B}}$	$0 \pm 0^{\text{A}}$	$433 \pm 147^{\text{A}}$	563 ± 103	138 ± 31	$701 \pm 106^{\text{A}}$	2142	3304
Control Hollows	$182 \pm 93^{\text{A}}$	$135 \pm 41^{\text{B}}$	$11 \pm 32^{\text{A}}$	$328 \pm 72^{\text{A}}$	484 ± 195	386 ± 425	$870 \pm 553^{\text{A}}$		
Drained Hummocks	$16 \pm 27^{\text{B}}$	$737 \pm 60^{\text{A}}$	$13 \pm 14^{\text{A}}$	$766 \pm 323^{\text{B}}$	470 ± 96	498 ± 262	$967 \pm 275^{\text{A}}$	1964	3676
Drained Hollows	$80 \pm 130^{\text{A}}$	$133 \pm 44^{\text{B}}$	$358 \pm 354^{\text{B}}$	$571 \pm 280^{\text{AB}}$	491 ± 60	626 ± 392	$1118 \pm 422^{\text{A}}$		

* The total site biomass is calculated considering measured hummock coverage of 56% and 52% at control and drained sites, respectively. Values are mean \pm SE. Superscript letters indicate statistically significant differences.

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Table 4. Growing Season CO₂ Flux Estimates (g CO₂ m⁻²) for 2011 and 2012.

	2011				2012			
	GEP	R _{tot}	NEE	Site NEE*	GEP	R _{tot}	NEE	Site NEE*
Control Hummock	-698 ± 296	825 ± 136	127	-6.9	-835 ± 153	791 ± 261	-44	71.7
Control Hollow	-653 ± 422	507 ± 161	-146		-664 ± 144	883 ± 112	219	
Drained Hummock	-1025 ± 257	1083 ± 78	58	769.5	-1220 ± 457	1315 ± 235	95	734.5
Drained Hollow	-426 ± 236	1907 ± 236	1481		-432 ± 453	1806 ± 611	1374	

* NEE of the sites were calculated by considering measured hummock to hollow coverage of 56/44 % and 52/48 % at control and drained sites.

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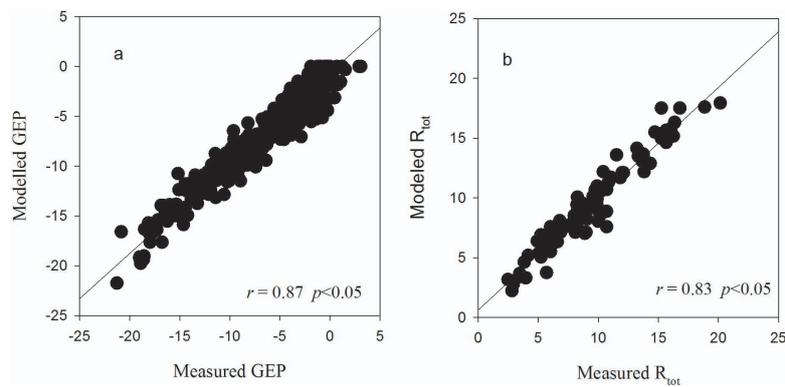


Fig. 1. Goodness of fit (r^2) between (a) modeled and measured GEP and (b) modeled and measured R_{tot}. Both 2011 and 2012 data from control and drained sites are presented. Lines represent the 1 : 1 fit.

15028

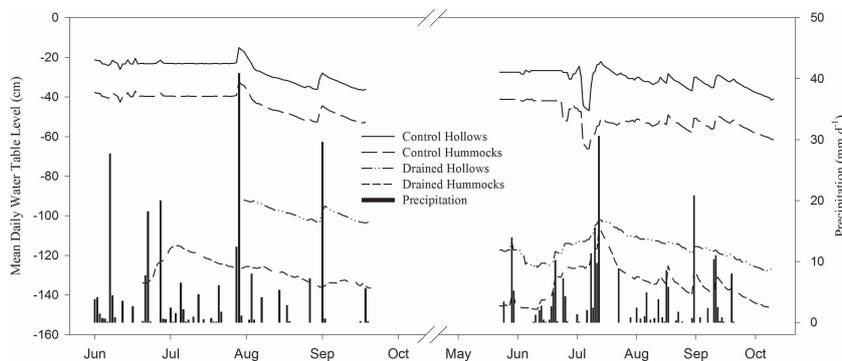


Fig. 2. Water table levels (lines) and daily precipitation (bars) during growing seasons of 2011 and 2012. The cumulative seasonal precipitation during 2012 was 30% less than that of 2011.

15029

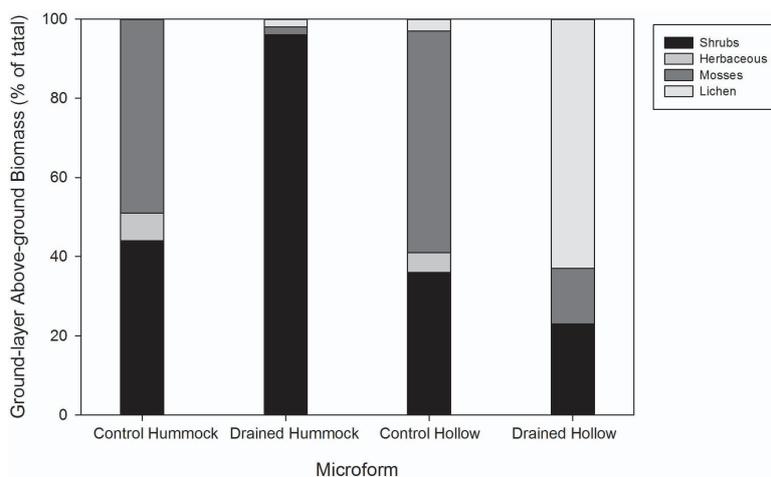


Fig. 3. Relationship between drainage/microform scenario and ground layer above ground biomass by category as a percentage of total.

15030

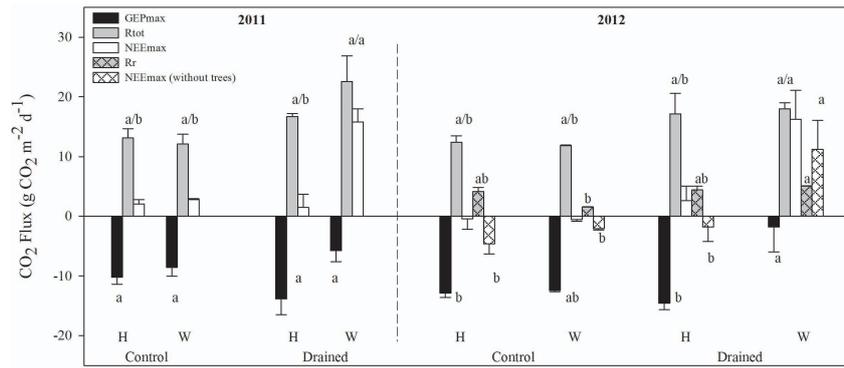


Fig. 4. GEP_{max} , R_{tot} and NEE_{max} at control and drained sites in 2011. The R_r measurements were added in 2012. NEE_{max} (without trees) was calculated by subtracting R_r from NEE_{max} and represents CO_2 exchange of the ground layer vegetation and peat. Error bars indicate \pm one standard deviation. Results are from two-way (drainage and microform) ANOVA performed separately for each year. Differences were evaluated between study plots grouped according to microform and drainage and are indicated by letters at each bar. Sites are significantly different at $p < 0.05$ if they have no letters in common (letters should be compared only within one CO_2 component in one year).