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

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Abstract. Northern peatland ecosystems represent large carbon (C) 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 (1 May to 31 October) 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 sink of −92 in 2011 and −70 g C m⁻² in 2012, while the drained site was a source of 27 and 23 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 %, 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 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).

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) predicts a 3–4 °C increase in mean annual air temperature 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 ecosystem functions of boreal peatlands (Tarnocai, 2006; Adkinson et al.,...
Carbon fluxes in peatlands occur in the forms of the uptake of CO$_2$ from the atmosphere via gross primary photosynthesis (GPP) and the release of CO$_2$ to the atmosphere by respiration (R) of plants (autotrophic) and microorganisms (heterotrophic). The sum of GPP and R is defined as the net ecosystem exchange (NEE) of CO$_2$. Net uptake of CO$_2$ causes the accumulation of carbon in the form of plant biomass and soil organic matter. The GPP, R and NEE of the forest floor are denoted by GPP$_{ff}$, R$_{ff}$ and NEE$_{ff}$, respectively.

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 CO$_2$ uptake by enhanced GPP (e.g. Moore and Dalva, 1993; Updegraff 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 tree productivity and fine root biomass significantly in a Canadian (Liefers and Rothwell, 1987) and a Finnish peatland (Heikurainen and Pakarinen, 1982). Cool temperatures and near-surface water 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 CO$_2$ emissions from northern peatland soils (Moore, 2002; Roulet et al., 1992) where fine tree root biomass may contribute to soil total respiration (Liefers 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 of GPP and R 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 forest floor respiration (R$_f$) 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$_t$) from R$_f$ 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$_t$ from R$_{ff}$ can make possible the comparison of CO$_2$ fluxes and plant biomass of a treed bog with those of an open bog, provided all controlling variables are similar. The contribution of R$_t$ to R$_{ff}$ 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$_t$ was 24% of the soil total respiration. The contribution of R$_t$ to soil total respiration was higher (37%) in a subtropical forest (Wang et al., 2008) in a similar trenching experiment. An even higher contribution of rhizomicrobial respiration was quantified by Hanson et al. (2000) for 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 could alter the above (Lohila et al., 2011) and belowground C dynamics (Blodau and Siems, 2012). Swedish peatlands drained for forestry have been reported to respire at very high rates of 513–6516 g CO$_2$ m$^{-2}$ yr$^{-1}$ (von Arnold et al., 2005). A net loss of soil carbon in Finnish peatlands drained for forestry has also been reported with mean value of 150 g C m$^{-2}$ yr$^{-1}$ (Simola et al., 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 CO$_2$ 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 GPP at hummocks and enhanced GPP 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 total respiration at bog hollows during a dry summer and no change at hummocks.

Drought response experiments have been conducted in Eastern Canada (for example Waddington and Price, 2000; Strack et al., 2006) where generally most of the peatlands are characterized by their open nature (minimal tree cover) and receive high precipitation that leads to high surface humidity. 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 were short-term responses to drought studies and differences in microtopographic response were not considered. Western Canadian continental treed bogs are expected to respond to predicted climate change differently for CO$_2$ 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 response CO$_2$ flux and biomass
change experiments in treed peatland that have measured contribution of $R_f$ to $R_f$ using the closed chamber technique.

Therefore, our research aimed: (1) to compare CO$_2$ fluxes along a microtopographic gradient (hummock vs. hollow) between natural (control) and drained sites at a continental ombrotrophic 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 forest floor 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′14.19″N; −112°31′3.69″W) and one section that was drained in 2001 (DRAINED) (+55°16′44.28″N, −112°28′8.22″W). The drained site was not specifically drained for forestry but inadvertently drained during horticultural peat extraction operations on nearby sites. The drained site is located near the corner of two main ditches that have effectively drained a large quadrant of the peatland. All plots were within 50 m of the ditches. The two sections were 9 km apart and located in north-central Alberta, approximately 85 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–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 and 281.6 mm and 13.06 °C and 13.08 °C for 2011 and 2012, respectively.

The Wandering River, Alberta bog comes under the class of treed low shrub bogs, with typical mosaic of hummock (H) and hollow (W) microforms (Riley, 2003). The hummocks and hollows at the control site were dominated by Sphagnum mosses with sparse shrubs. The drained site had higher coverage of shrubs on the hummocks and higher lichen coverage in the hollows. Common mosses included Sphagnum fuscum, Sphagnum magellanicum, Sphagnum capillifolium and Pleurozium schreberi while common shrubs included Labrador Tea (Rhododendron groenlandicum), Lingonberry (Vaccinium vitis-idaea), small bog cranberry (Oxyccoccus microcarpus) and cloudberry (Rubus chamaemorus). The most common tree in the bog was black spruce (Picea mariana) that constituted > 99% of the tree stand with 25 766 stems ha$^{-1}$ consisted of 37% taller trees (> 137 cm height) up to 769 cm. The black spruce stand had an average canopy height of 168 cm, projection coverage of 42% and basal area of 73.5 m$^2$ ha$^{-1}$. This description applies to the whole bog having control and drained sites.

2.2 CO$_2$ exchange

At each site, three hummocks and three hollows were chosen as the study plots before the growing season (May–October) of 2011. A 60 cm × 60 cm steel collar having grooves at the top was inserted about 6 cm into the peat at each plot to keep disturbance to roots minimal. The CO$_2$ fluxes were measured weekly during the growing seasons using a closed chamber having dimensions of 60 cm × 60 cm × 30 cm ($L \times D \times H$), made of clear acrylic and corrected for transmittance (88%). Two small battery-operated fans were installed inside the chamber to circulate the air and achieve equilibrium CO$_2$ concentration between measurements. The instantaneous CO$_2$ 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 1.75 min. At the time of flux measurements, soil temperatures at the depths of 2, 5, 10, 15, and 20 cm were measured with a thermocouple thermometer at all plots. Water table relative to moss surface was measured at each CO$_2$ flux measurement occasion from a permanently installed well associated with each plot. We used negative values for indicating belowground water table.

At each plot, a total of 184 CO$_2$ flux measurements were made during the daytime of growing seasons (May–October) of 2011 and 2012. During the two growing seasons we organized 20 flux measurement campaigns. Each campaign lasted for about eight days during which fluxes were measured on two to three occasions at each plot. At each flux measurement occasion we took a total of five measurements (four measurements for NE$_{f,f}$ (net exchange of CO$_2$ at the forest floor) under a range of PAR levels created using shades, and a last run for $R_{fl}$) each of 1.75 min: 2–3 full sun, single shade, double shade and finally opaque tarp (for $R_{fl}$). The chamber was flushed (vented) for enough time between the measurements to bring the headspace concentration in equilibrium with ambient air concentration. Therefore we measured respiration as the final measurement (after about 18 min) at each plot by using the clear chamber covered with an opaque shroud. In this way any buildup of CO$_2$ in the soil would have already been flushed. Thus problems in determining respiration rates caused by flushing CO$_2$ built up in the soil during night time chamber measurements (Lai et al., 2012; Koskinen et al., 2013) were not an issue for our measurements.

As noted above, CO$_2$ flux measurements in the dark (when the chamber was covered with an opaque shroud) represented $R_{f,f}$. We recognize that this $R_{f}$ represents only forest floor respiration including understory aboveground biomass.
respiration, heterotrophic soil respiration and tree root respiration, and ignores respiration of the overstory aboveground tree biomass. \( \text{GPP}_{\text{fl}} \) was determined as the difference between \( \text{NE}_{\text{fl}} \) and \( R_{\text{fl}} \). We used the convention that negative values indicate an uptake of \( \text{CO}_2 \) by the ecosystem.

Net exchange of \( \text{CO}_2 \) at the forest floor (\( \text{NE}_{\text{fl}} \)) was calculated using exponential change (Kutzbach et al., 2007) instead of linear change in \( \text{CO}_2 \) 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 \( \text{CO}_2 \) fluxes by altering the concentration gradients between the soil, the vegetation and the air inside the chamber. Due to the constantly changing controls on \( \text{CO}_2 \) flux within the chamber, no linear decrease or increase of \( \text{CO}_2 \) concentration inside the chamber can be expected. Kutzbach et al. (2007) found that the linear \( \text{CO}_2 \) fluxes compared with exponential fluxes were up to 40% lower, over \( \text{CO}_2 \) chamber closure time of only two minutes.

Maximum rates of \( \text{GPP}_{\text{fl}} \) (\( P_{\text{max}} \)) and \( \text{NE}_{\text{fl}} \) (\( N_{\text{max}} \)) represent \( \text{GPP}_{\text{fl}} \) and \( \text{NE}_{\text{fl}} \) when the photon flux density of photosynthetically active radiation is greater than 1000 \( \mu \text{mol m}^{-2} \text{s}^{-1} \). As modeled values of the maximum rate of photosynthesis are likely never achieved in reality, these values represent a more realistic estimate of \( \text{CO}_2 \) exchange when light is not limiting as discussed in Bubier et al. (2003). We use these to statistically compare plots to better understand processes (changes in plant cover, species type, water table, etc.) that affect \( \text{CO}_2 \) exchange. Data reported are averages for the study seasons (May–October) for all occasions when \( \text{PAR} > 1000 \mu \text{mol m}^{-2} \text{s}^{-1} \).

### 2.2.1 Seasonal \( \text{CO}_2 \) exchange model

The growing season (1 May to 31 October) \( \text{GPP}_{\text{fl}} \) was estimated using an empirical model following Riutta et al. (2007) parameterized separately for each microform type \( \times \) water table treatment. The parametrization was done separately for each of the growing seasons of 2011 and 2012. The seasonal \( \text{GPP}_{\text{fl}} \) was estimated by

\[
\text{GPP}_{\text{fl}} = \frac{\text{PAR} \times P_{\text{max}}}{\text{PAR} + k} \times e^{-0.5 \left( \frac{\text{WT}_{\text{opt}} - \text{WT}_{\text{tol}}}{\text{WT}_{\text{opt}} - \text{WT}_{\text{tol}}} \right)^2} \times e^{-0.5 \left( \frac{T_{\text{opt}} - T_{\text{tol}}}{T_{\text{opt}} - T_{\text{tol}}} \right)^2},
\]

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

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

After examining the data it appeared that the relationship of \( R_{\text{fl}} \) with soil temperature at 5 cm depth was not exponential. Therefore the growing season \( R_{\text{fl}} \) was estimated using multiple linear regressions with soil temperature at 5 cm

<table>
<thead>
<tr>
<th>Year</th>
<th>Site/Microform</th>
<th>( P_{\text{max}} ) (g CO(_2) m(^{-2})d(^{-1}))</th>
<th>( k ) (( \mu \text{mol m}^{-2}\text{s}^{-1}))</th>
<th>( \text{WT}_{\text{opt}} ) (cm)</th>
<th>( \text{WT}_{\text{tol}} ) (cm)</th>
<th>( T_{\text{opt}} ) (°C)</th>
<th>( T_{\text{tol}} ) (°C)</th>
<th>SEE</th>
<th>( r^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>2011</td>
<td>Control Hummocks</td>
<td>–22.2 ± 4.6</td>
<td>900 ± 422</td>
<td>–56.0 ± 13.0</td>
<td>30.0 ± 15.8</td>
<td>16.1 ± 3.7</td>
<td>10.0 ± 5.4</td>
<td>2.30</td>
<td>0.83</td>
</tr>
<tr>
<td></td>
<td>Control Hollows</td>
<td>–19.4 ± 7.1</td>
<td>950 ± 601</td>
<td>–28.3 ± 9.7</td>
<td>22.9 ± 21.3</td>
<td>14.1 ± 7.5</td>
<td>10.0 ± 12.5</td>
<td>2.05</td>
<td>0.63</td>
</tr>
<tr>
<td></td>
<td>Drained Hummocks</td>
<td>–35.9 ± 8.8</td>
<td>950 ± 440</td>
<td>–118.1 ± 8.3</td>
<td>30.0 ± 11.1</td>
<td>12.3 ± 1.5</td>
<td>10.0 ± 3.1</td>
<td>1.14</td>
<td>0.82</td>
</tr>
<tr>
<td></td>
<td>Drained Hollows</td>
<td>–29.2 ± 16.8</td>
<td>850 ± 639</td>
<td>–70.5 ± 31.6</td>
<td>30.0 ± 17.3</td>
<td>10.6 ± 2.7</td>
<td>10.0 ± 10.2</td>
<td>0.57</td>
<td>0.68</td>
</tr>
<tr>
<td>2012</td>
<td>Control Hummocks</td>
<td>–24.8 ± 4.7</td>
<td>900 ± 286</td>
<td>–34.9 ± 11.3</td>
<td>30.0 ± 14.0</td>
<td>15.2 ± 2.0</td>
<td>10.0 ± 3.8</td>
<td>1.84</td>
<td>0.86</td>
</tr>
<tr>
<td></td>
<td>Control Hollows</td>
<td>–21.8 ± 3.9</td>
<td>950 ± 299</td>
<td>–42.3 ± 13.8</td>
<td>30.0 ± 20.1</td>
<td>14.6 ± 1.3</td>
<td>9.9 ± 2.1</td>
<td>1.09</td>
<td>0.85</td>
</tr>
<tr>
<td></td>
<td>Drained Hummocks</td>
<td>–50.0 ± 14.3</td>
<td>950 ± 416</td>
<td>–104.8 ± 2.8</td>
<td>30.0 ± 2.9</td>
<td>10.1 ± 2.0</td>
<td>10.0 ± 2.0</td>
<td>0.96</td>
<td>0.82</td>
</tr>
<tr>
<td></td>
<td>Drained Hollows</td>
<td>–31.3 ± 10.1</td>
<td>850 ± 246</td>
<td>–99.5 ± 11.1</td>
<td>23.2 ± 6.7</td>
<td>10.0 ± 5.5</td>
<td>9.9 ± 4.6</td>
<td>1.55</td>
<td>0.83</td>
</tr>
</tbody>
</table>
Table 2. Estimated regression coefficient values (±SE), standard error of the estimate (SEE) and goodness of fit ($r^2$) for the forest floor respiration ($R_{ff}$) model (Eq. 2).  

<table>
<thead>
<tr>
<th>Year</th>
<th>Site/Microform</th>
<th>$a$</th>
<th>$b$</th>
<th>$c$</th>
<th>SEE (g CO$_2$ m$^{-2}$ d$^{-1}$)</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>2011</td>
<td>Control Hummocks</td>
<td>1.30 ± 0.29</td>
<td>-0.21 ± 0.12</td>
<td>-18.25 ± 6.80</td>
<td>0.80</td>
<td>0.81</td>
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<td></td>
<td>Control Hollows</td>
<td>1.70 ± 0.32</td>
<td>-0.61 ± 0.20</td>
<td>-32.33 ± 10.74</td>
<td>0.68</td>
<td>0.79</td>
</tr>
<tr>
<td></td>
<td>Drained Hummocks</td>
<td>0.31 ± 0.27</td>
<td>-0.02 ± 0.03</td>
<td>2.62 ± 7.26</td>
<td>0.38</td>
<td>0.49</td>
</tr>
<tr>
<td></td>
<td>Drained Hollows</td>
<td>0.55 ± 0.13</td>
<td>-0.02 ± 0.03</td>
<td>2.26 ± 3.63</td>
<td>0.19</td>
<td>0.85</td>
</tr>
</tbody>
</table>

| 2012       | Control Hummocks   | 0.39 ± 0.15   | -0.25 ± 0.09 | -10.71 ± 5.31 | 0.61                            | 0.53  |
|            | Control Hollows    | 0.93 ± 0.08   | -0.25 ± 0.05 | -12.77 ± 1.77 | 0.36                            | 0.81  |
|            | Drained Hummocks   | 0.65 ± 0.06   | -0.03 ± 0.05 | -3.40 ± 8.14  | 0.32                            | 0.91  |
|            | Drained Hollows    | 1.07 ± 0.09   | -0.15 ± 0.04 | -17.31 ± 5.55 | 0.86                            | 0.80  |

* The models were developed for each microform type ($n = 3$) at the control and drained sites separately for growing seasons of 2011 and 2012; $a$, $b$ and $c$ are regression coefficients. Negative values of $b$ represent greater respiration with deeper water table values (below ground WT having negative values). All modeled parameters are significant at $p = 0.05$ level.

depth and water table position by

$$R_{ff} = a \times T + b \times WT + c,$$

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

Seasonal GPP$_0$ and $R_{ff}$ 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 sites for PAR (LI-190, LI-COR, Nevada, USA), WT (Levelogger Junior, Solinst, USA) and temperature (Onset HOBOware Pro, MA, USA). Growing season ground-layer NE$_{ff}$ was determined by adding seasonal GPP$_{ff}$ to seasonal $R_{ff}$ estimates. The control site was instrumented with one additional soil temperature sensor (T 109, Campbell Scientific Inc., Utah, USA; depth = 5 cm) and one tipping bucket rain gauge (TE 525, Campbell Scientific Inc., Utah, USA; height = 150 cm) both wired to a data logger (CR 1000, Campbell Scientific Inc., Utah, USA) programmed to measure every minute and record the average at 20 min intervals.

### 2.2.2 Model validation

Of all the data measured in the field, we separated one third randomly and did not use it for model construction. The remaining two-thirds of the data were used for model construction. The unused data were later correlated with modeled data for validation of the GPP$_{ff}$ and $R_{ff}$ models. Validation of the model showed excellent agreement between predicted and measured values (Fig. 1a and b).

### 2.3 Tree root respiration

To exclude the contribution of $R_r$ to $R_{ff}$, a trenching method (Wang et al., 2008) was used. In May 2012, a total of 32 plots (eight hummocks and eight hollows at each site, in addition to the already described CO$_2$ flux plots) were chosen randomly from the available microtopography. At each site four hummock and four hollow plots of area 60 cm $\times$ 60 cm were cut around up to approximately 30 cm depth in three intervals (0–10 cm, 10–20 cm, 20–30 cm). It was assumed that cutting the peat would cut down most of the live root ingrowth. To make the cut loose enough to insert polyethylene sheet, we had to use a saw several times at each of the three depth intervals. Then the polyethylene sheet was inserted deep to 30 cm to prevent root ingrowth and the cuts were infilled with soil in the reverse order of removal (i.e., first we filled back the soil from 20–30 cm depth followed by 10–20 cm and lastly 0–10 cm). Although this procedure did not ensure that the backfilled soil occupied its original place, our intention was to keep disturbance minimal. The remaining four hummocks and four hollows were left intact to quantify the difference in CO$_2$ emission between cut (having minimal tree roots) and intact (with all tree roots) plots. During July to September 2012, all plots were clipped every two weeks to ensure that soil surface was free of live mosses, shrubs and herbs following Hanson et al. (2000), Riutta et al. (2007) and Hermle et al. (2010). The trenched and intact plots were clipped so that we could isolate soil respiration (measured at trenched plots) from $R_r$ and soil respiration (measured at intact plots). Had the plots not been clipped, we would have measured $R_r$ + soil respiration + autotrophic respiration of surface vegetation at intact plots and soil respiration + autotrophic respiration of surface vegetation at trenched plots. This way we could not have $R_r$ separated from soil respiration. The surface vegetation was clipped with Fiskars power lever shears (Model # 100017192) that clips horizontally to keep disturbance minimal.

The CO$_2$ emissions from all plots were measured using the same instruments and chamber used for the measurement of NE$_{ff}$ and $R_{ff}$ and hence GPP$_{ff}$. We had a methodological challenge that while the cutting separates $R_r$ from $R_{ff}$, it also adds fresh litter to the soil that can add to the existing heterotrophic soil respiration.

Trenching or cutting experiments have been performed to separate root autotrophic respiration from $R_{ff}$ (e.g. Hanson...
et al., 2000; Hermle et al., 2010; Wang et al., 2008; Díaz Pinés et al., 2010; Kuzyakov, 2006; Brant et al., 2006). In all cases the assumption has been made that the trenched roots die off within a short time and that afterwards the measured $R_f$ 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 or cutting experiments showed that C content of decomposing fine roots in trenched plots contribute little to $R_f$ and become stable in the four months after trenching. Therefore, no correction for extra CO$_2$ 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 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 $R_f$ while investigating $R_r$ to better understand and separate the contribution of various processes to shifts in $R_f$ following drainage.

### 2.4 Biomass and tree productivity

Forest floor biomass was measured by clipping 25 cm × 25 cm quadrats at nine hummocks and nine hollows, 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 triplicate of each microform at each site, soil cores of only 20 cm depth were collected due to frozen peat beyond this depth at the time of sample collection. 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 m × 10 m quadrats in areas directly surrounding the flux plots at each site. The total study areas were not large and these plots covered most of the trees in the study areas. 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 (dry biomass = 0.153(tree DBH)$^{2.248}$) from Grigal and Kernik (1984). Trees < 137 cm were not measured for DBH as their total height was below a standard DBH measurement height. A subsample of 20 smaller trees > 125 cm were harvested parallel to the forest floor and taken back to the lab and oven dried at 80°C for 48 hours. The height and dry biomass of each tree was measured and an exponential regression was performed. An allometric equation was generated by regressing height with oven-dried weight as dry biomass = 0.0085(tree height)$^{2.2088}$ ($R^2 = 0.93$, $p < 0.001$).

For calculating NPP of the tree stand, we adapted methods of Szumigalski and Bayley (1996) and Thormann and Bayley (1997). In addition to fens, they also estimated NPP of an Alberta ombrotrophic treed bog of hummock-hollow microtopography by adding aboveground incremental biomass to stand litter production (17% of incremental biomass m$^{-2}$ yr$^{-1}$ for Picea mariana). We quantified the incremental biomass of tall trees for 2011 and 2012 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), Summation of biomass increments of tall and short trees for a year represented incremental biomass of tree stand for aboveground parts of the trees (ICbiom_ag) for that year at either site. However, litterfall was not estimated. Therefore we predicted a value of stand litter production based on Szumigalski and Bayley (1996; 17% of incremental biomass) for Alberta ombrotrophic bogs. We also did not measure incremental biomass of the belowground parts of the tree (ICbiom/bg) due to the difficulty in measuring this component without disturbing our study sites for future monitoring. Therefore, we use an allometric equation (tree root biomass = 0.222* tree aboveground biomass) from Li et al. (2003) for estimating incremental biomass of tree roots.

### 2.5 CO$_2$-C balance calculations

The CO$_2$-C balances of the treed control and drained sites (NEE) were calculated separately for the growing seasons (1 May to 31 October) of 2011 and 2012 as

\[
\text{NEE} = \text{NE}_\text{ff} + \text{IC}_{\text{tree-ag}} + \text{IC}_{\text{tree-bg}} + \text{L}_{\text{tree}} - R_t, \tag{3}
\]

where NEE denotes net ecosystem exchange, NE$_{\text{ff}}$ represents net exchange of CO$_2$-C of the forest floor, IC$_{\text{tree-ag}}$ and IC$_{\text{tree-bg}}$ represent incremental biomass growth of the aboveground and belowground parts of the trees, respectively, \(L_{\text{tree}}\) is tree litter production and \(R_t\) is tree root respiration.

Seasonal CO$_2$ fluxes at hummocks and hollows were upscaled by multiplying mean estimated growing season CO$_2$ 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 trees and their litter production was added to the forest floor CO$_2$ exchange assuming that biomass had a carbon content of 50%. \(R_t\) was excluded to avoid double counting while determining CO$_2$-C balance of sites as IC$_{\text{tree-bg}}$ already accounts for \(R_t\). We estimated a seasonal value of \(R_t\) by determining it as a proportion of \(R_{\text{ff}}\) based on instantaneous measurements and then estimating it as this proportion of the modelled seasonal \(R_{\text{ff}}\).

### 2.6 Statistical analysis

Differences in GPP$_{\text{max}}, R_{\text{ff}}, NE_{\text{max}},$ and aboveground biomass between sites and microforms were tested by two-way ANOVA, using Minitab 16.0 (Minitab Inc., PA, USA). Differences in \(R_t\) between sites, microforms and cut and intact plots were tested for significance employing a three-way ANOVA using SPSS 20.1. The nonlinear and linear regression models (Eqs. 1, 2 and 3) were used to construct GPP$_{\text{ff}}$ and \(R_{\text{ff}}\) models (SPSS 20.1) and to estimate seasonal CO$_2$-C 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. 2). The growing seasons of 2011 and 2012 were warmer by 1.36 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. In 2012, the reduction in rainfall by 121 mm led to a decrease in water table 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 ditched around in 2001 and the data on pre-drawdown hydrology and vegetation were not available. However, given that the control and drained sites were part of the same bog and had similar vegetation layers (canopy layer consisted of Picea mariana and ground layer consisted of similar shrubs and mosses), air temperature, peat depth and underlain substrate are assumed to be similar before start of this study in 2001. As a result of 10 yr drainage, Sphagnum coverage at the drained site was significantly reduced by 97% (\(F(3, 32) = 33.40, p < 0.001\)) compared to the control site, but no significant difference in Sphagnum coverage was observed between microforms at either site (Fig. 3). Sphagnum at drained site was replaced by shrubs at hummocks and lichens at hollows (field observation, data not presented here). The significant reduction in coverage of Sphagnum at the drained site was due to the unfavourable condition of very low water potential in the surface soil.
F plots (biomass at drained hummocks was significantly lowest of all and drained hollows (Table 3, Fig. 3). Conversely, moss biomass was significantly higher than that in the control (Table 3). However, total root biomass was higher in the drained site compared to the control. Moisture and nutrients from the drainage water table were likely similar and we did see a clear change in tree growth determined represent a clear response to the changing water table.

### 3.2 Biomass and incremental tree growth

Vascular plant biomass at the drained hummocks was significantly higher than that at the control hummocks ($F(1, 32) = 17.07, p < 0.001$) 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 at 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 hollows that had the highest lichen biomass (over 30 times higher than 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$^{-2}$, the annual aboveground tree increment during the study years (2011 and 2012) was significantly higher in the drained site (66 and 60 g C m$^{-2}$) than the control (38 and 33 g C m$^{-2}$) ($F(1, 3) = 30.25, p = 0.012$). Using equations presented in Li et al. (2003) belowground tree increment was estimated as 6 and 7 g C m$^{-2}$ at the control site and 15 and 13 g C m$^{-2}$ at the drained site in 2011 and 2012, respectively (Table 4).

Spatial variability in tree stands is a generic characteristic of natural/peatland ecosystems and we did not have tree stand data prior to the study period. Heterogeneity even between the three quadrats constructed at each site was large; however, the size of the study areas precluded our ability to include more replicates. Therefore, while we cannot be certain that the biomass was identical before the study, they were likely similar and we did see a clear change in tree growth (based on the tree rings) coinciding with the ditching 10 yr ago. Thus we are confident that the changes in incremental growth determined represent a clear response to the changing water table.

### 3.3 CO$_2$ fluxes

#### 3.3.1 Measured CO$_2$ Fluxes

Drainage did not change GPP$_{max}$ significantly in 2011 or 2012 (Fig. 4; two-way ANOVA, 2011: $F = 0.06, p = 0.813$, 2012: $F = 4.13, p = 0.08$). However, GPP$_{max}$ 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 2012 leading to significantly different GPP$_{max}$ at drained microforms. Drainage resulted in significantly higher $R_{ff}$ (2011: $F = 6.85, p = 0.037$, 2012: $F = 8.52, p = 0.019$), but $R_{ff}$ remained statistically similar between microforms at both sites in both years. The drained hollows were the largest sources of CO$_2$ emission largely due to the significantly higher contribution of $R_t$ (5.03 g CO$_2$ m$^{-2}$ d$^{-1}$) to $R_{ff}$ (18.02 g CO$_2$ m$^{-2}$ d$^{-1}$) than that of the $R_t$ contribution of 1.51 g CO$_2$ m$^{-2}$ d$^{-1}$ to $R_{ff}$ (11.84 g CO$_2$ m$^{-2}$ d$^{-1}$) at control hollows (see 2012 in Fig. 4). NEE$_{max}$ was positive in 2011 but became negative (net sink of CO$_2$) in 2012 at control microforms. Subtracting $R_t$ from NEE$_{max}$ switched the drained hummocks to a moderate sink and the control microforms to

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**Table 4.** Growing season CO$_2$-C flux estimates ($\pm$SE, g C m$^{-2}$)$^a$.

<table>
<thead>
<tr>
<th>Year</th>
<th>Site</th>
<th>GPP$_{ff}$</th>
<th>$R_{ff}$</th>
<th>NEE$_{ff}$</th>
<th>$R_t$</th>
<th>$L_{tree}$</th>
<th>IC$<em>{tree</em>{ag}}$</th>
<th>IC$<em>{tree</em>{bg}}$</th>
<th>NEE$^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>2011</td>
<td>CONTROL</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hummock</td>
<td>$-190 \pm 29$</td>
<td>$225 \pm 18$</td>
<td>$35 \pm 30$</td>
<td>$63 \pm 5.1$</td>
<td>$-6 \pm 1.4$</td>
<td>$-38 \pm 7.9$</td>
<td>$-6 \pm 1.4$</td>
<td>$-92 \pm 11.7$</td>
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<tr>
<td></td>
<td>Hollow</td>
<td>$-178 \pm 29$</td>
<td>$130 \pm 21$</td>
<td>$-48 \pm 9$</td>
<td>$12 \pm 0.3$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>DRAINED</td>
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<tr>
<td></td>
<td>Hummock</td>
<td>$-280 \pm 21$</td>
<td>$295 \pm 10$</td>
<td>$15 \pm 7$</td>
<td>$62 \pm 4.9$</td>
<td>$-11 \pm 1.4$</td>
<td>$-66 \pm 9.1$</td>
<td>$-15 \pm 1.7$</td>
<td>$27 \pm 13.6$</td>
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<tr>
<td></td>
<td>Hollow</td>
<td>$-116 \pm 19$</td>
<td>$536 \pm 9$</td>
<td>$420 \pm 23$</td>
<td>$123 \pm 0.6$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2012</td>
<td>CONTROL</td>
<td></td>
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</tr>
<tr>
<td></td>
<td>Hummock</td>
<td>$-228 \pm 43$</td>
<td>$216 \pm 33$</td>
<td>$-12 \pm 11$</td>
<td>$60 \pm 5.1$</td>
<td>$-6 \pm 1.2$</td>
<td>$-33 \pm 6.8$</td>
<td>$-7 \pm 1.2$</td>
<td>$-70 \pm 10.2$</td>
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<tr>
<td></td>
<td>Hollow</td>
<td>$-181 \pm 8$</td>
<td>$241 \pm 45$</td>
<td>$60 \pm 33$</td>
<td>$21 \pm 0.3$</td>
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<td></td>
<td>DRAINED</td>
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<td></td>
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<tr>
<td></td>
<td>Hummock</td>
<td>$-333 \pm 75$</td>
<td>$359 \pm 18$</td>
<td>$26 \pm 13$</td>
<td>$75 \pm 4.9$</td>
<td>$-10 \pm 1.8$</td>
<td>$-60 \pm 10.3$</td>
<td>$-13 \pm 1.9$</td>
<td>$23 \pm 14.9$</td>
</tr>
<tr>
<td></td>
<td>Hollow</td>
<td>$-118 \pm 20$</td>
<td>$507 \pm 35$</td>
<td>$389 \pm 47$</td>
<td>$116 \pm 0.6$</td>
<td></td>
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<td></td>
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</tbody>
</table>

$^a$ Negative values represent uptake of carbon by the peatland from the atmosphere. The forest floor respiration ($R_{ff}$) includes tree root respiration ($R_t$). $^b$ NEE is calculated using equation 3 (NEE = NEE$_{ff}$ + IC$_{tree_{ag}}$ + IC$_{tree_{bg}}$ + $L_{tree}$ = $R_t$). Forest floor carbon exchange was determined by weighting NEE$_{ff}$ measured at each microform by the proportion of hummocks and hollows at each site (control = 56% hummocks; drained = 52% hummocks).
larger sinks of CO$_2$, while considerably reduced emissions at the drained hollows (Fig. 4).

**3.3.2 Modeled CO$_2$ fluxes**

Based on empirical models (Eqs. 1 and 2), the ground layer at the control site was a small growing season sink of CO$_2$ taking up an estimated 6.9 g CO$_2$ m$^{-2}$ largely due to the significantly higher GPP$_{ff}$ at its hollows than that of its hummocks. In contrast, the ground layer at the drained site was a substantial source of CO$_2$, losing an estimated 770 g CO$_2$ m$^{-2}$ largely due to significantly higher $R_{ff}$ 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 CO$_2$, and the hollows became a substantial source. However, the drained microforms and site remained consistently sources of CO$_2$ (Table 4).

**3.4 CO$_2$-C balance**

In the growing season of 2011, the forest floor (including $R_I$) of control and drained sites were a small sink (2 g CO$_2$-C m$^{-2}$) and substantial source (210 g CO$_2$-C m$^{-2}$), respectively. In the growing season of 2012, the control site became a moderate source (20 g CO$_2$-C m$^{-2}$) while the drained site remained a substantial source (200 g CO$_2$-C m$^{-2}$). To calculate the final CO$_2$-C balance, we added estimated NE$_{ff}$ (-$R_I$)
to estimated tree incremental growth (IC$_{\text{tree,ag}}$ + IC$_{\text{tree,bg}}$) and tree litter production (L$_{\text{tree}}$) during the study years, and estimated that the control site was a larger sink of −92 g C m$^{-2}$ in 2011 than that of −70 g C m$^{-2}$ in 2012. However, the drained site remained a source through both study seasons, losing 27 g C m$^{-2}$ in 2011 and 23 g C m$^{-2}$ in 2012 growing season. Importantly, majority of the discussion in this study focuses on the differences in the measured components as opposed to the CO$_2$-C balance itself.

4 Discussion

The control site of this sub-humid, continental treed bog was a growing season sink of CO$_2$-C of 92 and 70 g C m$^{-2}$ in years slightly wetter and drier than average, respectively. Depending on time since fire, Wieder et al. (2009) report that treed bogs in the same region represent an annual CO$_2$ sink of 120 to 220 g C m$^{-2}$ and thus our value is slightly below this range. Within the same region of northern Alberta as the present study, Adkinson et al. (2011) report net growing season CO$_2$ exchange across three study years of −110.1 and −153.5 to −34.5 g C m$^{-2}$ at poor fen and rich fen sites, respectively.

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; Arneth et al., 2002; Bubier et al., 2003; Aurela et al., 2007). Similarly, in our experiment 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 increased $R_{\text{ff}}$ at the hollows greater than that of combined increase in GPP$\text{ff}$ at the microforms (Table 4). The enhanced $R_{\text{ff}}$ at hollows might be due to stressed vegetation growth observed at the drier hollows (Fig. 3). In contrast there was little change in GPP$\text{ff}$ or $R_{\text{ff}}$ at the drained site in 2012 and thus no real change in net CO$_2$ emission.

Ten years of water table drawdown, converted our bog site forest floor from a small sink of 2 g m$^{-2}$ in 2011 or a smaller source of 20 g m$^{-2}$ in 2012 to a large source of CO$_2$ of ∼ 200 g m$^{-2}$ in both years. This value of net source of CO$_2$ compares well with those of other drained peatlands as reported by Waddington et al. (2002), von Arnold et al. (2005) and Simola et al. (2012). Similar to our findings on response of warmer and drier weather, Aurela et al. (2007) and Lafleur and Humphreys (2008) also found increased GPP$\text{ff}$ with warmer growing season temperature but reduced GPP$\text{ff}$ and enhanced $R_{\text{ff}}$ 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; Wieder et al., 2009) demonstrate the important interaction between temperature and water availability for GPP$\text{ff}$ and $R_{\text{ff}}$ response, as either factor alone could not 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 peatland to drainage varied between microforms and over time. Drainage replaced mosses with shrubs at hummocks and lichens at hollows such that the ground-layer aboveground biomass increased...
significantly (Fig. 3). The aboveground biomass 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$2259 g m$^{-2}$) and 478 g m$^{-2}$ ($\pm$224 g m$^{-2}$), respectively (Moore et al., 2002). Our data for average total of the ground-layer and aboveground tree biomass (3490 $\pm$ 263 g m$^{-2}$) fall within the range of the published values. The drainage-induced increase in ground-layer biomass including above- 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 at the time of sampling and therefore it is likely that we may have underestimated the root biomass particularly at the drained site with large oxic zone. However, this still likely captured the majority of belowground 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, we found higher total biomass at the drained site due to 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 $R_t$ 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 determined the contribution of $R_t$ to $R_{GPP}$ in our treed peatland study, our main aim was to quantify and include $R_{GPP}$ 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 carbon balance estimates suggest that drainage has led to a shift from CO$_2$ sink to a CO$_2$ source as the drainage-induced increase in $R_{GPP}$ (supported by $R_t$) was substantially higher than that of increase in GPP 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 years of drainage, similar to our finding, that the drainage shifted the peatland from a sink of CO$_2$ 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 CO$_2$ exchange and respond differently to changes in environmental conditions. For example, Waddington and Roulet (2000) found significantly higher uptake of CO$_2$ at a wetter microform (lawn) than that at the drier one (ridge) in over two growing seasons. Strack et al. (2006) studied CO$_2$ 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 CO$_2$ at the wetter microform (hollow). They found that drained hummocks had lower GPP$_{max}$ 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 GPP$_{max}$ was in fact the highest at drained hummocks in both growing seasons. The increase in GPP$_{max}$ 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 GPP$_{max}$ (Table 4). Moreover, the drained hollows were the largest source of CO$_2$ 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 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; Belyea, 2009). 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 (reduced effect of water table change on peat accumulation at drier sites) would reduce this effect at already dry sites (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 CO$_2$ fluxes and plant biomass in the treed peatland complex. Drainage affected vegetation coverage, plant biomass and CO$_2$ 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 CO$_2$ to a source despite an increase in tree productivity. Net emission of CO$_2$ can decelerate the rate of vertical growth of microforms, whereas net uptake of CO$_2$ can accelerate the rate of vertical growth (Belyea, 2009). In this study we noticed significant increase in net CO$_2$ 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 CO\textsubscript{2}-C balance than determined following 10 yr of water table drawdown.

5 Conclusions

Ten years of drainage in an ombrotrophic tree 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 CO\textsubscript{2} but the loss via respiration was even higher due to peat oxidation and increased contribution of tree root respiration. The research strongly suggests that the deepening of the unsaturated zone affected C sequestration rates differently at hummocks and hollows, potentially resulting in steepened microtopographic gradient over time. Overall, drainage promoted CO\textsubscript{2} emissions but offset a portion of these losses by increasing total biomass in a dry continental boreal treed bog.

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