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Carbon dioxide flux and net primary production of a boreal treed bog: responses to warming and water table manipulations

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CO$_2$ flux and NPP of a boreal treed bog

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Abstract

Mid-latitude treed bogs are significant carbon (C) stocks and are highly sensitive to global climate change. In a dry continental treed bog, we compared three sites; control, recent (1–3 years; experimental) and older drained (10–13 years; drained) with water levels at 38, 74 and 120 cm below the surface, respectively. At each site we measured carbon dioxide (CO$_2$) fluxes and tree root respiration (R_r) (across hummock-hollow microtopography of the forest floor) and net primary production (NPP) of trees during the growing seasons (May to October) of 2011–2013. The carbon (C) balance was calculated by adding net CO$_2$ exchange of the forest floor (NE$_{ff}$ – R_r) to the NPP of the trees.

From cooler and wetter 2011 to driest and warmest 2013, The control site was a C sink of 92, 70 and 76 g m^{-2}, experimental site was a C source of 14, 57 and 135 g m^{-2}, and drained site was a progressively smaller source of 26, 23 and 13 g m^{-2}, respectively. Although all microforms at the experimental site had large net CO$_2$ emissions, the longer-term drainage and deeper water level at the drained site resulted in the replacement of mosses with vascular plants (shrubs) at the hummocks and lichens at the hollows leading to the highest CO$_2$ uptake at drained hummocks and significant losses at hollows. The tree NPP was highest at the drained site.

We also quantified the impact of climatic warming at all water table treatments by equipping additional plots with open-top chambers (OTCs) that caused a passive warming on average of $\sim 1\,°C$ and differential air warming of $\sim 6\,°C$ (at mid-day full sun) across the study years. Warming significantly enhanced the shrub growth and CO$_2$ sink function of the drained hummocks (exceeding the cumulative respiration losses at hollows induced by the lowered water level × warming). There was an interaction of water level with warming across hummocks that resulted in largest net CO$_2$ uptake at warmed drained hummocks. Thus in 2013, the warming treatment enhanced the sink function of control by 13 g m^{-2}, reduced the source function of experimental by 10 g m^{-2}, and significantly enhanced the sink function of the drained site by 73 g m^{-2}. Therefore, drying

and warming in continental bogs is expected to initially accelerate C losses via respiration but persistent drought and warming is expected to restore the peatland's original C sink function as a result of transitional shift of vegetation between the microforms and increased NPP of trees over time.

1 Introduction

Northern peatland ecosystems have accumulated ~ 547 Pg carbon (C; 1 Pg = 10^{15} g) as a result of functioning as a steady but persistent sink throughout the Holocene (Yu, 2012; Tarnocai et al., 2009). The accumulated peatland C stocks equal approximately a one third of the global terrestrial soil C pool (Grosse et al., 2011; Ciais et al., 2013) Mid-latitude peatlands in the north-west hemisphere are often covered by trees, in contrast to open bogs in the north-east (Turetsky et al., 2002). Forested bogs have greater net primary production (NPP) to decomposition ratios and hence return higher accumulation rates than those of open bogs (Clymo et al., 1998). The C stocks of the western boreal treed bogs may respond differently to warming and drought than those of eastern open fens (Kettles and Tarnocai, 1999), and may lead to an accelerated positive feedback to climate change (Gruber et al., 2004; Limpens et al., 2008; Bhatti et al., 2012). The large peatland C pools in the middle to high latitudes are expected to undergo significant changes in climate associated with growing atmospheric concentrations of carbon dioxide (CO$_2$) over time (Stocker et al., 2013). Future climatic changes are predicted to be the most severe at mid-latitudes including the southern boreal region (Vitt et al., 2009; Kettles and Tarnocai, 1999; IPCC, 2007) that has a dense coverage (50 %) of peatlands (Tarnocai, 2006).

Carbon exchange in peatlands occurs in the forms of the uptake of C from the atmosphere via gross primary photosynthesis (GPP) and the release of C 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 assimilation of C in the form of plant biomass and accumulation

of C in the form of soil organic matter. The GPP, R and NEE of the forest floor are represented by GPP$_{ff}$, R_{ff} and NE$_{ff}$, respectively. Tree root respiration is represented by R_r.

The changes in peatland air/soil temperature and water level can change GPP and R independently (Ow et al., 2008). Warm and dry conditions in peatlands can either promote CO$_2$ uptake by enhancing GPP or diminish uptake by limiting moisture (Roulet et al., 2007; Charman et al., 2013) or accelerate CO$_2$ release by enhancing R (Hanson et al., 2000; Davidson and Janssens, 2006; Lund et al., 2010; Ise et al., 2008; Cai et al., 2010). In a dwarf-shrub pine bog, Pihlatie et al. (2010) found that the CO$_2$ flux peak followed tightly the increase in air and soil temperature, being higher (uptake) on warm, and lower (up to emission) on cold days. They found increase in the net uptake and emission by $4.3\,\mathrm{g\,C\,m^{-2}\,d^{-1}}$ and $2.5\,\mathrm{g\,C\,m^{-2}\,d^{-1}}$, respectively, due to an average increase in air and soil temperature from 0 °C (late April) to 27 °C (early June). Long-term drawdown of water table in forested bogs significantly increased tree productivity of a Canadian (Lieffers and Rothwell, 1987) and a Finnish peatland (Heikurainen and Pakarinen, 1982; Lohila et al., 2011). For example, in a 35 year old forestry drained (40 cm below-ground at the end of study) pine bog, a highest ever NEE of -$871 \pm 100\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$, and a tree productivity of $240 \pm 30\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ were reported by Lohila et al. (2011). A sedge fen with water table 25 cm below-ground was reported to emit $8.21\,\mathrm{g\,CO_2\,m^{-2}\,d^{-1}}$ (Aurela et al., 2007). In a treeless fen, Riutta et al. (2007) reported average seasonal ecosystem respiration to be $810\,\mathrm{g\,CO_2\,m^{-2}}$. The ecosystem respiration increased by 18 % and 20 % due to lowering of water level by 14 cm and 22 cm, respectively. However, the variation in respiration may not always be linked to fluctuation in water table; it may be related more directly to variation in moisture availability. Therefore, water table is a major control on respiration in peatlands, and peat soil moisture is sensitive to lowering of water table (Moore et al., 2006; Parmentier et al., 2009; Moore, 2002).

Tree root respiration (R_r) may account for a significant proportion of forest floor respiration (R_{ff}) in forested bogs (Lohila et al., 2011). Therefore, isolating R_r from R_{ff} is critical

to attribute forest floor C to various sources of soil respiration and to fill knowledge gaps related to source/sink dynamics (Hanson et al., 2000; Janssens et al., 2001) of boreal treed bogs under a climate change scenario. The isolated R_r can be used to compare net exchange of the forest floor (NE$_{ff}$) and NPP of a treed peatland with those of an open peatland, provided the major controls (e.g. temperature and water table) remain unchanged. The contribution of R_r to R_{ff} has been quantified using the closed chamber technique in various forest ecosystems. The R_r was separated from R_{ff} by subtracting trenched plots' respiration from control plots at a black spruce forest in Quebec by Hermle et al. (2010) and R_r was found to be 24 % of R_{ff}. However, the percentage was found to be higher, at 37 % in a subtropical forest of mixed alder Cyprus plantations (Wang et al., 2008) in a similar trenching experiment. Hanson et al. (2000) have reported even higher mean root/rhizomicrobial respiration values of 46 % and 60 % for forest and nonforest vegetation, respectively. Munir et al. (2014) reported that the growing season R_r increased from 43 g C m^{-2} to 94 g C m^{-2} following ten years of lowered water table (~ 120 cm) in a boreal bog, but the time scale for the change remains unclear.

Continental peatlands are predicted to be drier under warming climatic conditions. The drier conditions may favour some species in peatland communities to yield more NPP than others and, as a result, plant composition will shift, leading to changes in species dominance (Sternberg et al., 1999). In northern bogs, the balance could shift towards a shrub/tree dominated system (Weltzin et al., 2001; Lohila et al., 2011), which in combination with deeper water tables could lead to an increase in both soil (Ise et al., 2008) and plant respiration (Tarnocai et al., 2009). A shift in species dominance after drainage in a Swedish peatland accelerated soil respiration rates ranging from 513 to 6516 g CO$_2$ m^{-2} d^{-1} (von Arnold et al., 2005). The shifts in species dominance (coverage) and composition vary between microforms (e.g. hummocks (H) and hollows (W)) in peatlands (e.g. Strack et al., 2006). Likewise, the responses of CO$_2$ flux and NPP to manipulations in local climate (warming) (Lafleur and Humphreys, 2008; Johnson

et al., 2013) and local environment (water table) (Strack et al., 2006; Munir et al., 2014) also varied between the microforms.

Warming response studies have used open-top chambers (OTCs) to manipulate ambient temperature to quantify the response of CO_2 exchange in peatlands at northern latitudes. For example, Sullivan et al. (2008) used OTCs in a Greenland rich fen for warming hollow and hummock microforms to evaluate responses of CO_2 fluxes and vegetation changes to warming manipulation. A significant increase in GPP_{ff} was found at both of the microforms in response to the OTC warming of $\sim 1\,°C$. However, Johnson et al. (2013) neither found any consistent increase in warming provided by the OTCs nor any effect on GPP_{ff} or R_{ff} of a treeless poor fen. Weltzin et al. (2003) used overhead infrared lamps to induce warming on bog mesocosms and found that the soil temperature at 15 cm below surface increased up to $4.5\,°C$ and water table dropped to 20 cm. The increase in soil temperature and decrease in water table elevation increased cover of shrubs by 50 % and decreased cover of graminoids by 50 %.

Although several studies have been conducted on NPP and CO_2 exchange in western Canadian peatlands, many unknowns remain. The CO_2 balance and tree biomass of 10 ombrotrophic treed bog sites in Alberta, were quantified by Wieder et al. (2009), but responses to the major controls of temperature and water table were not evaluated. The response of a bog to decade long water table manipulation was quantified by Munir et al. (2014), but the impact of the warming manipulations remained unexplored. The impact of warming manipulation and microtopography on CO_2 balance responses to was also not investigated by Adkinson et al. (2011) in their climatic temperature and short-term drought study on Alberta fens. They also did not estimate the tree productivity of the forested fen nor the contribution of R_r. The CO_2 fluxes at hummock and hollow (or lawn) microforms affected by OTC warming were quantified by Sullivan et al. (2008) in a Greenland fen and Johnson et al. (2013) in an Alaskan fen, but responses to water table fluctuations in the studied open fens remained indeterminate. Therefore, evaluation of peatland tree productivity and net forest floor CO_2 exchange responses to potential warming and water table lowering expected under a climate change scenario

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is required to fill the knowledge gaps on how a severely sensitive treed continental bog (Tarnocai et al., 2009) will feedback to the expected changes in climate. Thus, our unique investigation answers this question by quantifying C balance of a mid-latitude treed continental bog (having hummock and hollow microforms) subjected to warming and water table manipulations, by adding net forest floor CO_2-C exchange to tree productivity-C. Moreover, we isolate R_r from R_{ff} to better understand proportional response of R_r to potential short and longer-term droughts under climate change.

Thus, the goal of our research was to quantify the responses of CO_2 flux and NPP to potential climatic warming and subsequent lowering of water table. We used three sites within a continental boreal bog chosen at Wandering River, Alberta, Canada and monitored the CO_2 flux and the plant biomass over a three year study period (2011–2013). Our specific objectives were: (1) to compare CO_2 flux responses at microforms to warming and water level manipulations using control, experimental and drained sites in an ombrotrophic continental bog, (2) to quantify changes in tree NPP and R_r at the sites in response to the water level manipulations, and (3) to determine changes in ground layer biomass at the microforms and sites in response to the warming and water level manipulations.

2 Methods

2.1 Study sites

Research was conducted in a dry ombrotrophic bog located near the township of Wandering River, Alberta, Canada, during the growing seasons (May to October) of 2011–2013. Three sites were chosen or created having various water levels: an undisturbed water level site called CONTROL (55°21′ N, 112°31′ W), an experimentally lowered water level site ($\sim$ 35 cm lower than control) called EXPERIMENTAL (55°21′ N, 112°31′ W), and a 10 year old drained site ($\sim$ 74 cm lower than control) called DRAINED (55°16′ N, 112°28′ W). The creation of the experimental and drained

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sites has been described in detail by Munir and Strack (2014). Mean precipitation and temperature for the period May to October for this sub-humid continental region are 382 mm and 11.7 °C, respectively, based on 30 year (1971–2000) averages (Environment Canada, 2013). Mean precipitation and air temperature for the growing seasons of 2011, 2012 and 2013, measured using an on-site weather station, were 13.1 °C, 13.2 °C, 14.1 °C and 403 mm, 282 mm, 267 mm, respectively.

Mean water table position (± standard deviation) at the control site (−55.8 ± 21.6) was not different from that at the experimental site (−56.7 ± 20.4) prior to the water table manipulation in 2011 (negative values represented below-ground water table; ANOVA, $F_{1,5} = 0.55$, $p = 0.492$). Mean electrical conductivity (EC, µS cm^{-1}) and pH of pore water in the control (16.6 ± 0.7 and 4.1 ± 0.1, respectively) and experimental (15.2 ± 2.5 and 4.4 ± 0.3, respectively) sites were also found to be similar (ANOVA, EC: $F_{1,5} = 0.84$, $p = 0.401$; pH: $F_{1,5} = 2.63$, $p = 0.166$). All sites were underlain by sandy clay substrate and had peat depth exceeding 4 m.

The Wandering River bog has been classified as a treed low shrub bog with typical mosaic of hummock and hollow microforms (Riley, 2003). In 2011, the control and experimental site microforms were found equally dominated by *Sphagnum* mosses (e.g. *Sphagnum fuscum*) with sparse shrubs (e.g. *Rhododendron groenlandicum*) whereas the drained site hummocks had the greatest coverage of shrubs and the drained hollows had the greatest coverage of lichens. The most abundant type of tree in the bog was black spruce (*Picea mariana*) that constituted > 99 % of the tree stand with 25 766 stems ha^{-1} consisting of 37 % taller trees (> 137 cm height) up to 769 cm high. 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, experimental and drained sites (Munir et al., 2014).

We chose six hummocks and six hollows from the available microtopography at each of the control, experimental and drained sites. Each of the chosen microforms (plot) was fitted with a 60 cm × 60 cm permanent steel collar having groove at the top and inserted approximately 5–6 cm in to the peat surface (to keep disturbance minimal).

Adjacent to each plot, a perforated PVC water well (diameter = 3.5 cm) covered with nylon cloth at the lower 150 cm was inserted into the peat to measure water level manually every time CO$_2$ flux is measured. Two automatic water level loggers (Levelogger Junior 3001, Solinst, Georgetown, Ontario, Canada) were installed at each of the three sites in two randomly selected wells: one at a hummock and the other at a hollow plot. These leveloggers recorded temperature compensated water levels continuously at 20 min intervals throughout the three growing seasons (except at the drained hollow between May to early July 2011 due to malfunction of the levelogger). A Barologger (Barologger Gold, Solinst; height = 100 cm) was also installed to compensate water levels for barometric pressure changes. These records caught short-term water level fluctuations caused by precipitation events that were not captured by weekly manual measurements. In May 2011, at each site, randomly selected three hummocks and three hollows were equipped with 60 degree, 50 cm tall open-top hexagonal chambers (OTCs) of top and basal, side to side dimensions of 104 and 162 cm, respectively.

The OTCs (Molau and Mølgaard, 1996) were constructed using 3.5 mm thick, translucent plexiglas (SUN-LITE HP, Solar Components Corporation, Manchester, New Hampshire, USA) to passively warm internal air and soil (at 5 cm depth) by about 1 °C (Hollister and Webber, 2000). Inside each OTC, two automatic data loggers (HOBO Pro V2, Onset computer corporation, Bourne, MA, USA) were installed at a height of 25 cm above-ground and facing north to avoid direct solar radiation loading. One of the HOBOs logged OTC air temperature only, and the other logged OTC air as well as soil (5 cm) temperatures. To log ambient temperatures, duplicate sets of the two HOBOs were also installed outside the OTCs at all sites. The HOBOs continuously logged temperatures at 20 min intervals during the growing seasons. Snowpack disturbance was minimized by dismantling the OTCs each October and reinstalling back on plots early May.

2.2 CO$_2$ flux

We measured CO$_2$ flux in biweekly campaigns during the growing seasons (May to October) of 2011–2013 using a closed chamber having dimensions 60 cm × 60 cm × 30 cm (length × width × height), made of clear acrylic and corrected for transmittance (88 %). The inside of the chamber was equipped with two low speed battery-operated fans to circulate air inside the chamber during and between the measurements. The instantaneous CO$_2$ concentration inside the chamber headspace was measured with a portable infrared gas analyser (PP systems, USA, EGM-4) while photosynthetically active radiation (PAR) was being measured with a quantum sensor (PP systems, USA) placed at the top of the chamber. The temperature inside the chamber was being measured using a thermocouple thermometer (VWR Int., USA). All of the concomitant measurements were made during a short chamber deployment period (Lai et al., 2012) of 1.75 min at 15 s intervals. Synchronous to the 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 at each CO$_2$ flux measurement occasion from a permanently installed well associated with each plot.

At each plot, a total of 276 CO$_2$ flux measurements in 29 campaigns, were made during the daytime of growing seasons (May to October; 2011–2013). Each campaign lasted for about 7 days during which fluxes were measured at 2 to 3 occasions at each plot. At each flux measurement occasion we made a total of five or six measurements: 2–3 full sun, a single layer shroud, a double layer shroud and finally an opaque tarp (for R_{ff}). The chamber was air-flushed for enough time between the measurements to equilibrate the headspace concentration with that of the ambient air. Therefore we measured respiration as the final measurement (after about 18 min) at each plot and in this way any buildup of CO$_2$ in the soil would have already been flushed out. Thus, the problems Lai et al. (2012) and Koskinen et al. (2014) encountered in determining respiration rates caused by flushing out the soil CO$_2$ built up during nighttime chamber measurements were avoided.

The CO_2 flux measurements when the chamber was covered with an opaque tarp represented R_{ff}. The R_{ff} represents only forest floor respiration (ground-layer above-ground biomass respiration + soil respiration + root respiration (shrubs + herbs + trees)). GPP_{ff} was determined as the difference between NE_{ff} and R_{ff}. Negative values indicate an uptake of CO_2 by the ecosystem. The NE_{ff} was calculated using the exponential change in chamber headspace CO_2 concentration (Kutzbach et al., 2007) regressed with time, as a function of volume, pressure and air temperature inside the chamber, according to the ideal gas law. The exponential regression was applied because covering the soil and vegetation manipulates the spontaneous CO_2 fluxes across soil-vegetation-air continuum and therefore, no linear change in CO_2 concentration inside the chamber can convincingly be expected. The linear fluxes compared with the exponential fluxes have been found to be up to 40 % lower over chamber closure time of only two minutes (Kutzbach et al., 2007).

The GPP_{ff} and NE_{ff} were represented by GPP_{max} and NE_{max}, respectively, when the photon flux density of PAR was greater than $1000\,\mu mol\,m^{-2}\,s^{-1}$. As modeled values of the GPP_{max} were most likely never achieved in reality, these values represented a more realistic estimate of CO_2 exchange when light was not limiting, as reported by Bubier et al. (2003). We used these to statistically compare CO_2 exchange at the microforms and to better understand its controls (e.g., changes in water level, air and soil temperature, and vegetation coverage). The instantaneous CO_2 flux component data presented (Fig. 4) are three growing seasons' averages for all occasions when $PAR > 1000\,\mu mol\,m^{-2}\,s^{-1}$.

2.2.1 Seasonal CO_2 flux modeling and validation

The growing season (May to October) GPP_{ff} was estimated using an exponential empirical model (Munir et al., 2014) parameterized separately for each water level treatment × warming × microform type × year combination. The seasonal GPP_{ff} was esti-

mated according to (modified from Riutta et al., 2007):

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

where $P_{\max}$ denotes the potential maximum rate of GPP_{ff} ($g\,CO_2\,m^{-2}\,d^{-1}$) not constrained by water level and/or temperature, and k represents the PAR level at which half of the $P_{\max}$ occurs. The WL represents water level (cm), WL_{opt} and WL_{tol} are parameters in a GPP_{ff} Gaussian response to WL when GPP_{ff} is optimum, and the width of the curve, respectively. The T denotes soil temperature at 5 cm deep ($T_{\text{soil 5 cm}}$; °C), T_{opt} and T_{tol} are parameters in a GPP_{ff} Gaussian response to T when GPP_{ff} is optimum, and the width of the curve, respectively. The GPP_{ff} model parameters (standard errors), r^2 values, and standard errors of the estimates at control, experimental and drained microforms are presented in Supplement Table S1.

The relationship between R_{ff} with $T_{\text{soil 5 cm}}$ was found to be linear. Therefore, the seasonal R_{ff} was estimated using a multiple linear regression with $T_{\text{soil 5 cm}}$ and water table position by:

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

where a, b and c are regression coefficients, and their values for each water level treatment × warming × microform type × year combination are presented in Supplement Table S2.

Applying Eqs. (1) and (2), seasonal GPP_{ff} and R_{ff} were estimated for each 20 min period between 1 May and 31 October of 2011–2013, averaged daily and summed separately for the growing seasons using continuous PAR (LI-190, LI-COR, Nevada, USA, connected to a CR1000 data logger, Campbell Scientific Canada, Edmonton, AB), WL (Levelogger Junior, Solinst, USA) and $T_{\text{soil 5 cm}}$ (Onset HOBOware Pro, MA, USA) measurements made on site. The seasonal NE_{ff} was calculated by adding seasonal estimates of GPP_{ff} and R_{ff}. The field measured values of GPP_{ff} and R_{ff} were

compared with the model predicted values obtained using SPSS 21. Validation of the models showed excellent agreement between the measured and the modeled values (Fig. 1).

2.2.2 Tree root respiration

To isolate R_r from R_{ff}, a trenching method was used following Wang et al. (2008). From the available microtopography adjacent to the regularly monitored flux plots, we chose an additional eight hummocks and eight hollows at each of control and drained sites, and a fewer four hummocks and four hollows at experimental site (due to its smaller area). Each microform plot had an area of 60 cm × 60 cm. At all sites, half of the chosen microform types were incised around up to a depth of 30 cm and wrapped with a thick polythene sheet to prevent root ingrowth, while disturbance was kept minimal. The other half of the microform plots were left intact (having all tree roots) to quantify the respiration rate difference from those of trenched (having minimal tree roots) plots. All of the R_r plots were kept free of surface vegetation during the trenching experiment in the growing season of 2012. The CO_2 emissions from all R_r plots were measured on average weekly using the same instruments and chamber (with opaque shroud) used for the measurement of NE_{ff}.

2.3 Biomass and tree productivity

2.3.1 Ground-layer biomass

At the end of our field work in October 2013, we collected the ground-layer biomass samples from triplicate of each microform type at each of the three sites. The above-ground biomass samples were collected by clipping duplicate representative quadrats (each measuring 10 cm × 10 cm) adjacent to each of the ambient plots, and from be-tween the OTC wall and the plot collar from warmed plots. The biomass was clipped (using sharp scissors) at the base of capitulum at 1 cm below moss surface following

Loisel et al. (2012). The below-ground biomass samples were collect by soil coring (using a serrated saw) to 20 cm depth only, due to difficulty in collecting and processing a large number of samples to deeper depth. The cores were sectioned into 0–10 cm and 10–20 cm depths at the time of sample collection and taken to the Ecohydrology laboratory, University of Calgary, and sorted into fine (< 2 mm) and coarse (> 2 mm) diameter fractions.

2.3.2 Tree biomass and productivity

Three 10 m × 10 m quadrats in the areas directly surrounding the NE_{ff} flux plots at each of the control and drained sites, and one quadrat at experimental site (due to its smaller area) were laid out in May 2011. The total study areas were not large and these quadrats covered most of the trees in the study areas. The trees were categorized into tall (> 137 cm height) and short (< 137 cm height) for biomass and productivity estimation. The taller trees were measured for their height, diameter at breast height (DBH) and basal diameter (DB), and their biomass was calculated by using an allometric equation (dry biomass = $0.153(\text{tree DBH})^{2.248}$) from Grigal and Kernik (1984). All short trees were also measured for their heights only. Twenty short trees were harvested parallel to the forest floor and transported to the laboratory, oven dried at 80 °C for 48 h (until constant weight), and their biomass used to create an an allometric equation (dry biomass = $0.0085(\text{tree height})^{2.2088}$; $R^2 = 0.93$; $p < 0.001$) we generated by regressing height with oven-dried weight. This was used to estimate the biomass of all other short trees.

NPP of the tree stand for above-ground parts was estimated for 2011 and 2012, following Szumigalski and Bayley (1996) and Thormann and Bayley (1997). They estimated NPP of an Alberta ombrotrophic bog of hummock-hollow microtopography by adding incremental biomass of the trees to their litter production (17 % of above-ground incremental biomass $m^{-2} yr^{-1}$ for *Picea mariana*). We estimated tall trees incremental biomass based on tree ring widths measured using DendroScan (Varem-Sanders et al., 1996). The incremental biomass of the short trees was estimated by re-

gressing leader length with height following Macdonald and Lieffers (1990) and Mullin et al. (1992). Summation of tall and short tree biomass increments for a year represented incremental biomass of the tree stand for above-ground parts of trees for that year. To account for litter, an additional 17 % was added to this summation. The new
5　summation represented NPP for above-ground parts of the tree stand (Szumigalski and Bayley, 1996). We did not measure incremental biomass of the below-ground parts of trees due to the desire to limit disturbance to our research sites and allow for future monitoring. Therefore, we used an allometric equation (tree root biomass = 0.222·tree above-ground biomass) generated by Li et al. (2003) for estimating the incremental
10　biomass of the tree roots. We did not measure tree productivity for 2013, instead used 2012 values for calculating the CO$_2$ and productivity derived C balance for this last year of the study.

2.4　C balance (NE$_{ff}$ + NPP – R_r)

To calculate C balance, the NE$_{ff}$ (–GPP$_{ff}$ + R_{ff}) and NPP (incremental tree biomass
15　of above-ground and below-ground parts of tree stand + stand litter) in term of mass of C were added together separately for the sites and the growing seasons (1 May to 31 October) of 2011–2013. The R_r was excluded to avoid double counting as incremental biomass of below-ground parts of the tree stand already accounted for R_r. Assuming that the dry biomass has a C content of 50 %, the C balance equation for
20　the treed bog sites is as:

$$\text{NEE} = \text{NE}_{ff} + \text{IC}_{tree\_ag} + \text{IC}_{tree\_bg} + L_{tree} - R_r \qquad (3)$$

where NEE denotes Net Ecosystem Exchange, NE$_{ff}$ represents net exchange of the forest floor, IC$_{tree\_ag}$ and IC$_{tree\_bg}$ represent incremental C from biomass growth of the above-ground and below-ground parts of the tree stand, respectively, L_{tree} is tree litter
25　production and R_r is tree root respiration. We estimated a seasonal value of R_r by determining it as a proportion of R_{ff} based on instantaneous measurements and then estimating it as this proportion of the modelled seasonal R_{ff}. 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 %, 55 and 45 %, and 52 and 48 % at the control, experimental and drained sites, respectively (Table 4).

2.5 Data analysis

To estimate treatment effects on instantaneous CO$_2$ flux components (GPP$_{ff}$, R_{ff}, NE$_{ff}$, R_r, NE$_{ff}$ without R_r) we used separate linear mixed-effects models (SPSS 21.0) with CO$_2$ flux component as the response variable, and water level treatment, warming (OTC), microtopography and year as fixed effects. Since the same plots were measured in each study season, year was also taken as repeated measures within the same model (Table 3). We used the same fixed effects and repeated measures in all mixed-effects ANOVA models (described below). All two-way, three-way and four-way interactions between fixed effects were also included in the models. We used compound symmetry covariance structure for repeated measures analysis (Jennrich and Schluchter, 1986). A mean value of flux determined at each plot in each growing season was used for all analyses. Mean CO$_2$ flux components data were normally distributed in all years (Kolmogorov–Smirnov Z: 2011, $p = 0.910$; 2012, $p = 0.767$; 2013, $p = 0.624$).

To quantify treatment effects on ground-layer biomass, we also used multiple response linear mixed-effects model (SPSS 21.0) with moss biomass, vascular biomass, lichen biomass and total biomass as the response variables, and water level treatment, warming (OTC) and microtopography as fixed effects. All two-way and three-way interactions between fixed effects were also included in the models. A mean value of biomass quantified at each plot was used for all analyses. Mean biomass data were normally distributed (Kolmogorov–Smirnov Z: 1.189, $p = 0.118$).

3   Results

3.1   Microclimate and environment

At the Wandering River bog air and soil temperatures and precipitation were monitored during the growing seasons (May to October) of 2011–2013. The weather during the study period was warmer by 1.36 °C, 1.38 °C and 2.44 °C, and wetter by 42 mm in 2011 and drier by 79 mm and 94 mm in 2012 and 2013, respectively, than 30 year means at Athabasca, Alberta (meteorological data have been described under "Methods"). The average undisturbed water level at the control, and manipulated water levels at the experimental and drained sites were clearly different at the start of the study period in 2011 at 38 cm, 73 cm and 112 cm (below moss surface), respectively. The declining precipitation and rising air temperature from 2011 to 2013 further lowered the water level at all sites and microforms. From 2011 to 2013 the water level declined at hummocks by 9 cm, 8 cm and 8 cm and at hollows by 6 cm, 6 cm and 4 cm at control, experimental and drained sites, respectively. Three and thirteen years after initial drainage, the water levels at the experimental and drained sites were lower than at the control site by on average 36 cm and 82 cm, respectively (Fig. 2).

The OTCs resulted in significantly warmer growing season air temperature (T_{air}; ANOVA, $F_{2,24} = 215.87$, $p < 0.001$) by an average (±SD) of 1.0 ± 0.0 °C at the control, 0.9 ± 0.0 °C at the experimental and 0.8 ± 0.5 °C at the drained site (Table 1) consistently over the three study years. The OTC warming at hollows was also significantly greater than at hummocks (ANOVA, $F_{1,24} = 4.85$, $p = 0.037$). The increasing T_{air} significantly warmed the growing season soil temperature at 5 cm depth ($T_{soil\,5\,cm}$; ANOVA, $F_{1,24} = 37.59$, $p < 0.001$) by an average of $1. \pm 0.3$ °C at the control, 0.7 ± 0.1 °C at experimental and 0.7 ± 0.3 °C at the drained site (Table 1) consistently over the three study years. The rising T_{air} warmed the $T_{soil\,5\,cm}$ the least (0.4 ± 0.3 °C) at drained hummocks and the most (1.3 ± 0.2 °C) at the control hummocks. Average soil temperature at 30 cm depth ($T_{soil\,30\,cm}$) below the OTC equipped plots was not significantly different than that at the same depth at non-OTC plots across all sites (ANOVA, $F_{2,24} = 0.71$, $p = 0.053$)

and microforms (ANOVA, $F_{1,24} = 0.95$, $p = 0.339$). Diurnal T_{air} and $T_{soil\,5\,cm}$ patterns in the OTCs were significantly related to PAR ($R^2 = 0.81$, 0.87, respectively) across the microtopography at all sites. During mid-day bright sunny conditions the air warming at OTC equipped plots was greater than that at non-OTC plots by averages of 4 °C, 5 °C and 9 °C at hummocks, and by 5 °C, 7 °C and 6 °C at hollows in the control, experimental and drained sites, respectively. Similarly, the direct solar loading increased the $T_{soil\,5\,cm}$ at the OTC plots greater than at non-OTC plots by averages of 5 °C, 3 °C and 8 °C at hummocks, and by 2 °C, 4 °C and 8 °C at hollows in the control, experimental and drained sites, respectively (Fig. 2).

3.2 Biomass and incremental tree growth

3.2.1 Ground-layer biomass

The moss biomass at the drained site was significantly lower compared to the control site ($F_{2,24} = 3.78$, $p = 0.013$), but not different compared to the experimental site ($p = 0.076$), while the control and experimental sites were not significantly different compared to each other ($p = 0.412$; Table 2). This indicates a strong decline of moss biomass with long-term and deeper drainage. The moss biomass were not significantly different across microtopography ($F_{1,24} = 0.10$, $p = 0.749$) or warming treatments ($F_{1,24} = 0.51$, $p = 0.481$). Also no interaction between the treatments was found.

The vascular plant biomass (mostly woody shrubs) at the control and experimental sites was not significantly different compared to each other ($F_{2,24} = 36.79$, $p < 0.970$), but was significantly lower compared to the drained site ($p < 0.001$; Table 2). Of all the three plant functional groups (moss, vascular, lichen), only vascular plants were significantly affected by warming ($F_{1,24} = 6.83$, $p = 0.015$) and microform type ($F_{1,24} = 41.99$, $p < 0.001$). There were interactions of water level with microform leading to significantly greater vascular plant growth at drained hummocks ($F_{2,24} = 33.70$, $p < 0.001$), and with warming resulting in significantly greater growth at the drained warmed plots ($F_{2,24} = 3.78$, $p = 0.013$), compared to control and experimental ambient and warmed

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microforms. There was a significant interaction between water level, microform and warming resulting in significantly greater biomass of vascular plants at the warmed drained hummocks ($p < 0.001$) compared to control and experimental ambient and warmed microforms. In fact, the long-term deep water level at hummocks had a significant interaction with warming ($F_{1,24} = 8.72$, $p = 0.007$) to increase vascular plant growth. The vascular plant biomass at the ambient drained hollows was the lowest of all plots (Table 2).

The lichen biomass also grew significantly more over the course of longer-term deeper drainage at the drained site ($F_{2,24} = 13.52$, $p = 0.002$) compared to short-term shallower drainage at the experimental and control sites, which were not significantly different compared to each other ($p = 0.958$; Table 2). There was a significant interaction between water level and microform ($F_{2,24} = 3.86$, $p = 0.035$) resulting in significantly greater lichen biomass at the warmed drained hollows ($p = 0.011$), although warming did not increased lichen biomass significantly ($p = 0.441$). There was limited growth of lichen in the control site (Table 2).

As a whole, there was a significant interaction between water level, warming and microform that resulted in a significant increase in the overall ground-layer, above-ground biomass at the warmed drained hummocks ($F_{2,36} = 32.95$, $p = 0.030$). The lowest above-ground biomass was found at the ambient experimental hummocks (Table 2). The total below-ground root biomass (including tree roots) was not statistically different between the sites or the microforms. However, total root biomass was highest at the warmed, drained microforms (Table 2).

3.2.2 Canopy-layer biomass

Above-ground tree biomass was higher in the control site than that in the experimental and drained sites by an average of $156\,\mathrm{g\,m^{-2}}$ and $178\,\mathrm{g\,m^{-2}}$, respectively (Tables 2 and 4). However, the above-ground tree growth during 2011–2012 were significantly higher in the drained site (66 and $60\,\mathrm{g\,C\,m^{-2}}$) than that at the experimental (42 and $39\,\mathrm{g\,C\,m^{-2}}$) and the control (38 and 33) sites ($F_{2,11} = 6.95$, $p = 0.011$). There

was no significant difference between the control and experimental sites ($F_{2,11}$ = 0.87, p = 0.712). Below-ground incremental tree biomass was estimated using equations given by Li et al. (2003). The tree root productivity was calculated to be 8 and 7 g C m^{-2} at the control, 9 and 9 at the experimental, and 15 and 13 g C m^{-2} at the drained sites in 2011 and 2012, respectively.

Tree stand data prior to the study period was not available. We measured the data at the start of our study in 2011 and have described this in detail under "study sites" section. Heterogeneity between the tree quadrats laid out at each site was large; however, the small size of the study sites limited our ability to construct more replicates with the study area. We cannot be certain that the tree biomass at each study site was identical before the study. However, based on the tree ring growth, we did see that the increase in tree productivity coincided with the inadvertent drainage at the drained site 10 years prior to the start of this study. The productivity at the drained site trees was clearly different from that of the control and experimental site trees. Thus, we are confident that the changes in the productivity estimated represent a clear response to the interaction of water level elevation and the duration of drainage.

3.3 CO$_2$ fluxes

3.3.1 Measured CO$_2$ fluxes

GPP$_{max}$ was significantly affected by water level, microtopography and year, but there was no direct significant effect of OTC warming on GPP$_{max}$ (Table 3). The GPP$_{max}$ at the control (-15.4 g CO$_2$ m^{-2} d^{-1}) and drained (-12.8 g CO$_2$ m^{-2} d^{-1}) sites were not significantly different from each other but were different from that at the experimental site (-7.8 g CO$_2$ m^{-2} d^{-1}). There was a higher GPP$_{max}$ at hummocks (-14.4 g CO$_2$ m^{-2} d^{-1}) than at hollows (-9.8 g CO$_2$ m^{-2} d^{-1}). Microform and warming had a significant interaction with each other as well as interactions each individually with water level. The GPP$_{max}$ in 2011 and 2012 were not significantly different from each other but from the highest value that occurred in the warmest 2013. Year had sig-

nificant interactions individually with water level leading to higher GPP_{max} at the control site by 2013; with microform increasing GPP_{max} to $-21.2\,g\,CO_2\,m^{-2}\,d^{-1}$ at hummocks by 2013; and with warming, increasing GPP at warmed but not unwarmed plots by 2013. Although OTC warming did not have a significant effect directly on productivity, there was a significant interaction with water level, microform and year resulting in significantly higher productivity ($-25.8\,g\,CO_2\,m^{-2}\,d^{-1}$) at the warmed drained hummocks in 2013.

R_{ff} was significantly affected individually by all four study factors; water level, microtopography, OTC warming and year (Table 3). The R_{ff} at the control ($13.1\,g\,CO_2\,m^{-2}\,d^{-1}$) and experimental ($14.5\,g\,CO_2\,m^{-2}\,d^{-1}$) sites were not significantly different from each other but were lower compared to that at the drained site ($16.9\,g\,CO_2\,m^{-2}\,d^{-1}$). The R_{ff} was significantly different between hollow ($16.9\,g\,CO_2\,m^{-2}\,d^{-1}$) and hummock ($14.2\,g\,CO_2\,m^{-2}\,d^{-1}$) microforms, and between ambient ($13.5\,g\,CO_2\,m^{-2}\,d^{-1}$) and warmed ($16.7\,g\,CO_2\,m^{-2}\,d^{-1}$) plots. The R_{ff} in 2011 ($14.3\,g\,CO_2\,m^{-2}\,d^{-1}$) and 2013 ($14.7\,g\,CO_2\,m^{-2}\,d^{-1}$) were not significantly different from each other but from the highest ($16.3\,g\,CO_2\,m^{-2}\,d^{-1}$) that occurred in the first drier than average year 2012. There was an interaction between microform and year leading to significantly higher emissions at hollows ($16.8\,g\,CO_2\,m^{-2}\,d^{-1}$) in 2012. Warming had a significant interaction with microform and year resulting in significantly higher R_{ff} at warmed hollows in 2012 ($19.1\,g\,CO_2\,m^{-2}\,d^{-1}$). The significantly greater emissions were likely due to the significantly higher contributions of R_r (5.03 and $6.80\,g\,CO_2\,m^{-2}\,d^{-1}$) to R_{ff} at the experimental and drained hollows, respectively, compared to $1.51\,g\,CO_2\,m^{-2}\,d^{-1}$ at the control hollows. The R_r at the drained hummocks ($3.3\,g\,CO_2\,m^{-2}\,d^{-1}$) was not significantly different compared to that at the experimental hummocks ($3.4\,g\,CO_2\,m^{-2}\,d^{-1}$), but significantly different compared to that at the control hummocks ($4.3\,g\,CO_2\,m^{-2}\,d^{-1}$).

NE_{max} (including R_r) was significantly affected individually by water level, microtopography, OTC warming and year, and all four interactively (Table 3). All sites were significantly different from each other: control site forest floor was a sink of $1.4\,g\,CO_2\,m^{-2}\,d^{-1}$

while experimental and drained sites were sources of 6.5 and 4.1 g CO_2 m^{-2} d^{-1}, respectively. There was a significant interaction of water level with microform resulting in net emissions at experimental hollows (10 g CO_2 m^{-2} d^{-1}) and drained hollows (9.8 g CO_2 m^{-2} d^{-1}) compared to net uptake at the control microforms (hollows = -1.1 g CO_2 m^{-2} d^{-1}; hummocks = -1.8 g CO_2 m^{-2} d^{-1}) and the drained hummocks (-1.5 g CO_2 m^{-2} d^{-1}). The water level also had a significant interaction with warming leading to net emissions from warmed plots at experimental site (10.2 g CO_2 m^{-2} d^{-1}) and drained site (4.2 g CO_2 m^{-2} d^{-1}) compared to net uptake at ambient control plots (-2.1 g CO_2 m^{-2} d^{-1}), while warmed plots had significantly higher emissions (NE$_{ff}$ = 4.5 g CO_2 m^{-2} d^{-1}) than ambient plots (1.7 g CO_2 m^{-2} d^{-1}). The water level also had a significant interaction with study year with highest net uptake of -6.3 g CO_2 m^{-2} d^{-1} at control site in 2013, the year not significantly different compared with 2011 and 2012. Subtracting R_r from NE$_{max}$ (to consider the net exchange of the ground layer only), converts the control microforms and drained hummocks to larger sinks of CO_2, while considerably reduces emissions at the drained hollows and experimental microforms (Table 4).

3.3.2 Modeled CO$_2$ fluxes (excluding R_r)

Based on empirical models (Eqs. 1 and 2), in 2011, the ground layer at the control site was a sink of 42 g CO_2-C m^{-2}, while drained and experimental sites were large sources of 118 and 72 g CO_2-C m^{-2}, respectively (Table 4). The warmer and drier weather in 2012 and 2013 stressed the sink function of the control site, reduced the source function of drained and enhanced the source function of the experimental microforms. Thus in 2012 and 2013, the ground layer at the control site was a reduced CO_2-C sink of 24 and 30 g m^{-2}, respectively; drained site was a reduced CO_2-C source of 106 and 96 g m^{-2}, respectively; while experimental site was an enhanced CO_2-C source of 112 and 189 g m^{-2}, respectively.

In 2011, OTC warming of the forest floor microforms converted the control site to a greater CO_2-C sink of $52\,\mathrm{g\,m^{-2}}$, drained site to a smaller CO_2-C source of $84\,\mathrm{g\,m^{-2}}$ and experimental site to a greater CO_2-C source of $177\,\mathrm{g\,m^{-2}}$. Across the study years, warming of the microforms at control and drained sites on average increased the up-

5 take of carbon (Table 4). In contrast, warming at the experimental site on average enhanced CO_2 emissions much higher than uptake and resulted in net larger release of CO_2 to the atmosphere. The highest emissions at the experimental and drained hollows were largely due to a substantial contribution by R_r. Averaged across years, exclusion of R_r from NE_{ff} makes the control site a greater sink and experimental and

10 drained sites a smaller source of forest floor CO_2 (Table 4, Fig. 4).

3.4 C balance (NE_{ff} + NPP − R_r)

To calculate the final balance of CO_2 fluxes and tree biomass productivity, we added seasonal estimated NE_{ff} ($-R_r$) to estimated tree incremental growth (above and below-ground) and tree litter production. We estimated the C balance separately for the three

15 growing seasons of 2011–2013. The control site was a larger sink of $92\,\mathrm{g\,C\,m^{-2}}$ in 2011 than that of 70 and $76\,\mathrm{g\,C\,m^{-2}}$ in 2012 and 2013, respectively. The experimental site was a progressively increasing source of 14, 57 and $135\,\mathrm{g\,C\,m^{-2}}$ in 2011, 2012 and 2013, respectively. On the other hand, the drained site was a progressively declining source of 26, 23 and $13\,\mathrm{g\,C\,m^{-2}}$ through 2011–2013, respectively. OTC warming of mi-

20 croforms consistently increased uptake at the control site by −13, −19 and $-6\,\mathrm{g\,C\,m^{-2}}$ from 2011 to 2013, respectively. The warming also converted the drained site to a sink of C by 34, 52 and $71\,\mathrm{g\,C\,m^{-2}}$ in 2011, 2012 and 2013, respectively. In contrast, the warming enhanced emissions at the experimental site resulting in losses of 105, 100 and $10\,\mathrm{g\,C\,m^{-2}}$ through the study years, respectively. In all cases, as warming was not

25 applied directly to the trees and so any impact on their growth could not be included in the study. The warming treatment overall increased the carbon uptake at hummocks and enhanced the emissions at hollows. Averaged across the study years, the warm-

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ing interacted with deeper and longer drainage to restore the peatland's original sink function (Fig. 5).

4   Discussion

This study estimated the C balance of a sub-humid, continental treed bog by combining the C exchange values derived from modeled CO$_2$ flux and tree productivity, separately for the growing seasons (May to October) of 2011, 2012 and 2013. The control site in this bog was a growing season sink of 92, 70 and 76 g C m^{-2} along years from slightly wetter and warmer to drier and warmer than average, respectively (Table 4). Depending on the length of time interval after fire, Wieder et al. (2009) reported that the ombrotrophic bogs in the same region represented an annual CO$_2$ sink of 120 to 220 g C m^{-2} and thus our values are slightly below this range. Within the same boreal region of northern Alberta as the present study, Adkinson et al. (2011) also reported net growing season CO$_2$ uptake across three study years of −110 and −35 to −154 g C m^{-2} at the poor fen and rich fen sites, respectively, and thus our control site sink values are close to the value at the poor fen. However, a higher yearly CO$_2$ accumulation rate of −144 g C m^{-2} in a treed fen in the same boreal region is reported by Syed et al. (2006).

Previous findings have revealed that dry and warm summer conditions can reduce net CO$_2$ uptake in peatlands by enhancing respiration greater than production (Aurela et al., 2007; Cai et al., 2010; Bhatti et al., 2012; Alm et al., 1999). Likewise, the net CO$_2$ uptake (NE$_{ff}$) at our control and experimental sites were lower in the drier and warmer growing seasons (2011 and 2012) of the study. This reduction was due to the substantial increase in R_{ff} at the hollows exceeding the combined increase in GPP$_{ff}$ at the microforms especially in 2012 (Table 4). The steady and consistent increase in R_{ff} at control hollows might be due to the weather-driven moderate decline in water level (Fig. 2) and stressed vegetation (data not presented here) observed at the hollows. However, the abrupt increase in R_{ff} noticed at the experimental hollows might be due to the influence of experimental lowering of water table negatively affecting hollow veg-

etation more than adjacent hummocks. In contrast, there was only a minor fluctuation in GPP$_{ff}$ or R_{ff} at the drained site in 2012 and 2013 compared to 2011, and thus stability in net CO$_2$ exchange at this long-term drained site could be due to the dominance of vascular ground-layer vegetation, as opposed to the control and short-term drained sites having greater coverage of mosses (Fig. 3, Tables 2 and 3).

The one to three years of water table drawdown, converted our bog site forest floor (excluding R_r) from a sink of 42, 24 and 30 g C m^{-2} in 2011, 2012 and 2013, respectively, to a progressively larger source of 72, 112 and 189 g C m^{-2} in 2011, 2012 and 2013, respectively. A net loss of CO$_2$-C in response to a short-term disturbance has been reported by Laiho (2006) in a bog and Chivers et al. (2009) in a fen ecosystem. The 11–13 years of deeper water level also showed a net loss that was higher in 2011 (118 g C m^{-2}) and declined slightly through the later years (106 and 96 g C m^{-2} in 2012 and 2013, respectively). The drained and experimental sites had consistently increasing emissions at the hollows and decreasing emissions at the hummocks from 2011 to 2013, although the emissions at the experimental site were highest. These net loss values of C at the short and longer-term drained sites compare well with those of other experimentally drained peatlands as reported by von Arnold et al. (2005), Cai et al. (2010) and Simola et al. (2012). The rapid decline in water table in the experimental site possibly initiated vegetation desiccation that progressed through the study years. In contrast, the longer-term drainage drove hummock habitat to be more favourable for woody shrubs of higher water use efficiency and longer root system. That was likely why the drained site hummocks had declining net emissions with warming and drying of the growing seasons.

The control site sink strength was enhance by OTC warming leading to greater C uptake as NEE (including NE$_{ff}$ and trees) by 13, 19 and 6 g C m^{-2} (represented by C_w in Table 4) in the growing seasons from 2011 to 2013, respectively. The lowest sink differential (warmed – ambient) of 6 g C m^{-2} was noticed in the warmest and driest year 2013 similar to the findings of Aurela et al. (2007) and Lafleur and Humphreys (2008). They also reported that increased growing season temperature enhanced GPP$_{ff}$ but

extreme seasonal temperature reduced the GPP$_{ff}$ and accelerated R_{ff} in a sub-arctic fen. The increase in GPP$_{ff}$ and/or R_{ff} has also been reported by Sullivan et al. (2008) in a Greenland rich fen and Weltzin et al. (2001) in bog mesocosms, both in disagreement with Johnson et al. (2013) that reported that there was no consistent effect of OTC warming on the CO$_2$ flux components because of subtle warming. At our short-term drained (experimental) site, the OTC warming greatly accelerated emissions, causing differential increases of 105, 100 and 10 g C m^{-2} from 2011 to 2013, respectively (Table 4). An abrupt differential increase in the first year of water table drawdown could be due to an accelerated microbial decomposition of easily decomposable substrate (Keller and Bridgham, 2007; Cai et al., 2010) due to the limiting capillary rise to the drying moss (Waddington and Price, 2000) and extremely stressed vegetation observed in the first two years of warming treatment. However, our long-term drained site had 13 years of transitioning to a habitat favourable for the drought resistant vascular vegetation. A peatland forest floor subjected to long-term deeper drainage developed drought resistant vascular vegetation and trees with deeper root system compared to that under shallower water level conditions. The stable increase in the growth of shrubs and trees in the thicker oxic zone can accelerate accumulation rate equal to or exceeding its original productivity before forestry drainage (Hermle et al., 2010; Lohila et al., 2011). Thus our drained site microforms equipped with OTCs, responded with consistently increasing differential NEE of −34, −52 and −73 g C m^{-2} in 2011, 2012 and 2013, respectively. Thus, warming led to greater CO$_2$ uptake. Our findings together with those of others (e.g. Bubier et al., 2003; Aurela et al., 2007; Sullivan et al., 2008; Weider et al., 2009; Lohila et al., 2011) demonstrate the critical interaction of temperature with wetness for GPP$_{ff}$ and R_{ff} response as either of the factors alone could not illustrate the overall growth response of bog vegetation under changing microclimatic and environmental conditions.

Peatland microforms have been reported to respond with different magnitudes and in different directions to changes in water table, warming, and other climatic and environmental conditions. For example, Waddington and Roulet (2000) reported signifi-

cantly greater CO_2 uptake at the wetter lawn than that at the drier ridge in an eccentric raised bog in Sweden, over two growing seasons. Similarly, in a cool temperate fen in Canada, Strack et al. (2006) demonstrated higher GPP_{max} at drained hollows than that at drained hummocks in contrast to control microforms and speculated that the persistently lowered water tables would result in flattening of the peatland microtopography. Contrastingly, in this study in a dry continental treed bog in Alberta, we found that after thirteen years of deepest drainage treatment the GPP_{max} and GPP_{ff} were in fact the highest at drained hummocks, increasing from cooler 2011 to warmer 2013. Conversely, R_{ff} and R_r were the highest at the experimental and drained hollows, also increasing towards warmer 2013. Interestingly, the CO_2 uptake was even higher at the warmed drained hummocks, while CO_2 release was also even higher at the warmed drained hollows and experimental microforms compared to the ambient microforms at these sites (Fig. 4, Table 4). The significantly increased GPP_{max} at ambient and even higher at warmed drained hummocks were probably due to enhanced growth and greater biomass of vascular vegetation (shrubs; Table 2, Fig. 3). Conversely, replacement of most of the moss (dominantly *Sphagnum*) biomass by lichens at ambient and warmed drained hollows led to the measured reduction in GPP_{max} and GPP_{ff} (Fig. 3, Tables 2 and 4). Moreover, drained and experimental hollows were the largest sources of CO_2 in all years. Thus, we expect hummocks to have increasing equilibrium peat depth and hollows to have decreasing equilibrium peat depth as an effect of drainage over the long run. These predictions contradict with those of Strack et al. (2006) due to contrasting microclimatic and environmental conditions of the two studies but corroborate with those of Munir et al. (2014) due to same climatic and environmental conditions. However, these studies together support a general humpbacked relationship of peat accumulation with water level (Belyea, 2009). Therefore, combining the CO_2 dynamics at the ambient and warmed experimental and drained microforms demonstrates that climate forced declining water levels in ombrotrophic continental bogs would result in hummocks growing higher and hollows deepening.

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Methane (CH_4) is also an important component of the C balance in peatland ecosystems. However, over-all seasonal CH_4-C losses were reported to be 0.34, 0.61 and 0.07 g C m^{-2} at our control, experimental and drained sites, respectively (Munir and Strack, 2014). Therefore, the CH_4 fluxes are a minor component of the seasonal C balance at our dry continental bog sites. The carbon can also be lost from the system with hydrologic flows. This would include particulate and dissolved organic carbon. Given the deep water level and dry conditions in these continental bogs, discharge from the study areas during the growing season was also likely small.

Interactions between soil and plant communities have been predicted to play a major role in determining the response of net exchange of CO_2 in peatlands to a climate change scenario (Weltzin et al., 2001; Kardol et al., 2010; Moore et al., 2002) of water level lowering and global warming (Ciais, 2013). Ground-layer biomass was significantly affected in response to thirteen years of drainage (water level ∼ 120 cm; $F_{2,36} = 49.42$, $p < 0.001$) and OTC average warming of ∼ 1 °C or mid-day full sun diurnal air warming of ∼ 6 °C or 5 cm deep soil warming of ∼ 5 °C ($F_{2,36} = 6.46$, $p = 0.015$; Figs. 2 and 3). The shift in biomass coverage and composition was also different between the microforms ($F_{2,36} = 24.14$, $p < 0.001$); increased biomass at hummocks compared to that at hollows. However, no significant difference in vegetation biomass or composition was found after a three years of drainage of water level ∼ 76 cm ($p = 0.162$). Interestingly, along a gradient of decreasing water level, shrub biomass increased at hummocks, lichens biomass increased at hollows, while moss biomass decreased at all microforms at the continental bog sites. Along the same gradient of decreasing water level, the warming treatment enhanced shrub biomass at the hummocks from 2011–2013, indicated by an interaction of water table × warming × microform × year ($F_{2,36} = 8.24$, $p = 0.001$). The accumulated NPP ratio of below-ground : above-ground shifted from 1.86 before warming to 2.00 after warming, suggesting a shift in C allocation in response to warming treatment. The three bog functional plant groups (moss, shrub, lichen) differed in their response to water level and warming due to their differential response of life-forms and species characteristics of each community (Weltzin

et al., 2000). The drainage-driven and warming-induced increases in vascular biomass we found had also been reported by Moore et al. (2002); Laine et al. (2011) and Weltzin et al. (2000), respectively.

We report above-ground biomass (including ground-layer and canopy-layer) to be within the range of values previously published for bogs. The published data for ground-layer biomass across 16 bogs and above-ground tree biomass across 20 bogs varied quite broadly with means of 1900 g m^{-2} (± 224) and 2177 g m^{-2} (± 2259), respectively (Moore et al., 2002). Our data for above-ground tree biomass (2031 ± 379) fall within the range of published values. However our ground-layer biomass average (1236 ± 130 g m^{-2}) is less than those reported by Moore et al. (2002) because they drew 110 cm deep peat cores for quantifying below-ground biomass vs. our core depth of only 20 cm. Therefore, it is likely that we might have underestimated the below-ground biomass particularly at the drained site with up to 120 cm thick oxic zone. However, this still more likely included almost all of the below-ground biomass as Lieffers and Rothwell (1987) could find only 6 % of the root biomass below 20 cm depth in a drained bog (water level below 80 cm) in north central Alberta.

Although above-ground tree biomass decreased along our gradient of deeper water level, productivity of the trees (measured by determining above-ground incremental tree growth) increased along the same gradient (Tables 2 and 4). The highest above-ground tree biomass estimated at the control site was due to thinner oxic zone supporting mainly denser stand but smaller diameter trees and higher number of shorter trees. The higher productivity in the drier sites was due to thicker aerated peat and supporting higher availability of nutrients (Paavilainen and Päivänen, 1995). Therefore, trees react almost instantly to changes in the local water table (Linderholm and Leine, 2004), as occurred in experimental site that showed higher productivity than control but lesser than drained site. The response time to reach maximum tree productivity after drainage has been reported to be ∼ 10 years (Seppala, 1969; Linderholm and Leine, 2004) which strongly supports significantly highest productivity at our 10–13 years old drained site of deepest water table of ∼ 120 cm. The measured R_r consistently increased at all sites

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along a gradient of warming year (growing season), but was highest at the experimental site in all years due to readily available substrate and desiccating vegetation at this short-term lowered water level site. Drainage induces significantly higher coverage and biomass of vascular plants that offset some of the loss of CO_2 occurring due to deepening of oxic zone and increasing of decay rates (Ise et al., 2008). Therefore, although our drained site forest floor was always a source of CO_2, warming induced significantly increased ground-layer biomass that shifted this site to be a sink of C. This sink function coupled with higher tree productivity significantly enhanced the sink function of the drained site (Fig. 5). Conversely, the dramatic lowering of water table at the experimental site severely destabilized the ecosystem functioning that was further deteriorating with warming treatment along the study seasons (2011–2013). However, the differential emissions (warmed – ambient) were noticed to be declining through the study years, indicating that the bog ecosystem may have been reaching a new equilibrium after an initial stress.

5   Conclusions

In a mid-latitude dry continental treed bog, there was a transitional shift in biomass coverage and composition between the microforms in response to a longer-term water level lowering and OTC warming. The moss cover decreased slightly in response to a short-term (1–3 years) experimental water level lowering of ~ 36 cm and with a significantly greater decline in response to a longer-term (11–13 years) and deeper water level lowering of ~ 82 cm. In fact, the moss biomass was replaced by vascular plant biomass (mostly woody shrubs) at hummocks and lichen biomass at hollows. The shrub biomass growth was significantly increased in response to a three year OTC warming of $\sim 1\,^\circ$C in the longer-term and deeper water level treatment.

The deeper water level combined with OTC warming induced enhanced growth of woody shrubs and drove the drained hummocks to become a the largest net sink of CO_2 across all sites and microforms. Conversely, the short-term, as well as the longer-

term, water level lowering converted the hollows to be the largest net sources of CO_2. However, the 11–13 years of deeper water level lowering coupled with OTC warming increased the forest floor net uptake of CO_2 exceeding well above the losses via respiration at the drained microforms. The significantly increased tree productivity in response to the longer-term deeper drainage (NPP – C) added to the NE_{ff} – C ($-R_r$) converted the drained site from a moderate C source, to become a sink of C close to the bog's original sink strength (Fig. 5).

Averaged across study years, an OTC warming of $\sim 1\,^\circ$C (and differential mid-day full sun air warming of $\sim 6\,^\circ$C) interacted with water level treatment to increase the sink function of the undisturbed site by $-13\,\mathrm{g\,m^{-2}\,yr^{-1}}$, increased source strength of the experimental site by $72\,\mathrm{g\,m^{-2}\,yr^{-1}}$ and increased the sink strength of the drained site by $53\,\mathrm{g\,m^{-2}\,yr^{-1}}$. This pattern is a strong indicator that climatic warming that drives persistent lowering of water level for longer-term (~ 13 years or more) is expected to restore the original sink function of continental treed bogs after an initial short duration (~ 3 years) of net C losses, driven by the initial lowering of water level in response to climatic warming and drying. It also infers that mid-latitude continental treed bogs are sensitive but resilient ecosystems that are expected to respond to climatic warming and drying almost instantly by thickening the aerated peat and developing woody roots that penetrate deeper for optimum supply of moisture and nutrients to the newly adapted surface vegetation. Although the aerated peat thickening initially leads to larger net emissions to the atmosphere, persistent drying and warming transforms the moss habitat (characterized by near surface water level) to vascular plant habitat (characterized by deeper water level) leading to a shift to woody shrubs with longer root system and greater water use efficiency. The bog trees adapt better to lower water levels and increase productivity by widening ring width, lengthening leader length and increasing belowground biomass allocation.

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Table 1. Mean seasonal air temperatures (T_{air}), soil temperatures at 5 cm depth ($T_{soil\,5\,cm}$) and soil temperatures at 30 cm depth ($T_{soil\,30\,cm}$) at all the sites, measured during growing seasons (May to October) of 2011–2013[a].

		CONTROL		EXPERIMENTAL		DRAINED	
		Hummock	Hollow	Hummock	Hollow	Hummock	Hollow
T_{air} (°C)	Ambient	13.6 ± 0.3^A	13.5 ± 0.2^A	13.8 ± 0.1^A	13.9 ± 0.1^A	14.3 ± 0.3^A	14.3 ± 0.2^A
	Warmed	14.4 ± 0.5^B	14.4 ± 0.4^B	14.7 ± 0.3^B	14.7 ± 0.6^B	14.6 ± 0.2^A	15.2 ± 0.8^B
$T_{soil\,5\,cm}$ (°C)	Ambient	12.3 ± 0.2^A	12.3 ± 0.0^A	13.1 ± 0.0^A	13.1 ± 0.1^A	13.7 ± 0.0^A	13.7 ± 0.1^A
	Warmed	12.9 ± 0.2^B	13.6 ± 0.6^B	13.8 ± 0.9^B	13.7 ± 0.6^B	14.1 ± 0.6^A	14.6 ± 0.4^B
$T_{soil\,30\,cm}$ (°C)	Ambient	10.8 ± 2.5^A	11.0 ± 2.8^A	9.9 ± 2.7^A	11.2 ± 3.2^A	12.0 ± 3.7^A	13.2 ± 3.8^A
	Warmed	11.7 ± 2.3^A	12.4 ± 2.5^A	11.2 ± 2.7^A	12.2 ± 3.8^A	12.3 ± 3.8^A	12.7 ± 3.8^A

[a] All temperatures are mean (± SD). At each site, all the OTC-equipped hummocks ($n = 3$) and hollows ($n = 3$) were instrumented with HOBOs to log OTC warming of air (T_{air}) and 5 cm deep soil ($T_{soil\,5\,cm}$). The 30 cm deep soil temperatures ($T_{soil\,30\,cm}$) were measured using thermocouple, during the measurement of CO$_2$ fluxes in the growing seasons of the study years. Means sharing same letters do not differ significantly. Letters should be compared only within one column separately for T_{air}, $T_{soil\,5\,cm}$ and $T_{soil\,30\,cm}$.

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Table 2. Ground-layer and tree biomass (g m^{-2}) at control, experimental and drained sites[a].

| SITE/ MICROFORM | ABOVE-GROUND | | | | BELOW-GROUND | | | TREES | TOTAL |
	Moss	Vascular	Lichen	Total	Fine (< 2 mm)	Coarse (> 2 mm)	Total		Ambient/ Warmed
CONTROL								2142 ± 376	
Ambient Hummock	208 ± 51[A]	191 ± 62[A]	0 ± 0[A]	399 ± 24[A]	335 ± 15	233 ± 61	568 ± 48		3168 ± 604
Ambient Hollow	134 ± 17[A]	216 ± 11[A]	0 ± 0[A]	350 ± 82[A]	486 ± 67	266 ± 102	751 ± 332		
Warmed Hummock	113 ± 46[A]	172 ± 97[A]	0 ± 0[A]	285 ± 140[A]	477 ± 118	71 ± 36	548 ± 147		3150 ± 578
Warmed Hollow	269 ± 98[A]	166 ± 32[A]	0 ± 0[A]	435 ± 130[A]	418 ± 68	378 ± 84	796 ± 122		
EXPERIMENTAL								1986[b]	
Ambient Hummock	63 ± 24[A]	185 ± 68[A]	3 ± 2[B]	251 ± 78[A]	329 ± 148	112 ± 176	441 ± 96		2836 ± 540
Ambient Hollow	138 ± 29[A]	190 ± 24[A]	0 ± 0[A]	327 ± 51[A]	385 ± 112	330 ± 188	715 ± 116		
Warmed Hummock	178 ± 69[A]	238 ± 37[A]	0 ± 0[A]	416 ± 80[A]	581 ± 313	138 ± 70	719 ± 169		3048 ± 731
Warmed Hollow	88 ± 89[A]	139 ± 44[A]	2 ± 1[B]	228 ± 89[A]	495 ± 119	250 ± 118	745 ± 171		
DRAINED								1964 ± 381	
Ambient Hummock	143 ± 95[A]	462 ± 91[B]	38 ± 49[BC]	643 ± 18[B]	625 ± 220	300 ± 154	925 ± 247		3429 ± 639
Ambient Hollow	146 ± 70[A]	80 ± 39[C]	378 ± 6[A]		631 ± 194	344 ± 409	975 ± 301		
Warmed Hummock	38 ± 12[B]	870 ± 66[C]	12 ± 3[B]	919 ± 63[C]	895 ± 242	397 ± 58	1292 ± 249		3970 ± 767
Warmed Hollow	24 ± 33[B]	226 ± 99[A]	200 ± 91[C]	450 ± 23[A]	999 ± 266	335 ± 219	1334 ± 332		

[a] Values are means ±SE ($n = 3$ for each of above-ground, belowground and trees' biomass). Means sharing same letters do not differ significantly. Letters should be compared only within one column. Total biomass was determined by weighing ground-layer by the proportion of hummocks and hollows at each site (control = 56 % hummocks, experimental = 55 % hummocks, drained = 52 % hummocks).
[b] $n = 1$ (only one quadrat was available due to limited size of experimental site).

Table 3. Mixed-effects ANOVA F and p values for the fixed effects of water level treatments (control, experimental, drained), warming treatments (non-OTC, OTC), microform types (hummock, hollow) and years (2011, 2012, 2013) with repeated measures of year, on CO$_2$ fluxes at the peatland surface[a].

Effect	df	CO$_2$ Flux Components					
		GPP$_{max}$		R		NE$_{max}$	
		F	p	F	p	F	p
Water level	2, 108	57.78	0.000	12.61	0.000	53.87	0.000
Microform	1, 108	56.71	0.000	12.60	0.001	92.55	0.000
Warming	1, 108	0.21	0.651	37.68	0.000	19.52	0.000
Year	2, 108	31.43	0.000	5.77	0.004	33.15	0.000
Water level × Microform	2, 108	12.85	0.000	19.42	0.000	22.26	0.000
Water level × Warming	2, 108	11.79	0.000	0.88	0.420	11.33	0.000
Water level × Year	4, 108	8.11	0.000	4.75	0.001	2.86	0.027
Microform × Warming	1, 108	7.57	0.007	1.39	0.242	2.26	0.136
Microform × Year	2, 108	1.51	0.003	3.88	0.024	1.61	0.205
Warming × Year	2, 108	8.96	0.000	5.25	0.007	6.45	0.002
Water level × Microform × Warming	2, 108	0.60	0.519	0.83	0.441	1.58	0.211
Water level × Microform × Year	4, 108	0.17	0.954	2.17	0.077	1.02	0.400
Water level × Warming × Year	4, 108	0.31	0.871	0.31	0.873	0.37	0.831
Microform × Warming × Year	2, 108	1.57	0.213	3.72	0.027	0.27	0.768
Water level × Microform × Warming × Year	4, 108	2.63	0.039	0.54	0.710	3.30	0.014

[a] GPP$_{max}$ and NE$_{max}$ represent GPP$_{ff}$ and NE$_{ff}$ when the photon flux density of PAR was greater than 1000 μmol m^{-2} s^{-1}. R represents R_{ff} (forest floor respiration).

CO2 flux and NPP of a boreal treed bog

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Table 4. Growing season CO_2-C flux estimates ($\pm$SE; $g\,C\,m^{-2}$)[a].

Yr	Site	GPP_{ff}	R_{ff}	NE_{ff}	R_r	L_{tree}	IC_{tree_ag}	IC_{tree_bg}	NEE[b]	C_w
2011	CONTROL									
	Ambient Hummock	−190 ± 29	225 ± 18	35 ± 30	63 ± 5	−6 ± 1	−38 ± 8	−8 ± 1	−92 ± 12	−13
	Ambient Hollow	−178 ± 29	130 ± 21	−48 ± 09	2 ± 0					
	Warmed Hummock	−206 ± 41	251 ± 63	45 ± 21	70 ± 6	−6 ± 1	−38 ± 8	−8 ± 1	−105 ± 16	
	Warmed Hollow	−207 ± 37	134 ± 52	−74 ± 22	12 ± 3					
	EXPERIMENTAL									
	Ambient Hummock	−106 ± 44	182 ± 75	76 ± 12	53 ± 14	−7 ± 0	−42 ± 15	−9 ± 3	14 ± 5	105
	Ambient Hollow	−102 ± 52	349 ± 89	246 ± 55	115 ± 68					
	Warmed Hummock	−104 ± 04	422 ± 83	317 ± 94	122 ± 56	−7 ± 0	−42 ± 15	−9 ± 3	119 ± 48	
	Warmed Hollow	−136 ± 13	435 ± 95	299 ± 83	144 ± 55					
	DRAINED									
	Ambient Hummock	−280 ± 21	295 ± 10	15 ± 7	62 ± 5	−11 ± 1	−66 ± 9	−15 ± 2	26 ± 14	−34
	Ambient Hollow	−116 ± 19	536 ± 09	420 ± 23	123 ± 01					
	Warmed Hummock	−333 ± 91	343 ± 86	10 ± 9	72 ± 17	−11 ± 1	−66 ± 9	−15 ± 2	−8 ± 5	
	Warmed Hollow	−118 ± 19	468 ± 95	350 ± 92	108 ± 24					
2012	CONTROL									
	Ambient Hummock	−228 ± 43	216 ± 33	−12 ± 11	60 ± 5	−6 ± 1	−33 ± 7	−7 ± 1	−70 ± 10	−19
	Ambient Hollow	−181 ± 8	241 ± 45	60 ± 33	21 ± 0					
	Warmed Hummock	−226 ± 99	222 ± 87	−4 ± 2	62 ± 19	−6 ± 1	−33 ± 7	−7 ± 1	−89 ± 27	
	Warmed Hollow	−197 ± 29	201 ± 88	4 ± 0	18 ± 17					
	EXPERIMENTAL									
	Ambient Hummock	−33 ± 23	165 ± 53	132 ± 12	48 ± 14	−7 ± 2	−39 ± 11	−9 ± 0	57 ± 44	100
	Ambient Hollow	−89 ± 77	351 ± 96	261 ± 67	116 ± 55					
	Warmed Hummock	−119 ± 44	443 ± 88	324 ± 87	129 ± 17	−7 ± 2	−39 ± 11	−9 ± 0	157 ± 90	
	Warmed Hollow	−77 ± 12	459 ± 59	382 ± 64	151 ± 82					
	DRAINED									
	Ambient Hummock	−333 ± 75	359 ± 18	26 ± 13	75 ± 05	−10 ± 2	−60 ± 10	−13 ± 2	23 ± 15	−52
	Ambient Hollow	−118 ± 20	507 ± 35	390 ± 47	116 ± 01					
	Warmed Hummock	−391 ± 44	356 ± 79	−36 ± 12	75 ± 27	−10 ± 2	−60 ± 10	−13 ± 2	−29 ± 11	
	Warmed Hollow	−136 ± 16	478 ± 63	342 ± 98	110 ± 29					
2013	CONTROL									
	Ambient Hummock	−233 ± 82	217 ± 59	−17 ± 1	61 ± 9	−6 ± 0	−33 ± 7	−7 ± 1	−76 ± 38	−6
	Ambient Hollow	−195 ± 29	248 ± 41	53 ± 14	22 ± 7					
	Warmed Hummock	−259 ± 92	203 ± 56	−56 ± 23	57 ± 12	−6 ± 1	−33 ± 7	−7 ± 1	−82 ± 40	
	Warmed Hollow	−232 ± 97	322 ± 46	90 ± 22	29 ± 20					
	EXPERIMENTAL									
	Ambient Hummock	−51 ± 18	288 ± 22	237 ± 15	84 ± 18	−7 ± 2	−39 ± 11	−9 ± 0	135 ± 44	10
	Ambient Hollow	−93 ± 55	486 ± 58	394 ± 67	161 ± 56					
	Warmed Hummock	−81 ± 34	330 ± 55	249 ± 69	96 ± 19	−7 ± 2	−39 ± 11	−9 ± 0	145 ± 90	
	Warmed Hollow	−104 ± 16	535 ± 51	431 ± 99	177 ± 81					
	DRAINED									
	Ambient Hummock	−347 ± 65	365 ± 84	17 ± 18	77 ± 21	−10 ± 2	−60 ± 10	−13 ± 2	13 ± 15	−73
	Ambient Hollow	−123 ± 22	502 ± 33	380 ± 74	116 ± 61					
	Warmed Hummock	−517 ± 42	398 ± 58	−120 ± 11	83 ± 25	−10 ± 2	−60 ± 10	−13 ± 2	−58 ± 11	
	Warmed Hollow	−122 ± 36	513 ± 33	391 ± 91	118 ± 25					

[a] Negative values represent uptake of carbon by the peatland from the atmosphere. The forest floor respiration (R_{ff}) includes tree root respiration (R_r). C_w (NEE warmed – NEE ambient) represents warming induced net ecosystem exchange at site.

[b] NEE is calculated using Eq. (3) (NEE = NE_{ff} + IC_{tree_ag} + IC_{tree_bg} + L_{tree} − R_r). Forest floor carbon exchange was determined by weighting NE_{ff} measured at each microform by the proportion of hummocks and hollows at each site (control = 56 % hummocks, experimental = 55 %, drained = 52 % hummocks).

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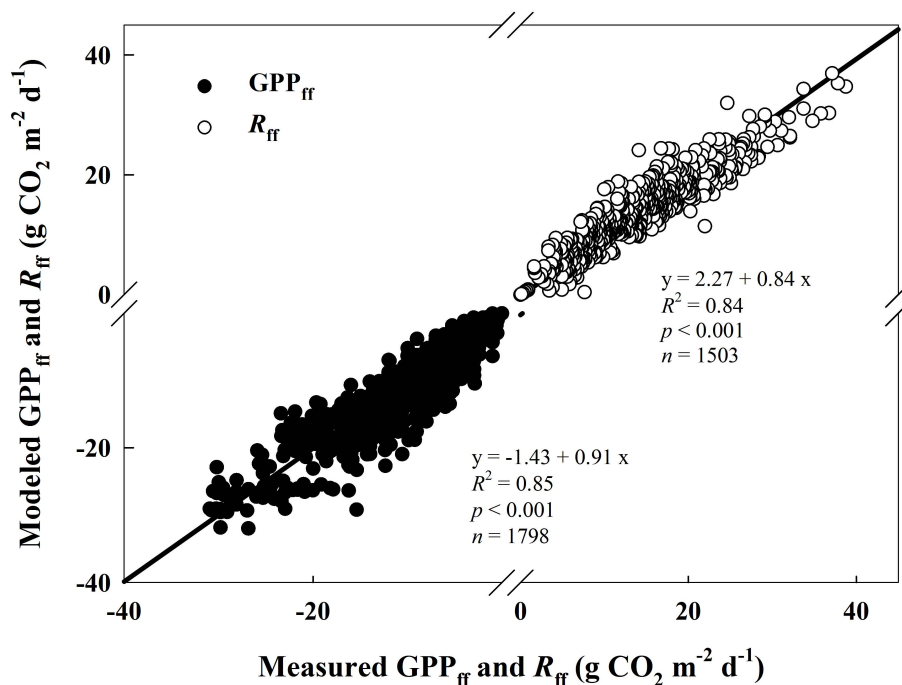Printer-friendly Version

Interactive Discussion

Figure 1. Goodness of fit (r^2) between modeled and measured GPP_{ff} and modeled and measured R_{ff} values. The figure presents all data for control, experimental and drained sites for the study years (2011–2013). Lines represent the 1 : 1 fit.
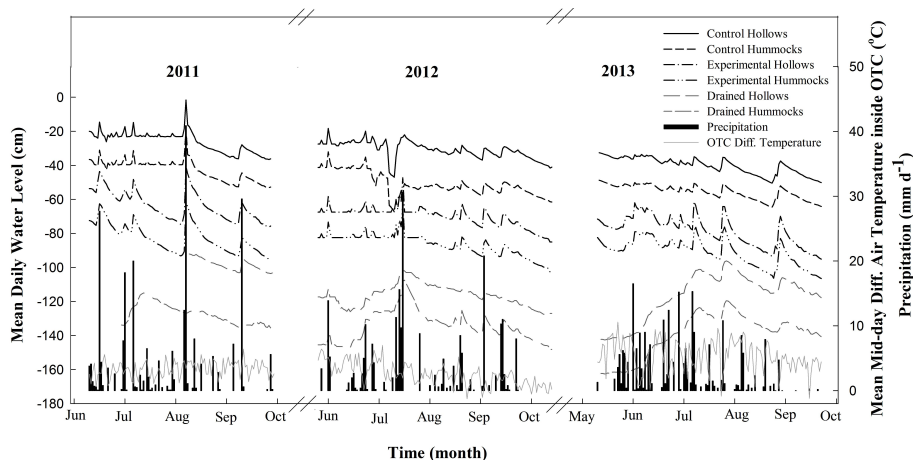
Figure 2. Mean daily water level, mid-day differential (warmed – ambient) air temperature and precipitation at hummock and hollow microforms during growing seasons of 2011, 2012 and 2013. Note the right y-axis has two values using the same scale: mean mid-day differential air temperature and daily precipitation. The x-axis breaks separate 2011, 2012 and 2013. The partially missing water level data at drained hummocks in 2011 was due to levelogger's malfunction. The cumulative seasonal precipitation during 2012 and 2013 was 30.0 % and 35.3 % lesser respectively than that in 2011.
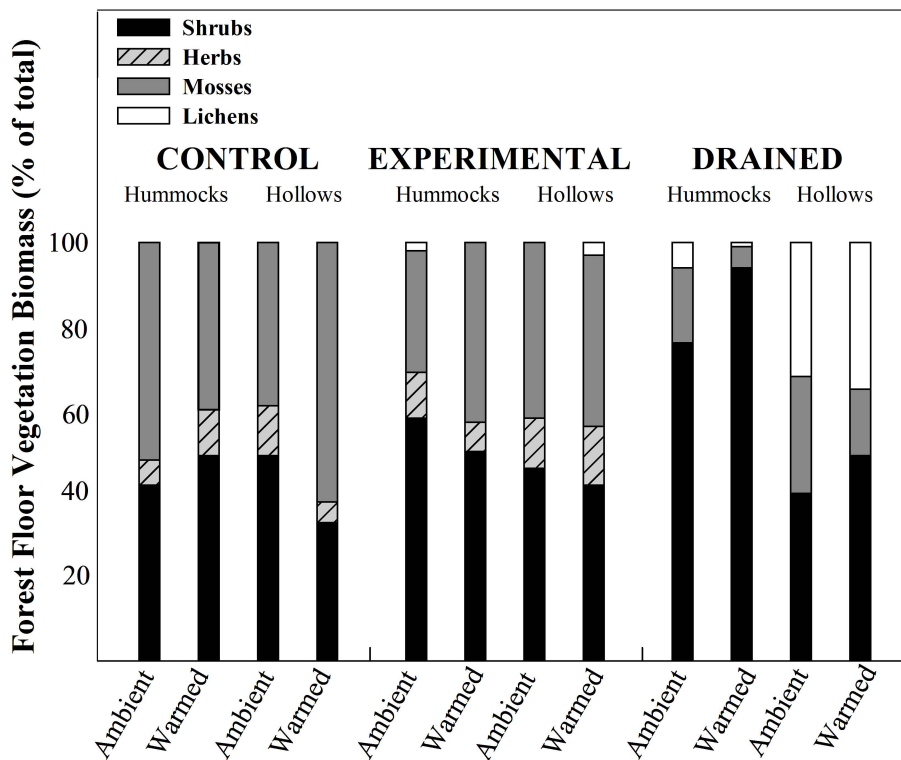
Figure 3. Relationship between drainage, warming and microform scenario and ground layer above-ground biomass by category as a percentage of total.
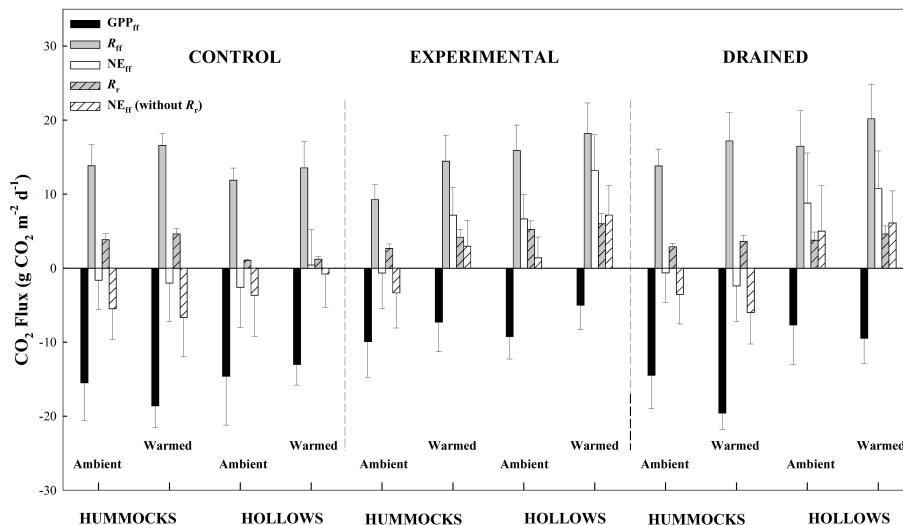
Figure 4. GPP$_{max}$, R_{ff} and NE$_{max}$ and R_r at control, experimental and drained sites averaged across 2011–2013. NE$_{max}$ (without above and below-ground parts of trees) was calculated by subtracting R_r from NE$_{max}$ and represents net exchange of CO$_2$ of the ground-layer vegetation (including peat). Error bars indicate ± standard deviation. Results are from linear mixed-effects model with water table, OTC (warming) and microform and year as fixed effects and year as repeated measures. Only averaged fluxes across all study years are being graphed as the impacts of treatments were consistent in all growing seasons.

Figure 5. CO$_2$-C balance averaged across study years (2011–2013). Error bars indicate ± standard deviation. Differences were evaluated between ambient and warmed sites (micro-forms) indicted by letters at each bar. Sites are significantly different at $p < 0.05$ if they have no letters in common.