- 1 Carbon dioxide flux and net primary production of a boreal treed bog: responses to warming and water
- 2 table lowering simulations of climate change

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Abstract

- Mid-latitude treed bogs represent 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 (CO₂) fluxes and estimated tree root
- 16 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 CO₂-C
- balance was calculated by adding net CO_2 exchange of the forest floor (NE_{ff}- R_r) to the NPP of the
- 19 trees.
- From cooler and wetter 2011 to the driest and the warmest 2013, the control site was a CO₂-C sink of
- 21 92, 70 and 76 g m⁻², the experimental site was a CO₂-C source of 14, 57 and 135 g m⁻², and the drained
- site was a progressively smaller source of 26, 23 and 13 g CO₂-C m⁻², respectively. The short-term
- drainage at the experimental site resulted in small changes in vegetation coverage and large net CO₂
- 24 emissions at the microforms. In contrast, 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 lichen at
- 26 the hollows leading to the highest CO₂ uptake at the drained hummocks and significant losses at the
- 27 hollows. The tree NPP (including above- and below-ground growth and litter fall) in 2011 and 2012
- were significantly higher at the drained site (92 and 83 g C m⁻²) than at the experimental (58 and 55 g C
- m^{-2}) and control (52 and 46 g C m^{-2}) sites.

We also quantified the impact of climatic warming at all water table treatments by equipping additional 30 31 plots with open-top chambers (OTCs) that caused a passive warming on average of ~1 °C and 32 differential air warming of ~6 °C at mid-day full sun across the study years. Warming significantly enhanced shrub growth and CO₂ sink function of the drained hummocks (exceeding the cumulative 33 respiration losses at hollows induced by the lowered water level × warming). There was an interaction 34 35 of water level with warming across hummocks that resulted in the largest net CO₂ uptake at the warmed 36 drained hummocks. Thus in 2013, the warming treatment enhanced the sink function of the control site by 13 g m⁻², reduced the source function of the experimental by 10 g m⁻², and significantly enhanced the 37 sink function of the drained site by 73 g m⁻². Therefore, drying and warming in continental bogs is 38 expected to initially accelerate CO₂-C losses via ecosystem respiration but persistent drought and 39 40 warming is expected to restore the peatland's original CO₂-C sink function as a result of the shifts in vegetation composition and productivity between the microforms and increased NPP of trees over time. 41 42

1 Introduction

- Northern peatland ecosystems have accumulated \sim 547 Pg carbon (C: 1Pg = 10^{15} g) as a result of 43
- 44 functioning as a steady but persistent sink throughout the Holocene (Yu. 2012; Tarnocai et al., 2009).
- 45 The accumulated peatland C stocks equal approximately one third of the global terrestrial soil C pool
- 46 (Grosse et al., 2011; Ciais et al., 2013). Mid-latitude peatlands in north-west North America are often
- covered by trees, in contrast to open bogs in north-east North America (Turetsky et al., 2002). Forested 47
- bogs have greater net primary production (NPP) to decomposition ratios and hence return higher 48
- 49 accumulation rates than those of open bogs (Clymo et al., 1998). The C stocks of the western boreal
- 50 treed bogs may respond differently to warming and drought than those of eastern boreal open fens
- (Kettles and Tarnocai, 1999), and may lead to an accelerated positive feedback to climate change 51
- 52 (Gruber et al., 2004; Limpens et al., 2008; Bhatti et al., 2012; Stocker et al., 2013). Future climatic
- 53 changes are expected to be severe at mid-latitudes (Vitt et al., 2009; Kettles and Tarnocai, 1999; IPCC,
- 54 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 55
- primary photosynthesis (GPP) and the release of C to the atmosphere by respiration (R) of plants 56
- 57 (autotrophic) and microorganisms (heterotrophic). The sum of GPP (-) and R(+) is defined as the net
- 58 ecosystem exchange (NEE) of CO₂. Net uptake of CO₂ 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 59
- 60 floor are represented by GPP_{ff}, $R_{\rm ff}$ and NE_{ff}, respectively. Tree root respiration is represented by $R_{\rm r}$.

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The changes in peatland air/soil temperature and water level can change GPP and R independently (Ow
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- et al., 2008). Warm and dry conditions in peatlands can either promote CO₂ uptake by enhancing GPP
- or diminish uptake by limiting moisture (Roulet et al., 2007; Charman et al., 2013) or accelerate CO₂
- 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 CO₂ flux peak
- 66 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 g C m⁻² d⁻¹ and 2.5
- 68 g C m⁻² d⁻¹, respectively, coincident with an average increase in air and soil temperature from 0 °C (late
- 69 April) to 27 °C (early June). Long-term drawdown of water table in forested bogs significantly increased
- 70 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 very high NEE of -871 ± 100 g C m⁻² yr⁻¹, and a tree
- productivity of 240 ± 30 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 g CO₂ m⁻² d⁻¹ (Aurela et al., 2007). In a treeless fen,
- Riutta et al. (2007) reported average seasonal ecosystem respiration to be 810 g CO₂ m⁻². The ecosystem
- respiration increased by 18% and 20% due to lowering of water level by 14 cm and 22 cm, respectively.
- 77 However, the variation in respiration may not always be linked to fluctuation in water table; it may be
- 78 related more directly to variation in moisture availability. Therefore, water table is a major control on
- 79 respiration in peatlands, and peat soil moisture is sensitive to lowering of water table (Moore et al.,
- 80 2006; Parmentier et al., 2009; Moore, 2002).
- 81 Tree root respiration (R_r) may account for a significant proportion of forest floor respiration $(R_{\rm ff})$ in
- forested bogs (Lohila et al., 2011). Therefore, isolating R_r from $R_{\rm ff}$ 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.
- 87 The contribution of $R_{\rm r}$ to $R_{\rm ff}$ has been quantified using the closed chamber technique in various forest
- ecosystems. The R_r was separated from $R_{\rm ff}$ 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,
- 90 the percentage was found to be higher, at 37% in a subtropical forest of mixed alder Cyprus plantations
- 91 (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

95 change remains unclear. Continental peatlands are predicted to be drier under warming climatic conditions. The drier conditions 96 97 may favour some species in peatland communities to yield more NPP than others and, as a result, plant 98 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., 99 100 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 101 Swedish peatland accelerated soil respiration rates ranging from 513 to 6516 g CO₂ m⁻² d⁻¹ (Von-Arnold 102 103 et al., 2005). The shifts in species dominance (coverage) and composition varied between microforms (e.g. hummocks (H) and hollows (W)) in peatlands (e.g. Strack et al., 2006). Likewise, the responses of 104 105 CO₂ 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 106 107 between the microforms. 108 Warming response studies have used open-top chambers (OTCs) to manipulate ambient temperature to 109 quantify the response of CO₂ exchange in peatlands at northern latitudes. For example, Sullivan et al. 110 (2008) used OTCs in a Greenland rich fen for warming hollow and hummock microforms to evaluate responses of CO₂ fluxes and vegetation changes to warming manipulation. A significant increase in 111 GPP_{ff} was found at both of the microforms in response to the OTC warming of ~1 °C. However, 112 Johnson et al. (2013) neither found any consistent increase in warming provided by the OTCs nor any 113 effect on $GPP_{\rm ff}$ or $R_{\rm ff}$ of a treeless poor fen. Weltzin et al. (2003) used overhead infrared lamps to 114 induce warming on bog mesocosms and found that the soil temperature at 15 cm below surface 115 116 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%. 117 Although several studies have been conducted on NPP and CO₂ exchange in western Canadian 118 119 peatlands, many unknowns remain. The CO₂ 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 120 121 temperature and water table were not evaluated. The response of a bog to decade long water table 122 manipulation was quantified by Munir et al. (2014), but the impact of the warming manipulations 123 remained unexplored. The impact of warming manipulation and microtopography on CO₂ balance 124 responses was also not investigated by Adkinson et al. (2011) in their climatic temperature and short-125 term drought study on Alberta fens. They also did not estimate the tree productivity of the forested fen

C m⁻² following ten years of lowered water table (~120 cm) in a boreal bog, but the time scale for the

nor the contribution of R_r . The CO₂ 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 CO₂ exchange responses to potential warming and water table lowering expected under a climate change scenario is required to fill the knowledge gaps on how a treed continental bog will feedback to the expected changes in climate. Thus, our unique investigation answers this question by quantifying CO₂-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 CO₂-C exchange to tree productivity-C uptake. Moreover, we isolate R_r from $R_{\rm ff}$ to better understand proportional response of R_r to potential short and longer-term water table draw down 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 the 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 (1st May to 31st October) of 2011-2013. Three sites were chosen or created having various water levels: an undisturbed water level site (~38 cm below surface) called CONTROL (55° 21' N, 112° 31' W), an experimentally lowered water level site (~35 cm lower than the control) called EXPERIMENTAL (55° 21' N, 112° 31' W), and a 10 year old drained site (~74 cm lower than the control) called DRAINED (55° 16' N, 112° 28' W). The creation of the experimental and drained 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 (\pm standard deviation) at the control site (-55.8 \pm 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
- 161 conductivity (EC, μ S cm⁻¹) and pH of pore water in the control (16.6 ± 0.7 and 4.1 ± 0.1, respectively)
- and experimental (15.2 \pm 2.5 and 4.4 \pm 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.
- 168 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
- 171 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 m² ha⁻¹. This
- description applies to the whole bog having the control, experimental and drained sites (Munir et al.,
- 174 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 $60 \text{ cm} \times 60 \text{ cm}$
- 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)
- 179 covered with nylon cloth at the lower 150 cm was inserted into the peat to measure water level
- manually every time CO₂ 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 minute 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
- 190 104 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-minute intervals during the growing seasons. Snowpack disturbance was minimized by dismantling the OTCs each October and reinstalling back on plots early May.

CO_2 flux

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We measured CO₂ flux in biweekly campaigns during the growing seasons (May to October) of 2011-2013 using a closed chamber having dimensions 60 cm \times 60 cm \times 30 cm (length \times width \times 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. However, the chamber had no pressure equilibrium port installed. The instantaneous CO₂ concentration inside the chamber headspace was measured with a portable infrared gas analyser (PP systems, USA, EGM-4) having a built-in sampling pump operating at a flow rate of 350 ml minute⁻¹ and compensating automatically for pressure and temperature fluctuations during the measurements. The photosynthetically active radiation (PAR) was measured with a quantum sensor (PP systems, USA) placed at the top of the chamber. All PAR data collected using the portable PAR sensor was multiplied with a factor of 0.88 to obtain corrected values of the PAR inside the chamber accounting for its transmittance. The temperature inside the chamber was 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 minutes at 15 seconds 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 CO₂ flux measurement occasion from a permanently installed well associated with each plot.

At each plot, a total of 276 CO₂ 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 $R_{\rm ff}$). The chamber was air-flushed for enough time between the measurements to
- equilibrate the headspace concentration with that of the ambient air.
- The CO_2 flux measurements when the chamber was covered with an opaque tarp represented $R_{\rm ff}$. The
- $R_{\rm ff}$ 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 $R_{\rm ff}$. Negative values indicate an uptake of CO₂ by the ecosystem. The NE_{ff} was calculated
- using the exponential change in chamber headspace CO₂ 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 following Munir et al. (2014)
- because covering the soil and vegetation can manipulate the spontaneous CO₂ fluxes across soil-
- vegetation-air continuum (Hanson et al., 1993; Davidson et al., 2002; Denmead and Reicosky, 2003;
- Kutzbach et al., 2007) likely due to suppression of natural pressure fluctuations (Hutchinson and
- Livingston, 2001) and possible alteration in turbulence between measured intervals (Hutchinson et al.,
- 236 1993). Therefore, the CO₂ fluxes determined using linear regression likely result in underestimation of
- fluxes under closed chamber environment (Kutzbach et al., 2007). 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 μmol m⁻² s⁻¹. As modeled values of maximum GPP were most likely
- 242 never achieved in reality, these values represented a more realistic estimate of CO₂ exchange when light
- was not limiting, as reported by Bubier et al. (2003). We used these to statistically compare CO₂
- 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 CO₂ flux component data presented (e.g.,
- Fig. 4) are three growing seasons' averages for all occasions when PAR $> 1000 \mu mol m^{-2} s^{-1}$.

2.2.1 Seasonal CO₂ flux modeling and validation

- The growing season (May to October) GPP_{ff} was estimated using an exponential empirical model
- 249 (Munir et al., 2014) parameterized separately for each water level treatment × warming × microform
- 250 type × year combination. The seasonal GPP_{ff} was estimated according to (modified from Riutta et al.,
- 251 2007):

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

- where P_{max} denotes the potential maximum rate of GPP_{ff} (g CO₂ 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 ($_{Tsoil\ 5cm}$;
- °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 $_{\rm ff}$ model parameters (standard errors), r^2 values, and standard errors
- of the estimates at the control, experimental and drained microforms are presented in Appendix A.
- The relationship between $R_{\rm ff}$ with $T_{\rm soil\ 5cm}$ was found to be linear. Therefore, the seasonal $R_{\rm ff}$ was
- estimated using a multiple linear regression with $T_{\text{soil 5cm}}$ and water table position by:

$$R_{\rm ff} = a \times T + b \times WT + c \tag{2}$$

- where a, b and c are regression coefficients, and their values for each water level treatment \times warming \times
- 264 microform type \times year combination are presented in Appendix B.
- Applying equations (1) and (2), seasonal GPP_{ff} and $R_{\rm ff}$ were estimated for each 20 minute period
- between 1st May and 31st 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 $T_{\text{soil 5cm}}$ (Onset
- 269 HOBOware Pro, MA, USA) measurements made on site. The seasonal NE_{ff} was calculated by adding
- seasonal estimates of GPP $_{\rm ff}$ and $R_{\rm ff}$. Because some environmental variables were missing for first 5 days
- of May 2011 and first 21 days of May 2012, they were filled by assuming that the first measured value
- was representative of the whole missing period. The field measured values of $GPP_{\rm ff}$ and $R_{\rm ff}$ were
- compared with the model predicted values obtained using SPSS 21.0. 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
- 277 microtopography adjacent to the regularly monitored flux plots, we chose an additional eight hummocks
- and eight hollows at each of the 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 $60 \text{ cm} \times 60 \text{ cm}$. 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 plots were kept free of surface
- vegetation during the trenching experiment in the growing season of 2012 so that R_r could be estimated

by difference without the additional complicating factors of differences in autotrophic respiration 285 286 between plots due to slight difference in vegetation (Wang et al., 2008). The CO₂ emissions from all 287 plots were measured on average weekly using the same instruments and chamber (with opaque shroud) 288 used for the measurement of NE_{ff}. 289 The plots were trenched in early May 2012 while respiration measurements were carried out in July-290 September 2012. While the trenching is used to separate R_r from R_{ff} , it also adds fresh litter to the peat 291 that can add to the initial heterotrophic soil respiration. However, it has been assumed in trenching experiments that the trenched roots die off within a short time and that afterwards the measured $R_{\rm ff}$ can 292 293 solely be attributed to heterotrophic soil respiration (Hanson et al., 2000; Hermle et al., 2010; Wang et al., 2008). Trenching immediately disrupts the supply of recent photosynthates to the roots, and 294 295 mycorrhiza and associated bacteria that suffer from the lack of labile C. In trenching experiments Bowden et al. (1993), Boone et al. (1998) and Rey et al. (2002) have shown that C content of 296 decomposing fine roots in trenched plots contributed little to R_r and becomes stable a few months after 297 trenching. Also, the root exclusion experiment may not be useful if extended through a complete annual 298 299 cycle, as over such a long period there is the possibility of reinvasion of roots into the previously rootfree trenched plot (Edwards and Norby, 1999). While it is clear that findings from such trenching 300 measurements should be interpreted carefully, the primary focus of this paper is to quantify $R_{\rm ff}$ while 301 investigating R_r to better understand and separate the contribution of various processes to shifts in $R_{\rm ff}$ 302 303 following drainage.

2.3 Biomass and tree productivity

2.3.1 Ground-layer biomass

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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 between 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 317 318 and drained sites, and one quadrat at experimental site (due to its smaller area) were laid out in May 319 2011. The study areas were not large and these quadrats covered most of the trees in the study areas. 320 The trees were categorized into tall (> 137 cm height) and short (< 137 cm height) for biomass and 321 productivity estimation. The taller trees were measured for their height, diameter at breast height (DBH) 322 and basal diameter (DB), and their biomass was calculated by using an allometric equation (dry biomass = 0.153(tree DBH)^{2.248}) from Grigal and Kernik (1984). All short trees were also measured for their 323 heights only. Twenty short trees were harvested parallel to the forest floor and transported to the 324 325 laboratory, oven dried at 80 °C for 48 hours (until constant weight), and their biomass used to create an an allometric equation (dry biomass = 0.0085(tree height)^{2.2088}; $R^2 = 0.93$; p < 0.001) we generated by 326 regressing height with oven-dried weight. This was used to estimate the biomass of all other short trees. 327 328 NPP of the tree stand for above-ground parts was estimated for 2011 and 2012, following Szumigalski 329 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 330 production (17% of above-ground incremental biomass m⁻² yr⁻¹ for *Picea mariana*). We estimated tall 331 trees incremental biomass based on tree ring widths measured using DendroScan (Varem-Sanders and 332 Campbell, 1996). The incremental biomass of the short trees was estimated by regressing leader length 333 334 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-335 336 ground parts of trees for that year. To account for litter, an additional 17% was added to this 337 summation. The new summation represented NPP for above-ground parts of the tree stand (Szumigalski 338 and Bayley, 1996). We did not measure incremental biomass of the below-ground parts of trees due to 339 the desire to limit disturbance to our research sites and allow for future monitoring. Therefore, we used 340 an allometric equation (tree root biomass = 0.222*tree above-ground biomass) generated by Li et al. 341 (2003) for estimating the incremental biomass of the tree roots. We did not measure tree productivity 342 for 2013, instead used 2012 productivity values to calculate NEE for this last year of the study.

2.4 CO_2 -C balance (NE_{ff} + NPP - R_r)

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To calculate CO_2 -C balance, the NE_{ff} (- $GPP_{ff} + R_{ff}$) and NPP (incremental tree biomass 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 (May 1 to October 31) 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 CO_2 -C balance equation for the treed bog sites is as: $NEE = NE_{ff} + IC_{tree ag} + IC_{tree bg} + L_{tree} - R_{r}$ (3)

where NEE denotes Net Ecosystem Exchange, NEff represents net exchange of the forest floor, ICtree 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 production and R_{r} is tree root respiration. We estimated a

seasonal value of R_r by determining it as a proportion of $R_{\rm ff}$ based on instantaneous measurements and

then estimating it as this proportion of the modelled seasonal $R_{\rm ff}$. Seasonal CO_2 fluxes at hummocks and

hollows were upscaled by multiplying mean estimated growing season CO₂ exchange by their

respective coverage of 56 and 44%, 55 and 45%, and 52 and 48% at the control, experimental and

358 drained sites, respectively (Table 4).

2.5 Data analysis

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- To estimate treatment effects on instantaneous CO_2 flux components (GPP_{ff}, R_{ff} , NE_{ff}, NE_{ff}, without
- 361 R_r) we used separate linear mixed-effects models (SPSS 21.0) with CO₂ 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 CO₂ flux components data were normally
- distributed in all years (Kolmogorov-Smirnov Z: 2011, p = 0.910; 2012, p = 0.767; 2013, p = 0.624).
- 370 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).

376 3 Results

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3.1 Microclimate and environment

- 378 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
- 380 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
- 381 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 the 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).
- 390 The OTCs resulted in significantly warmer growing season air temperature (T_{air} ; ANOVA, $F_{2, 24}$ =
- 391 215.87, p < 0.001) by an average (\pm 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 ($T_{\text{soil 5cm}}$;
- 395 ANOVA, $F_{1,24} = 37.59$, p < 0.001) by an average of 1.0 ± 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 $T_{\text{soil},5\text{cm}}$ the least $(0.4 \pm 0.3 \,^{\circ}\text{C})$ at drained hummocks and the most $(1.3 \pm 0.2 \,^{\circ}\text{C})$
- at the control hollows. Average soil temperature at 30 cm depth ($T_{\text{soil }30\text{cm}}$) below the OTC equipped
- 399 plots was not significantly different than that at the same depth at non-OTC plots across all sites
- 400 (ANOVA, $F_{2,24} = 0.71$, p = 0.053) and microforms (ANOVA, $F_{1,24} = 0.95$, p = 0.339). Diurnal T_{air} and
- 401 $T_{\text{soil 5cm}}$ patterns in the OTCs were significantly related to PAR ($R^2 = 0.81, 0.87$, respectively) across the
- 402 microtopography at all sites. During mid-day bright sunny conditions the air warming at OTC equipped
- 403 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 $T_{\text{soil 5cm}}$ at the OTC plots greater than at non-OTC plots by averages of
- 406 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).

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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 ($F_{2,24} = 3.78$,
- 411 p = 0.013), but not different compared to the experimental site (p = 0.076), while the control and
- 412 experimental sites were not significantly different compared to each other (p = 0.412; Table 2). This
- 413 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 ($F_{1,24} = 0.10, p = 0.749$) or warming treatments ($F_{1,24} = 0.10, p = 0.749$)
- 415 $_{24} = 0.51, p = 0.481$). 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
- 418 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 the control and experimental ambient and warmed 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 the control and
- 426 the 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 increase 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
- 437 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 Above-ground tree biomass

- Above-ground tree biomass was higher in the control site than that in the experimental and drained sites
- by an average of 156 g m⁻² and 178 g m⁻², respectively (Table 2, 4). However, the above-ground tree
- growth during 2011-2012 was significantly higher in the drained site (66 and 60 g C m⁻²) than that at the

- experimental (42 and 39 g C m⁻²) and the control (38 and 33 g C m⁻²) 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
- 452 study in 2011 and have described this in detail under "study sites" section. Heterogeneity between the
- 453 tree quadrats laid out at each site was large; however, the small size of the study sites limited our ability
- 454 to construct more replicates in 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.

460 3.3 CO_2 fluxes

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3.3.1 Measured CO₂ fluxes

- 462 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 CO₂ m⁻² d⁻¹)
- and drained (-12.8 g CO₂ m⁻² d⁻¹) sites were not significantly different from each other but were
- different from that at the experimental site (-7.8 g CO₂ m⁻² d⁻¹). There was a higher GPP_{max} at
- hummocks (-14.4 g CO₂ m⁻² d⁻¹) than at hollows (-9.8 g CO₂ m⁻² d⁻¹). Microform and warming had a
- significant interaction with each other as well as interactions each individually with water level. The
- 468 GPP_{max} in 2011 and 2012 were not significantly different from each other but from the highest value
- 469 that occurred in the warmest 2013. Year had significant 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 CO₂
- 471 m⁻² d⁻¹ at hummocks by 2013; and with warming, increasing GPP at warmed but not unwarmed plots by
- 472 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 CO₂ m⁻² d⁻¹) at the warmed drained hummocks in 2013.
- $R_{\rm ff}$ was significantly affected individually by all four study factors; water level, microtopography, OTC
- warming and year (Table 3). The $R_{\rm ff}$ at the control (13.1 g CO₂ m⁻² d⁻¹) and experimental (14.5 g CO₂ m⁻²
- 477 ² d⁻¹) sites were not significantly different from each other but were lower compared to that at the

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drained site (16.9 g CO_2 m<sup>-2</sup> d<sup>-1</sup>). The R_{\rm ff} was significantly different between hollow (16.9 g CO_2 m<sup>-2</sup> d<sup>-1</sup>)
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          and hummock (14.2 g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) microforms, and between ambient (13.5 g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) and warmed
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          (16.7 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}) plots. The R_{\text{ff}} in 2011 (14.3 g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) and 2013 (14.7 g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) were not
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          significantly different from each other but from the highest (16.3 g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) that occurred in the first
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          drier than average year 2012. There was an interaction between microform and year leading to
          significantly higher emissions at hollows (16.8 g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) in 2012. Warming had a significant
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          interaction with microform and year resulting in significantly higher R_{\rm ff} at warmed hollows in 2012
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          (19.1 g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>). The significantly greater emissions were likely due to the significantly higher
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          contributions of R_r (5.03 and 6.80 g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) to R_{\rm ff} at the experimental and drained hollows,
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          respectively, compared to 1.51 g CO_2 m<sup>-2</sup> d<sup>-1</sup> at the control hollows. The R_r at the drained hummocks
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          (3.3 g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) was not significantly different compared to that at the experimental hummocks (3.4
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          g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>), but significantly different compared to that at the control hummocks (4.3 g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>).
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          NE_{max} (including R_r) was significantly affected individually by water level, microtopography, OTC
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          warming and year, and all four interactively (Table 3). All sites were significantly different from each
          other: the control site forest floor was a sink of 1.4 g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup> while the experimental and drained
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          sites were sources of 6.5 and 4.1 g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>, respectively. There was a significant interaction of water
          level with microform resulting in net emissions at experimental hollows (10 g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) and drained
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          hollows (9.8 g CO_2 m<sup>-2</sup> d<sup>-1</sup>) compared to net uptake at the control microforms (hollows = -1.1 g CO_2 m<sup>-2</sup>
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          d^{-1}; hummocks = -1.8 g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) and the drained hummocks (-1.5 g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>). The water level
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          also had a significant interaction with warming leading to net emissions from warmed plots at the
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          experimental site (10.2 g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) and the drained site (4.2 g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) compared to net uptake at
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          the ambient control plots (-2.1 g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>), while warmed plots had significantly higher emissions
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          (NE_{ff} = 4.5 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}) than ambient plots (1.7 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}). The water level also had a significant
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          interaction with study year with highest net uptake of -6.3 g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup> at the control site in 2013, the
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          year not significantly different compared with 2011 and 2012. Subtracting R_r from NE<sub>max</sub> (to consider
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          the net exchange of the ground layer only), converts the control microforms and drained hummocks to
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          larger sinks of CO<sub>2</sub>, while considerably reduces emissions at the drained hollows and experimental
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          microforms (Table 4).
                           Modeled CO<sub>2</sub> fluxes (excluding R_r) for growing season (1<sup>st</sup> May to 31<sup>st</sup> October)
          3.3.2
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          Based on empirical models (Eqs. 1 and 2), in 2011, the ground layer at the control site was a sink of 42
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          g CO<sub>2</sub>-C m<sup>-2</sup>, while the drained and experimental sites were large sources of 118 and 72 g CO<sub>2</sub>-C m<sup>-2</sup>,
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respectively (Table 4). In 2012 and 2013, the ground layer at the control site was a reduced CO₂-C sink

of 24 and 30 g m⁻², respectively; the drained site was a reduced CO₂-C source of 106 and 96 g m⁻²,

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respectively; while the experimental site was an enhanced CO₂-C source of 112 and 189 g m⁻²,

respectively.

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In 2011, OTC warming of the forest floor microforms converted the control site to a greater CO₂-C sink

of 52 g m⁻², drained site to a smaller CO₂-C source of 84 g m⁻² and experimental site to a greater CO₂-C

source of 177 g m⁻². Across the study years, warming of the microforms at the control and drained sites

on average increased the uptake of carbon (Table 4). In contrast, warming at the experimental site on

average enhanced CO₂ emissions much higher than uptake and resulted in net larger release of CO₂ 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 drained sites a smaller source of forest floor CO₂ (Table 4, Fig. 4).

3.4 CO_2 -C- balance $(NE_{ff} + NPP - R_r)$

- To calculate the final balance of CO₂ 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 CO₂-C balance separately for the three growing seasons of 2011-2013. The control site
- was a larger sink (\pm SD) of 92 (\pm 12) g C m⁻² in 2011 than that of 70 (\pm 10) and 76 (\pm 38) g C m⁻² in
- 526 2012 and 2013, respectively. The experimental site was a progressively increasing source of 14 (\pm 5),
- 527 57 (\pm 44) and 135 (\pm 45) g C m⁻² in 2011, 2012 and 2013, respectively. On the other hand, the drained
- site was a progressively declining source of 26 (\pm 14), 23 (\pm 15) and 13 (\pm 2) g C m⁻² through 2011-
- 529 2013, respectively. OTC warming of microforms consistently increased uptake at the control site by -
- 13, -19 and -6 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 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 g C m⁻² through the
- study years, respectively. In all cases, as warming was not applied directly to the trees any impact on
- their growth could not be included in the study. The warming treatment overall increased the CO₂-C
- 535 uptake at hummocks and enhanced the emissions at hollows. Averaged across the study years, the
- warming interacted with deeper and longer drainage to restore the peatland's original CO₂-C sink
- function (Fig. 5).

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4 Discussion

- This study estimated the CO₂-C balance of a sub-humid, continental treed bog by combining the C
- exchange values derived from modeled CO₂ 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 since fire, Wieder et al. (2009) reported that the ombrotrophic bogs in the same region represented an annual CO₂ 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 CO₂ uptake across three study years of -110 and -35 to -154 g C m⁻² at 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 CO₂ accumulation rate of -144 g C m⁻² in a treed fen in the same boreal region is reported by Syed et al. (2006).Methane (CH₄) is also an important component of the C balance in peatland ecosystems. However, over-all seasonal CH₄-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 CH₄ fluxes are a minor component of the seasonal C balance at our dry continental bog sites. Carbon can also be lost from the system with hydrologic flows. This would include dissolved organic C, particulate organic C and dissolved inorganic C. 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. This suggests the CO₂-

C exchange likely represents the majority of the C balance at these sites.

4.1 Weather effects

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 (2012 and 2013) of the study. This reduction was due to the substantial increase in $R_{\rm ff}$ at the hollows exceeding the combined increase in $GPP_{\rm ff}$ at the microforms especially in 2012 (Table 4). The steady and consistent increase in $R_{\rm ff}$ at the 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 $R_{\rm ff}$ noticed at the experimental hollows might be due to the influence of experimental lowering of water table negatively affecting hollow vegetation more than adjacent hummocks. In contrast, there was only a minor fluctuation in $GPP_{\rm ff}$ or $R_{\rm ff}$ 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, Table 2, 3).

4.2 Water table manipulation effects

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 CO₂-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 CO₂-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.

4.3 OTC warming effects

The control site sink strength was enhanced by OTC warming leading to greater CO₂-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 $R_{\rm ff}$ in a sub-arctic fen. The increase in GPP_{ff} and/or $R_{\rm ff}$ 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) who reported that there was no consistent effect of OTC warming on the CO₂ 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 CO₂-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 CO₂ 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.

4.4 Microform effects

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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 significantly greater CO₂ 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 the 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, $R_{\rm ff}$ and $R_{\rm r}$ were the highest at the experimental and drained hollows, also increasing towards warmer 2013. Interestingly, the CO₂ uptake was even higher at the warmed drained hummocks, while CO₂ 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, Table 2, 4). Moreover, drained and experimental hollows were the largest sources of CO₂ 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 CO₂ 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.

4.5 Water table manipulation and warming effects on vegetation

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Interactions between soil and plant communities have been predicted to play a major role in 647 648 determining the response of net exchange of CO₂ in peatlands to a climate change scenario (Weltzin et 649 al., 2001; Kardol et al., 2010; Moore et al., 2002) of water level lowering and global warming (Ciais et 650 al., 2013). Ground-layer biomass was significantly affected in response to thirteen years of drainage (water level \sim 120 cm; $F_{2.36}$ = 49.42, p < 0.001) and OTC average warming of \sim 1 °C or mid-day full sun 651 diurnal air warming of ~6 °C or 5 cm deep soil warming of ~5 °C ($F_{2,36} = 6.46$, p = 0.015; Fig. 2, 3). 652 653 The shift in biomass coverage and composition was also different between the microforms ($F_{2,36}$ = 654 24.14, p < 0.001); increased biomass at hummocks compared to that at hollows. However, no 655 significant difference in vegetation biomass or composition was found after a three years of drainage of 656 water level \sim 76 cm (p = 0.162). Interestingly, along a gradient of decreasing water level, shrub biomass 657 increased at hummocks, lichens biomass increased at hollows, while moss biomass decreased at all 658 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 659 water table \times warming \times microform \times year ($F_{2.36} = 8.24$, p = 0.001). The accumulated NPP ratio of 660 661 below-ground: above-ground shifted from 1.86 before warming to 2.00 after warming, suggesting a 662 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 663 life-forms and species characteristics of each community (Weltzin et al., 2000). The drainage-driven 664 and warming-induced increases in vascular biomass we found were also reported by Moore et al. (2002) 665 and Laine et al. (2011), and Weltzin et al. (2000), respectively. 666

4.6 Water table manipulation and warming effects on biomass and NPP

We report above-ground biomass (including ground-layer and canopy-layer) to be within the range of values previously published for bog studies. 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 (\pm 224) and 2177 g m⁻² (\pm 2259), respectively (Moore et al., 2002). Our data for above-ground tree biomass (2031 \pm 379) fall within the range of published values. However our ground-layer biomass average (1236 \pm 130 g m⁻²) is less than 1900 g m⁻² (\pm 224) reported by Moore et al. (2002) because they

drew 110 cm deep peat cores for quantifying below-ground biomass versus 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 (Table 2, 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 the experimental site that showed higher productivity than the control but lesser than the 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 \sim 120 cm. The measured R_r consistently increased at all sites 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 CO₂ 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 CO₂, 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

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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. In fact, the moss biomass was replaced by vascular plant biomass (mostly woody shrubs) at

706 hummocks and lichen biomass at hollows. The shrub biomass growth was significantly increased in 707 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 708 709 drove the drained hummocks to become the largest net sink of CO₂ across all sites and microforms. 710 Conversely, the short-term, as well as the longer-term, water level lowering converted the hollows to be 711 the largest net sources of CO₂. However, the 11-13 years of deeper water level lowering coupled with 712 OTC warming increased the forest floor net uptake of CO₂ exceeding well above the losses via 713 respiration at the drained microforms. The significantly increased tree productivity in response to the 714 longer-term deeper drainage (NPP-C) added to the NE_{ff} -C (- R_r) converted the drained site from a 715 moderate C source, to become a sink of C close to the bog's original sink strength (Fig. 5). 716 Averaged across study years, an OTC warming of ~1 °C (and differential mid-day full sun air warming 717 of $\sim 6^{\circ}$ C) interacted with water level treatment to enhance the sink function of the undisturbed site, 718 enlarge source strength of the experimental site and restore the sink strength of the drained site. This 719 pattern is a strong indicator that climatic warming that drives persistent lowering of water level for 720 longer-term is expected to restore the original sink function of continental treed bogs after an initial short duration of net C losses. We also infer that mid-latitude continental treed bogs are sensitive but 721 722 adaptive ecosystems that are expected to respond to climatic warming and drying almost instantly by 723 supporting development of woody roots that penetrate deeper for optimum supply of moisture and 724 nutrients to the newly adapted surface vegetation. Although the deepening of water table initially leads 725 to larger net emissions to the atmosphere, persistent drying and warming transforms the moss habitat 726 (characterized by near surface water level) to vascular plant habitat (characterized by deeper water 727 level) leading to a shift to woody shrubs and trees with deeper root systems. The bog trees adapt better 728 to lower water levels and increase productivity by widening ring width, lengthening leader length and 729 increasing belowground biomass allocation.

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

| Air / Soil | Treatment | CONTROL | | EXPERI | MENTAL | DRAINED | | |
|-----------------------------|-----------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|--|
| Temperature | | Hummock | Hollow | Hummock | Hollow | Hummock | Hollow | |
| T _{air} (°C) | Ambient | $13.6 \pm 0.3^{\text{A}}$ | $13.5 \pm 0.2^{\text{A}}$ | $13.8 \pm 0.1^{\mathbf{A}}$ | $13.9 \pm 0.1^{\mathbf{A}}$ | $14.3 \pm 0.3^{\mathbf{A}}$ | $14.3 \pm 0.2^{\mathbf{A}}$ | |
| | Warmed | $14.4 \pm 0.5^{\mathbf{B}}$ | $14.4 \pm 0.4^{\mathbf{B}}$ | $14.7 \pm 0.3^{\mathbf{B}}$ | $14.7 \pm 0.6^{\mathbf{B}}$ | $14.6 \pm 0.2^{\mathbf{A}}$ | $15.2 \pm 0.8^{\mathbf{B}}$ | |
| $T_{\text{soil 5 cm}}$ (°C) | Ambient | $12.3\pm0.2^{\mathbf{A}}$ | $12.3 \pm 0.0^{\mathbf{A}}$ | $13.1 \pm 0.0^{\mathbf{A}}$ | $13.1 \pm 0.1^{\mathbf{A}}$ | $13.7 \pm 0.0^{\mathbf{A}}$ | $13.7 \pm 0.1^{\mathbf{A}}$ | |
| | Warmed | $12.9 \pm 0.2^{\mathbf{B}}$ | $13.6 \pm 0.6^{\mathbf{B}}$ | $13.8 \pm 0.9^{\mathbf{B}}$ | $13.7 \pm 0.6^{\mathbf{B}}$ | $14.1 \pm 0.6^{\mathbf{A}}$ | $14.6 \pm 0.4^{\mathbf{B}}$ | |
| $T_{ m soil~30~cm}$ (°C) | Ambient | $10.8 \pm 2.5^{\mathbf{A}}$ | 11.0 ± 2.8^{A} | $9.9 \pm 2.7^{\mathbf{A}}$ | 11.2 ± 3.2^{A} | $12.0 \pm 3.7^{\mathbf{A}}$ | $13.2 \pm 3.8^{\mathbf{A}}$ | |
| | Warmed | $11.7 \pm 2.3^{\text{A}}$ | 12.4 ± 2.5^{A} | 11.2 ± 2.7^{A} | $12.2 \pm 3.8^{\mathbf{A}}$ | $12.3 \pm 3.8^{\mathbf{A}}$ | $12.7 \pm 3.8^{\mathbf{A}}$ | |

^a All temperatures are mean (\pm 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 ($T_{\rm air}$) and 5 cm deep soil ($T_{\rm soil\ 5cm}$). The 30 cm deep soil temperatures ($T_{\rm soil\ 30cm}$) were measured using thermocouple, during the measurement of CO₂ 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 $T_{\rm air}$, $T_{\rm soil\ 5cm}$ and $T_{\rm soil\ 30cm}$.

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

| Site/ Microforms | | ABOVE-GROUND | | | BEL | BELOW-GROUND | | | TOTAL |
|---------------------|---------------------------|---------------------------|-------------------------|---------------------------|---------------|---------------|----------------|-------------------|----------------|
| | Moss | <u>Vascular</u> | <u>Lichen</u> | <u>Total</u> | Fine | <u>Coarse</u> | <u>Total</u> | | Ambient/ |
| | | | | | < 2 mm | > 2 mm | | Ambient | Warmed |
| CONTROL | <u>-</u> | | | | | | | | |
| AMBIENT | | | 4 | | | | | 2142 ± 376 | 3168 ± 604 |
| Hummock | $208 \pm 51^{\text{A}}$ | 191 ± 62^{A} | $0 \pm 0^{\mathbf{A}}$ | $399 \pm 24^{\text{A}}$ | 335 ± 15 | 233 ± 61 | 568 ± 48 | | |
| Hollow | 134 ± 17^{A} | $216 \pm 11^{\mathbf{A}}$ | $0 \pm 0^{\mathbf{A}}$ | $350 \pm 82^{\mathbf{A}}$ | 486 ± 67 | 266 ± 102 | 751 ± 332 | | |
| WARMED | | | | | | | | | 3150 ± 578 |
| Hummock | $113 \pm 46^{\text{A}}$ | $172 \pm 97^{\text{A}}$ | 0 ± 0^{A} | $285\pm140^{\text{A}}$ | 477 ± 118 | 71 ± 36 | 548 ± 147 | | |
| Hollow | $269 \pm 98^{\text{A}}$ | $166 \pm 32^{\text{A}}$ | $0 \pm 0^{\text{A}}$ | $435\pm130^{\text{A}}$ | 418 ± 68 | 378 ± 84 | 796 ± 122 | | |
| | | | | | | | | | |
| EXPERIMEN | NTAL | | | | | | | | |
| AMBIENT | | - | | | | | | 1986 ^b | 2836 ± 540 |
| Hummock | $63 \pm 24^{\text{A}}$ | $185\pm68^{\text{A}}$ | $3 \pm 2^{\mathbf{B}}$ | $251 \pm 78^{\text{A}}$ | 329 ± 148 | 112 ± 176 | 441 ± 96 | | |
| Hollow | $138\pm29^{\text{A}}$ | $190\pm24^{\text{A}}$ | $0 \pm 0^{\mathbf{A}}$ | $327 \pm 51^{\text{A}}$ | 385 ± 112 | 330 ± 188 | 715 ± 116 | | |
| WARMED | | | | | | | | | 3048 ±731 |
| Hummock | $178 \pm 69^{\mathbf{A}}$ | $238 \pm 37^{\text{A}}$ | $0 \pm 0^{\mathbf{A}}$ | $416\pm80^{\text{A}}$ | 581 ± 313 | 138 ± 70 | 719 ± 169 | | |
| Hollow | $88\pm89^{\rm A}$ | $139 \pm 44^{\text{A}}$ | $2 \pm 1^{\mathbf{B}}$ | $228\pm89^{\text{A}}$ | 495 ± 119 | 250 ± 118 | 745 ± 171 | | |
| | | | | | | | | | |
| DRAINED | | | | | | | | | |
| AMBIENT | - | | | | | | | 1964 ± 381 | 3429 ± 639 |
| Hummock | $143 \pm 95^{\text{A}}$ | $462 \pm 91^{\text{B}}$ | $38 \pm 49^{\text{BC}}$ | $643 \pm 18^{\text{B}}$ | 625 ± 220 | 300 ± 154 | 925 ± 247 | | |
| Hollow | $146 \pm 70^{\text{A}}$ | $152 \pm 51^{\text{A}}$ | $80 \pm 39^{\text{C}}$ | $378 \pm 6^{\text{A}}$ | 631 ± 194 | 344 ± 409 | 975 ± 301 | | |
| WARMED | | | | | | | | | 3970 ± 767 |
| Hummock | $38 \pm 12^{\mathbf{B}}$ | $870 \pm 66^{\mathrm{C}}$ | $12\pm03^{\rm B}$ | $919 \pm 63^{\mathrm{C}}$ | 895 ± 242 | 397 ± 58 | 1292 ± 249 | | |
| Hollow | $24\pm33^{\text{B}}$ | $226 \pm 99^{\text{A}}$ | $200 \pm 91^{\rm C}$ | $450\pm23^{\text{A}}$ | 999 ± 266 | 335 ± 219 | 1334 ± 332 | | |

^a Values are means \pm SE (n = 3 for each of above-ground, below-ground and trees biomasses). Means sharing same letters do not differ significantly. Letters should be compared only within one column. Total biomass was determined by weighting 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 | | | | | |
|------------------------------------------|--------|---------------------------------|-----------------------------------------|---------------------------|-------|------------------|-------|
| | | GP. | \underline{GPP}_{max} \underline{R} | | NE | <u>'max</u> | |
| | | $\boldsymbol{\mathit{F}}$ | P | $\boldsymbol{\mathit{F}}$ | p | \boldsymbol{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 \geq 1000 μmol m⁻² s⁻¹. *R* represents $R_{\rm ff}$ (forest floor respiration).

Table 4. Growing season CO₂-C flux estimates (± SE; g CO₂-C m⁻²) a.

| Year | Site / Microforms | GPP_{ff} | $R_{ m ff}$ | NE _{ff} | $R_{\rm r}$ | $L_{ m tree}$ | IC _{tree_ag} | IC _{tree_bg} | NEEb | C_{w} |
|------|---------------------|---------------|--------------|------------------|--------------|---------------|-----------------------|-----------------------|---------------|---------|
| 2011 | CONTROL | | | | | | | | | |
| | Ambient Hummock | -190 ± 29 | 225 ± 18 | 35 ± 30 | 63 ± 05 | -6 ± 1 | -38 ± 08 | -8 ± 1 | -92 ± 12 | |
| | Ambient Hollow | -178 ± 29 | 130 ± 21 | -48 ± 09 | 2 ± 00 | -0 ± 1 | -30 ± 00 | -0 ± 1 | -92 ± 12 | -13 |
| | Warmed Hummock | -206 ± 41 | 251 ± 63 | 45 ± 21 | 70 ± 06 | -6 ± 1 | -38 ± 08 | -8 ± 1 | -105 ± 16 | -13 |
| | Warmed Hollow | -207 ± 37 | 134 ± 52 | -74 ± 22 | 12 ± 03 | -0 ± 1 | -30 ± 00 | -0 ± 1 | -105 ± 10 | |
| | EXPERIMENTAL | | | | | | | | | |
| | Ambient Hummock | -106 ± 44 | 182 ± 75 | 76 ± 12 | 53 ± 14 | -7 ± 0 | -42 ± 15 | -9 ± 3 | 14 ± 05 | |
| | Ambient Hollow | -102 ± 52 | 349 ± 89 | 246 ± 55 | 115 ± 68 | -/ ± 0 | -4 2 ± 13 | - 9 ± 3 | 14 ± 03 | 105 |
| | Warmed Hummock | -104 ± 04 | 422 ± 83 | 317 ± 94 | 122 ± 56 | -7 ± 0 | -42 ± 15 | -9 ± 3 | 119 ± 48 | 103 |
| | Warmed Hollow | -136 ± 13 | 435 ± 95 | 299 ± 83 | 144 ± 55 | -/ ± 0 | -4 2 ± 13 | - 9 ± 3 | 119 ± 40 | |
| | DRAINED | | | | | | | | | |
| | Ambient Hummock | -280 ± 21 | 295 ± 10 | 15 ± 07 | 62 ± 05 | -11 ± 1 | -66 ± 09 | -15 ± 2 | 26 ± 14 | |
| | Ambient Hollow | -116 ± 19 | 536 ± 09 | 420 ± 23 | 123 ± 01 | -11 ± 1 | -00 ± 09 | -13 ± 2 | 20 ± 14 | -34 |
| | Warmed Hummock | -333 ± 91 | 343 ± 86 | 10 ± 09 | 72 ± 17 | -11 ± 1 | -66 ± 09 | -15 ± 2 | -8 ± 05 | -34 |
| | Warmed Hollow | -118 ± 19 | 468 ± 95 | 350 ± 92 | 108 ± 24 | -11 ± 1 | -00 ± 09 | -13 ± 2 | -0 ± 03 | |
| 2012 | CONTROL | | | | | | | | | |
| | Ambient Hummock | -228 ± 43 | 216 ± 33 | -12 ± 11 | 60 ± 05 | -6 ± 1 | -33 ± 07 | -7 ± 1 | -70 ± 10 | |
| | Ambient Hollow | -181 ± 08 | 241 ± 45 | 60 ± 33 | 21 ± 00 | -0 ± 1 | -33 ± 07 | -/ ± 1 | -70 ± 10 | -19 |
| | Warmed Hummock | -226 ± 99 | 222 ± 87 | -04 ± 02 | 62 ± 19 | -6 ± 1 | -33 ± 07 | -7 ± 1 | -89 ± 27 | -19 |
| | Warmed Hollow | -197 ± 29 | 201 ± 88 | 04 ± 00 | 18 ± 17 | -0 ± 1 | -33 ± 07 | -/ ± 1 | -09 ± 21 | |
| | EXPERIMENTAL | | | | | | | | | |
| | Ambient Hummock | -33 ± 23 | 165 ± 53 | 132 ± 12 | 48 ± 14 | -7 ± 2 | -39 ± 11 | -9 ± 0 | 57 ± 44 | |
| | Ambient Hollow | -89 ± 77 | 351 ± 96 | 261 ± 67 | 116 ± 55 | -/ ± 2 | -39 ± 11 | -9 ± 0 | 31 ± 44 | 100 |
| | Warmed Hummock | -119 ± 44 | 443 ± 88 | 324 ± 87 | 129 ± 17 | -7 ± 2 | -39 ± 11 | -9 ± 0 | 157 ± 90 | 100 |
| | Warmed Hollow | -77 ± 12 | 459 ± 59 | 382 ± 64 | 151 ± 82 | -/ ± Z | -39 ± 11 | -9 ± U | 137 ± 90 | |
| | DRAINED | | | | | | | | | |
| | Ambient Hummock | -333 ± 75 | 359 ± 18 | 26 ± 13 | 75 ± 05 | 10 + 2 | 60 + 10 | 12 + 2 | 22 + 15 | |
| | Ambient Hollow | -118 ± 20 | 507 ± 35 | 390 ± 47 | 116 ± 01 | -10 ± 2 | -60 ± 10 | -13 ± 2 | 23 ± 15 | 52 |
| | Warmed Hummock | -391 ± 44 | 356 ± 79 | -36 ± 12 | 75 ± 27 | 10 + 2 | 60 + 10 | 12 + 2 | -29 ± 11 | -52 |
| | Warmed Hollow | -136 ± 16 | 478 ± 63 | 342 ± 98 | 110 ± 29 | -10 ± 2 | -60 ± 10 | -13 ± 2 | -29 ± 11 | |
| 2013 | CONTROL | | | | | | | | | |
| | Ambient Hummock | -233 ± 82 | 217 ± 59 | -17 ± 01 | 61 ± 09 | 6 ± 0 | -33 ± 07 | -7 ± 1 | -76 ± 38 | |
| | Ambient Hollow | -195 ± 29 | 248 ± 41 | 53 ± 14 | 22 ± 07 | -6 ± 0 | -33 ± 07 | -/ ± 1 | -70 ± 36 | -6 |
| | Warmed Hummock | -259 ± 92 | 203 ± 56 | -56 ± 23 | 57 ± 12 | 6 + 1 | 22 + 07 | 7 . 1 | 92 + 40 | -0 |
| | Warmed Hollow | -232 ± 97 | 322 ± 46 | 90 ± 22 | 29 ± 20 | -6 ± 1 | -33 ± 07 | -7 ± 1 | -82 ± 40 | |
| | EXPERIMENTAL | | | | | | | | | |
| | Ambient Hummock | -51 ± 18 | 288 ± 22 | 237 ± 15 | 84 ± 18 | -7 ± 2 | -39 ± 11 | -9 ± 0 | 135 ± 44 | |
| | Ambient Hollow | -93 ± 55 | 486 ± 58 | 394 ± 67 | 161 ± 56 | -/ ± Z | -39 ± 11 | -9 ± U | 133 ± 44 | 10 |
| | Warmed Hummock | -81 ± 34 | 330 ± 55 | 249 ± 69 | 96 ± 19 | -7 ± 2 | -39 ± 11 | -9 ± 0 | 145 ± 90 | 10 |
| | Warmed Hollow | -104 ± 16 | 535 ± 51 | 431 ± 99 | 177 ± 81 | -/ ± Z | -39 ± 11 | -9 ± U | 143 ± 90 | |
| | DRAINED | | | | | | | | | |
| | Ambient Hummock | -347 ± 65 | 365 ± 84 | 17 ± 18 | 77 ± 21 | -10 ± 2 | -60 ± 10 | 12 + 2 | 13 ± 15 | |
| | Ambient Hollow | -123 ± 22 | 502 ± 33 | 380 ± 74 | 116 ± 61 | -10 ± 2 | -00 ± 10 | -13 ± 2 | 15 ± 15 | 72 |
| | Warmed Hummock | -517 ± 42 | 398 ± 58 | -120 ± 11 | 83 ± 25 | -10 ± 2 | -60 ± 10 | -13 ± 2 | -58 ± 11 | -73 |
| | Warmed Hollow | -122 ± 36 | 513 ± 33 | 391 ± 91 | 118 ± 25 | -10 ± 2 | -00 ± 10 | -13 ± Z | -30 ± 11 | |

^a Negative values represent uptake of carbon by the peatland from the atmosphere. The forest floor respiration ($R_{\rm ff}$) includes tree root respiration ($R_{\rm f}$). C_w (NEE warmed - NEE ambient) represents warming induced net ecosystem exchange at site. ^b NEE (net ecosystem exchange) is calculated using equation 3 (NEE = NE_{ff} + IC_{tree_bg} + IC_{tree_bg} + L_{tree} - $R_{\rm f}$). 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).

Appendix A. Estimated parameter values (\pm SE), standard error of the estimate (SEE) and goodness of fit (r^2) for the gross primary production of forest Floor (GPP_{ff}) model (Eq. 1) ^a.

| Year | Site / Microforms | GPP _{ff} v | s. PAR | GPP _{ff} v | vs. WT | <u>GPP_{ff}</u> | vs. <i>T</i> | <u>SEE</u> | <u>r</u> ² |
|------|-----------------------|----------------------------------|--------------------------------|-------------------------------|-----------------------------------------|-----------------------------|--------------------------------|----------------------|-----------------------|
| | | \underline{P}_{\max} | <u>k</u> | WT _{opt} | $\overline{\mathrm{WT}_{\mathrm{tol}}}$ | $\underline{T}_{	ext{opt}}$ | $\underline{T}_{\mathrm{tol}}$ | | |
| | | $g~CO_2~m^{2}d^{1}$ | $\mu mol \ m^{-2} \ s^{-1}$ | cm | cm | °C | °C | $g~CO_2~m^{2}~d^{1}$ | |
| 2011 | CONTROL | | | | | | | | |
| | Ambient Hummock | -22.2 ± 04 | 900 ± 422 | -56 ± 13 | 30 ± 16 | 16 ± 04 | 10 ± 05 | 2.3 | 0.83 |
| | Warmed Hummock | -27.2 ± 06 | 999 ± 468 | -48 ± 04 | 15 ± 11 | 9 ± 15 | 20 ± 16 | 3.4 | 0.77 |
| | Ambient Hollow | -19.4 ± 07 | 950 ± 601 | -28 ± 10 | 23 ± 21 | 14 ± 08 | 10 ± 13 | 2.0 | 0.63 |
| | Warmed Hollow | -15.7 ± 04 | 500 ± 318 | -36 ± 02 | 11 ± 03 | 17 ± 13 | 18 ± 30 | 3.0 | 0.54 |
| | EXPERIMENTAL | | | | | | | | |
| | Ambient Hummock | -26.2 ± 24 | 999 ± 805 | -64 ± 04 | 18 ± 09 | 30 ± 07 | 16 ± 02 | 3.2 | 0.75 |
| | Warmed Hummock | -23.0 ± 15 | 999 ± 994 | -57 ± 15 | 30 ± 11 | 30 ± 05 | 17 ± 16 | 5.4 | 0.54 |
| | Ambient Hollow | -40.5 ± 15 | 999 ± 729 | -58 ± 01 | 7 ± 01 | 13 ± 00 | 3 ± 00 | 3.3 | 0.82 |
| | Warmed Hollow | -26.1 ± 18 | 999 ± 753 | -82 ± 06 | 30 ± 08 | 15 ± 09 | 20 ± 06 | 5.0 | 0.62 |
| | DRAINED | | | | | | | | |
| | Ambient Hummock | -35.9 ± 09 | 950 ± 440 | -118 ± 08 | 30 ± 11 | 12 ± 02 | 10 ± 03 | 1.0 | 0.82 |
| | Warmed Hummock | -35.6 ± 14 | 999 ± 398 | -111 ± 03 | 30 ± 06 | 15 ± 08 | 20 ± 08 | 1.0 | 0.80 |
| | Ambient Hollows | -29.2 ± 17 | 850 ± 639 | -71 ± 32 | 30 ± 17 | 11 ± 03 | 10 ± 10 | 0.9 | 0.68 |
| | Warmed Hollow | -19.4 ± 27 | 998 ± 779 | -124 ± 06 | 21 ± 10 | 9 ± 02 | 2 ± 02 | 3.2 | 0.56 |
| | Warmed Hummock | -35.6 ± 14 | 999 ± 398 | -111 ± 03 | 30 ± 06 | 15 ± 08 | 20 ± 08 | 1.0 | 0.80 |
| 2012 | CONTROL | | | | | | | | |
| | Ambient Hummock | -24.8 ± 05 | 900 ± 286 | -35 ± 11 | 30 ± 14 | 15 ± 02 | 10 ± 04 | 1.8 | 0.86 |
| | Warmed Hummock | -32.9 ± 05 | 999 ± 335 | -54 ± 10 | 30 ± 17 | 21 ± 01 | 9 ± 01 | 1.9 | 0.85 |
| | Ambient Hollow | -21.8 ± 04 | 950 ± 299 | -42 ± 14 | 30 ± 20 | 15 ± 01 | 10 ± 02 | 1.1 | 0.85 |
| | Warmed Hollow | -38.8 ± 12 | 999 ± 382 | -25 ± 43 | 30 ± 09 | 17 ± 01 | 10 ± 02 | 1.2 | 0.85 |
| | EXPERIMENTAL | | | | | | | | |
| | Ambient Hummock | -28.4 ± 10 | 998 ± 638 | -29 ± 12 | 30 ± 12 | 20 ± 04 | 12 ± 11 | 2.2 | 0.75 |
| | Warmed Hummock | -27.8 ± 26 | 500 ± 463 | -42 ± 31 | 30 ± 12 | 17 ± 21 | 20 ± 05 | 3.4 | 0.74 |
| | Ambient Hollow | -40.1 ± 18 | 999 ± 574 | -73 ± 03 | 30 ± 04 | 11 ± 00 | 3 ± 01 | 2.4 | 0.74 |
| | Warmed Hollow | -12.6 ± 05 | 738 ± 679 | -48 ± 13 | 23 ± 11 | 20 ± 02 | 5 ± 03 | 7.4 | 0.50 |
| | DRAINED | | | | | | | | |
| | Ambient Hummock | -50.0 ± 14 | 950 ± 416 | -105 ± 03 | 30 ± 03 | 10 ± 02 | 10 ± 02 | 0.9 | 0.82 |
| | Warmed Hummock | -50.0 ± 19 | 950 ± 444 | -107 ± 02 | 30 ± 04 | 11 ± 03 | 12 ± 01 | 0.9 | 0.83 |
| | Ambient Hollow | -31.3 ± 10 | 850 ± 246 | -100 ± 11 | 23 ± 07 | 10 ± 06 | 10 ± 05 | 1.6 | 0.83 |
| | Warmed Hollow | -18.5 ± 28 | 999 ± 779 | -125 ± 06 | 21 ± 13 | 8 ± 01 | 1 ± 01 | 4.1 | 0.55 |
| 2013 | CONTROL | | | | | | | | |
| 2010 | Ambient Hummock | -32.1 ± 05 | 837 ± 219 | -51 ± 07 | 30 ± 12 | 11 ± 07 | 20 ± 04 | 1.8 | 0.68 |
| | Warmed Hummock | -38.7 ± 10 | 500 ± 136 | -45 ± 06 | 30 ± 20 | 20 ± 09 | 20 ± 04 | 1.1 | 0.85 |
| | Ambient Hollow | -46.8 ± 05 | 554 ± 121 | -31 ± 01 | 12 ± 01 | 9 ± 01 | 6 ± 01 | 5.4 | 0.85 |
| | Warmed Hollow | -45.5 ± 24 | 500 ± 157 | -24 ± 08 | 23 ± 09 | 19 ± 05 | 11 ± 10 | 1.2 | 0.85 |
| | EXPERIMENTAL | 73.3 - 27 | 300 = 137 | 24 = 00 | 23 = 07 | 17 = 05 | 11 ±10 | 1.2 | 0.05 |
| | Ambient Hummock | -38.0 ± 13 | 634 ± 292 | -63 ± 03 | 30 ± 04 | 14 ± 05 | 10 ± 17 | 3.1 | 0.85 |
| | Warmed Hummock | -28.3 ± 28 | 500 ± 314 | -67 ± 02 | 13 ± 02 | 14 ± 03 15 ± 07 | 10 ± 17 20 ± 10 | 3.4 | 0.85 |
| | Ambient Hollow | -26.3 ± 26 -26.3 ± 14 | 500 ± 314 500 ± 156 | -64 ± 09 | 30 ± 08 | 15 ± 07 15 ± 07 | 13 ± 09 | 2.1 | 0.85 |
| | Warmed Hollow | -26.9 ± 14 | 557 ± 461 | -74 ± 05 | 11 ± 05 | 13 ± 07 20 ± 26 | 13 ± 09 17 ± 12 | 0.4 | 0.85 |
| | DRAINED | -10.7 ± 14 | JJ / ± 401 | -/ - /05 | 11 ± 03 | 20 ± 20 | 1/ - 12 | 0.4 | 0.03 |
| | Ambient Hummock | 50 0 ± 27 | 500 ± 190 | -102 ± 03 | 26 ± 07 | 30 ± 26 | 9 ± 05 | 0.6 | 0.82 |
| | Warmed Hummock | -50.0 ± 37 | 500 ± 180 | | 26 ± 07 | 30 ± 26 | | 0.6 | |
| | Ambient Hollow | -50.0 ± 41 | 500 ± 241 820 ± 591 | -115 ± 05 -76 ± 02 | 28 ± 07 | 21 ± 18 | 9 ± 11 | 2.0 | 0.85 |
| | Warmed Hollow | -40.0 ± 41 -28.0 ± 43 | | | 2 ± 01 | 18 ± 05 | 2 ± 02 | 1.5 | 0.83 0.85 |
| | models were developed | | 500 ± 456 | -89 ± 17 | 7 ± 29 | 16 ± 01 | 1 ± 00 | 1.6 | |

^a The models were developed for each microform type (n=3) at the control, experimental and drained sites separately for growing seasons of 2011, 2012 and 2013. PAR, WT and T represent photosynthetically active radiation, water table (negative values show belowground water level) and 5 cm soil temperature, respectively. P_{max} denotes potential maximum rate of GPP_{ff} and k is level of PAR at which half of GPP_{ff} occurs. WT_{opt} and T_{opt} are Gaussian response parameters for optimum GPP_{ff} while WT_{tol} and T_{tol} are Gaussian response parameters describing the width of the curve. All modeled parameters are significant at p=0.05 level.

Appendix B. Estimated regression coefficient values (\pm SE), standard error of the estimate (SEE) and goodness of fit (r^2) for the forest floor respiration ($R_{\rm ff}$) model (Eq. 2) ^a.

| Year | Site / Microforms | a | b | \boldsymbol{c} | SEE | r^2 |
|------|-------------------|----------------|-----------------|---------------------------------------------------|-----|-------|
| | | | dimensionless | g CO ₂ m ⁻² d ⁻¹ | | |
| 2011 | CONTROL | | | | | |
| | Ambient Hummock | 1.30 ± 0.3 | -0.21 ± 0.1 | -18.3 ± 6.8 | 0.8 | 0.81 |
| | Warmed Hummock | 0.49 ± 0.1 | -0.16 ± 0.0 | -1.8 ± 2.5 | 3.8 | 0.37 |
| | Ambient Hollow | 1.70 ± 0.3 | -0.61 ± 0.2 | -32.3 ± 9.7 | 0.7 | 0.79 |
| | Warmed Hollow | 0.54 ± 0.1 | -0.38 ± 0.1 | -8.1 ± 2.0 | 1.8 | 0.75 |
| | EXPERIMENTAL | | | | | |
| | Ambient Hummock | 1.32 ± 0.1 | -0.07 ± 0.0 | -5.7 ± 2.0 | 2.0 | 0.83 |
| | Warmed Hummock | 0.71 ± 0.1 | -0.06 ± 0.1 | -3.9 ± 3.6 | 2.8 | 0.56 |
| | Ambient Hollow | 0.67 ± 0.2 | -0.37 ± 0.1 | -17.1 ± 4.7 | 5.5 | 0.51 |
| | Warmed Hollow | 1.65 ± 0.3 | -0.15 ± 0.1 | -18.5 ± 5.1 | 5.3 | 0.60 |
| | DRAINED | | | | | |
| | Ambient Hummock | 0.31 ± 0.3 | -0.02 ± 0.0 | -2.62 ± 7.3 | 0.4 | 0.49 |
| | Warmed Hummock | 0.66 ± 0.1 | -0.09 ± 0.0 | -7.2 ± 4.2 | 3.4 | 0.45 |
| | Ambient Hollow | 0.55 ± 0.1 | -0.02 ± 0.0 | -2.3 ± 3.6 | 0.2 | 0.85 |
| | Warmed Hollow | 1.80 ± 0.1 | -0.10 ± 0.1 | -20.7 ± 4.7 | 3.6 | 0.84 |
| 2012 | CONTROL | | | | | |
| | Ambient Hummock | 0.39 ± 0.2 | -0.25 ± 0.1 | -10.7 ± 5.3 | 0.6 | 0.53 |
| | Warmed Hummock | 0.57 ± 0.1 | -0.20 ± 0.1 | -1.3 ± 2.2 | 2.9 | 0.57 |
| | Ambient Hollow | 0.93 ± 0.1 | -0.25 ± 0.1 | -12.8 ± 1.8 | 0.4 | 0.81 |
| | Warmed Hollow | 0.90 ± 0.1 | -0.16 ± 0.1 | -2.8 ± 2.0 | 3.1 | 0.71 |
| | EXPERIMENTAL | | | | | |
| | Ambient Hummock | 0.61 ± 0.1 | -0.22 ± 0.1 | -9.4 ± 2.9 | 3.2 | 0.68 |
| | Warmed Hummock | 1.08 ± 0.1 | -0.15 ± 0.1 | -13.5 ± 4.9 | 4.6 | 0.62 |
| | Ambient Hollow | 1.56 ± 0.2 | -0.18 ± 0.1 | -19.6 ± 9.4 | 6.0 | 0.67 |
| | Warmed Hollow | 0.63 ± 0.1 | -0.25 ± 0.0 | -12.4 ± 1.4 | 3.2 | 0.85 |
| | DRAINED | | | | | |
| | Ambient Hummock | 0.65 ± 0.1 | -0.03 ± 0.1 | -3.4 ± 8.1 | 0.3 | 0.91 |
| | Warmed Hummock | 0.89 ± 0.1 | -0.00 ± 0.0 | -4.4 ± 4.5 | 4.4 | 0.60 |
| | Ambient Hollow | 1.07 ± 0.1 | -0.15 ± 0.0 | -17.3 ± 5.6 | 0.9 | 0.80 |
| | Warmed Hollow | 1.27 ± 0.1 | -0.00 ± 0.0 | -1.5 ± 3.7 | 5.0 | 0.67 |
| 2013 | CONTROL | | | | | |
| | Ambient Hummock | 1.74 ± 0.1 | -0.01 ± 0.1 | -5.3 ± 3.1 | 3.0 | 0.67 |
| | Warmed Hummock | 2.02 ± 0.2 | -0.03 ± 0.0 | -8.3 ± 3.4 | 4.2 | 0.56 |
| | Ambient Hollow | 1.18 ± 0.1 | -0.15 ± 0.1 | -3.8 ± 1.7 | 3.1 | 0.68 |
| | Warmed Hollow | 1.56 ± 0.2 | -0.18 ± 0.1 | -5.4 ± 2.1 | 3.7 | 0.71 |
| | EXPERIMENTAL | | | | | |
| | Ambient Hummock | 0.75 ± 0.5 | -0.53 ± 0.1 | -10.3 ± 3.3 | 3.5 | 0.70 |
| | Warmed Hummock | 1.29 ± 0.3 | -0.47 ± 0.1 | -45.9 ± 7.5 | 6.2 | 0.53 |
| | Ambient Hollow | 0.48 ± 0.3 | -0.61 ± 0.1 | -29.8 ± 2.5 | 2.5 | 0.83 |
| | Warmed Hollow | 0.96 ± 0.3 | -0.19 ± 0.1 | -10.3 ± 5.5 | 6.9 | 0.38 |
| | DRAINED | | | | | |
| | Ambient Hummock | 1.44 ± 0.2 | -0.17 ± 0.0 | -27.5 ± 2.7 | 2.8 | 0.82 |
| | Warmed Hummock | 2.17 ± 0.2 | -0.17 ± 0.0 | -32.1 ± 3.2 | 2.9 | 0.80 |
| | Ambient Hollow | 1.70 ± 0.3 | -0.32 ± 0.0 | -41.5 ± 5.5 | 6.5 | 0.61 |
| | Warmed Hollow | 0.77 ± 0.2 | -0.20 ± 0.0 | -23.2 ± 4.8 | 3.5 | 0.63 |

^a The models were developed for each microform type (n = 3) at the control, experimental and drained sites separately for growing seasons of 2011, 2012 and 2013. 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.

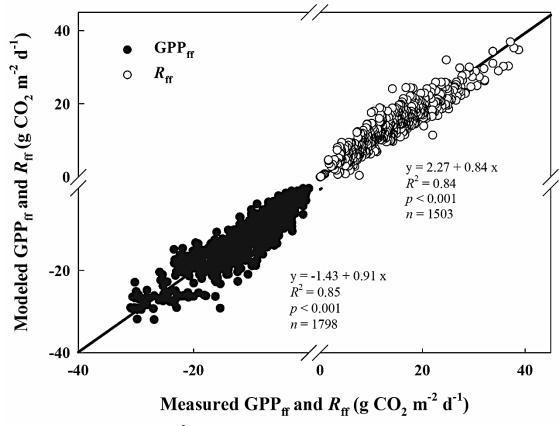


Figure 1. Goodness of fit (R^2) between modeled and measured $GPP_{\rm ff}$ and modeled and measured $R_{\rm ff}$ values. The figure presents all data for control, experimental and drained sites for the study years (2011-2013). Lines represent the 1:1 fit.

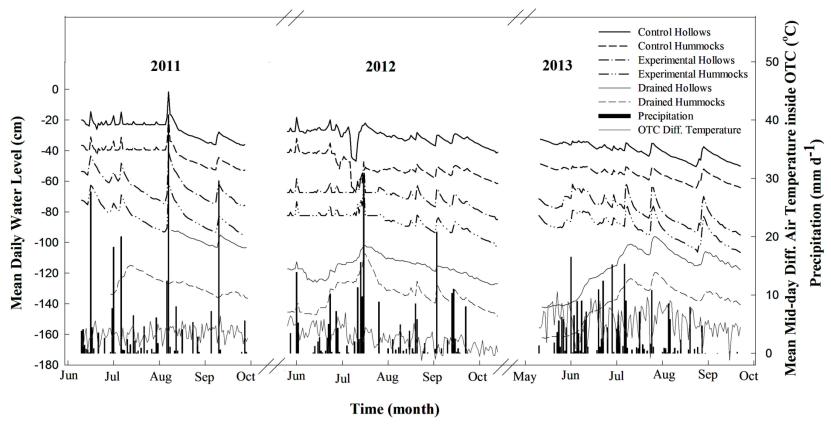


Figure 2. Mean daily water level, mid-day differential (warmed – Ambient) air temperature and precipitation at hummock and hollow microforms during growing seasons of 2011, 2012 and 2013. Note the right y-axis has two values using the same scale: mean mid-day differential air temperature and daily precipitation. 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.

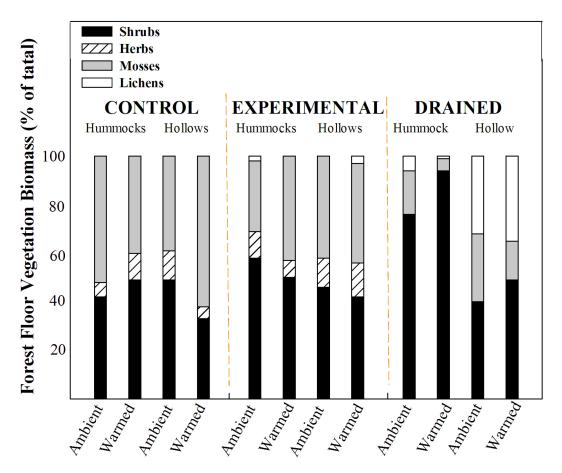


Figure 3. Relationship between drainage, warming and microform scenario and ground layer above-ground biomass by category as a percentage of total.

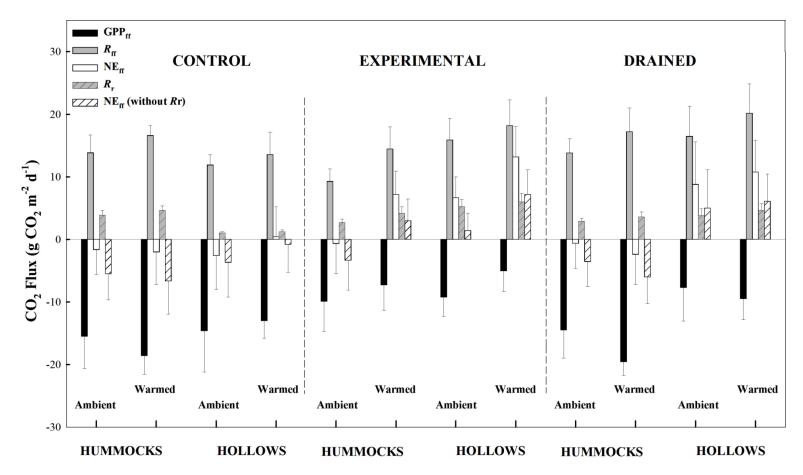


Figure 4. GPP_{max}, $R_{\rm ff}$ and NE_{max} and $R_{\rm r}$ at control, experimental and drained sites averaged across 2011-2013. NE_{max} (without above and below-ground parts of trees) was calculated by subtracting $R_{\rm r}$ from NE_{max} and represents net exchange of CO₂ of the ground-layer vegetation (including peat). Error bars indicate \pm 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.

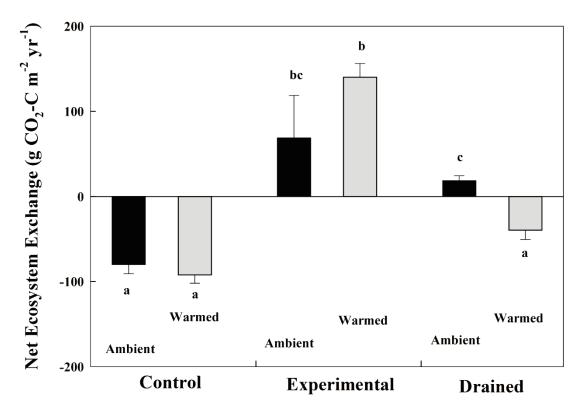


Figure 5. CO_2 -C balance averaged across study years (2011-2013). Error bars indicate \pm standard deviation. Differences were evaluated between ambient and warmed sites (microforms) indicted by letters at each bar. Sites are significantly different at p < 0.05 if they have no letters in common.