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

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Abstract. Midlatitude 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), with water levels at 38, 74 and 120 cm below the surface, respectively. At each site we measured carbon dioxide (CO_2) fluxes and estimated tree root respiration (R_r; across hummock–hollow microtopography of the forest floor) and net primary production (NPP) of trees during the growing seasons (May to October) of 2011–2013. The CO_2–C balance was calculated by adding the net CO_2 exchange of the forest floor ($NE_{ff} - R_r$) to the NPP of the trees.

From cooler and wetter 2011 to the driest and the warmest 2013, the control site was a CO_2–C sink of 92, 70 and 76 g m^{-2}, the experimental site was a CO_2–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 CO_2–C m^{-2}. The short-term drainage at the experimental site resulted in small changes in vegetation coverage and large net CO_2 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) on the hummocks and lichen in the hollows leading to the highest CO_2 uptake at the drained hummocks and significant losses in the hollows. The tree NPP (including above- and belowground growth and litter fall) in 2011 and 2012 was 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 plots with open-top chambers (OTCs) that caused a passive warming on average of ∼ 1 °C and differential air warming of ∼ 6 °C at midday full sun over the study years. Warming significantly enhanced shrub growth and the CO_2 sink function of the drained hummocks (exceeding the cumulative respiration losses in hollows induced by the lowered water level $\times$ warming). There was an interaction of water level with warming across hummocks that resulted in the largest net CO_2 uptake at the warmed 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 sink function of the drained site by 73 g m^{-2}. Therefore, drying and warming in continental bogs is expected to initially accelerate CO_2–C losses via ecosystem respiration, but persistent drought and warming is expected to restore the peatland's original CO_2–C sink function as a result of the shifts in vegetation composition and productivity between the microforms and increased NPP of trees over time.

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1 Introduction

Northern peatland ecosystems have accumulated ~ 547 Pg carbon (C; $1\,\text{Pg} = 10^{15}$ g) as a result of functioning as a steady but persistent sink throughout the Holocene (Yu, 2012; Tarnocai et al., 2009). The accumulated peatland C stocks equal approximately one third of the global terrestrial soil C pool (Grosse et al., 2011; Ciais et al., 2013). Midlatitude 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 bogs have greater net primary production (NPP) to decomposition ratios and hence return higher accumulation rates than those of open bogs (Clymo et al., 1998). The C stocks of the western boreal treed bogs may respond differently to warming and drought than those of eastern boreal open fens (Kettles and Tarnocai, 1999) and may lead to an accelerated positive feedback to climate change (Gruber et al., 2004; Limpens et al., 2008; Bhatti et al., 2012; Stocker et al., 2013). Future climatic changes are expected to be severe at midlatitudes (Vitt et al., 2009; Kettles and Tarnocai, 1999; IPCC, 2007) where there is a dense coverage (50 %) of peatlands (Tarnocai, 2006).

Carbon exchange in peatlands occurs in the forms of the uptake of C from the atmosphere via gross primary photosynthesis (GPP) and the release of C to the atmosphere by respiration (R) of plants (autotrophic) and microorganisms (heterotrophic). The sum of GPP ($-$) and R ($+$) is defined as the net ecosystem exchange (NEE) of CO_2. Net uptake of CO_2 causes assimilation of C in the form of plant biomass and accumulation of C in the form of soil organic matter. The GPP, R and NEE of the forest floor are represented by GPP_{ff}, R_{ff} and NE_{ff}, respectively. Tree root respiration is represented by R_{r}.

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

Tree root respiration (R_{r}) may account for a significant proportion of forest floor respiration (R_{ff}) in forested bogs (Lohila et al., 2011). Therefore, isolating R_{r} from R_{ff} is critical in attributing forest floor C to various sources of soil respiration and in filling 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 the net exchange of the forest floor (NE_{ff}) and the NPP of a treed peatland with those of an open peatland, provided the major controls (e.g. temperature and water table) remain unchanged. The contribution of R_{r} to R_{ff} has been quantified using the closed-chamber technique in various forest ecosystems. The R_{r} was separated from R_{ff} by subtracting trenched plots' respiration from that of control plots at a black spruce forest in Quebec by Hermle et al. (2010), and R_{r} was found to be 24 % of R_{ff}. However, the R_{r} percentage was found to be higher (37 %) in a subtropical forest of mixed alder and cypress plantation (Wang et al., 2008) in a similar trenching experiment. Hanson et al. (2000) have reported even higher mean root and 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 to $94\,\text{g C m}^{-2}$ following 10 years of lowered water table (~ 120 cm) in a boreal bog, but the timescale of the change remains unclear.

Continental peatlands are predicted to be drier under warming climatic conditions. The drier conditions may favour some species in peatland communities to yield more NPP than others, and, as a result, plant composition will shift, leading to changes in species dominance (Sternberg et al., 1999). In northern bogs, the balance could shift towards a shrub- or tree-dominated system (Weltzin et al., 2001; Lohila et al., 2011), which in combination with deeper water tables could lead to an increase in both soil (Ise et al., 2008) and plant respiration (Tarnocai et al., 2009). A shift in species dominance after drainage in a Swedish peatland accelerated soil respiration rates, ranging from 513 to $6516\,\text{g CO}_2\,\text{m}^{-2}\,\text{d}^{-1}$ (Von-Arnold 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 CO_2 flux and NPP to manipulations in local climate (warming) (Lafleur and Humphreys, 2008; Johnson et al., 2013) and local environment (water table) (Strack et al., 2006; Munir et al., 2014) also varied between the microforms.

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

Although several studies have been conducted on NPP and CO_2 exchange in western Canadian peatlands, many unknowns remain. The CO_2 balance and tree biomass of 10 ombrotrophic treed bog sites in Alberta were quantified by Wieder et al. (2009), but responses to the major controls of temperature and water table were not evaluated. The response of a bog to decade-long water table manipulation was quantified by Munir et al. (2014), but the impact of the warming manipulations remained unexplored. The impact of warming manipulation and microtopography on CO_2 balance responses was also not investigated by Adkinson et al. (2011) in their climatic temperature and short-term drought study on Alberta fens. They also did not estimate the tree productivity of the forested fen nor the contribution of R_r. The CO_2 fluxes in 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 open fens studied remained indeterminate. Therefore, the evaluation of peatland tree productivity and net forest floor CO_2 exchange responses to potential warming and water table lowering expected under a climate change scenario is required in order to fill the knowledge gaps on how a treed continental bog will feed back to the expected changes in climate. Thus, our unique investigation answers this question by quantifying the CO_2–C balance of a midlatitude treed continental bog (having hummock and hollow microforms) subjected to warming and water table manipulations, by adding net forest floor CO_2–C exchange to tree productivity C uptake. Moreover, we isolate R_r from R_{ff} to better understand the proportional response of R_r to potential short- and longer-term water table drawdown 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 the 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 3-year study period (2011–2013). Our specific objectives were (1) to compare CO_2 flux responses in 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 (1 May to 31 October) of 2011–2013. Three sites were chosen or created, having various water levels: an undisturbed water level site (water level ∼ 38 cm below surface) called CONTROL (55°21′ N, 112°31′ W), an experimentally lowered water level site (water level ∼ 35 cm lower than the control) called EXPERIMENTAL (55°21′ N, 112°31′ W) and a 10-year-old drained site (water level ∼ 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 subhumid 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, 13.2 and 14.1 °C and 403, 282 and 267 mm, respectively.

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

The Wandering River bog has been classified as a treed low shrub bog with typical mosaic of hummock and hollow microforms (Riley, 2003). In 2011, the control and experimental site microforms were found equally dominated by *Sphagnum* mosses (e.g. *Sphagnum fuscum*) with sparse shrubs (e.g. *Rhododendron groenlandicum*), whereas the drained-site hummocks had the greatest coverage of shrubs and the drained hollows had the greatest coverage of lichens. The most abundant type of tree in the bog was black spruce (*Picea mariana*), which constituted > 99 % of the tree stand, with 25 766 stems ha^{-1} consisting of 37 % of 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 a basal area of 73.5 $\text{m}^2\,\text{ha}^{-1}$. This description applies to the whole bog, including the control, experimental and drained sites (Munir et al., 2014).

We chose six hummocks and six hollows from the available microtopography at each of the control, experimental and drained sites. Each of the chosen microforms (plot) was fitted with a 60 cm × 60 cm permanent steel collar with a groove at the top inserted approximately 5–6 cm into the peat surface (to keep disturbance minimal). Adjacent to each plot, a perforated PVC water well (diameter = 3.5 cm) with a nylon cloth covering the lower 150 cm was inserted into the peat to measure the water level manually every time CO_2 flux is measured. Two automatic water level loggers (Levelogger Junior 3001, Solinst, Georgetown, Ontario, Canada) were installed at each of the three sites in two randomly selected wells: one at a hummock and the other in a hollow plot. These leveloggers recorded temperature-compensated water levels continuously at 20 min intervals throughout the three growing seasons (except in the drained hollow between May to early July 2011 due to a malfunction of the levelogger). A Barologger (Barologger Gold, Solinst; height = 100 cm) was also installed to adjust 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, three hummocks and three hollows selected at random were equipped with 60 °C, 50 cm tall, open-top hexagonal chambers (OTCs) with a top and basal width of 104 and 162 cm, respectively.

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

2.2 CO_2 flux

We measured CO_2 flux in biweekly campaigns during the growing seasons (May to October) of 2011–2013 using a closed chamber with dimensions 60 cm × 60 cm × 30 cm (length × width × height), made of clear acrylic and corrected for transmittance (88 %). The inside of the chamber was equipped with two low-speed battery-operated fans to circulate air inside the chamber during and between the measurements. However, the chamber had no pressure equilibrium port installed. The instantaneous CO_2 concentration inside the chamber headspace was measured with a portable infrared gas analyser (PP systems, USA, EGM-4) with a built-in sampling pump operating at a flow rate of 350 mL min^{-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 were multiplied by a factor of 0.88 to obtain corrected values of the PAR inside the chamber to account 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 min at 15 s intervals. Synchronous with the flux measurements, soil temperatures at the depths of 2, 5, 10, 15 and 20 cm were measured with a thermocouple thermometer in all plots. The water table relative to moss surface was measured at each CO_2 flux measurement occasion from a permanently installed well associated with each plot.

In each plot, a total of 276 CO_2 flux measurements in 29 campaigns were made during the daytime of the growing seasons (May to October, 2011–2013). Each campaign lasted for about 7 days during which fluxes were measured on two to three occasions in each plot. At each flux measurement occasion, we took a total of five or six measurements: two to three in full sun, one with a single-layer shroud, one with a double-layer shroud and, finally, one with an opaque tarp (for R_{ff}). The chamber was air-flushed for enough time between the measurements to equilibrate the headspace concentration with that of the ambient air.

The CO_2 flux measurements when the chamber was covered with an opaque tarp represented R_{ff}. The R_{ff} represents only forest floor respiration (ground-layer aboveground biomass respiration + soil respiration + root respiration (shrubs + herbs + trees)). GPP_{ff} was determined as the difference between NE_{ff} and R_{ff}. Negative values indicate an uptake of CO_2 by the ecosystem. The NE_{ff} was calculated using the exponential change in chamber headspace CO_2 concentration (Kutzbach et al., 2007) regressed with time, as a function of volume, pressure and air temperature inside the chamber, according to the ideal gas law. The exponential regression was applied following Munir et al. (2014) because covering the soil and vegetation can manipulate the spontaneous CO_2 fluxes across the 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 alterations in turbulence between measured intervals (Hutchinson et al., 1993). Therefore, the CO_2 fluxes determined using linear regression likely result in an underestimation of fluxes in a 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 a chamber closure time of only 2 min (Kutzbach et al., 2007).

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

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

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

where P_{max} denotes the potential maximum rate of GPP_{ff} ($g\,CO_2\,m^{-2}\,d^{-1}$) not constrained by water level and/or temperature, and k represents the PAR level at which half of the P_{max} occurs. The WL represents water level (cm); WL_{opt} and WL_{tol} are parameters in a GPP_{ff} Gaussian response to WL when GPP_{ff} is optimum and the width of the curve, respectively. The T denotes soil temperature at 5 cm deep ($T_{soil\ 5\,cm}$; °C); T_{opt} and T_{tol} are parameters in a GPP_{ff} Gaussian response to T when GPP_{ff} is optimum and the width of the curve, respectively. The GPP_{ff} model parameters (standard errors), r^2 values and standard errors of the estimates at the control, experimental and drained microforms are presented in Table A1 in the Appendix.

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

$$R_{ff} = a \cdot T + b \cdot WT + c, \quad (2)$$

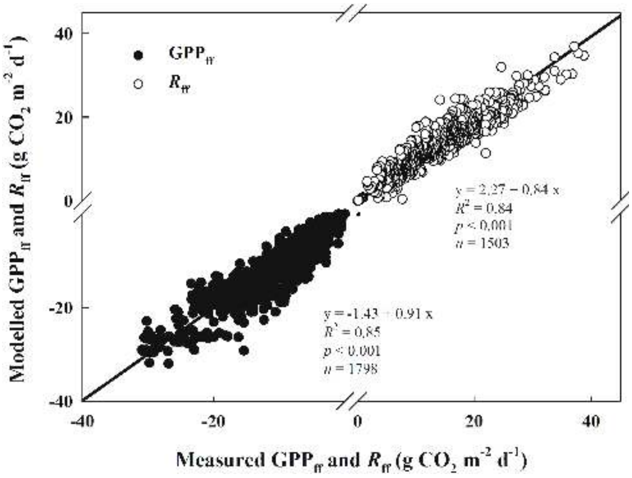

Figure 1. Goodness of fit (R^2) between modelled and measured GPP_{ff} and modelled and measured R_{ff} values. The figure presents all data for control, experimental and drained sites for the study years (2011–2013). Lines represent the 1 : 1 fit.

where a, b and c are regression coefficients, and their values for each water level treatment, warming, microform type and year combination are presented in Table A2 in the Appendix.

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

2.2.2 Tree root respiration

To isolate R_r from R_{ff}, a trenching method was used following Wang et al. (2008). From the available microtopography adjacent to the regularly monitored flux plots, we chose an additional eight hummocks and eight hollows at each of the control and drained sites and four hummocks and four hollows at the experimental site (due to its smaller area). Each microform plot had an area of 60 cm × 60 cm. At all sites, an incision was made around half of the chosen microform types 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 was 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 between plots due to slight difference in vegetation (Wang et al., 2008). The CO_2 emissions from all plots were, on average, measured weekly using the same instruments and chamber (with opaque shroud) used for the measurement of NE_ff.

The plots were trenched in early May 2012 while respiration measurements were carried out in July–September 2012. While the trenching is used to separate R_r from R_ff, it also adds fresh litter to the peat 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_ff can 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 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 decomposing fine roots in trenched plots contributed little to R_r and becomes stable a few months after trenching. Also, the root exclusion experiment may not be useful if extended through a complete annual cycle, as, over such a long period, there is the possibility of reinvasion of roots into the previously root-free trenched plot (Edwards and Norby, 1999). While it is clear that findings from such trenching measurements should be interpreted carefully, the primary focus of this paper is on quantifying R_ff while investigating R_r to better understand and separate the contribution of various processes to shifts in R_ff following drainage.

2.3 Biomass and tree productivity

2.3.1 Ground-layer biomass

At the end of our field work in October 2013, we collected the ground-layer biomass samples from triplicates 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. The quadrats were clipped 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 the 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 from a greater depth. The cores were sectioned into 0–10 and 10–20 cm depths at the time of sample collection, taken to the ecohydrology laboratory, University of Calgary, and sorted into fine- (< 2 mm) and coarse- (> 2 mm) diameter fractions.

2.3.2 Tree biomass and productivity

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

The NPP of the tree stand for above-ground parts was estimated for 2011 and 2012, following Szumigalski and Bayley (1996) and Thormann and Bayley (1997). They estimated the NPP of an Alberta ombrotrophic bog of hummock–hollow microtopography by adding incremental biomass of the trees to their litter production (17 % of above-ground incremental biomass $m^{-2}\,yr^{-1}$ for *Picea mariana*). We estimated tall-tree incremental biomass based on tree ring widths measured using DendroScan (Varem-Sanders and Campbell, 1996). The incremental biomass of the short trees was estimated by regressing leader length with height following Macdonald and Lieffers (1990) and Mullin et al. (1992). The summation of tall- and short-tree biomass increments for a year represented the incremental biomass of the tree stand for above-ground parts of trees for that year. To account for litter, an additional 17 % was added to this summation. The new summation represented NPP for above-ground parts of the tree stand (Szumigalski and Bayley, 1996). We did not measure incremental biomass of the below-ground parts of trees due to the desire to limit disturbance to our research sites and allow for future monitoring. Therefore, we used an allometric equation (tree root biomass $= 0.222 \times$ tree above-ground biomass) generated by Li et al. (2003) for estimating the incremental biomass of the tree roots. We did not measure tree productivity for 2013 and instead used 2012 productivity values to calculate NEE for this last year of the study.

2.4 CO_2–C balance ($NE_\mathrm{ff} + NPP - R_\mathrm{r}$)

To calculate CO_2–C balance, the NE_ff ($-GPP_\mathrm{ff} + R_\mathrm{ff}$) and NPP (incremental tree biomass of above-ground and below-

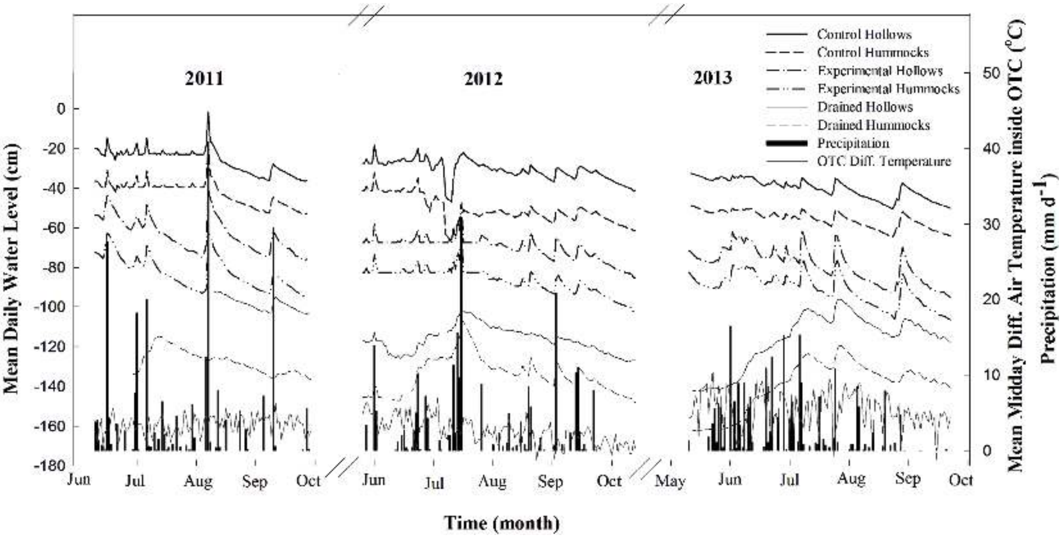

Figure 2. Mean daily water level, midday differential (warmed – ambient) air temperature and precipitation in hummock and hollow microforms during growing seasons of 2011, 2012 and 2013. Note the right *y* axis has two values using the same scale: mean midday differential air temperature and daily precipitation. The *x* axis 2011, 2012 and 2013 separately. The partially missing water level data at drained hummocks in 2011 were due to levelogger's malfunction. The cumulative seasonal precipitation during 2012 and 2013 was 30.0 and 35.3 % less, respectively, than that in 2011.

ground parts of tree stand + stand litter) in terms 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

$$\mathrm{NEE} = \mathrm{NE}_{\mathrm{ff}} + \mathrm{IC}_{\mathrm{tree\_ag}} + \mathrm{IC}_{\mathrm{tree\_bg}} + L_{\mathrm{tree}} - R_{\mathrm{r}}, \qquad (3)$$

where $\mathrm{NE}_{\mathrm{ff}}$ represents net exchange of the forest floor, $\mathrm{IC}_{\mathrm{tree_{ag}}}$ and $\mathrm{IC}_{\mathrm{tree_{b}g}}$ 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_{ff} based on instantaneous measurements and then estimating it as this proportion of the modelled seasonal R_{ff}. Seasonal CO_2 fluxes at hummocks and hollows were upscaled by multiplying mean estimated growing season CO_2 exchange by their respective coverage of 56 and 44 %, 55 and 45 %, and 52 and 48 % at the control, experimental and drained sites, respectively (Table 4).

2.5 Data analysis

To estimate treatment effects on instantaneous CO_2 flux components ($\mathrm{GPP}_{\mathrm{ff}}$, R_{ff}, $\mathrm{NE}_{\mathrm{ff}}$, R_r, $\mathrm{NE}_{\mathrm{ff}}$ without R_r), we used separate linear mixed-effects models (SPSS 21.0) with a CO_2 flux component as the response variable and water level treatment, warming (OTC), microtopography and year as fixed effects. Since the same plots were measured in each study season, the 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 a compound symmetry covariance structure for repeated measures analysis (Jennrich and Schluchter, 1986). A mean value of flux determined in each plot in each growing season was used for all analyses. Mean CO_2 flux components data were normally distributed across all years (Kolmogorov–Smirnov Z: 2011, $p = 0.910$; 2012, $p = 0.767$; 2013, $p = 0.624$).

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

3 Results

3.1 Microclimate and environment

At the Wandering River bog, air and soil temperatures and precipitation were monitored during the growing seasons (May to October) of 2011–2013. The weather during the

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

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

* All temperatures are mean (±SD). At each site, all the OTC-equipped hummocks ($n = 3$) and hollows ($n = 3$) were instrumented with HOBOs to log OTC warming of air (T_{air}) and 5 cm deep soil ($T_{\mathrm{soil\ 5\,cm}}$). The 30 cm deep soil temperatures ($T_{\mathrm{soil\ 30\,cm}}$) were measured using thermocouple during the measurement of CO_2 fluxes in the growing seasons of the study years. Means sharing same letters do not differ significantly. Letters should be compared only within one column for T_{air}, $T_{\mathrm{soil\ 5\,cm}}$ and $T_{\mathrm{soil\ 30\,cm}}$.

study period was warmer by 1.36, 1.38 and 2.44 °C, wetter by 42 mm in 2011 and drier by 79 and 94 mm in 2012 and 2013, respectively, than the 30-year means at Athabasca, Alberta (meteorological data have been described under "Methods"). The average undisturbed water level at the control site, and manipulated water levels at the experimental and drained sites were clearly different at the start of the study period in 2011 at 38, 73 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, 8 and 8 cm and in hollows by 6, 6 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 and 82 cm, respectively (Fig. 2).

The OTCs resulted in significantly warmer growing season air temperature (T_{air}; ANOVA, $F_{2,\,24} = 215.87$, $p < 0.001$) by an average (±SD) of 1.0 ± 0.0 °C at the control, 0.9 ± 0.0 °C C at the experimental and 0.8 ± 0.5 °C at the drained site (Table 1) consistently over the 3 study years. The OTC warming in 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 ($T_{\mathrm{soil 5\,cm}}$; 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 3 study years. The rising T_{air} warmed the T_{soil5cm} the least (0.4 ± 0.3 °C) at drained hummocks and the most (1.3 ± 0.2 °C) at the control hollows. Average soil temperature at 30 cm depth ($T_{\mathrm{soil\,30\,cm}}$) below the OTC-equipped plots was not significantly different from that at the same depth in non-OTC plots across all sites (ANOVA, $F_{2,\,24} = 0.71$, $p = 0.053$) and microforms (ANOVA, $F_{1,\,24} = 0.95$, $p = 0.339$). Diurnal T_{air} and $T_{\mathrm{soil\ 5\,cm}}$ patterns in the OTCs were significantly related to PAR ($R^2 = 0.81$, 0.87, respectively) across the microtopography at all sites. During midday bright sunny conditions the air warming in OTC-equipped plots was greater than that in non-OTC plots by averages of 4, 5 and 9 °C at hummocks, and by 5, 7 and 6 °C in hollows at the control, experimental and drained sites, respectively. Similarly, the direct solar loading increased the $T_{\mathrm{soil\ 5\,cm}}$ in the OTC plots by more than at non-OTC plots, by averages of 5, 3 and 8 °C at hummocks, and by 2, 4 and 8 °C in hollows in the control, experimental and drained sites, respectively (Fig. 2).

3.2 Biomass and incremental tree growth

3.2.1 Ground-layer biomass

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

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

Table 2. Ground-layer and tree biomass ($g\,m^{-2}$) at control, experimental and drained sites *.

	ABOVE-GROUND				BELOW-GROUND			TREES	TOTAL
Site/microforms	Moss	Vascular	Lichen	Total	Fine < 2 mm	Coarse > 2 mm	Total	Ambient	Ambient/ warmed
CONTROL									
AMBIENT								2142 ± 376	3168 ± 604
Hummock	208 ± 51^{a}	191 ± 62^{a}	0 ± 0^{a}	399 ± 24^{a}	335 ± 15	233 ± 61	568 ± 48		
Hollow	134 ± 17^{a}	216 ± 11^{a}	0 ± 0^{a}	350 ± 82^{a}	486 ± 67	266 ± 102	751 ± 332		
WARMED									3150 ± 578
Hummock	113 ± 46^{a}	172 ± 97^{a}	0 ± 0^{a}	285 ± 140^{a}	477 ± 118	71 ± 36	548 ± 147		
Hollow	269 ± 98^{a}	166 ± 32^{a}	0 ± 0^{a}	435 ± 130^{a}	418 ± 68	378 ± 84	796 ± 122		
EXPERIMENTAL									
AMBIENT								1986 **	2836 ± 540
Hummock	63 ± 24^{a}	185 ± 68^{a}	3 ± 2^{b}	251 ± 78^{a}	329 ± 148	112 ± 176	441 ± 96		
Hollow	138 ± 29^{a}	190 ± 24^{a}	0 ± 0^{a}	327 ± 51^{a}	385 ± 112	330 ± 188	715 ± 116		
WARMED									3048 ± 731
Hummock	178 ± 69^{a}	238 ± 37^{a}	0 ± 0^{a}	416 ± 80^{a}	581 ± 313	138 ± 70	719 ± 169		
Hollow	88 ± 89^{a}	139 ± 44^{a}	2 ± 1^{b}	228 ± 89^{a}	495 ± 119	250 ± 118	745 ± 171		
DRAINED									
AMBIENT								1964 ± 381	3429 ± 639
Hummock	143 ± 95^{a}	462 ± 91^{b}	38 ± 49^{bc}	643 ± 18^{b}	625 ± 220	300 ± 154	925 ± 247		
Hollow	146 ± 70^{a}	152 ± 51^{a}	80 ± 39^{c}	378 ± 6^{a}	631 ± 194	344 ± 409	975 ± 301		
WARMED									3970 ± 767
Hummock	38 ± 12^{b}	870 ± 66^{c}	12 ± 03^{b}	919 ± 63^{c}	895 ± 242	397 ± 58	1292 ± 249		
Hollow	24 ± 33^{b}	226 ± 99^{a}	200 ± 91^{c}	450 ± 23^{a}	999 ± 266	335 ± 219	1334 ± 332		

* Values are means ± 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 the ground layer by the proportion of hummocks and hollows at each site (control: 56 % hummocks; experimental: 55 % hummocks; drained: 52 % hummocks). ** $n = 1$ (only one quadrat was available due to limited size of experimental site).

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 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 in the warmed drained hollows ($p = 0.011$), although warming did not increase lichen biomass significantly ($p = 0.441$). There was limited growth of lichen at the control site (Table 2).

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

3.2.2 Above-ground tree biomass

Above-ground tree biomass was greater at the control site than that at the experimental and drained sites by an average of 156 and 178 $g\,m^{-2}$, respectively (Tables 2, 4). However, the above-ground tree growth during 2011–2012 was significantly higher at the drained site (66 and 60 $g\,C\,m^{-2}$) than 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 $g\,C\,m^{-2}$ 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 were not available. We measured the data at the start of our study in 2011 and have described this in detail in the Study sites section. Heterogeneity between the tree quadrats laid out at each site was large; however, the small size of the study sites limited our ability to construct more replicates 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 of the drained-site trees was clearly different from that of the control- and experimental-site trees. Thus, we are confident that the changes in the productivity estimated represent a clear response to the interaction of water level elevation and the duration of drainage.

3.3 CO_2 fluxes

3.3.1 Measured CO_2 fluxes

GPP_{max} was significantly affected by water level, microtopography and year, but there was no direct significant effect of OTC warming on GPP_{max} (Table 3). The GPP_{max} at the control ($-15.4\,g\,CO_2\,m^{-2}\,d^{-1}$) and drained ($-12.8\,g\,CO_2\,m^{-2}\,d^{-1}$) sites was not significantly different, but it was different from that at the experimental site ($-7.8\,g\,CO_2\,m^{-2}\,d^{-1}$). There was a higher GPP_{max} at hummocks ($-14.4\,g\,CO_2\,m^{-2}\,d^{-1}$) than in hollows ($-9.8\,g\,CO_2\,m^{-2}\,d^{-1}$). Microform and warming had a significant interaction with each other as well as individually with water level. The GPP_{max} in 2011 and 2012 was not significantly different, but it was different from the highest value that occurred in the warmest year, 2013. The 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 $-21.2\,g\,CO_2\,m^{-2}\,d^{-1}$ at hummocks by 2013; and with warming, increasing GPP at warmed but not at unwarmed plots by 2013. Although OTC warming did not have a significant effect directly on productivity, there was a significant interaction with water level, microform and year, resulting in significantly higher productivity ($-25.8\,g\,CO_2\,m^{-2}\,d^{-1}$) at the warmed drained hummocks in 2013.

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

NE_{max} (including R_r) was significantly affected individually by water level, microtopography, OTC warming and year, and all the four factors interactively (Table 3). All sites were significantly different from each other: the control site forest floor was a sink of $1.4\,g\,CO_2\,m^{-2}\,d^{-1}$ while the experimental and drained sites were sources of 6.5 and $4.1\,g\,CO_2\,m^{-2}\,d^{-1}$, respectively. There was a significant interaction of water level with microform resulting in net emissions at experimental hollows ($10\,g\,CO_2\,m^{-2}\,d^{-1}$) and drained hollows ($9.8\,g\,CO_2\,m^{-2}\,d^{-1}$) compared to net uptake at the control microforms (hollows $= -1.1\,g\,CO_2\,m^{-2}\,d^{-1}$; hummocks $= -1.8\,g\,CO_2\,m^{-2}\,d^{-1}$) and the drained hummocks ($-1.5\,g\,CO_2\,m^{-2}\,d^{-1}$). The water level also had a significant interaction with warming, leading to net emissions from warmed plots at the experimental site ($10.2\,g\,CO_2\,m^{-2}\,d^{-1}$) and the drained site ($4.2\,g\,CO_2\,m^{-2}\,d^{-1}$) compared to net uptake in the ambient control plots ($-2.1\,g\,CO_2\,m^{-2}\,d^{-1}$), while warmed plots had significantly higher emissions ($NE_{ff} = 4.5\,g\,CO_2\,m^{-2}\,d^{-1}$) than ambient plots ($1.7\,g\,CO_2\,m^{-2}\,d^{-1}$). The water level also had a significant interaction with study year, with the highest net uptake of $-6.3\,g\,CO_2\,m^{-2}\,d^{-1}$ at the control site in 2013, this year not being significantly different from 2011 and 2012. Subtracting R_r from NE_{max} (to consider the net exchange of the ground layer only) converts the control microforms and drained hummocks to larger sinks of CO_2, while it considerably reduces emissions in the drained hollows and experimental microforms (Table 4).

3.3.2 Modelled CO_2 fluxes (excluding R_r) for growing season (1 May to 31 October)

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

In 2011, OTC warming of the forest floor microforms converted the control site to a greater CO_2–C sink ($52\,g\,m^{-2}$), the drained site to a smaller CO_2–C source ($84\,g\,m^{-2}$) and the experimental site to a greater CO_2–C source ($177\,g\,m^{-2}$).

Table 3. Mixed-effects ANOVA F and p values on CO$_2$ fluxes at the peatland surface 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*.

Effect		CO$_2$ flux components					
		GPP$_{\mathrm{max}}$		R		NE$_{\mathrm{max}}$	
	df	F	p	F	p	F	p
Water level	2.108	57.78	**0.000**	12.61	**0.000**	53.87	**0.000**
Microform	1.108	56.71	**0.000**	12.60	**0.001**	92.55	**0.000**
Warming	1.108	0.21	0.651	37.68	**0.000**	19.52	**0.000**
Year	2.108	31.43	**0.000**	5.77	**0.004**	33.15	**0.000**
Water level × microform	2.108	12.85	**0.000**	19.42	**0.000**	22.26	**0.000**
Water level × warming	2.108	11.79	**0.000**	0.88	0.420	11.33	**0.000**
Water level × year	4.108	8.11	**0.000**	4.75	**0.001**	2.86	**0.027**
Microform × warming	1.108	7.57	**0.007**	1.39	0.242	2.26	0.136
Microform × year	2.108	1.51	**0.003**	3.88	**0.024**	1.61	0.205
Warming × year	2.108	8.96	**0.000**	5.25	**0.007**	6.45	**0.002**
Water Level × microform × warming	2.108	0.60	0.519	0.83	0.441	1.58	0.211
Water Level × microform × year	4.108	0.17	0.954	2.17	0.077	1.02	0.400
Water Level × warming × year	4.108	0.31	0.871	0.31	0.873	0.37	0.831
Microform × warming × year	2.108	1.57	0.213	3.72	**0.027**	0.27	0.768
Water Level × microform × warming × year	4.108	2.63	**0.039**	0.54	0.710	3.30	**0.014**

* GPP$_{\mathrm{max}}$ and NE$_{\mathrm{max}}$ represent GPP$_{\mathrm{ff}}$ and NE$_{\mathrm{ff}}$ when the photon flux density of PAR was $\geq 1000\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$. R represents R_{ff} (forest floor respiration). Bold values are significant at $p = 0.05$ level.

Over the study years, the 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 CO$_2$ emissions more than uptake and resulted in a larger net release of CO$_2$ to the atmosphere. The highest emissions at the experimental and drained hollows were largely due to a substantial contribution by R_{r}. Averaged over years, the exclusion of R_{r} from NE$_{\mathrm{ff}}$ makes the control site a greater sink and experimental and drained sites a smaller source of forest floor CO$_2$ (Table 4, Fig. 4).

3.4 CO$_2$–C- balance (NE$_{\mathrm{ff}}$ + NPP − R_{r})

To calculate the final balance of CO$_2$ fluxes and tree biomass productivity, we added seasonal estimated NE$_{\mathrm{ff}}$ ($-R_{\mathrm{r}}$) to estimated tree incremental growth (above and below ground) and tree litter production. We estimated the CO$_2$–C balance separately for the three growing seasons of 2011–2013. The control site was a larger sink (±SD) (92 (±12) g C m^{-2} in 2011 compared to 70 (±10) and 76 (±38) g C m^{-2} in 2012 and 2013, respectively). The experimental site was a progressively increasing source (14 (±5), 57 (±44) and 135 (±45) g C m^{-2} in 2011, 2012 and 2013, respectively). On the other hand, the drained site was a progressively declining source (26 (±14), 23 (±15) and 13 (±2) g C m^{-2} through 2011–2013). OTC warming of microforms consistently increased uptake at the control site by −13, −19 and −6 g C m^{-2} from 2011 to 2013. The warming also converted the drained site to a sink of C (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. 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 CO$_2$–C uptake at hummocks and enhanced the emissions in hollows. Averaged over the study years, the warming interacted with deeper and longer drainage to restore the peatland's original CO$_2$–C sink function (Fig. 5).

4 Discussion

This study estimated the CO$_2$–C balance of a subhumid, continental treed bog by combining the C exchange values derived from modelled CO$_2$ flux and tree productivity separately for the growing seasons (May to October) of 2011, 2012 and 2013. The control site in this bog was a growing season sink of 92, 70 and 76 g C m^{-2} along a gradient of slightly wetter and warmer years to drier and warmer than average years (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 CO$_2$ sink of 120 to 220 g C m^{-2}, and thus our values are slightly below this range. Within the same boreal region of northern Alberta as the present study, Adkinson et al. (2011) also reported net growing season CO$_2$ uptake over 3 study years of −110 and −35 to −154 g C m^{-2} at poor-fen and rich-fen sites, respec-

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

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

[a] Negative values represent the uptake of carbon by the peatland from the atmosphere. The forest floor respiration (R_{ff}) includes tree root respiration (R_r). C_w (NEE warmed – NEE ambient) represents warming-induced net ecosystem exchange at site. [b] NEE (net ecosystem exchange) is calculated using Eq. (3) ($NEE = NE_{ff} + IC_{tree_a g} + IC_{tree_b g} + L_{tree} - R_r$). Forest floor carbon exchange was determined by weighting NE_{ff} measured at each microform by the proportion of hummocks and hollows at each site (control: 56 % hummocks; experimental: 55 % hummocks; drained: 52 % hummocks).

tively, and thus our control site sink values are close to the value at the poor fen. However, a higher yearly CO_2 accumulation rate of $-144\,g\,C\,m^{-2}$ in a treed fen in the same boreal region is reported by Syed et al. (2006).

Methane (CH_4) is also an important component of the C balance in peatland ecosystems. However, overall seasonal CH_4–C losses were reported to be 0.34, 0.61 and $0.07\,g\,C\,m^{-2}$ at our control, experimental and drained sites, respectively (Munir and Strack, 2014). Therefore, the CH_4 fluxes are a minor component of the seasonal C balance at our dry continental bog sites. 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 CO_2–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 to a greater extent 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 was lower in the drier and warmer growing seasons (2012 and 2013) of the study. This reduction was due to the substantial increase in R_{ff} in the hollows exceeding the combined increase in GPP_{ff} at the microforms, especially in 2012 (Table 4). The steady and consistent increase in R_{ff} in 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 in the hollows. However, the abrupt increase in R_{ff} noticed in the experimental hollows might be due to the influence of the experimental lowering of the water table negatively affecting hollow vegetation more than adjacent hummocks. In contrast, there was only a minor fluctuation in GPP_{ff} or R_{ff} at the drained site in 2012 and 2013 compared to 2011, and thus stability in net CO_2 exchange at this long-term drained site could be due to the dominance of vascular ground-layer vegetation, as opposed to the control and short-term drained sites having greater moss coverage (Fig. 3, Tables 2, 3).

4.2 Water table manipulation effects

The 1–3 years of water table drawdown converted our bog site forest floor (excluding R_r) from a sink of 42, 24 and $30\,g\,C\,m^{-2}$ in 2011, 2012 and 2013, respectively, to a progressively larger source of 72, 112 and $189\,g\,C\,m^{-2}$ in 2011, 2012 and 2013, respectively. A net loss of CO_2–C in response to a short-term disturbance has been reported by Laiho (2006) for a bog and Chivers et al. (2009) for 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 in 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 CO_2–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 the water table at the experimental site possibly initiated vegetation desiccation that progressed through the study years. In contrast, the longer-term drainage drove the hummock habitat to be more favourable for woody shrubs with a higher water use efficiency and longer root system. That was likely why the drained-site hummocks had declining net emissions as the growing seasons became warmer and drier.

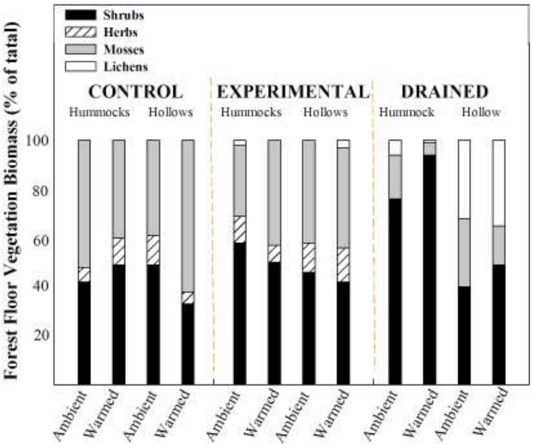

Figure 3. Relationship between drainage, warming and microform scenario and ground-layer above-ground biomass by category as a percentage of the total.

4.3 OTC warming effects

The control site sink strength was enhanced by OTC warming leading to greater CO_2–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. The lowest sink differential (warmed – ambient) of $6\,g\,C\,m^{-2}$ was noticed in the warmest and driest year 2013, similar to the findings of Aurela et al. (2007) and Lafleur and Humphreys (2008). They also reported that increased growing season temperature enhanced GPP_{ff} but extreme seasonal temperature reduced the GPP_{ff} and accelerated R_{ff} in a subarctic fen. The increase in GPP_{ff} and/or R_{ff} has also been reported by Sullivan et al. (2008) in a Greenland rich fen and Weltzin et al. (2001) in bog mesocosms, both in disagreement with Johnson et al. (2013), who reported that there

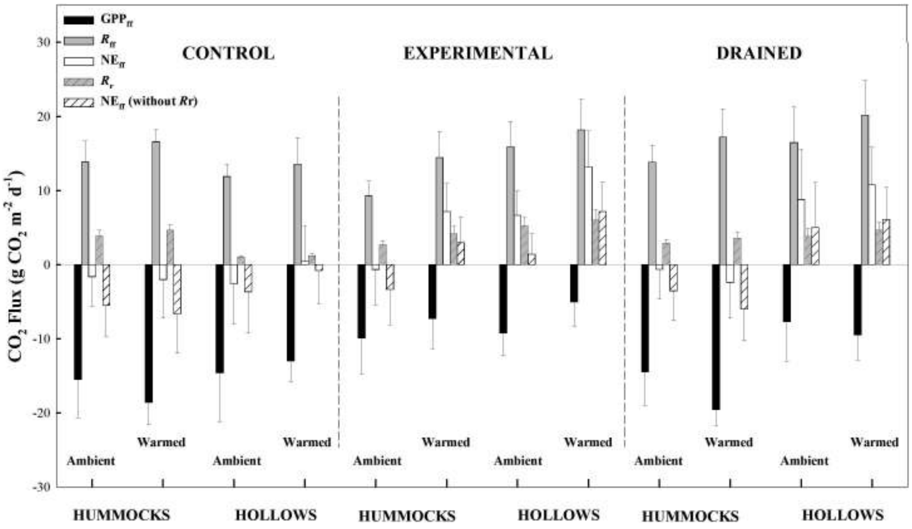

Figure 4. GPP$_{\mathrm{max}}$, R_{ff}, NE$_{\mathrm{max}}$ and R_{r} at control, experimental and drained sites averaged over 2011–2013. NE$_{\mathrm{max}}$ (without above- and below-ground parts of trees) was calculated by subtracting R_{r} from NE$_{\mathrm{max}}$ and represents net exchange of CO_2 of the ground-layer vegetation (including peat). Error bars indicate ± standard deviation. Results are from linear mixed-effect models with water table, OTC (warming) and microform and year as fixed effects and year as repeated measures. Only averaged fluxes over all study years are being graphed as the impacts of treatments were consistent in all growing seasons.

was no consistent effect of OTC warming on the CO_2 flux components because of subtle warming. At our short-term drained (experimental) site, the OTC warming greatly accelerated emissions, causing differential increases of 105, 100 and 10 g CO_2–C m^{-2} from 2011 to 2013 (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 2 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 a 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 rates 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 a consistently increasing differential NEE of −34, −52 and −73 g C m^{-2} in 2011, 2012 and 2013, respectively. Thus, warming led to greater CO_2 uptake. Our findings together with those of others (e.g. Bubier et al., 2003; Aurela et al., 2007; Sullivan et al., 2008; Wieder et al., 2009; Lohila et al., 2011) demonstrate the critical interaction of temperature with wetness for GPP$_{\mathrm{ff}}$ 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

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 CO_2 uptake at the wetter lawn than that at the drier ridge in an eccentric raised bog in Sweden over two growing seasons. Similarly, in a cool temperate fen in Canada, Strack et al. (2006) demonstrated higher GPP$_{\mathrm{max}}$ 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 a flattening of the peatland microtopography. Contrastingly, in this study in a dry continental treed bog in Alberta, we found that after 13 years of deepest drainage treatment the GPP$_{\mathrm{max}}$ and GPP$_{\mathrm{ff}}$ were in fact the highest at drained hummocks, increasing from cooler (2011) to warmer (2013). Conversely, R_{ff} and R_{r} were the highest at the experimental and drained hollows, also increasing towards the warmer year 2013. Interestingly, the CO_2 uptake was even higher at the warmed drained hummocks, while CO_2 release was also even higher in the warmed drained hollows and experimental microforms compared to the ambient microforms at these sites (Fig. 4, Table 4). The significantly increased GPP$_{\mathrm{max}}$ at ambient hummocks, which was even higher at warmed drained hummocks, was probably due to enhanced growth and the greater biomass of vascular vegetation (shrubs; Table 2, Fig. 3). Conversely, the replacement of most of the moss (dominantly *Sphagnum*) biomass by lichens in ambient and warmed drained hollows led to the reduction in GPP$_{\mathrm{max}}$

and GPP_{ff} (Fig. 3, Tables 2, 4) that was measured. Moreover, drained and experimental hollows were the largest sources of CO_2 in all years. Thus, we expect hummocks to have increasing equilibrium peat depth and hollows to have decreasing equilibrium peat depth as an effect of drainage in the long run. These predictions contradict those of Strack et al. (2006) due to contrasting microclimatic and environmental conditions of the two studies but corroborate those of Munir et al. (2014) due to the same climatic and environmental conditions. However, these studies together support a general unimodal relationship of peat accumulation with water level (Belyea, 2009). Therefore, combining the CO_2 dynamics at the ambient and warmed experimental and drained microforms demonstrates that climate-forced declining water levels in ombrotrophic continental bogs would result in hummocks growing higher and hollows deepening.

4.5 Water table manipulation and warming effects on vegetation

Interactions between soil and plant communities have been predicted to play a major role in determining the response of the net exchange of CO_2 in peatlands to a climate change scenario (Weltzin et al., 2001; Kardol et al., 2010; Moore et al., 2002) of water level lowering and global warming (Ciais et al., 2013). Ground-layer biomass was significantly affected by 13 years of drainage (water level ∼ 120 cm; $F_{2,36} = 49.42$, $p < 0.001$) and OTC average warming of ∼ 1 °C, midday full sun diurnal air warming of ∼ 6 °C or 5 cm deep soil warming of ∼ 5 °C ($F_{2,36} = 6.46$, $p = 0.015$; Figs. 2, 3). The shift in biomass coverage and composition was also different between the microforms ($F_{2,36} = 24.14$, $p < 0.001$); biomass increased at hummocks compared to hollows. However, no significant difference in vegetation biomass or composition was found after 3 years of drainage of the water level to ∼ 76 cm ($p = 0.162$). Interestingly, along a gradient of decreasing water level, shrub biomass increased at hummocks and lichen biomass increased in hollows, while moss biomass decreased at all microforms at the continental bog sites. Along the same gradient of decreasing water level, the warming treatment enhanced shrub biomass at the hummocks from 2011 to 2013, indicated by an interaction of water table, warming, microform and year ($F_{2,36} = 8.24$, $p = 0.001$). The accumulated NPP ratio of below-ground : above-ground shifted from 1.86 before warming to 2.00 after warming, suggesting a shift in C allocation in response to warming treatment. The three bog functional plant groups (moss, shrub, lichen) differed in their response to water level and warming due to their differential response of life forms and species characteristics of each community (Weltzin et al., 2000). The drainage-driven and warming-induced increases in vascular biomass that we found were also reported by Moore et al. (2002), Laine et al. (2011) and Weltzin et al. (2000).

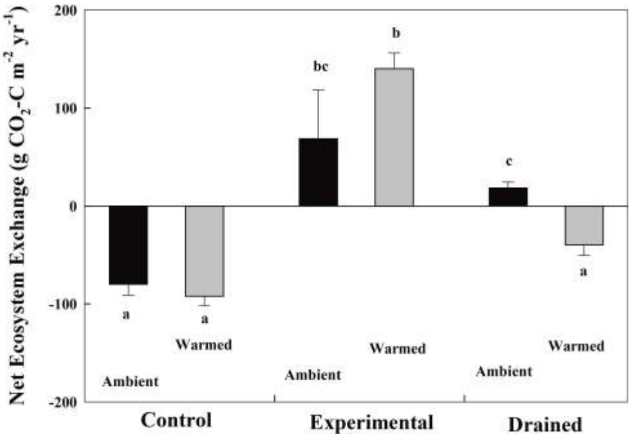

Figure 5. CO_2–C balance averaged over study years (2011–2013). Error bars indicate ±standard deviation. Differences were evaluated between ambient and warmed sites (microforms) indicted by letters at each bar. Sites are significantly different at $p < 0.05$ if they have no letters in common.

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} (±224) and 2177 g m^{-2} (±2259), respectively (Moore et al., 2002). Our data for above-ground tree biomass (2031 ± 379) fall within the range of published values. However, our ground-layer biomass average (1236 ± 130 g m^{-2}) is less than 1900 g m^{-2} (±224) reported by Moore et al. (2002) because they drew peat cores from a depth of 110 cm for quantifying below-ground biomass, whereas our core depth was only 20 cm. Therefore, it is likely that we might have underestimated the below-ground biomass, particularly at the drained site with an oxic zone up to 120 cm thick. However, this still 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 water level gradient, productivity of the trees (measured by determining above-ground incremental tree growth) increased along the same gradient (Tables 2, 4). The highest above-ground tree biomass estimated at the control site was due to a thinner oxic zone supporting stand that was mainly denser but had smaller-diameter trees and a higher number of smaller trees. The higher productivity at the drier sites was due to thicker aerated peat which supported a 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 at the experimental site, which showed higher productivity than the control site but less productivity 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 the by far highest productivity at our 10–13-year-old drained site with deepest water table (∼ 120 cm). The measured R_r consistently increased at all sites along a gradient of warming years (growing season) but was highest at the experimental site in all years due to readily available substrate and desiccating vegetation at this site where the water level had been lowered for a short time. Drainage induces significantly higher coverage and biomass of vascular plants that offset some of the loss of CO_2 occurring due to the deepening of the oxic zone and the increasing of decay rates (Ise et al., 2008). Therefore, although our drained site forest floor was always a source of CO_2, warming induced significantly increased ground-layer biomass that shifted this site to be a sink of C. This sink function coupled with higher tree productivity significantly enhanced the sink function of the drained site (Fig. 5). Conversely, the dramatic lowering of the water table at the experimental site severely destabilized the ecosystem functioning that further deteriorated with warming treatment over the study seasons (2011–2013). However, it was noted that differential emissions (warmed – ambient) to declined over the study years, indicating that the bog ecosystem may have been reaching a new equilibrium after an initial stress.

5 Conclusions

In a midlatitude 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, moss biomass was replaced by vascular plant biomass (mostly woody shrubs) at hummocks and lichen biomass in hollows. The shrub biomass growth was significantly increased in response to a 3-year OTC warming of ∼ 1 °C in the longer-term and deeper-water-level treatment.

The deeper water level combined with OTC warming induced enhanced growth of woody shrubs and drove the drained hummocks to become the largest net sink of CO_2 across all sites and microforms. Conversely, the short-term, as well as the longer-term, water level lowering converted the hollows to be the largest net sources of CO_2. However, the 11–13 years of deeper-water-level lowering coupled with OTC warming increased the forest floor net uptake of CO_2, leading it to clearly exceed the losses via respiration at the drained microforms. The significantly increased tree productivity in response to the longer-term deeper drainage (NPP–C) added to the NE_ff–C ($-R_\mathrm{r}$) converted the drained site from a moderate C source to a sink of C with a sink strength close to the bog's original strength (Fig. 5).

Averaged over study years, an OTC warming of ∼ 1 °C (and differential midday full sun air warming of ∼ 6 °C) interacted with water level treatment to enhance the sink function of the undisturbed site, enlarge the source strength of the experimental site and restore the sink strength of the drained site. This pattern is a strong indicator that climatic warming that drives persistent lowering of the water level in the 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 midlatitude continental treed bogs are sensitive but adaptive ecosystems that are expected to respond to climatic warming and drying almost instantly by supporting the development of woody roots that penetrate deeper for an optimum supply of moisture and nutrients to the newly adapted surface vegetation. Although the deepening of water table initially leads to larger net emissions to the atmosphere, persistent drying and warming transforms the moss habitat (characterized by near-surface water level) to a vascular plant habitat (characterized by a deeper water level), leading to a shift to woody shrubs and trees with deeper root systems. The bog trees adapt better to lower water levels and increase productivity by widening ring width, increasing leader length and increasing below-ground biomass allocation.

Appendix A

Table A1. Estimated parameter values (±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)*.

Year	Site/microforms	GPP_{ff} vs. PAR		GPP_{ff} vs. WT		GPP_{ff} vs. T		SEE	r^2
		P_{max}	k	WT_{opt}	WT_{tol}	T_{opt}	T_{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	−458 ± 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
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								
	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								
	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	15 ± 07	20 ± 10	3.4	0.85
	Ambient hollow	−26.3 ± 14	500 ± 156	−64 ± 09	30 ± 08	15 ± 07	13 ± 09	2.1	0.85
	Warmed hollow	−16.9 ± 14	557 ± 461	−74 ± 05	11 ± 05	20 ± 26	17 ± 12	0.4	0.85
	DRAINED								
	Ambient hummock	−50.0 ± 37	500 ± 180	−102 ± 03	26 ± 07	30 ± 26	9 ± 05	0.6	0.82
	Warmed hummock	−50.0 ± 41	500 ± 241	−115 ± 05	28 ± 07	21 ± 18	9 ± 11	2.0	0.85
	Ambient hollow	−40.0 ± 41	820 ± 591	−76 ± 02	2 ± 01	18 ± 05	2 ± 02	1.5	0.83
	Warmed hollow	−28.0 ± 43	500 ± 456	−89 ± 17	7 ± 29	16 ± 01	1 ± 00	1.6	0.85

* The models were developed for each microform type ($n = 3$) at the control, experimental and drained sites separately for the growing seasons of 2011, 2012 and 2013. PAR, WT and T represent photosynthetically active radiation, water table (negative values show below-ground 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 modelled parameters are significant at $p = 0.05$ level.

Table A2. Estimated regression coefficient values (±SE), standard error of the estimate (SEE) and goodness of fit (r^2) for the forest floor respiration (R_{ff}) model (Eq. 2)*.

Year	Site/microforms	*a*	*b*	*c*	SEE	r^2
			dimensionless		$\mathrm{g\,CO_2\,m^{-2}\,d^{-1}}$	
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

* The models were developed for each microform type ($n = 3$) at the control, experimental and drained sites separately for the 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 modelled parameters are significant at $p = 0.05$ level.

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