

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

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9

10 **Abstract**

11 Mid-latitude treed bogs represent significant carbon (C) stocks and are highly sensitive to global climate
12 change. In a dry continental treed bog, we compared three sites; control, recent (1-3 years;
13 experimental) and older drained (10-13 years; drained) with water levels at 38, 74 and 120 cm below
14 the surface, respectively. At each site we measured carbon dioxide (CO₂) fluxes and estimated tree root
15 respiration (R_r ; across hummock-hollow microtopography of the forest floor) and net primary
16 production (NPP) of trees during the growing seasons (May to October) of 2011-2013. The CO₂-C
17 balance was calculated by adding net CO₂ exchange of the forest floor ($NE_{ff} - R_r$) to the NPP of the
18 trees.

19 From cooler and wetter 2011 to the driest and the warmest 2013, the control site was a CO₂-C sink of
20 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
21 site was a progressively smaller source of 26, 23 and 13 g CO₂-C m⁻², respectively. The short-term
22 drainage at the experimental site resulted in small changes in vegetation coverage and large net CO₂
23 emissions at the microforms. In contrast, the longer-term drainage and deeper water level at the drained
24 site resulted in the replacement of mosses with vascular plants (shrubs) at the hummocks and lichen at
25 the hollows leading to the highest CO₂ uptake at the drained hummocks and significant losses at the
26 hollows. The tree NPP (including above- and below-ground growth and litter fall) in 2011 and 2012
27 were significantly higher at the drained site (92 and 83 g C m⁻²) than at the experimental (58 and 55 g C
28 m⁻²) and control (52 and 46 g C m⁻²) sites.

29 We also quantified the impact of climatic warming at all water table treatments by equipping additional
30 plots with open-top chambers (OTCs) that caused a passive warming on average of ~1 °C and

31 differential air warming of ~6 °C at mid-day full sun across the study years. Warming significantly
32 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 of water level with warming across hummocks that resulted in the largest net CO₂ uptake at the warmed
35 drained hummocks. Thus in 2013, the warming treatment enhanced the sink function of the control site
36 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 warming is expected to restore the peatland's original CO₂-C sink function as a result of the shifts in
40 vegetation composition and productivity between the microforms and increased NPP of trees over time.

41 1 Introduction

42 Northern peatland ecosystems have accumulated ~547 Pg carbon (C; 1Pg = 10¹⁵ g) as a result of
43 functioning as a steady but persistent sink throughout the Holocene (Yu, 2012; Tarnocai et al., 2009).
44 The accumulated peatland C stocks equal approximately one third of the global terrestrial soil C pool
45 (Grosse et al., 2011; Ciais et al., 2013). Mid-latitude peatlands in north-west North America are often
46 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 accumulation rates than those of open bogs (Clymo et al., 1998). The C stocks of the western boreal
49 treed bogs may respond differently to warming and drought than those of eastern boreal open fens
50 (Kettles and Tarnocai, 1999), and may lead to an accelerated positive feedback to climate change
51 (Gruber et al., 2004; Limpens et al., 2008; Bhatti et al., 2012; Stocker et al., 2013). Future climatic
52 changes are expected to be severe at mid-latitudes (Vitt et al., 2009; Kettles and Tarnocai, 1999; IPCC,
53 2007) that has a dense coverage (50%) of peatlands (Tarnocai, 2006).

54 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 (autotrophic) and microorganisms (heterotrophic). The sum of GPP (-) and *R* (+) is defined as the net
57 ecosystem exchange (NEE) of CO₂. Net uptake of CO₂ causes assimilation of C in the form of plant
58 biomass and accumulation of C in the form of soil organic matter. The GPP, *R* and NEE of the forest
59 floor are represented by GPP_{ff}, *R*_{ff} and NE_{ff}, respectively. Tree root respiration is represented by *R*_r.

60 The changes in peatland air/soil temperature and water level can change GPP and *R* independently (Ow
61 et al., 2008). Warm and dry conditions in peatlands can either promote CO₂ uptake by enhancing GPP
62 or diminish uptake by limiting moisture (Roulet et al., 2007; Charman et al., 2013) or accelerate CO₂

63 release by enhancing R (Hanson et al., 2000; Davidson and Janssens, 2006; Lund et al., 2010; Ise et al.,
64 2008; Cai et al., 2010). In a dwarf-shrub pine bog, Pihlatie et al. (2010) found that the CO₂ flux peak
65 followed tightly the increase in air and soil temperature, being higher (uptake) on warm, and lower (up
66 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
67 g C m⁻² d⁻¹, respectively, coincident with an average increase in air and soil temperature from 0 °C (late
68 April) to 27 °C (early June). Long-term drawdown of water table in forested bogs significantly increased
69 tree productivity of a Canadian (Lieffers and Rothwell, 1987) and a Finnish peatland (Heikurainen and
70 Pakarinen, 1982; Lohila et al., 2011). For example, in a 35 year old forestry drained (40 cm below-
71 ground at the end of study) pine bog, a very high NEE of -871 ± 100 g C m⁻² yr⁻¹, and a tree
72 productivity of 240 ± 30 g C m⁻² yr⁻¹ were reported by Lohila et al. (2011). A sedge fen with water table
73 25 cm below-ground was reported to emit 8.21 g CO₂ m⁻² d⁻¹ (Aurela et al., 2007). In a treeless fen,
74 Riutta et al. (2007) reported average seasonal ecosystem respiration to be 810 g CO₂ m⁻². The ecosystem
75 respiration increased by 18% and 20% due to lowering of water level by 14 cm and 22 cm, respectively.
76 However, the variation in respiration may not always be linked to fluctuation in water table; it may be
77 related more directly to variation in moisture availability. Therefore, water table is a major control on
78 respiration in peatlands, and peat soil moisture is sensitive to lowering of water table (Moore et al.,
79 2006; Parmentier et al., 2009; Moore, 2002).

80 Tree root respiration (R_r) may account for a significant proportion of forest floor respiration (R_{ff}) in
81 forested bogs (Lohila et al., 2011). Therefore, isolating R_r from R_{ff} is critical to attribute forest floor C to
82 various sources of soil respiration and to fill knowledge gaps related to source/sink dynamics (Hanson
83 et al., 2000; Janssens et al., 2001) of boreal treed bogs under a climate change scenario. The isolated R_r
84 can be used to compare net exchange of the forest floor (NE_{ff}) and NPP of a treed peatland with those of
85 an open peatland, provided the major controls (e.g., temperature and water table) remain unchanged.
86 The contribution of R_r to R_{ff} has been quantified using the closed chamber technique in various forest
87 ecosystems. The R_r was separated from R_{ff} by subtracting trenched plots' respiration from control plots
88 at a black spruce forest in Quebec by Hermle et al. (2010) and R_r was found to be 24% of R_{ff} . However,
89 the percentage was found to be higher, at 37% in a subtropical forest of mixed alder Cyprus plantations
90 (Wang et al., 2008) in a similar trenching experiment. Hanson et al. (2000) have reported even higher
91 mean root/rhizomicrobial respiration values of 46% and 60% for forest and nonforest vegetation,
92 respectively. Munir et al. (2014) reported that the growing season R_r increased from 43 g C m⁻² to 94
93 g C m⁻² following ten years of lowered water table (~120 cm) in a boreal bog, but the time scale for the
94 change remains unclear.

95 Continental peatlands are predicted to be drier under warming climatic conditions. The drier conditions
96 may favour some species in peatland communities to yield more NPP than others and, as a result, plant
97 composition will shift, leading to changes in species dominance (Sternberg et al., 1999). In northern
98 bogs, the balance could shift towards a shrub/tree dominated system (Weltzin et al., 2001; Lohila et al.,
99 2011), which in combination with deeper water tables could lead to an increase in both soil (Ise et al.,
100 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 et al., 2005). The shifts in species dominance (coverage) and composition varied between microforms
103 (e.g. hummocks (H) and hollows (W)) in peatlands (e.g. Strack et al., 2006). Likewise, the responses of
104 CO₂ flux and NPP to manipulations in local climate (warming) (Lafleur and Humphreys, 2008; Johnson
105 et al., 2013) and local environment (water table) (Strack et al., 2006; Munir et al., 2014) also varied
106 between the microforms.

107 Warming response studies have used open-top chambers (OTCs) to manipulate ambient temperature to
108 quantify the response of CO₂ exchange in peatlands at northern latitudes. For example, Sullivan et al.
109 (2008) used OTCs in a Greenland rich fen for warming hollow and hummock microforms to evaluate
110 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_{ff} or R_{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 increased up to 4.5 °C and water table dropped to 20 cm. The increase in soil temperature and decrease
116 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 peatlands, many unknowns remain. The CO₂ balance and tree biomass of 10 ombrotrophic treed bog
119 sites in Alberta, were quantified by Wieder et al. (2009), but responses to the major controls of
120 temperature and water table were not evaluated. The response of a bog to decade long water table
121 manipulation was quantified by Munir et al. (2014), but the impact of the warming manipulations
122 remained unexplored. The impact of warming manipulation and microtopography on CO₂ balance
123 responses was also not investigated by Adkinson et al. (2011) in their climatic temperature and short-
124 term drought study on Alberta fens. They also did not estimate the tree productivity of the forested fen
125 nor the contribution of R_r. The CO₂ fluxes at hummock and hollow (or lawn) microforms affected by
126 OTC warming were quantified by Sullivan et al. (2008) in a Greenland fen and Johnson et al. (2013) in
127 an Alaskan fen, but responses to water table fluctuations in the studied open fens remained

128 indeterminate. Therefore, evaluation of peatland tree productivity and net forest floor CO₂ exchange
129 responses to potential warming and water table lowering expected under a climate change scenario is
130 required to fill the knowledge gaps on how a treed continental bog will feedback to the expected
131 changes in climate. Thus, our unique investigation answers this question by quantifying CO₂-C balance
132 of a mid-latitude treed continental bog (having hummock and hollow microforms) subjected to warming
133 and water table manipulations, by adding net forest floor CO₂-C exchange to tree productivity-C uptake.
134 Moreover, we isolate R_r from R_{ff} to better understand proportional response of R_r to potential short and
135 longer-term water table draw down under climate change.

136 Thus, the goal of our research was to quantify the responses of CO₂ flux and NPP to potential climatic
137 warming and subsequent lowering of water table. We used three sites within a continental boreal bog
138 chosen at Wandering River, Alberta, Canada and monitored the CO₂ flux and the plant biomass over a
139 three year study period (2011-2013). Our specific objectives were: 1) to compare CO₂ flux responses at
140 microforms to warming and water level manipulations using the control, experimental and drained sites
141 in an ombrotrophic continental bog, 2) to quantify changes in tree NPP and R_r at the sites in response to
142 the water level manipulations, and 3) to determine changes in ground layer biomass at the microforms
143 and sites in response to the warming and water level manipulations.

144 2 Methods

145 2.1 Study Sites

146 Research was conducted in a dry ombrotrophic bog located near the township of Wandering River,
147 Alberta, Canada, during the growing seasons (1st May to 31st October) of 2011-2013. Three sites were
148 chosen or created having various water levels: an undisturbed water level site (~38 cm below surface)
149 called CONTROL (55° 21' N, 112° 31' W), an experimentally lowered water level site (~35 cm lower
150 than the control) called EXPERIMENTAL (55° 21' N, 112° 31' W), and a 10 year old drained site (~74
151 cm lower than the control) called DRAINED (55° 16' N, 112° 28' W). The creation of the experimental
152 and drained sites has been described in detail by Munir and Strack (2014). Mean precipitation and
153 temperature for the period May to October for this sub-humid continental region are 382 mm and 11.7
154 °C, respectively, based on 30-year (1971-2000) averages (Environment Canada, 2013). Mean
155 precipitation and air temperature for the growing seasons of 2011, 2012 and 2013, measured using an
156 on-site weather station, were 13.1 °C, 13.2 °C, 14.1 °C and 403 mm, 282 mm, 267 mm, respectively.

157 Mean water table position (\pm standard deviation) at the control site (-55.8 ± 21.6) was not different from
158 that at the experimental site (-56.7 ± 20.4) prior to the water table manipulation in 2011 (negative

159 values represented below-ground water table; ANOVA, $F_{1,5} = 0.55$, $p = 0.492$). Mean electrical
160 conductivity (EC, $\mu\text{S cm}^{-1}$) and pH of pore water in the control (16.6 ± 0.7 and 4.1 ± 0.1 , respectively)
161 and experimental (15.2 ± 2.5 and 4.4 ± 0.3 , respectively) sites were also found to be similar (ANOVA,
162 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
163 and had peat depth exceeding 4 m.

164 The Wandering River bog has been classified as a treed low shrub bog with typical mosaic of hummock
165 and hollow microforms (Riley, 2003). In 2011, the control and experimental site microforms were
166 found equally dominated by *Sphagnum* mosses (e.g. *Sphagnum fuscum*) with sparse shrubs (e.g.
167 *Rhododendron groenlandicum*) whereas the drained site hummocks had the greatest coverage of shrubs
168 and the drained hollows had the greatest coverage of lichens. The most abundant type of tree in the bog
169 was black spruce (*Picea mariana*) that constituted $> 99\%$ of the tree stand with $25,766$ stems ha^{-1}
170 consisting of 37% taller trees (> 137 cm height) up to 769 cm high. The black spruce stand had an
171 average canopy height of 168 cm, projection coverage of 42% and basal area of $73.5 \text{ m}^2 \text{ ha}^{-1}$. This
172 description applies to the whole bog having the control, experimental and drained sites (Munir et al.,
173 2014).

174 We chose six hummocks and six hollows from the available microtopography at each of the control,
175 experimental and drained sites. Each of the chosen microforms (plot) was fitted with a $60 \text{ cm} \times 60 \text{ cm}$
176 permanent steel collar having groove at the top and inserted approximately 5-6 cm in to the peat surface
177 (to keep disturbance minimal). Adjacent to each plot, a perforated PVC water well (diameter = 3.5 cm)
178 covered with nylon cloth at the lower 150 cm was inserted into the peat to measure water level
179 manually every time CO_2 flux is measured. Two automatic water level loggers (Levellogger Junior
180 3001, Solinst, Georgetown, Ontario, Canada) were installed at each of the three sites in two randomly
181 selected wells: one at a hummock and the other at a hollow plot. These levelloggers recorded
182 temperature compensated water levels continuously at 20 minute intervals throughout the three growing
183 seasons (except at the drained hollow between May to early July 2011 due to malfunction of the
184 levellogger). A Barologger (Barologger Gold, Solinst; height = 100 cm) was also installed to
185 compensate water levels for barometric pressure changes. These records caught short-term water level
186 fluctuations caused by precipitation events that were not captured by weekly manual measurements. In
187 May 2011, at each site, randomly selected three hummocks and three hollows were equipped with 60
188 degree, 50 cm tall open-top hexagonal chambers (OTCs) of top and basal, side to side dimensions of
189 104 and 162 cm, respectively.

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

200 **2.2 CO₂ flux**

201 We measured CO₂ flux in biweekly campaigns during the growing seasons (May to October) of 2011-
202 2013 using a closed chamber having dimensions 60 cm × 60 cm × 30 cm (length × width × height),
203 made of clear acrylic and corrected for transmittance (88%). The inside of the chamber was equipped
204 with two low speed battery-operated fans to circulate air inside the chamber during and between the
205 measurements. **However, the chamber had no pressure equilibrium port installed.** The instantaneous
206 CO₂ concentration inside the chamber headspace was measured with a portable infrared gas analyser
207 (PP systems, USA, EGM-4) **having a built-in sampling pump operating at a flow rate of 350 ml minute⁻¹**
208 **and compensating automatically for pressure and temperature fluctuations during the measurements.**
209 **The photosynthetically active radiation (PAR) was measured with a quantum sensor (PP systems, USA)**
210 **placed at the top of the chamber. All PAR data collected using the portable PAR sensor was multiplied**
211 **with a factor of 0.88 to obtain corrected values of the PAR inside the chamber accounting for its**
212 **transmittance.** The temperature inside the chamber was measured using a thermocouple thermometer
213 (VWR Int., USA). All of the concomitant measurements were made during a short chamber deployment
214 period (Lai et al., 2012) of 1.75 minutes at 15 seconds intervals. Synchronous to the flux measurements,
215 soil temperatures at the depths of 2, 5, 10, 15, 20 cm were measured with a thermocouple thermometer
216 at all plots. Water table relative to moss surface was measured at each CO₂ flux measurement occasion
217 from a permanently installed well associated with each plot.

218 At each plot, a total of 276 CO₂ flux measurements in 29 campaigns, were made during the daytime of
219 growing seasons (May to October; 2011-2013). Each campaign lasted for about 7 days during which
220 fluxes were measured at 2 to 3 occasions at each plot. At each flux measurement occasion we made a
221 total of five or six measurements: 2-3 full sun, a single layer shroud, a double layer shroud and finally

222 an opaque tarp (for R_{ff}). The chamber was air-flushed for enough time between the measurements to
223 equilibrate the headspace concentration with that of the ambient air.

224 The CO_2 flux measurements when the chamber was covered with an opaque tarp represented R_{ff} . The
225 R_{ff} represents only forest floor respiration (ground-layer above-ground biomass respiration + soil
226 respiration + root respiration (shrubs + herbs + trees)). GPP_{ff} was determined as the difference between
227 NE_{ff} and R_{ff} . Negative values indicate an uptake of CO_2 by the ecosystem. [The \$NE_{ff}\$ was calculated](#)
228 [using the exponential change in chamber headspace \$CO_2\$ concentration \(Kutzbach et al., 2007\)](#)
229 [regressed with time, as a function of volume, pressure and air temperature inside the chamber,](#)
230 [according to the ideal gas law. The exponential regression was applied following Munir et al. \(2014\)](#)
231 [because covering the soil and vegetation can manipulate the spontaneous \$CO_2\$ fluxes across soil-](#)
232 [vegetation-air continuum \(Hanson et al., 1993; Davidson et al., 2002; Denmead and Reicosky, 2003;](#)
233 [Kutzbach et al., 2007\) likely due to suppression of natural pressure fluctuations \(Hutchinson and](#)
234 [Livingston, 2001\) and possible alteration in turbulence between measured intervals \(Hutchinson et al.,](#)
235 [1993\). Therefore, the \$CO_2\$ fluxes determined using linear regression likely result in underestimation of](#)
236 [fluxes under closed chamber environment \(Kutzbach et al., 2007\). The linear fluxes compared with the](#)
237 [exponential fluxes have been found to be up to 40% lower over chamber closure time of only two](#)
238 [minutes \(Kutzbach et al., 2007\).](#)

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

246 2.2.1 Seasonal CO_2 flux modeling and validation

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

$$251 \quad GPP_{ff} = \frac{PAR \times P_{max}}{PAR + k} \times e^{\left[-0.5 \times \left(\frac{WL - WL_{opt}}{WL_{tol}}\right)^2\right]} \times e^{\left[-0.5 \times \left(\frac{T - T_{opt}}{T_{tol}}\right)^2\right]} \quad (1)$$

252 where P_{\max} denotes the potential maximum rate of GPP_{ff} ($g\ CO_2\ m^{-2}\ d^{-1}$) not constrained by water level
253 and/or temperature, and k represents the PAR level at which half of the P_{\max} occurs. The WL represents
254 water level (cm), WL_{opt} and WL_{tol} are parameters in a GPP_{ff} Gaussian response to WL when GPP_{ff} is
255 optimum, and the width of the curve, respectively. The T denotes soil temperature at 5 cm deep ($T_{soil\ 5cm}$;
256 $^{\circ}C$), T_{opt} and T_{tol} are parameters in a GPP_{ff} Gaussian response to T when GPP_{ff} is optimum, and the width
257 of the curve, respectively. The GPP_{ff} model parameters (standard errors), r^2 values, and standard errors
258 of the estimates at the control, experimental and drained microforms are presented in Appendix A.

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

$$261\ R_{ff} = a \times T + b \times WT + c \quad (2)$$

262 where a , b and c are regression coefficients, and their values for each water level treatment \times warming \times
263 microform type \times year combination are presented in Appendix B.

264 Applying equations (1) and (2), seasonal GPP_{ff} and R_{ff} were estimated for each 20 minute period
265 between 1st May and 31st October of 2011-2013, averaged daily and summed separately for the growing
266 seasons using continuous PAR (LI-190, LI-COR, Nevada, USA, connected to a CR1000 data logger,
267 Campbell Scientific Canada, Edmonton, AB), WL (Levellogger Junior, Solinst, USA) and $T_{soil\ 5cm}$ (Onset
268 HOBOware Pro, MA, USA) measurements made on site. The seasonal NE_{ff} was calculated by adding
269 seasonal estimates of GPP_{ff} and R_{ff} . Because some environmental variables were missing for first 5 days
270 of May 2011 and first 21 days of May 2012, they were filled by assuming that the first measured value
271 was representative of the whole missing period. The field measured values of GPP_{ff} and R_{ff} were
272 compared with the model predicted values obtained using SPSS 21.0. Validation of the models showed
273 excellent agreement between the measured and the modeled values (Fig. 1).

274 2.2.2 Tree root respiration

275 To isolate R_r from R_{ff} , a trenching method was used following Wang et al. (2008). From the available
276 microtopography adjacent to the regularly monitored flux plots, we chose an additional eight hummocks
277 and eight hollows at each of the control and drained sites, and a fewer four hummocks and four hollows
278 at experimental site (due to its smaller area). Each microform plot had an area of 60 cm \times 60 cm. At all
279 sites, half of the chosen microform types were incised around up to a depth of 30 cm and wrapped with
280 a thick polythene sheet to prevent root ingrowth, while disturbance was kept minimal. The other half of
281 the microform plots were left intact (having all tree roots) to quantify the respiration rate difference
282 from those of trenched (having minimal tree roots) plots. All of the plots were kept free of surface
283 vegetation during the trenching experiment in the growing season of 2012 so that R_r could be estimated

284 by difference without the additional complicating factors of differences in autotrophic respiration
285 between plots due to slight difference in vegetation (Wang et al., 2008). The CO₂ emissions from all
286 plots were measured on average weekly using the same instruments and chamber (with opaque shroud)
287 used for the measurement of NE_{ff}.
288 The plots were trenched in early May 2012 while respiration measurements were carried out in July-
289 September 2012. While the trenching is used to separate R_r from R_{ff} , it also adds fresh litter to the peat
290 that can add to the initial heterotrophic soil respiration. However, it has been assumed in trenching
291 experiments that the trenched roots die off within a short time and that afterwards the measured R_{ff} can
292 solely be attributed to heterotrophic soil respiration (Hanson et al., 2000; Hermle et al., 2010; Wang et
293 al., 2008). Trenching immediately disrupts the supply of recent photosynthates to the roots, and
294 mycorrhiza and associated bacteria that suffer from the lack of labile C. In trenching experiments
295 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 cycle, as over such a long period there is the possibility of reinvasion of roots into the previously root-
299 free 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_{ff} while
301 investigating R_r to better understand and separate the contribution of various processes to shifts in R_{ff}
302 following drainage.

303 **2.3 Biomass and tree productivity**

304 **2.3.1 Ground-layer biomass**

305 At the end of our field work in October 2013, we collected the ground-layer biomass samples from
306 triplicate of each microform type at each of the three sites. The above-ground biomass samples were
307 collected by clipping duplicate representative quadrats (each measuring 10 cm × 10 cm) adjacent to
308 each of the ambient plots, and from between the OTC wall and the plot collar from warmed plots. The
309 biomass was clipped (using sharp scissors) at the base of capitulum at 1 cm below moss surface
310 following Loisel et al. (2012). The below-ground biomass samples were collect by soil coring (using a
311 serrated saw) to 20 cm depth only, due to difficulty in collecting and processing a large number of
312 samples to deeper depth. The cores were sectioned into 0-10 cm and 10-20 cm depths at the time of
313 sample collection and taken to the Ecohydrology laboratory, University of Calgary, and sorted into fine
314 (< 2 mm) and coarse (> 2 mm) diameter fractions.

315 **2.3.2 Tree biomass and productivity**

316 Three 10 m × 10 m quadrats in the areas directly surrounding the NE_{ff} flux plots at each of the control
317 and drained sites, and one quadrat at experimental site (due to its smaller area) were laid out in May
318 2011. The study areas were not large and these quadrats covered most of the trees in the study areas.
319 The trees were categorized into tall (> 137 cm height) and short (< 137 cm height) for biomass and
320 productivity estimation. The taller trees were measured for their height, diameter at breast height (DBH)
321 and basal diameter (DB), and their biomass was calculated by using an allometric equation (dry biomass
322 = $0.153(\text{tree DBH})^{2.248}$) 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 laboratory, oven dried at 80 °C for 48 hours (until constant weight), and their biomass used to create an
325 an allometric equation (dry biomass = $0.0085(\text{tree height})^{2.2088}$; $R^2 = 0.93$; $p < 0.001$) we generated by
326 regressing height with oven-dried weight. This was used to estimate the biomass of all other short trees.

327 NPP of the tree stand for above-ground parts was estimated for 2011 and 2012, following Szumigalski
328 and Bayley (1996) and Thormann and Bayley (1997). They estimated NPP of an Alberta ombrotrophic
329 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 with height following Macdonald and Lieffers (1990) and Mullin et al. (1992). Summation of tall and
334 short tree biomass increments for a year represented incremental biomass of the tree stand for above-
335 ground parts of trees for that year. To account for litter, an additional 17% was added to this
336 summation. The new summation represented NPP for above-ground parts of the tree stand (Szumigalski
337 and Bayley, 1996). We did not measure incremental biomass of the below-ground parts of trees due to
338 the desire to limit disturbance to our research sites and allow for future monitoring. Therefore, we used
339 an allometric equation (tree root biomass = $0.222 * \text{tree above-ground biomass}$) generated by Li et al.
340 (2003) for estimating the incremental biomass of the tree roots. We did not measure tree productivity
341 for 2013, instead used 2012 productivity values to calculate NEE for this last year of the study.

342 **2.4 CO_2 -C balance ($NE_{ff} + NPP - R_r$)**

343 To calculate CO_2 -C balance, the NE_{ff} ($-GPP_{ff} + R_{ff}$) and NPP (incremental tree biomass of above-ground
344 and below-ground parts of tree stand + stand litter) in term of mass of C were added together separately
345 for the sites and the growing seasons (May 1 to October 31) of 2011-2013. The R_r was excluded to
346 avoid double counting as incremental biomass of below-ground parts of the tree stand already
347 accounted for R_r . Assuming that the dry biomass has a C content of 50%, the CO_2 -C balance equation
348 for the treed bog sites is as:

349 $NEE = NE_{ff} + IC_{tree_ag} + IC_{tree_bg} + L_{tree} - R_r$ (3)

350 where NEE denotes Net Ecosystem Exchange, NE_{ff} represents net exchange of the forest floor, IC_{tree_ag}
351 and IC_{tree_bg} represent incremental C from biomass growth of the above-ground and below-ground parts
352 of the tree stand, respectively, L_{tree} is tree litter production and R_r is tree root respiration. We estimated a
353 seasonal value of R_r by determining it as a proportion of R_{ff} based on instantaneous measurements and
354 then estimating it as this proportion of the modelled seasonal R_{ff} . Seasonal CO_2 fluxes at hummocks and
355 hollows were upscaled by multiplying mean estimated growing season CO_2 exchange by their
356 respective coverage of 56 and 44%, 55 and 45%, and 52 and 48% at the control, experimental and
357 drained sites, respectively (Table 4).

358 **2.5 Data analysis**

359 To estimate treatment effects on instantaneous CO_2 flux components (GPP_{ff} , R_{ff} , NE_{ff} , R_r , NE_{ff} without
360 R_r) we used separate linear mixed-effects models (SPSS 21.0) with CO_2 flux component as the response
361 variable, and water level treatment, warming (OTC), microtopography and year as fixed effects. Since
362 the same plots were measured in each study season, year was also taken as repeated measures within the
363 same model (Table 3). We used the same fixed effects and repeated measures in all mixed-effects
364 ANOVA models (described below). All two-way, three-way and four-way interactions between fixed
365 effects were also included in the models. We used compound symmetry covariance structure for
366 repeated measures analysis (Jennrich and Schluchter, 1986). A mean value of flux determined at each
367 plot in each growing season was used for all analyses. Mean CO_2 flux components data were normally
368 distributed in all years (Kolmogorov-Smirnov Z: 2011, $p = 0.910$; 2012, $p = 0.767$; 2013, $p = 0.624$).

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

375 **3 Results**

376 **3.1 Microclimate and environment**

377 At the Wandering River bog air and soil temperatures and precipitation were monitored during the
378 growing seasons (May to October) of 2011-2013. The weather during the study period was warmer by
379 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
380 2013, respectively, than 30 year means at Athabasca, Alberta (meteorological data have been described

381 under “Methods”). The average undisturbed water level at the control, and manipulated water levels at
382 the experimental and drained sites were clearly different at the start of the study period in 2011 at 38
383 cm, 73 cm and 112 cm (below moss surface), respectively. The declining precipitation and rising air
384 temperature from 2011 to 2013 further lowered the water level at all sites and microforms. From 2011
385 to 2013 the water level declined at hummocks by 9 cm, 8 cm and 8 cm and at hollows by 6 cm, 6 cm
386 and 4 cm at the control, experimental and drained sites, respectively. Three and thirteen years after
387 initial drainage, the water levels at the experimental and drained sites were lower than at the control site
388 by on average 36 cm and 82 cm, respectively (Fig. 2).

389 The OTCs resulted in significantly warmer growing season air temperature (T_{air} ; ANOVA, $F_{2, 24} =$
390 215.87 , $p < 0.001$) by an average (\pm SD) of 1.0 ± 0.0 °C at the control, 0.9 ± 0.0 °C at the experimental
391 and 0.8 ± 0.5 °C at the drained site (Table 1) consistently over the three study years. The OTC warming
392 at hollows was also significantly greater than at hummocks (ANOVA, $F_{1, 24} = 4.85$, $p = 0.037$). The
393 increasing T_{air} significantly warmed the growing season soil temperature at 5 cm depth ($T_{\text{soil } 5\text{cm}}$;
394 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
395 experimental and 0.7 ± 0.3 °C at the drained site (Table 1) consistently over the three study years. The
396 rising T_{air} warmed the $T_{\text{soil } 5\text{cm}}$ the least (0.4 ± 0.3 °C) at drained hummocks and the most (1.3 ± 0.2 °C)
397 at the control hollows. Average soil temperature at 30 cm depth ($T_{\text{soil } 30\text{cm}}$) below the OTC equipped
398 plots was not significantly different than that at the same depth at non-OTC plots across all sites
399 (ANOVA, $F_{2, 24} = 0.71$, $p = 0.053$) and microforms (ANOVA, $F_{1, 24} = 0.95$, $p = 0.339$). Diurnal T_{air} and
400 $T_{\text{soil } 5\text{cm}}$ patterns in the OTCs were significantly related to PAR ($R^2 = 0.81$, 0.87 , respectively) across the
401 microtopography at all sites. During mid-day bright sunny conditions the air warming at OTC equipped
402 plots was greater than that at non-OTC plots by averages of 4 °C, 5 °C and 9 °C at hummocks, and by 5
403 °C, 7 °C and 6 °C at hollows in the control, experimental and drained sites, respectively. Similarly, the
404 direct solar loading increased the $T_{\text{soil } 5\text{cm}}$ at the OTC plots greater than at non-OTC plots by averages of
405 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
406 drained sites, respectively (Fig. 2).

407 3.2 Biomass and incremental tree growth

408 3.2.1 Ground-layer biomass

409 The moss biomass at the drained site was significantly lower compared to the control site ($F_{2, 24} = 3.78$,
410 $p = 0.013$), but not different compared to the experimental site ($p = 0.076$), while the control and
411 experimental sites were not significantly different compared to each other ($p = 0.412$; Table 2). This
412 indicates a strong decline of moss biomass with long-term and deeper drainage. The moss biomass were

413 not significantly different across microtopography ($F_{1,24} = 0.10, p = 0.749$) or warming treatments ($F_{1,24}$
414 $= 0.51, p = 0.481$). Also no interaction between the treatments was found.

415 The vascular plant biomass (mostly woody shrubs) at the control and experimental sites was not
416 significantly different compared to each other ($F_{2,24} = 36.79, p < 0.970$), but was significantly lower
417 compared to the drained site ($p < 0.001$; Table 2). Of all the three plant functional groups (moss,
418 vascular, lichen), only vascular plants were significantly affected by warming ($F_{1,24} = 6.83, p = 0.015$)
419 and microform type ($F_{1,24} = 41.99, p < 0.001$). There were interactions of water level with microform
420 leading to significantly greater vascular plant growth at drained hummocks ($F_{2,24} = 33.70, p < 0.001$),
421 and with warming resulting in significantly greater growth at the drained warmed plots ($F_{2,24} = 3.78, p$
422 $= 0.013$), compared to the control and experimental ambient and warmed microforms. There was a
423 significant interaction between water level, microform and warming resulting in significantly greater
424 biomass of vascular plants at the warmed drained hummocks ($p < 0.001$) compared to the control and
425 the experimental ambient and warmed microforms. In fact, the long-term deep water level at hummocks
426 had a significant interaction with warming ($F_{1,24} = 8.72, p = 0.007$) to increase vascular plant growth.
427 The vascular plant biomass at the ambient drained hollows was the lowest of all plots (Table 2).

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

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

441 **3.2.2 Above-ground tree biomass**

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

445 experimental (42 and 39 g C m⁻²) and the control (38 and 33 g C m⁻²) sites ($F_{2, 11} = 6.95, p = 0.011$).
446 There was no significant difference between the control and experimental sites ($F_{2, 11} = 0.87, p = 0.712$).
447 Below-ground incremental tree biomass was estimated using equations given by Li et al. (2003). The
448 tree root productivity was calculated to be 8 and 7 g C m⁻² at the control, 9 and 9 at the experimental,
449 and 15 and 13 g C m⁻² at the drained sites in 2011 and 2012, respectively.

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

459 **3.3 CO₂ fluxes**

460 **3.3.1 Measured CO₂ fluxes**

461 GPP_{max} was significantly affected by water level, microtopography and year, but there was no direct
462 significant effect of OTC warming on GPP_{max} (Table 3). The GPP_{max} at the control (-15.4 g CO₂ m⁻² d⁻¹)
463 and drained (-12.8 g CO₂ m⁻² d⁻¹) sites were not significantly different from each other but were
464 different from that at the experimental site (-7.8 g CO₂ m⁻² d⁻¹). There was a higher GPP_{max} at
465 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
466 significant interaction with each other as well as interactions each individually with water level. The
467 GPP_{max} in 2011 and 2012 were not significantly different from each other but from the highest value
468 that occurred in the warmest 2013. Year had significant interactions individually with water level
469 leading to higher GPP_{max} at the control site by 2013; with microform increasing GPP_{max} to -21.2 g CO₂
470 m⁻² d⁻¹ at hummocks by 2013; and with warming, increasing GPP at warmed but not unwarmed plots by
471 2013. Although OTC warming did not have a significant effect directly on productivity, there was a
472 significant interaction with water level, microform and year resulting in significantly higher
473 productivity (-25.8 g CO₂ m⁻² d⁻¹) at the warmed drained hummocks in 2013.

474 R_{ff} was significantly affected individually by all four study factors; water level, microtopography, OTC
475 warming and year (Table 3). The R_{ff} at the control (13.1 g CO₂ m⁻² d⁻¹) and experimental (14.5 g CO₂ m⁻²
476 d⁻¹) sites were not significantly different from each other but were lower compared to that at the

477 drained site ($16.9 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$). The R_{ff} was significantly different between hollow ($16.9 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$)
478 and hummock ($14.2 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) microforms, and between ambient ($13.5 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) and warmed
479 ($16.7 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) plots. The R_{ff} in 2011 ($14.3 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) and 2013 ($14.7 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) were not
480 significantly different from each other but from the highest ($16.3 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) that occurred in the first
481 drier than average year 2012. There was an interaction between microform and year leading to
482 significantly higher emissions at hollows ($16.8 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) in 2012. Warming had a significant
483 interaction with microform and year resulting in significantly higher R_{ff} at warmed hollows in 2012
484 ($19.1 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$). The significantly greater emissions were likely due to the significantly higher
485 contributions of R_r (5.03 and $6.80 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) to R_{ff} at the experimental and drained hollows,
486 respectively, compared to $1.51 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ at the control hollows. The R_r at the drained hummocks
487 ($3.3 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) was not significantly different compared to that at the experimental hummocks (3.4
488 $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$), but significantly different compared to that at the control hummocks ($4.3 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$).

489 NE_{max} (including R_r) was significantly affected individually by water level, microtopography, OTC
490 warming and year, and all four interactively (Table 3). All sites were significantly different from each
491 other: the control site forest floor was a sink of $1.4 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ while the experimental and drained
492 sites were sources of 6.5 and $4.1 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$, respectively. There was a significant interaction of water
493 level with microform resulting in net emissions at experimental hollows ($10 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) and drained
494 hollows ($9.8 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) compared to net uptake at the control microforms (hollows = $-1.1 \text{ g CO}_2 \text{ m}^{-2}$
495 d^{-1} ; hummocks = $-1.8 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) and the drained hummocks ($-1.5 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$). The water level
496 also had a significant interaction with warming leading to net emissions from warmed plots at the
497 experimental site ($10.2 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) and the drained site ($4.2 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) compared to net uptake at
498 the ambient control plots ($-2.1 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$), while warmed plots had significantly higher emissions
499 ($\text{NE}_{\text{ff}} = 4.5 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) than ambient plots ($1.7 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$). The water level also had a significant
500 interaction with study year with highest net uptake of $-6.3 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ at the control site in 2013, the
501 year not significantly different compared with 2011 and 2012. Subtracting R_r from NE_{max} (to consider
502 the net exchange of the ground layer only), converts the control microforms and drained hummocks to
503 larger sinks of CO_2 , while considerably reduces emissions at the drained hollows and experimental
504 microforms (Table 4).

505 **3.3.2 Modeled CO_2 fluxes (excluding R_r) for growing season (1st May to 31st October)**

506 Based on empirical models (Eqs. 1 and 2), in 2011, the ground layer at the control site was a sink of 42
507 $\text{g CO}_2\text{-C m}^{-2}$, while the drained and experimental sites were large sources of 118 and $72 \text{ g CO}_2\text{-C m}^{-2}$,
508 respectively (Table 4). In 2012 and 2013, the ground layer at the control site was a reduced $\text{CO}_2\text{-C}$ sink
509 of 24 and 30 g m^{-2} , respectively; the drained site was a reduced $\text{CO}_2\text{-C}$ source of 106 and 96 g m^{-2} ,

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

512 In 2011, OTC warming of the forest floor microforms converted the control site to a greater CO₂-C sink
513 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
514 source of 177 g m⁻². Across the study years, warming of the microforms at the control and drained sites
515 on average increased the uptake of carbon (Table 4). In contrast, warming at the experimental site on
516 average enhanced CO₂ emissions much higher than uptake and resulted in net larger release of CO₂ to
517 the atmosphere. The highest emissions at the experimental and drained hollows were largely due to a
518 substantial contribution by R_r. Averaged across years, exclusion of R_r from NE_{ff} makes the control site a
519 greater sink and experimental and drained sites a smaller source of forest floor CO₂ (Table 4, Fig. 4).

520 **3.4 CO₂-C- balance (NE_{ff} + NPP - R_r)**

521 To calculate the final balance of CO₂ fluxes and tree biomass productivity, we added seasonal estimated
522 NE_{ff} (-R_r) to estimated tree incremental growth (above and below-ground) and tree litter production. We
523 estimated the CO₂-C balance separately for the three growing seasons of 2011-2013. The control site
524 was a larger sink (± SD) of 92 (± 12) g C m⁻² in 2011 than that of 70 (± 10) and 76 (± 38) g C m⁻² in
525 2012 and 2013, respectively. The experimental site was a progressively increasing source of 14 (± 5),
526 57 (± 44) and 135 (± 45) g C m⁻² in 2011, 2012 and 2013, respectively. On the other hand, the drained
527 site was a progressively declining source of 26 (± 14), 23 (± 15) and 13 (± 2) g C m⁻² through 2011-
528 2013, respectively. OTC warming of microforms consistently increased uptake at the control site by -
529 13, -19 and -6 g C m⁻² from 2011 to 2013, respectively. The warming also converted the drained site to
530 a sink of C by 34, 52 and 71 g C m⁻² in 2011, 2012 and 2013, respectively. In contrast, the warming
531 enhanced emissions at the experimental site resulting in losses of 105, 100 and 10 g C m⁻² through the
532 study years, respectively. In all cases, as warming was not applied directly to the trees any impact on
533 their growth could not be included in the study. The warming treatment overall increased the CO₂-C
534 uptake at hummocks and enhanced the emissions at hollows. Averaged across the study years, the
535 warming interacted with deeper and longer drainage to restore the peatland's original CO₂-C sink
536 function (Fig. 5).

537 **4 Discussion**

538 This study estimated the CO₂-C balance of a sub-humid, continental treed bog by combining the C
539 exchange values derived from modeled CO₂ flux and tree productivity, separately for the growing
540 seasons (May to October) of 2011, 2012 and 2013. The control site in this bog was a growing season
541 sink of 92, 70 and 76 g C m⁻² along years from slightly wetter and warmer to drier and warmer than

542 average, respectively (Table 4). Depending on the length of time since fire, Wieder et al. (2009)
543 reported that the ombrotrophic bogs in the same region represented an annual CO₂ sink of 120 to 220 g
544 C m⁻² and thus our values are slightly below this range. Within the same boreal region of northern
545 Alberta as the present study, Adkinson et al. (2011) also reported net growing season CO₂ uptake across
546 three study years of -110 and -35 to -154 g C m⁻² at poor fen and rich fen sites, respectively, and thus
547 our control site sink values are close to the value at the poor fen. However, a higher yearly CO₂
548 accumulation rate of -144 g C m⁻² in a treed fen in the same boreal region is reported by Syed et al.
549 (2006).

550 Methane (CH₄) is also an important component of the C balance in peatland ecosystems. However,
551 over-all seasonal CH₄-C losses were reported to be 0.34, 0.61 and 0.07 g C m⁻² at our control,
552 experimental and drained sites, respectively (Munir and Strack, 2014). Therefore, the CH₄ fluxes are a
553 minor component of the seasonal C balance at our dry continental bog sites. Carbon can also be lost
554 from the system with hydrologic flows. This would include dissolved organic C, particulate organic C
555 and dissolved inorganic C. Given the deep water level and dry conditions in these continental bogs,
556 discharge from the study areas during the growing season was also likely small. This suggests the CO₂-
557 C exchange likely represents the majority of the C balance at these sites.

558 **4.1 Weather effects**

559 Previous findings have revealed that dry and warm summer conditions can reduce net CO₂ uptake in
560 peatlands by enhancing respiration greater than production (Aurela et al., 2007; Cai et al., 2010; Bhatti
561 et al., 2012; Alm et al., 1999). Likewise, the net CO₂ uptake (NE_{ff}) at our control and experimental sites
562 were lower in the drier and warmer growing seasons (2012 and 2013) of the study. This reduction was
563 due to the substantial increase in R_{ff} at the hollows exceeding the combined increase in GPP_{ff} at the
564 microforms especially in 2012 (Table 4). The steady and consistent increase in R_{ff} at the control hollows
565 might be due to the weather-driven moderate decline in water level (Fig. 2) and stressed vegetation
566 (data not presented here) observed at the hollows. However, the abrupt increase in R_{ff} noticed at the
567 experimental hollows might be due to the influence of experimental lowering of water table negatively
568 affecting hollow vegetation more than adjacent hummocks. In contrast, there was only a minor
569 fluctuation in GPP_{ff} or R_{ff} at the drained site in 2012 and 2013 compared to 2011, and thus stability in
570 net CO₂ exchange at this long-term drained site could be due to the dominance of vascular ground-layer
571 vegetation, as opposed to the control and short-term drained sites having greater coverage of mosses
572 (Fig. 3, Table 2, 3).

573 **4.2 Water table manipulation effects**

574 The one to three years of water table drawdown, converted our bog site forest floor (excluding R_f) from
575 a sink of 42, 24 and 30 g C m⁻² in 2011, 2012 and 2013, respectively, to a progressively larger source of
576 72, 112 and 189 g C m⁻² in 2011, 2012 and 2013, respectively. A net loss of CO₂-C in response to a
577 short-term disturbance has been reported by Laiho (2006) in a bog and Chivers et al. (2009) in a fen
578 ecosystem. The 11-13 years of deeper water level also showed a net loss that was higher in 2011 (118 g
579 C m⁻²) and declined slightly through the later years (106 and 96 g C m⁻² in 2012 and 2013, respectively).
580 The drained and experimental sites had consistently increasing emissions at the hollows and decreasing
581 emissions at the hummocks from 2011 to 2013, although the emissions at the experimental site were
582 highest. These net loss values of CO₂-C at the short and longer-term drained sites compare well with
583 those of other experimentally drained peatlands as reported by Von-Arnold et al. (2005), Cai et al.
584 (2010) and Simola et al. (2012). The rapid decline in water table in the experimental site possibly
585 initiated vegetation desiccation that progressed through the study years. In contrast, the longer-term
586 drainage drove hummock habitat to be more favourable for woody shrubs of higher water use efficiency
587 and longer root system. That was likely why the drained site hummocks had declining net emissions
588 with warming and drying of the growing seasons.

589 **4.3 OTC warming effects**

590 The control site sink strength was enhanced by OTC warming leading to greater CO₂-C uptake as NEE
591 (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
592 from 2011 to 2013, respectively. The lowest sink differential (warmed – ambient) of 6 g C m⁻² was
593 noticed in the warmest and driest year 2013 similar to the findings of Aurela et al. (2007) and Lafleur
594 and Humphreys (2008). They also reported that increased growing season temperature enhanced GPP_{ff}
595 but extreme seasonal temperature reduced the GPP_{ff} and accelerated R_{ff} in a sub-arctic fen. The increase
596 in GPP_{ff} and/or R_{ff} has also been reported by Sullivan et al. (2008) in a Greenland rich fen and Weltzin
597 et al. (2001) in bog mesocosms, both in disagreement with Johnson et al. (2013) who reported that there
598 was no consistent effect of OTC warming on the CO₂ flux components because of subtle warming. At
599 our short-term drained (experimental) site, the OTC warming greatly accelerated emissions, causing
600 differential increases of 105, 100 and 10 g CO₂-C m⁻² from 2011 to 2013, respectively (Table 4). An
601 abrupt differential increase in the first year of water table drawdown could be due to an accelerated
602 microbial decomposition of easily decomposable substrate (Keller and Bridgham, 2007; Cai et al.,
603 2010) due to the limiting capillary rise to the drying moss (Waddington and Price, 2000) and extremely
604 stressed vegetation observed in the first two years of warming treatment. However, our long-term
605 drained site had 13 years of transitioning to a habitat favourable for the drought resistant vascular
606 vegetation. A peatland forest floor subjected to long-term deeper drainage developed drought resistant

607 vascular vegetation and trees with deeper root system compared to that under shallower water level
608 conditions. The stable increase in the growth of shrubs and trees in the thicker oxic zone can accelerate
609 accumulation rate equal to or exceeding its original productivity before forestry drainage (Hermle et al.,
610 2010; Lohila et al., 2011). Thus our drained site microforms equipped with OTCs, responded with
611 consistently increasing differential NEE of -34, -52 and -73 g C m⁻² in 2011, 2012 and 2013,
612 respectively. Thus, warming led to greater CO₂ uptake. Our findings together with those of others (e.g.
613 Bubier et al., 2003; Aurela et al., 2007; Sullivan et al., 2008; Weider et al., 2009; Lohila et al., 2011)
614 demonstrate the critical interaction of temperature with wetness for GPP_{ff} and R_{ff} response as either of
615 the factors alone could not illustrate the overall growth response of bog vegetation under changing
616 microclimatic and environmental conditions.

617 **4.4 Microform effects**

618 Peatland microforms have been reported to respond with different magnitudes and in different
619 directions to changes in water table, warming, and other climatic and environmental conditions. For
620 example, Waddington and Roulet (2000) reported significantly greater CO₂ uptake at the wetter lawn
621 than that at the drier ridge in an eccentric raised bog in Sweden, over two growing seasons. Similarly, in
622 a cool temperate fen in Canada, Strack et al. (2006) demonstrated higher GPP_{max} at drained hollows
623 than that at drained hummocks in contrast to the control microforms and speculated that the persistently
624 lowered water tables would result in flattening of the peatland microtopography. Contrastingly, in this
625 study in a dry continental treed bog in Alberta, we found that after thirteen years of deepest drainage
626 treatment the GPP_{max} and GPP_{ff} were in fact the highest at drained hummocks, increasing from cooler
627 2011 to warmer 2013. Conversely, R_{ff} and R_r were the highest at the experimental and drained hollows,
628 also increasing towards warmer 2013. Interestingly, the CO₂ uptake was even higher at the warmed
629 drained hummocks, while CO₂ release was also even higher at the warmed drained hollows and
630 experimental microforms compared to the ambient microforms at these sites (Fig. 4, Table 4). The
631 significantly increased GPP_{max} at ambient and even higher at warmed drained hummocks were probably
632 due to enhanced growth and greater biomass of vascular vegetation (shrubs; Table 2, Fig 3).
633 Conversely, replacement of most of the moss (dominantly *Sphagnum*) biomass by lichens at ambient
634 and warmed drained hollows led to the measured reduction in GPP_{max} and GPP_{ff} (Fig. 3, Table 2, 4).
635 Moreover, drained and experimental hollows were the largest sources of CO₂ in all years. Thus, we
636 expect hummocks to have increasing equilibrium peat depth and hollows to have decreasing
637 equilibrium peat depth as an effect of drainage over the long run. These predictions contradict with
638 those of Strack et al. (2006) due to contrasting microclimatic and environmental conditions of the two
639 studies but corroborate with those of Munir et al. (2014) due to same climatic and environmental

640 conditions. However, these studies together support a general humpbacked relationship of peat
641 accumulation with water level (Belyea, 2009). Therefore, combining the CO₂ dynamics at the ambient
642 and warmed experimental and drained microforms demonstrates that climate forced declining water
643 levels in ombrotrophic continental bogs would result in hummocks growing higher and hollows
644 deepening.

645 **4.5 Effects of water table manipulation and warming on vegetation**

646 Interactions between soil and plant communities have been predicted to play a major role in
647 determining the response of net exchange of CO₂ in peatlands to a climate change scenario (Weltzin et
648 al., 2001; Kardol et al., 2010; Moore et al., 2002) of water level lowering and global warming (Ciais et
649 al., 2013). Ground-layer biomass was significantly affected in response to thirteen years of drainage
650 (water level ~120 cm; $F_{2,36} = 49.42$, $p < 0.001$) and OTC average warming of ~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 The shift in biomass coverage and composition was also different between the microforms ($F_{2,36} =$
653 24.14 , $p < 0.001$); increased biomass at hummocks compared to that at hollows. However, no
654 significant difference in vegetation biomass or composition was found after a three years of drainage of
655 water level ~76 cm ($p = 0.162$). Interestingly, along a gradient of decreasing water level, shrub biomass
656 increased at hummocks, lichens biomass increased at hollows, while moss biomass decreased at all
657 microforms at the continental bog sites. Along the same gradient of decreasing water level, the warming
658 treatment enhanced shrub biomass at the hummocks from 2011-2013, indicated by an interaction of
659 water table × warming × microform × year ($F_{2,36} = 8.24$, $p = 0.001$). The accumulated NPP ratio of
660 below-ground: above-ground shifted from 1.86 before warming to 2.00 after warming, suggesting a
661 shift in C allocation in response to warming treatment. The three bog functional plant groups (moss,
662 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 Effects of water table manipulation and warming on biomass and NPP**

667 We report above-ground biomass (including ground-layer and canopy-layer) to be within the range of
668 values previously published for bog studies. The published data for ground-layer biomass across 16
669 bogs and above-ground tree biomass across 20 bogs varied quite broadly with means of 1900 g m⁻² (±
670 224) and 2177 g m⁻² (± 2259), respectively (Moore et al., 2002). Our data for above-ground tree
671 biomass (2031 ± 379) fall within the range of published values. However our ground-layer biomass
672 average (1236 ± 130 g m⁻²) is less than 1900 g m⁻² (± 224) reported by Moore et al. (2002) because they

673 drew 110 cm deep peat cores for quantifying below-ground biomass versus our core depth of only 20
674 cm. Therefore, it is likely that we might have underestimated the below-ground biomass particularly at
675 the drained site with up to 120 cm thick oxic zone. However, this still more likely included almost all of
676 the below-ground biomass as Lieffers and Rothwell (1987) could find only 6% of the root biomass
677 below 20 cm depth in a drained bog (water level below 80 cm) in north central Alberta.

678 Although above-ground tree biomass decreased along our gradient of deeper water level, productivity of
679 the trees (measured by determining above-ground incremental tree growth) increased along the same
680 gradient (Table 2, 4). The highest above-ground tree biomass estimated at the control site was due to
681 thinner oxic zone supporting mainly denser stand but smaller diameter trees and higher number of
682 shorter trees. The higher productivity in the drier sites was due to thicker aerated peat and supporting
683 higher availability of nutrients (Paavilainen and Päivänen, 1995). Therefore, trees react almost instantly
684 to changes in the local water table (Linderholm and Leine, 2004), as occurred in the experimental site
685 that showed higher productivity than the control but lesser than the drained site. The response time to
686 reach maximum tree productivity after drainage has been reported to be ~10 years (Seppala, 1969;
687 Linderholm and Leine, 2004) which strongly supports significantly highest productivity at our 10-13
688 years old drained site of deepest water table of ~120 cm. The measured R_t consistently increased at all
689 sites along a gradient of warming year (growing season), but was highest at the experimental site in all
690 years due to readily available substrate and desiccating vegetation at this short-term lowered water level
691 site. Drainage induces significantly higher coverage and biomass of vascular plants that offset some of
692 the loss of CO₂ occurring due to deepening of oxic zone and increasing of decay rates (Ise et al., 2008).
693 Therefore, although our drained site forest floor was always a source of CO₂, warming induced
694 significantly increased ground-layer biomass that shifted this site to be a sink of C. This sink function
695 coupled with higher tree productivity significantly enhanced the sink function of the drained site (Fig.
696 5). Conversely, the dramatic lowering of water table at the experimental site severely destabilized the
697 ecosystem functioning that was further deteriorating with warming treatment along the study seasons
698 (2011-2013). However, the differential emissions (warmed – ambient) were noticed to be declining
699 through the study years, indicating that the bog ecosystem may have been reaching a new equilibrium
700 after an initial stress.

701 **5 Conclusions**

702 In a mid-latitude dry continental treed bog, there was a transitional shift in biomass coverage and
703 composition between the microforms in response to a longer-term water level lowering and OTC
704 warming. In fact, the moss biomass was replaced by vascular plant biomass (mostly woody shrubs) at

705 hummocks and lichen biomass at hollows. The shrub biomass growth was significantly increased in
706 response to a three year OTC warming of $\sim 1^{\circ}\text{C}$ in the longer-term and deeper water level treatment.

707 The deeper water level combined with OTC warming induced enhanced growth of woody shrubs and
708 drove the drained hummocks to become the largest net sink of CO_2 across all sites and microforms.
709 Conversely, the short-term, as well as the longer-term, water level lowering converted the hollows to be
710 the largest net sources of CO_2 . However, the 11-13 years of deeper water level lowering coupled with
711 OTC warming increased the forest floor net uptake of CO_2 exceeding well above the losses via
712 respiration at the drained microforms. The significantly increased tree productivity in response to the
713 longer-term deeper drainage (NPP-C) added to the $\text{NE}_{\text{ff}}\text{-C}$ ($-R_r$) converted the drained site from a
714 moderate C source, to become a sink of C close to the bog's original sink strength (Fig. 5).

715 Averaged across study years, an OTC warming of $\sim 1^{\circ}\text{C}$ (and differential mid-day full sun air warming
716 of $\sim 6^{\circ}\text{C}$) interacted with water level treatment to enhance the sink function of the undisturbed site,
717 enlarge source strength of the experimental site and restore the sink strength of the drained site. This
718 pattern is a strong indicator that climatic warming that drives persistent lowering of water level for
719 longer-term is expected to restore the original sink function of continental treed bogs after an initial
720 short duration of net C losses. We also infer that mid-latitude continental treed bogs are sensitive but
721 [adaptive](#) ecosystems that are expected to respond to climatic warming and drying almost instantly by
722 supporting development of woody roots that penetrate deeper for optimum supply of moisture and
723 nutrients to the newly adapted surface vegetation. Although the deepening of water table initially leads
724 to larger net emissions to the atmosphere, persistent drying and warming transforms the moss habitat
725 (characterized by near surface water level) to vascular plant habitat (characterized by deeper water
726 level) leading to a shift to woody shrubs and trees with deeper root systems. The bog trees adapt better
727 to lower water levels and increase productivity by widening ring width, lengthening leader length and
728 increasing belowground biomass allocation.

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

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

^a All temperatures are mean (± SD). At each site, all the OTC-equipped hummocks ($n = 3$) and hollows ($n = 3$) were instrumented with HOBOS to log OTC warming of air (T_{air}) and 5 cm deep soil ($T_{\text{soil } 5\text{cm}}$). The 30 cm deep soil temperatures ($T_{\text{soil } 30\text{cm}}$) 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_{air} , $T_{\text{soil } 5\text{cm}}$ and $T_{\text{soil } 30\text{cm}}$.

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

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

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

^b $n = 1$, only one quadrat was available due to limited size of experimental site. All data were collected in 2012 and 2013.

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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 CO₂ fluxes at the peatland surface ^a.

| Effect | df | CO ₂ Flux Components | | | | | |
|--|--------|---------------------------------|----------|----------|----------|-------------------|----------|
| | | GPP _{max} | | <i>R</i> | | NE _{max} | |
| | | <i>F</i> | <i>p</i> | <i>F</i> | <i>p</i> | <i>F</i> | <i>p</i> |
| 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 |

965 ^a GPP_{max} and NE_{max} represent GPP_{ff} and NE_{ff} when the photon flux density of PAR was greater than 1000 μmol m⁻² s⁻¹. *R* represents *R*_{ff} (forest
966 floor respiration).

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969 Table 4. Growing season CO₂-C flux estimates (\pm SE; g CO₂-C m⁻²)^a.

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

^a Negative values represent uptake of carbon by the peatland from the atmosphere. The forest floor respiration (R_{ff}) includes tree root respiration (R_r). C_w (NEE warmed - NEE ambient) represents warming induced net ecosystem exchange at site. Growing season represents a period from 1st May to 31 October in all study years.

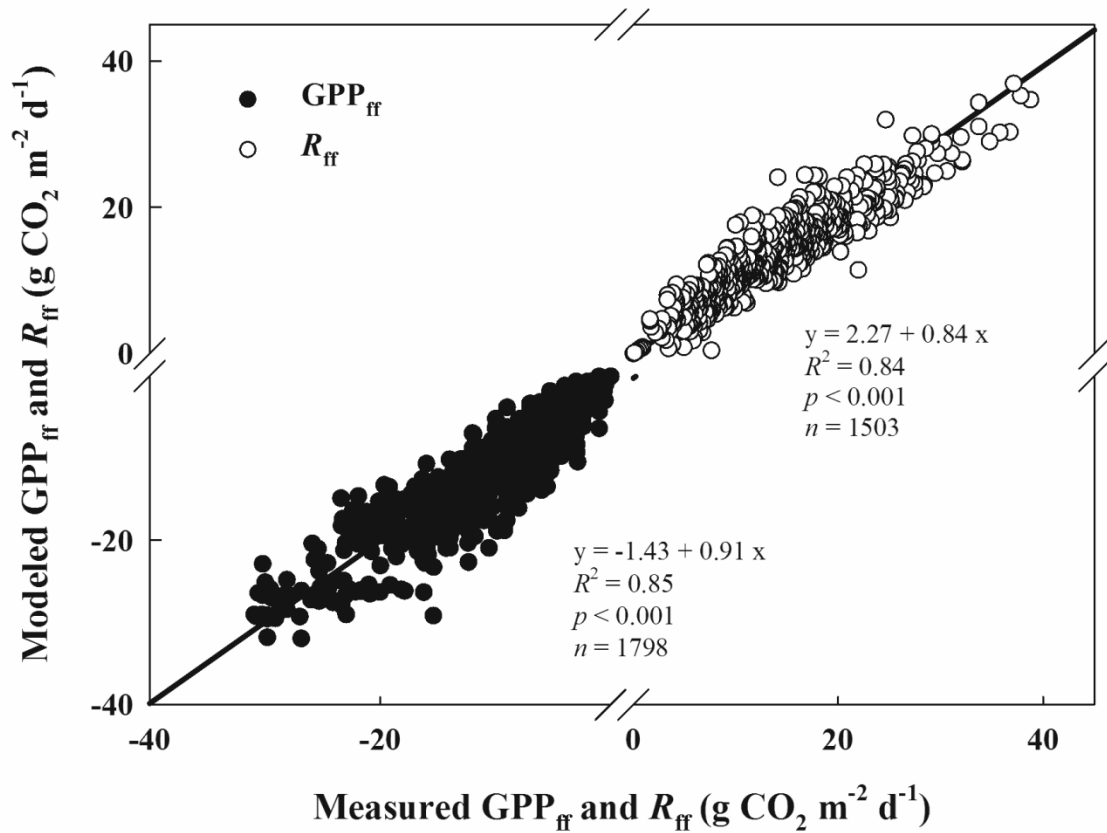
^b NEE is calculated using equation 3 ($NEE = NE_{ff} + IC_{tree_ag} + IC_{tree_bg} + L_{tree} - R_r$). Forest floor carbon exchange was determined by weighting NE_{ff} measured at each microform by the proportion of hummocks and hollows at each site (control = 56% hummocks, experimental = 55%, drained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

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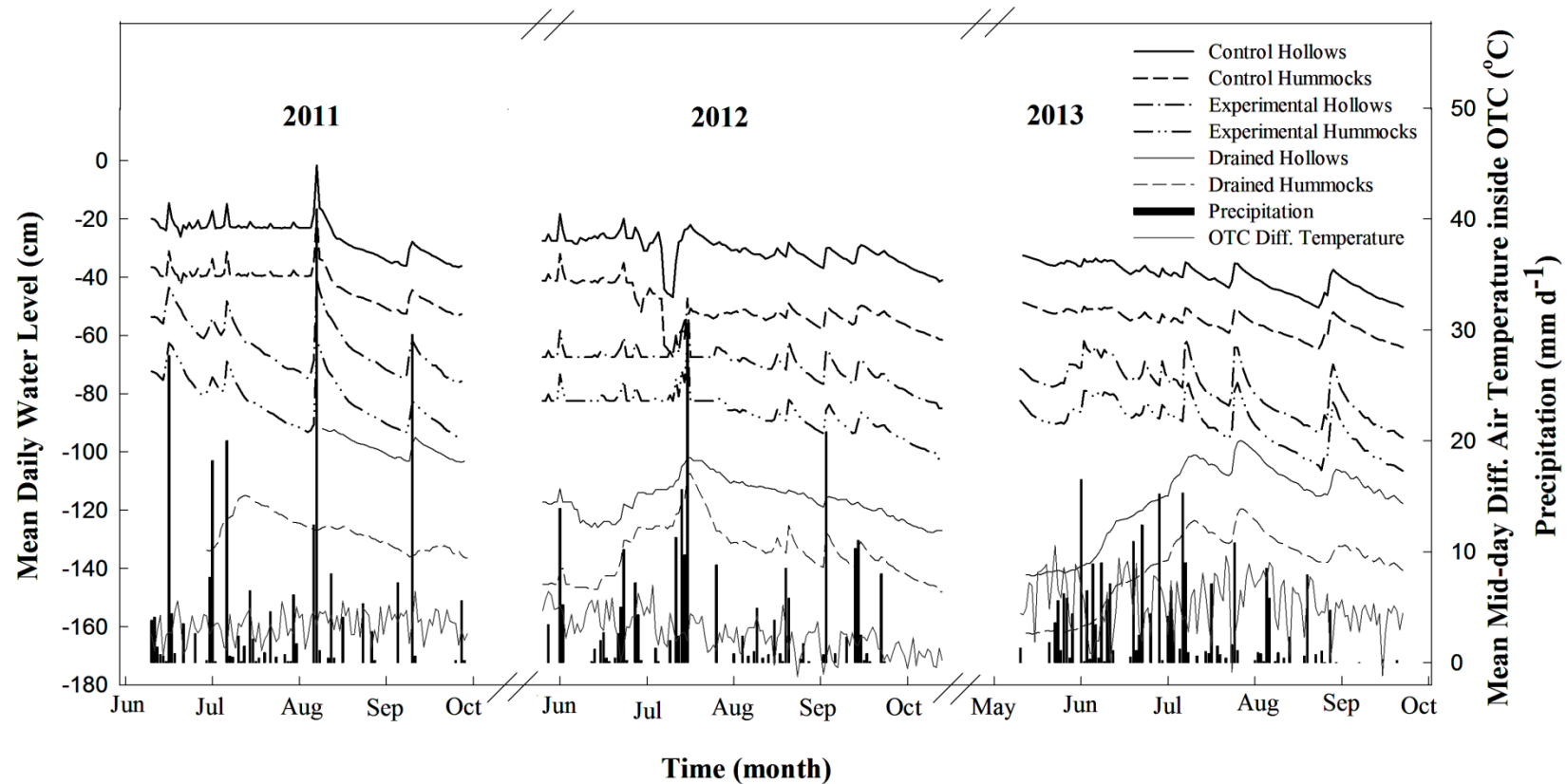
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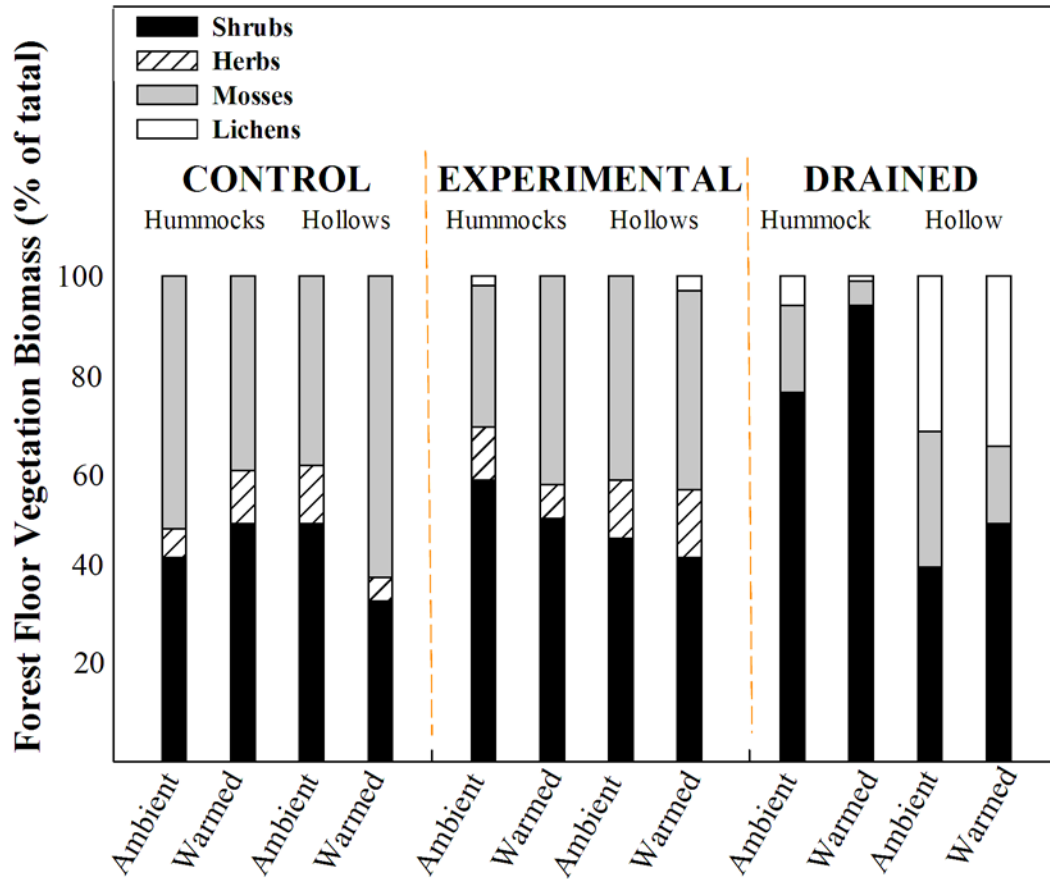
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 975 Figure 1. Goodness of fit (R^2) between modeled and measured GPP_{ff} and modeled and measured R_{ff}
 976 values. The figure presents all data for control, experimental and drained sites for the study years (2011-
 977 2013). Lines represent the 1:1 fit.

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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 levellogger’s malfunction. The cumulative seasonal precipitation during 2012 and 2013 was 30.0% and 35.3% lesser respectively than that in 2011.

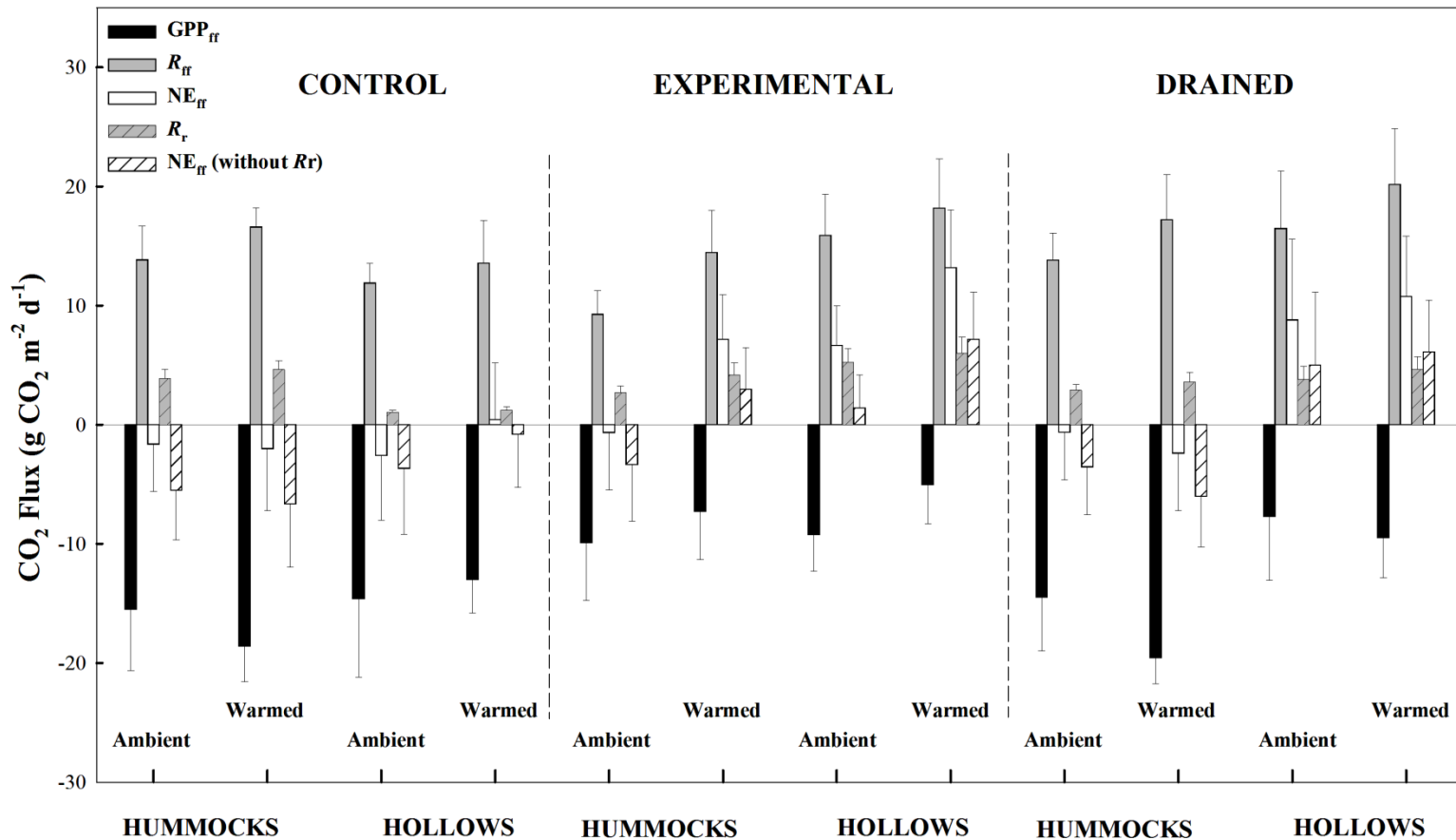


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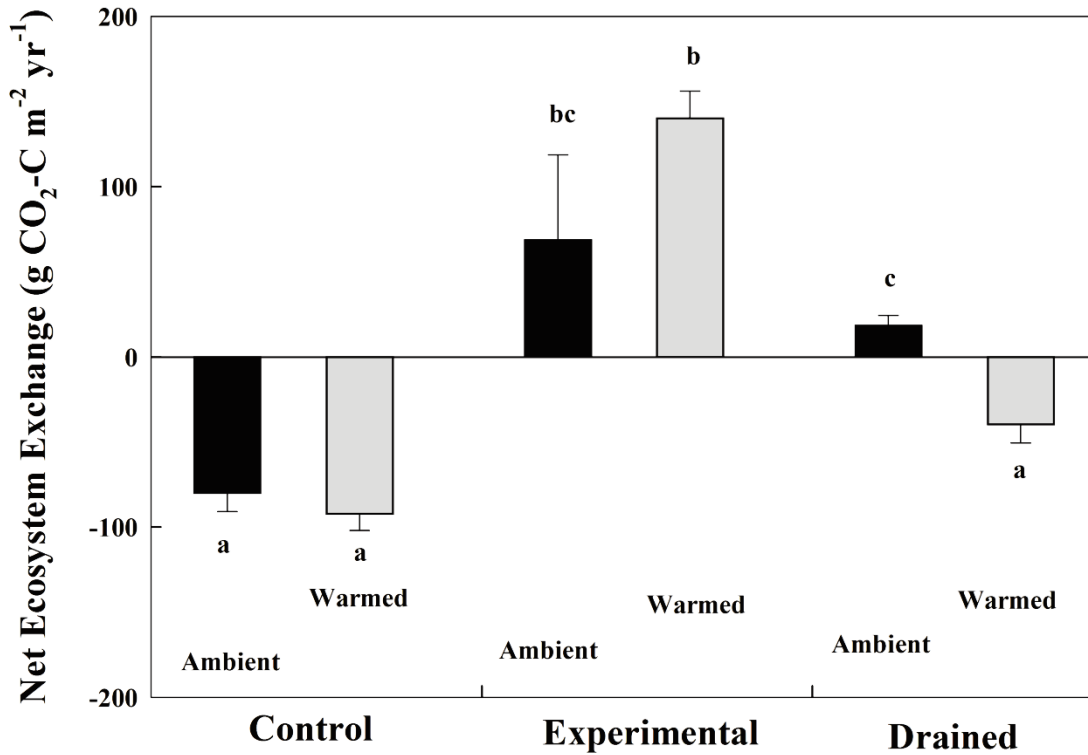
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Figure 3. Relationship between drainage, warming and microform scenario and ground layer above-ground biomass by category as a percentage of total.



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1009 Figure 4. GPP_{max}, R_{fr} and NE_{max} and R_r at control, experimental and drained sites averaged across 2011-2013. NE_{max} (without above
 1010 and below-ground parts of trees) was calculated by subtracting R_r from NE_{max} and represents net exchange of CO₂ of the ground-layer
 1011 vegetation (including peat). Error bars indicate ± standard deviation. Results are from linear mixed-effects model with water table,
 1012 OTC (warming) and microform and year as fixed effects and year as repeated measures. Only averaged fluxes across all study years
 1013 are being graphed as the impacts of treatments were consistent in all growing seasons.



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1015 Figure 5. CO₂-C balance averaged across study years (2011-2013). Error bars indicate ±
 1016 standard deviation. Differences were evaluated between ambient and warmed sites
 1017 (microforms) indicated by letters at each bar. Sites are significantly different at $p < 0.05$ if they
 1018 have no letters in common.

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