Partitioning Forest-Floor Respiration into Source Based Emissions in a Boreal Forested Bog: Responses to Experimental Drought

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Abstract: Northern peatlands store globally significant amounts of soil carbon that could be released to the atmosphere under drier conditions induced by climate change. We measured forest floor respiration (R_{FF}) at hummocks and hollows in a treed boreal bog in Alberta, Canada and partitioned the flux into aboveground forest floor autotrophic, belowground forest floor autotrophic, belowground tree respiration, and heterotrophic respiration using a series of clipping and trenching experiments. These fluxes were compared to those measured at sites within the same bog where water-table (WT) was drawn down for 2 and 12 years. Experimental WT drawdown significantly increased R_{FF} with greater increases at hummocks than hollows. Greater R_{FF} was largely driven by increased autotrophic respiration driven by increased growth of trees and shrubs in response to drier conditions; heterotrophic respiration accounted for a declining proportion of R_{FF} with time since drainage. Heterotrophic respiration was increased at hollows, suggesting that soil carbon may be lost from these sites in response to climate change induced drying. Overall, although WT drawdown increased R_{FF}, the substantial contribution of autotrophic respiration to R_{FF} suggests that peat carbon stocks are unlikely to be rapidly destabilized by drying conditions.

Keywords: forest floor respiration; root respiration; autotrophic respiration; heterotrophic respiration; disturbance; water table; drought; climate change; modeling; soil temperature

1. Introduction

Peatlands contain one of the largest terrestrial carbon (C) stocks, estimated at ~600 Gt C [1], with northern peatland C storage accounting for ~390–440 Gt [1,2]. The large C stock has been accumulated as a result of only a marginal difference, over millennia, between photosynthetic C uptake and loss of C as ecosystem respiration, methane (CH_4) emissions, and water-borne outflows [3]. The stored C is present in the form of highly mineralizable organic C [4,5] protected in water-saturated, anoxic conditions and is highly sensitive to warmer and drier climate [5–7]. Therefore, any increase in carbon dioxide (CO_2) emissions in response to the expected changes in climate has the potential to provide a positive feedback to global warming [4,7–9]. In general, many northern peatlands are expected to be drier under future climates [10,11], and while the response of peatland ecosystem respiration to water-table drawdown has been extensively studied [12–17], controlled field experimentation for partitioning ecosystem respiration into its source-based major components remains largely unexplored [18]. Research is needed to investigate source-based respiration fluxes in relation to potential changes in environmental conditions to improve our understanding of changes in ecosystem C storage or emissions to the atmosphere under climate change scenarios [19,20].

Ecosystem respiration includes the emission of CO_2 to the atmosphere from above and belowground parts of vegetation (autotrophic respiration; R_A), and from microbial decomposition of the soil organic matter including litter (heterotrophic respiration; R_H). The aboveground parts mainly include plant leaves and stems while the belowground parts comprise living roots with their associated mycorrhizal fungi and microbial populations [21,22]. Many northern peatlands are treed [23,24]. When respiration is measured at the ground layer of a treed peatland, this forest floor respiration (R_{FF}) includes respiration associated with tree roots, while respiration of the aboveground tree biomass is excluded. This research partitioned the bulk R_{FF} into source-based above and belowground respiration flux components as: (1) forest floor aboveground autotrophic respiration ($R_{FF\_A\_ag}$) and, (2) belowground shrub + herb (roots) autotrophic respiration ($R_{A\_SH\_bg}$) and belowground tree (roots) autotrophic respiration ($R_{A\_T\_bg}$). Separating the $R_{A\_SH\_bg}$ from $R_{A\_T\_bg}$ is important as specific vascular plant functional types may respire at different rates [25,26] due to the difference in their respective above and belowground productivities [27], and therefore modify the response of R_{FF} to changes in water-table (WT) level and soil temperature at 5 cm depth (T_5) [4,28].

Peatland respiration flux components are highly responsive to environmental changes such as WT level [26,29–32], T_5 [15,33,34], and plant functional (shrubs + herbs, trees) type [35–38]. Therefore, increased atmospheric or soil temperatures and subsequent WT lowering [39,40] may increase soil respiration rates [22] and ultimately alter the peatland C sink or source strength ([37] resulting from increasing atmospheric CO_2 [41]. However, increases in R_{FF} alone do not necessarily indicate a loss of soil C if only autotrophic respiration increases, illustrating the importance of determining the source of respiration and the relative response of each component to changing environmental conditions [42].

Ericaceous shrubs (e.g., *Rhododendron groenlandicum*) are important contributors to ecosystem productivity in many northern bogs [43,44], also making important contributions to ecosystem respiration. The contribution of shrub autotrophic respiration to R_{FF} in a shrub-dominated bog in Patuanak, Saskatchewan, Canada was estimated to be ~75% [45]. A median value of root: shoot ratios estimated from 14 sites in boreal forest was found to be 0.39 [46], suggesting that root respiration is likely to make a significant contribution to measured autotrophic respiration. Overall, root/rhizospheric respiration has been found to account for between 10% and 90% of R_{FF} depending upon vegetation type and season of year [28,47]. As similar controls apply to the above and belowground productivities of shrubs [48,49], therefore, the response of above and belowground respiration to environmental change should be similar [46].

Experimental partitioning of soil autotrophic and heterotrophic respiration components has been attempted using different methods with varying results. For example, methods include application of stable isotopes [50,51], root biomass regression with R_{FF} to determine belowground root respiration [52], and comparison of soils with and without root exclusion to determine tree root respiration [17,28]; however, evaluating the responses of various respiration sources ($R_{FF\_A\_ag}$, $R_{A\_SH\_bg}$, $R_{A\_T\_bg}$, and R_H) to environmental change has not been completed. Moreover, responses may vary between microforms (hummocks and hollows) due to initial differences in WT level, soil properties, and vegetation community [16,17,32]. Therefore, this study focused on partitioning R_{FF} emissions along a microtopographic gradients in order to evaluate responses of each respiration component to short (2 years) and longer term (12 years) water-table drawdown.

Our specific objectives were to:

1. Partition R_{FF} between the aboveground ground-layer autotrophic respiration ($R_{FF\_A\_ag}$), belowground autotrophic respiration of shrubs + herbs ($R_{A\_SH\_bg}$) and trees ($R_{A\_T\_bg}$), and heterotrophic respiration (R_H) across water-table (WT) treatments (control, experimental, drained),

2. Evaluate differences in source contributions to R_{FF} along a microtopographic (hummock, hollow) gradient in a boreal forested bog and how these contributions changed in response to WT treatments, and

3.   Assess the respiration components' responses to the WT and soil temperature at 5 cm depth (T_5) over one growing season.

We hypothesized that experimental WT lowering would lead to increases in all respiration components, with greatest increases at hollows. We also hypothesized that increases in R_H would be greatest at hollows, while hummocks would have greater increases in autotrophic respiration (both above and belowground) and that all components of R_{FF} would have significant positive correlations with depth to WT and T_5.

2. Materials and Methods

2.1. Sites Description and Experimental Design

During the growing season (1 May to 31 October) of 2012, this research was conducted in a forested bog within the southern boreal forest and near the town of Wandering River, Alberta, Canada. Based on 30-year (1981–2010) averages, the mean growing season (May to October) temperature and precipitation for this region are 11.7 °C and 382 mm, respectively [53]. The mean growing season air temperature and precipitation measured during the 2012 study using a meteorological station installed at the study sites were 13.2 °C and 282 mm, respectively.

Within the dry ombrotrophic forested bog, three research sites, CONTROL (55°21′ N, 112°31′ W), EXPERIMENTAL (55°21′ N, 112°31′ W), and DRAINED (55°16′ N, 112°28′ W), were chosen or created (Figure 1). The control was an undisturbed site with a mean WT level of −38 cm whereas the experimental site was created adjacent to the control by ditching around, lowering the mean WT level to 78 cm below surface. One year prior to this study, WT level (± Standard Deviation (SD)) at the control (−56 ± 22 cm) and experimental (−57 ± 20 cm) sites were not different (negative values denote belowground WT; ANOVA, $F_{1, 5} = 0.55$, $p = 0.492$). The drained site (part of the same bog and located 9 km to southwest) was drained inadvertently 12 years prior to the study as a result of a peat harvesting preparation on an adjacent section, and had a mean WT level of ~−120 cm in 2012 (Figure 2).
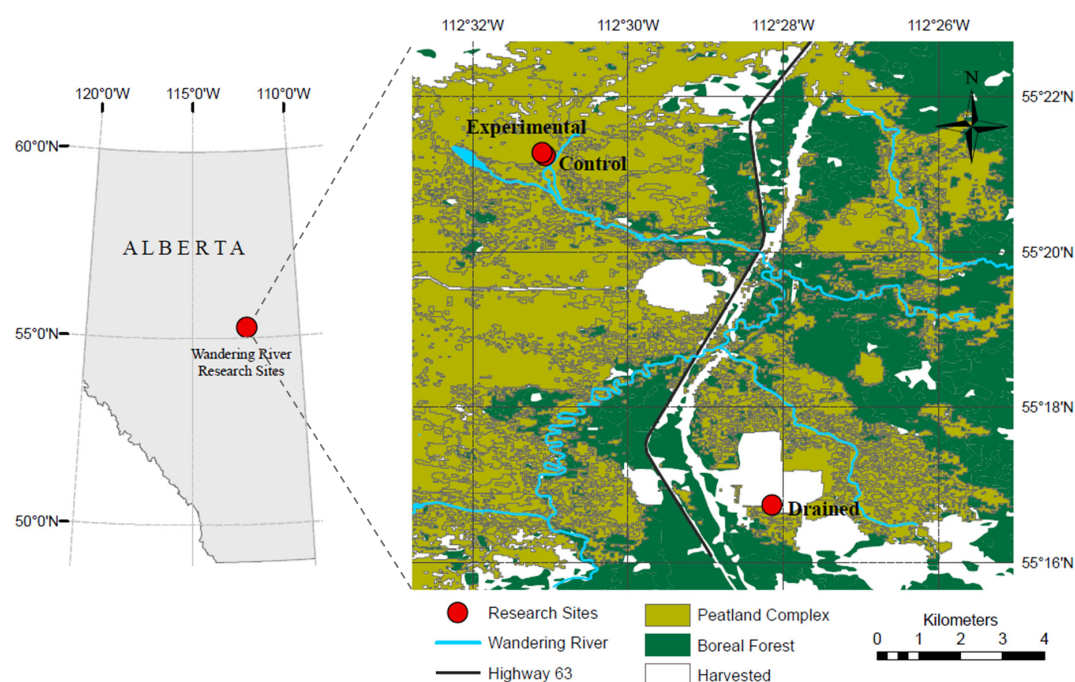

Figure 1. Geographical map of the Wandering River study sites located in a forested peatland complex within boreal forest in Alberta, Canada [54].

Based on plant species indicators, the studied bog was classified as a forested low shrub bog [55] with two distinct microtopographic features: hummock and hollow. One year prior to this study, the control and experimental site microforms had equal coverage of mosses with sparse shrubs, whereas the drained hummocks had the highest coverage of shrubs and the drained hollows had the greatest coverage of lichens [44]. At all sites, black spruce (*Picea mariana* (Mill.) B.S.P.) was the most abundant type of tree constituting >99% of the tree stand, with 25,766 stems·ha^{-1} consisting of 37% taller trees (>137 cm height) up to 769 cm high [44]. The black spruce stand had an average canopy height of 168 cm, projection coverage of 42%, and basal area of 73.5 m^2·ha^{-1} [17]. Trees were generally evenly distributed across the study plots (i.e., not clustered).
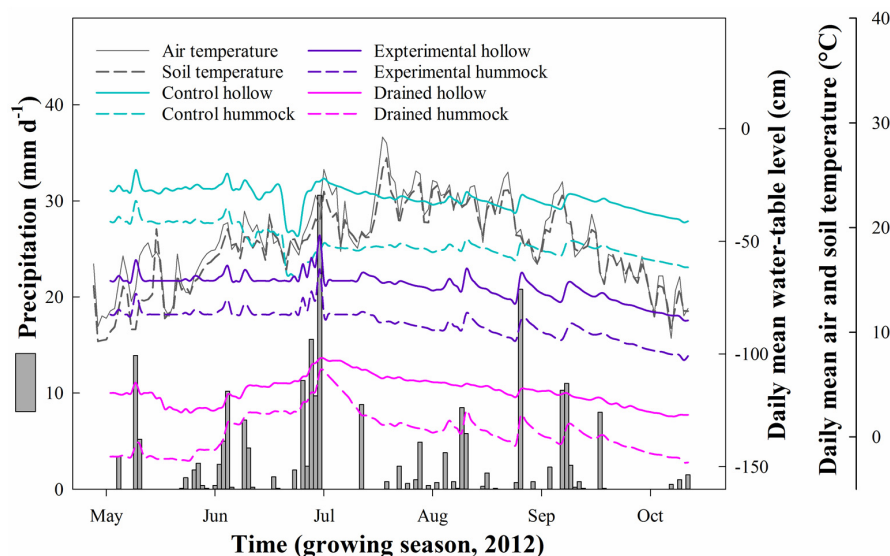

Figure 2. Daily mean site air temperature (°C), soil temperature (°C) at 5 cm depth, total precipitation (mm), representative hollow and hummock water-table (WT) level (cm) over the 2012 growing season (May to October). Note the two *y*-axes on the right side: daily mean WT level, and air and soil temperatures.

Mean (±SD) pH and electrical conductivity (µS·cm^{-1}) of pore water in the control (4.1 ± 0.1 and 16.6 ± 0.7, respectively) and experimental (4.4 ± 0.3 and 15.2 ± 2.5, respectively) sites were similar (ANOVA, pH: $F_{1,5}$ = 2.6, p = 0.166; EC: $F_{1,5}$ = 0.84, p = 0.401) prior to any manipulation. All the study sites had an average peat depth exceeding 4 m, and were underlain by a sandy clay substrate. Because all the study sites were part of the same bog and their initial primary characteristics of vegetation composition, WT levels, and chemistry were similar, their secondary attributes (e.g., respiration rates) were also assumed to be similar prior to WT manipulation.

From the available microtopography, we chose eight hummock and eight hollow microforms at each of the control and drained sites, and four of each microform type at the experimental site (due to its smaller area). In early May 2012, each of the chosen microform plots was fitted with a 60 cm × 60 cm collar having a groove at the top for placing the CO_2 flux chamber. The collar was carefully inserted into the peat surface to a depth of ~5 cm to keep the disturbance minimal [56]. Outside each collar, a Polyvinyl Chloride (PVC) well (length = 200 cm, diameter = 3.5 cm) with perforation and a nylon cloth covering on the lower 150 cm was inserted into a bore-hole drilled to a depth of 150 cm. WT level was manually measured at all the water wells every time CO_2 flux was measured during the growing season of 2012. The WT levels were also monitored during the study period at 20-min intervals using automatic, temperature compensating pressure transducers (Levelogger Junior 3001, Solinst, Georgetown, Ontario, Canada) installed in two randomly selected water wells at each site: one at a hummock and the other at a hollow plot.

2.2. CO$_2$ Flux Measurements

All CO$_2$ flux measurements were made during the day time of the growing season (May to October, 2012) using the same equipment. We used a closed chamber with dimensions 60 cm × 60 cm × 30 cm (width × length × height), made of opaque acrylic and fitted with a low-speed battery-operated fan to circulate air within the chamber headspace during and between CO$_2$ concentration measurements. The chamber had no pressure equilibrium port installed. A portable infrared gas analyzer (EGM-4, PP Systems, Amesbury, MA, USA) with a built-in CO$_2$ sampling pump operating at a flow rate of 350 mL·min^{-1} and compensating for temperature fluctuations within the chamber headspace was used to measure the instantaneous CO$_2$ concentration inside the chamber headspace. The chamber headspace temperature was measured using a thermocouple thermometer (VWR International, Edmonton, AB, Canada). The CO$_2$ concentration and temperature measurements were made every 15 s during a short chamber deployment period [57,58] of 1.75 min. Immediately after the CO$_2$ concentration measurements at a plot, soil temperature at a depth of 5 cm (T$_5$) was measured using a thermocouple thermometer, and the WT level relative to moss surface was manually measured from a permanently installed water well adjacent to the plot. The CO$_2$ flux was calculated from the linear change in CO$_2$ concentration in chamber headspace over time [17], as a function of air temperature, pressure, and volume within the chamber headspace, following the ideal gas law.

2.2.1. Forest Floor Respiration (R$_{FF}$)

Prior to any manipulation at a plot, a CO$_2$ efflux measurement represented forest floor respiration (R$_{FF}$). During a 5-day long R$_{FF}$ measurement campaign in May 2012, we measured the fluxes on four to five occasions in each plot. The measured R$_{FF}$ is divided into major source-based respiration flux components as:

$$R_{FF} = R_{FF\_A\_ag} + R_{A\_SH\_bg} + R_{A\_T\_bg} + R_H, \tag{1}$$

where R$_{FF}$ accounts for forest floor aboveground autotrophic respiration (R$_{FF\_A\_ag}$), belowground shrub + herb and tree autotrophic (rhizospheric) respiration (R$_{A\_SH\_bg}$ + R$_{A\_T\_bg}$, respectively), and soil heterotrophic respiration (R$_H$). At the end of the R$_{FF}$ measurement campaign, we clipped all plots using sharp scissors at the base of capitulum at 1 cm below the moss surface [27,59]. All the plots had their surface carefully cleared of any plant litter. The clipped shrubs + herbs were placed in labelled paper bags, taken to the Ecohydrology Lab, University of Calgary, AB, oven dried at 60 °C for 48 hours and weighed to calculate mean biomass (g·m^{-2}) at each plot at each site.

2.2.2. Partitioning Forest Floor Respiration

Following the R$_{FF}$ measurement campaign, a 5-day long campaign for measuring the post-clipping CO$_2$ emissions from every plot was performed. During the campaign, we measured the emissions on four to five occasions in each plot. At plot level, the CO$_2$ emissions (g·CO$_2$·m^{-2}·day^{-1}) at clipped plots subtracted from R$_{FF}$ (g·CO$_2$·m^{-2}·day^{-1}) represented R$_{FF\_A\_ag}$ (g·CO$_2$·m^{-2}·day^{-1}).

To estimate R$_{A\_T\_bg}$ at hummock or hollow microform at each site, we used a trenching method [17,52]. One half of the instrumented hummock or hollow plots (60 cm × 60 cm) were chosen at each site for the trenching procedure, whereas the other half of the plots were left untrenched. The trenched hummock or hollow plot R$_{FF}$ was not significantly different from those of the untrenched plots at control (ANOVA, Hummock: $F_{1,25} = 0.667$, $p = 0.422$; Hollow: $F_{1,23} = 0.316$, $p = 0.580$), experimental (ANOVA, Hummock: $F_{1,7} = 0.000$, $p = 0.990$; Hollow: $F_{1,7} = 0.605$, $p = 0.466$), or drained (ANOVA, Hummock: $F_{1,23} = 0.041$, $p = 0.841$; Hollow: $F_{1,23} = 0.070$, $p = 0.790$) site. Therefore, in June 2012, we incised around the trenched plots to a depth of 30 cm and installed a thick polythene sheet to prevent root ingrowth while keeping the disturbance minimal. All the trenched and intact, untrenched plots were measured for CO$_2$ emission between July and September, 2012 to quantify the difference in the respiration rate for estimation of R$_{A\_T\_bg}$. The trenching method at this site had already been used at this bog [17].

We did not measure $R_{A\_SH\_bg}$ and calculated it by using regression equations ($y = a + bx$) generated by regressing the aboveground biomass of shrubs + herbs (x) with $R_{FF\_A\_ag}$ (y) following a previous study [52]. We did not sample/measure shrub + herb root biomass (B_{SH_bg}) to avoid disturbance to plots used for ongoing research and instead calculated B_{SH_bg} as: $B_{SH\_ag} \times 0.39$ [46], as previous research found the median root:shoot ratio of shrubs + herbs for 14 data points in boreal forest to be 0.39. Similar factors control net production both above and belowground, and the two rates were found to be related with each other [47]. The generated regression equations were used to determine the ($R_{A\_SH\_bg}$) by substituting B_{SH_ag} with B_{SH_bg} in the equation. The R_H was calculated from Equation (1) once all other components were estimated.

2.3. Seasonal Modeling

Only the measured respiration components (R_{FF}, $R_{FF\_A\_ag}$, $R_{A\_T\_bg}$) during the growing season (May to October) of 2012 were modeled using a multiple linear regression model with T_5 and WT level as:

$$R_{FF} = a \times T_5 + b \times \text{WT level} + c, \tag{2}$$

where a, b, and c are regression coefficients (Table 1). Seasonal R_{FF}, $R_{FF\_A\_ag}$, and $R_{A\_T\_bg}$ were estimated for each 20-min period between 1 May to 31 October 2012, averaged daily, and summed separately for the growing season using T_5 (Onset®, HOBO®, Bourne, MA, USA) and WT level (Levelogger Junior, Solinst Canada Ltd., Georgetown, ON, Canada) measurements made on site. As the environmental variable logs were missing for the 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 R_{FF}, $R_{FF\_A\_ag}$, and $R_{A\_T\_bg}$ were plotted against the model predicted values obtained using SPSS 24.0.0.1. Validation of the models showed excellent agreement between the measured and the modeled values (Appendix A: Figure A1).

The seasonal respiration rates (R_{FF}, $R_{FF\_A\_ag}$, $R_{A\_T\_bg}$) at hummock and hollow microforms were up-scaled by multiplying mean estimated growing season respiration by their corresponding coverage of 56% and 44% at the control, 55% and 45% at the experimental, and 52% and 48% at the drained site, respectively [60]. The seasonal value of $R_{A\_SH\_bg}$ was calculated separately for each microform/site combination by determining it as a proportion of corresponding instantaneous R_{FF} value and then estimating it as this proportion of the modeled seasonal R_{FF}. Seasonal R_H was determined by difference according to Equation (1).

2.4. Statistical Analyses

To test the effects of WT level and microform on R_{FF}, $R_{FF\_A\_ag}$, $R_{A\_SH\_bg}$, and $R_{A\_T\_bg}$, we conducted a repeated, linear mixed-effects model analysis (LMEM; IBM SPSS Statistics 24.0.0.1, IBM corporation, Armonk, New York, USA) with WT level (control, experimental, drained) and microform (hummock, hollow) as predictor variables and R_{FF}, $R_{FF\_A\_ag}$, $R_{A\_SH\_bg}$, or $R_{A\_T\_bg}$ as response variables, including the random effect of plot and repeated effect of time (as the same plots were used sequentially for all the measurements). We also tested the effect of B_{SH_ag} in combination with site and microform on $R_{FF\_A\_ag}$ with random effect of plot using a repeated, LMEM. In this case, non-significant terms were removed from the model one at a time, starting with the highest p-value and the model was re-run until only significant terms remained. In all the LMEMs used in this study, a combined symmetry covariance structure was used. The relationships of WT level and T_5 with R_{FF}, $R_{FF\_A\_ag}$, $R_{A\_SH\_bg}$, and $R_{A\_T\_bg}$ were also tested for their significance using linear regression model fitting where applicable. Differences between regression slopes were tested [61] where applicable.

3. Results

The microclimate of the study sites was monitored over the growing season (May to October) of 2012 and was warmer by 1.4 °C and drier by 79 mm than the 30-year (1981–2010) regional averages

measured at Athabasca, Alberta, Canada. The WT levels at the experimental and drained sites were as much as 36 cm and 82 cm lower than at the control site (Figure 2). In general, as a result of 12 years of drainage, the mosses at the drained hummocks were replaced by shrubs and mosses at the drained hollows were replaced by lichens. Detailed site hydrological responses to the warmer and drier climate at these sites have been reported [17].

Table 1. Fitted model parameters, their values ($\pm$SE), residual standard error (RSE), *p* values, adjusted r^2, and the number of values (*n*) included in the regression analyses for the forest floor respiration (R_{FF}), forest floor aboveground autotrophic respiration ($R_{FF\_A\_ag}$), and belowground autotrophic respiration of tree roots ($R_{A\_T\_bg}$) models (Equation (2)) *.

Site/Microform	Flux	a	b	c	RSE	*p*	r^2	*n*
		Dimensionless			$g \cdot CO_2 \cdot m^{-2} \cdot day^{-1}$			
Control Hummock	R_{FF}	0.52 ± 0.14	-0.47 ± 0.15	-19.90 ± 5.1	1.09	<0.001	0.80	24
	$R_{FF\_A\_ag}$	0.36 ± 0.10	-0.45 ± 0.13	-22.51 ± 5.3	1.16	<0.001	0.67	24
	$R_{A\_T\_bg}$	0.43 ± 0.17	0.25 ± 0.17	7.88 ± 5.1	1.46	0.044	0.17	26
Hollow	R_{FF}	1.08 ± 0.21	-0.29 ± 0.14	-15.74 ± 5.1	2.45	<0.001	0.61	24
	$R_{FF\_A\_ag}$	0.85 ± 0.19	-0.54 ± 0.18	-24.59 ± 5.5	1.55	<0.001	0.75	24
	$R_{A\_T\_bg}$	0.86 ± 0.23	-0.21 ± 0.14	14.80 ± 5.7	2.34	0.002	0.43	22
Experimental Hummock	R_{FF}	0.05 ± 0.10	-0.24 ± 0.11	-15.67 ± 11.8	0.24	0.010	0.77	8
	$R_{FF\_A\_ag}$	0.96 ± 0.50	-0.83 ± 0.57	-86.98 ± 55.9	2.02	0.049	0.58	8
	$R_{A\_T\_bg}$	0.91 ± 0.52	-0.72 ± 0.63	-75.24 ± 61.5	1.24	0.032	0.83	6
Hollow	R_{FF}	2.59 ± 0.80	0.70 ± 0.09	-15.09 ± 13.2	1.59	0.058	0.55	8
	$R_{FF\_A\_ag}$	0.82 ± 1.60	-0.27 ± 0.18	-29.44 ± 10.0	2.56	0.061	0.54	8
	$R_{A\_T\_bg}$	0.94 ± 0.39	-0.69 ± 0.87	-61.08 ± 70.1	2.06	0.021	0.79	7
Drained Hummock	R_{FF}	-0.32 ± 0.16	-1.40 ± 0.20	-167.53 ± 30.9	3.27	<0.001	0.76	24
	$R_{FF\_A\_ag}$	0.93 ± 0.31	-0.49 ± 0.18	-70.88 ± 19.3	2.43	<0.001	0.75	24
	$R_{A\_T\_bg}$	1.69 ± 0.35	0.39 ± 0.64	34.86 ± 89.9	2.41	<0.001	0.79	24
Hollow	R_{FF}	0.79 ± 0.33	-0.58 ± 0.17	-61.70 ± 16.9	2.29	<0.001	0.70	20
	$R_{FF\_A\_ag}$	0.70 ± 0.23	-0.32 ± 0.10	-40.53 ± 10.6	2.15	<0.001	0.56	24
	$R_{A\_T\_bg}$	0.26 ± 0.19	-1.08 ± 0.42	-113.87 ± 46.4	1.28	<0.001	0.77	25

* R_{FF}, $R_{FF\_A\_ag}$, and $R_{A\_T\_bg}$ models were developed for each microform type (*n* = 3) at the control, experimental, and drained sites for the growing season of 2012. a and b are soil temperatures at 5 cm depth and WT level (below-ground) coefficients, respectively, and c is a regression constant. All modeled parameters are significant at α = 0.05.

3.1. Controls on Respiration Flux Components

All the measured component fluxes (R_{FF}, $R_{FF\_A\_ag}$, $R_{A\_SH\_bg}$, $R_{A\_T\_bg}$) were well correlated to T_5 and WT (Figure 3) and therefore the modeled values matched the measured values well (Appendix A: Figure A1). Generally, the highest respiration occurred with warm temperatures and deep WT position.

3.2. Measured Respiration Components

3.2.1. Mean Forest Floor Respiration Rate (R_{FF})

There were significant effects of each of the WT (control, experimental, drained) and microform (hummock, hollow) types on R_{FF} measured in May, 2012; however, their interaction term did not significantly affect R_{FF} (Table 2). The drained site had significantly higher R_{FF} value ($\pm$SE) of 21.0 ± 2.1 $g \cdot CO_2 \cdot m^{-2} \cdot day^{-1}$ compared with those measured at the experimental (13.2 ± 2.5 $g \cdot CO_2 \cdot m^{-2} \cdot day^{-1}$; *p* = 0.042) and control (9.3 ± 2.1 $g \cdot CO_2 \cdot m^{-2} \cdot day^{-1}$; *p* = 0.006) sites that were not different (*p* = 0.455) from each other. Bonferroni pairwise comparisons revealed that the hummocks had overall significantly higher R_{FF} (17.9 ± 1.8 $g \cdot CO_2 \cdot m^{-2} \cdot day^{-1}$) than hollows ($11.2 \pm 1.8$ $g \cdot CO_2 \cdot m^{-2} \cdot day^{-1}$). Comparing microforms across sites (Figure 4) revealed that R_{FF} at

hummocks was significantly different among all sites with highest rates at drained, followed by experimental, and then control, while hollows were not different (p = 0.526) across sites.
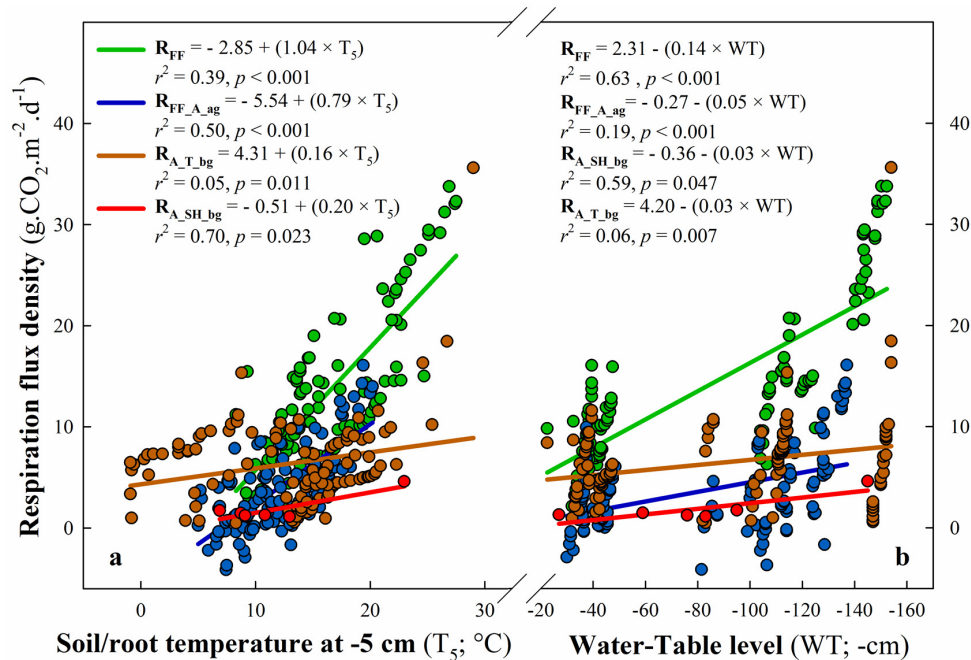

Figure 3. (**a**) Forest floor respiration flux (R_{FF}; $g \cdot CO_2 \cdot m^{-2} \cdot day^{-1}$), aboveground autotrophic respiration flux of forest floor ($R_{FF\_A\_ag}$; $g \cdot CO_2 \cdot m^{-2} \cdot day^{-1}$), belowground autotrophic respiration of shrubs + herbs ($R_{A\_SH\_bg}$; $g \cdot CO_2 \cdot m^{-2} \cdot day^{-1}$), and belowground autotrophic respiration of tree roots ($R_{A\_T\_bg}$; $g \cdot CO_2 \cdot m^{-2} \cdot day^{-1}$) versus soil temperature at -5 cm (T_5) and (**b**) R_{FF}, $R_{FF\_A\_ag}$, $R_{A\_SH\_bg}$, and $R_{A\_T\_bg}$ versus water-table (WT) level, at all sites/microforms. All the respiration components were statistically related to both the T_5 and WT level.

Table 2. Statistical results of repeated, linear mixed effects models. The models tested the fixed effects of site and microform on respiration of forest floor (R_{FF}), aboveground autotrophic respiration of forest floor ($R_{FF\_A\_ag}$), and belowground autotrophic respiration of shrubs + herbs and trees ($R_{A\_SH\_bg}$ and $R_{A\_T\_bg}$, respectively), separately *.

	Flux Component							
Effect	R_{FF}		$R_{FF\_A\_ag}$		$R_{A\_SH\_bg}$		$R_{A\_T\_bg}$	
	F	p	F	p	F	p	F	p
Site	$F_{2,7} = 8.1$	0.015	$F_{2,15} = 4.9$	0.023	$F_{2,12} = 25.3$	<0.001	$F_{2,12} = 6.4$	0.012
Microform	$F_{1,7} = 6.9$	0.033	$F_{1,15} = 10.3$	0.005	$F_{2,12} = 44.4$	<0.001	$F_{2,27} = 2.5$	0.123
Site × Microform	$F_{2,7} = 3.5$	0.090	$F_{2,15} = 4.1$	0.037	$F_{2,12} = 35.6$	<0.001	$F_{2,12} = 0.9$	0.437

* All models included a random effect of plot at sites to account for repeated measurements made at each site.

3.2.2. Mean Forest Floor Aboveground Autotrophic Respiration Rate ($R_{FF\_A\_ag}$) and Belowground Autotrophic Respiration of Shrubs + Herbs ($R_{A\_SH\_bg}$)

There were significant effects of WT and microform treatments individually and interactively on both the $R_{FF\_A\_ag}$ and $R_{A\_SH\_bg}$ (Table 2). Similar to R_{FF}, the $R_{FF\_A\_ag}$ and $R_{A\_SH\_bg}$ values were highest at the drained site (5.2 ± 0.6 $g \cdot CO_2 \cdot m^{-2} \cdot day^{-1}$; 2.8 ± 0.6 $g \cdot CO_2 \cdot m^{-2} \cdot day^{-1}$, respectively), followed by values at the experimental (3.1 ± 0.9 $g \cdot CO_2 \cdot m^{-2} \cdot day^{-1}$, 1.5 ± 0.2 $g \cdot CO_2 \cdot m^{-2} \cdot day^{-1}$, respectively) and control (2.4 ± 0.6 $g \cdot CO_2 \cdot m^{-2} \cdot day^{-1}$; 1.4 ± 0.2 $g \cdot CO_2 \cdot m^{-2} \cdot day^{-1}$, respectively) sites. The $R_{FF\_A\_ag}$ and $R_{A\_SH\_bg}$ fluxes were also overall higher at the hummocks (4.9 ± 0.6 $g \cdot CO_2 \cdot m^{-2} \cdot day^{-1}$; 2.5 ± 0.1 $g \cdot CO_2 \cdot m^{-2} \cdot day^{-1}$, respectively) than that at the hollows (2.1 ± 0.6 $g \cdot CO_2 \cdot m^{-2} \cdot day^{-1}$;

1.3 ± 0.1 g·CO_2·m^{-2}·day^{-1}, respectively). Comparing microforms across sites, drained hummocks had significantly higher $R_{FF\_A\_ag}$ emissions than all other plots ($p = 0.005$; Figure 4) while $R_{A\_SH\_bg}$ at hummocks was significantly different between all three sites. There were no significant differences at hollows across the WT treatment sites for either $R_{FF\_A\_ag}$ or $R_{A\_SH\_bg}$.
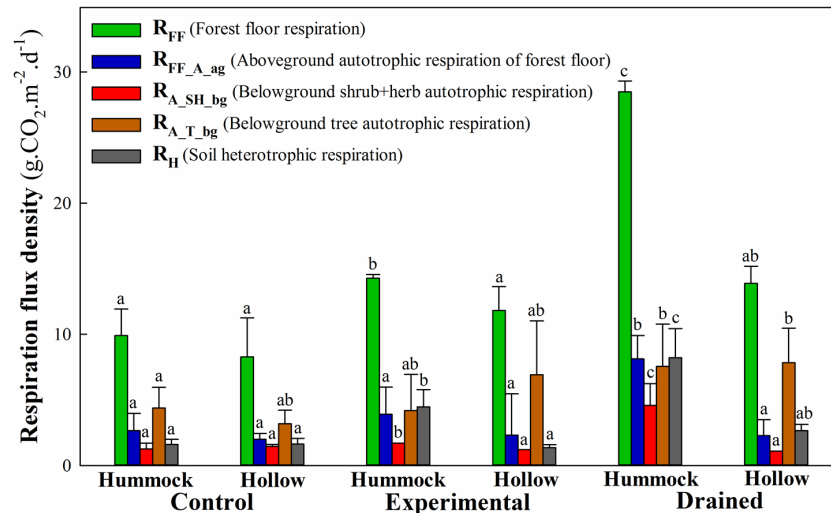

Figure 4. Mean ($\pm$SD) R_{FF}, $R_{FF\_A\_ag}$, $R_{A\_SH\_bg}$, and $R_{A\_T\_bg}$ measured during the growing season (May to October) of 2012 at all sites/microforms. Mean $R_{A\_SH\_bg}$ was determined by using a biomass regression method (Tables 3 and 4; Figure 5) [46,52]. Bars having no letters in common are significantly different ($p < 0.05$) while bars with same letters indicate no significant difference ($p > 0.05$); letters should be compared only within one flux component across all microforms.

We used B_{SH_ag} to calculate B_{SH_bg} ($B_{SH\_bg} = B_{SH\_ag} \times 0.39$; Table 3) and determine $R_{A\_SH\_bg}$ (Figures 4 and 5) using the regression equations we generated by regressing B_{SH_ag} with $R_{FF\_A\_ag}$ (explained in detail in Methods section). The B_{SH_ag} was not different among sites or microforms due to large variation between plots; however, the drained site had the highest, while experimental had the lowest B_{SH_ag} of all sites, and drained hummocks had higher B_{SH_ag} than those of control and experimental hummocks in that order (Table 4, Figure 4). The B_{SH_ag} and microform type significantly explained $R_{FF\_A\_ag}$ emissions individually and interactively (Table 4). Also, the $R_{FF\_A\_ag}$ was significantly related to an interaction between B_{SH_ag}, site and microform, where B_{SH_ag} was significantly related to the $R_{FF\_A\_ag}$ at all sites and microforms except at the experimental hollows which had the lowest or inconsistent B_{SH_ag} values (Table 4; Figure 5). The overall regression lines' slopes differed significantly at the hummocks and hollows ($z = 4.43$; 3.12, respectively). Regarding hollows, the slope was steeper at the drained site compared to control.

Table 3. Estimated aboveground biomass of shrubs + herbs (B_{SH_ag}) and trees (B_{T_bg}), and belowground biomass of shrubs + herbs and trees (B_{SH_bg}), at control, experimental, and drained sites *. All values ($\pm$SD) are in g·m^{-2}.

Vascular vegetation	Control			Experimental			Drained		
	Site	Hummock	Hollow	Site	Hummock	Hollow	Site	Hummock	Hollow
Shrubs + herbs									
B_{SH_ag}	90 ± 41	110 ± 54	65 ± 27	62 ± 34	70 ± 32	52 ± 36	152 ± 103	245 ± 180	52 ± 27
B_{SH_bg}	35 ± 16	43 ± 21	25 ± 10	24 ± 1	27 ± 0.6	20 ± 1	59 ± 35	95 ± 70	20 ± 1
Tree									
B_{T_ag}	2142 ± 376			1986			1964 ± 381		

* all values are mean $\pm$ SD ($n = 6$ for each of the B_{SH_ag} and B_{SH_bg}, and $n = 3$ (except experimental site with $n = 1$) for B_{T_ag}) [17]. Site biomass was determined by weighting the forest floor by the proportion of hummock and hollow microforms at each site (hummocks: control = 56%, experimental = 55%, drained = 52%), where applicable.

Table 4. Statistical results of a repeated, linear mixed effects model with fixed effects of site (control, experimental, drained), microform (hummock, hollow), and aboveground biomass of shrub + herb (B_{SH_ag}; covariate), random effect of plot, and an outcome variable of aboveground autotrophic respiration of shrubs + herbs at the forest floor ($R_{FF\_A\_ag}$) *.

Respiration	Effect	F	p
	B_{SH_ag}	$F_{1,\,34} = 10.63$	0.003
	Site	$F_{2,\,34} = 4.09$	0.026
$R_{FF\_A\_ag}$	Microform	$F_{1,\,34} = 6.00$	0.020
	$B_{SH\_ag} \times$ Microform	$F_{1,\,34} = 9.20$	0.005
	Site $\times$ Microform	$F_{2,\,34} = 9.57$	0.001
	$B_{SH\_ag} \times$ Site $\times$ Microform	$F_{4,\,34} = 3.93$	0.010

* Random effect of plot was included in the model to account for the repeated measurements made at each site.

3.3. Modeled Respiration Components

Overall, all modeled seasonal (May to October) respiration components ($g \cdot CO_2 \cdot m^{-2} \cdot$ growing season^{-1}) were in the order of drained > experimental > control site, with greater overall increases at hollows than at hummocks at all the sites (Table 5). R_H accounted for approximately 48%, 43%, and 37% of R_{FF} at control, experimental, and drained sites, respectively. The R_{FF} and $R_{A\_T\_bg}$ fluxes at the drained site were significantly higher than those at the control site, while $R_{FF\_A\_ag}$ and $R_{A\_SH\_bg}$ were not different among sites, but were different between drained hummocks and drained hollows. The seasonal $R_{A\_T\_bg}$ and R_H values were highest at the drained hollows.
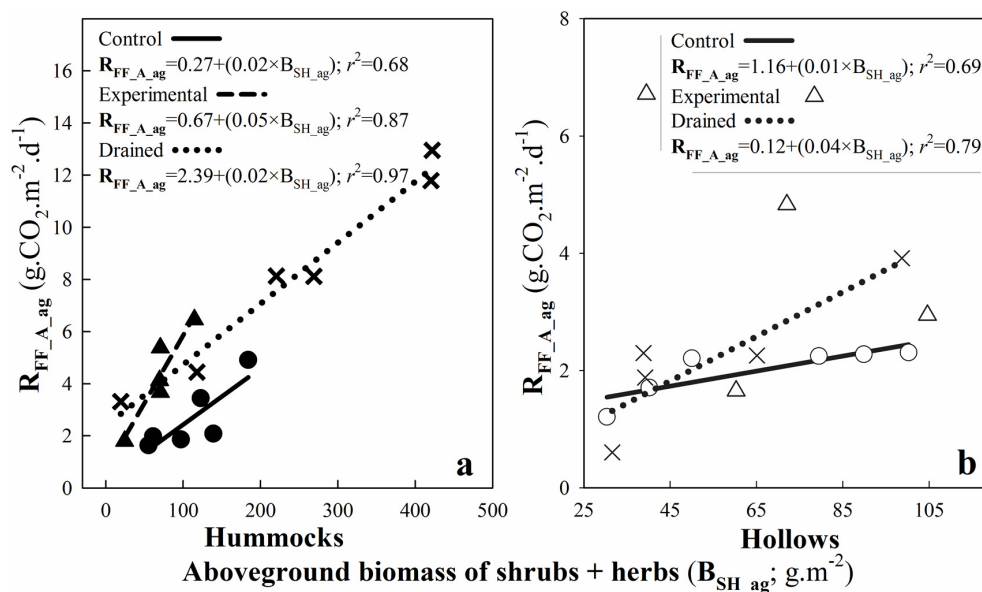

Figure 5. Aboveground autotrophic respiration of forest floor ($R_{FF\_A\_ag}$; $g \cdot CO_2 \cdot m^{-2} \cdot day^{-1}$) versus aboveground biomass of shrubs + herbs (B_{SH_ag}; $g \cdot m^{-2}$) at (**a**) hummock and at (**b**) hollow microforms at each site. Regression lines were plotted for each microform type at each site when statistically significant at $p < 0.05$.

4. Discussion

In agreement with the previous seasonal (2012) R_{FF} estimates made at these sites [17], this research found the greatest growing season R_{FF} values at the drained site (422 ± 22 $g \cdot CO_2 \cdot m^{-2}$), smaller values at the experimental site (354 ± 16 $g \cdot CO_2 \cdot m^{-2}$), and the smallest values at the control site (255 ± 10 $g \cdot CO_2 \cdot m^{-2}$; Table 2); however, in general, the values at hollows across sites were slightly lower in the present study, as these R_{FF} values were modeled using measurements made over a

shorter duration and from different plots (located in an area adjacent to the previous study plots [17]). The increased losses of CO_2 at the short- and long-term drained sites that we observed compare well with those reported by others from experimentally drained boreal peatlands [9,32,44,62,63]. Declining WT level promotes desiccation of aquatic vegetation and soil that progresses over time.

Table 5. Partitioning of the growing season (May to October, 2012) forest floor respiration ($\pm$SE; $g \cdot CO_2$-$C \cdot m^{-2}$) into major flux components *.

Site	Microform	R_{FF}	$R_{FF\_A\_ag}$	$R_{A\_SH\_bg}$	$R_{A\_T\_bg}$	R_H **
Control		255 ± 10.3 [a]	38 ± 6.7 [a]	37 ± 8.0 [a]	58 ± 8.9 [a]	122 ± 33.9 [a]
	Hummock	282 ± 4.6 [a,b]	42 ± 2.1 [a,b]	36 ± 6.2 [a,b]	80 ± 3.9 [a]	124 ± 16.8 [a]
	Hollow	221 ± 5.8 [a]	33 ± 4.6 [a,b]	39 ± 1.8 [a,b]	30 ± 5.1 [b]	119 ± 17.3 [a]
Experimental		354 ± 15.7 [a,b]	45 ± 11.8 [a]	40 ± 21.9 [a]	117 ± 11.1 [a,b]	152 ± 60.5 [a]
	Hummock	361 ± 2.2 [a,b]	57 ± 6.5 [a,b]	43 ± 6.8 [a,b]	101 ± 17.4 [a]	160 ± 22.9 [a]
	Hollow	346 ± 13.6 [a,b]	31 ± 5.3 [a,b]	36 ± 15.1 [a,b]	137 ± 13.8 [a]	142 ± 37.8 [a]
Drained		422 ± 21.9 [b]	66 ± 23.4 [a]	51 ± 22.7 [a]	150 ± 9.0 [b]	155 ± 77.0 [a]
	Hummock	429 ± 15.7 [b]	108 ± 11.2 [a]	69 ± 19.9 [a]	147 ± 5.2 [c]	105 ± 52.0 [a]
	Hollow	415 ± 6.2 [b]	21 ± 12.2 [b,c]	33 ± 2.8 [b,c]	154 ± 3.8 [c]	207 ± 25.0 [a]

* R_{FF}, $R_{FF\_A\_ag}$, and $R_{A\_T\_bg}$ denote forest floor respiration, above-ground autotrophic respiration of forest floor, and belowground autotrophic respiration of tree, respectively. $R_{A\_SH\_bg}$ represents belowground shrub + herb autotrophic respiration and was determined using biomass regression method (Tables 2 and 3). The seasonal value of $R_{A\_SH\_bg}$ is calculated by determining it as a proportion of instantaneous R_{FF} value and then estimating it as this proportion of the modeled seasonal R_{FF}. ** R_H was determined by difference using Equation (2). Values are significantly different if they have no letter in common; letters should be compared only within one flux component in a column between sites or microforms.

The R_{FF} was partitioned into major respiration components ($R_{FF\_A\_ag}$, $R_{A\_SH\_bg}$, $R_{A\_T\_bg}$) which were then modeled for seasonal estimates with WT level and T_5 as covariates. Model validations across sites/microforms showed excellent agreements within RSE of 0.24–2.41 $g \cdot CO_2 \cdot m^{-2}$ growing season^{-1} (Table 1, Figure A1). Many investigations on peatland or forest respiration components have shown that warm and dry conditions enhance autotrophic [9,30,64,65] and heterotrophic [25,26,39] respiration emissions with greater impact over longer time scales [17,32,66]. Warmer air and soil temperatures stimulate microbial activity, resulting in increased respiration fluxes; however, T_5 response of R_H depends on substrate type and availability of nutrients and moisture [67,68]. Water-table lowering in peatlands prompts increased respiration emissions that are enhanced with increase in peat surface temperature, as we noticed that R_{FF} values at our sites were well correlated to both WT level and T_5 (Tables 2 and 3; Figure 3). In contrast, a few studies suggest that the vascular vegetation (shrubs + herbs and trees) are less sensitive to WT lowering, as they can increase their rooting depth with deeper WT [15,30]. Peatland microforms have been observed to respond to changes in WT level and T_5 with different magnitudes and in different directions [16,60,69] mainly due to differences in vegetation coverage and composition. Counter to our hypothesis, we observed a significant increase in R_{FF} in response to WT lowering at hummocks, while R_{FF} at hollows was not significantly affected. Hummocks were drier and had significantly higher coverage of shrubs + herbs compared to hollows that were dominated by *Sphagnum* mosses at the research sites prior to WT manipulation. Therefore, differences in R_{FF} response to WT drawdown may be driven by changes in either autotrophic or heterotrophic respiration, or both.

At the control site, autotrophic respiration components ($R_{FF\_A\_ag}$, $R_{A\_SH\_bg}$, $R_{A\_T\_bg}$) were similar at hummocks and hollows. As for R_{FF}, drainage increased autotrophic respiration at hummocks, but only resulted in increased $R_{A\_T\_bg}$ at hollows. The greater $R_{FF\_A\_ag}$ and $R_{A\_SH\_bg}$ at hummocks (dominated by shrubs + herbs) was found to be related to B_{SH_ag} and B_{SH_bg} (Tables 4 and 5), respectively, indicating that drainage-induced increase in shrubs + herbs biomass had a strong control on above and belowground autotrophic respiration components at hummock microforms, which is similar to the findings of several studies [44,70,71]. Minimal change in B_{SH_ag} and B_{SH_bg} at hollows

(Table 3) resulted in the non-significant change in $R_{FF\_A\_ag}$ and $R_{A\_SH\_bg}$. As tree roots likely extend across all microforms, particularly as the depth of aerated peat is thickened by WT drawdown, the overall increase in tree productivity in response to drainage [17] resulted in increased $R_{A\_T\_bg}$ across both hummocks and hollows. Although $R_{FF\_A\_ag}$ did not increase significantly at hollows following drainage, the slope of the $R_{FF\_A\_ag}$ versus B_{SH_ag} became steeper, indicating increasing autotrophic respiration rates per unit increase in biomass. This may reflect the shift from moss dominated vegetation at the control site to more herbs and shrubs at the drained site, as vascular plants tend to have higher respiration rates than bryophytes [72,73].

Although R_H increased at some microforms (i.e. drained hollows) in response to WT drawdown, there was no significant difference across the WT treatments sites (Table 5). We hypothesized that R_{FF} increase would be greatest at hollows, as the WT drawdown would shift this microform position from largely anoxic to oxic conditions, resulting in large increases in R_H that would drive shifts in R_{FF}. We did observe substantial increases in R_H at hollows following WT lowering; however, these were masked by autotrophic respiration. Previous studies have also reported that $R_{FF\_A\_ag}$ can account for the majority of peatland respiration [45]. As WT drawdown enhanced plant productivity at the study site [17], R_H accounted for a declining proportion of growing season R_{FF} from 48% at control to 36% at the drained site. Hummock R_H did not change substantially in response to WT drawdown. As WT was initially deep below hummocks at the control site, due to the continental climate at the study site, the surface peat was well-aerated initially and R_H was likely rarely limited by saturated conditions. Drainage may actually result in desiccation of the surface peat that could result in conditions too dry for optimal rates of R_H [74]. The limited change in R_H between the WT treatments is therefore partially driven by the differential microform response where R_H is enhanced at hollows, with little change, or slight reduction at hummocks.

Overall, the substantial contribution of autotrophic respiration to R_{FF} suggests that the large increase in R_{FF} observed in response to WT drawdown will result in only slow loss of the C accumulated in peat, with these losses likely greatest at hollows [17]. However, comparison of R_H is partially complicated by the fact that it was calculated by difference once all the other partitioned flux components were estimated, and thus also contains error associated with the estimation of individual components. Isolated partitioning of the source-based respiration components remains to be developed, although the few manipulative field experiments that have investigated how climate change factors interact with one another to alter soil respiration [41,75] were not able to separate soil respiration into its components without significantly disrupting the soil [28]. Separating peat soil C into various major components is an important challenge for improving our understanding of peatland C cycling response to climate change [76].

5. Conclusions

Experimental water-table (WT) drawdown in a treed boreal bog increased forest floor respiration (R_{FF}). While all measured and estimated respiration components also increased following WT lowering, these were generally only significantly increased at hummock microforms. Increases in R_{FF} at hummocks were largely driven by increases in autotrophic respiration as shrub biomass increased. Drainage increased heterotrophic respiration at hollows, with less response at hummocks, suggesting that carbon is more likely to be released from stored peat at hollows. Overall, shifts in R_{FF} were largely driven by autotrophic respiration, indicating that rapid destabilization of peat carbon stocks under drying conditions are unlikely. Partitioning R_{FF} into its subcomponents accurately and without substantial disturbance to the soil is difficult and the development of partitioning methods are needed to better understand the fate of peat carbon stocks under various disturbances.
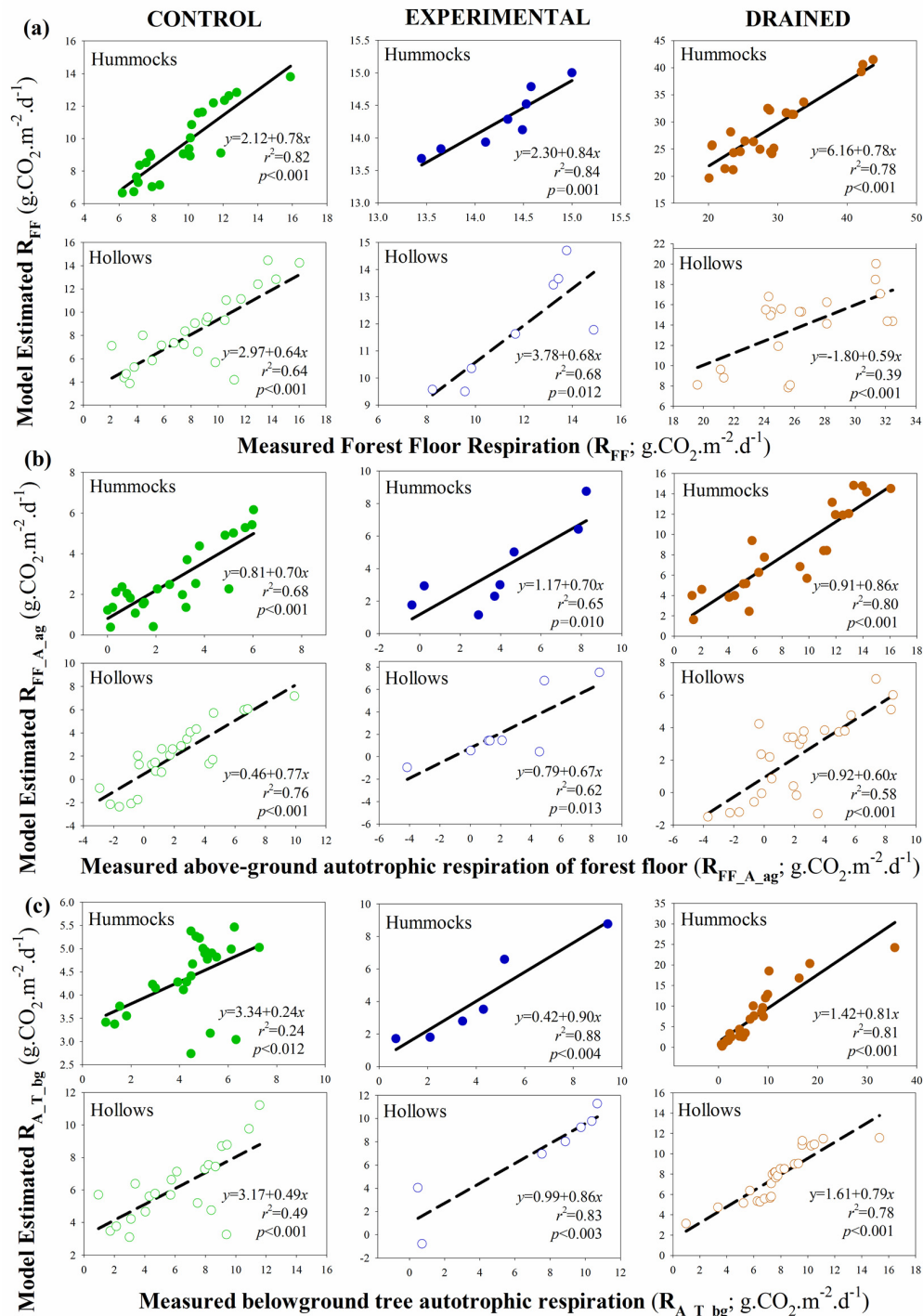
Appendix A

Figure A1. Goodness of fit between measured (year 2012) and model estimated values of (**a**) forest floor respiration (RFF), (**b**) aboveground autotrophic respiration of forest floor (RFF_A_ag), and (**c**) belowground autotrophic (rhizospheric) respiration of tree roots, across sites and microforms. Lines represent 1:1 fit.

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