

Mineral nitrogen and phosphorus pools affected by water-table lowering and warming in a boreal wooded bog

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Abstract

Changes in atmospheric temperature and lowering in water-table (WT) are expected to affect peatland nutrient dynamics. To understand the response of peatland nitrogen (N) and phosphorus (P) dynamics to warming and drainage in a continental wooded-bog of hummock – hollow microtopography, we compared three sites: 1) control, 2) recently drained (2-3 years; experimental), and 3) older drained (12-13 years; drained), during 2013. The WT was lowered at experimental and drained sites to 74 cm and 120 cm, respectively, while a warming of ~ 1 °C was created at one half of the microforms using open-top chambers. Responses of peat total-inorganic-nitrogen [TIN = nitrate nitrogen (NO_3^- -N) + ammonium nitrogen (NH_4^+ -N)] and phosphate-P [PO_4^{3-} -P] pools and, vegetation C:N ratio, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ to the experimental treatments were investigated across sites/microforms and over time.

Peat TIN available and extractable pools increased with deepening of WT and over time, and were greater at hummocks relative to hollows. In contrast, the PO_4 pools increased with short-term drainage but reverted to very close to their original (control) nutrient values in the longer-term. The WT and warming driven change in the peat TIN pool was strongly reflected in the vascular vegetation C:N ratio and, shrub $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, while moss nutrient dynamics did not vary between sites. Therefore, we suggest that atmospheric warming combined with WT deepening can increase availability of mineral N and P, which then can be reflected in vascular vegetation and hence modify the productivity and ecosystem functioning of the northern mid-latitude continental forested bogs in the long-term.

1 Introduction

Northern peatlands sequester ~547 Pg carbon (C; 1Pg = 10^{15} g), approximately one third of the total terrestrial soil C pool (Yu, Loisel, Brosseau, Beilman, & Hunt, 2010) and represent a stock of ~15.9 Pg nitrogen (N), approximately 10% of total terrestrial nitrogen pool (Loisel et al., 2014). These peatlands are predicted to be highly sensitive to climate change (Carlson et al., 2010; Dale H. Vitt, Wieder, Scott, & Faller, 2009) with warming likely to result in deeper ground water-table (WT). The warmer and drier conditions are predicted to significantly increase peat respiration and mineralization rates (Flanagan & Syed, 2011; Updegraff, Bridgham, Pastor, Weishampel, & Harth, 2001), and alter greenhouse gas (GHG) concentrations in the atmosphere (Bragg, 2002). While attempts have been made to investigate the C status and cycling in peatland in response to climate change (e.g., Ballantyne, Hribljan, Pypker, & Chimner, 2013; Chivers, Turetsky, Waddington, Harden, & McGuire, 2009; T. M. Munir, Perkins, Kaing, & Strack, 2015; Riutta, Laine, & Tuittila, 2007; Strack & Waddington, 2007), controlled field experimentation to evaluate the potential impacts of warming in combination with drainage on peatland nutrient biogeochemistry remains limited.

Temperature and WT position are among the most important environmental controls on net primary productivity (NPP) of peatland ecosystem of hummock-hollow microtopography (Ciais et al., 2013; T. M. Munir, Xu, Perkins, & Strack, 2014). The NPP is also strongly constrained by the soil total inorganic nitrogen (TIN = nitrate (NO_3^-) + ammonium (NH_4^+)), available phosphorus (P) and total extractable pools (Idol, Baker, & Meason, 2007; Iversen, Bridgham, & Kellogg, 2010). Nutrient availabilities are in turn driven by the microbial decomposition rate, which has been found to increase with temperature in peatland ecosystems (Dorrepaal, Cornelissen, Aerts, WallÉN, & Van Logtestijn, 2005; Ise, Dunn, Wofsy, &

Moorcroft, 2008). Experimental increases in temperature have been found to stimulate N mineralization (ammonification and nitrification) (C. H. Robinson, 2002; Verhoeven, Maltby, & Schmitz, 1990), and enhanced N availability may therefore be a realistic indirect consequence of climate warming (Dorrepaal et al., 2005; Nadelhoffer, Giblin, Shaver, & Laundre, 1991).

Experimental WT drawdown in peatlands has also been shown to increase the concentrations of available and extractable nutrients (Eppinga et al., 2010; Holden, Chapman, & Labadz, 2004; Laiho, Silvan, Cárcamo, & Vasander, 2001; Macrae, Devito, Creed, & Macdonald, 2006), although mobility of phosphate (PO_4) in response to drainage was dissimilar to NO_3 and NH_4 (Brady & Weil, 2010). Drainage has also been clearly shown to increase tree stand biomass and total stand nutrient pools in boreal peatlands, although biomass nutrient pools remained much smaller than the soil pool (Westman & Laiho, 2003). The WT or moisture driven changes in soil nutrient availability are also likely to shift plant community composition, and dominant plant functional type, thus modifying plant and litter C:N (W. J. Choi, Chang, & Bhatti, 2007; Smiljanić et al., 2014) and C:P ratios (Dorrepaal et al., 2005). Moreover, the forest floor litter C:N:P ratio is an important predictor of its decomposition rate and subsequent nutrient availability to plants in peatland ecosystems (D'Orangeville, Houle, Côté, Duchesne, & Morin, 2013). Lower peat N or P concentration may diminish microbial activity and mineralization rate (Johnson & Damman, 1993) differently in moss and shrub dominated bogs (Rien Aerts, Wallén, Malmer, & De Caluwe, 2001) due to differences in litter quality. Changes in vegetation composition in response to experimental warming in peatlands have been reported (e.g., T. M. Munir et al., 2015), however, to our knowledge, a combined effect of warming and WT drawdown on peat-vegetation nutrient relationships has not been investigated. Climate change is expected to result in drier conditions in continental peatlands (Vile, Scott, Brault, Wieder, &

Vitt, 2011; Dale H Vitt, Halsey, Bauer, & Campbell, 2000), and although drainage alters WT level more rapidly, investigating the response of peatland nutrient dynamics to drainage and warming will provide process-based information required to understand the role nutrients play in the potential peatland C feedback to environmental change.

Stable isotopes can be used to track changes in soil-plant-atmosphere water and nutrient use relationships in response to changes in environmental controls. The stable isotope ratio of C ($^{13}\text{C}/^{12}\text{C}$, expressed as $\delta^{13}\text{C}$) and N ($^{15}\text{N}/^{14}\text{N}$, expressed as $\delta^{15}\text{N}$) are directly related to discrimination against the heavier isotopes (^{13}C and ^{15}N) in soil-plant-atmosphere water and nutrient cycling (W. J. Choi et al., 2007). The discrimination during photosynthesis results in ^{13}C depletion in leaves of vascular plants (Cernusak et al., 2009). Discrimination against $^{13}\text{CO}_2$ during moss photosynthesis is related to water content with greater discrimination under drier conditions (Williams & Flanagan, 1996). Moss $\delta^{15}\text{N}$ signature is related with atmospheric N deposition rate, and increased from a lower negative value of -3‰ to a higher negative value of -8‰ in response to increasing atmospheric N deposition from $0.1 \text{ g m}^{-2}\text{yr}^{-1}$ to $2.0 \text{ g m}^{-2}\text{yr}^{-1}$ (Bragazza et al., 2005). Plant litter inputs lower soil $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values while decomposition increases $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (Rien Aerts, Callaghan, Dorrepaal, Van Logtestijn, & Cornelissen, 2009; Natelhoffer & Fry, 1988). Nitrogen uptake from soil results in ^{15}N enrichment in soil and corresponding depletion in plant as a result of isotope fractionation, under equilibrium conditions (P. Dijkstra et al., 2008).

Vegetation composition differences between hummocks and hollows result in differences in nutrient demands and potentially uptake (Turetsky, 2003), while differences in water table position likely affect mineralization rates (e.g., Macrae, Devito, Strack, & Waddington, 2013), both of which potentially influence local available and extractable nutrient pools (R. Aerts,

Verhoeven, & Whigham, 1999; Chapin, Bridgham, Pastor, & Updegraff, 2003). It is likely that patterns of nutrient distribution between microforms may change in response to WT drawdown and warming. Significant microtopographic differences in nutrient dynamics occurred following 10 years of drainage (Macrae et al., 2013). However, the time frame for these changes, and the individual and interactive effects of warming and WT lowering remains a knowledge gap.

In order to better understand how mineral nutrient supply rates (availabilities) and extractable nutrient pools will affect the vegetation nutrient content (C:N ratio) under atmospheric warming and WT lowering in both the short- and longer-terms, and how this response varies between microforms, a field-based experiment was conducted. The goal of our research was to quantify the peatland mineral nutrient dynamics in response to experimental warming and WT lowering using three sites at a continental wooded boreal bog, in Alberta, Canada. Our specific objectives were:

1. To quantify the effects of experimental changes in temperature and water-table level on peat available and extractable mineral nutrient pools and, vegetation C:N ratio, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, and
2. To investigate the controls (e.g., temperature, water-table level) on the nutrient dynamics across space (microforms) and over time (2 and 13 years).

We hypothesized that both drainage and warming would increase available and extractable mineral N and P pools, with the greatest change at warmed and drained sites, and that this response would be greater at hummocks than at hollows. Using the plant C:N ratio as an indicator of plant uptake from these pools, we hypothesized that C:N ratio would decline with both drainage and warming, particularly for vascular plants. Increased nutrient uptake was also hypothesized to result in depleted $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in plant tissues from warmed and drained plots compared to control plots.

2 Materials and methods

2.1 Study sites and experimental design

This research was conducted at three wooded bog sites in a peatland complex located near the township of Wandering River, Alberta, Canada, during 2012-2013 growing seasons (May to October). Based on 30-year (1981-2010) averages (Environment Canada, 2013), the mean precipitation and temperature for the period May to October for this region are 382 mm and 11.7 °C, respectively. During 2012-2013 growing seasons the control/experimental site mean precipitation and air temperature (measured using a meteorological station installed at the study sites) were 13.2 °C, 14.1 °C and 282 mm, 267 mm, respectively.

Within the peatland complex, three bog sites namely 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 in 2011 (geographical map is presented by Tariq Muhammad Munir, Khadka, Xu, and Strack (2017)). Based on hydrological, vegetational and chemical characteristics, the sites were classified as wooded bogs (Alberta Environment and Sustainable Resource Development, 2015). All sites were underlain by sandy-clay substrate and had peat depth exceeding 4 m. The control was an undisturbed site with a mean WT level of -38 cm (negative value represents belowground WT). Adjacent to the control, experimental site was created by ditching around and lowering the mean WT level to -78 cm. One year prior to the WT level manipulation, mean WT level (\pm SD) at the control site (-56 ± 22) was not significantly different from that at the experimental site (-57 ± 20 ; ANOVA, $F_{1,5} = 0.55$, $p = 0.492$). The drained site, located 9 km to southwest, was inadvertently drained in 2001 as a result of horticultural peat harvesting preparation on an adjacent section, and had a mean WT level of -120 cm.

The control and experimental site microforms were blanketed by thick mats of *Sphagnum* mosses (mainly *S. fuscum*, and *S. magellanicum* on hummocks and, *S. angustifolium*, in hollows) interspersed with sparse shrubs (mainly *Rhododendron groenlandicum*, *Rubus chamaemorus*, *Vaccinium vitis-idaea*, and *Vaccinium oxycoccos*), whereas the drained hummocks had the greatest coverage ($83 \pm 14\%$) of shrubs and drained hollows had the greatest coverage of lichen ($53 \pm 11\%$) as elaborated by Munir et al. 2014. To find out whether the drained site was similar to the control prior to drainage in 2001, we conducted a vegetation survey in 2013 along a 50 m transect located ~100 m farther from the drainage ditch (the survey data is used for Global Sphagnum Project). Drained site microforms were found blanketed by Sphagnum mosses and shrubs similar to the control microforms, indicating that the three sites under experiment were bogs and covered by similar ground-layer vegetation. Of all shrubs and across all sites, *Rhododendron groenlandicum* dominated at hummock and lichen dominated at hollow. Across all sites, black spruce (*Picea mariana* (Mill.) B.S.P.) was the most abundant type of tree with a projection coverage of >42% constituting ~99% of the tree stand with 25,766 stems ha⁻¹. To approximate the time-since-fire following Wieder et al. (2008), we determined age of the trees (n = 9) by counting annual rings at tree bases, and found that the oldest tree was aged at 52-yr in both control and drained sites.

Mean (\pm SD) electrical conductivity corrected for H⁺ (EC) and pH of pore water in the control ($16.6 \pm 0.7 \mu\text{S cm}^{-1}$ and 4.1 ± 0.1 , respectively) and experimental ($15.2 \pm 2.5 \mu\text{S cm}^{-1}$ and 4.4 ± 0.3 , respectively) sites were not different (one-way ANOVA, EC: $F_{1,5} = 0.84$, $p = 0.401$; pH: $F_{1,5} = 2.6$, $p = 0.166$) prior to any manipulation. As all the study sites were wooded bogs and their initial primary characteristics of vegetation composition, WT levels and chemistry were similar, therefore, secondary attributes of the sites were also assumed to be similar.

At each of the control, experimental and drained sites, we chose six hummock and six hollow microforms and fitted each with 60 cm × 60 cm permanent collars (3 sites × 12 microforms = 36 study plots) as described by T. M. Munir et al. (2015). At each of the plots, a perforated PVC water well (diameter = 3.5 cm), covered with a nylon cloth at the lower 150 cm, was inserted into the peat to manually measure WT levels bi-weekly. Two randomly selected wells (one hummock and one hollow) were instrumented with pressure transducers (Levelogger Junior 3001, Solinst, Georgetown, Ontario, Canada) to automatically monitor WT level. The leveloggers recorded temperature compensated WT levels continuously at 20-minute intervals during 2012-2013 growing seasons. The levels were also compensated for barometric pressure changes measured using a barologger (Barologger Gold, Solinst; above-ground height = 100 cm).

At each site, randomly selected three hummock and three hollow plots were equipped with 60 degree, 50 cm tall open-top hexagonal chambers (OTCs) of top and basal, side to side dimensions of 104 cm and 162 cm, respectively. The OTCs (Molau & Molgaard, 1996) were constructed using 3.5 mm thick, translucent plexiglas (SUN-LITE HP, Solar Components Corporation, Manchester, New Hampshire, USA) to passively warm the plot air and soil (at 5 cm depth) by ~1 °C (Hollister & Webber, 2000). Inside each OTC, two automatic data loggers (HOBO Pro V2, Onset computer corporation, Bourne, MA, USA) were installed at a height of 25 cm above-ground and facing north to minimize direct solar radiation loading. One of the HOBOS logged OTC air temperature only, and the other logged OTC air as well as soil (5 cm deep) temperatures. To log ambient temperatures, duplicate sets of the two HOBOS were also installed outside the OTCs at all sites. All the HOBOS continuously logged temperatures at 20-minute

intervals during 2012-2013 growing seasons. Snowpack disturbance was minimized by dismantling the OTCs each October and reinstalling back on plots in early May.

2.2 Peat nutrient supply rate (availability)

In-situ soil NH_4 , NO_3 and PO_4 supply rates were measured using ion-exchange membrane (IEM) probes (Plant root simulator (PRSTM), Western Ag Innovations, Saskatoon, Canada). The PRS probes have been extensively used for measuring in-situ nutrient supply rates (hereafter called availability) and have been found to be effective for bio-mimicking the nutrient adsorption by plant roots (e.g., D'Orangeville et al., 2013; Yan et al., 2012). Each PRS probe membrane has a 17.5 cm^2 surface area held in a $15.5 \text{ cm} \times 3 \text{ cm} \times 0.5 \text{ cm}$ (L \times W \times D) plastic support which is inserted into soil surface with minimal disturbance. Cation and anion availabilities are quantified using negatively- and positively-charged PRS probes, respectively. The charged membrane of the PRS probe acts as a surrogate for plant roots continuously adsorbing labile soil nutrients and allowing for evaluation of the soil nutrient availability in μg nutrient per 10cm^2 surface. During the burial period, once the ion concentrations at the PRS surface establish equilibrium with those of the soil solution, it may start acting as a dynamic exchanger (McGrath, Comerford, & Duryea, 2000). The PRS probe data will be referred to as “available” hereafter.

Two sets of PRS probes (each set consisted of four cation and four anion probes) were inserted into the moss surface of each plot vertically to a depth of approximately 5-10 cm on each of the June 28, 2012 and June 29, 2013. The inserted probes were uniformly distributed within the plot representative area. The two sets of probes were retrieved one by one at sequential intervals of 4 and 8 weeks in both years. After each of the retrievals, the probes were scrubbed of any soil particles, washed with de-ionized water, packed into clean and labelled

Ziploc bags and sent back to Western Ag Innovations (Saskatoon, SK, Canada) for nutrient analyses.

2.3 Peat sampling and extractable nutrient analyses

At the end of the study period in October 2013, we collected duplicate peat cores from all plots [3 sites \times (12 plots \times 2), ($n = 72$)] for determination of potassium chloride (KCl) extractable NH_4 and NO_3 , and water extractable PO_4 contents. Each core (collected using a stainless-steel saw) was 10 cm long \times 10 cm wide \times 0-20 cm deep. The cores were placed in labelled Ziploc bags. Excess air from the bags was removed to minimize sample oxidation. Samples were stored in a cooler and transported to the Wetland Soils and Ecohydrology Lab, University of Calgary and refrigerated at 4 °C. The peat samples, while still in their bags, were hand churned until the samples were visually homogenized and two 5 g (dry weight) sub-samples were taken following Macrae et al. (2013). One sub-sample was extracted in 50 ml 2M KCl for colorimetric analyses of NO_3^- and NH_4^+ while the second sub-sample was extracted in distilled deionized water for colorimetric analysis of soluble reactive PO_4 (Macrae et al., 2013). The remainder of the peat sample was oven-dried at 105 °C until constant weight to determine gravimetric moisture content.

2.4 Foliar sampling and analyses

At the end of the active growing season (October), each peat core's ($n = 72$; section 2.3) above-ground vegetation was clipped at the ground level and used for determination of total nitrogen (TN), C:N ratio, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Each vegetation sample was sorted for target plant functional types/species: shrub (*Rhododendron groenlandicum*) and moss (*Sphagnum fuscum*, *Sphagnum magellanicum* and *Sphagnum capillifolium*). We define the target species as the most common species across sites. Drained site lacked target moss species and therefore is not included in the

study. Nitrile gloves were worn during sampling and were changed between collections of different species.

Any non-target moss species (e.g., *Polytrichum strictum*) was removed from moss samples in the laboratory and the top 2 cm of the moss carpet (living portion including capitulum) were cut for analyses. Only green leaves of shrubs were chosen for TN, C:N ratio, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses. The prepared samples (living moss and shrub leaves) were placed in paper bags and dried in an oven at 60 °C until constant weight. Each dried sample was ground to fine powder form and sent to the Environmental Isotope Laboratory at University of Waterloo for determination of C and N contents and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Carbon and N stable isotope compositions were calculated as:

$$\delta (\text{‰}) = [(R_{\text{sample}}/R_{\text{standard}})-1] \times 10^3 \quad (1)$$

where δ is $\delta^{13}\text{C}$ ($\delta^{13}\text{C}$ IRMEA/VPDB) or $\delta^{15}\text{N}$ ($\delta^{15}\text{N}$ IRMEA/AIR), expressed in term of mil (‰). The R_{sample} is the ratio of $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ in plant tissue. The R_{standard} is the ratio of $^{13}\text{C}/^{12}\text{C}$ in immunoradiometric assay (IRMEA)/Vienna Pee Dee Belemnite (VPDB) or the ratio of $^{15}\text{N}/^{14}\text{N}$ in atmospheric N_2 . The error for the isotopic ratios is less than 0.2‰ and 0.3‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively.

Sample plots focused on understory species and trees could not be warmed given the small size of the OTCs. Therefore, only the WT lowering effect could be determined on the tree nutrient content and tree foliage samples were collected from the branches in the upper one-third of the crown and composited for each site ($n = 3$) following W. J. Choi et al. (2007). Isotopic ratios were not determined for tree samples.

2.5 Statistical Analysis

All statistical analyses were performed with SPSS 21.0 package (SPSS, Chicago, Illinois, USA). All dependent variables were studied during May-October 2013 except the PRS nutrient supply rate (availability), which was studied additionally during May-October 2012. To estimate treatment effects on each of the available nutrients (TIN, NH₄, NO₃, PO₄), we used separate linear mixed-effects models with nutrient availability as the response variable, and water-table level (control, experimental and drained), warming (non-TOC, OTC) and microtopography (hummock, hollow) as fixed effects. Since the same plots were measured in each study season (2012, 2013) for available nutrients, year was taken as repeated measures within the same model. The linear mixed-effects models were also used for analyzing the responses of peat extractable nutrients. We analyzed foliar TN, C:N ratio, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data separately for shrub and moss functional groups using the original mixed-effects model. For estimating the effect of WT lowering on tree TN and C:N ratio, the linear mixed-effects model included fixed effect of water-table level and response variables of foliar TN and C:N ratio. All two-way, three-way and four-way interactions between fixed effects were also included in the models where applicable. We used compound symmetry covariance structure for repeated measures analysis. A mean value of nutrient content determined at each plot in each growing season was used for all analyses. Prior to analyses, all data were tested for normality of distribution and homogeneity of variance using Kolmogorov-Smirnov test and Levene's test, respectively.

To test how well peat available and extractable nutrient pools could predict each other, mean peat available and extractable nutrient values of triplicate hummock and hollow microforms across the treatments were fitted with a linear regression model for each of the predictor nutrients. The peat available and extractable TIN pools were also separately regressed

with the C:N ratios of shrub and the moss tissue separately. The peat extractable TIN values were also regressed with the $\delta^{15}\text{N}$ values of shrub and moss separately, and the relationships were tested for their statistical significance. A significance level of 95% ($p < 0.05$) was used for each of the ANOVAs. Goodness of fit was reported as R^2 value.

3 Results

3.1 Site microclimate and hydrological conditions

The average temperatures of 2012 and 2013 growing seasons (May to October) were warmer by 1.4 °C and 2.4 °C, respectively, and drier by 79 mm and 94 mm, respectively, than 30 year (1981-2010) regional averages measured at Athabasca, Alberta, Canada. After three and thirteen years of WT lowering and recent atmospheric warming and drying, the WT levels at the experimental (moderate drainage) and drained (intensive drainage) sites were as much as 36 cm and 82 cm lower than at the control site (Fig. 1). Detailed hydrological responses to the warmer and drier conditions have been reported by T. M. Munir et al. (2015).

The average air temperature (T_{air}) within the OTCs was significantly greater than that of ambient air (ANOVA, $F_{2, 24} = 215.87$, $p < 0.001$) across WT treatments, microforms and years. Averaged over years, the OTC air warming (\pm SD) was 1.0 ± 0.1 °C at the control, 0.9 ± 0.0 °C at the experimental and 0.8 ± 0.5 °C at the drained site. The warming was significantly greater at hollows than at hummocks (ANOVA, $F_{1, 24} = 4.85$, $p = 0.037$). During midday bright sunny conditions, the air warming within the OTC-equipped plots was greater than that in ambient plots by averages of 5, 6 and 9 °C at hummocks, and by 5, 7 and 6 °C in hollows at the control, experimental and drained sites, respectively (Fig. 1).

The soil temperature at 5 cm depth ($T_{\text{soil } 5\text{cm}}$) within the OTCs was also significantly greater than that of the ambient soil temperature at the same depth across sites (ANOVA, $F_{1, 24} = 37.59$, $p < 0.001$). Across the WT gradient, the soil warming trend followed the air warming trend. Averaged over years, the OTC soil warming (\pm SD) was 1.0 ± 0.3 °C at the control, 0.7 ± 0.1 °C at the experimental and 0.7 ± 0.3 °C at the drained site. However, there was a site – microform interaction resulting in the largest soil warming (1.3 ± 0.2 °C) at the control hummocks and the smallest (0.4 ± 0.3 °C) at the drained hummocks. The midday direct solar loading increased the $T_{\text{soil } 5\text{cm}}$ in the OTC plots more than at ambient plots, by averages of 6, 4 and 8 °C at hummocks, and by 3, 5 and 8 °C in hollows at the control, experimental and drained sites, respectively. The soil temperature at 30 cm depth ($T_{\text{soil } 30\text{cm}}$) within the OTCs was overall higher but not significantly different than that at the same depth at ambient plots across sites (ANOVA, $F_{2, 24} = 0.71$, $p = 0.053$) and microforms (ANOVA, $F_{1, 24} = 0.95$, $p = 0.339$).

The average gravimetric moisture content (\pm SD) in the 0-20 cm deep peat profile at the control was significantly higher ($85 \pm 2\%$) than those in the same depth profile at the experimental ($79 \pm 4\%$) and drained ($74 \pm 5\%$) sites (ANOVA, $F_{2, 24} = 25.79$, $p < 0.000$) which were not significantly different from each other. Overall, the hollows were significantly moister than hummocks (ANOVA, $F_{1, 24} = 5.30$, $p = 0.030$), and the warming significantly reduced moisture across the microforms (ANOVA, $F_{1, 24} = 8.30$, $p = 0.008$). No interaction between the treatments was found.

3.2 Peat available nutrients (PRS probes)

The PRS probes buried for four-weeks and eight-weeks reflected similar nutrient supply rates (availabilities) of each of the TIN, NO₃, NH₄ and PO₄ ($p = 0.346$, 0.480 , 0.814 , 0.494 , respectively). Therefore, the two data sets were pooled for further analysis. Between years

(2012-2013) availabilities were also virtually the same so that year was dropped as a fixed effect and considered only as a repeated measure. The available TIN (\pm SE) at drained site ($18 \pm 0.9 \mu\text{g } 10\text{cm}^{-2}$) was significantly higher than that at experimental ($15 \pm 0.9 \mu\text{g } 10\text{cm}^{-2}$) and control ($13 \pm 0.9 \mu\text{g } 10\text{cm}^{-2}$) sites which did not differ significantly from each other (Table 1; Fig. 2A).

Available TIN was significantly higher at hummocks ($17 \pm 0.5 \mu\text{g } 10\text{cm}^{-2}$) than at hollows ($13 \pm 0.5 \mu\text{g } 10\text{cm}^{-2}$) while microform – warming interaction simultaneously increased TIN availability at hummocks and diminished at hollows (Table 1).

The available NH_4 , which comprised a substantial portion (~80 % across the data set) of TIN, had a similar microform – warming interaction (Table 1; Fig. 2B) and parallel overall higher availability at hummocks than hollows. However, NH_4 availability was also affected by a significant site – microform interaction with hummocks having higher availability than hollows at control and drained sites, while microforms were similar at experimental site.

The available NO_3 (\pm SE) was also affected by the WT gradient except the availability was the same at drained and control sites (Fig. 2C), which had higher NO_3 availability ($3 \pm 0.2 \mu\text{g } 10\text{cm}^{-2}$) than that at the experimental site ($2 \pm 0.2 \mu\text{g } 10\text{cm}^{-2}$). A microform – warming interaction was (Table 1) consistent with that of TIN and NH_4 availabilities.

The PO_4 availability was significantly higher at experimental site ($4.8 \pm 0.4 \mu\text{g } 10\text{cm}^{-2}$) than that at the control ($2.7 \pm 0.4 \mu\text{g } 10\text{cm}^{-2}$) and drained ($1.5 \pm 0.2 \mu\text{g } 10\text{cm}^{-2}$) sites which were not significantly different from each other (Table 1; Fig. 2D). There was a significant site – microform interaction effect on PO_4 availability where moderate drainage at the experimental site resulted in higher PO_4 availability at hollows ($6 \pm 0.6 \mu\text{g } 10\text{cm}^{-2}$) but not at hummocks compared to control and drained site. The warming did not affect the PO_4 availability at sites or microforms.

3.3 Peat extractable nutrients

The extractable TIN and NH₄ pools (\pm SE) were not significantly different among the WT treatments (Table 2), although an overall increasing TIN along the gradient of lowering WT level was observed from control ($51 \pm 3 \mu\text{g g}^{-1}$) to experimental ($52 \pm 3 \mu\text{g g}^{-1}$) to drained ($57 \pm 3 \mu\text{g g}^{-1}$; Fig. 3A) sites. However, the OTC warming significantly increased extractable TIN from $49 \pm 3 \mu\text{g g}^{-1}$ to $57 \pm 3 \mu\text{g g}^{-1}$, and the highest average value of $70 \pm 4 \mu\text{g g}^{-1}$ occurred at the warmed drained hummocks. The warming also significantly increased extractable NH₄ by 31% on average, with the highest value of $19 \pm 3 \mu\text{g g}^{-1}$ at the warmed drained hummocks (Table 2; Fig. 3B). The warming-induced increases were consistent across sites/microforms. There was no significant effect of microform type on any of the extractable nutrient pools determined in this study.

The extractable NO₃ constituted a large portion of the extractable TIN (~77% across the data set) and showed a similar trend of increasing with decreasing WT level. Contrary to the extractable TIN, the extractable NO₃ pool was significantly different between sites (Table 2) with higher value of $45 \mu\text{g g}^{-1}$ at drained and lower values of $38 \mu\text{g g}^{-1}$ and $40 \mu\text{g g}^{-1}$ at the experimental and control sites, respectively. (Fig. 3C) which were not different from each other. The NO₃ was the only extractable nutrient which was not affected by the warming treatment.

The extractable PO₄, similar to available PO₄ pool was significantly affected by the gradients of WT level and OTC warming, with the highest value at the experimental site followed by a lower value at the control and the lowest value at the drained site (Table 2, Fig. 3D).

3.4 Foliar C:N ratio, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

The shrub C:N ratio, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (\pm SE) significantly responded to drainage (Table 3, Fig. 4). The drained site had significantly smaller C:N ratio (36 ± 1.4) and significantly greater depletion values of $\delta^{13}\text{C}$ (-30.2 ± 0.1 ‰) and $\delta^{15}\text{N}$ (-4.0 ± 0.5 ‰) than the corresponding control site C:N ratio (44 ± 1.3), $\delta^{13}\text{C}$ (-29.4 ± 0.1 ‰) and $\delta^{15}\text{N}$ values (-1.9 ± 0.4 ‰). At the experimental site, C:N ratio (38 ± 1.3) and $\delta^{15}\text{N}$ (-2.1 ± 0.5 ‰) differed from control and drained sites, while $\delta^{13}\text{C}$ (-29.8 ± 0.2) was statistically similar.

The shrub C:N ratio (\pm SE) also significantly responded to the warming treatment (Table 3, Fig. 4) with the lowest C:N ratio of 33 ± 1.1 at the drained warmed hummocks and the highest value of 49 ± 1.0 at the control hollows. Although shrub C:N ratio, $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ were not different between the microforms, a significant site – microform interaction was present with the C:N ratio declining at experimental and drained hollows, but only at drained hummocks.

Moss C:N ratio varied significantly both between microforms and in response to drainage (Table 3, Fig. 4) with a smaller value (\pm SE) at experimental (35 ± 1.4) than that at the control (40 ± 1.3) site, and lower value at hollow (35 ± 1.4) than that at hummock (41 ± 1.3) microform. The moss at hollows had greater depletion of $\delta^{15}\text{N}$ (-2.5 ± 0.4 ‰) than that at the hummock (-1.3 ± 0.5 ‰) microform. No significant differences between sites or microforms (warmed or ambient) were found for moss $\delta^{13}\text{C}$. Tree C:N ratio at the drained site (59 ± 10.1) was significantly lower (ANOVA, $F_{2,8} = 7.42$, $p = 0.038$) than the tree C:N values at the experimental (77 ± 1.7) and control (84 ± 1.6) sites which did not differ from each other (Fig. 4).

3.5 Peat available – extractable nutrient relationships

Peat available – extractable nutrient correlations were positive for all and significant for each of TIN ($p = 0.028$, $R^2 = 0.40$), NH_4 ($p = 0.039$, $R^2 = 0.36$) and PO_4 ($p = 0.001$, $R^2 = 0.69$) in the 0-

20 cm deep profile (Fig. 5A). The available NO_3 , which constituted a small portion of available TIN, was poorly correlated with the extractable NO_3 ($p = 0.220$, $R^2 = 0.15$) which constituted a large fraction of extractable TIN.

3.6 Peat TIN – foliar C:N ratio and $\delta^{15}\text{N}$ relationships

The changes in peat available and extractable TIN in response to the combined WT lowering and warming along the microtopography gradient, were reflected in significant correlations with shrub C:N ratio (Fig. 5B, 5C; $p = 0.049$, $R^2 = 0.31$ and $p = 0.031$, $R^2 = 0.34$, respectively). The peat – shrub TIN cycling link was further supported by the significant inverse correlation of peat extractable TIN with shrub $\delta^{15}\text{N}$ (Fig. 5D; $p = 0.044$, $R^2 = 0.35$).

The moss C:N ratio also decreased with increased available and extractable TIN, however, no significant relationships were detected (Fig. 5B, 5C; $p = 0.834$, $R^2 = 0.01$ and $p = 0.275$, $R^2 = 0.19$, respectively). The poor peat – moss TIN cycling link was also illustrated by the lack of relationship between peat extractable TIN with moss $\delta^{15}\text{N}$ (Fig. 5D; $p = 0.848$, $R^2 = 0.07$).

4 Discussion

4.1 Available and extractable mineral nutrients

We investigated peat available and extractable, and foliar nutrient pools in a sub-humid, continental wooded bog across hummock and hollow microforms in response to drainage and warming treatments. Generally, the soil mineral nutrient pools were related to each other and their sizes enlarged with WT lowering and warming with a greater increase at hummocks than hollows. The extractable TIN was also related to shrub C:N ratio and $\delta^{15}\text{N}$ which suggests that nutrient mineralization in response to warming and WT lowering can play a vital role in

ecosystem functioning of treed continental bogs. The extractable TIN, NO₃ and PO₄ pools in the undisturbed (control) site (Figs. 3) are comparable to the values previously reported for undisturbed boreal peatlands in Canada (Macrae et al., 2006; Macrae, Redding, Creed, Bell, & Devito, 2005; Wind-Mulder, Rochefort, & Vitt, 1996) and in a fir forest in Quebec, Canada (D'Orangeville et al., 2013) but are higher than the values observed in the undisturbed temperate peatlands in the Netherlands (Verhoeven et al., 1990) and Minnesota, USA (Bridgham, Updegraff, & Pastor, 1998). The available TIN, NH₄ and NO₃ pools in our control site were overall ~20% lower compared to those observed in the forest floor in a fir forest in Quebec, Canada (D'Orangeville et al., 2013), and well within the range of those observed in a mixed wood forest, Fort McMurray, Canada (Yan et al., 2012) and in a fen in the Netherlands (Paulissen, Van Der Ven, Dees, & Bobbink, 2004). The moderate differences in the extractable and available values are likely due to local biogeochemical, climatic, environmental and biophysical conditions that inherently differ in space and time.

Similar to the findings of Macrae et al. (2013), NO₃ comprised a large proportion of extractable TIN in our undisturbed bog. However, our results are in contrast to other peatland (e.g., Verhoeven et al., 1990; Westbrook & Devito, 2004; Wood et al., 2015) and forest ecosystems (D'Orangeville et al., 2013), where NH₄ comprised the largest proportion of the TIN concentration, similar to the availability trend in this study. The difference in extractable and available pools of NO₃ relative to NH₄ likely results from differences in the timing of the measurements and period of time each represents. The available pool was measured by incubation of the PRS probes over July and August, a period of active plant growth and microbial activity. Available NH₄ was greater than NO₃, and comprised a substantial portion of available TIN across the data set (Fig. 2). The NO₃ availability in ombrotrophic acidic bogs has

been reported to be notoriously lower than NH_4 due to unfavorable acidic cold environment resulting in inhibition of nitrification (Ste-Marie & Houle, 2006; Wieder & Vitt, 2006), and instant local uptake and denitrification (Urban, Bayley, & Eisenreich, 1989). Compared to NO_3 availability, the NH_4 availability has been reported to be as much as 10 times higher in *Sphagnum* stands in a Dutch fen (Paulissen et al., 2004). In contrast, extractable pools were measured on samples collected in October when both plant growth and microbial activity slow as temperatures cool. This likely resulted in a reduction in NO_3 uptake leading to a larger extractable pool that made up the majority of extractable TIN. Similarly, Macrae et al. (2013) report reduced extractable NO_3 in July and August, with concentrations increasing in September. Ideally, extractable pools would have to be measured at multiple times throughout the study period, but given the small size of the OTCs used for the warming treatment and the destructive nature of the soil sampling, determination of extractable pools was limited to the end of the study.

All of the available nutrient (PRS) values except NO_3 were strong predictors of the respective extractable nutrient values (Fig. 5A), although slopes of the correlations were not similar. The slope differences are very likely the result of different affinities of the various ions for the PRS probes or for plant root exchange sites. The strong correlations between nutrient availabilities and respective extractable concentrations demonstrate that the two pools were affected by the same dominant controls (e.g., WT, warming, moisture contents, and vegetation composition) and were dependent upon each other. Once equilibrium is established between the two pools, they act as dynamic exchangers. Therefore the two nutrient pools (excluding NO_3) may be used as the proxy of each other as suggested by others (Hangs et al., 2002; Huang & Schoenau, 1996).

In the undisturbed bog (control site), the extractable and available nutrient pools were overall greater at hummocks relative to hollows (Figs. 2, 3). This finding supports those of Eppinga et al. (2010) for undisturbed patterned peatlands and Macrae et al. (2013) for a natural open bog. The reason of higher extractable and available nutrients in hummock relative to hollow is likely linked to a combination of increased transpiration and enhanced uptake of nutrients from adjacent hollows by vascular vegetation leading to advection of nutrients from hollow to hummock (Eppinga, de Ruiter, Wassen, & Rietkerk, 2009; Eppinga et al., 2010), and increased decomposition of vascular plant litter locally at hummocks (Strack, Kellner, & Waddington, 2006). The extractable and available nutrient pools have also previously been linked with vegetation community type (Macrae et al., 2013). *Sphagnum* uses nutrient pools derived from atmospheric deposition and N-fixation (Vile et al., 2014), whereas vascular plants depend more on nutrient pools released during decomposition of plant litter/organic matter (Malmer, Albinsson, Svensson, & Wallén, 2003; Wieder & Vitt, 2006). Our undisturbed site had significantly higher shrub coverage at hummocks relative to hollows (T. M. Munir et al., 2015) and this may drive nutrient distribution through water use and litter composition.

4.2 Effects of OTC warming on peat nutrient dynamics

Soil extractable and available nutrient pools responded differently to OTC warming across sites (Tables 1, 2; Figs. 2, 3). A warming – microform interaction was observed where available TIN and NH₄ increased at hummocks but decreased at hollows, while warming alone increased PO₄ pools at all sites and microforms. The opposite response of hummocks to warming than hollows for N pools may be due to the significantly greater warming induced growth of shrubs at hummocks at this bog (T. M. Munir et al., 2015), a pattern also reported in a bog mesocosm in Minnesota, USA (Weltzin, Bridgham, Pastor, Chen, & Harth, 2003; Weltzin, Harth, Bridgham,

Pastor, & Vonderharr, 2001). The shrubs and trees have well- developed root systems that consistently slough off old root membranes providing easily decomposable organic matter. An increase in soil temperature accelerates mineralization possibly leading to larger pools of available and exchangeable nutrients.

Unlike the variable response of available nutrients to OTC warming, all the extractable nutrients (except NO_3 that responded moderately, $p = 0.082$) across all microforms and sites increased significantly with warming (Table 2; Fig. 3). The clear warming response in the extractable pools may be partly explained by the timing of sampling in October when nutrient uptake would be lower, thus allowing a clearer pattern of enhanced mineralization in response to warming to be observed. The warming induced increases in extractable and available nutrients were consistent with our hypothesis and support the results of previous studies (F. A. Dijkstra et al., 2010; Frey, Lee, Melillo, & Six, 2013; Weltzin et al., 2001). The magnitudes of the warming-induced increases in extractable TIN, NO_3 and NH_4 pools were the highest at the drained hummocks at which the highest warming induced productivity has been reported (T. M. Munir et al., 2015) and in fact nutrient pools were related to the reported productivity (ANOVA, $F_{1, 23} = 41.69$, $p < 0.001$, $R^2 = 0.39$). This study, combined with changes in carbon exchange measured at the same site, demonstrates that warming very likely increases nutrient concentrations directly by enhancing decomposition and subsequent mineralization of peat, and indirectly by accelerating nutrient cycling between the peat and vegetation as reported by previous studies (Bubier, Moore, & Bledzki, 2007; McGrath et al., 2000; Riis, Christoffersen, & Baattrup-Pedersen, 2014).

4.3 Effect of water-table on peat nutrient dynamics

Along the gradients of decreasing water-table and decreasing surface moisture, the available and extractable nutrient pools (except PO_4) increased, although the amount of NO_3 captured by the

PRS-probes was not significantly different along these gradients. A coincident pattern of increasing productivity along the same gradients at this treed bog was observed (T. M. Munir et al., 2015; T. M. Munir et al., 2014). Similar findings at other treed bogs in northern Alberta, Canada (Lieffers & Rothwell, 1987; Wood et al., 2015) and Finland (Heikurainen & Pakarinen, 1982) have also been reported. These findings are consistent with our expectations, and corroborate those of White, Shannon, Weltzin, Pastor, and Bridgham (2008) in a bog mesocosm study in Minnesota and Macrae et al. (2013) in an open bog in Quebec. Lowering the WT decreases peat water content, deforms the peat surface (subsidence) and increases the peat bulk density (Strack et al., 2006; Waddington & Price, 2000) leading to increases in extractable and available nutrient pools.

Both the available and extractable PO_4 were consistently the highest in the short-term drained (i.e., experimental) site, although there was no consistent difference between the microforms. In contrast to TIN, PO_4 response to longer-term drainage resulted in values that returned to very close to their original (control) available and extractable values. A WT lowering in a low pH environment causes formation of chelates (called chemisorption) between PO_4^{3-} and available heavy metals (Al^{3+} and/or Fe^{2+} , Fe^{3+}) a phenomenon that limits the movement of PO_4 leading to increased local concentration (White et al., 2008). Three years of oxic conditions would have resulted in mineralization leading to increases in extractable and available PO_4 pools. The reversal could be due to the drained site's thick oxic zone that supported the growth of shrubs of extensive and deeper root system (T. M. Munir et al., 2015) that in turn required greater amounts of PO_4 (Cleve, Oliver, Schlentner, Viereck, & Dyrness, 1983; Rolo, Lopez-Diaz, & Moreno, 2012), removing it effectively from the peat. Macrae et al. (2013) also reported no difference in PO_4 concentrations between control peatlands and those drained for ~10 years, a

result that could be due to a more limited WT drawdown of only 20 cm in that study, or a similar return to pre-drainage pools as observed in this study.

4.4 Effect of warming and drainage on vegetation C:N ratio, $\delta^{13}C$ and $\delta^{15}N$

For moss C:N ratio, we report mean values of 48 ± 1.2 for control hummock and 38 ± 1.1 for control hollow (Fig. 4); average of which is slightly lower than the seasonal hummock – hollow mean value of 47 reported by Wang and Moore (2014) for Mer Bleue bog in Eastern Canada. They sampled sun-exposed capitula of mosses for determination of C:N mass ratios while our moss samples were from plots that were invariably shaded by shrubs and a > 42% coverage of black spruce. Shading has been found to significantly reduce the C:N ratio of *Sphagnum* capitula from ~54 to ~27 from peat mesocosms removed from a raised bog in Upper Teesdale, UK (Bonnett, Ostle, & Freeman, 2010). Although C:N over 100 has been reported for *Sphagnum* litter (Asada, Warner, & Aravena, 2005), several studies report values similar to the present study of 30-50 (e.g., Limpens, Berendse, & Klees, 2003; Péli, Nagy, & Cserhalmi, 2016; Toet et al., 2006). We also observed that C:N ratio of *Sphagnum* was similar to the leaves of *R. groenlandicum*, a result consistent with reported C:N ratios from a range of plant functional types in a shrubby ombrotrophic bog in eastern Canada (Wang et al., 2014).

Both warming and drainage increased TN or decreased C:N ratio of shrubs over the long-term with greater increases at hummocks than hollows. A lowered WT level combined with warming results in deeper rooting zone and promotes vascular vegetation (shrub, tree) coverage at the expense of moss coverage (T. M. Munir et al., 2015). As *Sphagnum* is known to restrict the availability of nutrients to shrubs (Malmer et al., 2003), the loss of moss in response to drainage may help increase the available nutrient pools. In addition, increased shrub growth in

response to both a thicker oxic zone and greater nutrient availability likely creates additional stress on mosses through shading, as has been observed in N-fertilization experiments in bogs (e.g., Bubier et al., 2007). Finally, shrubs under warmer conditions have higher leaf and litter polyphenol content which retards microbial N immobilization and facilitates the growth of symbiotic fungi and hence the acquisition of dissolved organic N (Bragazza, Parisod, Buttler, & Bardgett, 2013).

Tree C:N ratio also decreased with deeper WT position, indicating that the larger TIN pools in the soils at drier sites resulted in higher N content in the overstory biomass. Our findings corroborate with those of W. J. Choi et al. (2007) and Riis et al. (2014) for strong relationships between soil TIN and vascular vegetation C:N ratios. Moss TN and C:N values also changed slightly in response to warming and short-term drainage (very little moss was present at the longer term drained sites), but these shifts were limited. This suggests that vascular plants are better able to access the newly available soil N pool in the rhizosphere compared to mosses that rely largely on N deposition and N-fixation (Vile et al., 2014).

While only WT lowering was a strong enough control to enhance productivity with increased uptake of N (greater foliar depletion of $\delta^{15}\text{N}$) over the long-term, both warming and WT lowering resulted in a greater foliar depletion of $\delta^{13}\text{C}$ for shrubs. This increase in C isotope fractionation may indicate a decrease in stomatal conductance in response to period of water stress. W. J. Choi et al. (2007) also report small, but not significant depletion of $\delta^{13}\text{C}$ in shrubs following peatland drainage. Further research is required to evaluate shrub water use in response to changing water table and temperature. Increased productivity as observed at this site (T. M. Munir et al., 2015) accompanied greater N uptake, resulted in more negative values (depletion) of $\delta^{15}\text{N}$ in the plant leaf compared to the values in the rhizosphere soil or air (W.-J. Choi, Chang,

Allen, Kelting, & Ro, 2005; Mugasha, Pluth, & Macdonald, 1999; D. Robinson, 2001) unless the rhizosphere soil is highly mineralized which may lead to $\delta^{15}\text{N}$ enrichments instead.

4.5 Conclusions

Nutrient pools increased with deepening of the water-table and drying of the peat surface. The response was greater at hummocks relative to hollows. The increases along the decreasing WT gradient were enhanced by a warming of ~ 1 °C. The changes in peat mineral nutrients driven by warming, and WT and moisture decline, were reflected in vascular vegetation C:N ratio and, shrub $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ while the mosses remained largely unaffected by these changes. However, mosses were largely eliminated from the longer-term drained site, likely largely due to water stress, but possibly also linked to enhanced shrub growth and shading that was partially supported by greater nutrient availability. The shifts in peat nutrient pools were reflected in plant tissue and this suggests that the increased productivity we observed at this bog (T. M. Munir et al., 2015) was due in part to larger nutrient pools in response to the warming and WT lowering. The peat – shrub relationships are supported by the robust depletion of foliar $\delta^{15}\text{N}$. The changes in bog nutrient dynamics observed in this study likely mediated shifts in NPP, plant community composition, litter quality and hence overall ecosystem functioning. Therefore, peatland models need to integrate nutrient cycling modules with moisture (dynamic water-table) and temperature modifiers of growth and decay functions to derive C budgets under disturbance.

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6 Tables

Table 1. Mixed-effects ANOVA *F* and *p*-values for the fixed effects of water-table level (control, experimental, drained), warming (non-OTC, OTC) and microform (hummock, hollow) with repeated measures of year (2012, 2013), on TIN, NH₄, NO₃ and PO₄ availability (PRS nutrient supply rate) ^a.

Effect	df	Nutrient Availability (µg 10cm ⁻²)							
		TIN		NH ₄ -N		NO ₃ -N		PO ₄ -P	
		<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Water-table level	2, 24	19.63	0.000	31.70	0.000	4.23	0.027	18.25	0.000
Microform	1, 24	29.91	0.000	47.54	0.000	0.03	0.857	3.33	0.080
Warming	1, 24	0.22	0.644	0.27	0.607	0.00	0.971	0.72	0.405
Water-table level × Microform	2, 24	2.70	0.087	7.24	0.003	2.35	0.117	4.90	0.016
Water-table level × Warming	2, 24	0.01	0.992	0.13	0.883	0.87	0.432	0.28	0.761
Microform × Warming	1, 24	9.37	0.005	8.55	0.007	4.39	0.047	0.01	0.940
Water-table level × Microform × Warming	2, 24	0.90	0.421	1.72	0.200	0.98	0.389	0.59	0.943

^a TIN, NH₄, NO₃ and PO₄ represent total inorganic nitrogen, nitrate, ammonium and phosphate, respectively. Values in bold show significant differences at $\alpha = 0.05$.

Table 2. Mixed-effects ANOVA *F* and *p*-values for the fixed effects of water-table level (control, experimental, drained), warming (non-OTC, OTC) and microform (hummock, hollow), on TIN, NH₄, NO₃ and PO₄ extractable nutrients ^a.

Effect	df	Nutrient Concentration (µg g ⁻¹)							
		TIN		NH ₄ -N		NO ₃ -N		PO ₄ -P	
		<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Water-table level	2, 24	0.99	0.385	0.83	0.447	3.57	0.044	12.75	0.000
Microform	1, 24	0.56	0.816	0.64	0.802	0.13	0.724	1.17	0.289
Warming	1, 24	4.56	0.043	5.86	0.023	1.67	0.082	4.08	0.045
Water-table level × Microform	2, 24	0.74	0.490	0.64	0.538	0.29	0.754	0.47	0.954
Water-table level × Warming	2, 24	0.29	0.750	0.61	0.551	0.15	0.865	0.80	0.461
Microform × Warming	1, 24	0.17	0.687	0.83	0.372	0.01	0.935	0.01	0.943
Water-table level × Microform × Warming	2, 24	0.98	0.388	1.25	0.305	0.62	0.622	1.06	0.361

^a TIN, NH₄, NO₃ and PO₄ represent total inorganic nitrogen, nitrate, ammonium and phosphate, respectively. Values in bold show significant differences at $\alpha = 0.05$.

Table 3. Mixed-effects ANOVA *F* and *p*-values for the fixed effects of water-table level (control, experimental, drained), warming (non-OTC, OTC) and microform (hummock, hollow) on understory foliar C:N ratio and carbon and nitrogen isotope ratios.

Effect			C:N ratio				$\delta^{13}\text{C}$ (‰)				$\delta^{15}\text{N}$ (‰)			
	Shrub	Moss	Shrub		Moss		Shrub		Moss		Shrub		Moss	
	df	df	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Water-table level	2, 21	1, 15	9.96	0.001	7.50	0.015	5.41	0.013	0.00	0.971	5.16	0.015	0.27	0.613
Microform	1, 21	1, 15	0.33	0.574	8.90	0.009	0.10	0.754	0.16	0.697	0.26	0.619	3.19	0.094
Warming	1, 21	1, 15	4.55	0.045	1.39	0.257	8.29	0.009	0.80	0.384	0.51	0.482	0.10	0.763
Water-table level × Microform	2, 21	1, 15	4.53	0.023	4.03	0.063	1.29	0.296	1.19	0.293	0.08	0.924	0.98	0.339
Water-table level × Warming	2, 21	1, 15	0.51	0.606	0.41	0.529	0.54	0.590	0.01	0.945	0.16	0.858	0.33	0.574
Microform × Warming	1, 21	1, 15	0.00	0.961	1.41	0.253	0.37	0.548	2.22	0.157	2.68	0.117	0.95	0.345
Water-table level × Microform × Warming	2, 21	1, 15	0.09	0.911	0.43	0.522	3.68	0.043	0.02	0.898	1.16	0.334	0.00	0.979

Values in bold show significant differences at $\alpha = 0.05$.

7 Figures

Figure Captions

Figure 1. Mean daily water-table level, mid-day differential (warmed – ambient) air temperature and precipitation at hummock and hollow microforms during growing season of 2012-2013.

Note the right y-axis shows two different variables using the same scale: mean mid-day differential air temperature and daily precipitation. The x-axis breaks separate 2012 and 2013.

Figure 2. Mean peat available nutrients: **(A)** total inorganic nitrogen (TIN), **(B)** ammonium nitrogen ($\text{NH}_4\text{-N}$), **(C)** nitrate nitrogen ($\text{NO}_3\text{-N}$), and **(D)** phosphate phosphorus ($\text{PO}_4\text{-P}$) in peat profile as indicated by PRS probes at the ambient and warmed hummock (H, HO) and hollow (W, WO) microforms across sites. Each error bar indicates \pm SD of the mean ($n = 6$).

Figure 3. Mean peat extractable nutrients: **(A)** total inorganic nitrogen (TIN), **(B)** ammonium nitrogen ($\text{NH}_4\text{-N}$), **(C)** nitrate nitrogen ($\text{NO}_3\text{-N}$), and **(D)** phosphate phosphorus ($\text{PO}_4\text{-P}$) in peat profile of 0-20 cm within the ambient and warmed hummock (H, HO) and hollow (W, WO) microforms across sites. Each error bar indicates \pm SD of the mean ($n = 3$).

Figure 4. Mean foliar C:N ratio of shrub, moss and tree functional types at ambient and warmed hummock (H, HO) and hollow (W, WO) microforms across sites. Each bar with an error bar shows a mean ($n = 3$) C:N ratio (\pm SD) in a plant functional type sampled from microforms in 2013. Moss data from drained site which had different types of mosses than control and experimental sites, are not included. Trees could not be warmed given the small size of the plots/OTCs.

Figure 5: **A)** Relationship between peat available and extractable nutrients: total inorganic nitrogen (TIN; $y = 39 + 1.0x$, $R^2 = 0.40$, $p = 0.028$), ammonium nitrogen ($\text{NH}_4\text{-N}$; $y = 8 + 0.3x$, $R^2 = 0.36$, $p = 0.039$), nitrate nitrogen ($\text{NO}_3\text{-N}$; $y = 38 + 2.0x$, $R^2 = 0.15$, $p = 0.220$) and phosphate phosphorus ($\text{PO}_4\text{-P}$; $y = 3 + 4.4x$, $R^2 = 0.69$, $p = 0.001$). Each point shows means of available ($n = 3$) and extractable ($n = 3$) nutrient pools; **B)** Relationship of peat available TIN with shrub C:N ratio ($y = 49 - 0.6x$, $R^2 = 0.31$, $p = 0.049$) and moss C:N ratio ($y = 39 - 0.2x$, $R^2 = 0.01$, $p = 0.834$). Moss data from drained site which had different types of mosses than control and experimental sites, are not included; **C)** Relationship of peat extractable TIN with shrub C:N ratio ($y = 63 - 0.4x$, $R^2 = 0.34$, $p = 0.031$) and moss C:N ratio ($y = 64 - 0.5x$, $R^2 = 0.19$, $p = 0.275$); **D)** Relationship of peat extractable TIN with shrub $\delta^{15}\text{N}$ ($y = 0.3 - 0.1x$, $R^2 = 0.35$, $p = 0.044$) and moss $\delta^{15}\text{N}$ ($y = -1.5 - 0.0x$, $R^2 = 0.07$, $p = 0.848$). Non-significant relationship is indicated by dotted line.









