

# Effect of water table drawdown on peatland nutrient dynamics: implications for climate change

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**Abstract** It is anticipated that a lowering of the water table and reduced soil moisture levels in peatlands may increase peat decomposition rates and consequently affect nutrient availability. However, it is not clear if patterns will be consistent across different peatland types or within peatlands given the natural range of ecohydrological conditions within these systems. We examined the effect of persistent drought on peatland nutrient dynamics by quantifying the effects of an experimentally lowered water table position (drained for a 10-year period) on peat KCl-extractable total inorganic nitrogen (ext-TIN), peat KCl-extractable nitrate (ext-NO<sub>3</sub><sup>-</sup>), and water-extractable ortho-phosphorus (ext-PO<sub>4</sub><sup>3-</sup>) concentrations and net phosphorus (P) and nitrogen (N)

mineralization and nitrification rates at natural (control) and drained microforms (hummocks, lawns) of a bog and poor fen near Québec City, Canada. Drainage (water table drawdown) decreased net nitrification rates across the landscape and increased ext-NO<sub>3</sub><sup>-</sup> concentrations, but did not affect net N and P mineralization rates or ext-TIN and ext-PO<sub>4</sub><sup>3-</sup> concentrations. We suggest that the thick capillary fringe at the drained peatland likely maintained sufficient moisture above the water table to limit the effects of drainage on microbial activity, and a 20 cm lowering of the water table does not appear to have been sufficient to create a clear difference in nutrient dynamics in this peatland landscape. We found some evidence of differences in nutrient concentrations with microforms, where concentrations were greater in lawn than hummock microforms at control sites indicating some translocation of nutrients. In general, the same microtopographic differences were not observed at drained sites. The general spatial patterns in nutrient concentrations did not reflect net mineralization/immobilization rates measured at our control or drained peatlands. Rather, the spatial patterns in nutrient availability may be regulated by differences in vegetation (mainly *Sphagnum* moss) cover between control and drained sites and possibly differences in hydrologic connection between microforms. Our results suggest that microform distribution and composition within a peatland may be important for determining how peatland nutrient dynamics will respond to water table drawdown in northern

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peatlands, as some evidence of microtopographic differences in nutrient dynamics was found.

**Keywords** Peatlands · Nitrogen · Phosphorus · Drainage · Water table drawdown · Microtopography

## Introduction

Approximately 12 % of the Canadian land mass are covered by peatlands (Bridgman et al. 2006), many of which are under threat due to climate change (IPCC 2007). Non-permafrost peatlands are predicted to become drier with lower water tables under a warmer climate (Roulet et al. 1992) unless increased evapotranspiration rates are balanced by increases in precipitation. These hydrologic changes are likely to result in shifts in microbial activity and nutrient cycling that could represent an important feedback on plant community types, productivity and whole ecosystem function. However, these nutrient feedbacks to drying remain unclear. Here we examine the effects of peatland water table drawdown (drainage) on nutrient dynamics in a bog and poor fen, as a proxy for drying under a warmer climate.

The lowering of peatland water table position modifies peatland function hydrologically, biogeochemically and ecologically. A lower water table position leads to a drier peat and moss surface (Waddington et al. 2010) and altered watershed runoff quantity, timing and flowpaths, and moisture storage (Holden et al. 2004). Lowering the peatland water table position may also cause some peatlands to shift from carbon sinks to sources (Blodau 2002; Strack and Waddington 2007), increase the mineralization of organic material (Bayley et al. 2005; Holden et al. 2004; Wassen et al. 2006; Williams and Wheatley 1988), and potentially increase nutrient export (De Mars et al. 1996). Indeed, studies have reported an increase in nutrient concentrations post-drainage, and even greater increases in nutrient content ( $\text{kg ha}^{-1}$ ) due to the increases in bulk density (Sundstrom et al. 2000; Wells and Williams 1996; Williams and Wheatley 1988) that result from the subsidence and compression of the peat following drainage (Strack and Waddington 2007; Whittington and Price 2006). In the current study, we hypothesize that water table drawdown will increase nutrient mineralization rates

and consequently the concentrations of extractable nutrients in surface peat due to the lowered water table, reduced peat moisture and more oxic conditions, as has been observed by others (Devito and Dillon 1993; Devito and Hill 1997; Holden et al. 2004).

Although the effects of drainage on peatland nutrient dynamics have been examined previously (e.g. Holden et al. 2004; Williams and Wheatley 1988), this has not been systematically examined across different peatland types. It is widely accepted that fens are more productive and have faster decomposition rates than bogs and that fens more effectively mineralize nutrients (Bridgman et al. 1996). This has been related to CN ratios by some authors (e.g. Bayley et al. 2005; Moore et al. 2005), where bog peats, having larger CN ratios, decompose slowly and have lower mineralization rates than sites with lower CN ratios (e.g. fens). However, while bogs have lower total nutrient concentrations in soil organic matter in comparison to fens, the soil nutrients that are present are rapidly mineralized under aerobic conditions (Bridgman et al. 1996), suggesting that a lower water table may result in a greater increase in nutrient mineralization rates in bogs than in fens. Indeed, other studies on the effects of drying (Updegraff et al. 1995) and drainage (Wells and Williams 1996) on peat mineralization rates have observed increases in bogs but not fens. Thus, we hypothesized that nutrient concentrations and mineralization rates in our study would be larger in a natural (undisturbed) fen compared to an adjacent bog, but drainage would cause a larger increase in nutrient mineralization and nutrient concentrations in the bog.

Within peatlands, nutrient dynamics (and responses to drying) are also expected to vary between microforms (e.g. hummocks, lawns and hollows). In natural peatlands, microforms differ in their moisture content, oxic/anoxic conditions, and dominant vegetation species (Belyea and Baird 2006; Eppinga et al. 2010; Rydin and Jeglum 2006; Strack et al. 2006). These differences lead to differences in gross ecosystem production and peat decomposition rates (e.g. Strack et al. 2006) with intermediate water table position microforms such as lawns generally storing more carbon than the drier (hummocks) and wetter (hollows) microforms (e.g. Belyea and Clymo 2001; Moore 1989; Strack et al. 2006). Vegetation differences between hummocks and hollows result in different nutrient demands (Turetsky 2003), which

may affect available nutrient pools (Aerts et al. 1999). Larger peat total and extractable nutrient concentrations have frequently been observed in hummocks relative to hollows due to a combination of increased uptake of nutrients from surrounding hollows by vascular vegetation and increased decomposition of vascular plant litter locally within hummocks (Bruland and Richardson 2005; Eppinga et al. 2008, 2010; Rietkerk et al. 2004; Williams and Crawford 1983; Zimenko and Misnik 1970). However, recent work (Eppinga et al. 2009, 2010; Rietkerk et al. 2004) suggests that the nutrient-regulating mechanisms in patterned peatlands may differ between drainage-dominated systems (systems having a low evapotranspiration to precipitation ratio, Eppinga et al. 2010) and evapotranspiration-dominated systems (systems having a high evapotranspiration to precipitation ratio, Eppinga et al. 2010). The authors argue that in drainage-dominated systems nutrient pools are lower in hummocks relative to hollows due to the transfer of nutrients from hummocks to hollows via runoff, whereas in evapotranspiration-dominated systems nutrients are greater in hummocks relative to hollows, due to the advection of nutrients from hollows to hummocks and a positive feedback in peat production rates (Eppinga et al. 2008). This suggests that hydrology is an important control on the spatial patterns in nutrient transformations in peatlands, particularly those related to microtopography, and that a persistently lower water table position has the potential to modify these spatial patterns. Given that nutrient concentrations are also linked to vegetation community composition and microbial activity, these shifts have important implications for overall peatland form and function. In the current study, greater N concentrations are expected in hummocks at natural (undisturbed) sites due to increased N mineralization under drier, oxic conditions as previous work at this site (e.g. Strack et al. 2006, 2008) has shown that hummocks are drier than lawns. In contrast, larger ext- $\text{PO}_4^{3-}$  concentrations are expected in lawns, as P is more soluble under anoxic conditions (Moser et al. 2009).

Recent research suggests that peatland water table drawdown (an analog for persistent drought) may reduce the natural hydrological and biogeochemical differences between microforms, leading to a more homogeneous system. For example, Whittington and Price (2006) reported dampened hydrological differences between microforms at drained sites relative to

control sites in a poor fen in Québec, while Strack et al. (2006, 2008) observed that a lower water position caused hummocks to dry and degrade while hollows became more productive, leading to smaller differences in peatland-atmosphere carbon exchange rates between microforms. We hypothesized that differences in nutrient dynamics between microforms would be dampened following drainage in the current study, leading to a more homogeneous landscape, as was observed for rates of gaseous carbon exchange by Strack et al. (2006). More specifically, we expected to see a small increase in net mineralization and consequently nutrient concentrations in hummocks due to increased drying, while a larger increase in mineralization rates and nutrient concentrations would be observed in lawns due to a shift from anoxic to oxic conditions. However, it is equally plausible that that no changes may be observed as the capillary fringe (the region above the water table where groundwater migrates upwards under the forces of capillary suction) may maintain sufficient moisture above the water table in drained peatlands to limit the effect of drainage on microbial activity. Nevertheless, to our knowledge no studies on the impacts of peatland water table drawdown have considered the variability in nutrient dynamics between microforms within peatlands, and few have examined how this may vary between bogs and fens (e.g. Bayley et al. 2005; Bridgman et al. 1996; Verhoeven et al. 1990). Thus, the objectives of this study are to determine: (i) the effect of water table drawdown (drainage) on peatland ext-TIN, ext- $\text{NO}_3^-$  and ext- $\text{PO}_4^{3-}$  concentrations, and net N and P mineralization and nitrification rates; and (ii) if drainage dampens the microtopographic differences in peat extractable nutrient concentrations and transformations that are observed in the control (natural) fen and bog. We hypothesized that a general increase in net mineralization and net nitrification rates would be observed; however, the effects of drainage would be spatially variable and would not be consistent across peatlands and microforms.

## Materials and methods

### Study site

Research for this study was conducted in both an open bog and open poor fen in the St-Charles-de-Bellechasse (SCB) peatland complex near St-Charles-de-

Bellechasse, Québec (46°40'N, 71°10'N) between May and September, 2004. The SCB peatland complex includes portions of natural peatland as well as a section of bog and fen that was drained in 1993 lowering the water table by ~20 cm relative to the control plot. This drainage was maintained over the ten-year period. For this study we selected a site within the previously drained portion of the bog and fen (hereafter referred to as drained) and paired each with an adjacent natural (or control) site located far enough from any drainage activities that it was unaffected hydrologically (Pavey et al. 2007; Whittington and Price 2006). Within each of the paired drained and control sites of both the bog and fen, different microforms (hummocks, lawns and pools) were present. The hummocks form micro-topographic high regions above adjacent flat low-lying lawn areas. Pools, which accounted for a smaller proportion of the landscape relative to hummocks and lawns, were not considered in this study, primarily because of issues with our methodological approach (buried bag technique) to measuring extractable nutrients and net mineralization rates.

At the control fen, mean (standard deviation) water table positions during the study were -13.7 cm ( $\pm 3.0$  SD) and -6.2 cm ( $\pm 3.2$  SD) at hummocks and lawns, respectively. At the drained fen, mean water table position was -26.4 cm ( $\pm 5.7$  SD) at hummocks and -10.6 cm ( $\pm 7.3$  SD) at lawns. The magnitude of water table drawdown relative to the surface was limited due to the occurrence of soil subsidence in response to the drainage (Whittington and Price 2006). Water table position at hummocks was -24.7 cm ( $\pm 5.0$  SD) at the control bog site and -48.0 cm ( $\pm 7.5$  SD) at the drained bog site. Although detailed water table measurements were not available for bog lawns, soil moisture was determined at all study plots (see below).

Mean precipitation and air temperature for the period May to September for this region are 590 mm and 15.5 °C, respectively, based on 30-year averages (1971–2000) (Environment Canada 2003). 2004 was considered a normal year, receiving 601 mm of precipitation and averaging 14.2 °C.

Peat depths range from 0.8 to 1.5 m depth in the fen and are more than 4 m deep in the bog. The peat is underlain by clay mineral soil (Strack et al. 2008). Dominant vegetation cover on the control fen hummocks consisted of *Sphagnum rubellum*, *Chamaedaphne*

*calyculata*, *Carex oligosperma*, whereas the control fen lawns were dominated by *Sphagnum fallax*, *Sphagnum papillosum*, and *Carex limosa*. At the drained fen, hummocks were dominated by *Polytrichum strictum* and *Chamaedaphne calyculata* whereas lawns were dominated by *Sphagnum magellanicum* and *Carex oligosperma*. In the bog, dominant vegetation at the control hummocks consisted of *Sphagnum rubellum*, *S. magellanicum*, and *Chamaedaphne calyculata*, whereas the control lawns were dominated by *S. rubellum* and *Rhynchospora alba*. At the drained bog, hummocks were dominated by *Polytrichum strictum*, *Ledum groenlandicum*, and *Kalmia angustifolia* whereas the drained bog lawns were dominated by *S. rubellum*, *Rhynchospora alba*, and *Vaccinium macrocarpon*.

## Methods

Triplicate hummock and lawn peat cores were collected at the start and end of each month from May to September (2004) within the paired control and drained sites in both the bog and fen. Peat cores were collected with a stainless steel corer (10 × 10 × 20 cm deep) and divided into two 10 × 10 cm samples (0–10 and 10–20 cm), using a serrated knife to minimize core compaction and maintain a representative sample. Peat cores were placed in plastic bags, packed on ice and analyzed for gravimetric moisture content, bulk density, water-extractable  $\text{PO}_4^{3-}$ , and KCl-extractable  $\text{NO}_3^-$  and  $\text{NH}_4^+$ .

Peat samples were processed (nutrient extractions) within 12 to 24 h of collection. While it is possible that samples collected from anoxic environments were affected by oxygen within this time period, excess air was removed from collection bags to minimize contact with the air and these samples were processed as quickly as possible. In the laboratory, peat samples, while still in their bags, were hand mixed until visually homogenized and two ~5 g (dry weight) subsamples were removed. Using the approach of Binkley and Hart (1989), one subsample was extracted in 50 ml of distilled-deionized water for colorimetric analysis of soluble reactive phosphorus (SRP) and the second subsample was extracted in 50 ml of 2 M KCl for colorimetric analysis of  $\text{NO}_3^-$  and  $\text{NH}_4^+$  (Technicon, Tarrytown, USA). The remainder of the peat sample was dried at 105 °C for 24 h to determine gravimetric moisture content and bulk density in the Ecohydrology Lab at McMaster University.

In situ nutrient net mineralization and nitrification rates were estimated using the buried-bag method of Eno (1960). Cores were incubated in polyethylene bags in the field (at field water content) for approximately three weeks. After the incubation period, these soils were transported to the lab and extracted using the same methods described above. Net N and P mineralization for a site for a given incubation period were determined from the average difference between the amounts of ext-TIN ( $\text{ext-NH}_4^+ + \text{ext-NO}_3^-$ ) or  $\text{ext-PO}_4^{3-}$  in the triplicate cores at the beginning and end of an incubation period (Hart et al. 1994). Net nitrification was determined from the average difference in  $\text{ext-NO}_3^-$  between peat cores collected at the beginning and end of the incubation period.

For the final (September) sampling campaign, triplicate subsamples were composited for each site and analyzed for their total Kjeldahl phosphorus (Technicon, Ammonium-molybdate-ascorbic acid reduction), organic content (LOI) and total carbon and nitrogen content (Shimadzu TOC-V Model) in the Department of Renewable Resources at the University of Alberta.

### Statistical analyses

Due to the presence of frost during the May sampling period, we were unable to collect samples at 10–20 cm depth at some sites. Consequently, we did not have matching measurements for 0–10 and 10–20 cm across the entire study period. Thus, data were separated by depth and analyzed separately. In our examination of the data, patterns observed at 10–20 cm peat depth were generally the same as those observed at 0–10 cm depth, and consequently only results for 0–10 cm peat depths are presented in this paper. Given the objectives of the study, we ran a three-way (full factorial) analysis of variance (ANOVA) of nutrient concentrations ( $\mu\text{g g}^{-1}$  dry peat), mineralization rates ( $\mu\text{g g}^{-1}$  dry peat month $^{-1}$ ) and peat moisture content ( $\text{m}^3 \text{m}^{-3}$ ) using drainage (control, drained), peatland type (bog, fen), and microform (hummock, lawn) as fixed factors (SPSS Software, version 18). We also ran a three-way ANOVA on seasonal totals of net N and P mineralization and net nitrification (generated by summing monthly net mineralization and net nitrification rates). Data used in all ANOVA tests were normally distributed. Post hoc analyses (Tukey) were performed using

SAS Software. A Spearman Rank Correlation test was used to compare seasonal nutrient mineralization rates to peat total nutrient content. Differences were considered significant at the 0.05 level. Mean and standard deviation (SD) are presented in the results.

## Results

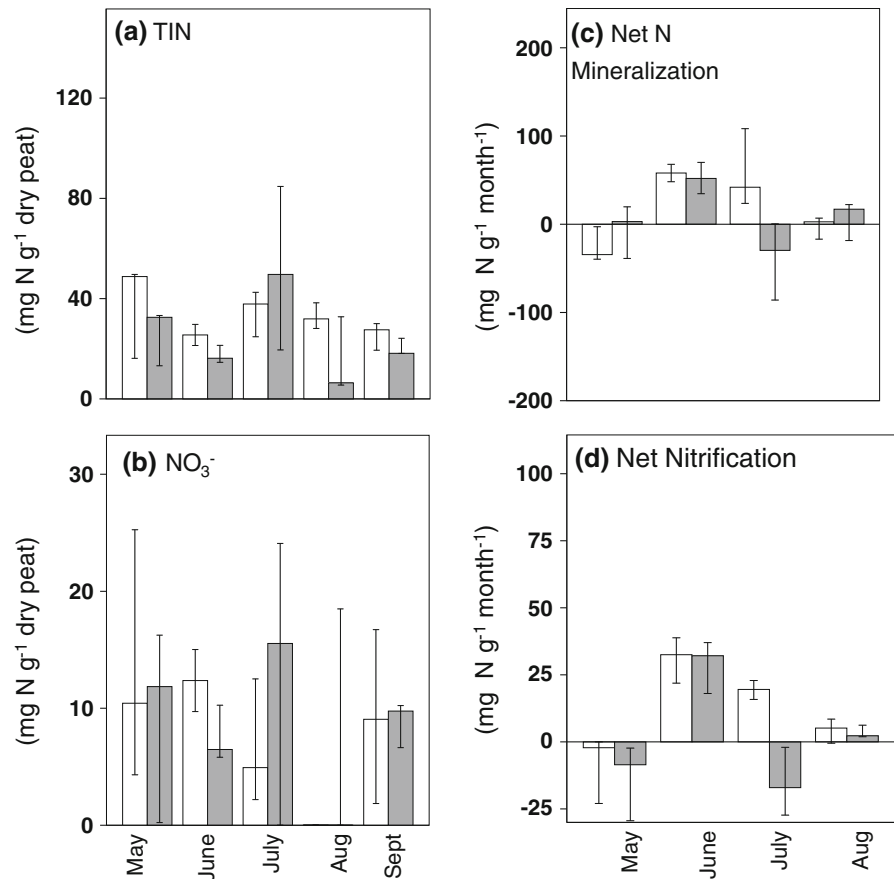
### Peat extractable nitrogen concentrations

Nitrate comprised a substantial portion ( $25 \pm 19\%$  SD across the data set) of ext-TIN concentrations and spatiotemporal patterns were similar between ext-TIN and  $\text{ext-NO}_3^-$ .

Peat nutrient concentrations in July are presented in this paper due to the dominance of this period in seasonal patterns in nutrient dynamics. Seasonal trends in median monthly ext-TIN and  $\text{ext-NO}_3^-$  concentrations of the bog lawn sites are shown as an example in Fig. 1a and b, and are similar to seasonal trends observed in the other microform and peatland sites. Monthly concentrations of surface peat extracts varied temporally over the season, with peak ext-TIN and  $\text{ext-NO}_3^-$  concentrations observed in July. A one-way ANOVA reported significant differences in both ext-TIN and  $\text{ext-NO}_3^-$  concentrations with date ( $P < 0.001$ ), and this pattern was observed across all sites. Post hoc (Tukey) analyses showed that ext-TIN concentrations were higher in July than the other dates sampled ( $P < 0.001$ ) but did not differ among the other four dates ( $P > 0.05$ ). A four-way ANOVA using all sampling dates (not shown) was run to test for the effects of drainage, peatland type, microform and date. However, the effect of date was significant, and there were complex interactions with the other three factors that were difficult to interpret. Consequently, given the dominance of the July period in seasonal nutrient dynamics, only the July sampling period was used when examining spatial differences in nutrient concentrations. In general, the same spatial patterns observed in July were also seen during the other sampling periods.

Mean July ext-TIN concentrations did not differ significantly between the control and drained sites ( $P = 0.093$ , Table 1) due to the large variability between and within peatland types (shown in table as WTD for water table drawdown). However, ext-TIN concentrations averaged over both microforms in the

**Fig. 1** Seasonal trends in concentrations of **a** extractable total inorganic nitrogen **b** extractable nitrate **c** net N mineralization rates and **d** net nitrification rates in surface peat at the bog lawn sites. *Control sites* are shown in white and *drained sites* are shown in grey. Medians are shown with bars and 95 % CI are shown with error bars. Samples collected in August produced very low nitrate concentrations



bog ( $55 \pm 21 \mu\text{g N g}^{-1}$ ) were significantly lower than in the fen ( $75 \pm 22 \mu\text{g N g}^{-1}$ ) ( $P < 0.001$ , Table 1). There was also a significant difference in ext-TIN concentrations between microforms across both peatlands, where hummocks had lower ext-TIN concentrations ( $47 \pm 26 \mu\text{g N g}^{-1}$ ) than lawns (mean =  $69 \mu\text{g N g}^{-1} \pm 36 \text{SD}$ ) ( $P = 0.02$ , Table 1).

There was a significant interaction in differences in surface peat ext-TIN concentrations between drained and control sites in both the bog and fen ( $P = 0.05$ , Table 1), where drainage increased peat ext-TIN concentrations in the bog but did not increase peat ext-TIN concentrations in the fen (Fig. 2a, b). The interaction between drainage and microform type was moderately significant ( $P = 0.058$ , Table 1). Hummocks had lower ext-TIN concentrations than lawns at control sites, but there was very little difference between hummocks and lawns at drained sites (Fig. 2a, b). This trend was observed in both the bog and the fen.

In contrast to ext-TIN, mean seasonal ext- $\text{NO}_3^-$  concentrations of all microforms on both drained peatlands (mean =  $14 \mu\text{g N g}^{-1} \pm 8 \text{SD}$ ) were significantly higher than at control peatlands (mean =  $4 \mu\text{g N g}^{-1} \pm 3 \text{SD}$ ) ( $P = 0.003$ , Table 1). However, in contrast to ext-TIN, mean July peat ext- $\text{NO}_3^-$  concentrations did not differ between the bog and fen ( $P = 0.759$ ) or between microforms ( $P = 0.908$ ) (Fig. 3a, b).

Although no significant interactions were observed between drainage and peatland type or microform ( $P > 0.05$ , Table 1), drainage appears to have increased ext  $\text{NO}_3^-$  concentrations in hummocks, but lead to more variability at lawn sites (Fig. 3a, b).

#### Net nitrogen mineralization and nitrification

Net N mineralization and net nitrification were temporally variable over the study period. At all sites, net N mineralization and net nitrification were usually



**Table 1** Environmental controls on peat nutrient concentrations in surface peat

	Source	df	Type III SS	F value	Sig. <sup>a</sup>
Results of analysis of variance comparing effects of water table drawdown (WTD, control, drained), peatland (bog, fen), and microform (hummock, lawn). Degrees of freedom (df), type III sum of squares (SS), F value and significance (Sig.) are presented in the Table. Results in Table reflect the July sampling period only	Ext-TIN ( $\mu\text{g N g}^{-1}$ dry peat)				
	WTD	1	1,398	3.2	0.093
	Peatland	1	8,560	19.6	<b>&lt;0.001</b>
	Microform	1	2,903	6.6	<b>0.020</b>
	WTD*peatland	1	1,961	4.5	<b>0.050</b>
	WTD*microform	1	1,830	4.2	0.058
	Peatland*microform	1	1,004	2.3	0.149
	WTD*peatland*microform	1	1	0.0	0.966
	Ext-NO <sub>3</sub> <sup>-</sup> ( $\mu\text{g N g}^{-1}$ dry peat)				
	WTD	1	635	11.9	<b>0.003</b>
	Peatland	1	5	0.1	0.759
	Microform	1	1	0.0	0.908
	WTD*peatland	1	1	0.0	0.891
WTD*microform	1	32	0.6	0.451	
Peatland*microform	1	11	0.2	0.652	
WTD*peatland*microform	1	5	0.1	0.767	
Ext-PO <sub>4</sub> <sup>3-</sup> ( $\mu\text{g P g}^{-1}$ dry peat)					
WTD	1	1	1.4	0.256	
Peatland	1	0	0.3	0.614	
Microform	1	2	3.0	0.105	
WTD*peatland	1	5	10.6	<b>0.005</b>	
WTD*microform	1	1	1.4	0.250	
Peatland*microform	1	0	1.0	0.337	
WTD*peatland*microform	1	1	1.7	0.205	

<sup>a</sup> Results significant at the 0.05 level are shown in *bold*

observed only for two months of the growing season (June, July) whereas N was immobilized in May and late August/early September (Fig. 1c, d). These seasonal trends were similar across peatland and microform type. These peak periods greatly influenced seasonal totals and consequently seasonal totals of net mineralization and net nitrification rates presented in this paper are generally a reflection of observations in June and July.

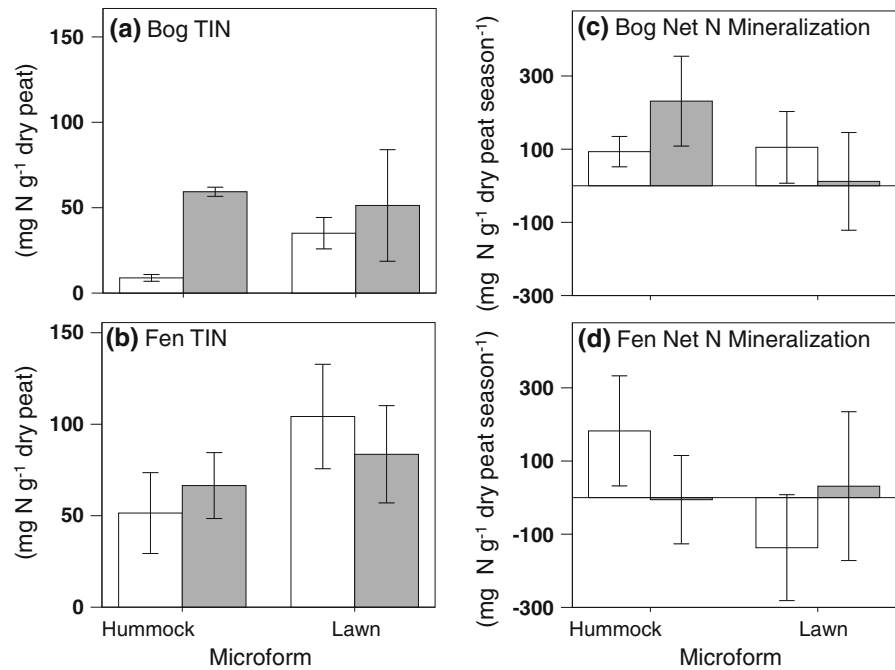
Similar to the ext-TIN concentrations, seasonal total net N mineralization rates (normalized to mass dry weight) over the entire study period at both peatland types did not vary between the control (mean  $61 \mu\text{g N g}^{-1} \text{ season}^{-1} \pm 160 \text{ SD}$ ) and drained sites ( $67 \pm 161 \mu\text{g N g}^{-1} \text{ season}^{-1}$ ) (Tables 2, 3) due to the large within- and between-peatland variability (Fig. 2c, d). Seasonal net N mineralization rates appeared to be larger in the bog (mean  $110 \pm 121 \mu\text{g N g}^{-1} \text{ season}^{-1} \text{ SD}$ ) than in the fen (mean  $18 \mu\text{g N g}^{-1} \text{ season}^{-1} \pm 179 \text{ SD}$ ) where considerable immobilization occurred; however, there was

substantial variability, and no significant difference was observed with peatland type ( $P = 0.110$ ). Seasonal net N mineralization rates were also larger in hummocks (mean  $125 \mu\text{g N g}^{-1} \text{ season}^{-1} \pm 137 \text{ SD}$ ) than in lawns (mean  $3 \mu\text{g N g}^{-1} \text{ season}^{-1} \pm 157 \text{ SD}$ ) ( $P = 0.04$ ; Fig. 2c, d; Table 2).

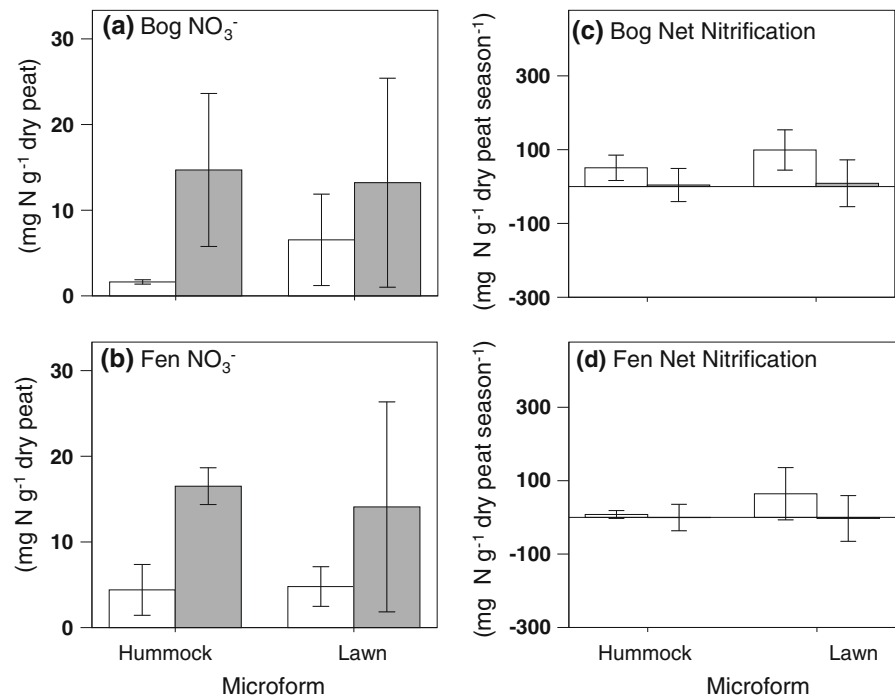
The influence of drainage may be inferred from the interaction with peatland type and microform. Although there was no significant interaction observed between drainage class (WTD) and peatland type or microform type ( $P > 0.05$ , Table 2), a significant interaction was observed between the effects of drainage (WTD), peatland type, and microform on net N mineralization ( $P = 0.016$ , Table 2). Drainage appears to have increased net N mineralization in bog hummocks, but the effects of drainage on N mineralization were highly variable across the fen microforms and the bog lawns (Fig. 2c, d).

In contrast, drainage appears to have lowered net nitrification at all sites ( $P = 0.02$ ) with a mean of  $56 \pm 54 \mu\text{g N g}^{-1} \text{ season}^{-1}$  at the control sites

**Fig. 2** Mean and standard deviations of extractable total inorganic nitrogen concentrations in surface peat of microforms at the bog (a) and fen (b) sites, sampled between May and September. Seasonal total net N mineralization rates are shown in c for the bog and d for the fen. Means (bars) and standard deviations (error bars) are shown and control sites are shown in white and drained sites are shown in grey



**Fig. 3** Mean and standard deviations of extractable nitrate concentrations in surface peat of microforms at the bog (a) and fen (b) sites, sampled between May and September. Seasonal total net nitrification rates are shown in c for the bog and d for the fen. Means (bars) and standard deviations (error bars) are shown and control sites are shown in white and drained sites are shown in grey



and mean of only  $2 \pm 45 \mu\text{g N g}^{-1} \text{ season}^{-1}$  at the drained sites (Tables 2, 3; Fig. 3c, d). There was considerable variability across sites and periodic immobilization was observed. Net N nitrification rates

did not differ with peatland type ( $P = 0.272$ ) or microform ( $P = 0.215$ ).

The seasonal trends in net N mineralization and net nitrification rates correspond with seasonal trends in N



**Table 2** Environmental controls on peat nutrient mineralization rates in surface peat

( $\mu\text{g g}^{-1}$ dry peat month $^{-1}$ )	df	Type III SS	F value	Sig. <sup>a</sup>
Net N mineralization				
WTD	1	242	0.0	0.909
Peatland	1	51,482	2.9	0.110
Microform	1	89,884	5.0	<b>0.040</b>
WTD*peatland	1	1,577	0.1	0.771
WTD*microform	1	5,851	0.3	0.576
Peatland*microform	1	2,085	0.1	0.738
WTD*peatland*microform	1	129,223	7.2	<b>0.016</b>
Nitrification				
WTD	1	16,924	0.0	<b>0.021</b>
Peatland	1	3,321	2.9	0.272
Microform	1	4,290	5.0	0.215
WTD*peatland	1	1,416	0.1	0.469
WTD*microform	1	3,937	0.3	0.234
Peatland*microform	1	0	0.1	0.989
WTD*peatland*microform	1	87	7.2	0.856
Net P mineralization				
WTD	1	38	0.0	0.197
Peatland	1	5	2.9	0.629
Microform	1	52	5.0	0.135
WTD*peatland	1	14	0.1	0.424
WTD*microform	1	8	0.3	0.535
Peatland*microform	1	9	0.1	0.529
WTD*peatland*microform	1	2	7.2	0.771

Results of analysis of variance comparing effects of water table drawdown (WTD, control, drained), peatland (bog, fen), and microform (hummock, lawn). Degrees of freedom (df), type III sum of squares (SS), *F* value and significance (Sig.) are presented in the table

<sup>a</sup> Results significant at the 0.05 level are shown in *bold*

concentrations that were observed at the sites. For example, increases in N concentrations were observed at many sites in early July, after peak net N mineralization and net nitrification rates were observed in June. Monthly changes in peat ext-TIN and ext-NO<sub>3</sub><sup>-</sup> concentrations at all sites correlated with net N mineralization and net nitrification rates, respectively, to an apparent upper threshold (Fig. 4). This upper threshold occurred mostly in June, and sometimes in July, where both net N mineralization and net nitrification rates increased at a greater rate than the observed changes in ext-TIN and ext-NO<sub>3</sub><sup>-</sup> concentrations. This corresponds to the period when vegetation uptake is the greatest.

No significant correlations between seasonal N mineralization and nitrification rates and environmental conditions (moisture, temperature) or substrate composition (peat TC, TN, TP, CN ratios) were observed using a Spearman rank correlation (data not shown). Although CN ratios were generally higher in the bog sites relative to the fen, there was no consistent

trend with microform and most sites had CN ratios greater than 25 (Table 3). The exception was the surface peat at the lawns of the drained fen, which had CN ratios of approximately 15 (Table 3).

#### Extractable ortho-phosphorus concentrations and net phosphorus mineralization rates

Water-extractable ortho-phosphorus (ext-PO<sub>4</sub><sup>3-</sup>) concentrations were low at all sites and were generally on the order of 0–4  $\mu\text{g g}^{-1}$  (Fig. 5a, b; Table 3). No significant differences in ext-PO<sub>4</sub><sup>3-</sup> concentrations with drainage ( $P = 0.256$ ), peatland type ( $P = 0.614$ ) or microform ( $P = 0.105$ ) were observed. There was a significant interaction in ext-PO<sub>4</sub><sup>3-</sup> concentrations with drainage and peatland type ( $P = 0.005$ ), where drainage increased ext-PO<sub>4</sub><sup>3-</sup> concentrations in the bog but decreased them in the fen. In the fen, ext-PO<sub>4</sub><sup>3-</sup> distributions between hummocks and lawns, and in control and drained sites had greater ext-PO<sub>4</sub><sup>3-</sup> concentrations in lawns than in hummocks at control

**Table 3** Summary of peat total and extractable nutrient contents, seasonal net mineralization rates and physical characteristics

Site	Peat moisture (m <sup>3</sup> m <sup>-3</sup> ) <sup>a</sup>	Bulk density (kg m <sup>-3</sup> ) <sup>a</sup>	Ext-NO <sub>3</sub> <sup>-</sup> (μg N g <sup>-1</sup> dry peat) <sup>b</sup>	Ext-TIN (μg N g <sup>-1</sup> dry peat) <sup>a</sup>	Ext-PO <sub>4</sub> <sup>3-</sup> (μg P g <sup>-1</sup> dry peat) <sup>a</sup>	Net N mineralization (μg N g <sup>-1</sup> dry peat season <sup>-1</sup> ) <sup>b</sup>	Net nitrification (μg N g <sup>-1</sup> dry peat season <sup>-1</sup> ) <sup>b</sup>	Net P mineralization (μg P g <sup>-1</sup> dry peat season <sup>-1</sup> ) <sup>b</sup>	OM (%) <sup>c</sup>	Total P in dry peat (%) <sup>c</sup>	Total N in dry peat (%) <sup>c</sup>	Total C in dry peat (%) <sup>c</sup>	CN <sup>c</sup>
BCH	0.63 (0.09)	45 (25)	2 (0.2)	9 (2)	0.8 (0.8)	92	54	5	96	0.051	1.19	51	43
BCL	0.91 (0.01)	56 (19)	7 (5)	35 (9)	1.0 (0.4)	98	101	0.2	97	0.033	0.89	47	53
BDH	0.94 (0.01)	67 (20)	15 (9)	59 (3)	2.0 (0.7)	240	6	-0.1	95	0.045	1.09	48	44
BDL	0.95 (0.00)	91 (26)	13 (1.2)	51 (33)	2.3 (1.5)	23	15	-3.1	92	0.049	1.92	48	25
FCH	0.88 (0.02)	35 (18)	4 (3)	51 (22)	0.9 (0.3)	177	10	1.2	93	0.05	1.76	49	28
FCL	0.92 (0.00)	51 (19)	5 (2)	104 (29)	2.4 (0.7)	-124	68	-2	94	0.045	1.31	46	35
FDH	0.85 (0.02)	80 (16)	16 (2)	66 (18)	1.0 (0.1)	15	-2	-1.3	92	0.049	1.52	47	31
FDL	0.91 (0.03)	75 (48)	14 (1.2)	84 (27)	1.1 (0.1)	41	-9	-1	91	0.054	3.08	49	16

<sup>a</sup> Mean and (standard deviation) are shown in the bog (B) and fen (F) at the control (C) and drained (D) sites in both hummocks (H) and lawns (L). Peat moisture and nutrient contents reflect the July sampling date only

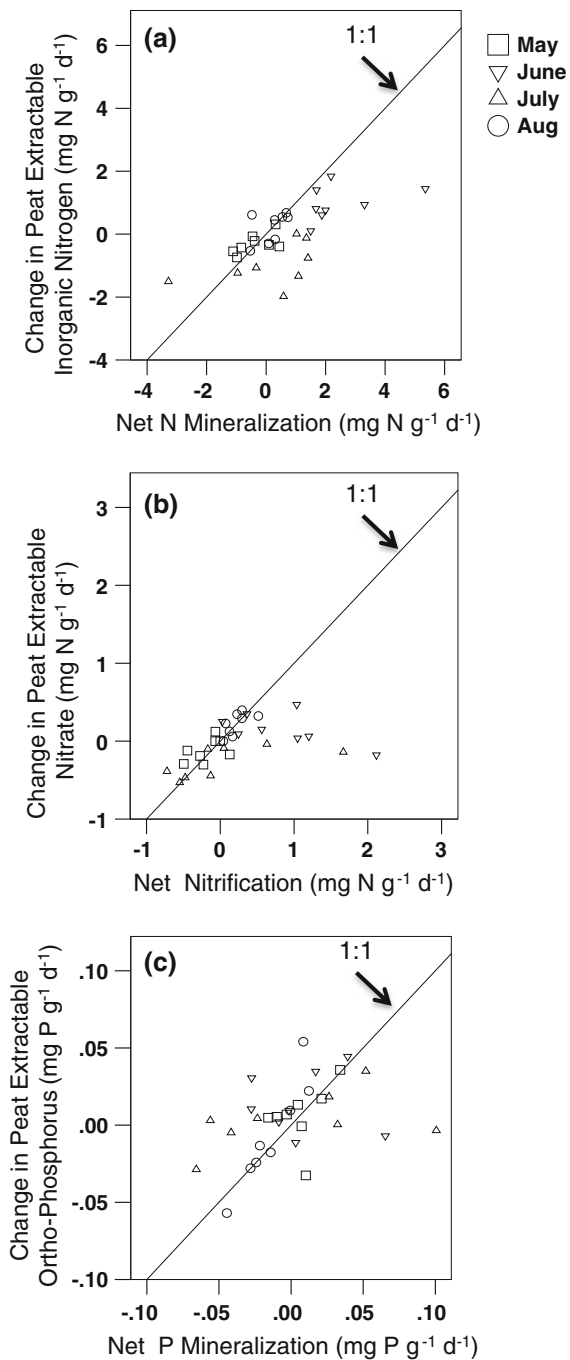
<sup>b</sup> Seasonal net N mineralization, net nitrification, and net P mineralization rates at the control (C) and drained (D) sites in the bog (B) and fen (F) in both hummocks (H) and lawns (L). Values are expressed as micrograms per gram of dry peat

<sup>c</sup> Phosphorus, nitrogen and carbon concentrations are for peat samples collected in September and are expressed as a percentage of peat dry weight and include both organic and inorganic nutrient fractions. Samples were collected in triplicate and composited for analysis ( $n = 1$  per site)

sites, and these differences were dampened following drainage (Fig. 5a, b). This pattern was not observed in the bog. A strong level of variability was observed in the data set and statistically significant trends were not found. Seasonal net P mineralization rates were also low at all sites, ranging from -2 (immobilization) to +5 μg g<sup>-1</sup> season<sup>-1</sup> (Tables 2, 3; Fig. 5). A significant positive correlation (Spearman rank correlation = 0.549;  $P = 0.034$ ) was found between seasonal net P mineralization and net N mineralization rates. Although drainage appeared to result in a shift to net P immobilization over the season, there was substantial variability (Fig. 5c, d) and these effects were not statistically significant (Table 2,  $P = 0.197$ ). Monthly net P mineralization rates were not as temporally variable as was observed for N, and net P mineralization rates were very low at all times. However, as was observed for N, monthly net P mineralization rates were more tightly coupled with observed changes in ext-PO<sub>4</sub><sup>3-</sup> concentrations in May and late August/September, but not in June and July (Fig. 4).

### Peat physical properties

Subtle differences in peat physical characteristics were observed both within and among peatland sites (Table 3). A significant three-way interaction between the effects of drainage, peatland type and microform on peat moisture (July sampling dates) was found [ $F(1,16) = 25.3$ ;  $P < 0.001$ ], demonstrating the variability throughout the landscape. Hummocks were drier than lawns [ $F(1,16) = 44.3$ ;  $P < 0.001$ ], although a significant interaction was observed between peatland type and microform [ $F(1,16) = 10.2$ ;  $P = 0.006$ ]. Significant main effects on peat moisture were found with both peatland type [ $F(1,16) = 4.8$ ;  $P = 0.044$ ] and drainage [ $F(1,16) = 26.2$ ;  $P < 0.001$ ]. However, the influence of drainage on peat moisture content differed throughout the landscape, as significant interactions were observed between the effects of drainage and peatland type [ $F(1,16) = 43.6$ ;  $P < 0.001$ ] and with drainage and microforms [ $F(1,16) = 18.9$ ;  $\leq 0.001$ ]. For example, while little difference was observed between drained and control sites in the bog, reductions in peat moisture content were apparent in the drained fen compared to the control fen (Table 3). The reduction in peat moisture in the drained fen is most apparent in the hummocks. The hummock site in the



**Fig. 4** Comparison of net nitrogen mineralization rates (a) net nitrification rates (b) and net phosphorus mineralization rates (c) with observed changes in peat extractable nutrient concentrations in the ambient (not incubated) peat over the same three-week period (y-axis). The four incubations are differentiated in the figures. Symbols falling below the 1:1 line indicate that larger quantities of N or P were mineralized than were found in soil samples, suggesting that these nutrients were used by vegetation uptake or loss through water transport. Symbols resting above the 1:1 line indicate an external source of N (runoff, deposition). Symbols that rest along the 1:1 line suggest that the observed changes in nutrient concentrations are similar in magnitude to measured mineralization rates

hummocks. A three-way ANOVA (fixed factor) testing for the effects of drainage, peatland type and microform on bulk density found significant differences with drainage [ $F(1,112) = 46.49$ ;  $P < 0.001$ ] and microform [ $F(1,112) = 5.05$ ;  $P = 0.027$ ] but not with peatland type [ $F(1,112) = 1.30$ ;  $P = 0.258$ ].

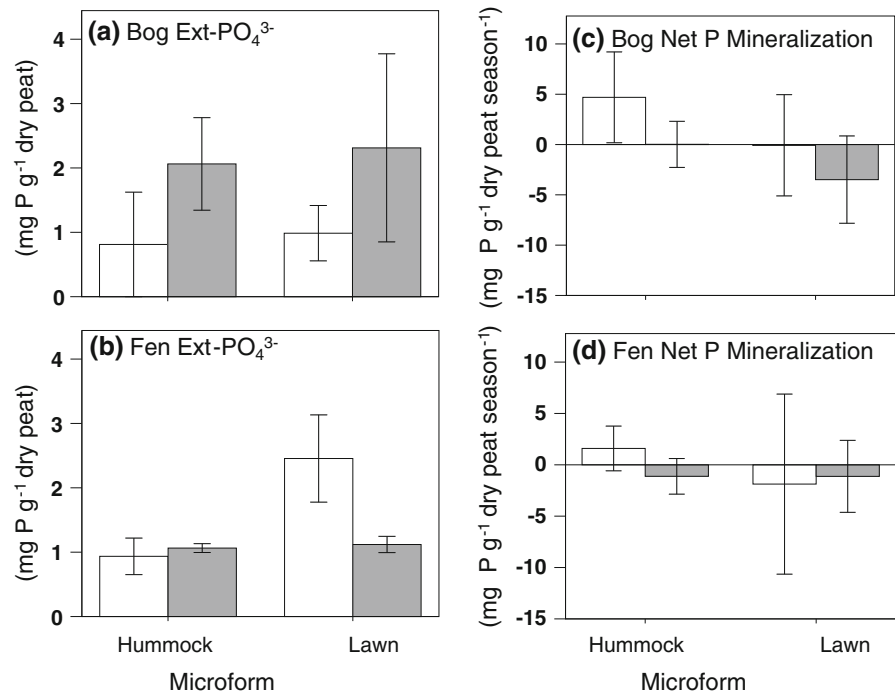
## Discussion

We expected that drainage would increase mineralization and consequently nutrient concentrations, as this has been observed in other landscapes (e.g. Holden et al. 2004). Although we expected a general increase in mineralization rates across the landscape, we also expected that the effects of drainage would vary among the landscape features within our sites. We expected to see microtopographic differences and N and P concentrations in mineralization rates and nutrient availability at the control sites as this has also been previously observed (e.g. Eppinga et al. 2010). We hypothesized that drainage would affect microforms in different ways but would ultimately dampen out microform differences and lead to a more homogeneous landscape as this has been observed for carbon dynamics at the fen site (Strack et al. 2006). However, we also expected to see differences in nutrient dynamics between bogs and fens as has been previously demonstrated (e.g. Bridgman et al. 1996). Indeed, nutrient mineralization rates and concentrations were highly variable at our sites. We observed a large degree of temporal variability in nutrient concentrations and transformation rates, and noted that seasonal nutrient dynamics were dominated by the July peak period. Consequently, we focused our analyses on this period to characterize the spatial differences in nutrient dynamics. Drainage affected

control bog dried considerably more in July than was observed at the other sites. This same level of drying was not observed during the other sampling periods.

In contrast to moisture content, peat bulk densities were greater in hummocks and lawns of both bog and fen drained sites compared to control sites (Table 3) and bulk densities in the lawns were greater than the

**Fig. 5** Mean and standard deviations of extractable phosphorus concentrations in surface peat of microforms at the bog (a) and fen (b) sites, sampled between May and September. Seasonal total net P mineralization rates are shown in c for the bog and d for the fen. Means (bars) and standard deviations (error bars) are shown and control sites are shown in white and drained sites are shown in grey



ext- $\text{NO}_3^-$  and net nitrification rates but did not affect ext-TIN, ext-P, net N mineralization or net P mineralization rates. There was also a large degree of spatial variability throughout the landscape. We found some evidence of microform and peatland (bog, fen) differences in nutrient dynamics, but this was only observed for ext-TIN.

#### Nitrogen and phosphorus contents in Quebec peatlands

The concentrations of ext-TIN, ext- $\text{NO}_3^-$  and ext- $\text{PO}_4^{3-}$  in peat at the control sites are comparable to what has been observed in undisturbed temperate peatlands in Minnesota, USA (Bridgman et al. 1998), the Netherlands (Verhoeven et al. 1990) and north-western Ontario, Canada (Westbrook and Devito 2004) but lower than what has been observed in the Western Boreal Plain in Canada (Macrae et al. 2005, 2006; Wind-Mulder et al. 1996). Most soil TN and TP are in organic forms (Table 3), which is typical of peatlands due to the rapid uptake of nutrients by plants and microbes (Turetsky 2003). Nitrate comprises a large proportion of ext-TIN in our peatlands relative to other peat systems (e.g. Bayley et al. 2005; Macrae et al. 2006; Verhoeven et al. 1990; Westbrook and

Devito 2004), where most ext-TIN was present as  $\text{NH}_4^+$ . This may be related to the regulation of  $\text{NH}_4^+$  by *Sphagnum* growth, as bryophytes assimilate  $\text{NH}_4^+$  more readily than  $\text{NO}_3^-$  (Turetsky 2003), and the peatlands in this study are dominated by *Sphagnum* mosses (Strack et al. 2006).

#### Effects of water table drawdown on peat nutrient dynamics

This study shows that micro-topographic variations typical of many bogs and fens (Belyea and Baird 2006) result in spatial variability in surface peat moisture, vegetation composition and nutrient cycling, and these may confound the effects of modest water table drawdown in peatlands. Although it is apparent that the water table drawdown at this site affected soil moisture and surface peat bulk density by peat deformation (subsidence) (Whittington and Price 2006; Strack et al. 2006), the effects of water table drawdown on both nutrient concentrations and mineralization rates were small and inconsistent across the peatland microforms. Indeed, the nutrient contents of surface peat in this study indicate a major increase in the top 20 cm of peat ext- $\text{NO}_3^-$  concentrations (hummock = 70–124 mg N m<sup>-2</sup>;

lawn = 13–26 mg N m<sup>-2</sup>) as well as for ext-TIN concentrations (hummock = 281–407 mg N m<sup>-2</sup>; lawn = 26–54 mg N m<sup>-2</sup>), when the surface compression and associated increases in bulk density in the drained peatlands are considered, but this is driven by the increases in bulk density rather than increased nutrient concentrations or mineralization rates.

We expected to observe an increase in net mineralization rates and a corresponding increase in nutrient concentrations at drained sites. However, we observed only a modest increase in ext-NO<sub>3</sub><sup>-</sup> concentrations and no increase in surface ext-TIN or ext-PO<sub>4</sub><sup>3-</sup> concentrations (Table 1). Rather, net nitrification was reduced and net P mineralization appeared to be reduced at the fen site (Figs. 3, 5; Table 2). Reductions in net mineralization or net nitrification rates may not be a reflection of smaller mineralization rates and may instead indicate increased microbial immobilization rates, as net nitrification/mineralization rates are a reflection of the balance between gross nitrification/mineralization rates and microbial immobilization (Westbrook and Devito 2004). Low or negative (immobilization) net N and P mineralization rates may demonstrate a large microbial demand for N, where microbes quickly immobilize N produced in the field through gross mineralization (Weintraub and Schimel 2003). Unfortunately, no estimates of gross mineralization were taken in this study. The reasons for the shift from net mineralization/nitrification to net immobilization are unclear. The dominance of immobilization over gross mineralization has been observed in nutrient limiting systems, especially for nitrification (Westbrook and Devito 2004). Net N immobilization rates are typically observed at CN ratios greater than 15–20 (Weintraub and Schimel 2003) whereas net N mineralization is typically observed at CN ratios lower than this. The CN ratios in this study were generally greater than 25, with the exception of drained lawn sites. However, net mineralization was generally observed in the control sites, with high CN ratios, and immobilization occurred on some drained sites with the lowest CN ratios. Thus, it appears to be difficult to determine potential immobilization using substrate composition (e.g. CN ratios) alone.

Although a reduction in nitrification was observed across sites, drainage did not cause an overall increase in net N or P mineralization rates at the sites and instead resulted in more variability within sites. The decrease in nitrification rates, and decreased

mineralization rates at some sites, observed in our study are similar to that observed by Willams (1974). He found that drainage of poorly drained blanket peat decreased the amount of N mineralized when the water table was lowered by 18 cm, but increased when the water table was lowered to depths greater than 18 cm. The lowering of the water table at drained sites was similar in magnitude to what Willams (1974) reported (i.e. <20 cm). It is possible that a greater lowering of the water table at our sites would have resulted in increased net N and P mineralization as Willams (1974) observed. Research on a Central Ontario peatland also showed that a water table drawdown of greater than 20 cm was required before rapid N, P and S mineralization and increased surface nutrient concentrations occurred, as the capillary fringe can often extend 20–40 cm above the water table (Devito and Dillon 1993; Devito and Hill 1997). Peat subsidence likely acted as a negative feedback by both potentially increasing the height of the capillary fringe through the collapse of the large pores and by reducing the thickness of the unsaturated zone. Together these processes may have maintained surface saturation and limited the influence of drainage on nutrient cycling. A 20 cm lowering of the water table may have been sufficient to enhance microbial and/or vegetation assimilation (immobilization) of nitrate, but not sufficient to change nutrient mineralization or nutrient concentrations at the SCB peatlands. Thus, while a lowering of the water table by 20 cm was sufficient to affect peat-atmosphere carbon fluxes (see Strack et al. 2006) it does not appear to have significantly affected nutrient pools or mineralization rates.

#### Spatial variability in nutrient distributions and mineralization rates

Characterizing the effects of drainage on nutrient concentrations and mineralization rates is complicated by the inherent natural spatial variability throughout the landscape. Based on previous research, we expected to see differences in nutrient dynamics between the bog and fen (e.g. Bridgham et al. 1996) and between microforms (e.g. Eppinga et al. 2010; Strack et al. 2006). Although we observed subtle differences in nutrient dynamics between the two peatland types (bog, fen) and between microforms (lawns, hummocks), this was not observed for all nutrients at all sites and there was a large level of

spatial variability. Nevertheless, we suggest that natural spatial variability should be accounted for when characterizing the effects of disturbance on nutrient dynamics.

We hypothesized that the fen would have larger nutrient concentrations and net mineralization rates than the bog at the control sites, but that the bog would show a larger increase in nutrient mineralization rates and concentrations following drainage. However, our bog sites had larger net N mineralization and net nitrification rates than the fen sites (Tables 2, 3). Despite the larger net N mineralization rates at the bog sites, ext-TIN concentrations were lower in the bog than in our fen, whereas ext-NO<sub>3</sub><sup>-</sup> and ext-PO<sub>4</sub><sup>3-</sup> did not differ. The effects of drainage were also consistent between the bog and fen. The similarity in nutrient concentrations and mineralization rates between the bog and fen in our study may be related to the fact that vegetation cover is similar between the sites, and both are dominated by *Sphagnum* species. Bryophytes (*Sphagnum* in particular) are also highly effective at scavenging N and can reduce N availability to vascular plants that rely on mineralized forms of N (Jonasson and Shaver 1999; Turetsky 2003).

Nutrient concentrations were also expected to vary between microforms, with the greatest N concentrations expected in hummocks and the greatest ext-PO<sub>4</sub><sup>3-</sup> concentrations expected in lawns. We observed the opposite trends in ext-TIN concentrations in our study, with greater concentrations of ext-TIN in lawns than in hummocks at control sites. Spatial patterns in ext-TIN concentrations between hummocks and lawns are similar to what was observed by Eppinga et al. (2009, 2010) in drainage-dominated peatlands, suggesting that the transfer of nutrients from hummocks to lawns may play an important role in peatlands in this region. This is supported by the work of Strack et al. (2008) who observed hydrologic exchange between hummocks and lawns at the control sites in our fen.

We hypothesized that natural differences in microforms would be observed at the control sites, but that drainage would dampen these microform differences, as has been observed for peat-atmosphere carbon exchange (Strack et al. 2006). Although there appears to be smaller differences between microforms at drained sites, there is a large amount of spatial variability and significant trends were not observed in our dataset. To our knowledge this is the first study

that has quantified the responses of peatland microform nutrient dynamics to water table drawdown. Wells and Williams (1996) observed increased TN concentrations in drained systems due to an increase in the retention of N by microbial immobilization as plant residues in the peat decomposed. Larger quantities of TN (based on samples collected in September) and a corresponding increase in seasonal net N immobilization rates were observed in the drained lawns at our sites, where Strack et al. (2006, 2008) observed substantial increases in vegetation growth and productivity although the quantity of *Sphagnum* did not change significantly at these sites (Strack et al. 2006; L. Rochefort unpublished data). The fact that ext-TIN, ext-NO<sub>3</sub><sup>-</sup> and ext-PO<sub>4</sub><sup>3-</sup> concentrations did not change may be related to the dense *Sphagnum* cover at these sites, which have been shown to affect nutrient concentrations (e.g. Aerts et al. 1999; Turetsky 2003; Westbrook and Devito 2004). Thus, *Sphagnum* growth may be regulating nutrients in this environment. The hypothesis that nutrient concentrations are being regulated by vegetation in this landscape is supported by temporal patterns in nutrient dynamics. Very little net N and P mineralization or immobilization occurred in May and September, and most activity was observed in June and July. This corresponds with the period of maximum vegetation growth (Strack et al. 2006). The net N mineralization and nitrification rates observed in June and July were much greater than the observed changes in nutrient concentrations over the same incubation period. It is likely that this surplus in nutrients is taken up rapidly by vegetation.

#### Conclusions and implications for climate change

Strack et al. (2006) and Strack and Waddington (2007) demonstrated that the response of CO<sub>2</sub> and CH<sub>4</sub> fluxes to water table drawdown varied between microforms owing to spatial variability in the initial ecohydrological differences between microforms. We saw some evidence of similar patterns in nutrient dynamics although such patterns were not consistent across the entire landscape and not consistent for all nutrients. As such, the effects of water table drawdown (and potential response to climate change) on nutrient dynamics may be complicated by microtopography and antecedent peat chemistry and vegetation type. Water table drawdown reduced net nitrification, likely



due to increased microbial immobilization, but this was not reflected in the ext-NO<sub>3</sub> concentrations at the sites. These patterns may be explained by changes in the hydrologic connection between hummocks and lawns at drained sites, or alternatively regulation by vegetation, the most important of which is *Sphagnum* growth. The current study has examined net nutrient mineralization rates and peat nutrient concentrations. Future studies should determine the specific pathways taken by nutrients (e.g. leaching in runoff, immobilization/uptake by vegetation and microbes). We suggest that in order to predict the response of climate change-mediated water table drawn in northern peatlands the distribution and composition of peatland microforms and initial ecohydrological conditions should be considered given that some variability was observed in the current study. However, our results suggest that the effects of climatic change on peatlands, at least during the initial draw down stages, may be less significant for nutrients than has been observed for carbon in other studies.

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