RESEARCH ARTICLE

Key Points:
- C:N:P:Ca:Mg:K stoichiometry is examined for >400 peat profiles from Ontario
- C:N ratios fall, and C:P ratios rise in the early stages of decomposition
- We estimate that 18 Pg of N and 0.3 Pg of P are stored in northern peatlands

The stoichiometry of carbon and nutrients in peat formation

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Abstract Northern peatlands have stored large amounts (~500 Pg) of carbon (C) since the last glaciation. Combined with peat C are nutrients such as nitrogen (N), phosphorus (P), calcium (Ca), magnesium (Mg), and potassium (K), each of which plays an important role in plant production, litter decomposition, and the biogeochemical functioning of peatlands. Yet little attention has been given to the amounts of these nutrients stored in northern peatlands and their stoichiometry with C. Here we use data on nutrient concentrations in over 400 peat profiles in Ontario, Canada, representing bogs, fens, and swamps and their vegetation. We show that the C:N ratio is high (>40:1) in vegetation and litter but declines through the peat profiles to reach ratios between 22:1 and 29:1 in peat below 50 cm. In contrast, the C:P ratio rises from vegetation and litter (500:1 to 1300:1) to 1500:1 to 2000:1 in the lower part of the peat profile. Ratios of C to Ca, Mg, and K vary with peatland type. Most of these stoichiometric changes occur in the early stages of organic matter decomposition, where the litter structure remains intact. We estimate that ~18 Pg of N has been stored in northern peatlands since deglaciation, reflecting high N accumulation rates (~0.8 g m^{-2} yr^{-1}), whereas P accumulation is small (~0.3 Pg, ~0.016 g m^{-2} yr^{-1}), indicating that P is quickly recycled in the surface layers.

1. Introduction

Northern peatlands cover ~4 · 10^6 km^2 and have accumulated large amounts of C in the Holocene, estimated between 436 and 547 Pg [*Yu et al.*, 2010; *Loisel et al.*, 2014]. This has generated considerable interest in the controls and rates of C accumulation in peatlands, with an average value of ~23 g C m^{-2} yr^{-1} [*Loisel et al.*, 2014] and average N accumulation rates of 0.3 to 0.6 g N m^{-2} yr^{-1} [*Limpens et al.*, 2006; *Loisel et al.*, 2014]. Yet little attention has been given to the stoichiometric changes between C and N and other nutrients such as P, Ca, Mg, and K as plant tissues senesce, litter forms and decomposes into peat, and elements accumulate in the peat profile and how this varies among different peatland types. To redress this, we used concentration data from ~400 peat profiles containing ~1600 individual peat samples, analyzed as part of a resource survey covering 208,000 km^2 of southeastern, northeastern, and northwestern Ontario, Canada. Sites included bogs, fens, and swamps, the major northern peatland types.

We analyzed the C:element stoichiometric patterns through multivariate analyses (principal component analysis) to assess the major controls, and we looked at the patterns of individual ratios. We also collated information on the nutrient concentrations of plants and litter that are found in these peatlands to create a cascade of C:nutrient stoichiometry, from vegetation to litter to peat decomposed over millennia. Using estimates of C accumulated and average C accumulation rates, we estimate the mass of these nutrients stored in northern peatlands and their average accumulation rate.

2. Methods

The sampled peatlands in southeastern [*Riley*, 1994b], northeastern [*Riley*, 1994a], and northwestern Ontario [*Riley and Michaud*, 1989] were large sites selected to represent typical peat resources and homogeneous vegetation (as training areas for remote sensing analysis). The sites were classified into bogs, fens, and swamps [*Riley and Michaud*, 1994]. Bogs are defined as wetlands with a pH lower than 5.2, where the surficial layers of peat are dominated by poorly decomposed *Sphagnum* and other typical bog indicator species.

Table 1. Results of the Principal Component Analysis on the C:Nutrient (g g^{-1}) Stoichiometry Data Set, Loading of the Main Variables on the Two Main Axes, and Predicting Value of the Main Environmental Variables[a]

	Axis 1	Axis 2
Eigenvalue	1.99	1.53
% of variance	40	31
Loading (Pearson)		
C:N	−0.60	0.31
C:P	−0.12	−0.83
C:K	−0.32	−0.81
C:Ca	−0.88	0.27
C:Mg	−0.87	−0.07
Predictors (Pearson)		
Depth	0.16	−0.43**
Humification	0.03	−0.39
Sphagnum content of sample	−0.19	0.25
Herbaceous/graminoid content of sample	0.00	−0.27
Wood content of sample	0.31	−0.04

[a]Statistically significant predictor correlations (alpha = 0.5) are identified with **.

Fens and swamps are predominantly minerotrophic wetlands developed on graminoid, woody, or brown moss peat. Swamps have a tree or tall shrub cover of at least 25% and are often seasonally flooded or flooded by beaver dams, whereas fens are open or sparsely wooded.

The individual sample sites had at least 40 cm of peat, were >100 ha in size, and were sampled for vegetation, depth to water table, and surface water pH measured in the field on water samples retrieved from about 10 to 15 cm below the water table. Peat stratigraphy was recorded by recovering a core with a Mini-Macaulay or Hiller sampler sectioned into intervals based on changes in peat type: *Sphagnum* moss, other mosses, sedge-herb, woody peat from shrubs, and woody peat from trees. The degree of humification was recorded using the von Post index based on color, recognizable plant fiber remains, and water release [*Riley and Michaud*, 1994].
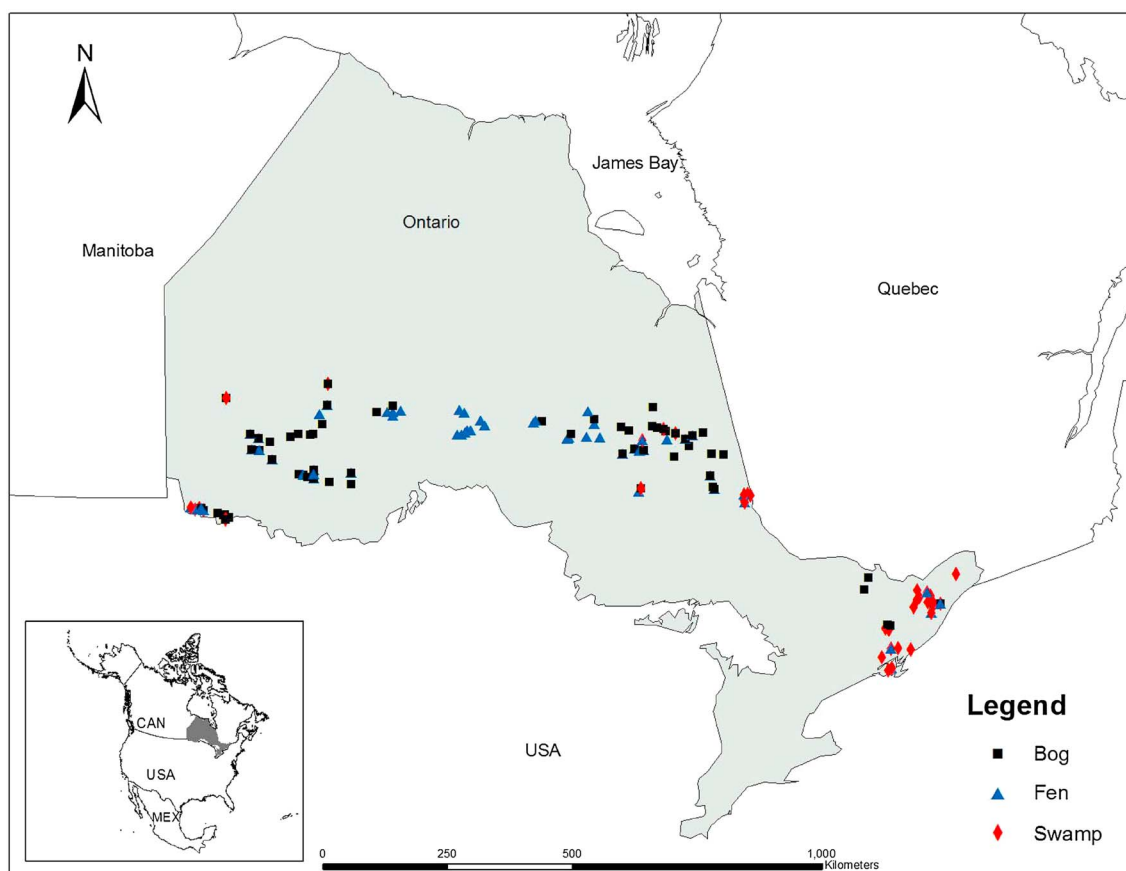
Figure 1. Location of the 400 peat cores in Ontario, Canada.
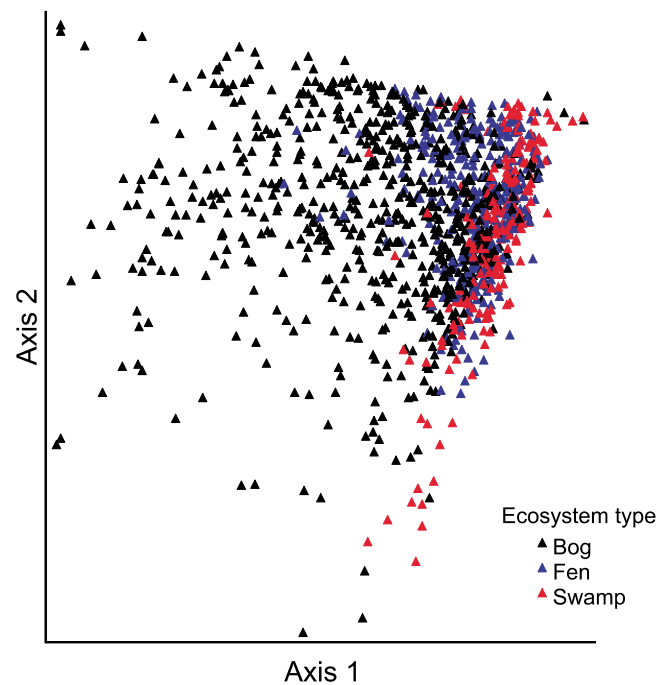
Figure 2. Biplot of the two main axes of variations of the stoichiometry data set as determined by the principal component analysis (PCA). The samples are classified based on ecosystem type.

The peat cores were divided into sample intervals on the basis of changes in botanical composition and degree of humification and combined into four sections: upper, upper middle, lower middle, and lower. The average depth of each section was recorded and used in our analysis of variations in stoichiometry with depth using averages of 10 cm increments in the upper 2 m and thicker increments deeper. Peat samples were frozen and in the laboratory were oven dried and analyzed for the following: organic C by ignition at 500°C after HCl treatment and carbon dioxide sorption in potassium hydroxide; N by micro-Kjeldahl digestion; P, Ca, Mg, and K by treating with HNO_3, HF, H_2SO_4, HC1, and H_2O_2, and determination by inductivity coupled argon plasma emission spectrometry [*Riley*, 1989].

To describe the main patterns of variation in peat stoichiometry, we conducted a principal component analysis (PCA) on the stoichiometric ratios (C:N, C:P, C:K, C:Ca, and C:Mg). Because of the large number of samples available, samples with missing values were omitted, leaving 1226 samples for analysis. The principal components with an eigenvalue >1 were retained. We used Pearson's coefficients to test for colinearity between the PCA axes and peat composition of samples, humification, and sample depth.

Table 2. Differences in C:N, C:P, N:P, C:K, C:Ca, and C:Mg Stoichiometric ratios (g g^{-1}) (Mean ± SE) Among Bog, Fen, and Swamp Peatlands and Poor and Rich Fens in the Complete Profile (All) and the 0–50 cm and >50 cm Sections[a]

Ratio	Bog	Fen	Swamp	Poor Fen	Rich Fen
All					
C:N	33.0 ± 0.5[b]	26.6 ± 9.6[c]	22.8 ± 6.1[d]	28.2 ± 0.8[b]	24.8 ± 0.6[c]
C:P	1338 ± 20[b]	1212 ± 29[c]	1360 ± 47[b]	1190 ± 45[b]	1260 ± 46[b]
N:P	46.4 ± 0.9[c]	50.2 ± 1.3[c]	60.2 ± 1.9[b]	47.7 ± 2.5[b]	54.6 ± 2.2[c]
C:K	1199 ± 41[b]	807 ± 34[c]	1111 ± 92[b]	793 ± 54[b]	837 ± 50[b]
C:Ca	129.9 ± 4.1[b]	34.8 ± 1.6[c]	27.1 ± 1.5[d]	40.1 ± 2.5[b]	25.3 ± 1.6[c]
C:Mg	850 ± 22[b]	338 ± 11[c]	224 ± 9[d]	361 ± 14[b]	283 ± 16[c]
C:K	1199 ± 41[b]	807 ± 34[c]	1111 ± 92[c]	793 ± 54[b]	837 ± 50[b]
0-50 cm					
C:N	42.0 ± 1.3[b]	32.0 ± 1.1[c]	24.9 ± 0.9[d]	35.0 ± 1.5[b]	28.8 ± 1.6[c]
C:P	892 ± 25[c]	768 ± 27[d]	923 ± 66[bcd]	772 ± 35[b]	736 ± 43[b]
N:P	24.5 ± 0.8[c]	26.4 ± 1.1[c]	36.5 ± 2.0[b]	24.0 ± 1.4[b]	28.1 ± 1.9[c]
C:Ca	172.1 ± 6.7[b]	43.3 ± 3.0[c]	32.8 ± 3.3[d]	54.2 ± 4.4[b]	29.2 ± 3.0[c]
C:Mg	759 ± 27[b]	292 ± 16[c]	210 ± 15[d]	342 ± 19[b]	221 ± 25[c]
C:K	592 ± 36[c]	439 ± 33[d]	768 ± 101[bcd]	445 ± 53[b]	412 ± 42[b]
>50 cm					
C:N	29.2 ± 0.4[b]	24.1 ± 0.5[c]	21.5 ± 0.3[d]	24.7 ± 0.6[b]	22.9 ± 0.5[c]
C:P	1531 ± 23[bc]	1414 ± 33[c]	1618 ± 52[b]	1391 ± 53[b]	1489 ± 498[c]
N:P	55.5 ± 1.0[d]	60.6 ± 1.5[c]	74.1 ± 2.2[b]	59.3 ± 3.0[b]	66.3 ± 2.4[c]
C:Ca	111.5 ± 4.8[b]	31.0 ± 1.8[c]	23.9 ± 1.2[c]	33.4 ± 2.9[b]	23.6 ± 1.9[c]
C:Mg	890 ± 29[b]	359 ± 14[c]	232 ± 11[d]	370 ± 18[b]	309 ± 21[c]
C:K	1466 ± 52[b]	984 ± 42[c]	1327 ± 132[c]	963 ± 70[b]	1042 ± 61[b]

[a]Different letters (b, c and d) indicate a significant difference among peatland types.
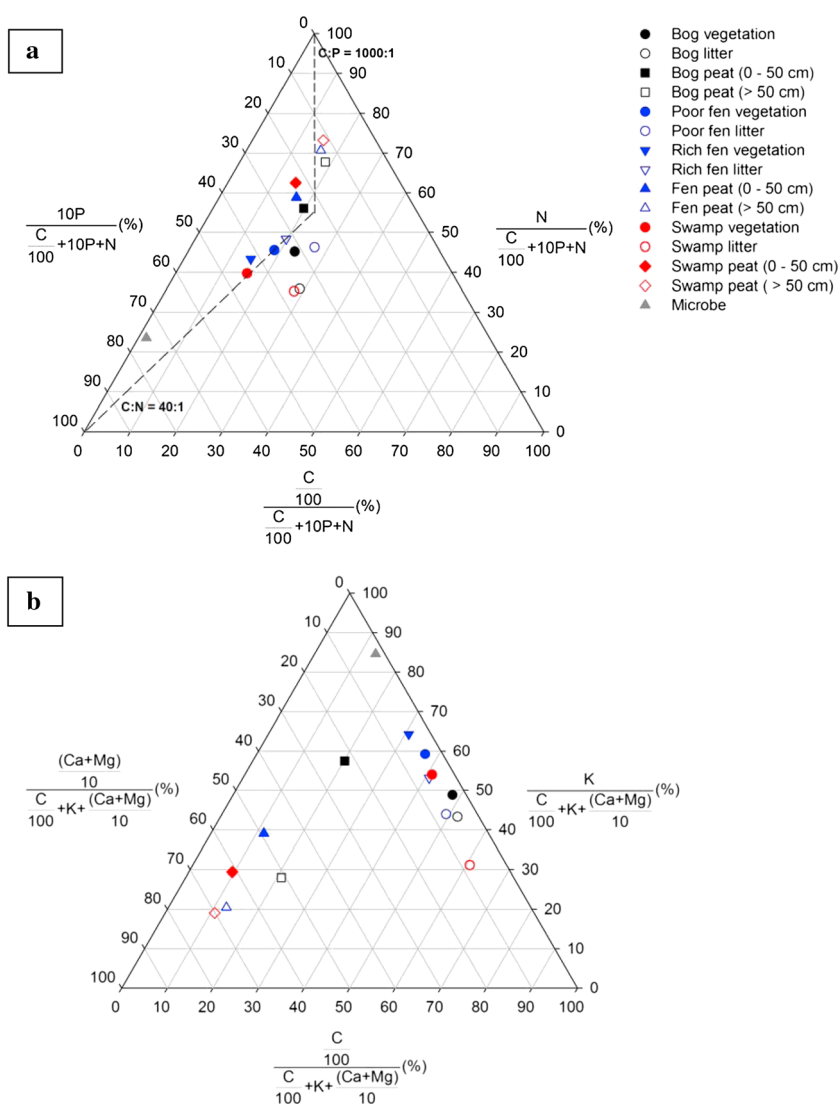
Figure 3. Ternary diagrams of (a) C, N, and P and (b) C, K, and Ca+Mg in vegetation, litter, and peat samples (0–50 and >50 cm depth) for bog, fen (poor and rich fens), and swamp in comparison with microbe. The dashed lines indicate the critical ratios (g g^{-1}) of C:N (40) and C:P (1000). For visual reasons, the C, Ca, and Mg concentrations are divided by a factor of 100 and 10, respectively; the P concentration is multiplied by a factor of 10.

3. Results

When taken as a whole, the peat stoichiometric ratios can be reduced to two main components with the first principal component being strongly loaded by the C:Ca and C:Mg ratios and explaining 40% of the total variation (Table 1 and Figure 1). The second component, mainly reflecting C:P and C:K ratios, explained 31% of the total variation. Correlation analyses show that the first axis is not related to any of the potential predictors we selected from the database (including the degree of decomposition of samples or their botanical composition) and that the second axis is mostly related to sample depth.

The C:N ratio in the near-surface bog peat ranges from 45 to 50:1 and decreases sharply to 30 to 35:1 before declining further to 20 to 30:1 throughout the lower profile (Figure 2a). In contrast, the fen and swamp peat profiles have a smaller C:N ratio near the surface (25 to 35:1) and decline to averages of 24 and 22:1, respectively, with significant differences among the three peatland types (Table 2).

The C:P ratio in the near-surface bog peat ranges from 800 to 1000:1 and increases with depth, reaching an average of 1531:1 at depths >50 cm (Figure 2a). The fen and swamp peat profiles show the same pattern

Table 3. Values Adopted for Ratios (g g^{-1}) in Vegetation and Litters of Bog, Fen (Poor and Rich Fen), and Swamp[a]

	C:N	C:P	N:P	C:Ca	C:Mg	C:K
Bog vegetation	60.5 ± 2.6	924 ± 44	16.1 ± 0.7	316 ± 20	655 ± 41	136.4 ± 8.7
Bog litter	129.2 ± 17.8	1051 ± 139	10.8 ± 1.4	194 ± 21	497 ± 18	197.2 ± 33.1
Fen vegetation	42.8 ± 1.5	573 ± 38	13.7 ± 0.7	200 ± 16	332 ± 24	77.7 ± 4.5
Fen litter	67.5 ± 8.0	1064 ± 130	17.4 ± 1.4	128 ± 10	310 ± 42	127.0 ± 12.7
Poor fen vegetation	52.7 ± 3.2	520 ± 86	12.7 ± 1.6	157 ± 21	251 ± 29	62.4 ± 9.0
Poor fen litter	93.0 ± 17.6	1008 ± 279	17.3 ± 2.0	108 ± 16	212 ± 91	111.9 ± 17.5
Rich fen vegetation	36.8 ± 1.1	347 ± 20	10.3 ± 0.5	110 ± 16	150 ± 45	48.0 ± 4.7
Rich fen litter	53.2 ± 6.7	619 ± 110	15.1 ± 2.0	97 ± 14	232 ± 41	76.9 ± 18.2
Swamp vegetation	45.6 ± 1.0	375 ± 6	9.1 ± 0.3	148 ± 4	414 ± 9	83.5 ± 1.6
Swamp litter	92.5 ± 2.0	821 ± 13	9.8 ± 0.3	128 ± 4	445 ± 9	215 ± 4
Microbe	6.6	13.6	2.2	104	621	21.1

[a]Vegetation and litter stoichiometric ratios are derived from Table S3 in the supporting information and microbe stoichiometry is derived from *Anderson and Domsch* [1980] with the assumption that Mg concentration is one sixth that of Ca.

butwith smaller ratios (600 to 900:1) close to the surface and increasing to averages of 1414 and 1618:1 at depths >50 cm, with few significant differences (Table 2). As a result of the changes in C:N and C:P ratios, the N:P ratio in the profiles starts at values of 20 to 30:1 and increases to averages of 56 to 74:1 at depth >50 cm, with swamp > fen > bog.

The C:Ca ratio is large (170 to 190:1) in the near-surface bog profiles and then declines with depth, falling to <80:1 at depths >3 m and an average of 112:1 for depths >50 cm. In stark contrast, the C:Ca ratio in the near surface layers of the fen and swamp profiles ranges between 30 and 50:1 and declines only slightly with the averages of 31 and 24:1 for samples >50 cm deep and no significant difference between them.

The C:Mg ratio is also large near the surface of bogs (600 to 800:1), increases with depth to an average of about 1000:1 at 50 to 100 cm depth and then declines to values <700:1 at >3 m in the profile. As with Ca, the fen and swamp peat profiles have C:Mg ratios ranging from 200 to 400:1 with little variation with depth, although the fen values are larger than those for the swamp values throughout. In both cases, this pattern likely reflects the flux of Ca and Mg-rich groundwater into fens and swamps.

The C:K ratio is similar for the three peat profiles close to the surface (250 to 400:1) and increases with depth, though with great variability, to values of 984 to 1466:1 at depths >50 cm, and with no strong distinction between the peat types.

Based on a differentiation of near-surface porewater pH of less than and greater than 5.5 into poor and rich fens, respectively, there are significantly larger C:N, smaller N:P, larger C:Ca, and larger C:Mg ratios in the poor fens than in the rich fens (Table 2).

The C:N and C:P ratios increase from vegetation to litter and decrease from litter to near-surface peat in all peatland types, except for the C:P ratio in swamps, which increases from litter to near surface peat (Figure 3a and Tables 2 and 3). The N:P ratio decreases from vegetation to litter in bogs and increases in fens and swamps, which increases consistently from litter to near-surface peat in all peatland types. The C:Ca ratio decreases from vegetation to litter and further to near-surface peat in all peatland types especially bogs (Figure 3b and Tables 2 and 3), while a contrary pattern occurs for the C:K ratio. No clear pattern is observed for the C:Mg ratio. Overall, the C:nutrient ratios from vegetation through litter to peat at depth >50 cm move away from that of the soil microbes, which have consistently smaller C:N, C:P, and C:K ratios than peat, while no similar pattern occurs for C:Ca and C:Mg ratios (Table 3).

Peat samples show consistent patterns of ratio changes with von Post humification index of decomposition (Figure 4). C:N ratio falls from 42:1 at 1 to 26:1 at 4 and remains similar with further decomposition. C:P ratio rises from 727:1 at 1 to 1446:1 at 4 and remains similar with further decomposition, and a similar pattern is shown by N:P ratio rising from 20:1 at 1 to 58:1 at 4. C:Ca ratio falls from 133:1 at 1 to 79:1 at 4 and then rises slightly with further decomposition, although the high variability is created by the pronounced differences between bog and fen and swamp (Figure 5b). C:Mg ratio rises from
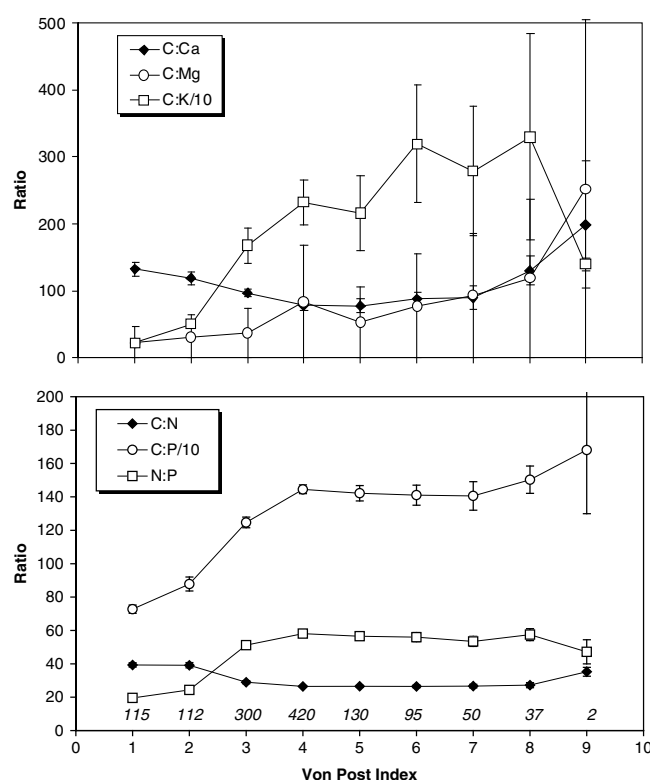
Figure 4. Relationship between von Post humification index of decomposition and (top) C:Ca, C:Mg, and C:K and (bottom) C:N, C:P, and N:P ratios in the peat samples (g g^{-1}). The bars represent the standard error of the mean.

416:1 at 1 to 771:1 at 4 and remains similar with further decomposition. C:K ratio rises from 230:1 at 1 to 2330:1 at 4 with larger ratios with further decomposition, although there is a high degree of variability among the samples. Thus, most of the changes in stoichiometry occur from von Post index 2 to 4. This corresponds to a change from almost entirely undecomposed peat with plant remains easily identifiable and no amorphous material to slightly decomposed peat with plant remains slightly pasty and having lost some of their identifiable features.

4. Discussion

Our analyses can be used to estimate the storage of N, P, K, Ca, and Mg in northern peatlands, based on C:element ratios. In Canada, about 65.5% of the peatland area of 1.06×10^6 km^2 comprises bogs, with 33.8% as fens, and very small coverage by swamps (0.5%) and marshes (0.2%) [*Tarnocai*, 2006]. As most of the peat accumulation occurs beneath a depth of 50 cm to avoid weighting our estimate with the surface layers, we took only samples from beneath 50 cm to estimate combined bog and fen (weighted for relative area) ratios of C:N 27.1, C:P 1481, C:K 1293, C:Ca 84, and C:Mg 704.

Assuming a C storage of 500 Pg in northern peatlands [*Yu et al.*, 2010; *Loisel et al.*, 2014] and stoichiometry similar to that in Ontario peatlands, we estimate that storage is 18.5 Pg N, 0.34 Pg P, 0.39 Pg K, 5.95 Pg Ca, and 0.71 Pg Mg, mainly over the last 10,000 years during the period of northern peatland initiation. At an average long-term accumulation rate of 23 g C m^{-2} yr^{-1} [*Loisel et al.*, 2014], the average rates (g m^{-2} yr^{-1}) of nutrient accumulation in northern peatlands would be 0.85 N, 0.016 P, 0.27 Ca, 0.033 Mg, and 0.018 K. The accumulation rates vary with the age of the peatland, with generally faster rates of accumulation in young peatlands, because of the limited degree of decomposition.

The C:N stoichiometry shows high initial vegetation ratios, increasing further with N resorption as tissues senesce to litter and then follows a pattern to similar forest litters [e.g., *Moore et al.*, 2011] falling to 20:1 to 30:1 in the lower sections of the peat, reflecting the differential loss of C, probably as carbon dioxide and methane, compared to N. These ratios are somewhat smaller than commonly reported elsewhere, such as 55:1 [*Loisel et al.*, 2014], the latter being derived primarily from peatlands sampled for paleoecological analyses and thus may show some bias, whereas the Ontario peatlands were sampled because of their representation in the landscape.

The main sources of N for peatlands are by atmospheric deposition, generally small (0.1–0.2 g N m^{-2} yr^{-1}) in the pre-Industrial Era [*Holland et al.*, 1997], and by N$_2$ fixation. Contemporary estimates of N$_2$ fixation of bogs, fens, and swamps range widely from 0.1 to >6 g N m^{-2} yr^{-1} [*Limpens et al.*, 2006], although this may be increased by 0.1 to 2.9 g N m^{-2} yr^{-1} by methanotrophy [*Larmola et al.*, 2014]. Although N$_2$ fixation is an energetically costly process, N accumulation rates are large given that many of these northern peatlands are believed to be N limited [*Aerts et al.*, 1992; *Gunnarsson and Rydin*, 2000]. Decomposition is conducted by microbes, so that one might expect that as decomposition progresses, microbial biomass makes up a larger proportion of the residual material and thus the "peat" may approach the stoichiometry of microbes.
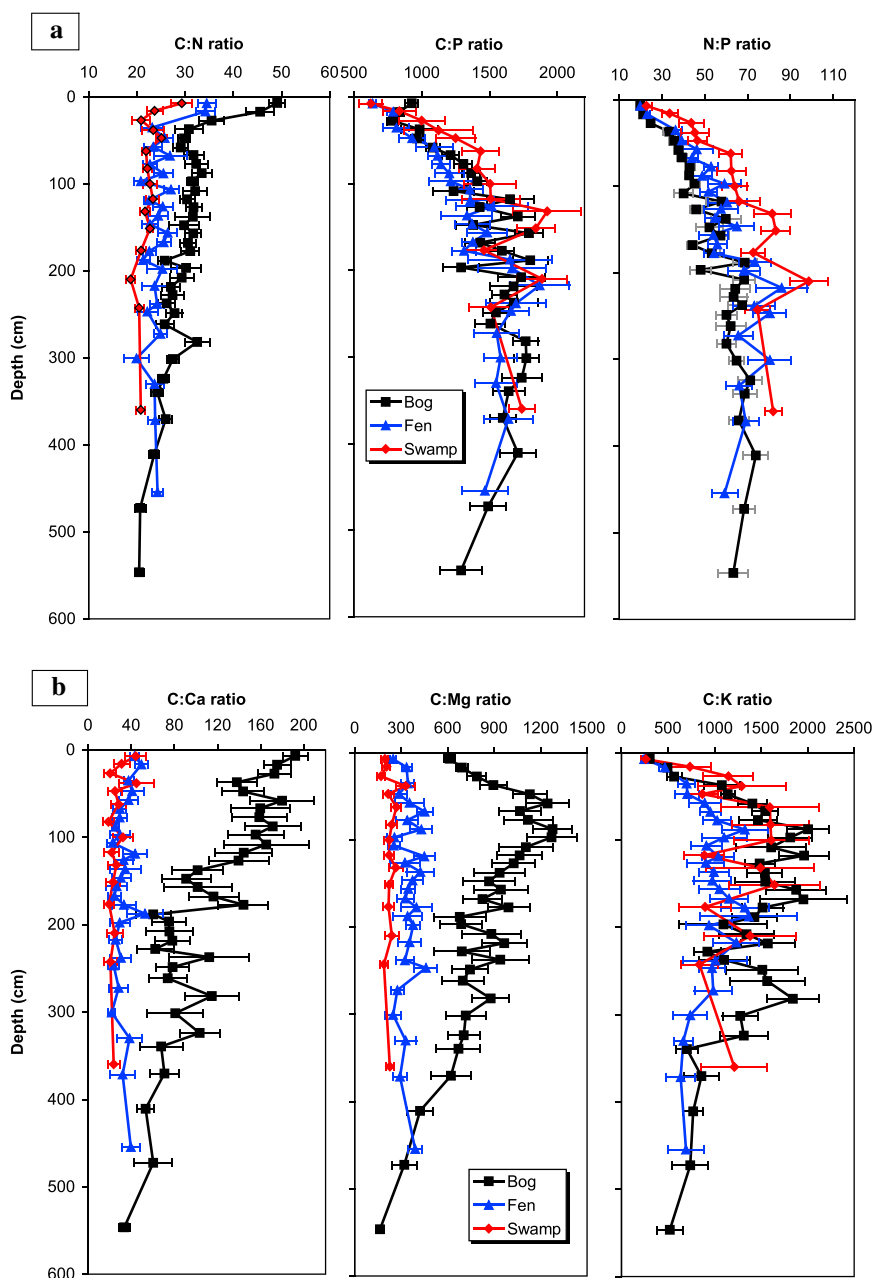
Figure 5. Patterns (g g^{-1}) of (a) C:N, C:P, and N:P and (b) C:Ca, C:Mg, and C:K with depth in peat cores for bog, fen, and swamp peatlands. The bars represent the standard error of the mean.

Although the peat C:N ratio is moving toward that of microbes, it is still far from it, with little change with the progression from poorly to well-decomposed peat (von Post indices 3 to 7).

The estimated global N accumulation in northern peatlands (~18 Pg) is larger than the 8 to 15 Pg estimated by *Limpens et al.* [2006] and *Loisel et al.* [2014], primarily because of the C:N ratio being smaller in our results. The 18 Pg global N accumulation is smaller than the 95 Pg in global soil N [*Post et al.*, 1985] but larger than the estimated 6 Pg stored in vegetation from Last Glacial Maximum to preindustrial Holocene and thus may have played a significant role if the global N cycle in the past 10,000 years [*McLauchlan et al.*, 2013].

The pattern of C:P ratio changes is the most interesting, showing that P is lost from peat at a faster rate than C, resulting in increases in C:P ratios, more or less independent of peat type. This is contrary to that observed in northern forest litter decomposition, where ratios decrease to ~400:1 in well-decomposed

litter [*Moore et al.*, 2011]. There may be several reasons for this strong recycling of P from peat, relative to C. There may be strong mycorrhizal and root uptake of P by peatland plants [*Turner*, 2008], and *Sphagnum* moss has a strong affinity for P [*Rydin and Clymo*, 1989], although the pattern appears to be similar for all of our peatland types despite their varied vegetation. Concentrations of P and Fe in high-resolution bog cores, such as Mer Bleue 775 and 930 [*Wang et al.*, 2014], are large in the aerobic section, decrease under anoxic conditions beneath the water table, and Fe concentration increases toward the base of the profile (unpublished data). Thus, P becomes more soluble as it is released via reduction of Fe [*Moore and Reddy*, 1994], permitting diffusion to the oxic-anoxic interface. Incubation of peat samples in laboratory incubation experiment under oxic and anoxic conditions by *Bridgham et al.* [1998] showed that the release of C and N follows the pattern of the peat C:N ratio, whereas the C:P ratio of released material is strongly affected by the peat C:P ratio and by the oxic/anoxic conditions. This leads to a tight organic P cycle, maintaining P near the surface, and as peat forms, its C:P ratio moves away from, rather than toward, that of microbes (Table 3).

Sources of P to peatlands are atmospheric deposition or P-rich groundwater, in the case of rich fens and swamps. Few atmospheric deposition P data are available for the area covered by northern peatlands but currently fall in the range of 7 to 34 mg m^{-2} yr^{-1} [*Newman*, 1995; *Schindler et al.*, 1976; *R. Vet, Environment Canada*, personal communication] and modeled total P atmospheric deposition for areas occupied by northern peatlands as <5 mg m^{-2} yr^{-1} [*Mahowald et al.*, 2008]. Thus, peatlands accumulate P at approximately the same rate as they gain P from the atmosphere, and changes in atmospheric deposition of P in dust may have profound effects on C cycling in peatlands, as shown for the Florida Everglades [*Craft and Richardson*, 2008; *Glaser et al.*, 2013].

A N:P ratio of ~15:1 is suggested as the differentiation between N (<15:1) and P (>16:1) limitation for plants growing in peatlands. Phosphorus as a potential limiting or colimiting nutrient has been overlooked in peatlands [*Wang and Moore*, 2014], and *Walbridge and Navaratnam* [2006] collated data from boreal peatlands showing a range of 5 to 37:1 for fens, bogs, and marshes. The increase in N:P ratio from averages of ~20:1 to ~55:1 as peat decomposes in our samples shows that, in general, peatlands lose P relative to N and have N:P ratios well above that regarded as critical for P limitation in plants.

5. Conclusions

Our study has shown that large amounts of nutrients can accumulate in northern peatlands. There is a consistent change in C:nutrient ratios as plant senesce and peat forms and decomposes, and this pattern varies among nutrients. The results show the significance of the recycling of P relative to C, as peat forms, resulting in a C:P ratio of about 1500:1 at lower depths. Given that average atmospheric deposition rates of P are about 15 mg m^{-2} yr^{-1}, it may be that P plays a critical role in the observed narrow range [*Loisel et al.*, 2014] of long-term C accumulation rate in northern peatlands through recycling and its influence on N fixation.

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