Article

Lake–landscape connections at the forest–tundra transition of northern Manitoba

Charles E. Umbanhowar Jr.,[1]* Philip Camill,[2] Mark B. Edlund,[3] Christoph Geiss,[4] Patrick Henneghan,[5] and Kendra Passow[5]

[1] *Departments of Biology and Environmental Studies, Saint Olaf College, Northfield, MN, USA*
[2] *Earth and Oceanographic Science Department and Environmental Studies Program, Bowdoin College, Brunswick, ME, USA*
[3] *St. Croix Watershed Research Station, Science Museum of Minnesota, Marine on St. Croix, MN, USA*
[4] *Department of Physics and Environmental Science Program, Trinity College, Hartford, CN, USA*
[5] *Saint Olaf College, Northfield, MN, USA*
* *Corresponding author: ceumb@stolaf.edu*

Received 16 April 2014; accepted 7 September 2014; published 9 Decmeber 2014

Abstract

To better understand aquatic–terrestrial linkages in the sub-Arctic, and specifically the relative importance of landscape position versus land cover, we surveyed lakes, soils, land cover, and lake/basin characteristics in a 14 000 km^2 region of acidic forest–tundra landscape near northern Manitoba, Canada (59.56°N, 97.72°W) in 2009. We analyzed 39 different biological, chemical, and physical variables for lakes and soils. We used a remote-sensing–based classification to determine that the landscape was 21% water, 46% peat-forming lowland, and 24.9% open tundra, and we assigned lake order to all lakes based on the order of the outlet stream for each lake. Lakes were oligotrophic to mesotrophic (median total phosphorus: TP = 11.8 µg L^{-1}), N-limited (median dissolved inorganic nitrogen: TP = 1.6), acidic (median pH 5.7), and had moderate amounts of dissolved organic carbon (median DOC = 5.2 mg L^{-1}). We identified 2 principle groups of variables represented by DOC and conductivity/cations, respectively, that captured major axes of lake variation. DOC, 2 measures of DOC quality (a_{250}/a_{365} [a proxy for molecular weight and aromaticity] and specific ultraviolet absorbance), and Fe and were significantly correlated with percent cover of lowland forest, but conductivity/cations were not correlated with variation in land cover. Soils were generally acidic (pH 2.7–4.4) and nutrient-poor, and wetland soils contained more carbon and higher concentrations of calcium, magnesium, and other cations than upland open tundra. Landscape position of lakes (measured as lake order) did not capture systematic differences in land cover or lake biogeochemistry. Our results highlight the importance of lowland export of DOC to lakes and further suggest the need for additional regional studies of aquatic–terrestrial connections in Arctic and sub-Arctic landscapes.

Key words: Arctic, biogeochemistry, DOC, lakes, lake order, land cover, landscape, sub-Arctic, tundra

Introduction

Intensified warming in the Arctic and sub-Arctic has resulted in a wide range of changes in terrestrial and aquatic ecosystems at local, regional, and global scales (Prowse et al. 2009, Bonfils et al. 2012). These changes include (a) increased terrestrial productivity (Bonfils et al. 2012, Epstein et al. 2012), (b) enhanced lake productivity (Smol et al. 2005), (c) fundamental shifts in lake primary producers (Rühland et al. 2008), and (d) changes in the number and area of lakes and ponds due to thawing permafrost and terrestrialization (Rouse et al. 1997, Roach et al. 2011).

Terrestrial, wetland, and aquatic ecosystem responses to climate change typically have been studied independently, but they need to be considered together as a way

DOI: 10.5268/IW-5.1.752

of understanding local to global dynamics of carbon (C), silica (Si), nitrogen (N), phosphorus (P), and other biogeochemical variables (Cole et al. 2007, Sobek et al. 2007, Prairie 2008, Frey and McClelland 2009, Rosa et al. 2012, Olefeldt et al. 2013). Dissolved organic carbon (DOC), for example, plays a critical role in the functioning of lakes and rivers (Prairie 2008); DOC is largely terrestrial in origin and strongly positively correlated with wetland cover (Gergel et al. 1999, Xenopoulos et al. 2003, Cardille et al. 2007, Sobek et al. 2007, Lottig et al. 2011). The importance of wetlands versus uplands as a source of aquatic DOC may be explained by a range of factors, including C concentration, C quality, pH, iron (Fe) and aluminum (Al) concentrations, proximity, and hydrological flow paths (Hobara et al. 2013). Recently, a number of authors have linked changes in DOC and other geochemical markers to increasing permafrost thaw depths and/or past or future changes in land cover (e.g., Frey and Mcclelland 2009, Olefeldt et al. 2013).

While there are a growing number of studies in the Arctic and sub-Arctic describing local and regional variability in lake biogeochemistry (Pienitz et al. 1997, Duff et al. 1998, Rühland and Smol 1998, Westover et al. 2009, Medeiros et al. 2012), there are relatively few studies directly linking lake biogeochemistry to wetland cover and, more broadly, to landscape position (as in Riera et al. 2000) in permafrost-dominated Arctic or sub-Arctic landscapes (Duff et al. 1998, Soranno et al. 1999, Kling et al. 2000). Documenting aquatic–terrestrial connections (e.g., DOC and wetland cover) in multiple regions may be key to extrapolating results from local studies to global scales (Fergus et al. 2011, Cheruvelil et al. 2013).

This study explored aquatic–terrestrial connections in a little-studied, peat-rich, nutrient-poor, acidic, low-relief landscape located in the sub-Arctic of north-central Manitoba, Canada. We combined chemical, biological, and physical measurements of lakes and soils with catchment and vegetation characteristics derived from remote-sensing imagery to address 3 main questions. First, to what extent do differences in cover of wetlands (for this study defined as peat-forming lowland areas) or lake and catchment morphometry explain major biogeochemical gradients among lakes, including DOC, nutrient/trophic status, and pH/conductivity? Second, how well does landscape position, as measured by lake order (Riera et al. 2000, Martin and Soranno 2006, Sadro et al. 2012), capture differences in wetland cover, basin and catchment morphometry, or lake biogeochemistry? Third, how much of the importance of wetland cover can be explained by differences in carbon, nutrient, or cation content of wetland versus upland soils?

Methods and materials

Study area

Nejanilini Lake is located at tree line just north of the western Hudson Bay Lowlands ~140 km west of Hudson Bay (59°33′N, 97°43′W) and just south of the border between Manitoba and Nunavut, Canada (Fig. 1). The region was labeled forest-tundra by Ritchie (1959) and is part of the Taiga Shield Ecozone (both Seal and Ennadai Lake Plains; National Atlas Information Service 1993), and ~21% of the region is covered by lakes and other bodies of water (described later). The area is at the edge of the zone of continuous permafrost (Brown et al. 1998 [revised 2001]). The area was glaciated and then covered by the last remnants of Lake Agassiz until ~8500 cal yr BP (Leverington et al. 2002). Mean elevation is 264 m, rising from southeast to northwest from ~170 m to ~300 m (Fig. 1). Soils are thin and poorly developed cryosols, and the surficial geology is dominated by a bouldery, sandy diamicton of Precambrian crystalline rocks (Matile and Keller 2006). The underlying bedrock is characterized as an Archean granitoid complex as well as charnockite-mangerite and gneiss (Manitoba Geological Survey 2006). Areas of unvegetated bedrock and exposed, frost-heaved, and frost-shattered bedrock blocks are common (Anderson et al. 2005).

Average temperatures in the region range from −25 to −30 °C in winter and 10 to 15 °C in summer; monthly precipitation ranges from 15 to 30 mm (winter) to 30 to 60 mm (summer; Plummer et al. 2006). Based on data from Churchill, Manitoba (58.73°N, 94.07°W), summer 2009 was relatively cool, with an average daily high temperature of 12.5 °C. July precipitation in 2009 was 91.5 mm (Environment Canada, http://www.climate.weatheroffice.ec.gc.ca/).

Water and soil sampling

We sampled 44 lakes during 14–24 July 2009 (Fig. 1). Lakes were chosen on the basis of (a) accessibility by float plane and (b) a goal of sampling catchments representing a range of wetland covers. Sampling occurred near what was determined from the air and on-lake direct measurement to be the deepest part of the lake. At each sample location, water depth was measured using a Depthmate portable depth sounder, and Secchi depth was recorded. A YSI 556 multimeter (1 m depth) was used for pH, dissolved oxygen (DO), oxidative reduction potential (ORP), and temperature. The probe was bobbed gently up and down until output was stabilized. We calibrated the pH probe on a daily basis using pH 4 and 7 buffers. The 2 L water samples were collected from a depth of ~0.25 m and kept refrigerated until processing.

 DOI: 10.5268/IW-5.1.752

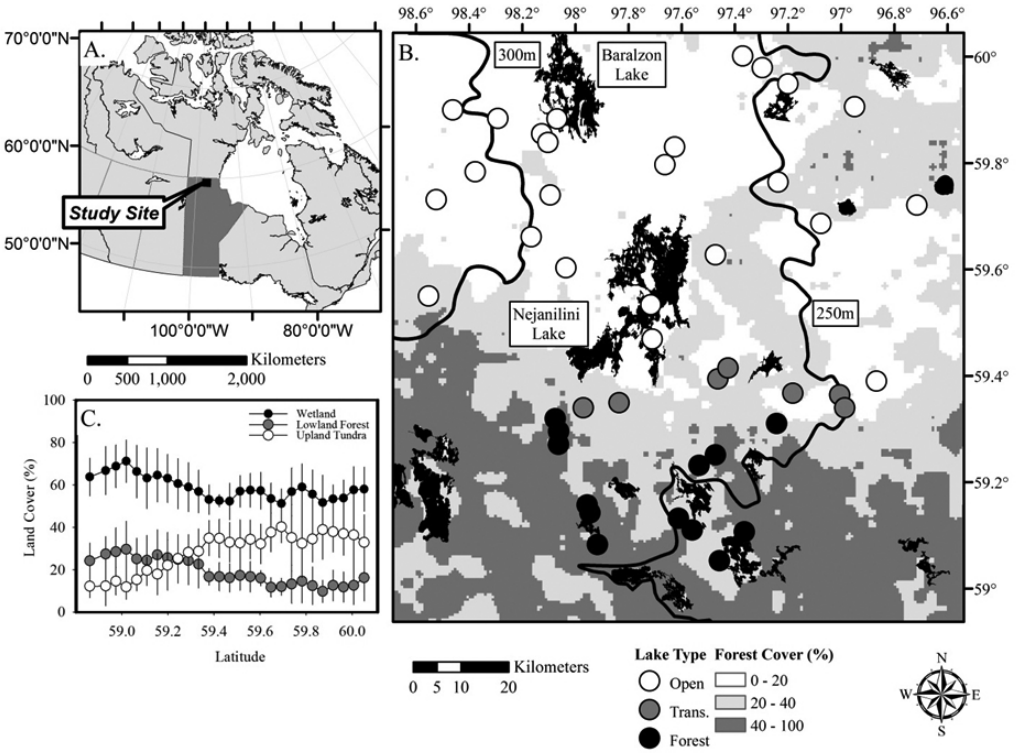

Fig. 1. Location of (A) study site in northern Manitoba, (B) distribution of 44 study lakes at site, and (C) latitudinal changes in land cover (see Table 2) based on 5 × 5 km blocks. In panel B, symbols denote whether lakes were located in forest-dominated (black), transitional (gray), or open tundra (white) regions. Landscape shading is based on relative forest cover in 5 × 5 km blocks. Lines represent 250 and 300 m elevation contours. Large study lakes, labeled for reference, are also based on 5 × 5 km.

We measured specific conductivity (EC) in the laboratory within 12 h of sample collection using an Oakton Instruments (Vernon Hills, IL) Con 6 conductivity meter calibrated using a 23 µS cm^{-1} standard. EC was measured in the lab because initial work in 2008 showed that the YSI field instrument was not reliable for the low EC values we observed for our lakes. All conductivity measurements were normalized to 25 °C.

Within 24 h of collection, water samples were processed and preserved. Samples for total phosphorus (TP) were unfiltered and acidified to pH < 2 with concentrated sulfuric acid. Water for element analysis was filtered through a 0.45 µm polycarbonate mesh and preserved with sulfuric acid for DOC, total dissolved nitrogen (TDN), and total dissolved phosphorus (TDP), or nitric acid for calcium (Ca^{2+}), sodium (Na^{+}), potassium (K^{+}), magnesium (Mg^{+}), total Fe ($Fe^{2+/3+}$), and total Al (Al^{-}). Filtered samples for ammonia (NH_4^{+}) and nitrate (NO_3^{-}) analysis were frozen. Filtered samples were refrigerated for anions and dissolved silica ($dSiO_2$). For chlorophyll *a* (Chl-*a*), 300–400 mL of water was passed through a 0.7 µm pore glass filter, and the filter was then immersed in 90% acetone and frozen prior to analysis (Arar and Collins 1997). For particulate Si ($pSiO_2$), additional unfiltered water (150–300 mL) was passed through 0.45 µm Durapore filters and the filters frozen (Triplett et al. 2008). For total suspended solids (TSS) and volatile suspended solids (VSS), 200–300 mL of water (in shaken bottles) was passed through pre-weighed, ashed glass filters (1.5 µm), and filters were frozen prior to analysis. Water for ultraviolet (UV) fluorescence analysis was filtered through a 0.7 µm GF/F filter and analyzed within 24 h of collection.

To document differences in wetland and upland soils in the region, we opportunistically sampled active layer soils from a range of dry upland tundra (n = 16), and wetland (n = 19) sites. Wetland sites were further divided between lowland, peat-forming forests (n = 10) and open peat (n = 9) sites; lowland forest sites had a nearly continuous cover of white spruce (*Picea glauca*) and/or tamarack (*Larix laricina*; see also Supplemental Table S1). At each upland site a small pit was excavated, and a volumetric sample was taken from the approximate center of each visible soil layer (A, E, B, or C horizons). For purposes of this study, we present results for our shallow (5 cm median depth) sample and a deeper (25 cm median depth) sample. In upland tundra, the shallow sample corresponded to the A

horizon and the deeper sample represented the C horizon at 12 of 16 sites. At the remaining 4 sites, large buried cobbles prevented deeper excavation, and therefore the deep sample was taken from the B horizon. In peat-forming sites, soil horizons were not differentiated; soils were simply collected at 5 cm and 25 cm depths. Thickness of the A horizon was recorded in the field. Soils were dried upon collection (~60 °C) in the laboratory prior to analysis.

Laboratory analyses of water and soil samples

For water samples, DOC and TDN were analyzed using a TOC-VCSN (Shimadzu). UV absorbance was measured using scans with a UV-Vis spectrophotometer (Cary 300, Varian Inc.) set to 1 nm intervals with DI blanks and absorption coefficients calculated as described in Kirk (1994). UV absorbance measurements were used to calculate (a) specific UV absorbance (SUVA) as a_{254}/DOC, which is a commonly used measure of aromaticity (Weishaar et al. 2003, Hanley et al. 2013); (b) a_{320} as a possible measure of the contribution to UV absorption of oxygenated Fe and Fe–DOM complexes (Maloney et al. 2005); and (c) a_{250}/a_{365} as a measure of molecular weight (Olefeldt et al. 2013). Color was estimated from a_{440} (Cuthbert and Del Giorgio 1992).

Initial evaluation of pH data suggested that our in-field numbers for lakes were too low, despite a strong positive correlation (0.93) between 2008 (not published) and 2009 measurements. A depression in pH associated with stirring or movement of low EC water (<20 µS cm^{-1}) has been previously noted in the literature (Hoenicke et al. 1991). Using an experimental approach in the lab, we compared stirred (125 rpm) and unstirred low conductivity (10–20 µS cm^{-1}) low pH solutions (4.5–5.5) and found a nearly identical pH depression of 0.65 units (SD = 0.22, n = 12) for 2 new YSI 5565 pH probes in the stirred solutions. The drop in pH due to stirring was nearly identical to a 0.71 drop in pH in 11 uS cm^{-1} water associated with the standard "bobbing" movement of YSI probe used in the field. As such, all reported pH values are adjusted upward by 0.65 units to account for the observed depression.

Ca, Mg, K, Fe, Al, K, and sodium (Na) were analyzed using a OES-ICP (Horiba Jobin Yvon Ultima 2) and multi-element standards obtained from Inorganic Ventures (Christiansburg, VA, USA). Chloride (Cl) and sulfate (SO_4) were analyzed using an ion chromatography system (Dionex DX-100). Samples for TP and TDP analysis were prepared using a persulfate digest (30 min at 121 °C, 0.11 MPa with ammonium persulfate and sulfuric acid) and then analyzed using an autoanalyser (Lachat QC8000, Hach Co; Liao 2002). We extracted $pSiO_2$ from filters using sodium hydroxide (NaOH) as described by Triplett et al. (2008); $pSiO_2$ extract and $dSiO_2$ were both analyzed colorimetrically using the autoanalyser (McKnight 2000). Nitrate was measured on the autoanalyser using a cadmium reduction method modified from Sechtig (2001). NH_4^+ was analyzed using a fluorometric method (Holmes et al. 1999) on a Trilogy fluorometer (Turner Designs Inc.). Chl-*a* and phaeophytin were measured using the Trilogy Fluorometer (http://www.turnerdesigns.com/t2/doc/appnotes/998-5101.pdf).

We calculated soil bulk density on a dry mass basis. Bulk density of mineral soils was corrected by subtracting the mass of stones and pebbles trapped by a 2 mm sieve prior to calculation of density. Mineral soil samples were passed through a 2 mm sieve prior to analysis and lightly ground. Soil pH was analyzed using either a 2:1 or 4:1 dilution with $CaCl_2$:soil extraction (Kalra and Maynard 1991) and measured in the laboratory using an Orion pH meter calibrated at pH 4 and 7; pH readings were taken from unstirred samples after 2 minutes. C and N content of soils was analyzed using an Element Analyzer (Costech 4010) after removing any possible carbonates with hydrogen chloride (HCl). A Mehlich III extraction (Mehlich 1984) was used to extract Fe, Al, Ca, Na, Mg, K, and P, and these were analyzed as described earlier. Concentrations are expressed on a mass basis, and for carbon are also given on an areal basis (kg m^{-2}).

Lake, landscape and catchment description

Using a combination of remote sensing imagery and digital elevation models, we calculated several lake and landscape properties useful for the analysis of terrestrial–aquatic linkages. Lake area was determined from polygons traced from the lake images in a 2002 Landsat image (ETM Mosaic, N-14-55, downloaded from the University of Maryland Global Land Cover Facility, http://glcf.umiacs.umd.edu/). Catchments were delineated using 50 K digital elevation models (DEMs; downloaded from Geobase Canada, http://www.geobase.ca/geobase/en/index.htmL, vertical positional accuracy ~3–4 m) using the Arc Hydro extension for ArcMap 10.0 (ESRI). Lake catchment area was calculated excluding the target lake. Average slope (excluding the target lake) was calculated for each catchment from the DEM using ArcMap. Because of possible problems with catchment delineation due to low relief relative to vertical positional accuracy, we also created a 100 m buffer for each lake using ArcMap to delineate land cover. Elevation of lake and maximum catchment elevation was taken from the DEM.

Lake order (LO) is generally defined by the order of the outlet stream (Riera et al. 2000) and was calculated for each lake using streams delineated in the Canadian

 DOI: 10.5268/IW-5.1.752

National Hydro Network dataset (downloaded from GeoBase) in combination with aerial photos, notes taken from the field, and high resolution imagery (Geoeye, 1 m resolution, flown in 2008–2009). LO is generally higher for lakes located lower in the landscape.

Land cover was classified using the Landsat image. The image was pan-sharpened first and then analyzed iteratively using ENVI EX 4.8 (Exelis Visual Information Solutions). A first pass was made through the data using ISODAT unsupervised classification to identify areas of open water and remove them from further analysis to focus on the terrestrial landscape. Next, 10 land cover types were identified using the Feature Extraction algorithm and ground-truth data from on-the-ground reconnaissance, aerial photographs, and 1 m Geoeye satellite imagery. Each of these 10 cover types was then separately analyzed and classified and the results of these 10 individual analyses combined for the final classification (see Supplementary Table S1 for descriptions of each cover type). Percent of area occupied by cover types was summarized for each catchment and separately within the 100 m buffer zone surrounding each lake (Table 1).

Statistical analysis

Summary statistics were calculated for all data using R (R Development Core Team 2006) and given as medians ± median absolute deviation (MAD). The median and MAD were used because they are much less sensitive to outliers present in the data than mean and standard error. Element molar ratios (DIN:TP, Ca:Na, C:N) were calculated to explore nutrient limitation and dominant weathering processes.

To explore major environmental gradients, we ordinated lake data using Sorenson's measure of dissimilarity and nonmetric multidimensional scaling (NMDS) with a varimax rotation (McCune and Mefford 2006). The ordination was based on measured chemical and biological variables (n = 30) of lake waters. Element ratio data, lake morphometry, catchment characteristics, and land cover were not used in the ordination. Data used in the ordination were transformed by dividing each variable by its sum total (McCune and Mefford 2006) to ensure a similar scaling and weight for all variables. The pH data were converted to concentration of H^+ prior to transformation.

Lake water variables, element ratios, and lake and catchment morphometric and cover characteristics were correlated with the first 2 axes of the ordination using Spearman Rank correlation. We used Spearman Rank correlation because we could not easily transform the data to meet parametric assumptions of normality, largely as a result of outliers. Uncorrected p-values are presented for all correlations to facilitate comparison with previous lakes studies, but assessment of statistical significance is based on Hochberg's correction for multiple comparisons (Hochberg 1988). We assessed the utility of lake order using Kruskal-Wallis nonparametric tests for individual water quality, physical, and land cover variables. To ensure more equal sample sizes, lakes classified as LO 0–1 or 4–6 were combined to total 4 LO classes (0–1, 2, 3, 4–6; n = 11, 16, 10, and 7, respectively). If the Kruskal-Wallis test was significant ($p \leq 0.05$), we used Mann-Whitney-U tests (Hochberg-corrected) to examine pairwise differences among LO classes. Differences among soils were also explored using the Kruskal-Wallis, Mann-Whitney procedure described earlier. We also examined whether lake proximity was a predictor of lake biogeochemistry by comparing geographical distances and the Sorenson's dissimilarity (discussed earlier) for all possible pairwise combinations of lakes.

Results

Lakes and landscape setting

Median surface area of sampled lakes was 69 ha (Table 1), and all lakes were of the same order of magnitude in area with the exception of Baralzon, Nejanilini, and Little Duck (Fig. 1), which were 1–2 orders of magnitude larger, as were their catchments. Median catchment area was 702 ha, and the median catchment:basin ratio was 8.8. The landscape was generally level, with a median maximum catchment elevation:lake elevation ratio of 1.1 and a median slope of 1.7% (Table 1). Lakes were generally shallow (median recorded max depth = 3.3 m). Median LO of lakes was 2 (Table 1); only 5 lakes were order 0 (no upstream lake), and 5 were order 5 or higher.

Wetland occupied 44% of the surface area in catchments (Table 1) of sampled lakes (n = 44), ranging from 26 to 79%. Upland tundra (28%) ranged from 4 to 67%, while open water (excluding target lakes) accounted for a median of 10% of area in catchments. Wetland cover was greater in the 100 m buffer from the lake edge (65 vs. 44%) than the catchment as a whole, although percent wetland in catchments and 100 m buffers was highly correlated ($r = 0.68$, $p < 0.001$). Percent lowland forest cover was only slightly higher in 100 m buffers (13 vs. 10%) versus catchments, and again buffer and catchment percentages were highly positively correlated ($r = 0.69$, $p < 0.001$). Cover of dry upland tundra in the100 m buffer was almost half (17 vs. 28%) of that for catchments, but cover values were again positively correlated ($r = 0.64$, $p < 0.001$) for the catchment and 100 m buffer.

Table 1. Summary of lake and catchment morphometry and land cover (%) characteristics (n = 44). Bold values represent sum of component cover types. Data for individual catchments available in data set are available in supplemental materials (Table S2).

	Median	MAD[a]	Min	Max
Lake Elevation (m)	268	27	195	317
Catch:Lake Elevation	1.1	0.1	1.0	1.3
Surface area (ha)	69	36	21	32 976
Perimeter (km)	5.6	1.7	3.0	719
Catchment area (ha)[b]	702	732	116	461 709
Catchment: Basin	8.8	9.6	1.0	701.3
Catchment slope (%)[c]	1.7	0.3	1.2	3.0
Max recorded depth (m)	3.4	2.3	1.0	15.7
Lake order[d]	2.0	1.5	0	6
Catchment Cover (%)				
Wetland	**44.2**	**8.1**	**25.5**	**79.0**
Open Peat	27.3	3.6	15.2	44.3
Sedge Peat	3.7	1.1	1.3	9.0
Picea-Larix Lowland Forest	10.2	4.7	3.2	43.8
Tundra	**37.0**	**11.0**	**11.1**	**72.4**
Moist-Wet Tundra	6.9	2.3	0.5	22
Upland Tundrae	27.9	21.2	4.0	63.5
Dry Heath	19.8	11.2	0.8	49.2
Exposed/Bare Till	0.1	0.07	0	2.5
Shrub	7.1	2.80	0.3	14.9
Rock	0.0	0.01	0.0	3.3
Upland Forest/Woodland	**3.2**	**1.4**	**0.2**	**43.1**
Open Water	**10.1**	**6.3**	**0**	**30.4**
Burn Recovery	**0.0**	**0.00**	**0.0**	**59.8**
Cover in 100 m Buffer (%)				
Wetland	**65.0**	**14.3**	**36.4**	**86.3**
Picea-Larix Lowland Forest	**13.2**	**10.2**	**2.7**	**40.2**
Upland Tundra	**16.6**	**12.2**	**4.3**	**44.8**

[a] Median Absolute Deviation = the median difference between individual observations and the median
[b] Does not include surface area of sampled lake
[c] Does not include sampled lake
[d] After (Riera et al. 2000)
[e] Composite of dry heath, exposed/barren, shrub, and rock cover classes

Lake water properties

A summary of lake water physical, chemical, and biological properties (Table 2) shows that waters were highly oxygenated (median = 10.2 mg L^{-1}) and cold (median = 12.5 °C). Lake waters had low pH (median = 5.4) and low conductivity (median = 12.2 µS cm^{-1}). Base cation levels were generally low, with Ca (median = 698 µg L^{-1}) and Na (median = 623 µg L^{-1}) being the 2 most abundant cations. Ca:Na ratios (median = 0.7) were generally low but ranged from 0.3 to a high of 3.4. Median $dSiO_2$ levels were between 0.35 and 0.76 mg L^{-1},

 DOI: 10.5268/IW-5.1.752

and median Chl-*a* was 1.86 mg L^{-1} and varied widely from 0.8 to 13.8 mg L^{-1}. TP was generally low (median = 18.5 ug L^{-1}), and median DIN:TP was 1.62, suggesting N limitation is more likely than P limitation (Bergstrom 2010); however, direct measurement of limitation through experimentation was not undertaken. The bulk of N was organic, with inorganic N representing ~5% of TDN.

Median DOC was 4.7 mg L^{-1}, and C:N ratios were generally high (24.7), consistent with allochthonous inputs. DOC, SUVA, color, and Fe were all strongly positively correlated, but these same variables were negatively correlated with a_{250}/a_{365} (corrected and uncorrected p-values; Table 3). C:N ratios were significantly correlated with DOC concentrations only when p-values were not corrected for multiple comparisons.

NMDS ordination (Fig. 2) and correlation analysis (Tables 3 and 4) indicated 2 different groups of lake variables. Group 1 included DOC concentration and quality (a_{320}, color, SUVA, a_{250}/a_{365}), Fe, Al, Secchi, TDN, TP, TSS, and pheophytin, and these properties were largely responsible for separation of lakes on the first ordination axis. Lakes higher in DOC on the first axis were generally warmer and shallower than lakes lower in in DOC (Tables 4 and 5). Group 2 variables include ORP, conductivity, pH, $dSiO_2$, Na, Mg, K, Ca, SO_4, and TDP, and were significantly correlated with the second ordination axis (Table 4).

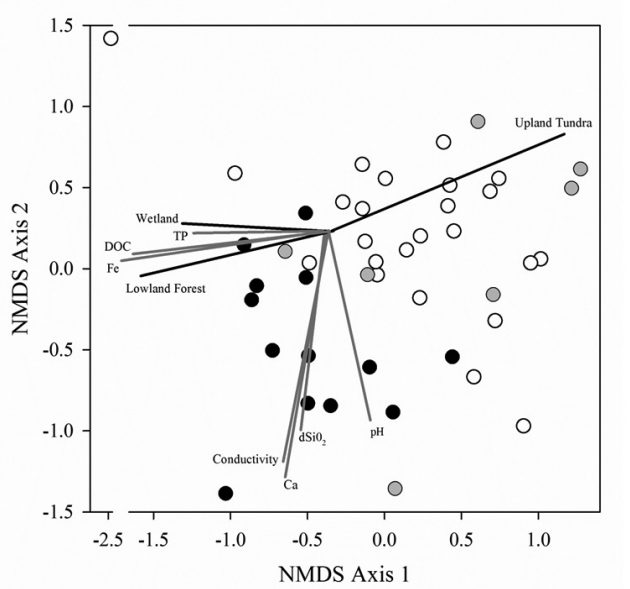

Fig. 2. Nonmetric multidimensional scaling (NMDS) ordination of lakes (n = 44) based on water characteristics (n = 39). Overlays are given for selected characteristics with direction and length of vectors representing relative strength of correlation with Axes 1 and 2; landscape vectors are passively plotted. Symbols colors denote whether lakes were located in forest-dominated (black), transitional (gray), or open tundra (white) regions.

Table 2. Summary of lake physical, chemical, and biological properties (n = 30). Unless otherwise noted, n = 44. Values for a_{320} are correlated with concentration of Fe and Fe-DOC complexes (Maloney et al. 2005), and a_{250}/a_{365} is inversely correlated with DOC molecular weight (Olefeldt et al. 2013). Full data set is available in supplemental materials (Table S2).

	Median	MAD	Min	Max
DOC (mg L^{-1})	4.7	1.8	2.1	9.8
SUVA (L mg C^{-1} m^{-1})	9.4	1.8	2.1	11.2
Color [(a_{440})] (mg L^{-1})	52.0	30.1	4.4	180.5
a_{320} (m^{-1})	18.8	12.1	3.1	43.1
a_{250}/a_{365}	5.3	0.6	4.6	6.9
Fe (µg L^{-1})	195	153	10	475
Al (µg L^{-1})	27	16	2	68
Secchi[a]	2.2	0.7	0.9	6.1
TDN (µg L^{-1})	209	63	135	647
NH_4^+ (µg L^{-1})	4.0	3.5	0.2	33.3
NO_3^- (µg L^{-1})	6.9	3.4	3.4	34.9
C:N (molar)	24.7	4.2	12.0	60.2
Conductivity (µS cm^{-1})	12.2	4.3	5.8	53.5
ORP (mV)	157.5	146.0	20.0	477.8
pH	5.3	0.7	4.0	6.8
Ca (µg L^{-1})	698	221	207	5452
Mg (µg L^{-1})	271	105	100	1638
Na (µg L^{-1})	623	171	340	1091
K (µg L^{-1})	219	82	76	474
Ca:Na (Molar)	0.7	0.1	0.3	3.4
Cl^- (µg L^{-1})	530	201	259	1076
SO_4^{2-} (µg L^{-1})	382	155	177	1256
$dSiO_2$ (µg L^{-1})	762	565	193	4381
$pSiO_2$[b] (mg L^{-1})	3.5	1.3	0.8	10.5
Chlorophyll *a* (µg L^{-1})	1.9	1.0	0.8	13.8
Pheophytin (µg L^{-1})	0.8	0.5	0.1	7.5
Total P (µg L^{-1})	18.5	9.4	6.6	101.6
TDP (µg L^{-1})	8.6	5.2	0.0	18.4
DIN:TP (Molar)	1.6	1.2	0.2	9.4
TSS (mg L^{-1})	2.9	1.5	1.1	12.4
VSS (mg L^{-1})	1.2	0.7	0.3	8.9
Temp (°C)	12.5	2.7	8.2	17.1
DO (mg L^{-1})	10.2	0.5	8.8	11.7

[a] Excludes lakes where Secchi disk was visible resting on bottom (final n = 38)
[b] $pSiO_2$

Lake and landscape connections

Physical distance between lakes, while statistically significant ($p < 0.01$), was not a useful predictor of lake biogeochemistry (Supplemental Fig. S1). Lakes north and south of treeline did separate along the first axis of the ordination, with southern lakes having higher concentrations of DOC (Table 4) and highest percent cover of lowland forest in the catchment. Across the region, wetland and lowland forest declined with increasing latitude (Fig. 1C). Lowland forest was the strongest correlate ($r = -0.80$, $p < 0.001$) with the first axis, despite representing only a median 10.2% of land cover in catchments (Table 1). Neither cover of open peat nor sedge peat (Table 1) was correlated with the first axis ($p > 0.05$), suggesting that the correlation of wetlands with Axis 1 was largely driven by lowland forest. Within the 100 m buffer, lowland forest and percent wetland were both significantly correlated with the first axis, as was upland tundra cover (Table 4). None of the land cover characteristics we measured were significantly correlated ($p > 0.05$) with the second axis of the ordination (Table 5). Percent area of bare till and exposed rock was significantly positively correlated with the first but not the second ordination axis (Table 5).

Based on the ordination results, we focused further analyses on the relationship of lowland forest cover and lake biogeochemistry. Concentrations of DOC were significantly positively correlated with lowland forest cover in the catchment (Fig. 3A; Table 3). Increasing DOC was accompanied by significantly higher SUVA (Fig. 3A), color, and Fe (Fig. 3B), and, marginally, C:N (Table 3). Ca, pH, TP, DIN: TP, $dSiO_2$, and Chl-*a* were not significantly correlated with percent lowland forest cover (Fig. 3; Table 3).

Catchment area was significantly different ($p < 0.05$) among LO groups (Fig. 4B), but lake surface area did not vary significantly, largely reflecting high variability in the area of LO 6 lakes (Fig. 4A). While not significant ($p > 0.15$), there was a slight tendency for higher-order lakes to have higher pH (Fig. 4K). LO showed little relation with any of the other measured physical, chemical, and biological properties of the terrestrial and aquatic systems (Fig. 4).

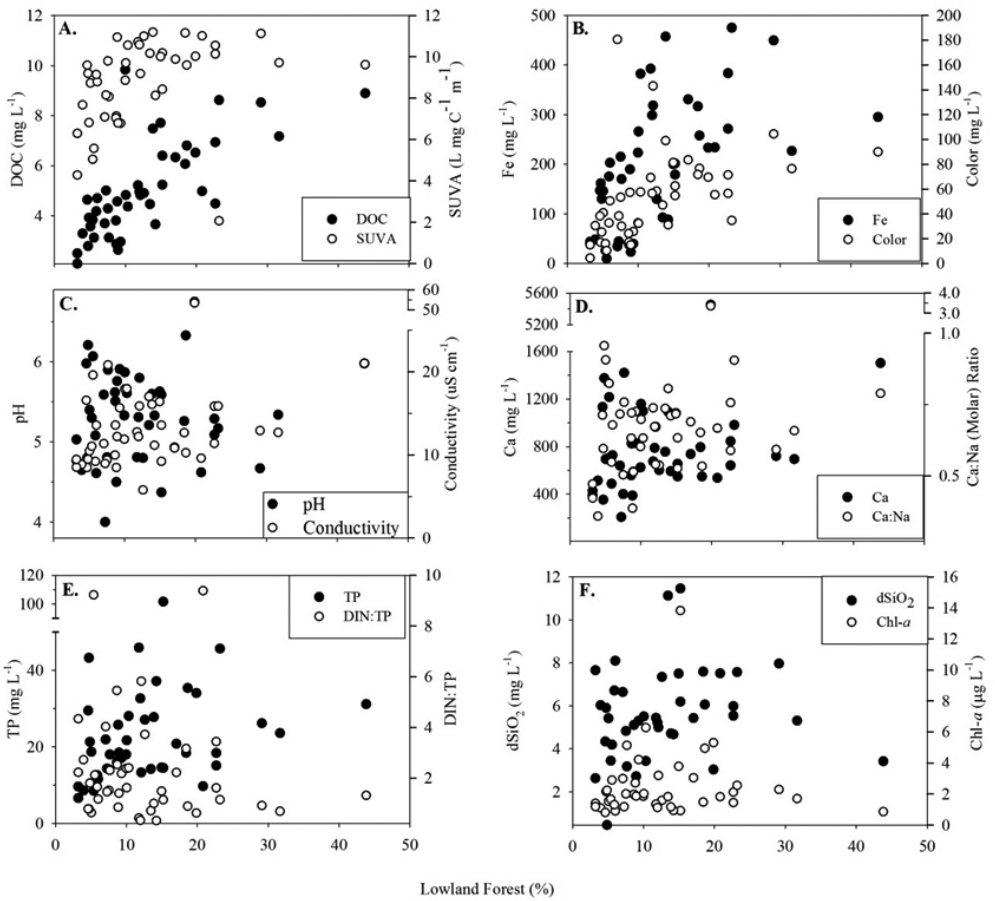

Fig. 3. Relations among selected lake water characteristics and lowland forest cover (%) for (A) DOC and SUVA; (B) Fe and Color; (C) pH and Conductivity; (D) Ca and Ca:Na ratio; (E) TP and DIN:TP; and (F) dissolved SiO_2 and Chl-*a*.

 DOI: 10.5268/IW-5.1.752

Table 3. Intercorrelation (Spearman) of selected lake variables. Significance (bold, $p < 0.01$; italics, $p < 0.05$) was assessed using Hochberg's family-wise adjustment to correct for multiple comparisons. Symbols following each correlation value represent uncorrected p-values (** $p < 0.01$, * $p < 0.05$).

	DOC	SUVA	Color	a_{250}/a_{320}	Fe	TN	CN	TP	DIN:TP	pH	Conductivity	Ca	Ca:Na	$dSiO_2$
SUVA	**0.56****													
Color	**0.74****	**0.69****												
a_{250}/a_{320}	***−0.51*****	**−0.78****	**−0.69****											
Fe	**0.74****	**0.67****	**0.68****	**−0.76****										
TN	**0.68****	0.29	**0.55****	−0.36*	0.51**									
CN	0.43**	0.49**	0.30*	−0.30*	0.38*	−0.29								
TP	0.39*	0.31*	0.39**	−0.35*	0.44**	0.27	0.18							
DIN:TP	0.04	−0.24	0.03	**−0.67****	−0.24	−0.18	−0.12	−0.10						
pH	−0.03	−0.18	−0.01	0.05	−0.08	0.02	0.01	0.16	0.24					
Conductivity	0.29	0.13	0.22	−0.15	0.30*	0.18	0.25	0.13	−0.11	**0.63****				
Ca	0.26	0.08	0.21	−0.17	0.29	0.20	0.23	0.19	0.29	**0.68****	**0.87****			
Ca:Na	0.20	−0.09	0.06	0.10	0.06	0.15	0.13	0.24	0.29	0.48**	**0.60****	**0.76****		
$dSiO_2$	0.11	0.26	0.26	−0.37*	0.27	0.06	0.19	−0.01	0.26	0.51**	**0.64****	**0.69****	0.25	
Low Forest	**0.76****	**0.56****	**0.68****	**−0.57****	**0.67****	**0.56****	0.30*	0.42**	−0.23	0.06	0.37*	0.27	0.16	0.14

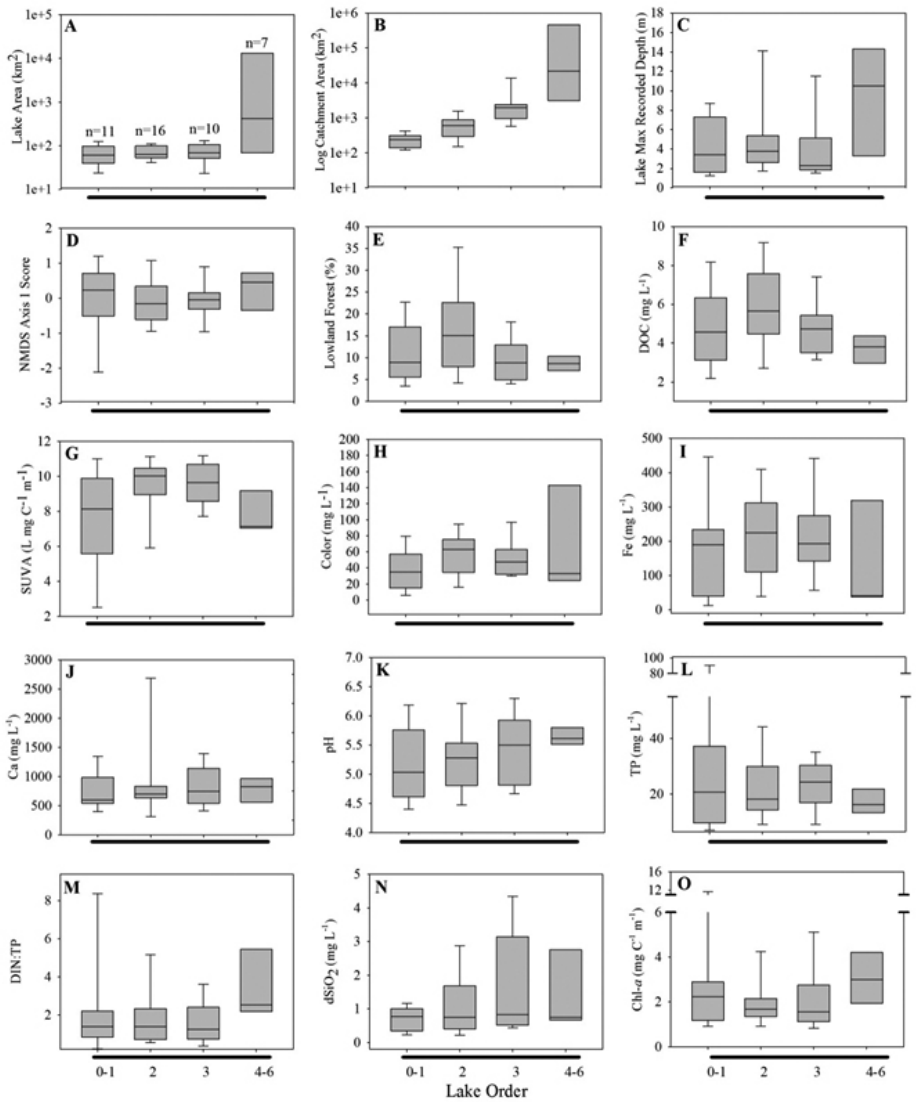

Fig. 4. Box plots of lake order versus (A) lake surface area; (B) catchment area; (C) maximum recorded depth; (D) wetland cover (open peat, sedge peat and lowland forest combined); (E) lowland forest cover; (F) DOC; (G) SUVA; (H) color; (I) Fe; (J) Ca; (K) pH; (L) TP; (M) DIN:TP; (N) dissolved SiO_2; and (O) Chl-*a*. Solid line in each box is median. Upper bound of box is 75th percentile while lower bound is 25th percentile; whiskers are 5th and 95th percentiles. If lake order (LO) was significant (Kruskal-Wallis, $p \leq 0.05$, Hochberg-corrected) then pairwise Mann-Whitney U tests (Hochberg-corrected) were performed. The solid line in each graph indicates groups not significantly different at ($p \leq 0.05$). Sample sizes for each LO class are given in Panel A.

Soil properties

Percent C (44%) on a mass basis was nearly 7 times greater in the shallow 0–10 cm of wetland soils versus upland tundra soil (Table 6), but greater soil bulk density for uplands means that soil C concentrations (~1.5 kg m^{-2}) were statistically similar across upland and the 2 wetland types ($p = 0.34$; Fig. 5A). Deeper (~25 cm) upland soils were mostly mineral (0.14% C), so when C concentrations were summed for the top 25 cm, C for open peat and lowland forest (~6 kg m^2) was twice that observed for upland tundra (Fig. 5B). C:N ratios were significantly higher for shallow lowland forest soils (Fig. 5C) but were significantly lower for deeper upland soils (Fig. 5D).

Soil cations, stoichiometric ratios, and pH varied significantly across landscape position, depth, and ecosystem type. Soil Fe and Al concentrations were highly variable within each of the 3 cover classes (Table 6). As also seen for lakes, we observed that Ca was the most abundant cation in our soils. While variable, Ca concentrations in lowland forest and open peat varied relatively little with depth. In upland tundra, Ca was largely concentrated in the shallow 0–5 cm depth (Table 6). Median Ca:Na ratios were highest (12.3, shallow; 25.8, deep) in lowland forest

 DOI: 10.5268/IW-5.1.752

soils (Fig. 5E and F). Differences in the Ca:Na ratio among the 3 soils were highly significant for deeper samples, but Ca:Na was much more variable for 0–5 cm samples, resulting in statistically nonsignificant differences. By contrast, Ca:Na ratios (0.3) we calculated for lakes were much lower than observed for soils (Table 2). Soil pH was lower than observed for lakes (Table 2), ranging from a median of 2.8 in shallow wetland soils to 4.4 in deeper upland soils (Table 6; Fig. 5G and H).

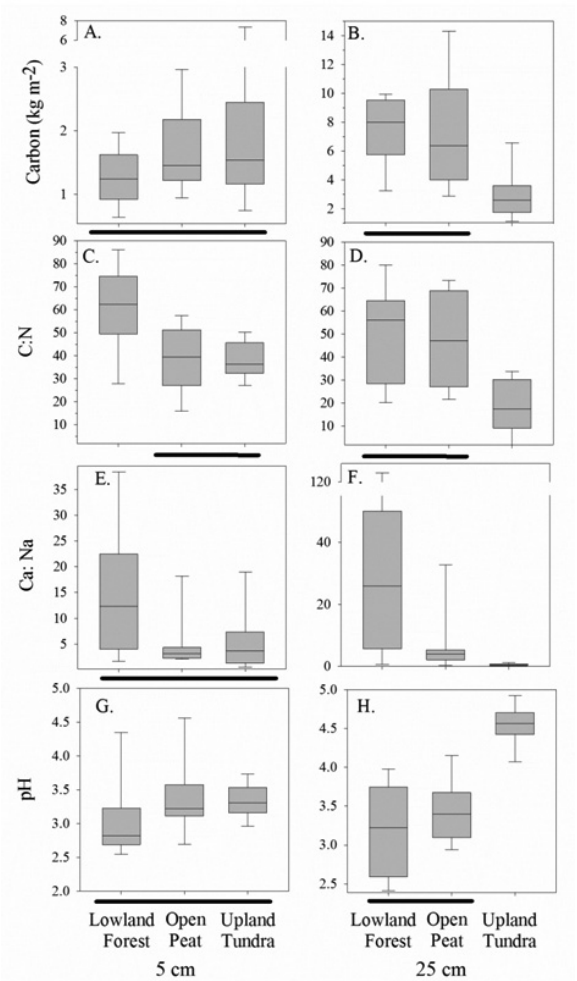

Fig. 5. Boxplots for selected characteristics of soils from lowland forest (n = 10), open peat (n = 9), and upland tundra. Data for shallow (0–10 cm) and deep (20–30 cm) samples are provided for (A, B) carbon (kg m^{-2}); (C, D) C:N (molar); (E,F) Ca:Na (molar); and (G, H) pH. Carbon is cumulative to a depth of 5 and 25 cm, respectively. Sample size is n = 12 for upland tundra in panel B and D because carbon and/or nitrogen levels were below detection limits for 4 samples. Upper bound of box is 75th percentile while lower bound is 25th percentile; whiskers are 5th and 95th percentiles. If difference among cover types was significant (Kruskal-Wallis, $p \leq 0.05$, Hochberg-corrected) then pairwise Mann-Whitney U tests (Hochberg-corrected) were performed. The solid line in each graph indicates groups not significantly different at $p \leq 0.05$.

Table 4. Correlation (Spearman) of lake water variables with first or second axis of ordination (Fig. 2). Italicized variables were not used in the ordination. P-values given in table are uncorrected but significance (bold, $p < 0.01$; italics, $p < 0.05$) was assessed using Hochberg's family-wise adjustment to correct for multiple comparisons.

	Axis 1		Axis 2	
	r	p	r	p
DOC[a]	**−0.83**	<0.001	−0.07	0.654
a_{320}	**−0.83**	<0.001	−0.01	0.878
Color (a_{440})	**−0.81**	<0.001	−0.03	0.827
SUVA	**−0.68**	<0.001	−0.01	0.961
a_{250}/ a_{365}	**0.72**	<0.001	0.02	0.910
Secchi (n = 38)	**0.90**	<0.001	−0.09	0.547
Al[a]	**−0.58**	<0.001	0.22	0.150
Fe	**−0.84**	<0.001	−0.09	0.534
TDN(n = 43)	**−0.64**	<0.001	0.01	0.932
TP(n = 43)	**−0.59**	<0.001	0.09	0.566
TSS	*−0.51*	<0.001	0.29	0.064
Pheophytin	**−0.59**	<0.001	−0.02	0.885
Conductivity	−0.33	0.028	**−0.83**	<0.001
ORP	−0.33	0.031	**0.75**	<0.001
pH	−0.04	0.804	**−0.70**	<0.001
Ca	−0.34	0.025	**−0.88**	<0.001
Mg	−0.31	0.043	**−0.77**	<0.001
Na	−0.31	0.038	**−0.86**	<0.001
K	−0.02	0.897	**−0.83**	<0.001
Ca:Na (molar)	−0.16	0.291	**−0.54**	<0.001
SO_4^{2-}	0.33	0.031	*−0.49*	<0.001
$dSiO_2$	−0.27	0.078	**−0.70**	<0.001
TDP	−0.16	0.308	*−0.52*	<0.001
DIN:TP (n = 43)	0.34	0.024	−0.10	0.510
DO	−0.43	0.029	0.19	0.230
Cl^-	−0.17	0.257	−0.02	0.913
Water Temperature	−0.39	0.009	−0.01	0.945
$pSiO_2$	−0.42	0.004	0.15	0.320
VSS	−0.31	0.041	0.12	0.452
C:N (molar)	−0.32	0.035	−0.21	0.162
Ammonia	0.15	0.334	−0.03	0.837
Nitrate	−0.29	0.061	−0.11	0.477
Chlorophyll *a*	−0.32	0.034	−0.18	0.234

Table 5. Correlation (Spearman) of basin and catchment morphometry and land cover with first or second axis of ordination (Fig. 2). Italicized variables were not used in the ordination. P-values given in table are uncorrected but significance (bold, $p < 0.01$; italics, $p < 0.05$) was assessed using Hochberg's family-wise adjustment to correct for multiple comparisons.

	Axis 1		Axis 2	
	r	p	r	p
Upland Tundra	**0.57**	0.000	0.43	0.007
Bare Till/Exposed Rock	0.49	0.001	−0.20	0.188
Wetlands (catchment)	**−0.64**	0.000	0.04	0.803
Lowland Forest (catchment)	**−0.80**	0.000	−0.15	0.339
Open Peat	−0.27	0.072	0.25	0.099
Sedge-Peat	−0.11	0.470	−0.05	0.751
Wetlands (100 m buffer)	**−0.58**	0.000	0.01	0.965
Lowland Forest (100 m buffer)	**−0.59**	0.000	−0.16	0.308
Upland Tundra (100 m buffer)	**0.73**	0.000	0.27	0.080
Lakes (# in catchment)	0.13	0.400	−0.25	0.103
Lake Max Recorded Depth	0.38	0.012	−0.38	0.011
Lake Area	0.24	0.121	0.00	0.991
Lake Perimeter	0.22	0.152	−0.14	0.372
Lake Elevation	0.48	0.001	−0.03	0.832
Catchment Area	−0.05	0.750	−0.32	0.033
Catch:Basin Ratio	−0.16	0.315	−0.31	0.042
Catch Elevation:Lake Elevation	−0.12	0.447	−0.30	0.046
% Slope in Catchment	0.03	0.832	−0.30	0.050

Table 6. Summary data for soils sampled at 0–10 cm and 20-30 cm from (A) lowland forest, (B) open peatland, and (C) upland tundra. bd = below detection limits. MAD = ± median absolute deviation.

	0–10 cm				20–30 cm			
	Median	MAD	min	max	Median	MAD	min	max
A. Lowland Forest (n = 10)								
Org Carbon (%)	43.9	0.6	40.1	50.1	44.0	2.5	bd	48.1
Org N (%)	0.8	0.3	0.6	1.8	0.9	0.4	bd	2.8
C:N	62.5	14.5	26.3	86.2	56.1	15.1	20.0	81.1
pH	2.8	0.3	2.5	4.4	3.2	0.8	2.4	4.0
Fe (mg kg^{-1})	221	213	71	2471	595	315	179	2562
Al (mg kg^{-1})	272	286	62	688	793	704	134	2708
Ca (mg kg^{-1})	1795	1300	697	6741	3457	3518	93	13 497
K (mg kg^{-1})	984	558.3	26.9	3223.3	310	217	33	1177
Mg (mg kg^{-1})	601	155	409	1339	586	580	18	1262
Na (mg kg^{-1})	137	74	59	315	77	16	57	272
P (mg kg^{-1})	12.6	13.4	2.3	296.9	5.2	4.6	2.2	33.5
Ca:Na	12.3	11.9	1.6	39.5	25.8	29.5	0.5	135.0
Bulk Density (kg m^{-3})	56	19	28	86	93	45	48	717

 DOI: 10.5268/IW-5.1.752

	0–10 cm				20–30 cm			
	Median	MAD	min	max	Median	MAD	min	max
B. Open Peatland (n = 9)								
Org Carbon (%)	42.3	4.2	37.6	48.0	44.6	2.0	1.4	47.1
Org N (%)	1.3	0.5	0.9	2.8	1.0	1.2	0.03	2.3
C:N	39.6	15.7	37.6	57.5	47.2	30.1	21.2	73.3
pH	3.2	0.3	2.7	4.6	3.4	0.4	2.9	4.2
Fe (mg kg^{-1})	799	521	88	1720	857	474	157	5742
Al (mg kg^{-1})	515	473	56	2386	792	413	297	3094
Ca (mg kg^{-1})	1033	309	825	2211	1140	685	55	2950
K (mg kg^{-1})	656	142	187	847	171	108	29	708
Mg (mg kg^{-1})	389	184	238	882	364	224	26	701
Na (mg kg^{-1})	227	92	69	407	129	77	52	258
P (mg kg^{-1})	11.1	4.5	2.2	27.4	3.7	3.1	1.4	31.9
Ca:Na	3.2	1.2	2.1	18.2	4.0	2.2	0.3	32.7
Bulk Density (kg m^{-3})	70	30	40	130	100	10	70	114
B. Upland Tundra (n = 16)								
Org Carbon (%)	6.6	3.6	1.8	49.2	0.14[a]	0.08	0.07	1.14
Org N (%)	0.2	0.1	0.04	1.3	0.01[a]	0.01	bd	0.12
C:N	36.4	9.8	21.3	57.4	17.5[b]	19.0	1.2	33.8
pH	3.3[a]	0.3	2.9	3.8	4.6[a]	0.2	4.0	5.0
Fe (mg kg^{-1})	253	92	167	509	127	87	58	735
Al (mg kg^{-1})	868	301	393	2094	1125	722	454	2751
Ca (mg kg^{-1})	314	231	16	89	28	14	16	89
K (mg kg^{-1})	91	34	22	313	10	9	2	21
Mg (mg kg^{-1})	28	20	8	761	11	8	3	29
Na (mg kg^{-1})	48	10	20	82	48	20	18	94
P (mg kg^{-1})	8.1	6.1	2.9	73.3	35.0	21.0	11.2	127.5
Ca:Na	3.7	4.0	0.2	25.2	0.5	0.4	0.2	1.8
Bulk Density (kg m^{-3})	459[a]	69	244	668	1021[a]	132	543	1423
Thickness A Horizon (cm)	5.0	1.0	4.0	12.0	--	--	--	--

[a] n = 12, [b] n = 7

Discussion

Understanding environmental change in Arctic landscapes requires more attention to terrestrial–aquatic linkages, especially in poorly studied landscape/geological provinces such as the Taiga Shield Ecozone west of Hudson Bay. Although an increasing body of research links variations in lake biogeochemistry to differences in catchment characteristics or landscape position (e.g., Wagner et al. 2011, Olefeldt and Roulet 2012, Sadro et al. 2012, Tank et al. 2012), relatively little of this work has occurred in Arctic or sub-Arctic areas where permafrost is common. Permafrost thaw is likely to alter quantitatively and qualitatively the production and transport of DOC and other materials to lakes (Olefeldt et al. 2014). We documented 2 groups of lake variables, similar to Lottig et al. (2011), representing 2 major gradients in lakes (Fig. 2; Table 3). Group 1 (DOC, Fe, TP, SUVA, and related) but not Group 2 (conductivity, Ca, Mg, pH, and other) was strongly positively correlated with relative cover of conifer-dominated lowland forest. None of the other measured landscape characteristics, including LO, catchment area, and slope, were significantly correlated with the 2 lake gradients.

DOC

DOC is a major controlling variable in lakes, and a large number of studies have shown that wetlands are a primary source of DOC (Prairie 2008). Xenopoulos et al. (2003) highlighted the importance of the relative area of forested, conifer-dominated wetlands in explaining among-lake variability in DOC. Our results point to lowland forest wetlands as being the most important potential source of DOC for our lakes, despite a median cover of only 10.2% within lake catchments (Tables 3 and 5; Fig. 3). At the tundra–forest border, higher concentrations of DOC associated with the shift from tundra to forest have been reported in a number of previous studies (Pienitz et al. 1997, Duff et al. 1998, Rühland and Smol 1998, Westover et al. 2009), and our results suggest this shift may be due to an increase in forested wetlands in particular.

The link between lowland forest and DOC in lakes may be further indicated by correlated changes in DOC quality and quantity (Fig. 3; Table 3). Higher concentrations of DOC in lakes were associated with increasing SUVA and C:N ratios and lower a_{250}/a_{365}. Fellman et al. (2008) found that soil solutions from forested wetlands had higher DOC, SUVA, and C:N ratios compared to bogs, fens, or upland forest. Wickland et al. (2007) showed that DOC derived from conifer litter had higher initial SUVA than *Sphagnum* mosses and emphasized the importance of biodegradation to understanding DOC properties in soil pore water. We did not sample soil pore water but did observe significantly higher C:N ratios in lowland forest soils compared to open peatland or upland tundra (Table 6). We also found lower Al and Fe concentrations in wetland peats (Table 6) than in upland tundra, possibly highlighting the importance of differences in DOC mobility. How water moves to lakes from lowland forest or open peatland is also an important determinant of DOC transport (Olefeldt and Roulet 2012, Olefeldt et al. 2013) but was not measured in this study.

Lower quality (SUVA, C:N, a_{250}/a_{365}) DOC associated with inputs from lowland forest may result in reduced mineralization and/or burial of C (Prairie 2008). A variety of aquatic and soil experiments have demonstrated reduced biodegradability of DOC associated with higher SUVA and C:N ratios and lower a_{250}/a_{365}. (Wickland et al. 2007, Fellman et al. 2008, Berggren et al. 2009). Conversely, abundant Fe, strong correlations of Fe and a_{320} with DOC, high oxygen levels, and low pH suggest that photodegradation may be an equally important process in our lakes (Maloney et al. 2005, Porcal et al. 2014).

Conductivity, cations, and pH

Conductivity, cations, and pH (Group 2 variables) for our lakes were low compared to other Arctic or sub-Arctic regional studies (Kling et al. 1992, Pienitz et al. 1997), but Medeiros et al. (2012) and Westover et al. (2009) reported similarly low values for conductivity and cations for lakes east and west, respectively, of our study region. In contrast to DOC and related Group 1 variables, we generally did not find any significant correlations of cations and other Group 2 variables with wetland cover, as reported by Lidman et al. (2014), or upland tundra. The lack of correlation may reflect a combination of similar tills and bedrock throughout our study site, generally low rock weathering rates (Rosa et al. 2012), and the limited (<1%) relative area of exposed till and bedrock (Table 1; Umbanhowar et al. 2013).

As expected, concentrations of cations in soils were low (Table 6) when compared to elsewhere in the Arctic (Ping et al. 2005, Michaelson et al. 2008), but our values are consistent with those reported by Timoney et al. (1993) for acid tundra located on noncalcareous tills/bedrock typical for our site. Higher concentrations of Ca and other cations in lowland forest and open peatlands (Table 6) are consistent with trapping and accumulation of metals by peats (Lidman et al. 2014). Lack of carbonates and carbonate buffering in waters and soils in our region is also clearly indicated by low Ca:Na ratios (<0.1) in lakes and deeper mineral soils (0.4) in upland tundra (Keller et al. 2007, Tank et al. 2012).

Similarly, low pH of soils and lakes likely reflects the lack of carbonates in the region. Soil pH values we observed for upland tundra soils are similar to those reported by Hobbie and Gough (2002) for acidic tundra in Alaska, while the soil pH in open peat and lowland forests was even lower but matches values reported by Wind-mulder et al. (1996) for peat in Quebec. Lake pH values were between 1 and 2 units lower than observed for soils in our study (Tables 2 and 6), and the median (5.3) for lakes is consistent with poor carbonate buffering, pointing to the likely importance of DOC as the principle buffer in these lakes (Munson and Gherini 1993, Hruska et al. 1999, Maloney et al. 2005). Poor buffering might explain why pH was strongly positively correlated with Ca but not DOC (Fig. 3). Dissolved inorganic carbon (DIC) was not measured but might also be a factor in explaining low pH.

Our lake pH values (median 5.3), when corrected for a 0.65 pH unit moving water depression, were similar to those reported by Westover et al. (2009) for lakes located in a similar tundra landscape in Nunuavut ~700 km northwest of our site, but our pH values were ~2 units

 DOI: 10.5268/IW-5.1.752

lower than a mean pH of 7.4 reported by Medeiros et al. (2012) for lakes located just east of our site. The lakes described Medeiros et al. (2012) were otherwise similar in biogeochemistry to our lakes, but they were larger (median 877 vs. 69 ha in our study). Even if our numbers are too low, we are confident in the relative pH readings given high positive interyear correlation noted in Methods. Large offsets in pH at low conductivity (<40 µS cm^{-1}) associated with moving water are discussed in some detail in the older literature (Covington et al. 1985, Davison and Woof 1985, Hoenicke et al. 1991). There is clearly a need for low EC pH calibration solutions when working in lakes with low conductivity.

Catchment and landscape

Similar relationships between Group 1 lake water variables and lowland forest cover for both catchments and 100 m buffers may highlight the greater impact of areas adjacent to lakes on lake water chemistry (Gergel et al. 1999). This may be especially true for our site because the flat (1.7% average slope), permafrost-dominated landscape means mass lateral water flow may be limited (Wright et al. 2009), creating weak connections between catchment and hydrological response units (Devito et al. 2005). Prepas et al. (2001) also noted minimal impact of slope for a boreal plain with little topographic (<11%) relief.

Alternatively, and more simply, a 100 m buffer may provide a representative sample of the entire catchment. Percent cover of wetland and upland tundra cover types for 100 m buffer and surrounding catchment were significantly positively correlated, although upland tundra and wetland cover types were respectively under- and over-represented in the 100 m buffer compared to the catchment as a whole (Table 1). Regardless, one practical outcome may be that there is no need to delineate entire catchments when exploring terrestrial influences on lakes in these and similarly flat, glaciated regions where reliable elevation information is not available.

Landscape position has been used recently in a variety of different studies as a way of systematically understanding lakes in the context of their landscape and, by extension, the physical, chemical, and biological characteristics of lakes (Martin and Soranno 2006, Wagner et al. 2011). In contrast to many of these other studies, landscape position, as measured by LO, provided little information about sub-Arctic lakes in northern Manitoba with regard to measured landscape or lake biogeochemical variables. The sole exception was catchment area, which did increase significantly with higher LO. This is not unexpected given the extensive stream connections among lakes. Lowland forest cover, the strongest correlate with DOC and other Group 1 variables, did not vary significantly among lakes as a function of LO, and this may explain why LO did not capture significant differences in DOC or Ca. Sadro et al. (2012) emphasized the importance of landscape effects on lakes but noted that high heterogeneity (e.g., Supplemental Fig. S1) among catchments limited the utility of landscape position as a predictor of lake biogeochemistry.

LO may not have been successful in predicting water chemistry changes in lakes for at least 3 additional reasons related to hydrology (Lottig et al. 2011). First, because of permafrost, both low- and high-order lakes may be largely dominated by surface flows or shallow subsurface flows (Woo 1986), with the result that any effects of landscape position due to shifts in the balance of surface flow:groundwater would be reduced. For example, Cardille et al. (2007) reported that only 11% of DOC entering lakes was from inlet streams, with the majority of the remainder coming from adjacent wetlands. Second, groundwater in this region may contain little or no Ca or other base cations because of the silicaceous rocks that underlie the area, despite low pH values that might increase weathering rates (Drever 1994). Third, concentrations of Ca and other base cations may be so low that they are consumed as they pass through lakes (Kling et al. 2000). Clearly, a much better understanding of groundwater connections to our lakes is needed (Smerdon et al. 2005).

Conclusions

In this study of 44 lakes in an acidic, nutrient-poor region of sub-Arctic northern Manitoba, we found that DOC quantity and quality and related variables (SUVA, C:N, color, Fe, Al) were positively correlated with relative cover of lowland forest surrounding lakes, but that conductivity and a second group of related variables (Ca, Mg, Na, pH, $dSiO_2$) could not be related to catchment or land cover characteristics. Lowland forest represented only 10% of terrestrial land cover, yet its importance for lake biogeochemistry underscores the need to better understand quality and quantity of DOC sources (Hanley et al. 2013). Low topographic relief, extensive wetland cover, permafrost, subsurface hydrology, and nutrient-poor acidic soils and tills typical of the region may explain the lack of correlation between landscape position with wetland cover and/or conductivity and cation concentrations.

Approximately 20% (global) of the Arctic/sub-Arctic is described as being Acidic Plain (Walker 2000, Walker et al. 2005). The extent to which our work can be extended to this 20% is less certain, but it is clear that additional

regional studies are needed (Cheruvelil et al. 2013) if broader scale conclusions are to be drawn about the impacts of climate warming on aquatic–terrestrial connections (Keller et al. 2007, Frey and McClelland 2009, Olefeldt et al. 2014).

Acknowledgements

Thanks to pilots Mark Leyden and Jason Essaunce as well as the staff at the Lodge at Little Duck for assistance in the field. Students Mark Krueger, Eric Emmons, Madison Kubis, and Megan Parker provided tremendous assistance in the field and/or laboratory. Thanks also to Manitoba Conservation for help with permits. This study was supported by National Science Foundation grants DEB-0743364, DEB-0743413, DEB-0743438, DEB-0743236, DEB-0904050, and DBI-1005817. Any opinions, findings, and conclusions or recommendations expressed are those of the authors and do not necessarily reflect the views of the NSF.

References

Anderson SD, Bohm CO, Matile GLD. 2005. Bedrock and surficial geological field investigations in the Nejanilini Lake area, northern Manitoba (parts of NTS 64P5, 12 and 13). In: Manitoba Industry Economic Development and Mines Manitoba Geological Survey, editor. Report of Activities 2005. Winnipeg (MB). p. 92–103.

Arar EJ, Collins GB. 1997. In vitro determination of chlorophyll a and pheophytin a in marine and freshwater algae by fluorescence (Method 445.0). US Environmental Protection Agency.

Berggren M, Laudon H, Jansson M. 2009. Aging of allochthonous organic carbon regulates bacterial production in unproductive boreal lakes. Limnol Oceanogr. 54(4):1333–1342.

Bergstrom AK. 2010. The use of TN:TP and DIN:TP ratios as indicators for phytoplankton nutrient limitation in oligotrophic lakes affected by N deposition. Aquat Sci. 72(3):277–281.

Bonfils CJW, Phillips TJ, Lawrence DM, Cameron-Smith P, Riley WJ, Subin ZM. 2012. On the influence of shrub height and expansion on northern high latitude climate. Environ Res Lett. 7(1):015503.

Brown J, Ferrians OJ Jr, Heginbottom JA, Melnikov ES. 1998 [revised 2001]. Circum-Arctic map of permafrost and ground-ice conditions. Boulder (CO): National Snow and Ice Data Center/World Data Center for Glaciology.

Cardille JA, Carpenter SR, Coe MT, Foley JA, Hanson PC, Turner MG, Vano JA. 2007. Carbon and water cycling in lake-rich landscapes: landscape connections, lake hydrology, and biogeochemistry. J Geophys Res. 112(G2):G02031.

Cheruvelil KS, Soranno PA, Webster KE, Bremigan MT. 2013. Multi-scaled drivers of ecosystem state: quantifying the importance of the regional spatial scale. Ecol Appl. 23(7):1603–1618.

Cole JJ, Prairie YT, Caraco NF, McDowell WH, Tranvik LJ, Striegl RG, Duarte CM, Kortelainen P, Downing JA, Middelburg JJ, et al. 2007. Plumbing the global carbon cycle: integrating inland waters into the terrestrial carbon budget. Ecosystems. 10(1):171–184.

Covington AK, Whalley PD, Davison W. 1985. Recommendations for the determination of pH in low ionic-strength fresh waters. Pure Appl Chem. 57(6):877–886.

Cuthbert ID, del Giorgio P. 1992. Toward a standard method of measuring color in freshwater. Limnol Oceanogr. 37(6):1319–1326.

Davison W, Woof C. 1985. Performance tests for the measurement of pH with glass electrodes in low ionic-strength solutions including natural-waters. Anal Chem. 57(13):2567–2570.

Devito K, Creed I, Gan T, Mendoza C, Petrone R, Silins U, Smerdon B. 2005. A framework for broad-scale classification of hydrologic response units on the Boreal Plain: Is topography the last thing to consider? Hydrol Processes. 19(8):1705–1714.

Drever JI. 1994. The effect of land plants on weathering rates of silicate minerals. Geochim Cosmochim Acta. 58(10):2325–2332.

Duff KE, Laing TE, Smol JP, Lean DRS. 1998. Limnological characteristics of lakes located across arctic treeline in northern Russia. Hydrobiologia. 391(1–3):205–222.

Epstein HE, Raynolds MK, Walker DA, Bhatt US, Tucker CJ, Pinzon JE. 2012. Dynamics of aboveground phytomass of the circumpolar Arctic tundra during the past three decades. Environ Res Lett. 7(1):015506.

Fellman JB, D'Amore DV, Hood E, Boone RD. 2008. Fluorescence characteristics and biodegradability of dissolved organic matter in forest and wetland soils from coastal temperate watersheds in southeast Alaska. Biogeochemistry. 88(2):169–184.

Fergus CE, Soranno PA, Cheruvelil KS, Bremigan MT. 2011. Multiscale landscape and wetland drivers of lake total phosphorus and water color. Limnol Oceanogr. 56(6):2127–2146.

Frey KE, McClelland JW. 2009. Impacts of permafrost degradation on arctic river biogeochemistry. Hydrol Process. 23:169–182.

Gergel SE, Turner MG, Kratz TK. 1999. Dissolved organic carbon as an indicator of the scale of watershed influence on lakes and rivers. Ecol Appl. 9(4):1377–1390.

Hanley KW, Wollheim WM, Salisbury J, Huntington T, Aiken G. 2013. Controls on dissolved organic carbon quantity and chemical character in temperate rivers of North America. Global Biogeochem Cycles. 27(2):492–504.

Hobara S, Koba K, Ae N, Giblin AE, Kushida K, Shaver GR. 2013. Geochemical influences on solubility of soil organic carbon in Arctic tundra ecosystems. Soil Sci Soc Am J 77(2):473–481.

Hobbie SE, Gough L. 2002. Foliar and soil nutrients in tundra on glacial landscapes of contrasting ages in northern Alaska. Oecologia. 131:453–462.

Hochberg Y. 1988. A sharper Bonferroni procedure for multiple tests of significance. Biometrika. 75:800–802.

Hoenicke R, Stapanian MA, Arent LJ, Metcalf RC. 1991. Consequences of pH measurement errors. Freshwater Biol. 25(2):261–278.

Holmes RM, Aminot A, Kerouel R, Hooker BA, Peterson BJ. 1999. A simple and precise method for measuring ammonium in marine and freshwater ecosystems. Can J Fish Aquat Sci. 56(10):1801–1808.

Hruska J, Kohler S, Bishop K. 1999. Buffering processes in a boreal

 DOI: 10.5268/IW-5.1.752

dissolved organic carbon-rich stream during experimental acidification. Environ Pollut. 106(1):55–65.

Kalra YP, Maynard DG. 1991. Methods manual for forest soil and plant analysis: information report NOR-X-319.

Keller K, Blum JD, Kling GW. 2007. Geochemistry of soils and streams on surfaces of varying ages in arctic Alaska. Arct Antarct Alp Res. 39(1):84–98.

Kirk JTO. 1994. Light and photosynthesis in aquatic ecosystems. Cambridge (NY): University Press.

Kling GW, Kipphut GW, Miller MM, O'Brien WJ. 2000. Integration of lakes and streams in a landscape perspective: the importance of material processing on spatial patterns and temporal coherence. Freshwater Biol. 43(3):477–497.

Kling GW, Obrien WJ, Miller MC, Hershey AE. 1992. The biogeochemistry and zoogeography of lakes and rivers in arctic Alaska. Hydrobiologia. 240(1–3):1–14.

Leverington DW, Mann JD, Teller JT. 2002. Changes in the bathymetry and volume of Glacial Lake Agassiz between 9200 and 7700 14C yr B.P. Quatern Res. 57:244–252.

Liao N. 2002. Deterimination of orthophosphate in waters by flow injection analysis colorimetry (Quikchem Method 10-115-01-1-M). Milwaukee (WI): Lachat Instruments.

Lidman F, Kohler SJ, Morth CM, Laudon H. 2014. Metal transport in the boreal landscape-the role of wetlands and the affinity for organic matter. Environ Sci Technol. 48(7):3783–3790.

Lottig NR, Stanley EH, Hanson PC, Kratz TK. 2011. Comparison of regional stream and lake chemistry: differences, similarities, and potential drivers. Limnol Oceanogr. 56(5):1551–1562.

Maloney KO, Morris DP, Moses CO, Osburn CL. 2005. The role of iron and dissolved organic carbon in the absorption of ultraviolet radiation in humic lake water. Biogeochemistry. 75(3):393–407.

Manitoba Geological Survey. 2006. Geology map of Manitoba. scale 1:1000000. Based on Manitoba Geological Services, 1979, Geological map of Manitoba, scale 1:1000000, Map 79-2.

Martin SL, Soranno PA. 2006. Lake landscape position: relationships to hydrologic connectivity and landscape features. Limnol Oceanogr. 51(2):801–814.

Matile GLD, Keller GR. 2006. Surficial geology of the Nejanilini Lake map sheet (NTS 64P), Manitoba. In: Manitoba Science T, Energy and Mines, Manitoba Geological Survey, editor. Surficial Geology Compilation Map Series, SG-64P, scale 1:250000.

McCune B, Mefford MJ. 2006. Multivariate Analysis of Ecological Data, Version 5. Gleneden Beach (OR): MjM Software Design.

McKnight R. 2000. Deterimination of silica in waters by flow injection analysis. Milwaukee (WI): Lachat Instruments.

Medeiros AS, Biastoch RG, Luszczek CE, Wang XA, Muir DCG, Quinlan R. 2012. Patterns in the limnology of lakes and ponds across multiple local and regional environmental gradients in the eastern Canadian Arctic. Inland Waters. 2(2):59–76.

Mehlich A. 1984. Mehlich 3 soil test extractant: a modification of Mehlich 2 extractant Commun Soil Sci Plant Anal. 15(12):1409–1416.

Michaelson GJ, Ping CL, Epstein H, Kimble JM, Walker DA. 2008. Soils and frost boil ecosystems across the North American Arctic Transect. J Geophys Res. 113(G3):G03S11.

Munson RK, Gherini SA. 1993. Influence of organic-acids on the pH and acid-neutralizing capacity of Adirondack Lakes. Water Resour Res. 29(4):891–899.

National Atlas Information Service. 1993. Canada Terrestrial Ecoregions. The National Atlas of Canada. 5th ed. Environment Canada.

Olefeldt D, Persson A, Turetsky MR. 2014. Influence of the permafrost boundary on dissolved organic matter characteristics in rivers within the Boreal and Taiga plains of western Canada. Environ Res Lett. 9:035005.

Olefeldt D, Roulet NT. 2012. Effects of permafrost and hydrology on the composition and transport of dissolved organic carbon in a subarctic peatland complex. J Geophys Res-Biogeosci. 117:G01005.

Olefeldt D, Roulet N, Giesler R, Persson A. 2013. Total waterborne carbon export and DOC composition from ten nested subarctic peatland catchments-importance of peatland cover, groundwater influence, and inter-annual variability of precipitation patterns. Hydrol Process. 27(16):2280–2294.

Pienitz R, Smol JP, Lean DRS. 1997. Physical and chemical limnology of 59 lakes located between the southern Yukon and the Tuktoyaktuk Peninsula, Northwest Territories (Canada). Can J Fish Aquat Sci. 54(2):330–346.

Ping CL, Michaelson GJ, Kimble JM, Walker DA. 2005. Soil acidity and exchange properties of cryogenic soils in Arctic Alaska. Soil Sci Plant Nutr. 51(5):649–653.

Plummer DA, Caya D, Frigon A, Cote H, Giguere M, Paquin D, Biner S, Harvey R, De Elia R. 2006. Climate and climate change over North America as simulated by the Canadian RCM. J Clim. 19(13):3112–3132.

Porcal P, Dillon PJ, Molot LA. 2014. Interaction of extrinsic chemical factors affecting photodegradation of dissolved organic matter in aquatic ecosystems. Photoch Photobio Sci 13(5):799–812.

Prairie YT. 2008. Carbocentric limnology: looking back, looking forward. Can J Fish Aquat Sci. 65(3):543–548.

Prepas EE, Planas D, Gibson JJ, Vitt DH, Prowse TD, Dinsmore WP, Halsey LA, McEachern PM, Paquet S, Scrimgeour GJ, et al. 2001. Landscape variables influencing nutrients and phytoplankton communities in Boreal Plain lakes of northern Alberta: a comparison of wetland and upland-dominated catchments. Can J Fish Aquat Sci. 58:1286–1299.

Prowse TD, Furgal C, Wrona FJ, Reist JD. 2009. Implications of climate change for northern Canada: Freshwater, marine, and terrestrial ecosystems. Ambio. 38(5):282–289.

R Development Core Team. 2006. R: A language and environment for statistical computing. Vienna, Austria.

Riera JL, Magnuson JJ, Kratz TK, Webster KE. 2000. A geomorphic template for the analysis of lake districts applied to the Northern Highland District, Wisconsin, U.S.A. Freshwater Biol. 43:301–318.

Ritchie JC. 1959. The vegetation of northern Manitoba: V. Establishing the major zonation. Arctic. 13:211–229.

Roach J, Griffith B, Verbyla D, Jones J. 2011. Mechanisms influencing

changes in lake area in Alaskan boreal forest. Global Change Biol. 17(8):2567–2583.

Rosa E, Gaillardet J, Hillaire-Marcel C, Helie JF, Richard LF. 2012. Rock denudation rates and organic carbon exports along a latitudinal gradient in the Hudson, James, and Ungava bays watershed. Can J Earth Sci. 49(6):742–757.

Rouse WR, Douglas MSV, Hecky RE, Hershey AE, Kling GW, Lesack L, Marsh P, McDonald M, Nicholson BJ, Roulet NT, et al. 1997. Effects of climate change on the freshwaters of arctic and subarctic North America. Hydrol Process. 11(8):873–902.

Rühland K, Paterson AM, Smol JP. 2008. Hemispheric-scale patterns of climate-related shifts in planktonic diatoms from North American and European lakes. Global Change Biol. 14:2740–2754.

Rühland K, Smol JP. 1998. Limnological characteristics of 70 lakes spanning Arctic treeline from Coronation Gulf to Great Slave Lake in the Central Northwest Territories, Canada. Int Rev Hydrobiol 83(3):183–203.

Sadro S, Nelson CE, Melack JM. 2012. The influence of landscape position and catchment characteristics on aquatic biogeochemistry in high-elevation lake-chains. Ecosystems. 15(3):363–386.

Sechtig A. 2001. Determination of nitrate in 2M KCl soil extracts by flow injection analysis (Quikchem Method 12-107-04-1-B). Milwaukee (WI): Lachat Instruments.

Smerdon BD, Devito KJ, Mendoza CA. 2005. Interaction of groundwater and shallow lakes on outwash sediments in the sub-humid Boreal Plains of Canada. J Hydrol. 314(1–4):246–262.

Smol JP, Wolfe AP, Birks HJ, Douglas MS, Jones VJ, Korhola A, Pienitz R, Rühland K, Sorvari S, Antoniades D, et al. 2005. Climate-driven regime shifts in the biological communities of arctic lakes. P Natl Acad Sci USA. 102(12):4397–4402.

Sobek S, Tranvik LJ, Prairie YT, Kortelainen P, Cole JJ. 2007. Patterns and regulation of dissolved organic carbon: An analysis of 7,500 widely distributed lakes. Limnol Oceanogr. 52(3):1208–1219.

Soranno PA, Webster KE, Riera JL, Kratz TK, Baron JS, Bukaveckas PA, Kling GW, White DS, Caine N, Lathrop RC, et al. 1999. Spatial variation among lakes within landscapes: ecological organization along lake chains. Ecosystems. 2(5):395–410.

Tank SE, Frey KE, Striegl RG, Raymond PA, Holmes RM, McClelland JW, Peterson BJ. 2012. Landscape-level controls on dissolved carbon flux from diverse catchments of the circumboreal. Global Biogeochem Cy. 26:GB0E02.

Timoney KP, Laroi GH, Zoltai SC, Robinson AL. 1993. Vegetation communities and plant-distributions and their relationships with parent materials in the forest-tundra of northwestern Canada. Ecography. 16(2):174–188.

Triplett LD, Engstrom DR, Conley DJ, Schellhaass SM. 2008. Silica fluxes and trapping in two contrasting natural impoundments of the upper Mississippi River. Biogeochemistry. 87(3):217–230.

Umbanhowar CE Jr, Camill P, Edlund M, Geiss C, Durham W, Kreger D, Molano W, Raskob C, Stocker M, Tvera A, et al. 2013. Contrasting changes in surface waters and barrens over the past 60 years for a subarctic forest-tundra site in northern Manitoba based on remote sensing imagery. Can J Earth Sci. 50(9):967–977.

Wagner T, Soranno PA, Webster KE, Cheruvelil KS. 2011. Landscape drivers of regional variation in the relationship between total phosphorus and chlorophyll in lakes. Freshwater Biol. 56(9):1811–1824.

Walker DA. 2000. Hierarchical subdivision of Arctic tundra based on vegetation response to climate, parent material and topography. Global Change Biol. 6:19–34.

Walker DA, Raynolds MK, Daniels FJA, Einarsson E, Elvebakk A, Gould WA, Katenin AE, Kholod SS, Markon CJ, Melnikov ES, et al. 2005. The Circumpolar Arctic vegetation map. J Veg Sci. 16(3):267–282.

Weishaar JL, Aiken GR, Bergamaschi BA, Fram MS, Fujii R, Mopper K. 2003. Evaluation of specific ultraviolet absorbance as an indicator of the chemical composition and reactivity of dissolved organic carbon. Environ Sci Technol. 37(20):4702–4708.

Westover KS, Moser KA, Porinchu DF, MacDonald GM, Wang XW. 2009. Physical and chemical limnology of a 61-lake transect across mainland Nunavut and southeastern Victoria Island, Central Canadian Arctic. Fund Appl Limnol. 175(2):93–112.

Wickland KP, Neff JC, Aiken GR. 2007. Dissolved organic carbon in Alaskan boreal forest: sources, chemical characteristics, and biodegradability. Ecosystems. 10(8):1323–1340.

Wind-Mulder HL, Rochefort L, Vitt DH. 1996. Water and peat chemistry comparisons of natural and post-harvested peatlands across Canada and their relevance to peatland restoration. Ecol Eng. 7(3):161–181.

Woo MK. 1986. Permafrost hydrology in North America. Atmos Ocean. 24(3):201–234.

Wright N, Hayashi M, Quinton WL. 2009. Spatial and temporal variations in active layer thawing and their implication on runoff generation in peat-covered permafrost terrain. Water Resour Res. 45:W05414.

Xenopoulos MA, Lodge DM, Frentress J, Kreps TA, Bridgham SD, Grossman E, Jackson CJ. 2003. Regional comparisons of watershed determinants of dissolved organic carbon in temperate lakes from the Upper Great Lakes region and selected regions globally. Limnol Oceanogr. 48(6):2321–2334.

Supplementary Material

Supplementary Material is available for download via the Inland Waters website, https://www.fba.org.uk/journals/index.php/IW:

Supplementary figure S1, supplementary tables S1 and S2.

 DOI: 10.5268/IW-5.1.752