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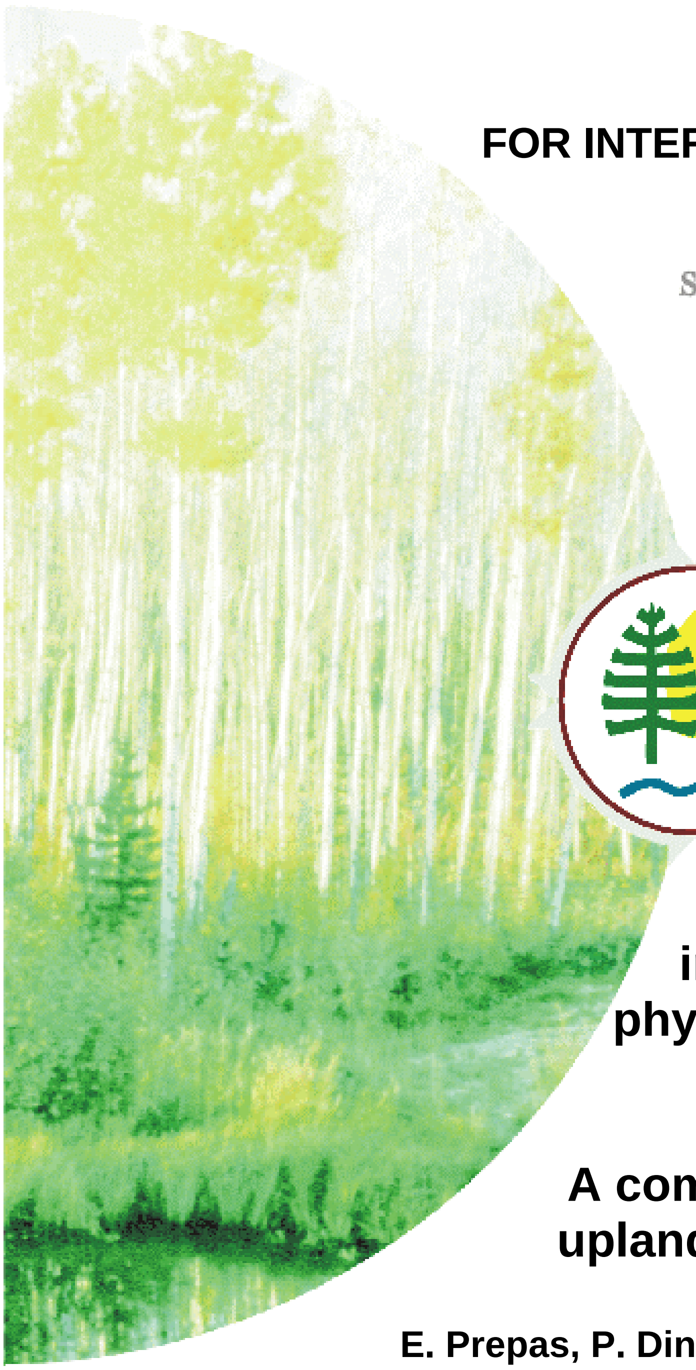

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Landscape variables influencing nutrients and phytoplankton communities in Boreal Plain lakes of northern Alberta: a comparison of wetland- and upland-dominated catchments

SFMN Project: Impacts of Natural Disturbance and Forest Harvesting on Water Quality, Primary Producers and Invertebrate Communities in Boreal Plain Lakes

by

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EXECUTIVE SUMMARY

Since the early 20th century, efforts to find patterns in water chemistry and biota in lakes focused on interactions between in-lake and catchment processes. Recent efforts to find patterns in the biogeochemistry of northern temperate lakes examined geographic characteristics such as lake morphometry, catchment hydrogeology, topography, drainage density, slope and land use. Drainage basin vegetation (e.g., coniferous or deciduous forests), as well as the amount and type of wetlands (e.g., bog or fen) can also be important for lakewater chemistry. Moderate wetland cover can impact the quality of water output of a catchment area. Wetlands are considered a source of dissolved organic carbon (DOC) and, under certain circumstances, may export much higher rates of nitrogen and/or other ions, compared to forested ecosystems.

The Boreal Forest covers 21% of Canada's land mass. Geological and climatic variation across this land base has resulted in two major sub regions: the larger and wetter Boreal Shield of central and eastern Canada and the drier Boreal Plain of western Canada. Lakes in these two sub-regions differ in water quality. Relative to lakes on the Boreal Shield, lakes on the Boreal Plain tend to be phosphorus (P) - and plankton-rich. For lakes on the Boreal Plain, internal P recycling from the bottom sediments is often the major P input to the euphotic zone on an annual basis. In pristine Shield lakes, the direct fallout of P on the lake surface is considered a major source of P. Most previous studies on catchment-surface water interactions have been undertaken on the Boreal Shield where wetlands are present, but represent a relatively minor portion of the watershed. Alberta has 21% coverage by wetlands versus only 9% coverage in Quebec.

Although there is a demand for information on the impact of various land uses on surface water quality in the Boreal Plain, no previous study has addressed catchment-lake interactions; recent studies in Alberta have focused on streams and wetlands. This study undertakes to assess the catchment-lake interactions for lakes in undisturbed watersheds on the Boreal Plain: specifically the relationship between wetlands (defined as bogs, fens, swamps and marshes), relative catchment area, watershed slope, deciduous and conifer cover, and water quality variables such as nutrients (e.g., total phosphorus (TP), DOC, NH_4^+) and dominant ions. Development of the land base of the Boreal Plain for resource-based industries is increasing exponentially. Knowledge of catchment-lake interactions in the absence of disturbance is a prerequisite for management of catchment development of aquatic resources in this region.

Combinations of catchment or drainage basin area to lake volume ratio (CA/LV and DBA/LV), terrestrial vegetation cover and lake morphometry explained 50 to 80% of total phosphorus (TP), total nitrogen (TN), dissolved organic carbon (DOC) and colour variability within 26 headwater lakes in northern Alberta. Morphometry and vegetation cover were the best predictors of nitrogen, while associations between CA/LV and DBA/LV and in-lake TP and DOC may reflect combined autochthonous and allochthonous inputs. Although TP, TN and chlorophyll *a* (chl *a*) concentrations were similar ($P>0.15$), lakes within wetland-dominated (>50% by area) drainages had higher colour and lower pH and dominant ions than upland-dominated systems (*P*<<0.01). Within wetland-dominated systems, TP, TN and DOC were positively and negatively linked with bog and upland conifer coverage respectively; in upland-dominated systems, these parameters were positively and negatively affiliated with CA/LV and mean depth respectively. Drainage basin slope was a relatively weak predictor of water quality, likely because of low topographic relief (≤11%). Higher Chlorophyceae and Cryptophyta biomasses in wetland- than in upland-dominated systems may coincide with greater NH_4^+availability. Apparently, different features influence nutrient inputs within wetland- and upland-dominated systems, suggesting that land-aquatic interactions within the two catchment types be evaluated separately.

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INTRODUCTION

Differences in lake morphometry, drainage basin topography and land use help explain variability in water quality on the Boreal Shield (Schindler 1971; Dillon et al. 1991; D'Arcy and Carignan 1997), but many Boreal Plain lakes in western Canada fall outside these established relationships. Boreal Plain lakes are situated on low-relief, often poorly-drained sedimentary tills in contrast to the typically higher relief of Shield drainages (Mitchell and Prepas 1990; D'Arcy and Carignan 1997). Euphotic total phosphorus (TP) is derived mainly through internal sediment P recycling (Shaw and Prepas 1990); atmospheric P inputs are relatively unimportant compared to Boreal Shield lakes (Shaw et al. 1989; D'Arcy and Carignan 1997). Boreal Plain phytoplankton communities typically feature high biomasses of cyanobacteria during summer stratification (Zhang and Prepas 1996), while chrysophytes and other flagellates dominate Boreal Shield communities (Kling and Holgrem 1972). Within the Boreal Plain and Shield ecozones, lake water quality can vary more than 10-fold within geologically similar, minimally perturbed catchments (Mitchell and Prepas 1990; D'Arcy and Carignan 1997). Relationships between physical and water quality parameters in Boreal Plain systems have yet to be addressed.

Some variation in water quality may be related to the extensive wetland coverage of the Boreal Plain. Wetlands greatly influence P and dissolved organic carbon (DOC) release and dissolved inorganic nitrogen (DIN) retention, and can increase runoff acidity through selective cation uptake and assimilation (Richardson 1989; Halsey et al. 1997). Wetlands that drain directly into lakes should influence lake water quality more than wetlands buffered by intervening uplands. These adjacent wetlands form an effective drainage basin area (eDBA) within the total drainage basin, the size of which depends in part on detention storage, soil moisture content and groundwater levels, and is ultimately dependent on seasonal variations in precipitation, evapotranspiration and runoff (Sorrano et al. 1996).

We used data from 26 headwater, minimally perturbed systems in northern Alberta to test the following: 1) even in low-relief systems (<10% slope), in-lake TP concentrations are inversely linked with mean drainage basin slope, since the degree of contact between surface runoff and orthophosphate-rich soil horizons should increase to some unknown point with decreasing slope (D'Arcy and Carignan 1997); 2) other physical features, such as water residence time, mean depth, drainage basin area to lake area ratio (DBA/LA) and vegetation cover are also effective predictors of TP concentrations; 3) in-lake DOC and colour are predictable from the extent of wetland coverage within drainage basins; 4) if wetlands act as a nitrogen sink, DIN concentrations will be lower in wetland- than in upland-dominated systems; 5) phytoplankton communities within wetland-dominated systems will have low biomasses of N-dependent taxa than upland-dominated systems; and 6) drainage basin indices including eDBA are better predictors of constituent inputs than those involving DBA or catchment area (CA: the sum of DBA and LA).

STUDY AREA

Euphotic water quality and phytoplankton, morphometric and drainage basin data were collected for 26 headwater lakes located within a 109 600-km^2 area (Fig. 1) within the Mixedwood ecoregion of the Boreal Plain ecozone (Strong 1992). Soil types within the study region range from eutric brunisols/gray luvisols in upland to organics/gleysols in wetland areas. Boreal Plain wetlands are categorized as peatland (bogs and fens) and non-peatland (swamps and marshes; Halsey et al. 1997). Bogs are dominated by bryophytes, notably *Sphagnum*; tree cover, when present, is limited to *Picea mariana*. Fens vary in cover from open (dominated by *Carex*, *Scirpus* and *Eriophorum*), shrubby (*Betula* and *Salix*) to wooded (*Picea mariana*, *Larix laricina*, *Betula* and *Salix*). Swamps and marshes are predominately forest/shrub (swamps) and *Carex*/*Scripus*/*Typha* (marshes). Boreal Mixedwood uplands are dominated by *Populus tremuloides*, *Populus balsamifera* and *Picea glauca* stands, with a diverse understory of herbs and shrubs (Strong 1992). Thirty-year average annual precipitation for the region ranged from 388 to 432 mm (33% as snow), while mean annual air temperature ranged from 0.7 to 1.4 °C. During the sampling periods (June to September 1996 and 1997, and August 1998), the region received between 4% less and 52% more precipitation than the 30-year normal, depending on location (Environment Canada, unpubl. data).

Drainage basins were defined as wetland-dominated if they contained >50% wetland by area, or upland-dominated with <50% wetland coverage (Table 1). Seven systems had a mean wetland coverage of 76% (range: 57 to 100%), while the remaining 19 upland-dominated systems had a mean wetland coverage of 17% (range: 0 to 44%). None of the study systems have been disturbed (>5% of vegetation removed by natural or human processes) within the past 50 years.

METHODS

Eleven lakes were sampled monthly by air during early to mid-July, August and September 1996 and 1997. Another 11 lakes were ground-accessible; nine of these lakes were sampled at 2- to 3-wk intervals, and two lakes were sampled at 1- to 2-wk intervals, between mid-June and mid-August 1996. Only one of the 11 ground-accessible lakes was sampled again at 3-wk intervals between mid-June and mid-August during 1997. Long, Moore, Narrow and Sauer lakes (Fig. 1) were sampled on one date during mid-August (Long, Moore and Narrow) or early September (Sauer) 1998. In summary, water quality data from two sampling periods (1996 and 1997) were available for all seven wetland-dominated systems (n=14); five of the 19 upland-dominated systems also had data for both sampling periods (n=10), while the remaining 14 upland-dominated systems had data for one sampling period (n=14), giving us a total of 38 independent estimates for our 26 study systems. Each of these 38 independent estimates represents summer mean euphotic water quality based on one (n=4), three (n=22), four to five (n=10) or 9 to 10 (n=2) sampling dates.

Vertically integrated water samples were collected from the euphotic region (depths receiving $\geq$1% of ambient surface light) at two sites along the longitudinal axis of each lake. Light extinction coefficient (ε) was calculated from profile data measured at one site per lake with a LiCor LI-1000 meter; data were unavailable for Long, Moore, Narrow and Sauer lakes. Samples for chlorophyll *a* (chl *a*) analysis were filtered through Whatman GF/C filters at -50 kPa and frozen within 12 h of collection. Unfiltered water was used for TP, NH_4^+, pH, colour, alkalinity (HCO_3^-, CO_3^{2-}) and conductivity analyses. Filtrate from distilled/deionized water-rinsed, 0.45-µm Millipore HAWP membranes was used for total dissolved phosphorus (TDP) and nitrate + nitrite (NO_3^- + NO_2^-) analyses. Samples for TP, TDP, pH, colour, alkalinity and conductivity were analysed within 24 h. NO_3^- + NO_2^- and NH_4^+ samples were preserved with 10 µL of 40% H_2SO_4, then refrigerated at 4°C for 1-2 wk prior to analysis. Total dissolved nitrogen (TDN) samples were filtered through pre-weighed, Whatman GF/C filters, stored at 4°C and analysed within 48 h; the remaining particulates were vacuum-dessicated and frozen for subsequent particulate nitrogen (PN) analysis. Samples for major cations (Ca^{2+}, Mg^{2+}, Na^+, K^+), major anions (Cl^-, SO_4^{2-}) and DOC were filtered through pre-combusted Whatman GF/C filters prior to long-term (1-2 mo) storage. Major cations were acidified to pH <2 with concentrated HNO_3 then refrigerated at 4°C;while DOC and major anions were refrigerated only.

Chl *a* was analysed by Ostrofsky's ethanol extraction technique (Bergmann and Peters 1980). TP and TDP were analyzed by the modified (Prepas and Rigler 1982) potassium persulfate method of Menzel and Corwin (1965). Euphotic pH was measured in the laboratory with a Fisher Scientific Accumet 925 pH meter equipped with a glass electrode. Colour was measured at 440 nm with a Milton Roy 1001 spectrophotometer (Cuthbert and del Giorgio 1992). Alkalinity was determined by potentiometric titration with 0.5-N H_2SO_4 on a Mettler DL 21 autotitrator equipped with a glass electrode (APHA 1994). NO_3^- + NO_2^-, NH_4^+ and TDN samples were analysed with a Technicon autoanalyser (Solórzano 1969; Stainton et al. 1977). PN was combusted at 700°C and analysed on a Control Equipment Corporation 440 Elemental Analyzer. DIN is the sum of NH_4^+ plus NO_3^- + NO_2^-; total nitrogen (TN) is the sum of TDN plus PN. SO_4^{2-} and Cl^- were analysed on a Dionex 2000i/SP ion chromatograph fitted with an AS4A-Sc high capacity anion exchange column, while major cations were analysed on a Perkin Elmer 3300 atomic absorption spectrophotometer. Silica (SiO_2) concentrations were determined spectrophotometrically (Environment Canada 1979). DOC was measured at 850°C from acidified (pH <2), sparged subsamples on an Ionics Corporation 1505 programmable carbon analyser with a platinum catalyst (Curtis and Prepas 1993). Specific conductivity was measured with a Radiometer CDM 83 conductivity meter. Where direct measurements were unavailable (14 lakes during 1996), conductivity (COND) was estimated from the sum of mean July-September Na^+, K^+, Ca^{2+} and Mg^{2+} concentrations ($mg \cdot L^{-1}$), weighted by atomic weight, based on an empirical model ($r^2 = 0.91$, df = 63) developed with data from this study ($n = 24$) and E. Prepas (unpubl. data; $n = 39$):

(1) $$\text{COND} = 13.77 + 102.43 \sum \text{cations}$$

Phytoplankton communities in the euphotic region were quantified for the 22 Boreal Plain lakes surveyed during 1996 and 1997; data were unavailable for Long, Moore, Narrow and Sauer lakes. Duplicate phytoplankton samples were collected concomitantly with water quality, preserved on-site with Lugol's solution and stored in amber glass bottles. Phytoplankton cells were identified, measured and counted, as per Lund et al. (1958), with a Leica DM-IRB inverted microscope. Cyanophyceae (cyanobacteria), Cryptophyceae, Diatomeae (diatoms), Euglenophyceae, Peridineae, Chlorophyceae and Chrysophyceae were identified following the keys of Prescott (1962). Cyanobacteria were subdivided into major taxa (Oscillatoriales, Nostocales, *Microcystis* spp. and other Chroococcales) and functional groups (N_2-fixing taxa: Nostocales and *Microcystis* spp.; and N_2 non-fixing taxa : non-*Microcystis* Chroococcales and Oscillatoriales). Total and taxa biomasses were estimated from cell biovolume measurements (Lewis 1976), using equivalent geometric forms and assuming $1 \mu m^3 = 1$ pg.

Lake morphometric variables (surface area, volume, mean and maximum depths) were estimated from bathymetric maps. Depths recorded along several transects per lake were digitized as binary point vector files with the software program DigiEdit. Bathymetric contour lines were created with the statistical package SYSTAT, Version 6.0. Drainage basin area and percent coverage by bogs, fens (rich and poor), swamps, marshes, upland deciduous and coniferous stands, and open water were estimated from 1:20 000 or 1:15 000 aerial photographs. Drainage basin and lake surface areas, lake volume and mean and maximum depths for Long, Moore, Narrow and Sauer lakes are from Mitchell and Prepas (1990). Mean drainage basin slopes (Table 1) were estimated for each drainage from 10 to 18 transects plotted from outer boundary to shoreline on 1:50 000 topographic maps.

Water residence times (τ; yr) were calculated for the 22 lakes sampled during 1996 and 1997 with a steady-state isotope mass-balance model, based on observed evaporative enrichment of lake water oxygen ($^{18}O/^{16}O$) and hydrogen ($^{2}H/^{1}H$) stable isotope ratios (Gibson et al. 1993).

(2) $$\tau = (xZ_{mean}) \cdot E^{-1}$$

x is the proportion of lake water lost by evaporation, Z_{mean} is mean lake depth (m), and E is long-term mean annual lake evaporation rate ($mm \cdot yr^{-1}$) for the region (Environment Canada 1978). The term x was calculated as

(2a) $$x = (\delta_L - \delta_P) \cdot [m(\delta^* - \delta_L)]^{-1},$$

where δ_L and δ_P are mean isotopic compositions of lake water and annual precipitation respectively; $m = h \cdot (1 - h)^{-1}$, where h is ambient atmospheric humidity. Limiting isotopic enrichment (δ^*) is equivalent to $\delta_h + \varepsilon \cdot h^{-1}$, where δ_h is the isotopic composition of atmospheric humidity, and ε is the isotopic fractionation factor, which is dependent upon mean annual air temperature (Gibson et al. 1993). Mean annual isotopic composition (δ_L) was determined from lake water collected in July, August and September of 1996 and 1997. Other parameters required to calculate x (δ_P, δ_h, h and mean annual air temperature) were interpolated for each lake from

Environment Canada climate station data and the Global Network for Isotopes in Precipitation (1998) database (International Atomic Energy Agency/ World Meteorological Organization, Vienna, Austria). Specific assumptions on the boundary layer regime and atmospheric parameters used in the model are discussed in Gibson and Prowse (1998). Water residence times for Long, Moore, Narrow and Sauer lakes are based on 25-yr averages of precipitation, runoff and evaporation (Mitchell and Prepas 1990),. Effective DBA (km^2) was calculated as

$$(3) \qquad \mathrm{eDBA} = (\mathrm{R}\cdot\mathrm{P}^{-1})\cdot\mathrm{DBA}^{-1};$$

R and P are mean annual drainage basin runoff and precipitation (both $mm\cdot yr^{-1}$) respectively.

Relationships between water quality and drainage basin/morphometric variables were examined by least squares methods of multivariate linear regression, for the combined (ALL; n=26) and wetland- (WETLAND) and upland- (UPLAND) dominated data sets (n=7 and 19 respectively). Variable data with non-normal distributions (Shapiro-Wilk test) were $\log_{10}$- or arcsine-transformed, where appropriate. Pearson correlation matrices were generated to select independent variables for regression analyses, based on significant ($P \leq 0.01$) correlations with dependent (water quality) variables and to detect inter-correlation between independent variables. Only the strongest, in terms of percent variation ($r^2 \times 100$) explained, and most limnologically meaningful relationships are presented. Each multivariate model is shown with its total r^2 value, adjusted to the degrees of freedom, and significance of each independent variable (*, $P < 0.05$; **, $P < 0.01$). Adjusted r^2 is an estimate of how well our models would fit another data set from the same population and is always smaller than unadjusted r^2, the square of the correlation coefficient. All analyses were performed with SPSS for Windows version 8.0.

RESULTS AND DISCUSSION

The lakes surveyed during 1996 and 1997 (Table 1) are smaller (mean LA, DBA and Z_{mean}: 0.9 km^2, 6.1 km^2 and 2.2 m respectively, n=22) than Boreal Plain lakes studied previously (Mitchell and Prepas 1990; Table 2). We added Long, Moore, Narrow and Sauer lakes (mean LA, DBA and Z_{mean}: 4.1 km^2, 32 km^2 and 7.8 m, respectively, n=4) to better reflect the range of physical characteristics reported for the Boreal Plain (Table 2). Mean DBA/LV and CA/LV of these four systems were one-quarter the size of the other upland-dominated systems (1.3 and 1.5, versus 4.9 and 5.6 respectively), but other physical parameters did not detectably differ despite noticeable extremes in individual systems (Table 1). Water quality in Long, Moore, Narrow and Sauer lakes, with the exception of colour (13 and 43 $mg\cdot L^{-1}$ Pt respectively), did not differ detectably from that of the other upland-dominated systems. We also looked at differences between water quality data for Long, Moore, Narrow and Sauer lakes collected on one date in 1998, and historical data collected on several dates over the open-water season during the early 1980s (Mitchell and Prepas 1990). Differences were as high as 21 and 25% (chl *a* and conductivity respectively), but were <13% for TP and dominant ions and only 4% for alkalinity and pH. Although many parameters such as nutrients and chl *a* exhibit seasonal variation, deep lakes such as Long, Moore, Narrow and Sauer are relatively stable compared to shallower lakes and thus one sampling date can give a reasonable approximation of water quality for pattern generation (Prepas and Trimbee 1988). The inclusion of these lakes allowed us to assemble the best data set available to address our objectives.

Most previously studied Boreal Plain lakes are located in road-accessible, inhabited areas of Alberta, where wetlands were sometimes drained for agricultural or other water management purposes (Mitchell and Prepas 1990). In these lakes, alkalinity, conductivity, pH and base cation concentrations were on average higher (Table 2) than in our study lakes with relatively unperturbed drainages (Table 3). However, ranges in TP, chl *a*, NO_3^- and DOC concentrations in this study are comparable to historical data for the region, suggesting that the study lakes reflect the range of trophic conditions present in the Boreal Plain.

Lake productivity indices were up to an order of magnitude higher compared to D'Arcy and Carignan's (1997) Boreal Shield lakes (mean TP: 54 and 8.7$\mu g \cdot L^{-1}$; chl *a*: 19 and 2.7 $\mu g \cdot L^{-1}$, respectively). Although mean DBA in this study is larger than that of D'Arcy and Carignan (1997) (10 and 2.3 km^2 respectively), drainage ratios were similar (mean DBA/LA: 8.0 and 7.5 respectively). Wetland coverage per drainage basin in this study was on average 25 times that reported by D'Arcy and Carignan (1997) (32 and 1.3% respectively), due to the lower relief of our study region. Upland conifer cover in Boreal Plain systems averaged less than half that of Shield systems (18 and 44% of DBA, respectively).

Some physical and chemical differences emerged following division into wetland- and upland-dominated systems (Tables 3 and 4). Mean and maximum depths were over 2.5-times greater in lakes with upland-dominated drainage basins, but other morphometric and drainage basin parameters were not detectably different. Bogs and deciduous forest were the dominant vegetation in wetland- and upland-dominated drainages respectively. Although mean in-lake TP, chl *a* and TN concentrations were similar ($P>0.5$), wetland-dominated systems were on average more coloured, with lower pH and conductivity than upland-dominated systems (186 vs. 38 $mg \cdot L^{-1}$ Pt, 5.7 vs. 7.6, and 265 vs. 80 $\mu S \cdot cm^{-1}$ respectively; $P<0.001$ for all comparisons).

Within the combined data set, CA/LV and DBA/LV were strongly linked with chl *a*, TP, TDP, DOC and colour, but not detectably with nitrogen (Table 5). Associations between CA/LV and DBA/LV and in-lake TP and DOC may reflect combined autochthonous and allochthonous inputs. Wetlands, particularly bogs, were positively linked with DOC and colour, and negatively associated with pH, alkalinity, base cations and conductivity ($P<0.001$; Table 5). Slope was a poor correlate of lake water quality in this study compared to D'Arcy and Carignan (1997), probably because slopes were on average lower and covered a smaller range (ranges: 0.3 to 11% and 6 to 31% respectively). We re-examined our correlation matrix after removing Long, Moore, Narrow and Sauer lakes to determine if these systems had influenced any of the relationships. Relationships between chl *a*, TP, TDP, DOC and colour and CA/LV, DBA/LV and water residence time did not change appreciably with the removal of the four deeper lakes, suggesting that our 26 lakes originate from the same population.

Phosphorus and Nitrogen

Phosphorus limits phytoplankton (particularly cyanobacteria) biomass and productivity in Boreal Plain lakes (Trimbee and Prepas 1987). In the combined data set, TP concentrations were most strongly related to CA/LV (Fig. 2A); about 50% of TP variability was explained by combinations of CA/LV and fen (FEN) and upland conifer (CONIF) cover (Eq. 4 and 5). DBA/LV explained essentially the same variability in TP compared to CA/LV (37 and 39% respectively), and was interchangeable with CA/LV in Eq. 4 and 5. CA/LV alone explained 53% of TP variability within upland-dominated systems, while percent wetland cover (WETL) explained 76% within wetland-dominated systems (Fig. 2B). Percent wetland cover combined with sampling year (YEAR) accounted for over 80% of TP variability within the wetland-dominated systems (Eq. 6). CA/LV and percent fen cover explained 73% of TP variation within the upland-dominated systems (Eq. 7).

(4) ALL: $\log(\mathrm{TP}) = 1.55 + 0.48 \log(\mathrm{CA/LV})^{**} - 0.46 \arcsin(\mathrm{FEN})^{**}$; $r^2 = 0.55$

(5) ALL: $\log(\mathrm{TP}) = 1.60 + 0.37 \log(\mathrm{CA/LV})^{**} - 0.37 \arcsin(\mathrm{CONIF})^{**}$; $r^2 = 0.48$

(6) WETLAND: $\log(\mathrm{TP}) = -222.17 + 0.01\ \mathrm{WETL}^{**} + 0.11\ \mathrm{YEAR}^{*}$; $r^2 = 0.82$

(7) UPLAND: $\log(\mathrm{TP}) = 1.55 + 0.56 \log(\mathrm{CA/LV})^{**} - 0.68 \arcsin(\mathrm{FEN})^{**}$; $r^2=0.73$

Phytoplankton (chl *a* and midsummer phytoplankton production and biomass) were positively related to CA/LV for Boreal Shield lakes in northwestern Ontario, suggesting that P and CA/LV are similarly related (Schindler 1971). In relatively shallow productive lakes, CA/LV may account for some in-lake P loading from bottom sediments along with allochthonous P inputs from organic-(wetland) and orthophosphate-based (upland) soils. TDP was similarly linked with CA/LV within the combined data set but the relationship was weaker than for TP (r = 0.49 and 0.64 respectively). The relationship between percent wetland coverage and TP concentration (Fig. 2B) suggests that our systems form two populations, one with a strong positive relationship between wetland cover and TP, the other with no detectable relationship. Dillon et al. (1991), D'Arcy and Carignan (1997) and Halsey et al. (1997) also reported positive relationships between wetland coverage and water-column P concentration, despite the relatively low wetland coverage of the first two studies (up to 6 and 25% respectively). Bogs appear to export P, as evidenced by a positive relationship between percent bog cover and in-lake TP concentration within wetland-dominated systems (r = 0.84, P<0.001), while fen and upland conifer cover retain terrestrial P (Table 5). Apparently, wetlands with organic soil do not retain P as effectively as forested systems (Richardson 1989); soils beneath upland conifer stands may be P-deficient compared to deciduous stands due to slower rates of leaf litter accumulation and decomposition. Fens, which are mineral-enriched compared to bogs, have increased decomposition rates and thus should have greater nutrient availability (Chee and Vitt 1989); in this study, the role of fens as a P-sink may reflect greater phosphorus uptake by vascular plants in fens, compared to bryophyte-dominated bog communities.

Nitrogen is also important in defining phytoplankton community structure and occurrence of cyanobacterial toxins in Boreal Plain lakes (Kotak et al. 1995). Most (~80%) DIN was NH_4^+

in our more productive Boreal Plain lakes, compared to NO_3^- in D'Arcy and Carignan's (1997) Boreal Shield study. Mean DIN concentration was three times higher in wetland- compared to upland-dominated systems, but differences were undetectable ($P \geq 0.3$; Table 3). Mean DIN for the upland-dominated Boreal Plain systems was comparable to values reported by D'Arcy and Carignan (1997) for Boreal Shield lakes (40 and 31 $\mu g \cdot L^{-1}$ respectively).

Few physical parameters were correlated with DIN concentrations in our lakes. Percent bog and upland conifer cover explained only 23 and 20% respectively of variation in DIN concentrations within the combined data set. Percent upland conifer cover and drainage basin slope combined explained two-thirds of NH_4^+ variability in wetland-dominated systems (Eq. 8), but similar relationships were not found for DIN and physical parameters within the upland-dominated systems.

(8) WETLAND: $\log(NH_4^+) = 2.23 - 2.52 \arcsin(\text{CONIF})^{**} + 0.32\ \text{SLOPE}^{*}$; $r^2 = 0.65$

While overall proportions of upland conifer cover per DBA were similar between wetland- and upland-dominated systems (21 and 17%, respectively; $P>0.53$), wetland-dominated systems had more conifer coverage per upland area (74 and 23%, respectively; $P<0.001$). The acidic soils beneath conifer stands may favour NH_4^+ retention. The positive relationship between drainage basin slope and NH_4^+ in Eq. 8 may represent greater terrestrial inputs via runoff, or a trend towards well-drained soils with less potential for N-retention.

The majority of the DIN pool in Boreal Plain lakes may originate from internal processes. NH_4^+ is released from sediments when overlying waters become anoxic (Mortimer 1971). Although thermal stratification data are incomplete for all study lakes, the 11 most frequently sampled lakes (maximum depths: 2.2 to 11m) became stratified with accompanying anoxia above the sediments for at least part of the 1996 and 1997 sampling periods (Prepas et al., unpubl. data). This suggests that NH_4^+ diffusion into the water column occurs at times in all Boreal Plain lakes. Thus, dissolved oxygen and water temperature profiles may prove useful correlates of DIN. N_2 fixation by cyanobacteria (Prepas and Trimbee 1988) and bacterial nitrification/denitrification activity may also have an impact on DIN concentrations in Boreal Plain lakes.

TDN comprised on average 75% of the TN pool in our study lakes (Table 3), of which >90% was dissolved organic nitrogen. In the combined data set, mean and maximum depth and percent rich fen and upland conifer coverage were inversely related with TN concentrations (Table 5) but explained ≤35%. Percent upland conifer, wetland, bog and fen cover and eDBA were strongly associated with TN in the wetland-dominated systems (r = -0.87, 0.68, 0.60, -0.57 and 0.66, respectively; $P<0.001$ for all), while mean depth was negatively linked with TN within upland-dominated systems (r = -0.75, $P<0.001$). Drainage basin and lake parameters together accounted for >70% of TN and TDN variation (Eq. 9 to 12):

(9) WETLAND: $\log(\text{TN}) = 3.47 - 0.80 \arcsin(\text{CONIF})^{**} - 0.15 \log(\text{eDBA/LV})^{*}$; $r^2 = 0.82$

(10) WETLAND: $\log(\mathrm{TDN}) = 2.52 - 0.64 \arcsin(\mathrm{CONIF})^{**} + 0.10\ \mathrm{pH}^{**}$; $r^2 = 0.86$
(11) WETLAND: $\log(\mathrm{TN}) = 2.00 + 0.01 (\mathrm{WETL})^{**} + 0.91 \log(Z_{mean})^{**}$; $r^2 = 0.84$
(12) UPLAND: $\log(\mathrm{TN}) = 3.39 - 0.57 \log(Z_{mean})^{**} - 0.52 \arcsin(\mathrm{FEN})^{**}$; $r^2 = 0.73$

Upland conifer stands appear to be an important sink for TN as well as DIN. The wetland-influenced parameter effective DBA to lake volume ratio (eBDA/LV) was inversely related to TN, while percent wetland cover itself was positively linked with TN. A possible explanation is that the wetlands immediately adjacent to the lakes in our wetland-dominated systems are primarily fens, which appear to retain nitrogen overall, whereas bogs form the majority of total wetland area per DBA. The inverse relationship between lake depth and TN/TDN in the upland-dominated systems suggests contributions by macrophytes to the dissolved and particulate organic nitrogen pools in shallow water bodies.

Dillon et al. (1991) suggested that Boreal Shield wetlands were important exporters of TP and total organic nitrogen in drainages with higher wetland coverage (up to 25%). Our results lend credence to this idea, but also indicate that in-lake production of nitrogen needs to be quantified to assess the importance of external nutrient contributions. Quantification of macrophyte contributions to primary production relative to those of phytoplankton in Boreal Plain lakes community may help in understanding these relationships.

Chlorophyll *a* and Phytoplankton Communities

Mean summer chl *a* concentrations covered 1.5 orders of magnitude (Table 3), and as expected, TP and TN concentrations were the best overall predictors of chl *a* (CHLA; Eq. 13 and 14). The chl *a*/TP relationship did not vary detectably among the combined, wetland- and upland-dominated data sets and was not enhanced by the addition of other independent variables. TDP concentrations may represent metabolically available P, but was less effective than TP in predicting chl *a* concentrations in the study lakes, explaining 30, 31 and 42% of chl *a* variability in the combined, wetland- and upland-dominated systems respectively.

(13) ALL: $\log(\mathrm{CHLA}) = -1.14 + 1.36 \log(\mathrm{TP})^{**}$; $r^2 = 0.69$
(14) ALL: $\log(\mathrm{CHLA}) = -2.46 + 1.18 \log(\mathrm{TN})^{**}$; $r^2 = 0.41$

Percent wetland cover and CA/LV explained 55 and 43% of chl *a* variability in wetland- and upland-dominated systems respectively. D'Arcy and Carignan (1997) reported similar, yet inconclusive, relationships between wetlands and chl *a* within Boreal Shield systems with less wetland cover. In a survey of 208 temperate lakes, chl *a* and mean depth were inversely related ($r = -0.60$; Duarte and Kalff 1989), as we found within our upland- ($r = -0.62$, $P<0.001$) but not wetland-dominated systems ($P>0.60$).

Cyanobacteria were the dominant phytoplankton in all study lakes, followed by Peridineae and Cryptophyceae within wetland- and upland-dominated systems respectively (Fig. 3). Within wetland-dominated systems, Chlorophyceae and Chrysophyceae biomasses were equally represented, but Chrysophyceae exceeded Chlorophyceae in upland-dominated systems. Diatoms were scarce during the July to September study period, relative to lakes on the Boreal Shield. We detected no differences in total phytoplankton biomasses between wetland- and upland-dominated systems, but Chlorophyceae and Peridineae biomasses were higher in wetland- than in upland-dominated systems (Fig. 3) and compared to historic data (Mitchell and Prepas 1990). Higher Chlorophyceae biomasses in wetland- than in upland-dominated systems, despite equivalent TP concentrations, may coincide with greater DIN availability in the former. In contrast, Cryptophyceae biomass was higher in lakes with upland-dominated catchments.

Although total cyanobacteria biomasses were similar, absolute and relative biomasses of Oscillatoriales were greater in upland- than in wetland-dominated systems (Fig. 4). Oscillatoriales are abundant in other upland-dominated systems in northern Alberta (Prepas et al., unpubl. data) and common in turbid, wind-mixed lakes (Scheffer et al. 1997). *Microcystis* spp. was highly linked with NO_3^- concentrations in wetland-dominated systems but N_2-fixing cyanobacteria overall, including *Microcystis* spp., were most strongly associated with TP in wetland-dominated systems (Table 6).

Total phytoplankton biomass (BIOM) was most closely related to TP concentration in both wetland- and upland-dominated systems (Eq. 15 and 16), but these relationships were weaker than those for chl *a*. Relationships between Cryptophyceae biomass (CRYTO) and NH_4^+ and DOC concentrations in wetland-dominated systems (Eq. 17 and 18) were suggestive of quadratic functions (Fig. 5).

(15) WETLAND: $\log(\text{BIOM}) = 1.80 + 1.19 \log(\text{TP})^{*}$; $r^2 = 0.42$
(16) UPLAND: $\log(\text{BIOM}) = 2.45 + 0.79 \log(\text{TP})^{**}$; $r^2 = 0.51$
(17) WETLAND: $\log(\text{CRYPTO}) = -1.01 + 4.18 \log(NH_4^+)^{**} - 1.05 (\log(NH_4^+))^{2**}$; $r^2=0.59$
(18) WETLAND: $\log(\text{CRYPTO}) = -14.7 + 25.6 \log(\text{DOC})^{*} - 9.3 (\log(\text{DOC}))^{2*}$; $r^2 = 0.45$

Cryptophyceae biomasses appeared to plateau at NH_4^+ and DOC concentrations of 94 $\mu g \cdot L^{-1}$ and 19 $mg \cdot L^{-1}$ respectively, and to decrease with increasing concentrations. The specific mechanisms by which Cryptophyceae biomass is limited by NH_4^+ and DOC concentrations above these optima are unclear; perhaps other factors, such as competition with other phytoplankton taxa, become important where nutrient concentrations are non-limiting. Cryptophyceae biomass was linearly related to TDP concentrations in upland-dominated systems (Table 6). Peridineae biomass was either poorly or negatively associated with euphotic-zone nutrients (Table 6). Many species of Peridineae exhibit can accumulate nutrients below the euphotic zone through diel migration, perhaps as a strategy to reduce interspecific competition (James et al. 1992). Similarly, the negative relationship between Oscillatoriales biomasses and NH_4^+ concentrations within upland-dominated systems suggests that non-N_2-fixing cyanobacteria like Oscillatoriales are inferior competitors compared to N_2-fixing taxa.

Colour and Dissolved Organic Carbon

Colour concentrations are dependent on dissolved humic matter and negatively influence underwater light penetration, limiting colonization depths for primary producers (Chambers and Prepas 1988). Colour was strongly associated with wetland, bog and fen cover in the combined data set (r = 0.81, 0.78 and 0.44 respectively). eDBA/LV was more strongly linked with colour (COL) than CA/LV and DBA/LV (r = 0.81, 0.69 and 0.64 respectively); eDBA/LV combined with drainage basin slope (SLOPE) explained 74% of colour variability (Eq. 19). Colour also coincided negatively with water residence time (r = -0.84), since in-lake humic matter degrades with prolonged photolysis and microbial activity (Engstrom 1987; Rasmussen et al. 1989).

(19) ALL: $\log(\text{COL}) = 1.82 + 0.51 \log(\text{eDBA/LV})^{**} - 0.06\ \text{SLOPE}^{**};\ r^2 = 0.74$

Drainage basin slope in Eq. 19 probably represents the transition from organic peatlands towards mineral soils, which export less humic matter. Although slopes are low in our study ($\leq$11%), they explained one-quarter of colour variability as a single predictor. Rasmussen et al. (1989) found no relationship between colour and percentage wetland cover, and interpreted the absence of pattern as due to the overriding influence of slope; within their study, slope was a strong inverse correlate of colour and wetland cover. DOC concentrations in this study explained only 46% of the colour variation, compared to 86% for Precambrian Shield lakes in Labrador (Rasmussen et al. 1989), and likely reflects the autochthonous DOC contributions by primary producers within Boreal Plain lakes (Curtis and Prepas 1993).

Almost four-fifths of the variability in light extinction coefficient within the combined data set was associated with colour and chl *a* concentration (Eq. 20). As expected, the positive trend between light extinction and chl *a* concentration suggests increased phytoplankton densities lead to reduced light penetration and macrophyte colonization depths in productive systems.

(20) ALL: $\varepsilon = -4.63 + 2.65 \log(\text{COL})^{**} + 2.35 \log(\text{CHLA})^{**};\ r^2 = 0.79$

Studies based in Labrador, Finland and northern Alberta with relatively high wetland coverage (up to 25, 58 and 85% respectively) noted strong relationships between wetland coverage and in-lake organic carbon concentrations (Engstrom 1987; Kortelainen 1993; Halsey et al. 1997). DOC concentrations in our combined data set were positively associated with percent wetland cover and CA/LV, but the relationships were relatively weak (r^2 = 0.30 and 0.25 respectively). Percent wetland cover and eDBA explained considerably more DOC variability in the wetland-dominated subset (r^2 = 0.68 and 0.61 respectively); DOC was also negatively related to percent upland conifer cover (r^2 = 0.73). Upland conifer cover and eDBA/LV together explained >80% of DOC variation in the wetland-dominated systems (Eq. 21). Within the upland-dominated systems, CA/LV and mean depth explained only 17 and 39% of DOC variability respectively, suggesting that a large proportion of DOC is autochthonously produced.

(21) WETLAND: $DOC = 27.23 - 25.53 \arcsin(CONIF)^{**} + 5.59 \log(eDBA/LV)^{**}$; $r^2 = 0.81$

Engstrom (1987) predicted that DOC and water residence time are strongly related in systems where DBA/LA is >4. In our study, DOC was inversely related to water residence time (r=-0.46) and not detectably related to DBA/LA (mean = 8.0), similar to Boreal Shield systems with mean DBA/LA = 7.5 (D'Arcy and Carignan 1997). A weak inverse relationship existed between DOC and slope ($r^2 = 0.13$, $P<0.02$), consistent with the low topographical relief of our study region. In contrast, drainage basin slope explained 40% of the variation in DOC of Boreal Shield lakes in Québec (D'Arcy and Carignan 1997).

Water Residence Times and Effective Drainage Basin Area

Mean water residence time (τ) was 22-fold longer for upland- than for wetland-dominated systems (11 and 0.5 yr respectively, Table 4), attributable to the greater lake volumes and mean depths and smaller eDBAs within the upland-dominated systems. Positive associations of r=0.65 or greater between water residence time and alkalinity, conductivity, HCO_3^-, Mg^{2+} and K^+ (Table 5) suggest the influence of hydrologic setting, specifically lake flushing rates. However, undetectable patterns between water residence time and other dominant ions suggests that the influence of in-lake as opposed to drainage basin processes depends on the chemical constituent.

Differences between estimated eDBA and DBA were less pronounced within wetland- compared to upland-dominated catchments (Table 4). On average, wetland- and upland-dominated eDBAs were 76 and 23% of the total DBA (Table 4). The first reflects a relatively higher wetted-fraction or contributing area within the drainage basin; the latter reflects lower overall runoff contributions from upland areas due to lower soil moisture content and enhanced evapotranspiration. Within the 26-lake data set, runoff (R from Eq. 3) was positively related to bog area ($r^2 = 0.87$; $P<0.001$), but was not detectably linked with DBA, suggesting that bogs play a key role in influencing runoff in our study region.

Effective DBA is dependent on drainage basin topography and hydrology, as suggested by strong positive and negative relationships with colour and percentage bog cover ($r^2 = 0.40$ and 0.37; $P<0.001$) and drainage basin slope and percent upland cover ($r^2 = 0.30$ and 0.47; $P<0.001$), respectively. Associations between DBA/wetland area and water quality parameters improved appreciably when eDBA was substituted as a correlate. The strongest relationship was between chl *a* concentrations and eDBA within the wetland-dominated systems ($r^2 = 0.70$, $P<0.001$). Constituent imports from wetland-dominated regions such as the Boreal Plain ecozone appear to vary annually with precipitation and snowmelt, as opposed to high-relief areas such as the Boreal Shield. DBA for the 26 lakes in our study was difficult to define using standard topographic methods. A more detailed knowledge of regional soil and groundwater regimes would likely provide a better definition of DBA and eDBA.

CONCLUSIONS

This study demonstrates the need to discriminate between wetland- and upland-dominated catchments to understand the impacts of land-based processes, both natural and human-related, on Boreal Plain surface waters. Our results also suggest that in upland-dominated systems, potential impacts of terrestrial disturbance on surface water quality will be related to catchment or drainage basin size, while in wetland-dominated systems, the impacts will be related to the proportion of wetlands affected. Boreal Plain wetlands are often extensively disturbed during fire events, but minimally affected during timber harvesting. Future studies should include an examination of how effective drainage basin dynamics change when catchment disturbance occurs in Boreal Plain systems.

LITERATURE CITED

American Public Health Association (APHA). 1994. Standard methods for the examination of water and wastewater. American Water Works Association, Hanover, MD.

Bergmann, M., and Peters, R. H. 1980. A simple reflectance method for the measurement of particulate pigment in lake water and its application to phosphorus-chlorophyll-seston relationships. Can. J. Fish. Aquat. Sci. **37**: 111-114.

Chambers, P. A., and Prepas, E. E. 1988. Underwater spectral attenuation and its effect on the maximum depth of angiosperm colonisation. Can. J. Fish. Aquat. Sci. **45**: 1010-1017.

Chee, W.-L., and Vitt, D.H. 1989. The vegetation, surface water chemistry and peat chemistry of moderate-rich fens in central Alberta. Wetlands **9**: 227-262.

Curtis, P. J., and Prepas, E. E. 1993. Trends of dissolved organic carbon (DOC) concentrations from freshwater to saltwater. Verh. Internat. Verein. Limnol. **25**: 75-81.

Cuthbert, I. D., and del Giorgio, P. 1992. Toward a standard method of measuring colour in fresh water. Limnol. Oceanogr. **37**: 1319-1326.

D'Arcy, P., and Carignan, R. 1997. Influence of catchment topography on water chemistry in southeastern Québec Shield lakes. Can. J. Fish. Aquat. Sci. **54**: 2215-2227.

Dillon, P. J., Molot, L. A., and Scheider, W. A. 1991. Phosphorus and nitrogen export from forested stream catchments in Central Ontario. J. Environ. Qual. **20**: 857-864.

Duarte, C. M., and Kalff, J. 1989. The influence of catchment geology and lake depth on phytoplankton biomass. Archiv Hydrobiol. **115**: 27-40.

Engstrom, D. 1987. Influence of vegetation and hydrology on the humus budgets of Labrador lakes. Can. J. Fish. Aquat. Sci. **44**: 1306-1314.

Environment Canada 1978. Hydrological atlas of Canada. Cat. No. En 37-26/1978. Supply and Services Canada, Ottawa, Ontario, Canada.

Environment Canada. 1979. Analytical methods manual. Inland Waters Directorate, Water Quality Branch, Ottawa, Ontario, Canada.

Gibson, J. J., Edwards, T. W. D., Bursey, G. G., and Prowse, T. D. 1993. Estimating evaporation using stable isotopes: quantitative results and sensitivity analysis for two catchments in northern Canada. Nordic Hydrol. **24**: 79-94.

Gibson, J.J., and Prowse, T.D. 1998. Water balance trends across northern treeline inferred from isotopic enrichment in lakes. *In* Isotope techniques in the study of environmental change. IAEA-SM-349/22. International Atomic Energy Agency, Vienna. 204-224.

Halsey, L. A., Vitt, D. H., and Trew, D. O. 1997. Influence of peatlands on the acidity of lakes in northeastern Alberta, Canada. Water, Air and Soil Pollut. **96**: 17-38.

James, W.J., Taylor, W.D., and Barko, J. W. 1992. Production and vertical migration of *Ceratium hirundinella* in relation to phosphorus availability in Eau Galle reservoir, Wisconsin. Can. J. Fish. Aquat. Sci. **49**: 694-700.

Kortelainen, P. 1993. Content of total organic carbon in Finnish lakes and its relationship to catchment characteristics. Can. J. Fish. Aquat. Sci. **50**: 1477-1483.

Kling, H.J., and Holgrem, S.K. 1972. Species composition and seasonal distribution in the Experimental Lakes Area, northwestern Ontario. Fish. Mar. Serv. Res. Dev. Tech. Rep. 337.

Kotak, B. G., Lam, A. K.-Y., Prepas, E.E., Kenefick, S.L., and Hrudey, S.E. 1995. Variability of the hepatotoxin microcystin-LR in hypereutrophic drinking water lakes. J. Phycol. **31**: 248-263.

Lewis, W.M., Jr., 1976. Surface/volume ratio: implication for phytoplankton morphology. Science **192**: 885-887.

Lund, J.W.G., Kippling, C., and Lecren, E.D. 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimation by counting. Hydrobiologia **136**: 31-46.

Menzel, D. W., and Corwin, N. 1965. the measurement of total phosphorus in seawater based on liberation of organically bound fractions by persulfate oxidation. Limnol. Oceanogr. **10**: 280-282.

Mitchell, P. A., and Prepas, E. E. 1990. Atlas of Alberta Lakes. University of Alberta Press, Edmonton, Alberta, Canada.

Mortimer, C.H. 1971. Chemical exchanges between sediments and water in the Great Lakes – speculations on possible regulatory mechanisms. Limnol. Oceanogr. **16**: 387-404.

Prepas, E. E., and Rigler, F. H. 1982. Improvements in quantifying the phosphorus concentration in lake water. Can. J. Fish. Aquat. Sci. **29**: 822-829.

Prepas, E. E., and Trimbee, A. M. 1988. Evaluation of indicators of N-limitation in deep prairie lakes with laboratory bioassays and limnocorrals. Hydrobiologia. **159**: 269-276.

Prescott, G.W., 1962. Algae of the western Great Lakes area. 2nd edition. Otto Koeltz Science Publishers, Koenigstein, Germany.

Rasmussen, J. B., Godbout, L., and Schallenberg, M. 1989. The humic content of lake water and its relationship to drainage basin and lake morphometry. Limnol. Oceanogr. **34**: 1336-1343.

Richardson, C. J. 1989. Freshwater wetlands: transformers, filters, or sinks? *In* Freshwater wetlands and wildlife. *Edited by* R.R. Sharitz and J.W. Gibbons. DOE Symposium Ser. No. 61. USDOE Office of Scientific and Technical Information, Oak Ridge, TN pp. 25-46.

Scheffer, M., Rinaldi, S., Gragnani, A., Mur, L.R., and van Ness, E.H. 1997. On the dominance of filamentous cyanobacteria in shallow turbid lakes. Ecology **78**: 272-282.

Schindler, D. W. 1971. A hypothesis to explain differences and similarities among lakes in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Bd. Can. **28**: 295-301.

Shaw, J. F. H., and Prepas, E. E. 1990. Exchange of P from shallow sediments at nine Alberta lakes. J. Environ. Qual. **19**: 249-256.

Shaw, R. D., Trimbee, A. M., Minty, A., Fricker, H., and Prepas, E. E. 1989. Atmospheric deposition of phosphorus and nitrogen in central Alberta with emphasis on Narrow Lake. Water, Air and Soil Pollut. **43**: 119-134.

Solórzano, L. 1969. Determination of ammonia in natural waters by phenolhypochlorite method. Limnol. Oceanogr. **14**: 799-801.

Soranno, P. A., Hubler, S. R., Carpenter, S. R., and Lathrop, R. C. 1996. Phosphorus loads to surface waters: A simple model to account for spatial patterns of land use. Ecol. Appl. **6**: 865-878.

Stainton, M. P., Capel, M. J., and Armstrong, F. A. J. 1977. The chemical analysis of freshwater. 2nd ed. Fisheries and Environment Canada Miscellaneous Special Publication 25.

Strong, W. L. 1992. Ecoregions and ecodistricts of Alberta. Volumes 1 and 2. Alberta Forestry, Lands and Wildlife, Land Information Services Division, Edmonton, Alberta, Canada.

Trimbee, A. M., and Prepas, E. E. 1987. Evaluation of total phosphorus as a predictor of the relative biomass of blue-green algae with emphasis on Alberta lakes. Can. J. Fish. Aquat. Sci. **44**: 1337-1342.

Table 1. Drainage basin and lake morphometry data for the 26 study lakes. Abbreviations are defined in Table 4. Drainage basin area, lake surface area and volume, mean and maximum depth data for Narrow, Sauer, Long and Moore lakes are from Mitchell and Prepas (1990).

Lake	Catchment Type	Year(s) Surveyed	DBA (km^2)	LA (km^2)	LV (m^3x10^6)	CA/LV	Z_{mean} (m)	Z_{max} (m)	SLOPE (%)	CONIF (%)	DECID (%)	WETL (%)
N4	Wetland	1996, 97	0.56	0.19	0.19	3.9	1.0	5.5	3.9	43	0	57
N6	Wetland	1996, 97	4.28	0.90	0.96	5.4	1.1	1.8	0.8	28	0	71
N7	Wetland	1996, 97	1.87	1.01	1.47	2.0	1.5	3.3	0.8	43	0	57
N8	Wetland	1996, 97	9.14	0.69	0.46	21.1	0.7	1.8	0.5	8	0	92
N9	Wetland	1996, 97	18.80	1.62	1.73	11.8	1.1	1.8	0.3	5	2	93
N16	Wetland	1996, 97	6.99	1.62	2.08	4.1	1.3	1.8	0.6	0	0	100
N26	Wetland	1996, 97	16.22	2.00	5.72	3.2	2.9	5.8	1.0	20	20	60
N5	Upland	1996, 97	5.15	1.20	1.38	4.6	1.1	4.6	1.4	29	28	44
N11	Upland	1996	5.75	0.84	2.64	2.5	3.2	5.4	8.0	7	83	10
N20	Upland	1996, 97	4.52	0.30	0.27	17.8	0.9	1.8	3.3	26	61	11
N24	Upland	1996, 97	1.51	0.25	0.49	3.6	1.9	4.0	6.6	14	65	20
N29	Upland	1996, 97	2.58	1.70	2.32	1.8	1.4	2.4	2.6	24	33	24
N31	Upland	1996	1.06	0.14	0.37	3.2	2.7	5.3	4.7	9	85	5
N32	Upland	1996	1.88	0.62	0.79	3.2	1.3	4.0	3.3	4	73	22
N33	Upland	1996	4.73	1.14	3.36	1.7	2.9	7.1	3.6	3	83	14
N34	Upland	1996	6.31	0.52	2.53	2.7	4.8	11.1	3.5	6	81	11
N35	Upland	1996	2.63	0.20	0.74	3.8	3.6	7.5	3.0	3	70	25
N37	Upland	1996, 97	6.50	0.77	1.69	4.3	2.2	2.8	1.1	1	82	16
N38	Upland	1996	10.02	1.59	7.17	1.6	4.5	8.3	4.5	43	45	13
N39	Upland	1996	7.02	0.56	0.73	10.5	1.3	2.2	3.9	19	59	21
N40	Upland	1996	9.53	0.47	2.02	4.9	4.3	8.9	3.7	29	59	13
N41	Upland	1996	6.19	0.65	1.57	4.4	2.4	3.7	3.9	15	59	21
Narrow	Upland	1998	8.06	1.14	16.40	0.6	14.4	38.0	3.4	25	52	21
Sauer	Upland	1998	0.49	0.09	0.35	1.6	4.2	8.5	10.6	40	60	0
Long	Upland	1998	82.40	5.84	29.30	3.0	4.3	9.0	3.4	15	83	0
Moore	Upland	1998	37.10	9.28	77.40	0.6	8.3	26.0	2.6	21	48	23

Table 2. Summary data for Boreal Plain lakes from Mitchell & Prepas (1990). Narrow, Sauer, Long and Moore lakes are excluded. *SE* = ± 1 standard error, Min. = minimum, Max. = maximum.

	n	Mean	*SE*	Min.	Max.
Lake area (km^2)	42	31	9.1	0.2	288
Drainage basin area (km^2)	42	369	110	1.5	4040
Mean depth (m)	41	6.7	0.7	1.3	17
Maximum depth (m)	42	17	1.9	3.5	60
Chlorophyll *a* ($\mu g \cdot L^{-1}$)	37	22	3.5	3.3	99
TP ($\mu g \cdot L^{-1}$)	39	57	7.8	9	193
NO_3^- ($\mu g \cdot L^{-1}$)	32	11	2.4	1	79
DOC ($mg \cdot L^{-1}$)	22	17	1.7	10	37
Alkalinity ($mg \cdot L^{-1}$)	42	176	14	49	556
pH	42	8.0	-----	7.3	9.2
Ca^+ ($mg \cdot L^{-1}$)	40	29	1.5	11	53
Cl^- ($mg \cdot L^{-1}$)	35	2.9	0.6	0.9	17
K^+ ($mg \cdot L^{-1}$)	40	8.5	1.0	0.8	25
Conductivity ($\mu S \cdot cm^{-1}$)	41	378	31	117	1143

Table 3. Summary water quality data for the 26 Boreal Plain study lakes. Data consist of independent annual estimates collected during the study period (1996-1998), or are from Mitchell and Prepas (1990). Water quality parameters in wetland- and upland-dominated systems were compared with two-tailed *t*-tests; probabilities (*P*) are included. *SE* = ± 1 standard error, Min. = minimum, Max. = maximum. Extinction coefficient data were unavailable for N37 (1997 only), Narrow, Sauer, Long and Moore lakes.

		Wetland-dominated (n = 14)				Upland-dominated (n = 24)				*P*	Total (n = 38)	
Variable	Abbreviation	Mean	*SE*	Min.	Max.	Mean	*SE*	Min.	Max.		Mean	*SE*
TP ($\mu g \cdot L^{-1}$)	TP	57	9.4	26	162	52	6.8	12	160	0.67	54	5.5
TDP ($\mu g \cdot L^{-1}$)	TDP	19	2.5	5.3	42	17	2.0	5.2	44	0.54	17	1.6
Chl *a* ($\mu g \cdot L^{-1}$)	CHLA	21	4.6	2.0	57	18	3.4	2.0	76	0.67	19	2.7
NH_4^+ ($\mu g \cdot L^{-1}$)	NH_4	136	90	6.4	1271	35	8.3	2.5	149	0.27	72	34
NO_3^- ($\mu g \cdot L^{-1}$)	NO_3	11	6.7	1.1	99	5.5	0.6	1.1	13	0.38	7.7	2.5
DIN ($\mu g \cdot L^{-1}$)	DIN	148	92	7.5	1281	40	8.6	5.2	154	0.26	80	34
TDN ($\mu g \cdot L^{-1}$)	TDN	858	123	373	2177	899	90	212	2129	0.79	884	72
TN ($\mu g \cdot L^{-1}$)	TN	1253	208	532	3297	1178	113	279	2825	0.75	1205	103
TN:TP	TN:TP	23	2.1	13	38	26	2.0	8.1	39	0.30	25	1.5
SO_4^{2-} ($mg \cdot L^{-1}$)	SO_4	4.2	2.2	0.2	25	7.2	3.1	0.1	74	0.44	6.0	2.1
Cl^- ($mg \cdot L^{-1}$)	Cl	0.3	0.03	0.1	0.6	1.5	0.8	0.1	20	0.18	1.0	0.5
Na^+ ($mg \cdot L^{-1}$)	Na	2.4	0.7	0.3	8.8	10	4.6	1.0	113	0.09	6.3	2.3
DOC ($mg \cdot L^{-1}$)	DOC	20	2.1	10	33	15	1.0	10	29	0.05	17	1.1
Extinction coefficient (m^{-1}), base e	ε	3.8	0.5	1.3	8.7	2.3	0.3	0.9	5.9	0.02	2.9	0.3
Colour ($mg \cdot L^{-1}$ Pt)	COL	186	29	29	358	38	5.2	8.0	125	<0.001	92	16
Alkalinity ($mg \cdot L^{-1}$)	ALK	28	8.4	2.9	95	110	14	40	389	<0.001	80	11
HCO_3^- ($mg \cdot L^{-1}$)	HCO_3	34	10	3.6	116	125	15	49	379	<0.001	91	12
pH	pH	5.7	-----	4.9	7.4	7.6	-----	6.9	8.7	<0.001	7.3	-----
Si ($\mu g \cdot L^{-1}$)	Si	703	194	40	2750	1563	235	56	4383	<0.001	1246	177
Ca^{2+} ($mg \cdot L^{-1}$)	Ca	10	3.2	0.9	37	24	1.9	10	52	<0.001	19	2.0
Mg^{2+} ($mg \cdot L^{-1}$)	Mg	2.3	0.6	0.3	7.1	11	1.7	3.7	48	<0.001	7.4	1.2
K^+ ($mg \cdot L^{-1}$)	K	0.6	0.2	0.2	2.4	3.6	0.5	0.7	11	<0.001	2.3	0.3
Conductivity ($\mu S \cdot cm^{-1}$)	COND	80	23	11	271	265	33	100	910	<0.001	197	27

Table 4. Drainage basin and lake morphometry summary data for the 26 study lakes; data are from this study and Mitchell and Prepas (1990). Physical parameters in wetland- and upland-dominated systems were compared with two-tailed *t*-tests; probabilities (*P*) are included. *SE* = ± 1 standard error, Min. = minimum, Max. = maximum. Data for eDBA, eDBA/LV and τ consist of independent annual estimates collected during 1996 and 1997, or were taken from Mitchell and Prepas (1990). Other parameters were assumed constant over the study period (1996-1998). eDBA and eDBA/LV were unavailable for Narrow, Sauer, Long and Moore lakes.

		Wetland-dominated (n = 7)				Upland-dominated (n = 19)				*P*	Total (n = 26)	
Parameter	Abbreviation	Mean	*SE*	Min.	Max.	Mean	*SE*	Min.	Max.		Mean	*SE*
Catchment area (km^2)	CA	9.41	2.82	0.75	20.42	11.90	4.55	0.58	88.24	0.78	11.41	3.55
Drainage basin area (km^2)	DBA	8.27	2.64	0.56	18.80	10.71	4.37	0.49	82.40	0.79	10.05	3.25
Effective DBA (km^2)	eDBA	6.30	1.15	2.63	15.88	2.46	0.52	0.10	9.45	0.007	4.04	0.65
Slope (%)	SLOPE	1.1	0.5	0.3	3.9	4.1	0.5	1.1	11	<0.001	3.3	0.5
Upland conifer (% of DBA)	CONIF	21	6.7	0	43	17	2.8	1.2	42	0.53	18	2.7
Upland deciduous (% of DBA)	DECID	3.1	2.8	0	20	64	4.0	30	85	<0.001	47	6.1
Wetlands (% of DBA)	WETL	76	7.1	57	100	17	2.3	0	44	<0.001	33	5.8
Bogs (% of DBA)	BOG	44	11	11	85	2.4	1.1	0	20	<0.001	14	4.7
Total fens (% of DBA)	FEN	30	5.6	7.8	45	8.8	1.9	0	30	<0.001	15	2.7
Rich fens (% of DBA)	RFEN	12	6.8	0	39	8.8	1.9	0	30	0.56	9.8	2.2
Poor fens (% of DBA)	PFEN	17	7.3	0	45	0.01	0.01	0	0.2	0.004	4.7	2.4
Swamps & marshes (% of DBA)	SWAMP	1.9	1.0	0	7.0	5.4	0.9	0	12	0.003	4.4	0.7
Lake elevation (m)	ELEV	613	36	505	730	633	11	549	740	0.44	625	12.5
Lake area (km^2)	LA	1.15	0.24	0.19	2.00	1.40	0.53	0.09	9.28	0.71	1.36	0.39
Mean depth (m)	Z_{mean}	1.3	0.3	0.7	2.5	3.6	0.7	0.9	14	0.004	3.0	0.6
Maximum depth (m)	Z_{max}	3.1	0.7	1.8	5.8	8.2	2.1	1.8	38	0.02	7.0	1.6
Lake volume (m^3 x 10^6)	LV	1.80	0.70	0.19	5.72	8.00	4.19	0.27	77.40	0.17	6.31	3.09
Water residence time (years)	τ	0.5	0.2	0.1	2.3	10.8	5.7	0.2	100	0.08	7.0	3.65
Drainage basin area/lake volume	DBA/LV	6.49	2.49	1.28	19.66	3.60	0.82	0.48	16.72	0.21	4.37	0.93
Effective DBA/lake volume	eDBA/LV	6.68	1.41	0.58	18.34	2.26	0.51	0.13	7.65	0.009	4.08	0.75
Drainage basin area/lake area	DBA/LA	6.69	1.66	1.86	13.21	8.48	1.05	1.52	20.15	0.33	8.00	0.92
Catchment area/lake volume	CA/LV	7.37	2.59	1.96	21.15	4.04	0.87	0.56	17.84	0.17	4.93	0.98

Table 5. Pearson correlation coefficients between water quality and drainage basin/lake morphometric variables. Data are from this study and Mitchell and Prepas (1990). Only significant coefficients are shown. *, $P \leq 0.01$; **, $P \leq 0.001$; ns, not significant. $n = 38$ for all correlations except for those involving ε (n=33) and eDBA/LV (n=34). Abbreviations as in Tables 3 and 4.

	log (LV)	log (Z_{mean})	Z_{max}	log (τ)	log (DBA/LV)	log (CA/LV)	log (eDBA/LV)	ELEV	SLOPE
ε	ns	-0.59**	-0.60**	-0.54**	0.54**	0.57**	0.55**	-0.45*	-0.50*
log(CHLA)	ns	-0.46*	-0.48*	ns	0.58**	0.59**	ns	ns	ns
log(TP)	ns	-0.54**	-0.60**	-0.45*	0.62**	0.64**	ns	ns	ns
log(TDP)	ns	ns	ns	ns	0.49*	0.49*	ns	ns	ns
NO_3	ns	ns	ns	ns	ns	ns	ns	ns	ns
log(NH_4)	ns	ns	ns	ns	ns	ns	ns	ns	ns
DIN	ns	ns	ns	ns	ns	ns	ns	ns	ns
log (TDN)	ns	-0.44*	-0.58**	ns	ns	ns	ns	ns	ns
log (TN)	ns	-0.45*	-0.59**	ns	ns	ns	ns	ns	ns
DOC	ns	-0.55**	ns	-0.46*	0.49*	0.52*	ns	-0.54**	ns
log (COL)	-0.44*	-0.82**	-0.58**	-0.84**	0.64**	0.69**	0.81**	-0.42*	-0.58**
ALK	0.57**	0.74**	0.68**	0.67**	-0.42*	-0.48*	-0.47*	ns	ns
HCO_3	0.57**	0.79**	0.69**	0.69**	-0.45*	-0.52*	-0.50*	ns	0.43*
pH	ns	0.45*	ns	ns	ns	ns	ns	ns	0.49*
Si	ns	ns	ns	ns	ns	ns	ns	ns	ns
log (SO_4)	0.47*	ns	ns	0.43*	ns	ns	ns	ns	ns
Cl	0.50*	ns	0.48*	0.49*	ns	-0.34*	ns	ns	ns
log (Na)	0.46*	0.58**	0.48*	0.49*	ns	ns	ns	ns	ns
K	ns	0.67**	0.42*	0.81**	-0.44*	-0.50*	-0.80**	ns	0.53*
Ca	ns	0.49*	ns	ns	ns	ns	-0.46*	ns	0.47*
Mg	0.53*	0.70***	0.68**	0.67**	-0.41*	-0.47*	-0.50*	ns	ns
COND	0.55**	0.68***	0.63**	0.65**	ns	-0.45*	-0.50*	ns	ns

Table 5. Continued.

	UPL	WETL	BOG	arcsin (FEN)	PFEN	RFEN	DECID	arcsin (CONIF)
ε	-0.64**	0.64**	0.75**	ns	ns	ns	-0.45*	ns
log (CHLA)	ns	ns	ns	ns	ns	-0.44*	ns	ns
log (TP)	ns	ns	ns	ns	ns	-0.49*	ns	-0.44*
log (TDP)	ns	ns	ns	ns	ns	-0.53*	ns	-0.46*
NO_3	ns	ns	0.43*	ns	ns	ns	ns	ns
log (NH_4)	ns	ns	ns	ns	ns	ns	ns	-0.52*
DIN	ns	ns	0.50*	ns	ns	ns	ns	-0.47*
log (TDN)	ns	ns	ns	ns	ns	-0.46*	ns	ns
log (TN)	ns	ns	ns	ns	ns	-0.42*	ns	-0.43*
DOC	-0.57**	0.57**	0.58**	ns	0.42*	ns	ns	ns
log (COL)	-0.80**	0.81**	0.78**	0.44*	ns	ns	-0.69**	ns
ALK	-0.56**	-0.58**	-0.58**	ns	ns	ns	0.56**	ns
HCO_3	0.59**	-0.61**	-0.61**	ns	ns	ns	0.59**	ns
pH	0.74**	-0.75**	-0.71**	ns	ns	ns	0.77**	ns
Si	ns	ns	-0.43**	ns	ns	ns	ns	ns
log (SO_4)	ns	ns	ns	ns	ns	ns	ns	ns
Cl	ns	ns	ns	ns	ns	ns	ns	ns
log (Na)	0.47*	-0.48*	-0.42*	ns	ns	ns	0.54*	ns
K	0.70**	-0.71**	-0.59**	-0.60**	ns	ns	0.69**	ns
Ca	0.63**	-0.63**	-0.68**	ns	ns	ns	0.66**	ns
Mg	0.53*	-0.55**	-0.55**	ns	ns	ns	0.53*	ns
COND	0.53*	-0.56**	-0.57**	ns	ns	ns	0.55**	ns

Table 6. Pearson correlation coefficients between phytoplankton taxa biomasses and water quality variables for 22 Boreal Plain lakes surveyed July – September 1996 and 1997. Phytoplankton biomass data were not available for Narrow, Sauer, Long and Moore lakes. *n* = 20 for upland-dominated (U), 14 for wetland-dominated (W), and 34 for all systems (All), respectively. DIN, dissolved inorganic nitrogen; TP, total phosphorus; TDP, total dissolved phosphorus; DOC, dissolved organic carbon; COL, colour; ALK, alkalinity. Only significant ($P \leq 0.05$) coefficients are shown; ns, not significant.

	NO_3			NH_4			DIN			TP			TDP		
	U	W	All	U	W	All	U	W	All	U	W	All	U	W	All
Total Biomass	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.72	0.65	0.66	0.59	ns	0.41
Cyanophyceae	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.73	0.43	0.74	0.55	0.55
Cryptophyceae	ns	ns	ns	ns	0.54	ns	ns	ns	ns	0.73	ns	0.54	0.73	ns	0.54
Diatomeae	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Euglenophyceae	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Peridineae	ns	-0.60	ns	ns	ns	ns	ns	-0.60	ns	ns	-0.60	ns	ns	ns	ns
Chlorophyceae	0.50	ns	0.40	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Chrysophyceae	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Chroococcales	0.47	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Oscillatoriales	ns	ns	ns	-0.50	ns	ns	-0.50	ns	ns	ns	ns	ns	ns	ns	ns
Nostocales	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Microcystis spp	ns	0.78	0.49	ns	ns	ns	ns	ns	ns	0.49	0.84	0.64	ns	ns	0.51
Non-Cyanophyceae	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.50	ns	0.44	ns	ns	ns
Heterocysts	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
N_2 fixing	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.57	0.37	ns	ns	0.35
N_2 non-fixing	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

Table 6. Continued

	DOC			COL			ALK			HCO_3			pH		
	U	W	All	U	W	All	U	W	All	U	W	All	U	W	All
Total Biomass	0.46	ns	0.36	ns	ns	ns	ns	-0.50	ns	ns	-0.50	ns	ns	ns	ns
Cyanophyceae	ns	0.65	0.35	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Cryptophyceae	ns	0.54	ns	ns	ns	ns	ns	ns	0.49	ns	ns	0.46	0.55	ns	0.61
Diatomeae	ns	ns	ns	ns	ns	0.37	ns	ns	ns	ns	ns	-0.50	ns	ns	-0.40
Euglenophyceae	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Peridineae	ns	-0.60	ns	ns	ns	ns	ns	-0.60	-0.50	ns	-0.60	-0.50	ns	-0.70	-0.60
Chlorophyceae	0.65	ns	0.56	ns	ns	0.44	-0.50	ns	-0.50	-0.50	ns	-0.50	-0.50	ns	-0.40
Chrysophyceae	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Chroococcales	ns	ns	ns	ns	ns	ns	ns	ns	ns	-0.50	ns	ns	-0.50	ns	ns
Oscillatoriales	ns	0.64	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.37	ns	ns	0.46
Nostocales	ns	0.53	ns	ns	ns	ns	ns	ns	ns	ns	0.56	0.41	ns	0.68	0.49
Microcystis spp	0.50	0.57	0.50	0.46	ns	ns	0.46	ns	ns	-0.50	ns	ns	-0.50	ns	ns
Non-Cyanophyceae	ns	ns	ns	ns	ns	0.36	ns	ns	0.36	ns	-0.70	-0.50	ns	ns	-0.40
Heterocysts	ns	0.59	ns	ns	ns	ns	ns	ns	0.43	ns	ns	0.39	ns	0.64	0.52
N_2 fixing	ns	0.76	0.38	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.67	0.41
N_2 non-fixing	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

Figures available in hard copy only.