

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

E.E. Prepas, D. Planas, J.J. Gibson, D.H. Vitt, T.D. Prowse, W.P. Dinsmore, L.A. Halsey, P.M. McEachern, S. Paquet, G.J. Scrimgeour, W.M. Tonn, C.A. Paszkowski, and K. Wolfstein

Abstract: A review of headwater lakes in undisturbed watersheds on the Boreal Plain, with indirect gradient analyses of chemical data, indicated a clear separation between those in wetland-dominated watersheds (57–100% wetland with variable proportions of bog, fen, swamp, and marsh cover) and those in upland-dominated watersheds (0–44% wetland cover). In the former, percentage wetland cover in the watershed was positively correlated with total phosphorus (TP, $r^2 = 0.78$, primarily bog), total nitrogen (TN, $r^2 = 0.50$), and dissolved organic carbon (DOC, $r^2 = 0.74$) concentrations. Rich fens appeared to sequester both TP and TN. In upland-dominated lakes, the ratio of catchment area to lake volume (CA/LV) was the strongest watershed correlate of TP concentration ($r^2 = 0.56$), whereas most limnetic nitrogen and DOC were generated in situ. Colour concentration, being highest in wetland lakes, was correlated with the ratio of isotopically defined effective drainage basin area to lake volume (eDBA/LV, $r^2 = 0.63$). Drainage basin slope was only weakly associated with water quality, likely because of low topographic relief ($\leq 11\%$). Higher Chlorophyta and Peridinea biomasses in wetland-dominated systems than in upland-dominated ones may coincide with greater NH_4^+ availability.

Résumé : Une analyse indirecte de gradient des données chimiques provenant de lacs situés en amont de bassins hydrographiques non perturbés de la Plaine boréale indique une nette séparation entre les lacs provenant de bassins dominés par les terres humides (57–100% de terres humides, avec des proportions variables de couverture de tourbières ombrotrophes, de tourbières minéralotrophes, de marécages et de marais) et ceux des bassins dominés par des terres hautes (0–44% de terres humides). Chez les premiers, le pourcentage de couverture par les terres humides dans le bassin est en corrélation positive avec les concentrations de phosphore total (TP, $r^2 = 0,78$, surtout des tourbières ombrotrophes), d'azote total (TN, $r^2 = 0,50$) et de carbone organique dissous (DOC, $r^2 = 0,74$). Les tourbières minéralotrophes productives semblent accaparer le TP et le TN. Dans les lacs provenant de bassins dominés par les terres hautes, le rapport de la surface du bassin hydrographique sur le volume du lac (CA/LV) est la variable qui montre la plus forte corrélation avec la concentration de TP ($r^2 = 0,56$); la majorité de l'azote et du DOC limnétiques y sont générés in situ. La couleur, qui est à son maximum dans les lacs des bassins dominés par les terres humides, est en corrélation avec le rapport de la surface effective du bassin de drainage (mesurée à l'aide d'isotopes) et le volume du lac (eDBA/LV, $r^2 = 0,63$). La pente du bassin versant n'est que peu associée à la qualité de l'eau, probablement parce que le relief topographique est faible ($\leq 11\%$). Les biomasses plus élevées des chlorophytes et des péridiniens dans les lacs dont le bassin est dominé par les terres humides sont sans doute associées à une disponibilité plus grande du NH_4^+ .

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E.E. Prepas,¹ D.H. Vitt, W.P. Dinsmore, L.A. Halsey, P.M. McEachern, G.J. Scrimgeour,² W.M. Tonn, C.A. Paszkowski, and K. Wolfstein.³ Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada.

D. Planas and S. Paquet. Département des sciences biologiques, Université du Québec à Montréal, Montréal, QC H3C 3P8, Canada.

J.J. Gibson⁴ and T.D. Prowse. Environment Canada, National Water Research Institute, 11 Innovation Boulevard, Saskatoon, SK S7N 3H5, Canada.

¹Corresponding author (e-mail: eprepas@ualberta.ca).

²Present address: Alberta Research Council, P.O. Bag 4000, Vegreville, AB T9C 1T4, Canada.

³Present address: Department of Marine Microbiology, NIOO-CEMO, P.O. Box 140, NL-4400 AC Yerseke, The Netherlands.

⁴Present address: Isotope Hydrology Section, International Atomic Energy Agency, Wagramer Strasse 5, P.O. Box 100, A-1400 Vienna, Austria.

Introduction

The Boreal Forest covers over one-fifth of Canada's landmass. Geological and climatic variation across this land base result in two major subregions: the larger, wetter, and nutrient-poor Boreal Shield of central and eastern Canada and the drier, nutrient-rich Boreal Plain of western Canada. On the Boreal Shield, differences in lake morphometry, drainage basin topography, and land use explain variability in water quality (Schindler 1971; Dillon et al. 1991; D'Arcy and Carignan 1997); similar relationships have yet to be developed for the Boreal Plain. Lakes on the Boreal Plain are situated on low-relief, often poorly drained sedimentary tills in contrast to the typically higher relief of Shield drainages (Mitchell and Prepas 1990). Relative to lakes on the Boreal Shield, lakes on the Boreal Plain tend to be phosphorus- (P) and plankton-rich (D'Arcy and Carignan 1997; Mitchell and Prepas 1990). On an annual basis, euphotic total phosphorus (TP) in lake water on the Boreal Plain is derived mainly through internal sediment P recycling (Shaw and Prepas 1990), atmospheric P inputs being relatively unimportant compared with Boreal Shield lakes (Shaw et al. 1989; D'Arcy and Carignan 1997). In summer, high cyanobacterial biomass is typical of phytoplankton communities on the Boreal Plain (Zhang and Prepas 1996), whereas Chrysophytes and other flagellates dominate Boreal Shield communities (Planas et al. 2000). Given differences in drainage basin geomorphology, nutrient dynamics, and phytoplankton communities, in situ models developed for drainage basin water quality interactions on the Boreal Shield (e.g., Rasmussen et al. 1989) for colour and dissolved organic carbon (DOC) will likely require modifications for the Boreal Plain.

Another feature distinguishing the two Boreal subregions is the amount and type of wetlands, the Boreal Plain (Alberta) having more than twice the wetland (bogs, fens, marshes, and swamps) coverage of the Boreal Shield (Québec) (NWWG 1998). The extent of peatland (i.e., bogs and fens) coincides with increased dissolved nitrogen, phosphorus, and organic carbon concentrations in lakes on the Boreal Plain (Halsey et al. 1997) and Boreal Shield (Dillon et al. 1991). Peatlands can vary markedly in water discharge and thus in their influence on surface water chemistry (Halsey et al. 1997). The amount of water produced by surface and subsurface flow forms an effective watershed (effective drainage basin area, eDBA, defined with stable isotopes by Gibson and Prowse 1998) within the total drainage basin. The size of an eDBA depends on the resistance that water encounters flowing from precipitation to lake and on surface storage, soil storage, hydraulic conductivity, groundwater levels, and the seasonal water balance (Soranno et al. 1996). Effective drainage basin area may be more closely linked with water quality in regions such as the Boreal Plain, where low drainage basin slope and variable runoff are associated with extensive peatland cover.

Data collected from headwater lakes having watersheds with minimal disturbance and near zero to 100% wetland cover in their watersheds were used to test hypotheses generated from studies based primarily on the Precambrian Shield and for peatland-dominated lake basins. These hypotheses are as follows: (i) physical features, such as water residence time, lake depth, drainage basin area (DBA) to lake area (LA) ratio (DBA/LA, where DBA = catchment

area (CA) – LA), slope, and vegetation cover are effective predictors of lakewater TP concentrations; (ii) nitrogen concentrations will be higher in wetland-dominated systems; (iii) phytoplankton communities within wetland-dominated systems will have higher biomasses of N-dependent (non-nitrogen-fixing) taxa than upland-dominated systems; (iv) in-lake DOC and colour are related to the extent of wetland coverage within drainage basins; and (v) eDBA is a better predictor of constituent inputs than DBA or CA, particularly in wetland-dominated watersheds.

Materials and methods

Study area

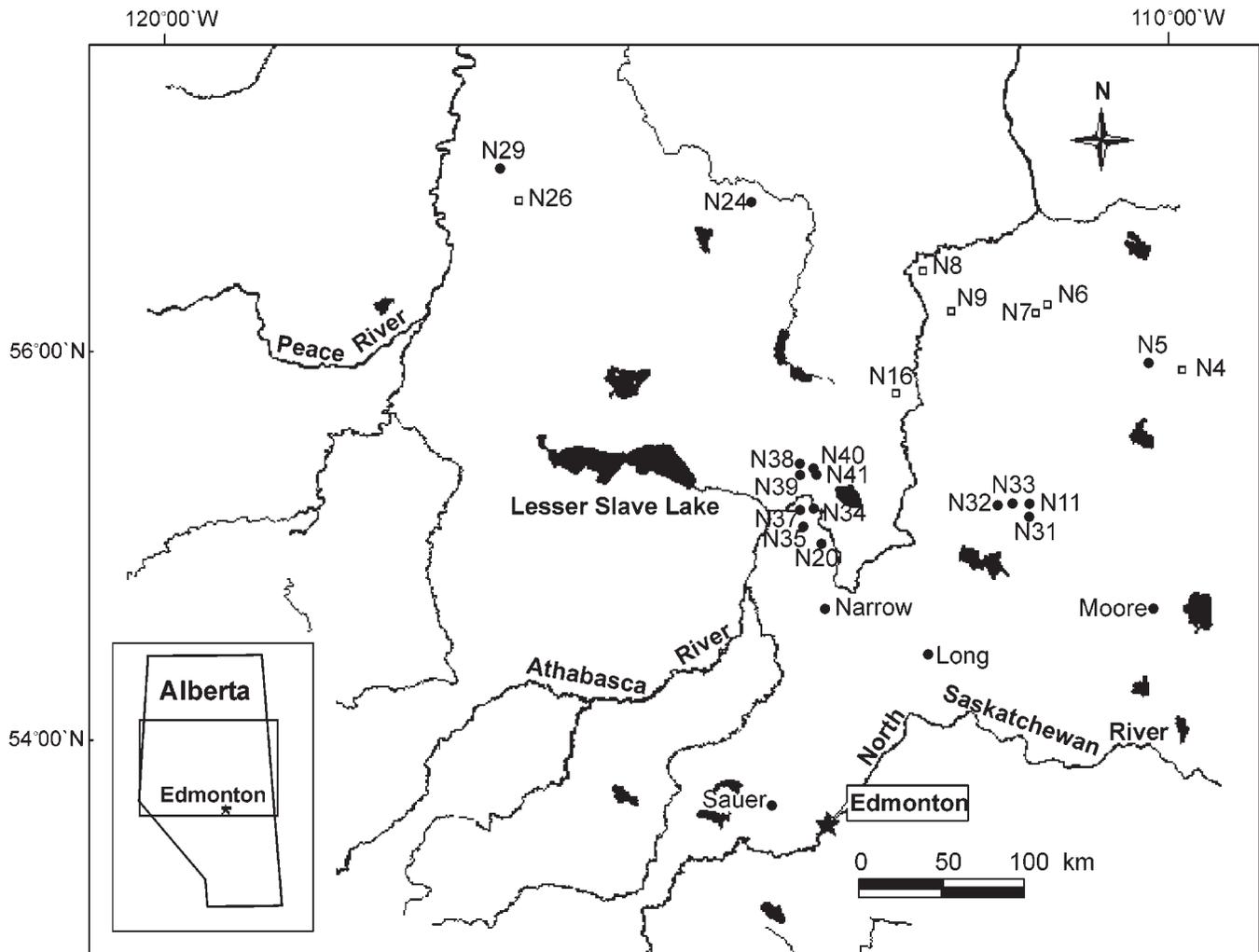
Euphotic water quality and phytoplankton samples and morphometric and watershed characteristics were collected for 26 headwater lakes located within a 109 600-km² area (Fig. 1) within the mixed-wood ecoregion of the Boreal Plain ecozone (Strong 1992). Soil types within the study region range from eutric brunisols–gray luvisols in upland areas to organics–gleysols in wetland areas. Boreal Plain wetlands are categorized as peatland (bogs, poor fens (PFEN), and rich fens (RFEN)) and non-peatland (swamps and marshes (SWAMP)) (Halsey et al. 1997). Bogs are dominated by Bryophytes, notably *Sphagnum*, and 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–Scirpus–Typha* (marshes). Boreal mixed-wood uplands are dominated by *Populus tremuloides*, *Populus balsamifera* (DECID), and *Picea glauca* (CONIF) stands, with a diverse understorey of herbs and shrubs (Strong 1992). Thirty-year average annual precipitation for the region ranged from 388 to 432 mm (33% as snow), and mean annual air temperature ranged from 0.7 to 1.4°C. During the main sampling periods (June–September 1996 and 1997), the region received twice the average precipitation compared with the 30-year normal, depending on location (Environment Canada, Commercial Weather Service, Edmonton, Alta., unpublished data). The two main sampling years were relatively wet. The lakes chosen were either slated for or near those slated for harvesting in or around 1997 or near areas burned in the 1995 wetland-dominated fires. None of the study systems has been disturbed (>5% of vegetation removed) within the past 50 years.

Sampling and analyses

Eleven lakes were sampled monthly by fixed-wing aircraft with pontoons during early to mid-July, August, and September 1996 and 1997. Another 11 lakes (N11, N31, N32, N33, N34, N35, N37, N38, N39, N40, and N41) were ground-accessible. Nine of these lakes were sampled at 2- to 3-week intervals and two lakes were sampled at 1- to 2-week intervals from mid-June to mid-August 1996. As the watersheds of 10 of the 11 ground-accessible lakes were harvested in winter of 1997, 1997 data from only one of these could be included in our analyses. Long, Moore, Narrow, and Sauer lakes (Fig. 1) were sampled on one date between mid-August to early September 1998. To summarize, 12 lakes had water quality data available for 1996 and 1997, 10 lakes had data available for 1996, and 4 lakes had data for 1998 only, for a total of 38 independent summer observations of water quality on 26 lakes. 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 nine to ten ($n = 2$) sampling dates.

Vertically integrated water samples were collected from the euphotic zone (depths receiving $\geq 1\%$ of ambient surface light) at two sites (including the deepest) along the longitudinal axis of each lake. Light extinction coefficient (ϵ) was calculated from pro-

Fig. 1. Location of the Boreal Plain study lakes. Open squares denote wetland-dominated systems; solid circles denote upland-dominated systems.



file data measured at the deepest site with a LiC or 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. Filtrate from distilled-deionized water-rinsed, $0.45\text{-}\mu\text{m}$ Millipore HAWP membranes was used for total dissolved phosphorus (TDP) and nitrate + nitrite ($\text{NO}_3 + \text{NO}_2$) analyses. Samples for TP, TDP, pH, colour, alkalinity, and conductivity were analysed within 24 h. $\text{NO}_3 + \text{NO}_2$ and ammonium (NH_4) samples were preserved with H_2SO_4 and then refrigerated for 1–2 weeks before analysis. Total dissolved nitrogen (TDN) samples were filtered through pre-weighed, Whatman GF/C filters, refrigerated, and analysed within 48 h. Filters were then vacuum-dried and frozen for subsequent particulate N (PN) analysis. Samples for major cations (Ca, Mg, Na, K), major anions (Cl, SO_4), and DOC were filtered through precombusted Whatman GF/C filters before long-term (1–2 months) storage. Samples for major cations and DOC analyses were acidified to $\text{pH} < 2$ with HNO_3 and then refrigerated. Samples for major anions were refrigerated only. Refrigeration was at 4°C .

Chl *a* was analysed by Ostrofsky's spectrophotometric-based ethanol extraction technique which does not correct for phaeo pigments (Bergmann and Peters 1980). TP and TDP were analysed by a modified potassium persulfate method (Prepas and Rigler 1982). pH was measured in the laboratory with a Fisher Scientific Accumet 925 pH meter. Colour (Col) was measured at 440 nm with a Milton Roy 1001 spectrophotometer (Cuthbert and del

Giorgio 1992) and reported as $\text{mg}\cdot\text{L}^{-1}$ platinum (Pt). Conductivity was measured with a Radiometer CDM 83 meter. Alkalinity (primarily HCO_3) was determined on a Mettler DL 21 autotitrator. TDN samples were photocombusted in an ultraviolet digester and analysed. $\text{NO}_3 + \text{NO}_2$ and NH_4 were analysed with a Technicon autoanalyser (Stainton et al. 1977). PN was combusted at 700°C and analysed on a Control Equipment Corporation 440 Elemental Analyzer. Dissolved inorganic nitrogen (DIN) is the sum of $\text{NH}_4 + \text{NO}_3 + \text{NO}_2$, and total nitrogen (TN) is the sum of TDN + PN. Sulphate (SO_4) and chloride (Cl) analyses were run on a Dionex 2000i/SP ion chromatograph fitted with an AS4A-Sc high-capacity anion exchange column, and major cations were analysed on a Perkin Elmer 3300 atomic absorption spectrophotometer. Silica (Si) concentrations were determined spectrophotometrically (Environment Canada 1979). For DOC, sparged subsamples were run on an Ionics Corporation 1505 programmable carbon analyser with a platinum catalyst. Where direct measurements were unavailable for conductivity (COND) (14 lakes during 1996), it was estimated from the sum of mean July to September Na, K, Ca, and Mg concentrations ($\text{mg}\cdot\text{L}^{-1}$), weighted by atomic weight, based on an empirical model ($r^2 = 0.91$, $\text{df} = 63$) developed with data from this study ($n = 24$) and unpublished data (E. Prepas; $n = 39$):

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

Phytoplankton were identified for the 22 Boreal Plain lakes sur-

veyed 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 with a Leica DM-IRB inverted microscope (for 40× magnification, 15 to 30 fields; for 10×, ½ the slide). Cyanobacteria, Cryptophyceae, Bacillariophyta (diatoms), Euglenophyceae, Peridineae, Chlorophyta, and Chrysophyceae were identified. Cyanobacteria were subdivided into major taxa (Oscillatoriales, Nostocales, *Microcystis* spp., and other Chroococcales) and functional groups (N₂-fixing taxa, Nostocales; non-N₂-fixing taxa, Chroococcales and Oscillatoriales). Total and taxa biomasses were estimated from cell biovolume measurements (Lewis 1976), using equivalent geometric forms and assuming 1 μm³ = 1 pg.

Lake morphometric variables (surface area (LA), volume (LV), and mean (Z_{mean}) and maximum (Z_{max}) 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 percentage 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 (DBA), lake surface area, and their sum, catchment area (DBA + LA = CA), 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 regularly to reflect the size of the drainage basin, from outer boundary to shoreline on 1 : 50 000 topographic maps.

Water residence times (τ , years) 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 (¹⁸O/¹⁶O) and hydrogen (²H/¹H) stable isotope ratios (Gibson et al. 1993). The isotope mass-balance reflects the major components of a water balance such that inflow (I), total outflow (Q), and total lake evaporation (E), in m³·year⁻¹, were multiplied by the respective isotope composition ($\delta^{18}\text{O}$ and $\delta^2\text{H}$, % Standard Mean Ocean Water (SMOW)) independently substituted for δ values to permit a comparative assessment of model uncertainty:

$$(2) \quad I \cdot \delta_I = Q \cdot \delta_Q + E \cdot \delta_E$$

where it was assumed that the isotope composition of outflow was equivalent to the composition of lake water (δ_L), the composition of inflows was equivalent to precipitation (δ_P), and the composition of evaporated moisture (δ_E) was predicted from a model for free-surface evaporation (Gibson et al. 1993). When rearranged eq. 2 becomes

$$(2a) \quad E/I = (\delta_L - \delta_P) \cdot [m(\delta^* - \delta_L)]^{-1}$$

where $m = h(1 - h)^{-1}$ and h is ambient atmospheric humidity. Limiting isotopic enrichment (δ^*) was 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 on 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 E/I (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 database (IAEA/WMO 1999). Specific assumptions on the boundary layer regime and atmospheric parameters used in the model are discussed in Gibson and Prowse (1998). Once the relative fraction of evaporation to inflow was calculated, lake water residence time was

$$(2b) \quad \tau = ((E/I) \cdot Z_{\text{mean}}) \cdot E_L^{-1}$$

where Z_{mean} is mean lake depth (m) and E_L^{-1} is long-term mean annual lake evaporation rate (mm·year⁻¹) for the region (Environment Canada 1978). Water residence times for Long, Moore, Narrow, and Sauer lakes are based on 25-year averages of precipitation, runoff, and evaporation (Mitchell and Prepas 1990). Effective DBA (eDBA, km²) was calculated as

$$(3) \quad \text{eDBA} = (R \cdot P^{-1}) \cdot \text{DBA}$$

where R and P are mean annual drainage basin runoff and precipitation (both in mm·year⁻¹), respectively.

To put the lakes surveyed in 1996 and 1997 in a context with others studied on the Boreal Plain, comparable summary information was prepared for lakes in the Atlas of Alberta Lakes (Mitchell and Prepas 1990); the latter analyses excluded the four headwater lakes added to our data analyses from the Atlas (Table 1). The data set for comparison consisted of 42 small to moderate-sized lakes north of the City of Edmonton.

To test hypotheses on the relationship between drainage basin vegetation and physiography and water quality, an indirect gradient analysis with a linear model was performed in CANOCO Version 4.0 (ter Braak and Smilauer 1998). Because of collinearity between environmental variables, only the following were included in the final analyses: LV, LA, τ , Z_{mean} , Z_{max} , DBA/LA, DBA/LV (km²·10⁶ m⁻²), CA/LV, % CONIF, % PFEN, % peatland (bog + fen), % bog, % upland, % DECID, slope, and elevation. Percentage vegetative cover is relative to drainage basin area throughout. A "passive analysis" of environmental variables and unconstrained ordination axes by correlation determined the relationship between lake chemistry and the corresponding DB vegetation and physiography.

Relationships between water quality and drainage basin – morphometric variables were examined by least squares methods of multivariate linear regression. Variable data with non-normal distributions (Shapiro–Wilks' test) were log₁₀- or arcsine-transformed, where appropriate. Pearson's 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 intercorrelation between independent variables. Only the strongest, in terms of percentage variation ($r^2 \times 100$) explained, and the most limnologically meaningful relationships are presented (*, $P < 0.05$; **, $P < 0.01$). Student's t tests were performed for data with heterogeneous variances, where appropriate. 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 and shallower (mean LA and $Z_{\text{mean}} = 0.8$ km² and 2.3 m, respectively, $n = 22$) than Boreal Plain lakes from the Atlas of Alberta Lakes (Mitchell and Prepas 1990) (mean LA and $Z_{\text{mean}} = 31$ km², $n = 42$, and 6.7 m, $n = 41$, respectively; Table 2). Consequently, four small headwater lakes in undisturbed watersheds, Long, Moore, Narrow, and Sauer (mean LA and $Z_{\text{mean}} = 4.1$ km² and 7.8 m, respectively, $n = 4$) were added to our survey set to better reflect the range of physical characteristics reported for the Boreal Plain (Table 2). Mean DBA/LV of these four systems was one-quarter that for the other upland-dominated systems in our data set (1.3 vs. 5.2, respectively), but other physical parameters did not differ overall despite noticeable extremes in individual systems (Table 1). Water quality in Long, Moore, Narrow, and Sauer lakes, with the exception of colour (13 mg·L⁻¹ and 43 mg·L⁻¹ Pt, respectively), did not differ detectably

Table 1. Drainage basin and lake morphometry data for the 26 study lakes.

Lake	Catchment type	Year(s) surveyed	DBA (km ²)	LA (km ²)	LV (m ³ × 10 ⁶)	DBA/LV	CA/LV	Z _{mean} (m)	Z _{max} (m)	SLOPE (%)	CONIF (%)	DECID (%)	WETL (%)
N4	Wetland	1996, 1997	0.56	0.19	0.19	2.9	3.9	1.0	5.5	3.9	43	0	57
N6	Wetland	1996, 1997	4.28	0.90	0.96	4.5	5.4	1.1	1.8	0.8	28	0	71
N7	Wetland	1996, 1997	1.87	1.01	1.47	1.3	2.0	1.5	3.3	0.8	43	0	57
N8	Wetland	1996, 1997	9.14	0.69	0.46	19.9	21.1	0.7	1.8	0.5	8	0	92
N9	Wetland	1996, 1997	18.80	1.62	1.73	10.9	11.8	1.1	1.8	0.3	5	2	93
N16	Wetland	1996, 1997	6.99	1.62	2.08	3.4	4.1	1.3	1.8	0.6	0	0	100
N26	Wetland	1996, 1997	16.22	2.00	5.72	2.8	3.2	2.9	5.8	1.0	20	20	60
N5	Upland	1996, 1997	5.15	1.20	1.38	3.7	4.6	1.2	4.6	1.4	29	28	44
N11	Upland	1996	6.12	0.62	2.40	2.6	2.8	3.9	5.8	8.0	7	83	10
N20	Upland	1996, 1997	4.52	0.30	0.27	16.7	17.8	0.9	1.8	3.3	26	61	11
N24	Upland	1996, 1997	1.51	0.25	0.49	3.1	3.6	1.9	4.0	6.6	14	65	20
N29	Upland	1996, 1997	2.58	1.70	2.32	1.1	1.8	1.4	2.4	2.6	24	33	24
N31	Upland	1996	1.09	0.14	0.37	2.9	3.3	2.7	5.5	4.7	9	85	5
N32	Upland	1996	1.89	0.33	0.56	3.4	4.0	1.7	4.1	3.3	4	73	22
N33	Upland	1996	4.55	1.04	3.30	1.4	1.7	3.2	7.2	3.6	3	83	14
N34	Upland	1996	6.78	0.52	2.53	2.7	2.9	4.9	11.2	3.5	6	81	11
N35	Upland	1996	2.92	0.18	0.72	4.1	4.3	3.9	7.6	3.0	3	70	25
N37	Upland	1996, 1997	7.42	0.75	1.67	4.4	4.9	2.2	2.9	1.1	1	82	16
N38	Upland	1996	10.53	1.57	7.16	1.5	1.7	4.6	8.5	4.5	43	45	13
N39	Upland	1996	8.40	0.56	0.72	11.7	12.5	1.3	2.3	3.9	19	59	21
N40	Upland	1996	9.64	0.45	2.00	4.8	5.1	4.4	9.1	3.7	29	59	13
N41	Upland	1996	6.50	0.65	1.57	4.2	4.6	2.4	3.9	3.9	15	59	21
Narrow	Upland	1998	7.17	1.14	16.40	0.4	0.5	14.4	38.0	3.4	25	52	21
Sauer	Upland	1998	0.49	0.09	0.35	1.4	1.6	4.2	8.5	10.6	40	60	0
Long	Upland	1998	82.40	5.84	29.30	2.8	3.0	4.3	9.0	3.4	15	83	0
Moore	Upland	1998	37.10	9.28	77.40	0.5	0.6	8.3	26.0	2.6	21	48	23

Note: DBA, drainage basin area; LA, lake area; LV, lake volume; DBA/LV, drainage basin area/lake volume; CA/LV, catchment area/lake volume; Z_{mean}, mean depth; Z_{max}, maximum depth; CONIF, conifer; DECID, deciduous; WETL, wetland. DBA, LA, LV, Z_{mean}, and Z_{max} for Narrow, Sauer, Long, and Moore lakes are from Mitchell and Prepas (1990).

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 the same lakes on several dates 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 parameters such as nutrients and Chl *a* vary seasonally, deep lakes such as Long, Moore, Narrow, and Sauer are relatively stable compared with 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, our study lakes reflect the range of trophic conditions in the Boreal Plain in that ranges in TP, Chl *a*, NO₃, and DOC concentrations are comparable with data for the region (Tables 2 and 3).

Lake productivity indices were up to an order of magnitude higher compared with those of D'Arcy and Carignan's (1997) Boreal Shield lakes (mean TP, 54 µg·L⁻¹ and 8.7 µg·L⁻¹; Chl *a*, 19 µg·L⁻¹ and 2.7 µg·L⁻¹, respectively). Although mean DBA in this study is larger than that of the Shield study (10 km² and 2.3 km², respectively), drainage ratios were similar (mean DBA/LA, 8.3 and 7.5, respectively). Wetland coverage per drainage basin in this study was on average 25 times that reported for the Shield study (32% and 1.3%, respectively). Upland conifer cover in Boreal Plain systems averaged less than half that of Shield systems (18% and 44% of DBA, respectively).

Indirect gradient analysis of chemical data indicated a clear separation between lakes with >50% wetland (range 57–100%) and those with <50% wetland (range 0–44%) in their watershed. Our division between wetland and upland is arbitrary and only a much larger study would permit evaluation of whether the relationship is a continuum or discontinuous. Four of the seven wetland-dominated systems were far to the right in the ordination (N6, N8, N9, N16, >71% wetland). Two more wetland lakes (N4, N7, both 57% wetland) were also to the right of all the upland-dominated systems, along with colour and inorganic nitrogen concentrations, whereas the remaining lakes were in the centre and left-hand portion (Fig. 2). The seventh lake (N26) with >50% wetland in the drainage was the only wetland-dominated lake with a substantive amount of deciduous trees (20% compared with 2% or less; Table 1) in its catchment; the remaining wetland-dominated catchments were conifer dominated in their upland sections. N26 rested in the middle of the lakes with upland-dominated drainages. Initial review of the data gave no indication of systematic changes introduced by having more data available for the first of the two wet years (1996, 1997) of this study. The gradient analysis confirmed that vegetative features of the catchment including percentage

wetland and percentage upland and physical features related to relative drainage basin area were substantive contributors to water chemistry. This initial data compilation suggested that in addition to relationships with the entire data set (ALL), we should explore independently those with wetland- and upland-dominated catchments.

When the lakes were divided into wetland- and upland-dominated systems, the physical and chemical differences suggested by gradient analyses were apparent (Tables 3 and 4). Mean and maximum depths were over 2.5-times greater as were drainage basin slopes, whereas eDBA were 2.5 times smaller in lakes with upland-dominated drainage basins; however, other morphometric and physical 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 mg·L⁻¹ vs. 38 mg·L⁻¹ TP, 5.7 µS·cm⁻¹ vs. 7.6 µS·cm⁻¹, and 265 µS·cm⁻¹ vs. 80 µS·cm⁻¹, respectively, $P < 0.001$ for all comparisons).

Within the combined data set, DBA/LV was strongly linked to Chl *a*, TP, and colour ($r = 0.58, 0.62, \text{ and } 0.64$, respectively, $P \ll 0.01$), less strongly to TDP ($r = 0.49, P < 0.05$), and not detectably to nitrogen. Associations between CA/LV and DBA/LV were indistinguishable. Water residence was negatively related to TP and DOC ($r = -0.45, -0.46$, respectively, $P < 0.05$) and colour ($r = -0.84, P \ll 0.01$). Presence of wetlands in the drainage, particularly bogs, were positively linked to lakewater DOC concentrations and colour ($r = 0.58 \text{ and } 0.78$, respectively) and negatively associated with lakewater pH, alkalinity, base cation concentrations, and conductivity (Na, $r = -0.42, P < 0.05$; for the rest, -0.55 to $-0.71, P < 0.001$). Drainage basin slope was not related to nutrient concentration in this study in direct contrast to the Precambrian Shield (D'Arcy and Carignan 1997), probably because slopes were on average lower and covered a smaller range compared with the Shield study (ranges 0.3–11% and 6–31%, respectively). We removed Long, Moore, Narrow, and Sauer lakes to determine if these deep lakes had influenced any of the relationships and re-examined our correlation matrix. Relationships between Chl *a*, TP, TDP, DOC, colour, DBA/LV, and water residence time did not change appreciably with the removal of the four deeper lakes.

Phosphorus and drainage basin features

In the combined data set, TP concentrations were most strongly related to CA/LV (Fig. 3a); almost 60% of TP variability was explained by a combination of CA/LV and RFEN cover (eq. 4). DBA/LV explained essentially the same variability in TP as CA/LV (39% and 42%, respectively). In contrast to our initial hypotheses, TP concentrations in Boreal Plain lakes with relatively low watershed slope ($\leq 11\%$) were unrelated to watershed slope.

$$(4) \quad \text{ALL: } \log(\text{TP}) = 1.57 + 0.38\log(\text{CA/LV})^{**} - 0.48\text{arcsin}(\text{RFEN})^{**}, r^2 = 0.59.$$

In upland-dominated systems, CA/LV alone explained 56% of TP variability, with percentage fen cover explaining an

Table 2. Summary data for Boreal Plain lakes from Mitchell and Prepas (1990).

	<i>n</i>	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 <i>a</i> (µg·L ⁻¹)	37	22	3.5	3.3	99
TP (µg·L ⁻¹)	39	57	7.8	9	193
NO ₃ ⁻ (µg·L ⁻¹)	32	11	2.4	1	79
DOC (mg·L ⁻¹)	22	17	1.7	10	37
Alkalinity (mg·L ⁻¹)	42	176	14	49	556
pH	42	8.0	—	7.3	9.2
Ca ⁺ (mg·L ⁻¹)	40	29	1.5	11	53
Cl ⁻ (mg·L ⁻¹)	35	2.9	0.6	0.9	17
K ⁺ (mg·L ⁻¹)	40	8.5	1.0	0.8	25
Conductivity (µS·cm ⁻¹)	41	378	31	117	1143

Note: Narrow, Sauer, Long, and Moore lakes are excluded. SE, ± 1 standard error; Min., minimum; Max., maximum; TP, total phosphorus; DOC, dissolved organic carbon.

additional 20% (eq. 5). Schindler (1971) suggests a similar relationship between P and CA/LV for Boreal Shield lakes, considering that phytoplankton (Chl *a* concentration and midsummer phytoplankton production and biomass) are positively related to CA/LV. Relative watershed size is a strong driving factor for TP concentration in our upland lakes, producing 10 times more phosphorus per unit DBA than lakes on the Precambrian Shield (Carignan et al. 2000).

$$(5) \quad \text{UPLAND: } \log(\text{TP}) = 1.55 + 0.54\log(\text{CA/LV})^{**} \\ - 0.67\arcsin(\text{RFEN})^{**}, r^2 = 0.76$$

In wetland-dominated systems, percentage wetland (WETL) and conifer cover explained most of the TP variance (78% and 87%, respectively). Addition of sampling year (YEAR) for lakes in the wetland-dominated drainages added 7% to the TP variability accounted for by percentage wetland cover (eq. 6).

$$(6) \quad \text{WETLAND: } \log(\text{TP}) = -222.17 + 0.01(\text{WETL})^{**} \\ + 0.11\text{YEAR}^*, r^2 = 0.85$$

Consistent with our preliminary data review, the relationship between percentage wetland coverage and lakewater TP concentration (Fig. 3b) suggests that our systems are from two populations, one with a positive link overall between wetland cover and TP, the other with a TP-sequestering aspect associated with rich fens. By separating wetland cover into its three constituents, we see that bogs apparently release TP ($r = 0.84$, $P \ll 0.01$), poor fens play a neutral role ($P > 0.3$), and like our upland-dominated systems, rich fens sequester TP ($r = -0.77$, $P \ll 0.01$). As reported with bogs in the watersheds of our study lakes, 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 25 and 6%, respectively). Apparently, wetlands with organic soil do not retain P as effectively as forested systems (Halsey et al. 1997).

Nitrogen and drainage basin features

Consistent with our hypotheses, nitrogen concentrations were related to type and extent of wetland cover. Mean DIN for our upland-dominated lakes was comparable with values reported by D'Arcy and Carignan (1997) for Boreal Shield lakes (40 µg·L⁻¹ and 31 µg·L⁻¹, respectively). Yet most (~80%) DIN was NH₄ in the Boreal Plain lakes compared to NO₃ in D'Arcy and Carignan's (1997) Boreal Shield study. The predominance of NH₄ in Boreal Plain lakes was due to greater wetland cover and water-logged soils, which should favour the export of reduced nitrogen species such as NH₄ (Dillon et al. 1991). As a result, percentage wetland cover explained 40% of NH₄ variability in the wetland-dominated systems ($r^2 = 0.39$, $P < 0.01$).

The TN pool in our study lakes was composed of 75% TDN on average (Table 3), of which >90% was dissolved organic nitrogen. In the combined data set, mean and maximum depth and percentage rich fen and upland conifer coverage were inversely related to TN concentrations but explained ≤35% of the variation. However, when watersheds were separated based on >50% and <50% wetland coverage, TN was strongly related with percentage upland conifer ($r = -0.88$, $P < 0.001$), wetland ($r = 0.71$, $P < 0.01$), bog ($r = 0.64$, $P < 0.05$), rich fen cover ($r = -0.61$, $P < 0.05$), and eDBA ($r = 0.69$, $P < 0.01$) in the former, whereas TN was negatively linked to Z_{max} in the latter ($r = -0.74$, $P < 0.001$). Mean lake depth and wetland parameters together accounted for >70% of TN concentration variation (eqs. 7 and 8):

$$(7) \quad \text{WETLAND: } \log(\text{TN}) = 1.99 + 0.89\arcsin(\text{WETL})^{**} \\ + 0.80\log(Z_{\text{mean}})^{**}, r^2 = 0.91$$

$$(8) \quad \text{UPLAND: } \log(\text{TN}) = 3.39 - 0.56\log(Z_{\text{mean}})^{**} \\ - 0.52\arcsin(\text{RFEN})^{**}, r^2 = 0.72$$

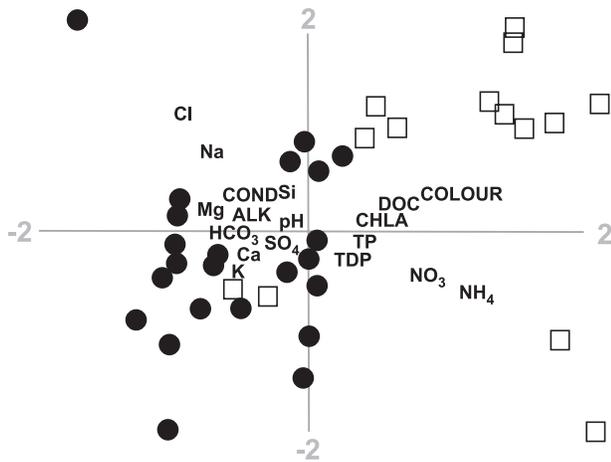
Wetlands immediately adjacent to our upland-dominated lakes are fens, which appear to retain nitrogen to some degree (Halsey et al. 1997), whereas bogs that form the majority of total wetland area export nitrogen, similar to the bogs elsewhere in Alberta (Halsey et al. 1997) and on the Shield

Table 3. Summary water quality data for the 26 Boreal Plain study lakes.

Variable	Abbreviation	Wetland-dominated (<i>n</i> = 14)				Upland-dominated (<i>n</i> = 24)				<i>P</i>	Total (<i>n</i> = 38)	
		Mean	SE	Min.	Max.	Mean	SE	Min.	Max.		Mean	SE
TP ($\mu\text{g}\cdot\text{L}^{-1}$)	TP	57	9.4	26	162	52	6.8	12	160	0.67	54	5.5
TDP ($\mu\text{g}\cdot\text{L}^{-1}$)	TDP	19	2.5	5.3	42	17	2.0	5.2	44	0.54	17	1.6
Chl <i>a</i> ($\mu\text{g}\cdot\text{L}^{-1}$)	CHLA	21	4.6	2.0	57	18	3.4	2.0	76	0.67	19	2.7
NH ₄ ⁺ ($\mu\text{g}\cdot\text{L}^{-1}$)	NH ₄	136	90	6.4	1271	35	8.3	2.5	149	0.27	72	34
NO ₃ ⁻ ($\mu\text{g}\cdot\text{L}^{-1}$)	NO ₃	11	6.7	1.1	99	5.5	0.6	1.1	13	0.38	7.7	2.5
DIN ($\mu\text{g}\cdot\text{L}^{-1}$)	DIN	148	92	7.5	1281	40	8.6	5.2	154	0.26	80	34
TDN ($\mu\text{g}\cdot\text{L}^{-1}$)	TDN	858	123	373	2177	899	90	212	2129	0.79	884	72
TN ($\mu\text{g}\cdot\text{L}^{-1}$)	TN	1227	194	604	3297	1208	126	279	2825	0.94	1215	106
TN:TP	TN:TP	23	2.1	13	38	26	2.0	8.1	39	0.30	25	1.5
SO ₄ ²⁻ (mg·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·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·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·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·L ⁻¹ Pt)	COL	186	29	29	358	38	5.2	8.0	125	<0.001	92	16
Alkalinity (mg·L ⁻¹)	ALK	28	8.4	2.9	95	110	14	40	389	<0.001	80	11
HCO ₃ ⁻ (mg·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 ($\mu\text{g}\cdot\text{L}^{-1}$)	Si	703	194	40	2750	1563	235	56	4383	<0.001	1246	177
Ca ²⁺ (mg·L ⁻¹)	Ca	10	3.2	0.9	37	24	1.9	10	52	<0.001	19	2.0
Mg ²⁺ (mg·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·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 ($\mu\text{S}\cdot\text{cm}^{-1}$)	COND	80	23	11	271	265	33	100	910	<0.001	197	27

Note: 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. TP, total phosphorus; TDP, total dissolved phosphorus; DIN, dissolved inorganic nitrogen; TDN, total dissolved nitrogen; TN, total nitrogen; DOC, dissolved organic carbon.

Fig. 2. Biplot of 26 lakes (19 upland lakes (14 for 1 year, 5 for 2 years) and 7 wetland lakes (all for 2 years) for an overall total of 38 observations) based on indirect gradient analysis of lake water chemistry. The contribution of individual water chemistry parameters to the two major ordination axes are superimposed. Lakes in wetland-dominated catchments are identified with open squares, lakes in upland catchments with solid circles. COND, conductivity; ALK, alkalinity; DOC, dissolved organic carbon; CHLA, chlorophyll *a*; TP, total phosphorus; TDP, total dissolved phosphorus.



(Dillon et al. 1991). The connection, although weaker than for TP, between watershed variables and lake TN concentrations is strongest in wetland-dominated systems. Denitrification and other in situ processes related to mean depth were the dominant forces controlling nitrogen concentration in lakes in upland-dominated watersheds.

Phytoplankton

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* ($r^2 = 0.70$ and 0.43 , respectively, $P < 0.01$). 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. Total phytoplankton biomass (BIOM) was most closely related to TP concentration in both wetland- and upland-dominated systems, but these relationships were weaker than those for Chl *a* ($r^2 = 0.42$ and 0.52 , respectively). In a survey of 208 temperate upland-dominated lakes, Chl *a* and mean depth were inversely related ($r = -0.60$; Duarte and Kalff 1989). We found a similar relationship within our upland-dominated systems ($r = -0.63$, $P < 0.001$) but not within our wetland-dominated systems ($P > 0.6$), which may be related to higher colour and, consequently, reduced light penetration in the latter systems (Table 3).

Cyanobacteria were the dominant phytoplankton in all study lakes, followed by Peridineeae and Cryptophyceae within wetland- and upland-dominated systems, respectively (Fig. 4a). Within wetland-dominated systems, Chlorophyta and Chrysophyceae were equally represented according to percentage phytoplankton composition, but Chrysophyceae were more prevalent than Chlorophyta in upland-dominated

systems (Fig. 4a). Diatoms were scarce during the July–September study period relative to lakes on the Boreal Shield (Planas et al. 2000). We detected no differences in total phytoplankton biomasses between wetland- and upland-dominated systems, but Chlorophyta and Peridineeae biomasses were higher in wetland-dominated systems than in upland-dominated ones (Fig. 4b) and compared with data collected on other lakes in the region (Mitchell and Prepas 1990). Cryptophyceae were relatively more abundant in upland- than in wetland-dominated systems (Fig. 4a). In contrast, higher Chlorophyta biomasses in wetland- than in upland-dominated systems, despite equivalent TP concentrations, may coincide with greater DIN availability in the former. This is consistent with the observed patterns in DIN and our original hypothesis that N-dependent Chlorophyta would be higher in lakes in wetland-dominated drainages than in upland-dominated ones.

Although total cyanobacterial biomasses were similar, absolute and relative biomasses of Oscillatoriales were greater in upland- than in wetland-dominated systems (Fig. 5). Oscillatoriales are also abundant in other upland-dominated systems in northern Alberta (Prepas and Planas, unpublished data). *Microcystis* spp. was positively linked to NO_3 concentrations in wetland-dominated systems ($r^2 = 0.61$, $P < 0.01$) as were, to a lesser extent, non-nitrogen-fixing Cyanobacteria as a group ($r^2 = 0.29$, $P < 0.05$). Of all the groupings we reviewed, biomass of *Microcystis* spp. was most strongly associated with TP concentrations particularly in wetland-dominated systems ($r^2 = 0.71$, $P < 0.1$).

Relationships between Cryptophyceae biomass (CRYTO) and NH_4 and DOC concentrations in wetland-dominated systems were suggestive of quadratic and linear functions, respectively (Fig. 6). Some Cryptophyceae species are mixotrophic and may prey on bacteria (Tranvik et al. 1989). In wetland-dominated systems, Cryptophyceae may be more dependent on heterotrophy rather than on autotrophy, because higher concentrations of coloured DOC and poorer light than in upland-dominated systems could limit photosynthesis. If bacterivory is the dominant source of energy for Cryptophyceae, the relationship between their biomass and DOC and NH_4 could be indirect, via their prey, the bacteria. Bacteria were not quantified in this study, but their dependence on DOC and competition with phytoplankton for nutrients are well known (e.g., Currie and Kalff 1984).

Cryptophyceae biomass was linearly related to TP and TDP concentrations in upland-dominated systems ($r^2 = 0.53$, $P < 0.01$). Peridineeae biomass was either poorly or negatively associated with euphotic-zone nutrients (NO_3 , TP, dissolved inorganic carbon (DIC), wetland only $P < 0.05$). Many species of Peridineeae can accumulate nutrients below the euphotic zone through diel migration, perhaps as a strategy to reduce interspecific competition (James et al. 1992). Similarly, a negative relationship between Oscillatoriales biomasses and NH_4 concentrations within upland-dominated systems ($r^2 = 0.25$, $P < 0.05$) suggests that non- N_2 -fixing Cyanobacteria like Oscillatoriales are inferior competitors compared with N_2 -fixing taxa.

Colour, DOC, and wetland coverage

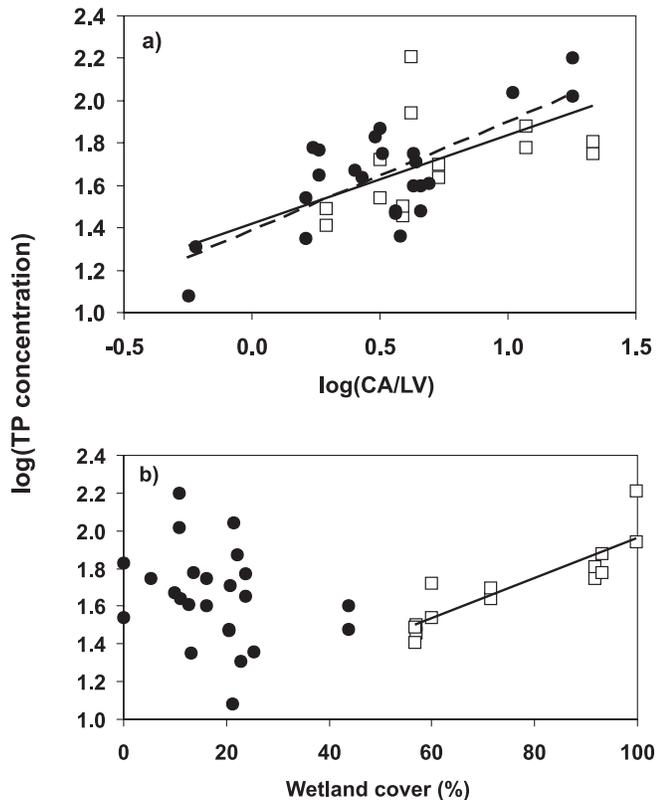
Colour concentrations are dependent on dissolved humic matter and negatively influence underwater light penetration,

Table 4. Drainage basin and lake morphometry summary data for the 26 study lakes.

Parameter	Abbreviation	Wetland-dominated (<i>n</i> = 7)				Upland-dominated (<i>n</i> = 19)				<i>P</i>	Total (<i>n</i> = 26)	
		Mean	SE	Min.	Max.	Mean	SE	Min.	Max.		Mean	SE
Catchment area (km ²)	CA	9.41	2.82	0.75	20.42	12.28	4.78	0.58	88.24	0.61	11.51	3.55
Drainage basin area (km ²)	DBA	8.27	2.64	0.56	18.80	10.88	4.36	0.49	82.40	0.61	10.18	3.24
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	0.67	1.33	0.39
Mean depth (m)	<i>Z</i> _{mean}	1.3	0.3	0.7	2.5	3.8	0.7	0.9	14	0.004	3.1	0.6
Maximum depth (m)	<i>Z</i> _{max}	3.1	0.7	1.8	5.8	8.5	2.0	1.8	38	0.02	7.1	1.6
Lake volume (m ³ × 10 ⁶)	LV	1.80	0.70	0.19	5.72	7.94	4.19	0.27	77.40	0.17	6.29	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	6.48	2.49	1.28	19.66	3.86	0.91	0.44	16.7	0.35	4.56	0.94
Effective DBA/lake volume	eDBA/LV	6.68	1.41	0.58	18.34	2.29	0.51	0.13	7.65	0.01	4.10	0.74
Drainage basin area/lake area	DBA/LA	6.69	1.66	1.86	13.21	9.30	1.19	1.52	21.42	0.23	8.60	0.99
Catchment area/lake volume	CA/LV	7.36	2.59	1.96	21.15	4.27	0.96	0.51	17.84	0.30	5.11	1.00

Note: Data are from this study and from 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.

Fig. 3. Relationships between mean July–September euphotic total phosphorus (TP) concentration and (a) catchment area/lake volume (CA/LV) (solid line, all systems, $r^2 = 0.42$, $P < 0.001$; broken line, upland systems, $r^2 = 0.56$) and (b) percentage wetland cover ($r^2 = 0.78$, $P < 0.001$) in Boreal Plain wetland- and upland-dominated systems. Open squares, wetland-dominated systems ($n = 14$ independent estimates from 7 lakes); solid circles, upland-dominated systems ($n = 24$ independent estimates from 19 lakes).

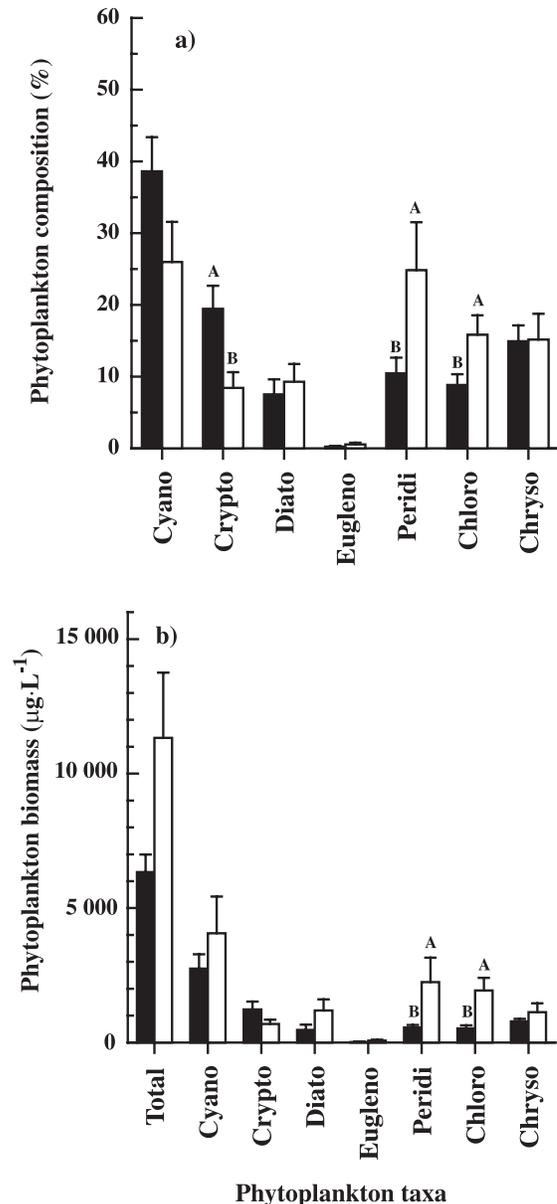


limiting colonization depths for primary producers (Chambers and Prepas 1988). Colour was strongly associated with wetland and bog and less so with fen cover in the combined data set ($r = 0.81$, 0.78 ($P < 0.01$), and 0.44 ($P < 0.05$), respectively). In contrast to relationships with TP, TN, and DOC, eDBA/LV was more strongly linked with colour (COL) than CA/LV and DBA/LV ($r = 0.80$, 0.69 , and 0.64 , respectively); eDBA/LV combined with drainage basin slope (SLOPE) explained 71% of colour variability (eq. 9). Colour also coincided negatively with water residence time ($r = -0.84$), which is consistent with in-lake degradation of humic matter (Rasmussen et al. 1989).

$$(9) \quad \text{ALL: } \log(\text{COL}) = 1.84 + 0.47\log(\text{eDBA/LV})^{**} - 0.06\text{SLOPE}^{**}, \quad r^2 = 0.71$$

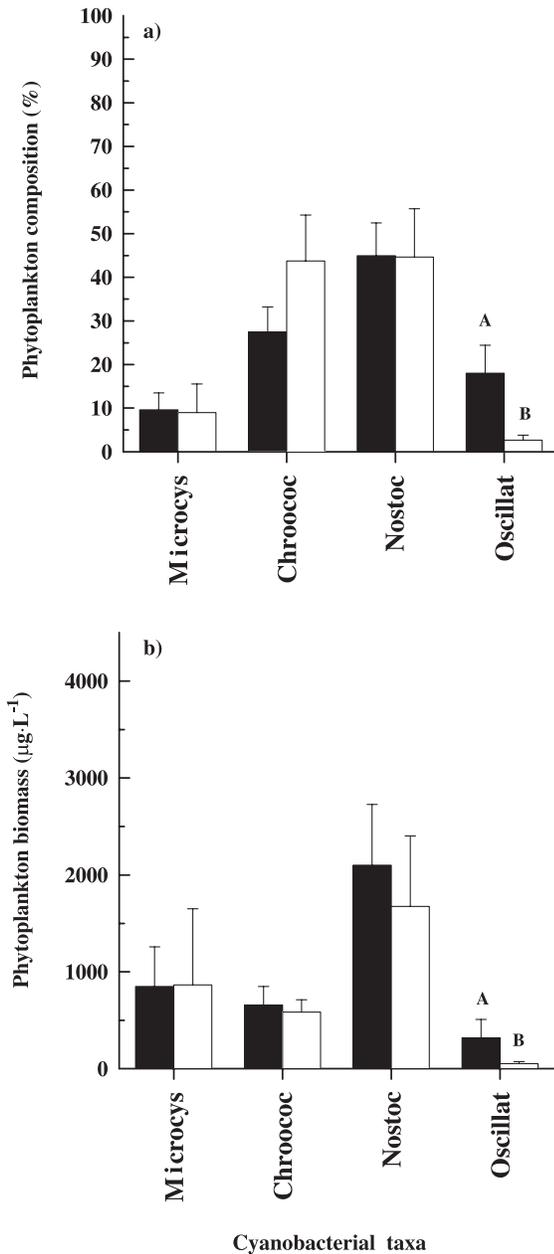
The drainage basin slope in eq. 9 could represent the transition from organic peatlands towards mineral soils, which export less humic matter, or distinct drainage patterns between upland- and wetland-dominated watersheds. Although catchment slopes are low in our study ($\leq 11\%$), they explained one-quarter of colour variability as a single predictor. Based on a study focused on the Precambrian Shield in Labrador, Rasmussen et al. (1989) interpreted the absence of a rela-

Fig. 4. Mean July–September euphotic biomasses of dominant phytoplankton taxa within the 22 Boreal Plain wetland- and upland-dominated systems surveyed during 1996 and 1997 compared as (a) relative and (b) absolute values. Summer means for 1996 and 1997 were averaged. Different letters over bars signify significant ($P < 0.05$) differences within a taxon between wetland-dominated (open bars) and upland-dominated (solid bars) systems. Cyano, Cyanobacteria; Crypto, Cryptophyceae; Diato, Diatoms; Eugleno, Euglenophyceae; Peridi, Peridinea; Chloro, Chlorophyta; Chryso, Chrysophyceae.



tionship between colour and wetland cover as due to the overriding influence of slope. In the Labrador study and peatland-dominated subarctic plateau (McEachern et al. 2000), DOC and colour were highly correlated ($r^2 = 0.86$ and 0.89 , respectively), whereas in our study, the relationship was much weaker ($r^2 = 0.48$). Much of the DOC in Boreal Plain lakes may be produced in situ (Curtis and Prepas 1993). As expected, within the combined data set, colour and Chl *a* concentration accounted for most of the variabil-

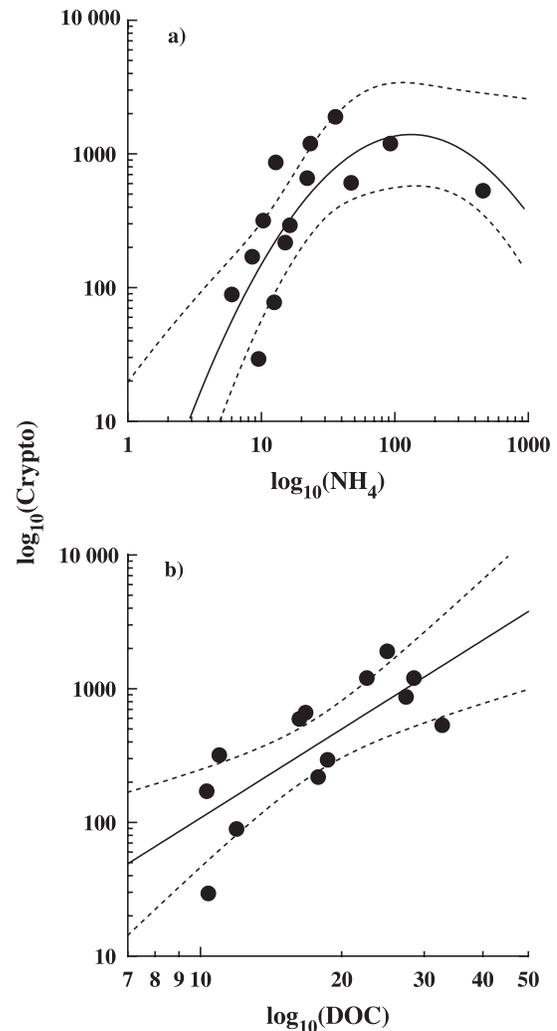
Fig. 5. Summer (July–September) cyanobacterial biomasses within the 22 Boreal Plain wetland- and upland-dominated systems surveyed during 1996 and 1997 compared as (a) relative and (b) absolute values. Summer means for 1996 and 1997 were averaged. For each graph, total cyanobacterial biomass is depicted by major taxa (*Microcys*, *Microcystis* spp.; *Chroococ*, *Chroococcales*; *Nostoc*, *Nostocales*; *Oscillat*, *Oscillatoriales*). Different letters over bars signify significant ($P < 0.05$) differences within a taxon between wetland-dominated (open bars) and upland-dominated (solid bars) systems.



ity in light extinction ($r^2 = 0.80$, $P < 0.01$). As predicted, wetland (primarily bog) coverage in the drainage, along with the variable eDBA/LV, were strongly associated with colour concentrations in all our lake water.

Studies based in Labrador, Finland, and northern Alberta with relatively high wetland coverage (up to 25%, 58%, and 85%, respectively) noted strong relationships between wet-

Fig. 6. Relationships between mean summer (July–September) Cryptophyceae (Crypto) biomass and (a) ammonia (NH_4^+) and (b) dissolved organic carbon (DOC) concentrations within the seven Boreal Plain wetland-dominated systems surveyed during 1996 and 1997. Broken lines represent 95% confidence intervals. WETLAND: $\log(\text{CRYPTO}) = -1.01 + 4.18\log(\text{NH}_4)^{**} - 1.05(\log(\text{NH}_4))^{2**}$, $r^2 = 0.59$.



land coverage and in-lake organic carbon concentrations (Engstrom 1987; Kortelainen 1993; Halsey et al. 1997). Although DBA/LA explained up to 70% of DOC variability in the peatland-dominated systems of the Caribou Mountains (McEachern et al. 2000), DOC concentrations in our combined data set were positively associated with percentage wetland cover and CA/LV, but relationships were relatively weak given the strong autochthonous input ($r^2 = 0.32$ and 0.28 , respectively). In upland-dominated systems, CA/LV and mean depth explained 21% and 38% of DOC variability, respectively. In contrast, in the wetland-dominated subset, percentage wetland cover and eDBA explained considerably more DOC variability ($r^2 = 0.74$ and 0.64 , respectively), whereas CA/LV explained 27% of DOC variability.

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). DOC concentration and watershed slope were weakly related ($r^2 = 0.16$, $P < 0.02$), whereas this relationship was much stronger ($r^2 = 0.40$) in lakes on the Boreal Shield (D'Arcy and Carignan 1997). In sharp contrast to colour, the connection between vegetative cover and DOC concentrations in lakewater on the Boreal Plain was stronger in wetland-dominated drainages than in upland-dominated ones. In situ generation of DOC was likely the prevailing force in upland-dominated drainages.

Effective drainage basin area as a predictor

Mean water residence time (τ) was more than 20-fold longer for upland-dominated lakes than for wetland-dominated ones (11 and 0.5 years, respectively; Table 4), attributable to the deeper lake basins and smaller eDBAs within the upland-dominated systems. Positive associations ($r = 0.65$) between lakewater residence time and alkalinity, conductivity, HCO_3^- , Mg^{2+} , and K^+ suggest the influence of hydrologic setting, specifically lake flushing rates for some but not all dominant ions. Differences between estimated isotopically defined eDBA and topographically defined DBA were less pronounced within wetland-dominated catchments compared with upland-dominated catchments. On average, wetland- and upland-dominated eDBAs were about three-quarters and one-quarter of the DBA, respectively (Table 4), the former reflecting a relatively higher wetted fraction or contributing area within the drainage basin and the latter reflecting lower overall runoff contributions from upland areas consistent with loss to groundwater. 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 surface runoff in our study region.

eDBA is positively related to colour and percentage bog cover ($r^2 = 0.40$ and 0.37 , respectively, $P < 0.001$) and negatively related to drainage basin slope and percentage upland cover ($r^2 = 0.30$ and 0.47 , respectively, $P < 0.001$). In wetland-dominated lakes, eDBA is a stronger correlate with DOC and TN than with DBA. Within the whole data set, eDBA was more strongly associated with lakewater colour than DBA, suggesting a connection with colour-producing wetlands.

In conclusion, this study found that bogs release more phosphorus than other vegetation categories, and rich fens appear to sequester more phosphorus and nitrogen than other vegetation categories in undisturbed lakes on the Boreal Plain. In upland-dominated lakes, the relative size of the watershed (DBA/LV) was the strongest predictive factor for TP concentration. In contrast, lakewater colour concentration was strongly linked to the wetland connectivity parameter eDBA/LV. In situ nitrogen concentrations were positively linked to percentage wetland cover. Phytoplankton community composition in these lakes was consistent with greater availability of inorganic nitrogen in the lakes with wetland-dominated catchments.

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