PROJECT REPORT
2001-19
FINAL PROJECT REPORT

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Forest fire-induced impacts on lake water chemistry, basin hydrology and pelagic algae in Boreal Sub-arctic lakes of northern Alberta

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ISBN 1-55261-129-9

Forest fire-induced impacts on lake water chemistry, basin hydrology and pelagic algae in Boreal Sub-arctic lakes of northern Alberta.

SFM Network Project: Impacts of natural disturbance and forest harvesting on water quality of lakes and streams of the boreal sub-arctic, highlands and wetland mixed wood ecoregions of northern Alberta

by

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June 2001

ABSTRACT

Biogeochemistry of 10 headwater lakes in burnt peatland-conifer catchments and 14 in unburnt catchments was evaluated throughout a summer, two years following forest fire in a boreal sub-arctic region of northern Alberta. Cation exchange within burnt catchments resulted in proton flux and a 9% reduction in mean pH. Lakes in burnt catchments contained > 2-fold higher ($P << 0.01$) mean concentrations of total, total dissolved and, soluble reactive phosphorus, 1.5-fold higher dissolved organic carbon (P << 0.01), and more than 1.2-fold higher ($P < 0.05$) concentrations of total and total dissolved nitrogen, nitrate/nitrite and ammonium compared to reference lakes. Total phosphorus concentration (TP) explained 86% of the variance in reference lake chlorophyll concentration (CHL) but was not related to CHL in burnt lakes. Analysis of CHL-TP residuals suggested algae in burn-impacted lakes were light-limited. With the addition of five lakes burnt between 1961 and 1985, time-since-disturbance and percent disturbance combined, explained 74% of variance in TP among burnt lakes. Fire caused increased flux of materials to the study lakes with slow recovery over decades.

To quantify how fire increased the flux of materials to the study lakes we determined three components describing relationships between catchment biogeochemistry and surface water chemistry. The three components were topographically defined drainage basin areas (DBA), contributing areas (CA) that generate runoff and effective areas (EA) that control the flux of solutes from the CA. Calculation of CA and EA require hydrologic data that are often difficult to assemble for remote areas. We applied a model using isotope composition of lake waters to estimate CA and catchment water yield. EA was subsequently determined from mass-balances for sodium. CA averaged 25 % of DBA for all 24 lakes, consistent with lacustrine soils on till. Catchment water yields determined from the isotope model (110 mm) were comparable to that determined from stream discharge measurements (114 mm) and published values for the region (75 to 100 mm). Water yield was negatively correlated with the ratio of DBA to lake volume (V) with steeper slope for lakes in burnt than unburnt catchments ($P = 0.04$). Burnt catchments produced as much as 3-fold more water than unburnt catchments when the DBA/V was < 10. The fire impact on water yield, when DBA/V < 10, was consistent with patterns in CA. Contributing area was negatively correlated with DBA/V ($r = -0.68$) and comprised a larger proportion of the DBA as DBA/V declined among lakes. EA averaged 2% of DBA when EA was calculated from flux rates consistent with published values for the region. The transport of solutes from the CA was either limited by poor drainage through peatlands with discontinuous permafrost or by exceptionally low flux rates. We discuss potential errors and failures in assumptions of isotope techniques for determining hydrologic parameters.

To determine some of the potential impacts of forest fire on lake biota, we tested nitrogen (N), phosphorus (P) and light limitation of pelagic algae with *in situ* microcosms in three Caribou Mountain lakes. To determine if low total nitrogen to total phosphorus ratios (TN:TP) in lake waters following fire influenced algal assemblages, algal species were identified from 10 lakes in unburnt (mean [TP] = 33$\mu g \bullet L^{-1}$, TN:TP = 20) and 10 burnt catchments (mean [TP] = 85 $\mu g \bullet L^{-1}$, TN:TP = 11). Phosphorus limitation of chlorophyll was apparent at low TP concentration

(14 μg•L^{-1}) and a high N to P ratio (TN:TP = 38, $P << 0.01$). Concurrent limitation of chlorophyll by both N and P were found at TP concentration (58 μg•L^{-1}) and TN:TP ratio (20, $P << 0.01$) typical for Caribou Mountain lakes in undisturbed basins. Nitrogen limitation of chlorophyll was observed at the elevated TP concentration (78 μg•L^{-1}) and reduced TN:TP ratio (8, $P << 0.01$) typical for a survey of 10 lakes in burnt catchments in the region. Light limitation was observed in the two lakes containing over 200 mg•L^{-1} [Pt] color. Algal species richness was 36% lower ($P << 0.01$) in burnt compared to reference lakes. Algal assemblages were dominated by Cyanophytes in most lakes. The proportion of Nostocales, capable of N-fixation, was not distinguishably different between burnt and unburnt lakes ($P > 0.5$).

ACKNOWLEDGEMENTS

Funding for this research was provided by The Sustainable Forest Management Network, Little Red River/ Tallcree First Nations High Level Lumber Division - TOLKO, and Daishowa-Marubeni International Ltd. We thank Chief J. Sewepagaham, C. Nanooch, and the Little Red River community for supporting this research on their traditional lands. We greatly appreciate contributions of stream gauging equipment and isotope analyses from T. Prowse, vegetation classification by L. Halsey and advice from D. Vitt. Administrative support was provided by B. MacLock, J. Webb, V. Neal and G. Scrimgeour. McEachern was supported by an NSERC-Postgraduate Scholarship. Comments from R. Carignan and two anonymous reviewers were greatly appreciated.

INTRODUCTION

Interest in fire as a natural disturbance impacting catchment biogeochemistry and surface water quality is rekindling as a relative benchmark for anthropogenic impacts. However, studies on the effects of fire on water quality suggest impacts are regionally or fire specific due to organic soil characteristics, severity of fire and hydrologic regime. The magnitude of ion flux from catchments is thought to depend on fire severity because of modifications to cation exchange and biochemical reactions in the organic soil layer (Grier 1975; Stark 1977; Schindler et al. 1980). In experimental fires where a third or less of the organic soil layer was burnt, no detectable changes in soil water and stream water carbon, nitrogen, phosphorus, their inorganic fractions or major cations were reported (e.g. Richter et al. 1982). Following more severe fires, increases in nutrient flux were large but usually short lived (< 5 yr) and changes in surface water concentrations did not exceed inter-annual variation (McColl and Grigal 1975; Bayley et al. 1992; Minshall et al. 1997). These studies have occurred primarily in regions with thin organic soils, whereas studies in burnt permafrost-peatland dominated systems such as those in northern Alberta are rare.

Water chemistry has been studied in burnt catchments with small proportions of peatlands. A comparison of burnt and unburnt portions of a *Sphagnum fallax / Picea mariana* mire demonstrated no detectable long-term (8 yr) impact of fire on water chemistry (Vitt and Bayley 1984). In a review of circumpolar studies MacLean et al. (1983) reported fire rarely burnt the entire organic layer and changes in soil water chemistry did not result in nutrient flux from peat-derived soils. However, wetland catchments had elevated phosphorus flux after severe fires (Bayley et al. 1992). The previous studies give little indication of potential impacts from forest fire in catchments with deep peat soils (0.5 m or more), underlain by glacial till and containing permafrost or seasonal frost lasting a majority of the summer which are common in northern Alberta.

A unique opportunity to examine extensive damage to peatlands was provided when 129 000 ha of the Caribou Mountains, a Sub-arctic plateau, were razed by fire in 1995. In this single event, one-third of the Plateau was burnt, equaling 50% of the mean annual area burnt in the province of Alberta between 1994 and 1998 (Alberta Environment unpubl. data). Impacts on lake water chemistry were expected because of high fire severity, large proportion of catchments burnt (between 60 and 100%) and hydrology dominated by flow through peatlands. We developed a study in the Caribou Mountains with partners from the Sustainable Forest Management Network (SFM), High Level Lumber Division (HLLD), Daishowa-Marubeni International (DMI), and the Little Red River Tallcree First Nation (LRRTC) to address questions on the effects of watershed disturbance on lake ecosystems in Alberta with the following specific objectives:

a) Determine patterns in nutrient concentrations and cycling among lakes in the Caribou Mountains and how these patterns are related to physical characteristics of the watersheds and lakes.

b) Determine the 1995 Caribou Mountains forest fire impacts on lake water chemistry through comparison of lakes in burnt and reference catchments.
c) Build simple predictive models that relate percent of watershed disturbance and time since disturbance to patterns in lake water chemistry.
d) Use these data, in cooperation with western and eastern aquatic SFM-NCE studies, to better understand nutrient-biota patterns in lakes across the entire Boreal forest and under a range of disturbance regimes.

We hypothesized that the 1995 fire in the Caribou Mountains would reduce base cation exchange capacity of peat and increase mineralization of nutrients to produce: a) increased base cation and nutrient concentrations in surface waters, b) corresponding increases in phytoplankton biomass, and c) increased suspended organic and inorganic seston. We also examined long-term (decades) impacts from fire and relationships between catchment characteristics and lake water chemistry. The goals of this project link LRRTC First Nations concerns for human and ecosystem health on traditional lands with management issues, such as allowable harvest, of concern to HLLD.

We began our study with a survey detailing lake water chemistry, algal biomass as represented by chlorophyll *a* (CHL), and physical characteristics of the surveyed lakes. With the survey data, we addressed patterns in lake chemistry and algal biomass resulting from landscape patterns, particularly between burnt and reference catchments. We followed our investigation of lake water chemistry with an assessment of the underling differences in hydrology between burnt and reference catchments. A method for describing hydrology from evaporative enrichment of isotopes in lake water was developed for the Caribou Mountains because other forms of hydrologic data did not exist for this remote region. In section two of this report we present both the isotope mass balance method and the basin water yields that account for differnces in water chemistry between burnt and reference lakes. Finally, we addressed nitrogen, phosphorus and light limitation of algal biomass to explain why increased phosphorus concentrations in burnt lakes did not result in increased CHL. Section three describes results from *in situ* algal bioassay experiments where nutrient and light limitation of algal biomass was tested in one burnt and two reference lakes. Section 3 also describes the algal species composition of mid-summer samples from the surveyed lakes with an emphasis on dominance by species adapted to low nitrogen or low light conditions. Section one has been published (McEachern et al. 2000). Sections two and three are currently in the review process for peer-reviewed journal publication.

SITE DESCRIPTION

The Caribou Mountains (59°N 115°W) are erosional remnants forming a large, relatively flat plateau 500 m above the Peace River valley. Peatlands cover 56% of the Caribou Mountains and are predominately underlain by poorly-drained cryosolic and brunisolic soils (Strong and Leggat 1992). Subsurface geology is shale, feldspathic sandstone, and siltstone of deltaic and marine origin. Open forest of black spruce (*Picea marianna*) and an understory of mixed *Sphagnum* spp., feathermosses, brown mosses and lichens dominate vegetation. Prior to the 1995 fire, most spruce stands in burnt and reference catchments originated between 1860 and 1910 (Alberta Vegetation Inventory 1:20000 map series 1983) indicating there had not been a stand-replacing fire in 90 years. Aspen (*Populus tremuloides*) is concentrated in upland areas. Mean percent upland per catchment is less than 30%, but is 83% in one burnt catchment (Table 1). Permafrost is estimated between 0.5 and 0.75 m beneath the organic soil surface within continental bogs (Strong and Leggat 1992) which cover an average of 62% of the study catchments. Collapse scars signify degraded permafrost (Vitt et al. 1994) and were present in bogs averaging an additional 19% of the study catchments prior to the fire. In the fire, understory herbaceous, sedge, and lichen cover were incinerated but damage to moss and peat varied. Impact from burning was mostly limited to 0 to 20 cm of peat. In some locations burning continued within deeper peat until the following summer. Late August testing in five catchments revealed no permafrost in the peat layer (down to mineral soil) of burnt areas, whereas it was present in five unburnt continental bogs. Mean May through August temperatures were 10.2 °C (automated climate station), typically with less than 800 growing degree days and between 400 and 450 mm of annual precipitation (Strong and Leggat 1992).

Ten headwater lakes were selected with catchments, where between 50 and 100% of the tree cover was killed by fire (mean 83%, median 90%, SD 15%). These, plus 14 headwater lakes in unburnt reference catchments and five headwater lakes in catchments burnt between 1961 and 1985, were sampled monthly after ice-out from late June to late August/early September (Fig. 1). The lakes selected from previously burnt catchments were used in time-since-disturbance and % disturbance analyses only. Among all combined lakes, differences in surface elevation were less than 90 m across the 120 Km distance of this study on the Plateau. Lake surface areas ranged from 2.6 to 1173 ha and mean depths from 0.3 to 11.6 m. All lakes were either polymictic or if stratification was observed (late July for deeper lakes) mixed conditions were restored by the next sampling event (Aug./Sept.) In all lakes, dissolved oxygen concentrations exceeded 5 $mg \bullet L^{-1}$, 0.5 m above the bottom through the summer. Three stream, four fen and six bog sites were also sampled during the summer of 1997. Two streams, MS1 and MS2, drained adjacent unburnt watersheds of 40 and 6 km^2, respectively. MS3, drained a 1 km^2 watershed that was entirely burnt. Thus the watershed ratios were 40:6:1 for the three streams. MS2, was gauged for discharge calculations. Samples were collected from MS1, MS2 and MS3 on the same four sample dates which included bank full and baseflow conditions. An automated sampler collected additional samples from MS2 through the summer. Our limited data show the ratio of discharge from MS3 relative to the reference streams was 20:1.5: 1. Based on this limited data set the burnt catchment, MS3, released between 2- and 4-fold more catchment-weighted discharge than the two unburnt catchments.

Watersheds were delineated from 1994 series 1:20000 aerial photographs. Ground cover in each catchment was classified as upland, peatland, or open water. Peatlands were subdivided into veneer bog, peat plateau, poor fen and rich fen based on vegetation and slope characteristics identified from the aerial photographs (Halsey et al. 1997). Percentage of fire disturbance per drainage basin was estimated from 1996 aerial photographs. The catchment slope index was calculated by computing elevation gain divided by linear distance to lake shore (CS1: D'Arcy and Carignan 1997). Bathymetric maps were constructed from depth measurements along 5 to 15 transects on each lake and became the basis for lake volume (V).

Lake water collection, preperation and analyses are described in McEachern et al. (2000). Precipitation (May-September) was collected from a rain gauge twice daily in 1998 and 1999 at a fire tower located at the southern edge of the Caribou Mountains. Snow depths were recorded at one site from 1996 to 1999. To convert snow depth to water equivalents, the density of four hundred snow samples collected along 20 transects during late March of 1999 and 2000 were applied to the 1997 snow depth data. Groundwater was collected in 1998 and 1999 from wells installed between 1.3 and 2 m into mineral soil at hill slope sites below the Caribou Mountain lakes.

Lake water residence times (τ; yr) were calculated for the 24 lakes with a steady-state isotope mass-balance model. The isotope mass-balance was 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). The isotope mass-balance reflects the major components of a water balance such that total inflow (I), total outflow (Q) and total lake evaporation (E), in $m^3 \bullet yr^{-1}$ were multiplied by the respective isotope composition ($\delta^{18}O$ and $\delta^{2}H$, ‰ Standard Mean Ocean Water or SMOW) of inflow, outflow and evaporated water:

(2) $I\ \delta_I = Q\ \delta_Q + E\ \delta_{E,}$

The isotope composition of outflow was assumed equivalent to the composition of lake water (δ_L), the composition of inflows equivalent to precipitation (δ_P), and the composition of evaporated moisture (δ_E) was replaced with a model for free-surface evaporation (Gibson et al. 1993). When rearranged (2) becomes:

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

where free-surface evaporation components, $m = h\cdot(1 - h)^{-1}$, and h is ambient atmospheric humidity. Limiting isotopic enrichment (δ^*) was equivalent to $\delta_h + \varepsilon\cdot h^{-1}$, where δ_h was the isotopic composition of atmospheric humidity, and ε 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 samples. The isotope composition of precipitation (δ_P) was calculated by three methods. Long term theoretical (δ_P) was determined as the intersection of the Mean Meteoric Water Line (MML) and the Local Evaporation Line (LEL) where the latter was determined by regression through mean δ_L for the study lakes. Observed δ_P was determined from means for summer precipitation and snow samples, volume weighted for relative contributions to total precipitation. Modeled δ_P was determined by adjusting values from the Global Network for Isotopes in Precipitation database (1998, International Atomic Energy Agency/ World Meteorological Organization, Vienna, Austria) for local climate conditions. Other parameters required to calculate E/I (δ_h, h and mean annual air temperature) were interpolated for each lake from Environment Canada climate station data. Specific assumptions on the boundary layer regime and atmospheric parameters used in the model are previously discussed (Gibson and Prowse 1998). Once the relative fraction of evaporation to inflow was calculated, lake water residence time (τ) was:

$$(2b) \qquad \tau = \frac{\frac{E}{I} * Z_{mean}}{E_L}$$

Z_{mean} was mean lake depth (m), and E_L was long-term mean annual lake evaporation rate (mm·yr^{-1}) for the region (Environment Canada Climate Records).

Catchment runoff was calculated from lake retention time, lake volume and DBA. Contributing area (CA, ha) was subsequently calculated as:

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

R and P are mean annual drainage basin runoff and precipitation (both mm·yr^{-1}), respectively. Catchment CA can change in response to precipitation which is consistent with its broader definition (Beven and Kirkby 1979) but a departure from the application by Soranno et al. (1996) where CA was fixed by catchment topography at a potential maximum for surface runoff.

In areas like the Boreal Wetlands of Alberta, flat topography, soils with high clay content and deep organic layers contribute to slow water movement and attenuated transport of solutes. The equation for solute loading proposed by Soranno et al. (1996) can be rearranged to reflect contributions from an unknown area (EA, m^2) with known total load. Total load was calculated as the product of lake discharge (Q_o, m^3•yr^{-1}) and observed lake concentration (mg•m^{-3}) which was divided by flux rate (F, mg•m^{-2}•yr^{-1}) and transmissivity (T, dimensionless) to obtain an aerial source for the solute:

$$(4) \qquad EA = \frac{Q_o[Na^+]}{\sum_{i=1}^{n} \frac{A_i * F_i * T_i}{CA}}$$

where A_i is the total area of a distinctive soil in the CA with flux rate F_i and transmissivity T_i. If EA is calculated from a conservative element such as Na^+ then T approaches 1, the $\sum A_i$ for n distinct soils equals CA and variation in EA relative to CA must be related to differences in F_i. Thus among catchment variation in Na^+ derived EA represents differences in soils through which water flows. The equation assumes Na^+ is a conservative element at equilibrium in the lake and its concentration is directly dependent on loading from the catchment.

In our study, the parameters A_i, and F_i, were not known, T_i was assumed to be 1. An approximation for the combined terms of 4.34 mg•m^{-2}•yr^{-1} (0.189 meq•m^{-2}•yr^{-1}) [Na^+] was chosen based on a mean of reported flux rates for similar soils in an arctic basin (Buttle and Fraser 1992) and from north-central Alberta (Shaw and Prepas 1990). The arbitrary selection of flux makes quantitative values of EA rough estimates only, however, the issue for this study was to describe variation in an unknown EA supplying solutes to each lake. Variation in EA was properly captured if the assumption that Na^+ loading reflected variation in A_i, and F_i, among basins. Na^+ flux rates were not adjusted for potential impacts of fire. Changes in Na^+ flux rates measured from podsolic soils after forest fire in Montana and burning of slash in British Columbia were reported as insignificant (Stark 1977, Feller and Kimmins 1984), however, these studies recognized accelerated Na^+ loss from some sites may have been obscured by high variability. The concentrations of non-conservative substances such as phosphorus, nitrogen and carbon will additionally be related to an unknown T_i and a term representing generation or removal in the lake. Transmission can vary widely but may be determined predominately by differences in weather and can approach one even for particulate bound phosphorus (Soranno et al. 1996).

To test nutrient and light limitation of phytoplankton we selected three lakes spanning a range of nutrient and light conditions observed in lakes from the Caribou Mountains (McEachern et al. 2000) and a broader dataset for wetland dominated catchments in northern Alberta (Prepas et al. In Press). The three lakes were named Lowratio, Midratio, and Highratio for this study. Lowratio lake (C24 from McEachern et al. 2000) water had the lowest TN:TP ratio (mean summer ratio = 8) and the highest TP concentration (70 $\mu g \cdot L^{-1}$). Midratio lake water had an intermediate TN:TP ratio of 20 and intermediate TP concentration (43 $\mu g \cdot L^{-1}$), whereas Highratio lake water had the highest TN:TP ratio of 38 and lowest TP concentration (15 $\mu g \cdot L^{-1}$).

Nutrient stimulation experiments (NSE) were set in Lowratio and Highratio lakes concurrently during the summer of 1997 and in Midratio lake during the summer of 1998. Each NSE consisted of 10-L polyethylene containers of lake water augmented with N, P, or N+P, plus an untreated control. Triplicate treatment containers were suspended at half the Secchi disk depth for 5 d (Knowlton & Jones 1996). NSEs from Midratio and Lowratio lakes received nutrient doses of 1000 $\mu g \cdot L^{-1}$ [N] and 100 $\mu g \cdot L^{-1}$ [P] while NSEs in oligotrophic Highratio lake received halved doses. In Lowratio lake, half the Secchi depth was 10% of incident light, a 5-fold improvement compared to the epilimnion which averaged 2% of incident light. Likewise, in Midratio and Highratio lakes, half the Secchi depth was a 2-fold and a 5-fold improvement compared to their respective epilimnia. Due to accessibility costs, replication through time was not feasible, therefore results represent a "snapshot" as a result of chemical conditions when the NSEs were initiated.

NSE response was determined by dividing final CHL by initial CHL and then comparing responses among treatments with replicate means (ANOVA, Bonferoni-Dunn comparison). Limitation by either N or P was inferred from elevated CHL in N or P treated containers compared to control containers. Concurrent limitation by both N and P was inferred from elevated CHL in N+P treated containers relative to controls and those treated by either N or P alone. Light limitation was inferred from increased CHL in control containers relative to changes occurring in lake CHL over the incubation period.

Algal species were identified from water samples collected during our 1997 survey of Caribou Mountain lakes (McEachern et al. 2000). The samples were stored in amber bottles and preserved with Lugol's solution at the time of collection. We selected samples collected between July 19 and 25 from those collected throughout the summer of 1997 to match dates when the NSEs were run in Lowratio and Highratio lakes. We selected one sample from each of the 10 lakes in burnt catchments and randomly chose samples from 10 lakes in reference catchments from the set of 14 lakes. Algae were identified, measured and counted with an inverted inferential microscope. Wet weight biomasses were determined from average species dimensions and assuming a density of $1 g/cm^3$ (Planas et al. 2000).

Data were tested for deviation from a normal distribution using Kolmogorov-Smirnov at $P \leq 0.05$. Data were either normally distributed, were $\log_{10}$-transformed to meet assumptions for normality and analyzed by *t*-test, Pearson's correlation and univariate least-squares regression or were analyzed by nonparametric Mann-Whitney tests. Probability values and correlation coefficients are reported for these tests. Standard error values are reported as ± values in parentheses after mean values. Intercept (α) and slope (β) values are reported from regression analyses. All analyses used Statistica 4.1 (© StatSoft, 1994) and StatView 4.5 (© Abacus 1995) for Macintosh.

RESULTS AND DISCUSSION

Section 1: Forest fire-induced impacts on phosphorus, nitrogen and chlorophyll *a* concentrations in Boreal Sub-arctic lakes of northern Alberta

Several physical characteristics of lakes and their catchments differed between burnt and reference systems (Table 1). Reference lakes tended towards larger surface areas (Mann-Whitney $P = 0.02$), lake volumes (Mann-Whitney $P = 0.05$) and percent open water cover per catchment (Mann-Whitney $P = 0.01$). Percent open water averaged 5 and 1 % of reference and burnt catchments, respectively. The small proportion of open water and its concentration in collapse scars, areas of degraded permafrost, makes it unlikely that it contributed to chemical differences in the lakes. Drainage ratios ($Wo \bullet Ao^{-1}$) and surface area to volume ratios, considered more important in determining land-water linkage than Wo or Ao alone, were not different between burn-impacted and reference lakes ($P = 0.6$, 0.3 respectively). Slope was also not different between burn-impacted and reference catchments ($P = 0.3$). Discriminant function analysis, containing drainage ratio, lake area : volume ratio, catchment slope and percent upland contained one root and was not significant (Wilks $\lambda = 0.75$, Canonical $r = 0.5$, $P = 0.3$). Likewise, substituting Ao, Wo and V for the Wo/V and Wo/Ao ratios did not produce a significant discriminant function ($P = 0.2$). Therefore, it is unlikely that chemical differences observed between reference and burn-impacted lakes resulted from physical characteristics alone.

Total base cation concentrations (Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}), of Caribou Mountain lake water (median 0.52 $meq \bullet L^{-1}$) were all below the world average for fresh water (2.33 $meq \bullet L^{-1}$). There were no detectable differences in mean total base cation concentrations between burnt (0.61 $meq \bullet L^{-1}$) and reference (0.72 $meq \bullet L^{-1}$) lakes ($P = 0.53$). As a percentage of total cations, Ca^{2+} was lower and K^{+} was higher in burnt compared to reference lakes ($P < 0.05$).

Fire affected lake acidity and ion balances possibly through increases in organic anions in burnt lakes. Lake water in burnt catchments was moderately acidic relative to reference lake water (mean pH = 6.9 and 7.6 respectively, $P = 0.04$). Burnt lakes demonstrated low total alkalinity compared to reference lakes, however, differences in means were not detectable (16.7 and 30.3 $mg \bullet L^{-1}$ $CaCO_3$, $P =$

0.07). Sulfate concentrations were elevated in burnt lakes (Mann-Whitney $P = 0.01$) compared to reference lakes with median concentrations of 2.4 and 1.5 mg•L^{-1}, respectively. Fire did not affect chloride concentrations, which averaged 0.15 and 0.13 mg•L^{-1}, for burnt and reference lake water, respectively ($P = 0.3$). Mean total anions (SO_4^{2-} , Cl^- , HCO_3^-, NO_3^-) balanced mean total cations in reference lake water (mean = 0.723 meq•L^{-1}, $P = 1.0$). All lakes in burnt catchments had a deficit in total anions (0.46 meq•L^{-1}, $P << 0.01$). The average deficit of 25% below mean total base cations, suggested a large pool of organic acids in burnt lakes. Most *Sphagnum*-derived acids contain –COOH groups which act as anions in solution while contributing protons (Clymo 1984). Anion deficits were linearly correlated with DOC in burnt ($r^2 = 0.84$, $P << 0.01$, $n = 10$) and less so in reference lakes ($r^2 = 0.26$, $P = 0.06$, $n = 14$). Fire apparently increased organic anion concentrations along a relationship with DOC that also existed in reference lakes.

Lake water in burnt catchments had elevated phosphorus and nitrogen concentrations. In reference lakes, mean TP, DP and SRP concentrations were 33, 14 and 4 µg•L^{-1}, respectively (Fig. 2). Lake water in burnt catchments had 2.6, 3.2 and 6.8-fold higher TP, DP and SRP concentrations, respectively than reference lakes ($P << 0.01$). In reference lakes, mean TN, DN, NO_3^--N, and NH_4^+-N were 655, 488, 3 and 15 µg•L^{-1}, respectively (Fig. 3). Burn-impacted lake water contained 1.2-fold higher DN ($P = 0.02$), 3-fold higher NO_3^--N ($P = 0.04$) and 1.4-fold higher NH_4^+-N (Mann-Whitney $P = 0.03$) concentrations. Mean TP and DP in the two reference streams (MS1 and MS2) were 48 and 28 µg•L^{-1} while the burn-impacted stream (MS3) contained 5.4-fold higher TP and half the DP. Mean TN and DN concentrations for water in MS1 and MS2 were 710 and 650 µg•L^{-1}, respectively, while MS3 contained 2.2-fold higher TN and 1.2-fold higher DN concentrations. Increased export of phosphorus and nitrogen from burnt relative to reference watersheds was likely given the 2- to 4-fold higher catchment weighted discharge from MS3.

Caribou Mountain water had high concentrations of DOC, particularly in burnt systems. Lake mean DOC concentration in burn-impacted lake water (25 mg•L^{-1}) was 1.6-fold higher ($P << 0.01$) than in reference lakes (16 mg•L^{-1}). Further, in reference streams, MS1 and MS2, DOC concentrations averaged 33 and 37 mg•L^{-1}, respectively. In MS3, which drains a burnt area, DOC averaged 28 mg•L^{-1}. The three sampled fens contained almost identical DOC (45, 45, 48 mg•L^{-1}) concentrations despite receiving drainage from burnt and unburnt areas. MS3 exported 3 and 2 times more DOC per unit catchment area than MS2 and MS1, respectively, given 2- to 4-fold higher weighted discharge from MS3.

Caribou Mountain water was highly coloured, especially within burnt catchments. Reference lake water mean colour was 151 and ranged from 26 to 388 mg•L^{-1} Pt, comparable to lake water in the boreal mixedwood ecoregion to the south, where colour ranged from 8 to 358 mg•L^{-1} Pt (Prepas In Press). Mean colour in burn-impacted lake waters (342 mg•L^{-1} Pt) was 2.3-fold higher ($P << 0.01$) than in reference lakes. Colour was related to DOC in all lake waters (Table 3). Variance in light penetration was closely associated with colour of lake water; The natural logarithm of Secchi transparencies were negatively related to colour while light extinction coefficients were positively related to colour (Table 3). Mean Secchi transparencies in burn-impacted lakes (0.73 m) were 54% of those in reference lakes ($P << 0.01$), while the mean light extinction coefficient (0.787 m^{-1}) was 1.7-fold higher in burn-impacted lakes ($P << 0.01$) compared to reference lakes. Secchi depth and light extinction were correlated ($r^2 = 0.36$, $P < 0.01$, $n = 24$); when lakes C24 and C45 were removed the relationship was stronger ($r^2 = 0.85$, $P << 0.01$, $n = 22$). Lake C24 had a high extinction coefficient (1.28 m^{-1}) for its Secchi depth (1.0 m) due to continuous surface bloom of Aphanizomenon sp. as flakes. Lake C45 had a high extinction (0.54 m^{-1}) for its Secchi depth (2.8 m) due to wind conditions during sampling. Elevated DOC and colour in burn-impacted lakes reduced transparency and likely enhanced the potential for light limitation of phytoplankton growth after fire.

Fire affected inorganic suspended solids concentrations. Mean nonvolatile suspended solids (NVSS) in reference lakes was 0.65 $mg \cdot L^{-1}$, whereas burnt lakes contained 2-fold higher NVSS (Mann-Whitney, $P = 0.04$). Volatile suspended solids (VSS) were not different between reference and burnt lakes, averaging 2.6 and 2.7 $mg \cdot L^{-1}$ respectively ($P = 0.88$). Increased transport of inorganic particles from burnt catchments is inferred.

Fire did not appear to affect lake water CHL concentrations. Among reference lakes, mean CHL was 12 $\mu g \cdot L^{-1}$ and $\log_{10}$-transformed values were strongly related to TP ($r^2 = 0.83$, $P << 0.01$, $n = 13$). Despite the much higher phosphorus concentrations observed in burn-impacted lake waters, CHL was not elevated, averaging 13 $\mu g \cdot L^{-1}$. There was no detectable relationship between CHL and TP concentrations for burn-impacted lakes ($r^2 = 0.06$, $P = 0.5$). We predicted CHL concentrations for burn-impacted lakes with the CHL-TP model for reference lakes. The residuals between predicted and observed values were positively related to Secchi depth ($r^2 = 0.44$, $P < 0.01$, $n = 10$) and to TN:TP ratio ($r^2 = 0.69$, $P << 0.01$, $n = 10$). The lack of response in CHL to elevated phosphorus in burn-impacted lake waters and the relationship with Secchi depth is consistent with light limitation.

General patterns relating lake chemistry to catchment features were poor. There were no detectable relationships between nitrogen or phosphorus concentrations of lake waters with drainage ratio ($r^2 < 0.25$, $P > 0.3$). However, colour and DOC were linearly related to log-drainage ratio (Table 3). Colour and DOC tended to increase at a faster rate with drainage ratio in burnt lakes compared to reference lakes (Table 3), however, the slopes of these relationships were not distinguishable (ANCOVA, $P = 0.09$ and $P = 0.20$ respectively).

Percent disturbance and time since disturbance

Water in the previously (1961-1985) burnt lakes had phosphorus concentrations intermediate between recently (1995) and non-burnt lakes. TP and DP concentrations for burnt lakes increased in a positive-linear relationship with percent disturbance (intercept forced through mean TP and DP for reference lakes). TP and DP appeared to decline with the natural logarithm of time-since-disturbance. Data were not normally distributed in time or percent disturbance and contained zero values for reference lakes so we combined both hypothesized disturbance patterns into a single disturbance index (DI):

$$\text{DI} = \%\text{Disturbance} \cdot e^{-Kt} \quad (8)$$

where t = time since disturbance (90 yr for reference lakes) and K = decay constant. The value for K was predicted from an exponential decay function $K = 0.693 \cdot T^{-1}$ where T = half-life which was estimated from the relationship between $\log_{10}$ DP and TP with the natural logarithm of time-since-disturbance. The half-life was estimated at 11 and 20 yr for DP and TP, respectively. The disturbance index explained 74 and 76% ($P << 0.01$) of the variance in TP and DP, respectively, among the 15 impacted lakes (Table 3). We included reference conditions in the analysis by forcing the intercept through mean TP and DP concentrations for reference lakes (intercept value from Table 3) assuming they represented a zero DI.

Section 1 Summary

Catchments in the Caribou Mountains are fundamentally different from those where fire effects have historically been studied. The large proportion of inundated peatlands in the Caribou Mountains created unique nutrient responses following fire. For example, forest fire usually augments nitrate and to a lesser degree, phosphorus export from granitic regions (Lewis 1974, McColl and Grigal 1975, Wright 1976). The relatively severe Caribou Mountains fire caused elevated phosphorus, and to a lesser degree, nitrogen concentrations in lakes which suggested higher phosphorus compared to nitrogen export following fire. Similar findings are reported from other wetland systems. Burnt fens exported phosphorus and retained nitrogen, while burnt upland catchments exported nitrogen and held phosphorus in the granitic Experimental Lakes Area (Bayley et al. 1992). Nitrogen retention in Alberta peatlands typically exceeds 98% (Li and Vitt 1997), a value comparable to the >85% retention reported by Bayley et al. (1992) for burnt fens. Surface water in northern Alberta, where peatlands dominate, could be more sensitive to eutrophication from elevated TP following fire than indicated by upland fire studies because of reduced phosphorus retention in peatlands after fire.

Increase in the flux of divalent cations and potassium from organic soils usually occurs after fire (Tiedmann et al. 1978). Increased flux rates of divalent ions from burned peat likely occurred in the Caribou Mountains. However, the cation exchange capacity of both living and dead peat likely remained intact, liberating protons as cations were exchanged (Clymo 1984). The result was a 5-fold median increase in $[H^+]$, decreased pH and reduced alkalinity in burnt lakes while base cation concentrations did not change. Organic acids associated with elevated DOC in burn-impacted lakes possibly added to overall acidification while contributing organic anions (presumably $R\text{–}COO^-$).

The relationship between CHL and TP in reference lakes on the plateau indicates a strong association between phytoplankton biomass and total phosphorus. The slope for $\log_{10}$-transformed values (2.31) was more positive and the intercept (-2.46) more negative than values reported for North America (Nurnberg 1996).

Time-since-disturbance and percent disturbance were important factors in nutrient enrichment among burnt lakes. When combined into a disturbance index (DI), they explained 74 and 76% of the variance in lake TP and DP concentrations. An exponential decay model for time-since-disturbance impacts was used because it matched the trend for our limited temporal data. The hypothesis is justifiable because recovery rates should initially be rapid as new growth and microbial communities are re-established followed by a decrease with increasing time as microbial and plant communities stabilize and nutrients are flushed from the lake and lost to sediments.

Our results suggest forest fire had a profound impact on surface water quality in lakes of the Caribou Mountains. These lakes responded to fire with elevated nutrient concentrations because phosphorus and to a lesser degree, nitrogen, liberated during fire and subsequent decomposition was not retained by peat. Though base cations were likely liberated from burnt material, cation exchange with peat resulted in an increase in the flux of protons. Elevated phosphorus concentrations slowly returned to reference conditions depending on both the magnitude of disturbance (% disturbance) and time-since-disturbance. A single disturbance index combining %disturbance and time proved effective, however, a larger range in time is needed to test the hypothesized exponential and linear components of this model. The effects of fire on water chemistry may be larger in peatland dominated catchments than elsewhere, due to elevated export of phosphorus and long recovery periods.

Section 2: Hydrology in burnt and unburnt catchments determined by isotopic and chemical methods

Canada's northern boreal forest is presently undergoing unprecedented changes related to development of mineral, petroleum and forest resources. Evaluating and predicting the impacts on aquatic systems requires models that link biogeochemistry and hydrology with surface water chemistry. Though a generation of such models exist (see review in: Ball and Trudgill 1995), most require hydrological data that may not be available for remote locations making them logistically difficult to calibrate. In the western boreal forest there has been only limited success in application of distributed hydrologic models because the landscape contains subdued local relief, abundant peatlands and discontinuous permafrost or long-lasting seasonal frost (Pietroniro et al. 1996). Methods for generating reliable hydrologic indices such as lakewater retention times and catchment water yields are needed before predictive loading models for solute transport to lakes and streams can be applied to remote locations like the western boreal forest.

One method of inferring hydrologic indices that is particularly suited to remote locations is based on the enrichment of the stable isotopes of water, deuterium (^{2}H) and oxygen-18 (^{18}O) in lakes compared to local precipitation (Gibson et al. 1993). Water molecules containing ^{2}H and ^{18}O are heavier than their ^{1}H and ^{16}O counterparts, and thus have distinct vapor pressures and molecular diffusion in air (Gat and Gonfiantini 1981). Heavier water molecules evaporate at a slower rate from open waterbodies. As water retention time increases, the waterbodies will become progressively enriched in heavy isotopes relative to local precipitation. A model that predicts lakewater retention times and catchment water yields from isotopic enrichment have been validated with detailed water budget measurements and shown to be accurate for two basins in northern Canada (Gibson et al. 1993).

Modeling catchment contributions of both water and solutes can be achieved by reducing the size of the catchment to contributing and effective areas respectively (e.g. Soranno et al. 1996). Once hydrologic parameters have been estimated, the mean contributing area (CA) for runoff can be derived from catchment water discharge divided by annual precipitation. There can be large variation in CA size, particularly among peatland catchments on glacial till, due to differences in groundwater recharge and discharge as well as transbasin transfers of groundwater (Shaw and Prepas 1990). Spatial variation in CA must be considered both within and among catchments when modeling runoff generation and solute transport (Beven and Kirkby 1979). Variable source areas (Betson and Marius 1969), similar to CA, are usually calculated for storm runoff and can range from 1.2% to 5% of DBAs in steeply sloped basins (Dunne and Black 1970, 1971) and from 15% to 36% of DBA in basins with moderate to low slopes (Dunne et al. 1975, Pierson and Taylor 1994). The importance of estimating CA and its variation among catchments is that solute transport depends partially on the amount of landscape contributing water.

Information describing CA is particularly important when runoff is routed through soils that form a minor and variable proportion of the total catchment (Beven and Kirkby 1979, Hill 1993). For example, riparian soils and peatlands have a strong influence on runoff generation and chemistry of receiving surface waters (Dunne 1978, Pierson and Taylor 1994, Soranno et al. 1996, Evans et al. 1999). However, determining the location of a variable CA and the flow pathways requires extensive water table and topographic data that are usually unavailable for remote catchments with low relief. A third index, effective area (EA), can be estimated as an analog for temporal variability in CA location, size, flux rates from soils, and transmission of solutes to surface waters. The EA represents the portion of CA contributing a solute such as phosphorus to surface waters as it is restricted by biological uptake, sorption and sedimentation. Models that predict solute load from a variable EA (e.g. Soranno et al. 1996), can be reformulated to predict EA from a mass-balance for conservative ions such as Na^+ or Cl^- if catchment water yield and lake ion concentrations are known. The importance of estimating EA is that its variation among catchments should explain some of the variation in catchment loading of solutes such as nitrogen, phosphorus and carbon to lakes.

Hydrologic indices such as CA and EA are particularly important for remote catchments because it is in these areas that impact from watershed disturbance is least known. Removal of forest cover is generally thought to cause increased water yield (Tiedemann et al. 1979, Hornbeck et al. 1993). Increased water yield should result in larger CA, EA and increased flux of nutrients. Increases in lake concentrations of phosphorus following fire have been observed in remote lakes from Canada's eastern (Carignan et al. 2000) and western boreal forests (McEachern et al. 2000). The parameters CA and EA aid initial examination of hydrologic and biogeochemical factors causing changes in lake chemistry following fire.

In this paper we calculate CA for runoff generation and EA for solute transport in a peatland region of low relief where discharge data were not available. We compare catchment water yields from CA with those determined from a topographically defined drainage basin area (DBA) and measured runoff in a gauged stream. We then compare DBA and EA as predictors of nitrogen, phosphorus and carbon concentrations in boreal Subarctic study lakes of Alberta. Finally, we compare water yields from lakes in burnt and unburnt catchments to test if forest fire resulted in increased water yield from SubArctic catchments.

The ^2H and ^{18}O composition of precipitation, runoff and groundwater (Fig. 4) were required to predict lakewater retention times. The most important index was mean isotope composition of precipitation (δ_P) because calculation of evaporative enrichment and lakewater retention time start from δ_P. The local evaporation line (LEL) intersected the mean meteoric line (MML) at –165.0 ^2H and –21.9 ^{18}O, which is the equivalent to the theoretical long-term mean isotope composition of precipitation (δ_P) in the region. For comparative purposes we attempted to calculate δ_P from a combination of precipitation measurements. Summer precipitation contained mean -138.3 ‰ ^2H SMOW and -19.0 ‰ ^{18}O SMOW. Snow samples contained -192.5 ‰ ^2H SMOW and -25.1 ‰ ^{18}O SMOW. Snow depth measurements combined with snow water equivalent data suggest snow typically comprised 20% of annual precipitation. Observed δ_P (Fig. 4) was thus calculated at -149.1 ^2H and -20.2 ‰ ^{18}O SMOW. Observed δ_P was enriched 9% compared to theoretical δ_P suggesting that methods for measuring annual precipitation were biased towards enriched summer precipitation.

In addition to precipitation, groundwater and runoff inflows to lakes must have isotope compositions similar to δ_P (Gibson et al. 1993). Groundwater sampling of springs and wells below the Plateau suggested groundwater had a mean isotope composition (δ_g) of -147.7 ‰ ^2H SMOW -19.0 ‰ ^{18}O SMOW which was virtually identical with observed δ_P (t-test$_{(0.05, 21)}$, $P > 0.7$) but was enriched 12% over theoretical δ_P (t-test$_{(0.05, 15)}$, $P \ll 0.01$). The mean isotope composition of stream waters in MS1, MS2, and MS3 were -138.0 ^2H SMOW and -17.8 ^{18}O SMOW, enriched 7% over observed δ_P (t-test$_{(0.05, 8)}$, $P \ll 0.01$). Enriched runoff measured in streams was likely due to sampling that did not adequately include snowmelt. The enrichment of sampled groundwater compared to theoretical δ_P suggested a less enriched source, perhaps from a deeper aquifer, contributed water to the lakes. Given the potential errors in measuring isotope compositions of precipitation, inflow and groundwater, we used theoretical δ_P for subsequent hydrologic calculations.

Mean water yield and thus retention time estimates from the isotope method were within expected values. Water residence times determined from ^2H and ^{18}O averaged 2.4 (± 0.6) yr in the 14 reference lakes. Reference catchment water yields averaged 110 (± 23) mm. Water yield from the gauged MS2 catchment was calculated at 114 mm. Published runoff for the region is from 75 to 150 mm (Fisheries and Environment Canada 1978). The range in water yield among reference basins was attributed to water storage in peatlands where porosity ranges over 3 orders of magnitude (Mulqueen 1986) and high variability of groundwater contributions among basins.

Mean water residence time for the 10 burnt lakes was 1.0 (± 0.2) yr which was lower than for reference catchments (P= 0.05). Lower residence times in burnt lakes was expected because, as a group, mean volume was less than in reference lakes. Water yield from burnt catchments averaged 120 (± 27) mm which was not detectably different from yield in reference basins (P = 0.8). Support for the hypothesis that water yield should be elevated from burnt catchments was not apparent in mean values.

A majority of runoff generation was limited to small hydrologically active areas that did not increase in size proportionally with DBA. The ratio CA/DBA declined with increasing DBA (r = -0.68). Catchment water yield declined with increasing DBA/V ratio in all lakes (Table 3). For example, lakes with DBA/V > 8 (median DBA/V) had a mean water yield of 74 mm, compared to 162 mm for lakes with a DBA/V less than 8. When reference and burnt catchment water yields to DBA/V were compared, the negative slope for burnt catchments was steeper (ANCOVA, $P = 0.04$, Table 3). Fire appeared to cause as much as 3-fold higher water yield from catchments at a DBA/V ratio of 1 but the effect diminished as DBA/V ratio approached 10 and intersected with reference catchments as DBA/V ratio increased to 100. Fire had a larger impact on the hydrology of small basins because CA was a larger proportion of DBA.

Drainage from variable source areas was represented by CA which averaged 24 and 26 % of reference and burnt DBAs, respectively. Although CA was within expected values for basins with low topographic relief, CA was not related to the sum of fens and open water on bogs in each drainage ($r = 0$), and thus was not a representation of surface saturation. The lack of a relationship between CA and surface saturation suggests that a significant portion of hydrologic loading derived from groundwater and that the magnitude of groundwater contribution was unrelated to our measures of surface saturation.

The combination of CA, variable flux rates and restricted transmission through soils within the CA was represented by a Na^+ mass-balance model for effective area (Eq. 4). Effective areas were an average of 1.7 % and 2.0 % of DBAs for reference and burnt lakes, respectively and were not distinguishable from each other (t-test$_{22,\,0.05}$, $P = 0.6$). The location of EA within each catchment could not be estimated. However, EA/DBA was related to the proportion of upland in the DBA and negatively related with the proportion of peatland in the DBA (Table 3). EA/DBA was not related to the proportion of fens and open water in the DBA ($r = -0.1$, $P = 0.6$). The positive relationship of EA/DBA to upland and lack of relationship with saturated land cover suggests a majority of water yield derived from groundwater and that the proportion of upland areas represented improved groundwater movement.

In reference lakes, dissolved nutrient concentrations were related to drainage basin and lake physical characteristics whereas total concentrations were not. For example, correlation coefficients between DP and DN concentration with DBA/V ratio were 0.38 and 0.28, respectively ($P = 0.02, 0.05$) whereas correlation coefficients for TP and TN concentration were less than 0.12 (Table 3). Except for DN and DOC concentration, correlation between nutrients and DBA/V were generally lower among lakes in burnt catchments (Table 3). We were unable to detect differences in TN, DN, TP and DP concentrations to DBA/V relationships for burnt and reference lakes because the relationships were generally poor.

Poor relationships for TN, DN, TP and DP concentrations with DBA/V ratio were expected when mass loading of solutes to Caribou Mountain lakes were limited to CAs that were less than 30 % and EAs less than 2% of DBAs. When the lakes were separated into burnt and reference groups, the EA/V model explained similar variance in nutrient concentrations among lakes as DBA/V. However, the EA/V model included a representation for export rates ($\sum A_i \bullet F_i \bullet T_i$) and should account for the impacts of fire on export in each catchment if the nutrients behaved similarly to Na^+. DN and DOC concentration fell along similar regression lines for burnt and reference lakes in the EA/V model (Table 3) suggesting the model adequately accounted for changes in DN and DOC loading following fire.

Reference and burnt lake data were subsequently combined. EA/V explained 50% and 67 % of variance in mean DN and DOC concentration, respectively for the combined dataset ($P << 0.01$). Relating lake concentrations with the physical parameter EA improved explained variance among lakes for DN and DOC concentration, however, it did not detectably improve explained variance in TN, TP or DP concentration.

The EA/V model assumed fire influenced nutrient flux rate to the same degree as Na^+. Substantially elevated flux rates of phosphorus following fire would explain the poor correlation between EA/V and phosphorus. The EA/V model consistently underestimated TP concentration in burnt lakes (residual mean = 0.3 for Log_{10} values). Total flux of TP and DP may have been on average 2-fold higher from burnt compared to reference effective areas of similar size.

Section 2 Summary

The isotopes ^2H and ^{18}O gave reasonable lakewater retention times and basin water yields that were consistent with measured and published runoff for the region. Water samples were easily collected and analyzed. We used three summer determinations to represent mean isotope composition in each lake at an average cost of $180 per lake. Three summer samples were adequate even for the Caribou Mountain lakes with retention times less than one year as June and late August samples were usually less than 5% different from the mean. To apply the isotope model in lakes with strong thermal stratification, more intensive sampling of outflow waters may be required because δ_Q may not equal δ_L.

For the isotope method, use of two independent tracers allowed for direct examination of model uncertainty. Residence times calculated from $\delta^{18}O$ were consistently lower by an average 17% and water yield consistently higher by an average 30% compared to values calculated from δ^2H. It is important to note that δ^2H is approximately 8-fold more sensitive to fractionation but that both tracers were equally sensitive to potential errors in humidity and evaporation rates used in the calculations. Consistently lower retention times from $\delta^{18}O$ indicate an underestimate of enrichment in δ_P. A 5% change in δ_P along the MML resulted in a 35% change in mean retention time estimates for Caribou Mountain lakes and brought the mean difference between $\delta^{18}O$ and δ^2H to 9%. Thus accuracy of an isotope model is determined primarily by uncertainty in estimating δ_P. The 95% confidence intervals for LEL (Fig. 4) intersected the MML at ± 6.6 δ^2H and $\pm$ 0.88 $\delta^{18}O$ or a total error of 8 % in the δ_P prediction. Error in Caribou Mountain lakes was exacerbated by low retention times. Errors in water yield exceeding 40% are common when measured discharge from gauged streams are used and can exceed 100% in estimates for groundwater yield (Winter 1981). Thus the isotope method appears to be at least as accurate as stream discharge measurements and has the added benefit of including groundwater yield.

A majority of studies indicate fire should cause increased catchment runoff (e.g. Wright 1976, Schindler et al. 1980, Hornbeck et al. 1993). However, several studies have noted no change or reduced runoff from burnt areas with deep mineral soils due primarily to reduced snow accumulation and soil moisture (e.g. Rouse 1976, Megahan 1983). Our data likewise suggest that it was difficult to detect a change in mean catchment water yield. However, fire did affect the relationship between water yield and catchment size with increased water yield from small catchments. In catchments where hydrologic contributing areas are limited in size by poor drainage such as the Caribou Mountains, fire caused increased water yields when DBA/V was below 10. In a survey of 100 northern Alberta headwater lakes, 80% had DBA/V < 10. Of those lakes, 100% (n = 18) and 62% (n = 27) of subsets with clear cut logging or forest fire in their catchments, respectively, had DBA/V < 10 (Prepas et al. in press) and are likely to be impacted by watershed disturbance.

In most basins, saturated areas along permanent and intermittent channels are believed to comprise the majority of source areas for solute transport (e.g. Pierson and Taylor 1994, Soranno et al. 1996). In the Caribou Mountains, EA would include solute movement from fens and bogs linked to surface inflows during saturated conditions. There was no apparent relationship between %EA and % saturated surface area, however, %EA was related to the proportion of upland. In peatland / lichen forest, upland is synonymous with improved drainage. Improved drainage was not well represented by our measure of catchment slope because upland areas were not uniformly distributed and often occurred as small ridges not represented on contour maps. The EA calculation did not depend solely on the extent of saturated areas such as fens but also on the amount of discharge flowing from those areas and from groundwater. The positive relationship between EA and upland implied that some catchments had higher discharge through saturated areas or groundwater or both via return flow (Dunne 1978) or subsurface flow (Hill 1993).

Actual EA sizes may have been larger than determined in our study if the combined term ($\sum A_i \cdot F_i \cdot T_i$) was smaller than 0.189 meq•m^{-2}•yr^{-1} [Na^+]. If EA were equivalent to CA, consistent with our assumption that Na^+ transmission was 1, flux rates averaged 0.020 meq•m^{-2}•yr^{-1} [Na^+] from the study catchments. Flux rates this low are not recorded in Alberta and are at the lower end of some Arctic Brunisols (Buttle and Fraser 1992). Our estimates of EA were likely conservative as Caribou Mountain soils undergo slow weathering, however, a lower constant flux rate would not have changed the outcome of the regression analyses we presented for nutrient and catchment linkage. The EA model presented here can be used to interpret the combined variation in source area and discharge among catchments. It cannot be used as a direct measurement of saturated area or areas producing surface runoff and groundwater discharge unless the parameters A_i, F_i, and T_i are known.

In survey studies of many remote catchments, the natural isotopes of water ^2H and ^{18}O may provide an economically feasible method for estimating hydrologic conditions. They may also assist in chemical tracer techniques for monitoring lakewater budgets that are complicated by the accuracy of precipitation to evaporation ratios (Stauffer 1985). Calibration data from one gauged catchment suggested the isotope method properly estimated water yield and retention time. Contributing areas, calculated from the isotope-derived hydrologic parameters suggested peatland dominated catchments were consistent in size with those determined for other basins with low topographic relief. Effective area provided an analogue to variability in source areas and total flux from these areas. Though theoretically a coarse filter, EA was the best physical parameter for explaining among lake variance in nutrient concentrations in the Caribou Mountains. However, variation in lakewater concentrations of phosphorus were not strongly linked to catchment descriptors including basin size and EA. The CA and EA data suggested increases in phosphorus concentrations exceeding 3-fold as a result of fire

(McEachern et al. 2000) must be related to combined changes in water yield and flow pathways as well as changes in flux rates and transmission through peat and mineral soils. Further work addressing the assumptions required in an EA model may lead to better predictive ability in determining land-water linkages in peatland dominated systems.

Section 3: Nutrient and light limitation of phytoplankton assemblages following forest fire in Boreal SubArctic catchments, Alberta

Nutrient limitation of algal biomass and the relative success of algal groups or individual species are determined largely by lake chemistry (e.g. Kilham and Kilham 1984, Tilman et al. 1986). In temperate lakes, algal biomass is typically limited by lake phosphorus (P) concentrations (Schindler 1975, Prepas and Trew 1983). In most boreal forest lakes, the total nitrogen to total phosphorus ratio (TN:TP) is above the cellular mass ratio of 20:1 for freshwater algae, indicating that N is in greater supply than P relative to cellular requirements (Hecky and Kilham 1988, Hecky et al. 1993). Phosphorus limitation of algal growth may not become severe until TN:TP ratios exceed 20 (Hecky et al. 1993) while TN:TP below 20 suggests algae may become nitrogen limited until N-fixation can balance N-deficits. Declines in lake water TN:TP ratios are associated with changes in nutrient limitation of algae, which subsequently can reduce the ability for non N-fixing species to compete for resources (Smith 1983).

When P supply is adequate, algal growth can be limited by nitrogen (Smith 1986, Jónasson 1996). Nitrogen limitation appears to be mediated by increased loading of P relative to N from either internal or external sources. Water column mixing of hypolimnia with surface water during the breakdown of thermal stratification results in internal P loading, promoting low TN:TP and potential N limitation (Riley and Prepas 1984, Jones 1990). External P loading can increase after disturbance of forested catchments while changes in land use towards non-intensive agriculture can also result in reduced TN:TP (Dillon and Kirchner 1975). Forest fire is one landscape disturbance common throughout the boreal forest causing increased P concentrations in lakes from the eastern boreal Shield (Carignan et al. 2000) to the western boreal SubArctic (McEachern et al. 2000). The soils of the western Canadian boreal region are generally nitrogen deficient, and lakes tend towards elevated TP concentration and low TN:TP ratio as a product of natural and anthropogenic sources. As a result, cyanobacterial blooms are common in lakes of the western boreal region (Riley and Prepas 1984) as are occurrences of winter oxygen depletion and poor water quality associated with algal blooms. The tendency of western boreal lakes towards eutrophication from internal and external P loading makes them perhaps more sensitive to catchment disturbance than lakes in other regions.

Increases in lake concentrations of dissolved organic carbon (DOC) and its correlates, colour and light extinction, have been observed following fire in boreal forest catchments (Carignan et al. 2000, McEachern et al. 2000). Light limitation of algal growth is mediated by reduced light penetration due to the presence of light absorbing material (e.g. DOC or suspended solids). A post-fire switch in lake water towards elevated colour and light extinction could cause increased occurrence of light limitation. Combined, potential light and nitrogen limitation following watershed disturbance could result in reduced algal diversity (Reynolds 1984). Changes towards increased P and colour concentrations in lake waters have been documented in the western boreal following fire (Prepas et al. In Press, McEachern et al. 2000), while little is known about the response of algae in these lakes. Burnt lakes in the western boreal SubArctic offer an excellent opportunity to assess N-limitation and changes in algal diversity following disturbance because a 1995 fire impacted 50 to 95% of some headwater lake catchments while leaving similar reference lakes untouched for comparison.

We tested N, P and light limitation of pelagic algae and impacts on species diversity in Boreal SubArctic lakes with experimental and field survey data. Our objective was to determine if lake waters with low TN:TP ratios were nitrogen limited and if so, what the impact would be on algal biomass and diversity. The hypotheses were that, in burnt lakes, lower TN:TP ratios and higher colour in lake water would cause N and light limitation of pelagic algae. Further, algal communities in burnt lakes would be less diverse and be dominated by species adapted to low N and light conditions. Nitrogen, P and light limitation were tested by modifying nutrient and light regimes within *in situ* microcosms. We subsequently compared algal assemblages from 20 lakes to determine if patterns in algal dominance were associated with TN:TP ratios, nutrient and colour concentrations similar to those suggesting N or light limitation in the bioassays.

Nutrient limitation

As TN:TP ratios declined in the study lakes, the three NSEs demonstrated P, concurrent N and P, and N limitation. In Highratio lake (TN:TP = 38), CHL increased 1.5 fold in response to P amendments (Fig. 5) compared to controls, indicating strong P limitation. In Midratio lake (TN:TP = 20), CHL in the combined N + P treatment increased 7 fold compared to control CHL (Fig. 5) indicating strong limitation by both N and P. A 2 fold improvement in N treatments over both control and P treatments (Fig. 5, $P << 0.01$) suggested that algal biomass in Midratio lake was particularly influenced by low N availability. Total N and P concentrations were at their lowest when the Midratio lake NSE was initiated. In Lowratio lake (TN:TP = 8), response was limited to N treatments with a 1.5 fold increase in CHL relative to controls ($P << 0.01$). Both N and N+P amended microcosms indicated nitrogen limitation in Lowratio lake.

Light Limitation

Increases in control CHL relative to initial and final lake CHL were consistent with light limitation of algal growth in the coloured lakes (Fig. 5). Midratio lake was not coloured and had the lowest DOC and the deepest Secchi depth (Table 4). CHL in control containers increased 1.5 fold over initial CHL (Fig. 5, $P << 0.01$). However, the increase in CHL obtained in the Midratio lake control microcosms was likely not associated with improved light in the experiment compared to the epilimnion because CHL response in the lake suggest *in situ* growing conditions improved over the incubation period. CHL in the lake increased 2.7 fold from minimum to maximum summer values over the same period. The increase in Midratio lake CHL above control microcosms was likely a response to 40% and 16% increases in lake P and N concentrations, respectively, over the incubation period. Of the two coloured lakes, Highratio lake had intermediate DOC, colour and light penetration (Table 4). CHL in control containers increased 2 fold over initial CHL and 1.5 fold over final CHL ($P << 0.01$). The 1.3 fold increase in lake CHL over the incubation period coincided with an increase in Secchi disc depth by 0.2 m (14%) while the 2 fold increase in control containers was likely due to the 5 fold improved light conditions in the NSEs. Lowratio lake water contained the highest DOC and colour concentrations and exhibited the shortest Secchi disk depth (Table 4). CHL increased 2.5 fold over both initial and final lake CHL in response to the 5 fold improved light conditions in control containers. Light was not limiting pelagic algal growth in Midratio lake where light extinction was 1.5 m^{-1} but appeared to strongly limit algal growth in both Lowratio and Highratio lakes where light extinction was above 2.5 m^{-1}.

Phytoplankton Assemblages

Reference lakes contained TN:TP ratios and mesotrophic to eutrophic nutrient concentrations similar to Midratio lake. From the 10 reference lakes, 125 algal species were identified. Average species richness was 36, consistent with richness from other lakes in Alberta's northern Boreal Plain (Prepas unpubl. data). *Cyanophyceae* represented between 15% and 89% of total algal biomass and over 90% of cell densities in reference lakes. Dominance patterns within *Cyanophyceae* were variable with, for example, Nostocales representing from 8% to 88% of total algal biomass. Taxa adapted to low N conditions tended to dominate reference lakes consistent with concurrent N+P limitation indicated by Midratio lake, however, clear taxa patterns with N among lakes were not apparent.

Burnt lakes contained TN:TP ratios below 20 with a majority below 10 and eutrophic nutrient concentrations similar to Lowratio. Burnt lakes contained similar algal species to reference lakes (Table 5) but lower species diversity. A total of 71 species were identified from the burnt lakes, just over half that found in the reference lakes. Average species richness in burnt lakes was 23, or 36% lower than richness in reference lakes ($P << 0.01$). *Cyanophyceae* represented from 17% to 99% and Nostocales from 0% to 99% of total algal biomass in the burnt lakes. *Aphanizomenon* dominated mean biomass for burnt lakes at 40% of total algal biomass compared to *Anabaena,* which dominated in reference lakes (Table 5). No genera comprising more than 5% of total biomass were unique to burnt lakes. Two genera, *Chroomonas* and *Gymnodinium,* identified in three or more reference lakes, were absent from burnt lakes. Discriminant analyses did not separate burnt from reference lake algal communities at the order, suborder or genus levels ($P > 0.5$). Clear dominance patterns within *Cyanophyceae* were not apparent in burnt lakes and differences in assemblage from reference lakes were not detected. Like reference lakes, burnt lakes were dominated by taxa adapted to N-deficient conditions.

Correlation analyses of the combined lake plankton data with lake water chemistry suggested nitrate concentration, pH and DOC or colour were primary variables influencing algal community composition. Data from burnt and reference lakes were combined because treatment was not a detectable factor in algal response to chemical variables (ANCOVA, $P > 0.4$). As a proportion of total cells, Cyanophytes were negatively related to nitrate ($r = -0.56$, $P << 0.01$). Chrysophytes decreased with pH and increased with DOC while Cyanophytes increased with pH and decreased with DOC. In addition, Cyanophytes increased with TN while relative abundance in other orders declined with increasing TN. Nostocales showed similar patterns with Cyanophyta as a whole and declined with nitrate while increasing with TN. Increases in Nostocales with decreased nitrate suggested a response of N-fixing plankton to low inorganic N availability. Two of the three NSEs suggested light was a limiting factor; colour and DOC, which were closely associated with reduced light penetration (McEachern et al. 2000), appeared to benefit Chrysophytes and Cryptophytes ($r > 0.5$, $P < 0.05$). In addition to advantages under low light conditions, Cryptophytes may have benefited from heterotrophy under elevated DOC concentration. Relationships between order or sub-order cell densities with TN:TP and light extinction were not detectable ($-0.3 < r < 0.3$, $P > 0.3$) despite burnt-lake TN:TP ratios that were less than half and light rates almost double that in reference lakes. Identification of plankton samples from dates through the summer may have improved our ability to detect differences in burnt and reference lake groups. Algal assemblages from our mid-summer samples were related to chemical concentrations impacted by fire. However, differences in plankton assemblage between burnt and reference lakes were not apparent because plankton were dominated by species adapted to low N and low light conditions in both lake groups.

Section 3 Summary

Phosphorus limitation of algal biomass is characteristic of lakes in Alberta's Boreal Forest (Prepas and Trew 1983). Nitrogen limitation has been suggested for Alberta's eutrophic lakes where frequent blooms of nitrogen-fixing plankton occur (Zhang and Prepas 1996). We demonstrated P limitation in one oligotrophic lake (Highratio lake) and combined N and P limitation in a eutrophic lake (Midratio lake). Nitrogen limitation alone was demonstrated in the burnt lake (Lowratio lake) where TN:TP was 8, less than half and one-quarter that in Midratio and Highratio lakes, respectively. Nitrate concentration and TN:TP ratio in Midratio and Lowratio lakes were within a range reported for Alberta lakes (Mitchell and Prepas 1992, McEachern et al. 2000, Prepas et al. In Press) suggesting N limitation of phytoplankton may be common in Alberta's boreal lakes. Reduced TN:TP ratio following fire in boreal SubArctic lakes results from increased export of P relative to N from burnt peatlands (McEachern et al. 2000) suggesting that forest fire increases the likelihood of N limitation in these lakes.

Light limitation has been demonstrated for lakes with low light penetration (Knowlton and Jones 1996). We demonstrated light limitation in lakes with light extinction above 2.5 m^{-1} and no evidence of light limitation at an extinction of 1.5 m^{-1}. Light extinction was associated with high DOC and colour content of lake water both of which increase following burning of peatland catchments (McEachern et al. 2000). The NSE placed in Lowratio and Highratio lakes suggested light limitation of algal growth at light extinction coefficients exceeded by 88% and 67% of lakes in the burnt and reference catchments, respectively. Light limitation is likely a common feature of lakes in peatland dominated catchments and increases in DOC, colour and light extinction following fire should increase the severity of light limitation.

Phytoplankton species richness was expected to decline in burnt lakes because fewer species can survive as N and light limitation become severe (Reynolds 1984, 1994). Declines in phytoplankton species richness have been observed under conditions of increasing external P load and reduced TN:TP (e.g. Tilman 1978) similar to changes following fire in the Caribou Mountains. The decline in algal species richness by 36% in the Caribou Mountains was more severe than following either fire, or logging, on the Boreal Shield (Planas et al. 2000) and logging in Finland (Rask et al. 1998).

Plankton communities in burnt lakes should have contained greater proportions of Nostocales if N limitation was more pervasive. Nostocales biomass was not consistently higher in our mid summer sample from 10 burnt lakes despite TN:TP ratios predominantly below 10. However, Nostocales increased relative to other algae as nitrate concentrations declined, indicating low available N concentration may be a stronger determinant in promoting N-fixing plankton than low TN:TP ratio. Fire may provide no advantage for nitrogen-fixing plankton because nitrate export increases following forest fire (Minshall et al. 1997) particularly from peatland catchments (Bayley et al. 1992). Fire may even reduce potential bloom formation in SubArctic and possibly other boreal lakes because of enhanced nitrate concentrations in lake waters. Within Nostocales, there appeared to be a shift from dominance by *Anabaena* in unburnt lakes to *Aphanizomenon* in burnt lakes (Table 5). The dominance of phytoplankton by Nostocales in lakes from undisturbed catchments makes it unlikely that increases in N-fixing taxa after fire would be detectable, however, shifts in dominant genera were suggested and require further investigation.

The limitation assays demonstrated a range in nutrient limitation from N through concurrent N+P to P limitation in association with increasing TN:TP ratio. Algal community compositions were ambiguous in describing linkages between nutrient limitation and nutrient ratio. However, both NSEs and community composition suggested N-deficient conditions result in N limitation that may be common among the naturally productive lakes of Alberta's Boreal Forest. Disturbances such as forest fire cause elevated P loading relative to N in boreal catchments and appears to increase the tendency towards N limitation of algal growth but also provides nitrate which may inhibit dominance by N fixing plankton. Lakes in northern boreal forests provide new opportunities to review the implications of enhanced allochthonous loading to lake waters following catchment disturbance because algal communities appear to exist along a fine balance between P, N and light limitation.

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Table 1: Physical parameters for Caribou Mountain study lakes. Symbols are: watershed area (Wo), lake surface area (Ao), lake mean depth (Z_m), residence time (τ). Slope, upland and peatland are percentages for each catchment and Disturb is the percent of impacted by forest fire.

ID	Wo (ha)	Ao (ha)	Volume (10^3 m^3)	Z_m (m)	Slope (%)	Upland (%)	Peatland (%)	Disturb (%)	τ (d)
				Reference lakes					
C1	663.2	52.3	510	1.07	1.5	1	94	0	75
C2	614.8	93.4	1910	2.17	2.3	2	95	0	217
C5	1068	76.5	568	0.75	2.4	6	79	0	80
C6	260.4	91.1	261	0.30	3.1	16	79	0	55
C7	569.0	90.0	578	0.66	2.9	6	87	0	61
C8	8208	60.8	612	0.99	1.4	5	85	0	49
C9	146.3	86.1	1563	1.83	2.6	13	86	0	551
C11	204.8	134.4	4071	3.06	6.1	65	35	0	887
C30	3218	536.1	55564	11.60	2.0	28	67	0	770
C32	3018	953.4	27318	2.90	3.0	12	81	0	314
C34	5571	166.5	5840	3.50	4.0	22	77	0	194
C35W	825.0	175.0	18240	5.50	6.1	32	66	0	419
C45	4627	1173	93840	8.00	4.0	14	83	0	660
C47	2732	59.0	697	1.18	6.0	72	25	0	56
				Lakes in catchments burnt in 1995					
C17	700.9	164.8	2300	1.54	1.9	83	16	80	105
C23	1053	65.8	2436	4.10	1.9	19	80	90	32
C24	1761	159.8	10332	6.36	3.6	35	62	95	42
C25	820.1	151.9	4278	2.87	4.2	25	72	90	171
C26	1520	36.6	523	1.68	3.3	25	73	75	36
C27	581.1	28.1	220	0.85	6.0	30	69	60	43
C41	32.6	2.6	22	0.86	2.0	43	57	100	68
C42	34.3	7.4	53	0.72	3.0	51	49	98	96
C43	691.9	8.3	50	0.60	4.0	51	45	95	26
C46	359.4	4.4	25	0.58	6.0	44	51	60	44
				Lakes in catchments burnt between 1961 and 1985					
C12	642.9	40.5	440	1.22	2.9	6	88	20	101
C13	483.8	175.5	1745	1.04	1.3	12	81	80	133
C14	268.9	62.4	1779	2.93	4.3	27	73	80	298
C15	2257	128.3	2013	1.67	2.8	6	91	70	77
C16	995.1	53.4	1056	2.04	4.2	42	55	80	129

Table 2: Summary of chemical characteristics for Caribou Mountain lakes. Numbers are summer means. Abbreviations are: CHL = chlorophyll *a*, TP, DP and SRP are total, total, dissolved and soluble reactive phosphorus, TN and DN are total and total dissolved nitrogen, NO_3 is NO_3^{-}N, NH_4 is NH_4^+-N, all in $\mu g \bullet L^{-1}$. DOC and DIC are dissolved organic and inorganic carbon, VSS and NVSS are volatile and non-volatile suspended solids, Ca^{2+}, Mg^{2+}, Na^+, and K^+ are the cations, SO_4^{2-}, SO_4^{2-} is $^-$, Alkalin. is total alkalinity all in $mg \bullet L^{-1}$. TC-TA is total cations – total anions in millequivalents per liter.

ID	CHL	TP	DP	SRP	TN	DN	NO_3	NH_4	DOC	DIC	VSS	NVSS	Ca	Mg	Na	K	SO_4	Alkalin.	Colour	TC-TA	pH
				($\mu g \bullet L^{-1}$)									($mg \bullet L^{-1}$)					$CaCO_3$	Pt	$meq \bullet L^{-1}$	
C1	9.87	31	16	6	609	514	2.6	17.8	22	6.3	1.35	0.34	4.40	1.20	0.83	0.08	1.35	9.75	317	-0.1307	6.70
C2	16.58	38	20	9	744	527	11.6	31.2	18	5.8	3.49	0.37	5.24	1.33	0.28	0.25	1.13	15.00	209	-0.0623	7.70
C5	12.17	34	11	6	688	452	1.1	10.1	17	5.4	3.21	0.42	4.37	0.95	0.32	0.17	0.70	12.25	172	-0.0505	7.29
C6	14.51	36	10	5	823	474	3.2	13.3	12	4.7	4.63	0.43	5.65	1.18	0.42	0.31	0.95	19.75	76	0.0128	7.86
C7	24.94	46	17	2	756	470	1.4	10.6	17	4.3	4.64	1.13	4.12	0.94	0.41	0.22	0.82	11.25	205	-0.0601	7.08
C8	4.68	40	25	14	661	612	5.0	13.6	27	7.6	1.57	0.91	7.30	1.59	0.37	0.09	1.55	15.25	389	-0.1755	6.69
C9	9.42	32	13	3	729	528	4.6	9.3	12	7.6	4.28	0.83	8.06	1.91	0.54	0.43	1.05	32.50	34	0.0823	7.88
C11	6.79	31	11	2	750	585	1.2	15.4	12	14.8	1.73	0.36	18.89	4.17	2.00	0.52	7.69	71.75	26	0.2147	8.49
C30	4.74	22	9	3	412	349	7.0	14.4	13	8.3	0.80	1.00	10.40	2.00	0.60	0.40	2.30	36.75	105	0.0687	7.47
C32	7.73	32	12	2	445	345	1.0	10.9	11	3.5	2.20	0.40	6.00	1.40	0.40	0.30	2.10	10.88	77	-0.1759	7.00
C34	6.66	26	13	1	550	466	1.7	11.5	18	11.5	1.40	1.00	14.60	2.90	0.90	0.40	2.50	54.38	140	0.1287	7.82
C35W	22.72	38	12	4	710	429	0.6	25.2	16	11.2	3.60	0.90	11.00	2.40	0.90	0.50	4.20	40.50	112	0.1053	8.27
C45	9.22	26	11	1	454	361	4.9	12.2	10	7.7	1.80	0.60	8.50	2.30	0.50	0.30	1.40	35.25	55	0.0965	7.77
C47	12.59	35	17	5	840	723	1.1	13.5	27	10.6	1.76	0.41	27.01	7.67	6.01	0.49	48.73	59.00	196	-0.0542	7.68
C17	39.23	125	66	36	1086	561	31.8	48.6	18	6.7	5.92	1.84	6.46	1.62	0.85	0.62	2.71	16.50	240	-0.1192	8.38
C23	5.94	79	55	40	552	468	6.1	12.9	22	6.3	1.70	2.28	7.18	1.35	0.47	0.57	1.63	16.25	331	-0.1395	7.06
C24	10.67	78	62	40	622	505	16.3	18.7	19	6.4	1.71	0.84	6.04	1.36	0.57	0.82	2.66	15.50	250	-0.0886	6.94
C25	24.31	55	21	9	751	421	2.6	12.7	14	6.2	4.16	1.09	7.84	2.27	0.53	0.79	2.70	27.75	112	-0.0052	7.96
C26	5.15	109	47	32	718	636	5.7	14.4	30	7.6	1.46	1.02	12.07	3.06	0.82	0.50	7.04	25.25	480	-0.2479	7.10
C27	3.89	98	43	24	649	583	12.6	16.1	27	8.4	1.12	2.87	10.24	2.38	0.91	0.34	1.96	26.50	396	-0.1819	7.17
C41	11.77	48	28	15	871	741	3.0	16.1	32	9.6	1.78	0.51	5.37	1.78	0.69	1.11	9.51	1.13	424	-0.2474	4.75
C42	5.97	40	21	4	757	668	5.6	22.2	21	14.6	1.59	0.30	5.98	1.85	0.74	0.70	5.43	16.00	212	-0.0638	6.61
C43	20.05	166	79	52	811	664	1.9	30.0	31	7.1	5.51	1.51	6.54	1.59	1.20	0.61	7.96	6.75	456	-0.2174	6.06
C46	7.26	54	33	17	779	734	4.2	15.5	35	8.9	2.02	0.82	10.20	2.68	2.76	0.24	16.62	15.00	523	-0.2079	6.48
C12	11.59	36	19	12	809	630	20.3	18.3	23	6.8	2.76	0.65	7.35	1.58	0.63	0.05	1.23	16.25	312	-0.1728	7.20
C13	19.74	46	14	2	799	534	3.8	70.9	14	6.5	4.27	0.62	6.71	1.94	1.30	0.25	1.54	26.50	112	0.0070	7.55
C14	9.03	36	15	5	588	456	11.4	91.7	12	12.0	1.42	0.64	14.28	3.76	1.26	0.63	5.12	54.75	87	0.1132	7.93
C15	4.89	80	64	51	607	556	9.0	19.9	27	6.3	1.09	0.81	5.67	1.47	0.81	0.33	3.49	10.00	454	-0.1741	6.60
C16	14.29	67	40	21	907	728	42.4	76.2	27	5.4	2.85	0.89	7.91	1.98	0.51	0.29	5.34	12.75	344	-0.2161	7.26

Table 3: Univariate regressions for independent (X) and dependant (Y) variables.

X	Y	*n*	α	β	r^2	*SE* (β)	MSE	*F*	*P*
DOC	Colour	24	-156	19.3	0.89	1.44	2595	175	< 0.0001
Colour	LnSecchi	24	0.62	-0.003	0.72	0.0004	0.066	53.6	< 0.0001
Colour	ε	24	0.32	0.001	0.58	0.0002	0.026	30.9	< 0.0001
Log_{10}DBA/Ao	DOC	24	8.7	10.7	0.62	1.78	21.4	36.3	< 0.0001
Burnt		10	10.1	12.2	0.69	2.87	17.2	17.9	0.003
Ref.		14	9.04	8.0	0.68	1.60	10.8	25.1	0.0003
Log_{10}DBA/Ao	Colour	24	9.17	210	0.57	38.9	10205	29.2	< 0.0001
Burnt		10	41.0	248	0.78	45.9	4377	29.3	0.0006
Ref.		14	18.4	141	0.59	34.8	5131	16.4	0.0016
DI	Log_{10}TP	15	1.52	0.005	0.74	0.001	0.038	40.58	< 0.0001
DI	Log_{10}DP	15	1.13	0.007	0.76	0.001	0.059	43.74	<0.0001
Log_{10} Wo/V	Log_{10} τ	24	0.51	-0.51	0.78	0.058	0.042	77.6	< 0.0001
Log_{10}DBA/V	Log_{10}R	24	2.27	-0.38	0.56	0.0572	0.071	27.6	< 0.0001
Burnt		10	2.54	-0.55	0.96	0.039	0.007	192.7	< 0.0001
Ref.		14	2.12	-0.35	0.48	0.107	0.091	11.0	< 0.006
Arc%Upland	Ar%EA	24	0.06	0.129	0.51	0.027	0.001	22.8	< 0.0001

Regression parameters are, the number of lakes in the regression (n), intercept (α),slope (β), regression coefficient (r^2), standard error (*SE*), mean square error (MSE), F-value (*F*), and probability (*P*). Variables are, lake volume (V, m^3), lake surface area (Ao, m^2), drainage basin area (DBA, m^2), residence time (τ, yr), water yield (R, mm), disturbance index (DI), light extinction coefficient (ε, m^{-1}), total, dissolved and soluble reactive phosphorus (TP, DP and SRP, $\mu g \cdot L^{-1}$), total and dissolved nitrogen (TN, DN, $\mu g \cdot L^{-1}$), water colour ($mg \cdot L^{-1}$ [Pt]) and dissolved organic carbon (DOC, $mg \cdot L^{-1}$).

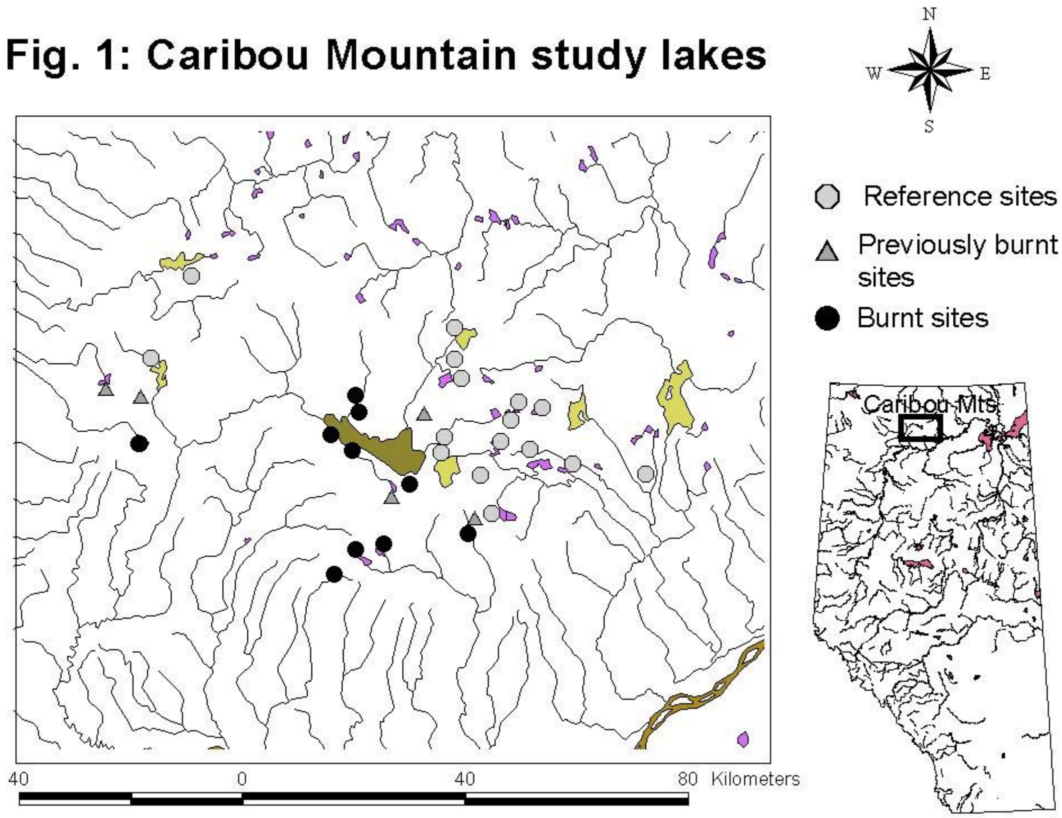
Table 4: Summer mean values for lakes containing nutrient stimulation experiments. Summary data are included from lakes in reference and burnt catchments described by McEachern et al. 2000. Standard deviations are in parentheses.

	Highratio n = 4	Midratio n = 5	Lowratio n = 4	Reference (n = 14)	Burnt (n = 10)
TP (µg/L)	14 (3)	58 (56)	78 (16)	33 (6)	85 (40)
TN (µg/L)	510 (57)	1036 (141)	622 (86)	655 (140)	749 (148)
TN:TP	38 (3)	20 (6)	8 (2)	20 (3)	11 (5)
NO3 (µg/L)	51 (28)	4 (2)	16 (11)	3 (3)	9 (9)
DOC (mg/L)	16.7 (0.5)	15.5 (6.5)	19.2 (0.8)	16.6 (6)	24.9 (7)
CHL (µg/L)	5 (4)	22 (10)	11 (5)	12 (6)	13 (11)
Colour (mg/L [Pt])	210 (105)	83 (35)	250 (5)	151 (106)	342 (135)
Extinction (m^{-1})	2.47 (0.1)	1.56 (0.2)	3.68 (0.2)	3.19 (1.18)	5.44 (1.69)
Secchi Depth (m)	1.9 (0.4)	2.2 (0.5)	1.0 (0.2)	1.4 (0.6)	0.7 (0.2)

Table 5: The 20 genera observed in the greatest number of reference lakes. Data summarizes taxa identification for 10 reference and 10 burnt lakes in the Caribou Mountains. %Biomass is an average percent of total algal biomass and the number (*n*) of lakes in which the genera was identified. The number in parentheses following each genera is an average rank of contribution to total algal biomass within the lakes in which it was observed. For example Ceratium ranks third in % Biomass (8%, *n* = 3) but is not shown because it was present in only 3 reference lakes.

20 most common genera	Reference		Burnt	
in Reference lakes	% Biomass	*n*	% Biomass	*n*
Anabaena (1)	20.5	10	10.4	10
Cryptomonas (14)	1.9	10	4.2	10
Chromulina (54)	0.2	10	0.4	10
Aphanothece (27)	1.1	10	1.7	9
Chlamydomonas (30)	0.2	10	1.0	6
Coelosphaerium (8)	4.1	9	3.1	7
Aphanizomenon (2)	13.6	8	40	8
Asterionella (15)	2.4	8	2.2	6
Erkenia (23)	1.4	8	2.0	7
Katablepharis (40)	0.8	8	1.2	9
Rhodomonas (16)	2.1	8	6.1	8
Ankistrodesmus (25)	1.3	7	1.0	8
Ochromonas (22)	1.4	7	2.3	7
Uroglena (24)	1.4	7	1.0	4
Dinobryon (17)	2.0	6	0.5	2
Monoraphidium (43)	0.6	6	0	3
Oocystis (41)	0.7	5	5.5	4
Scenedesmus (38)	0.9	5	0	4
Gymnodinium (39)	0.9	5	0	0
Melosira (14)	2.8	5	1.8	6
Trace, more common in Burnt Lakes				
Ankyra	0	0	1.0	4
Cyclotella	0.5	3	1.3	4
Mallomonas	0	3	1.3	4

Fig. 1: Caribou Mountain study lakes



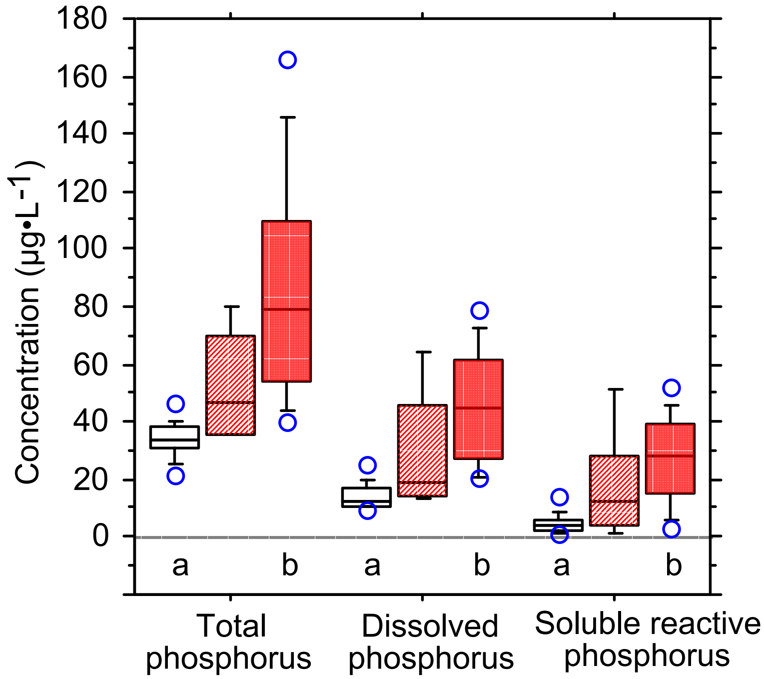


Fig. 2: Summer mean concentrations of total phosphorus (TP), dissolved phosphorus (DP) and soluble reactive phosphorus (SRP) for reference (clear boxes, n = 15), burnt (shaded boxes n = 10) and previously burn-impacted (striped boxes, n = 5) lakes. Letters (a&b) indicate difference between reference and burnt means at $P < 0.05$. Analytical statistics were not applied to previously burnt lakes.

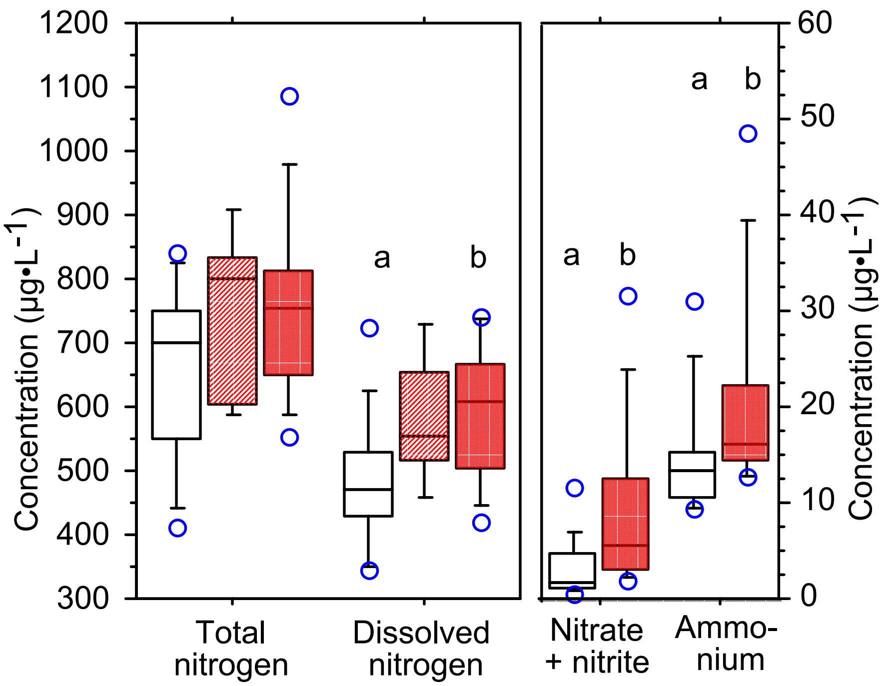


Fig. 3: Summer mean total nitrogen and dissolved nitrogen for reference (clear boxes, *n*= 15), burnt (shaded boxes, *n*=10) and previously burn-impacted (striped boxes, n = 5) lakes. Nitrate-nitrite and ammonium for reference and burnt lakes only. Letters (a & b) indicate differences in mean concentrations between reference and burnt at *P*Š0.05.

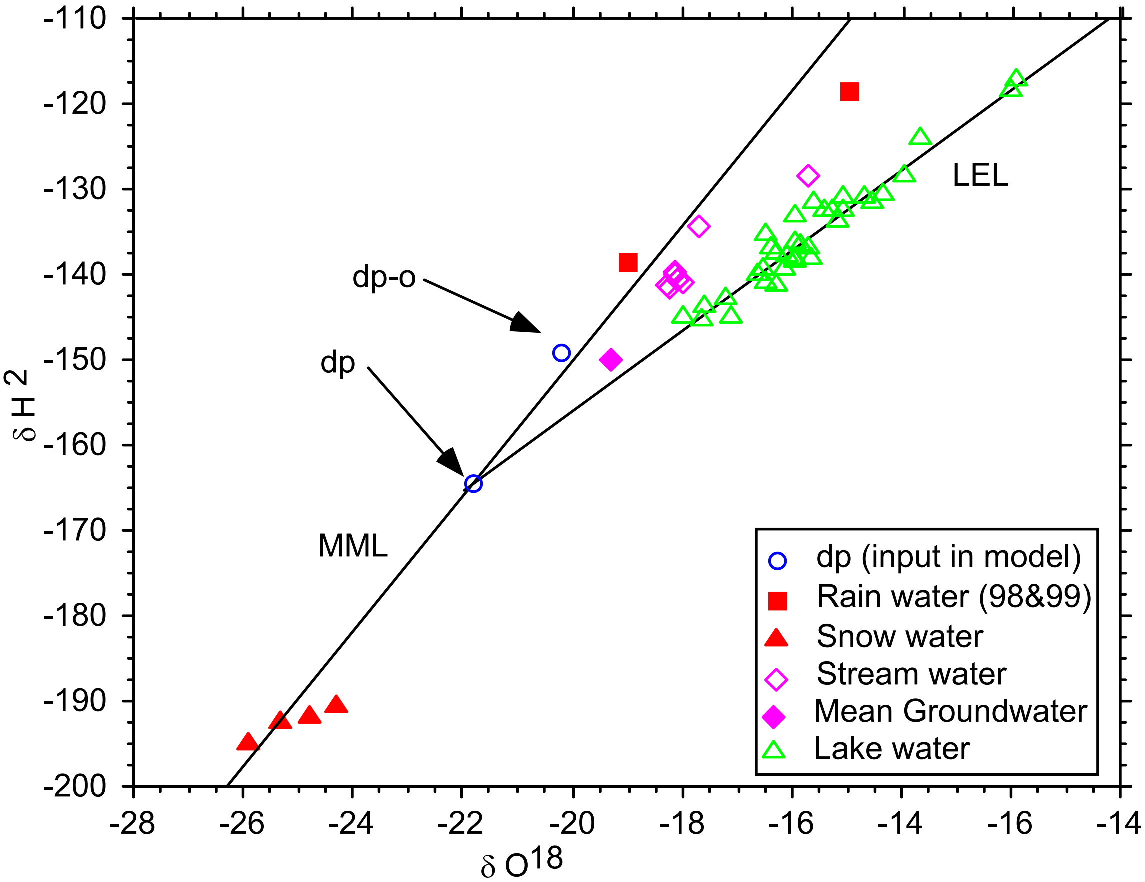


Fig. 4: Deuterium and oxygen-18 composition of source waters and lake waters in the Caribou Mountains. Both theoretical (dp) and volume weighted observed (dp-o) composition of percipitation are shown. The global mean meteoric evaporation line (MML) and the local evaporation line (LEL) are plotted. Also shown are isotope compositions of stream samples and the mean composition of groundwater samples.

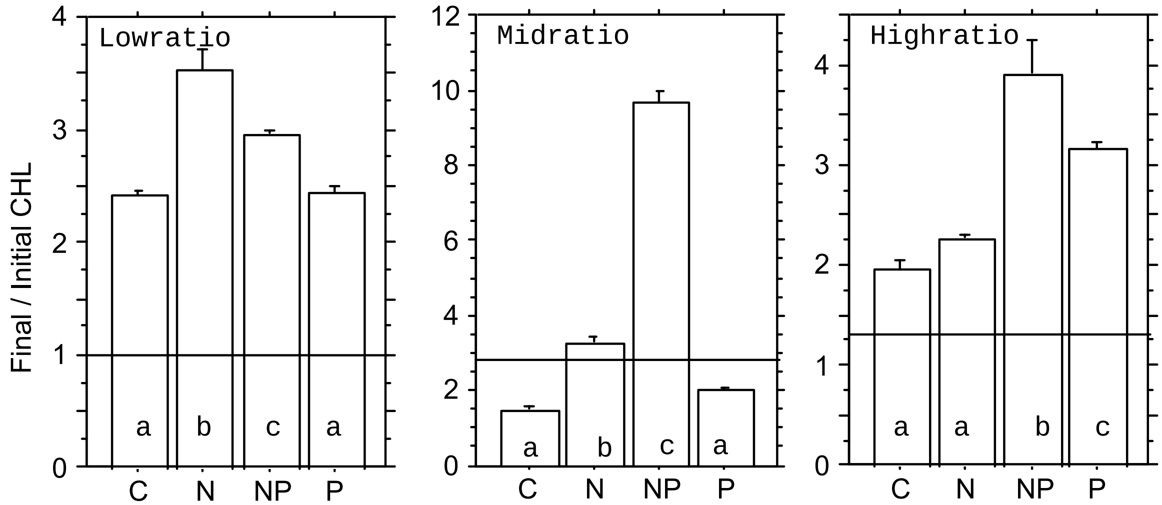


Fig. 5: Response of chlorophyll a (CHL) in nutrient stimulation experiments (10 L microcosms) in three lakes. Response is final CHL divided by initial CHL and thus represents growth in response to nutrient ammendments and light. The treatments are C= control, N= +1000 µg/L [N], P = +100 µg/L [P] and NP = combined +N & +P. Response in C is due to improved light conditions in the microcosms relative to the lake. Error bars represent one standard error from the mean. Small case letters represent differences in mean CHL at P < 0.0001. Horizontal line represents final/ initial CHL observed in the lake over the incubation period. All NSE responses are different from final lake CHL at P < 0.01.