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Interannual variability in trophic status of shallow lakes on the Boreal Plain: Is there a climate signal?

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[1] We explored relations between climate and trophic status of shallow lakes (lake area > 5 ha, mean depth < 3.2 m) located on the subhumid western Boreal Plain of Canada. Correlation and regression analyses were used to assess the association between indicators of climate and satellite-based estimates of trophic status (chlorophyll *a* (Chl *a*)). Chl *a* was derived using red band reflectance of Landsat satellite images for 76 lakes, which were then averaged for each year to produce a landscape median for summer (August) over a 20-year period from 1984 and 2003. Our results showed that climate was related to interannual changes in trophic status. Average May temperature was positively correlated to Chl *a*, suggesting the importance of conditions in the early part of the growing season. Growing season effective precipitation (P − PET) was negatively correlated to Chl *a* such that wetter conditions seemed to lead to a dilution of Chl *a*. Very wet years resulted in a larger Chl *a* drop than one expected by a linear model, suggesting greater water contribution from the landscape. P − PET explained 64% of the variance in Chl *a* using a nonlinear regression tree. Our study offers clues as to how shallow lake systems may behave on the subhumid Boreal Plain as a function of future climate change.

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1. Introduction

[2] Fundamental changes in the climate of the Boreal Plain of western Canada are expected to occur. Some studies suggest that the climate will become warmer and drier [*Schindler and Donahue*, 2006], while others suggest that the climate might become warmer but not become significantly drier [*Fernandes et al.*, 2007]. Climate change, coupled with climatic oscillations, is expected to have significant impacts on the ecology of the many shallow lakes populating the western Boreal Plain [*Schindler*, 1998]. Some of these impacts may be manifested through abiotic controls on biological production, such as changes in phosphorus concentrations in lakes [e.g., *Brown et al.*, 2000] or changes in lake level [e.g., *Coops et al.*, 2003]. Alternatively, these impacts may be manifested through biotic controls on biological production, such as changes in trophic dynamics [e.g., *Zimmer et al.*, 2002; *Norlin et al.*, 2005]. Ongoing research is focusing on understanding the dominant processes controlling the trophic structure of shallow lakes on the Boreal Plain.

[3] Dominant processes influencing the ecological functioning of lakes may be identified by analyzing changes in spatial and/or temporal patterns of key lake characteristics, such as trophic status. Trophic status is a measure of the fertility of lakes, and as such plays an important role in influencing the biological production (i.e., algae, macrophytes, zooplankton, fish, and water birds) in lakes [*Naumann*, 1929]. Trophic status may be estimated using chemical (e.g., phosphorus), physical (e.g., turbidity) or biological (e.g., algal biomass) characteristics of lakes [*Carlson*, 1977]. Proxies of algal biomass, such as the concentration of chlorophyll *a* (Chl *a*) give the most direct estimate of trophic status, since algal biomass is one of the major components of primary production. Traditionally, Chl *a* has been measured using spectrophotometry of water samples taken in situ. Recent work has shown that Chl *a* can also be estimated from remotely sensed images [e.g., *Sass et al.*, 2007]. Depending on the scale of analysis, field and remote sensing offer complementary approaches to understanding dominant processes controlling the ecology of lakes.

[4] The natural variation in trophic status of lakes can be studied at various temporal scales. At daily to seasonal timescales, trophic status is likely to respond to changes in weather, hydrology, and trophic interactions. Because of the chaotic nature of these controls [*Benincà et al.*, 2008], the response in trophic status is often different from lake-to-lake. However, at annual to decadal timescales, trophic status is likely to respond to changes in climate and land cover (e.g., burned forest). Because of the larger footprint of climate, the response in trophic status may be more similar among lakes within a region. Understanding the natural variation in trophic status at these longer temporal and broader spatial scales is important for improved land management of boreal landscapes in the face of climate and environmental change.

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[5] *Sass et al.* [2007] explored the natural variation in trophic status of 76 shallow lakes (lake area > 5 ha, mean depth < 3.2 m) on the western Boreal Plain in a regional drainage basin on the Utikuma Uplands of northern Alberta. The study indicated that of the overall variation in trophic status as measured by Chl *a*, fifty percent was explained by spatial factors, ten percent was explained by temporal factors and forty percent was explained by interactive spatiotemporal factors. Drawing on conceptual frameworks such as the ones offered by *Wiley et al.* [1997], *Blenckner* [2005], and *Devito et al.* [2005a], *Sass et al.* [2007] hypothesized that the sources of spatial and temporal variation in trophic status were climate and biophysical properties of the landscape that influence the transmission of water from catchments to lakes.

[6] The goal of this paper and the companion paper [*Sass et al.*, 2008] was to test to what degree climate and biophysical properties of the landscape, such as geology and topography, explain the spatial and temporal variation in lake trophic status as mapped by *Sass et al.* [2007]. Spatial variation refers to the lake-to-lake variation in Chl *a* based on a long-term record. Temporal variation refers to the landscape level fluctuation of Chl *a* of all lakes combined. Chl *a* was estimated from 17 Landsat images captured between 1984 and 2003 during end of summer period from late July to end of August. One image per year was used to characterize the end of summer Chl *a* conditions. For both papers, we relied on field observations to make the assumption that the inter-annual variability in Chl *a* was substantially greater than intra-annual (late July to end of August) variability. In this paper, we addressed the question: do climatic factors play a role in controlling the landscape level fluctuation of trophic status?

[7] We hypothesized that climate controls landscape level fluctuations of trophic status, as estimated by remotely sensed Chl *a* in algae, and that the nature of this control may be expressed through temperature or precipitation mediated processes. We identified a priori the main ways climate may control landscape level fluctuations of trophic status on this boreal landscape. Temperature mediated processes control lake ice depth, freezing of sediment and ice break-up in spring. For example, colder winters may suppress the emergence of submersed aquatic vegetation and therefore favor high Chl *a* [*Bayley et al.*, 2007]. On the other hand, earlier ice break-up, due to warmer temperatures, may cause higher nutrient resuspension [*Weyhenmeyer*, 2001] and hence favor higher Chl *a*. Growing season temperatures may affect Chl *a* by favoring the growth of certain species of algae. For example, warmer water favors quickly growing cyanobacteria that attain large biomass by the end of growing season [*Paerl*, 1988]. Precipitation or water mediated processes control the transport of nutrients from catchment to lake. Studies have found that wetter conditions increase Chl *a* by mobilizing nutrients that are limiting algal growth from land to lakes through surface and subsurface flow paths [*Devito et al.*, 2000; *Evans et al.*, 2000; *Macrae et al.*, 2005]. Precipitation also controls changes in lake water levels. Some studies have found an increase in Chl *a* after lake level drops due to concentration of limiting nutrients [e.g., *Vollenweider*, 1968; *Markensten*, 2006] and some have found a decrease in Chl *a* after a drop in lake levels due to enhanced gr f aquatic vegetation under more favorable light conditions [*Beklioglu et al.*, 2006]. In interconnected lakes, changes in Chl *a* may also be driven by the flushing of nutrients and algal cells from lakes to downstream water bodies [*Dickman*, 1969].

[8] We tested our hypothesis by completing the following objectives: (1) to estimate interannual changes in climate and Chl *a*, (2) to explore the relation between climate and Chl *a*, and (3) to provide explanation of what mechanisms could be responsible for the patterns observed. Our study covered a 20-year period from 1984 to 2003, which captured both the dry and wet extremes of climatic variation for our study region. This time period was chosen because of the availability of satellite imagery from which we estimated our indicator of trophic status (i.e., Chl *a*).

2. Study Area

[9] The study area is situated on the Utikuma Uplands, in the upper reaches of the Utikuma River drainage basin (Figure 1), which is located in north-central Alberta in the western part of the Boreal Plain ecozone (Figure 1 inset). The climate of the Utikuma Uplands is continental, characterized by long, cold winters and short, warm summers. Slave Lake meteorological recording station (55°18′ N, 114°46′ W; 581 m above sea level (asl)) is the closest year-round station to the study lakes within the Utikuma Uplands. On the basis of 30-year normals (1971–2000), the average annual temperature was 1.7°C, with average monthly temperatures ranging from −14.6°C in January to 15.6°C in July. Average annual precipitation was 503 mm. Most of this precipitation (P) fell during the summer months (May–August) coinciding with the peak evapotranspirative demand by vegetation [*Devito et al.*, 2005b]. Average annual potential evapotranspiration (PET) was 497 mm. Therefore, in most years P was less than PET. P was substantially greater than PET, only once every 5–10 years [*Sass and Creed*, 2008].

[10] Overall topographic relief is approximately 100 m on the Utikuma Uplands. Locally, the landscape is differentiated into wetter low-lying areas that are on average 5–10 m lower than the surrounding drier upland areas. Vegetation in low-lying areas is dominated by black spruce (*Picea mariana* (Mill.) B.S.P.) and tamarack (*Larix laricina* (Du Roi) K. Koch) in peat forming fens and bogs and by willow (*Salix* spp.), birch (*Betula* spp.), alder (*Alnus* spp.), sedges (*Carex* spp.) and grasses in non-peat-forming swamps and marshes [*Whitehouse and Bayley*, 2005]. Vegetation on the uplands is dominated by trembling aspen (*Populus tremuloides* Michx.) with occasional stands of white spruce (*Picea glauca* (Moench) Voss) [*Mitchell and Prepas*, 1990].

[11] Surficial geology comprises three major glacial units: moraine (undulating areas with silt and clay), glaciofluvial outwash (undulating areas with sand), and glaciolacustrine plain (flat areas with clay) [*Paulen et al.*, 2004]. Complex glacial deposits coupled with low topographic relief have given rise to a disintegrated drainage network, where water collects in hundreds of shallow lakes, most of which are surrounded by wetlands.

[12] Lakes on the Utikuma Uplands have a median size of 3 ha (0.01–3000 ha) and have a median depth of 1.26 m (0.30–3.20 m) [*Sass*, 2006; *Bayley et al.*, 2007]. Lakes are naturally eutrophic to hypereutrophic with respect to total phosphorus (12.4–670.4 μg TP L^{-1}) [*Bayley et al.*, 2007]. Anthropogenic sources of phosphorus are minimal [*Shaw et*

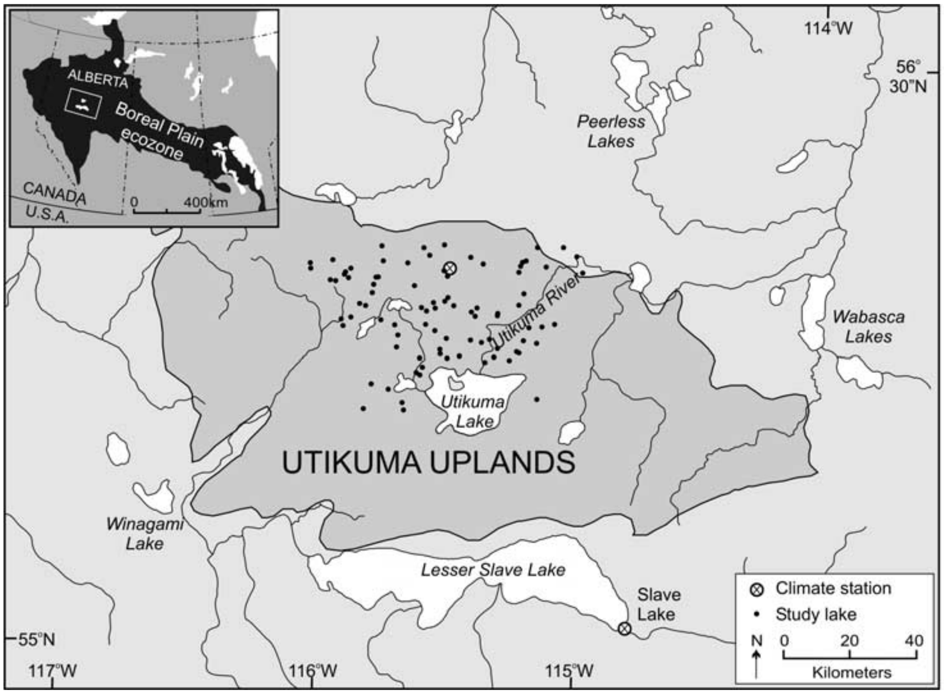

Figure 1. Study region showing locations of lakes. Maps are based on the ecological classification of the *Ecological Stratification Working Group* [1995].

al., 1989]. Despite being rich in phosphorus, phosphorus is still the limiting factor to algal production [*Bayley et al.*, 2007]. Lakes also have high dissolved organic content (DOC) (>10 mg L^{-1}) and high nitrogen content (>600 μg TN L^{-1}). Primary production is dominated either by algae, especially blue green algae, or by submersed aquatic vegetation (SAV) [*Bayley and Prather*, 2003]. Because of the severe winter cold and shallow water, many lakes freeze to the bottom or develop anoxic water beneath the ice. The ecological consequence is that most lakes are fishless [*Norlin et al.*, 2005] and that both the vegetative (e.g., SAV) and grazing (e.g., zooplankton) trophic levels are reduced substantially each year [*Bayley et al.*, 2007]. Primary production generally peaks near the end of the growing season from late July to end of August [*Bayley et al.*, 2007].

3. Methods

3.1. Climate

[13] For growing season climate, we used data from the Whitefish Lookout meteorological recording station (56°10′ N, 115°28′ W; 610 m asl) (Figure 1). We recognized the potential heterogeneity of precipitation and therefore we acquired meteorological data from the closest meteorological recording station to the study lakes. Although this station was operational only from 1 May to 31 August we felt justified using it as this is a period when the majority (>60%) of precipitation falls. Snowmelt does not play a significant role in the growing season water budget on the Boreal Plain since the snowpack is substantially reduced by sublimation by the spring melt period [*Devito et al.*, 2005b]. We compiled a daily time series for P, mean temperature (T), PET, and P − PET from 1 May to 31 August. PET was estimated using the following equation on the basis of *Hamon* [1964]:

$$\mathrm{PET} = 0.0138 \cdot D \cdot [\rho_{\mathrm{vsat}}(T)],$$

where PET is in mm d^{-1}, D is day length in h, and $\rho_{\mathrm{vsat}}(T)$ is the saturation absolute humidity at the mean daily temperature in g m^{-3}. We computed P − PET as a metric of effective precipitation [e.g., *Sass and Creed*, 2008]. From this daily data set, we computed monthly and growing season totals of P, PET, and P − PET and monthly and growing season averages of T. We also computed P, PET and P − PET totals and T averages for time periods of 1, 3, 7, 30 days prior to satellite image acquisition dates in order to test for any shorter-term effects on trophic status. For non-growing season (i.e., winter and spring) conditions, we used daily T data recorded at Slave Lake meteorological recording station (Figure 1). We computed average winter temperature on the basis of the months of November through to March and monthly averages for the three months preceding the start of growing season. To test for the confounding effect of wind induced turbidity on trophic status, we also computed average wind speeds for the various time periods considered for the other climatic variables using data from the Slave Lake meteorological recording station.

3.2. Trophic Status

[14] We used a time series of archived Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper (ETM) satellite images to determine the inter-annual changes in trophic status in 76 lakes from 1984 to 2003. Images were selected if they satisfied the following criteria: (1) the image captured the end of summer period from late July to late August; and (2) the image had no or minimal cloud. Within

the 20-year period from 1984 to 2003, 17 images satisfied the criteria.

[15] Our image selection targeted the end of the growing season, late July to the end of August, when algal biomass generally reaches its maximum for the year. Given the potential for daily to weekly variation in Chl *a* during this period, which might have overwhelmed the inter-annual variation in Chl *a*, we quantified the relative proportions of intra-annual versus interannual variation. We used a field-based data set of Chl *a* from a set of lakes in an adjacent lake region, 200 km to the southeast with similar physiographic setting. These lakes were studied as part of the Terrestrial and Riparian Organisms, Lakes, and Streams (TROLS) study [*Prepas et al.*, 2001]. There were 12 lakes sampled in mid-August over a 4-year period (1995–1998) with additional 1–2 measurements in two of those 4 years. For each lake, we estimated the between-year and within-year variation using a one-way ANOVA. On average, 84% of the variation in Chl *a* was interannual and 16% of the variation was intra-annual. Visual assessment of trophic status for some of the lakes used in the current study confirmed this relative stability during the end of summer period. From these field-based assessments, we concluded that the trophic status in August tended to be fairly stable and that a time series of trophic status estimates observed in August over many years can be expected to reveal interannual differences. While we feel confident with the assumption that interannual variability dominates over intra-annual variability from field monitoring program, our limited remotely sensed data set could not provide direct confirmation for this critical assumption. Obtaining multiple scenes in a month was a challenge because of limited satellite overflights (every 16 days) and the presence of clouds.

[16] For our time series, each image was georectified using maps of streams, lakes, and roads and then radiometrically normalized using a pseudoinvariant features correction method [c.f., *Kloiber et al.*, 2002] creating images with normalized exoatmospheric reflectance (%) at 25 m pixel resolution. For each year, study lakes were identified from band 5 (B5) images (λ: 1.55–1.75 μm), a band for which water strongly absorbs radiation [*Frazier et al.*, 2003]. A threshold in reflectance equal to the local minimum in the bimodal distribution that differentiated water and land pixels was used to identify lakes (i.e., pixels with reflectance less than the threshold were classified as lakes). Lakes were included in the analysis if they met the following criteria: (1) minimum area of 5 ha to avoid errors resulting from "mixed" pixels that combined lake and shoreline; (2) $B5_{\text{standard deviation}} < 2$ (%) to avoid errors resulting from "mixed" pixels that combined open water and water with emergent and floating aquatic vegetation (water is a strong absorber of radiation in B5 and therefore water alone would have a small standard deviation); and (3) lakes had no cloud or haze cover.

[17] Chl *a* in the study lakes was estimated from a regression model ($\ln(\text{Chl } a) = 0.42 \times \text{B3} - 1.66$; $R^2 = 0.68$, $p < 0.001$, SE = 0.65, $n = 18$) that related Chl *a* (measured in situ) to normalized exoatmospheric reflectance of band 3 (B3) (λ: 0.63–0.69 μm) [*Sass et al.*, 2007]. The largest sources of error in the estimation of Chl *a* from a satellite-based sensor were atmospheric effects and the effects of optically active tuents of the water column other than algal cells. These sources of error most likely accounted for the 32% of variance in Chl *a* that was not explained by red band reflectance [*Sass et al.*, 2007]. Given that Chl *a* was not normally distributed we estimated the natural logarithm transform of Chl *a*. Therefore, our estimate of trophic status for each of the 76 lakes and for each of 17 years was based on the natural logarithm of Chl *a* ($(\text{Chl } a)_{\text{sat}}$) computed from satellite-derived red band reflectance. There were no statistically significant effects of other optically active substances such as DOC and SAV [*Bayley et al.*, 2007; *Sass et al.*, 2007]. From this we concluded that our estimate of trophic status was based mainly on algal Chl *a*.

3.3. Landscape Level Estimation of Trophic Status

[18] From the individual lake data set of $(\text{Chl } a)_{\text{sat}}$ we computed the landscape median $(\text{Chl } a)_{\text{sat}}$ ($med(\text{Chl } a)_{\text{sat}}$) for all lakes (n = 76) for a given year. We used median instead of mean for capturing central tendency because individual lake $(\text{Chl } a)_{\text{sat}}$ were not normally distributed for some of the years. Given the different sources of error in estimating Chl *a* for 76 lakes over a 20-year period from red band reflectance, we used a Monte Carlo approach to quantify the uncertainty in the landscape median $(\text{Chl } a)_{\text{sat}}$ by simulating the effect of random error within our regression model (spatial error) and the effect of using this model over the 17-year data set (temporal error). For modeling spatial error, we randomly sampled normal distributions centered on the original $(\text{Chl } a)_{\text{sat}}$ values with a standard deviation equal to the standard error of the regression model ($0.65 \ln (\mu\text{g L}^{-1})$) and added it as white noise to the original individual lake data set. We created 1000 new realizations of the data set and computed $med(\text{Chl } a)_{\text{sat}}$ for each year of each realization. For modeling temporal error we randomly sampled normal distributions centered on the $med(\text{Chl } a)_{\text{sat}}$ for each year with a standard deviation equal to the standard deviation of $(\text{Chl } a)_{\text{sat}}$ of pseudo-invariant features ($0.26 \ln (\mu\text{g L}^{-1})$) that were used to assess the temporal stability of images [see *Sass et al.*, 2007, Figure 2]. From the 1000 realizations of $med(\text{Chl } a)_{\text{sat}}$, we computed the coefficient of variation (CV) to use as an assessment of uncertainty.

3.4. Statistical Analyses of Relation Between Climate and Trophic Status

[19] We used Spearman rank's correlation analysis to select climatic variables that correlated best with $med(\text{Chl } a)_{\text{sat}}$. Then, we used regression analysis to quantify the relation between climate and $med(\text{Chl } a)_{\text{sat}}$. In addition to parametric (i.e., linear) regression, we used non-parametric regression trees [*Breiman et al.*, 1984] to incorporate any nonlinearities that might have existed in the relations. Regression tree models were generated by iteratively partitioning the samples of the dependent variable (i.e., $med(\text{Chl } a)_{\text{sat}}$) into mutually exclusive groups. The partitioning was based on independent variables (i.e., T, P – PET), where the partitions were selected such that the sum of squares of the dependent variable were minimized within groups and maximized between groups. We determined optimal tree size by implementing a tenfold cross validation where we selected the tree whose estimated cross-validation error was within one standard deviation of the minimum cross-validation error (1 – SE rule) [*Breiman et al.*, 1984]. We used RPART implemented in SPLUS 4.0 to develop the regression tree models [*Therneau and Atkinson*, 1997]. For

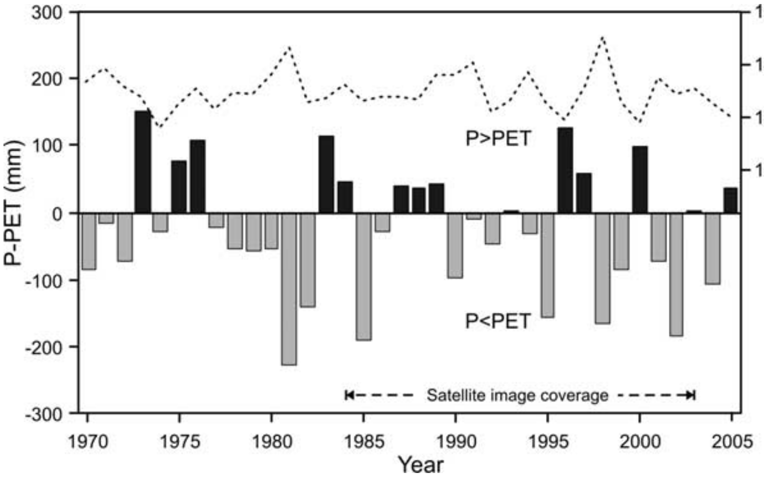

Figure 2. Interannual climate variability for the Utikuma Uplands. The climate data were compiled for the Whitefish Lookout station (56°10′N, 115°28′W; 610 m asl), which recorded climate data from May to August only. T, growing season average of daily mean air temperature; P – PET, growing season total of daily total precipitation minus daily total potential evapotranspiration.

both types of regression models, we tested for any interactive effects of climate variables on the temporal variation in *med*(Chl *a*)$_{\text{sat}}$.

4. Results

4.1. Interannual Variation in Climate

[20] There was large variability in growing season (May–August) P – PET and T from 1970 to 2005 (Figure 2). P – PET ranged from −227 mm (1981) to 151 mm (1973) with a 36-year average P – PET of −28.3 mm (Figure 2). Growing season T ranged from a minimum of 11.6°C in 1974 to a maximum of 15.0°C in 1998 (Figure 2). Winter season T ranged from a minimum of −14.7°C in 1974 to a maximum of −6.7°C reached in both 1977 and 1998. Although the extremes in growing season and winter temperature occurred during the same years, the overall correlation between the two variables was not significant ($r = 0.20$, $p = 0.26$). There was a weak but significant correlation between growing season P – PET and T ($r = -0.36$, $p < 0.05$), where wetter years tended to be cooler. The period from 1984 to 2003 for which satellite images were available captured the longer-term (1970–2005) extremes in both growing season P – PET and T (Figure 2).

4.2. Interannual Variation in Trophic Status

[21] There was large lake-to-lake variability in trophic status in each of the study years (Figure 3). However, this lake-to-lake variability exhibited temporal dependence. ANOVA on ranks indicated that the mean ranks between years were significantly different (Kruskal-Wallis $H = 163.9$, $df = 17$, $p < 0.001$). The ANOVA compared the mean ranks of (Chl *a*)$_{\text{sat}}$ between years computed from (Chl *a*)$_{\text{sat}}$

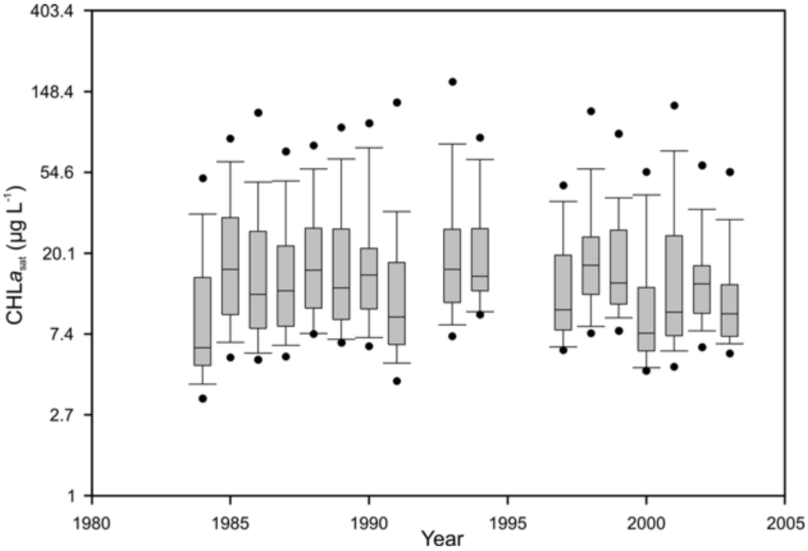

Figure 3. Wit - d among-year variability of (Chl *a*)$_{\text{sat}}$ from 1984 to 2003 (1992, 1995, and 1996 are missing because o ack of suitable imagery). Note log scale for *y* axis.

Table 1. Spearman's Correlation Matrix for Climatic Variables and Landscape Median (Chl *a*)$_{sat}$[a]

Spearman's rho	P − PET	T	Wind Speed
1 days prior	0.19	−0.34	0.14
3 days prior	0.07	−0.39	0.07
7 days prior	0.23	−0.29	0.04
30 days prior	−0.49[b]	−0.12	−0.16
1 May to image	−0.62[b]	0.26	−0.22
Month of May	−0.50[b]	0.48[b]	−0.16
Month of June	−0.16	−0.01	0.00
Month of July	−0.04	−0.10	0.03
November–March	na	−0.06	na
Month of February	na	−0.31	na
Month of March	na	0.38	na
Month of April	na	0.13	na

[a] T, daily mean air temperature; P − PET, daily total precipitation minus daily total potential evapotranspiration. P − PET represents totals, whereas T and wind speed represent averages for the different time periods used in aggregation. Na means data not available.
[b] Significant at $p < 0.05$.

values for each individual lake. Landscape median (Chl *a*)$_{sat}$ ranged from 6.2 μg L^{-1} to 17.3 μg L^{-1} (values back transformed using exponential function for ease of interpretation) indicating a large shift in median trophic status over the 20-year study period. The uncertainty analysis revealed that *med*(Chl *a*)$_{sat}$ was not sensitive to random error added either to the individual lake (Chl *a*)$_{sat}$ estimates or random error added to *med*(Chl *a*)$_{sat}$. The CV in *med*(Chl *a*)$_{sat}$ computed from 1000 realizations of the individual lake Chl *a* data set ranged between 3.4 and 4.9% over the 17 years of data with a mean CV of 4.0%.

4.3. Exploring the Link Between Climate and Trophic Status

[22] Our results showed the strongest correlation between cumulative growing season P − PET (1 May to image date), from here on referred to as P − PET$_{cum}$ and *med*(Chl *a*)$_{sat}$ (i.e., rho = −0.62, $p < 0.05$) (Table 1). There was also significant correlation between average May temperature, from here on referred to as T$_{may}$ and *med*(Chl *a*)$_{sat}$ (i.e., rho = 0.48, $p < 0.05$). We did not find any significant correlations between wind speed and *med*(Chl *a*)$_{sat}$ (Table 1). The nature of the relation was positive between T$_{may}$ and *med*(Chl *a*)$_{sat}$ (Figure 4a) and negative between P − PET$_{cum}$ and *med*(Chl *a*)$_{sat}$ (Figure 4b). Both relations exhibited nonlinearity. *med*(Chl *a*)$_{sat}$ seemed to reach an upper limit of around 20 μg L^{-1} as T$_{may}$ reached 10°C (Figure 4a). P − PET$_{cum}$ ≈ 0 mm appeared to indicate a threshold in the P − PET$_{cum}$ and *med*(Chl *a*)$_{sat}$ relation (Figure 4b). When P − PET$_{cum}$ < 0 mm (i.e., drier conditions), the slope of the line relating P − PET$_{cum}$ and *med*(Chl *a*)$_{sat}$ was less steep than when P − PET$_{cum}$ > 0 mm (i.e., wetter conditions).

[23] Of the univariate linear models T$_{may}$ and P − PET$_{cum}$ explained 33% and 35% of the variance in *med*(Chl *a*)$_{sat}$, respectively. The variance explained increased to 39% when both T$_{may}$ and P − PET$_{cum}$ were included as explanatory variables in a multivariate linear model predicting *med*(Chl *a*)$_{sat}$. Although the multivariate model for *med*(Chl *a*)$_{sat}$ was statistically significant, the coefficients for T$_{may}$ and P − PET$_{cum}$ were not, suggesting inappr e model structure. Nonlinear tree regressions provided only one significant model, in which *med*(Chl *a*)$_{sat}$ was regressed on P − PET$_{cum}$. The regression tree contained two significant splits, which altogether explained 64% of the total variation in *med*(Chl *a*)$_{sat}$ (Figure 5). The splits reflected a negative relation between P − PET$_{cum}$ and *med*(Chl *a*)$_{sat}$, where wet years (P − PET$_{cum}$ ≥ 67 mm) were associated with low *med*(Chl *a*)$_{sat}$, mesic years (P − PET$_{cum}$ > −53.5 mm and < 67 mm) were associated with moderate *med*(Chl *a*)$_{sat}$ and dry years (P − PET$_{cum}$ < −53.5 mm) were associated with high *med*(Chl *a*)$_{sat}$. While the overall trend was negative between P − PET$_{cum}$ and *med*(Chl *a*)$_{sat}$, the drop in *med*(Chl *a*)$_{sat}$ when P − PET$_{cum}$ > 67 mm was larger than expected under a linear model (Figure 5).

5. Discussion

[24] *Sass et al.* [2007] have shown that there is a common temporal signal in the natural variation of trophic status among 76 lakes on the Boreal Plain of Alberta. Herein we explored the role climate plays in regulating this temporal signal. We tested if there is a link between climate and trophic status, established the strength and nature (i.e., linearity versus nonlinearity) of this link, and provided

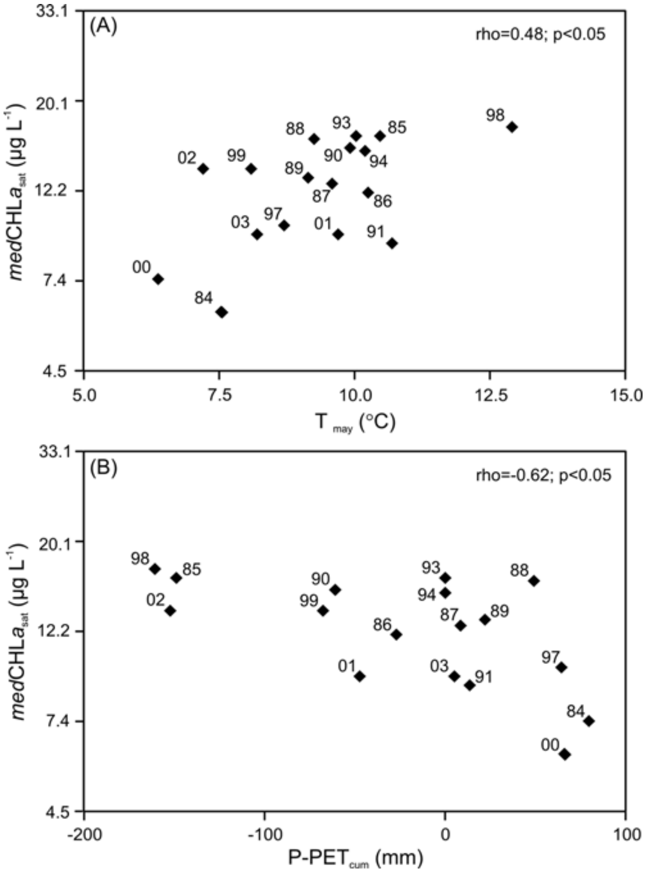

Figure 4. Landscape median (Chl *a*)$_{sat}$ as a function of (a) average May temperature (T$_{may}$) and (b) growing season total of daily total precipitation minus daily total potential evapotranspiration (P − PET$_{cum}$). Scatterplot pairs were chosen on the basis of the highest correlations in Table 1. Note log scale for *y* axis.

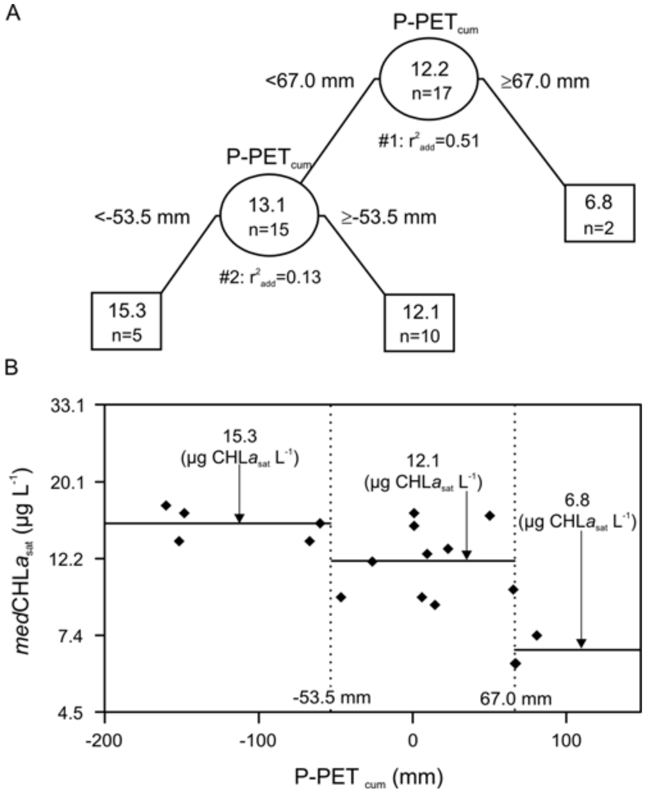

Figure 5. (a) Regression tree and (b) corresponding annotated scatterplot quantifying the relation between landscape median (Chl *a*)$_{sat}$ and growing season total of daily total precipitation minus daily total potential evapotranspiration ($P - PET_{cum}$). The model explained 64% of the total variance in (Chl *a*)$_{sat}$. In Figure 5a, ovals and rectangles represent splitting and terminal nodes, respectively, and numbers within node symbols indicate average (Chl *a*)$_{sat}$ (μg L^{-1}) (back transformed using exponential function) and sample size of that node.

some explanation of what mechanisms could be responsible for the patterns observed.

5.1. Evidence for Climatic Control on Trophic Status

[25] We found evidence for both T and $P - PET$ mediated control on trophic status. Warm springs, as indicated by T_{may} were correlated with high *med*(Chl *a*)$_{sat}$ (Table 1 and Figure 4a). Warmer temperatures in May can potentially affect the growth of algae either directly or indirectly. First, higher temperatures increase the rate of metabolic activity of algae [*Paerl*, 1988]. This is especially true in the case of cyanobacteria, which usually outcompete other algal species in warmer waters [*Elliott et al.*, 2006]. However, our results showed no significant correlations between growing season T and *med*(Chl *a*)$_{sat}$. On the other hand, higher T_{may} may indirectly influence summer trophic status through earlier ice-melt and hence earlier start of resuspension of nutrients from bottom sediments to the water column during windy conditions. Alternatively, it is possible that in years with warmer than usual spring conditions, algae are given a competitive growth advantage over the establishment of submersed aquatic vegetation (SAV) which translates into higher Chl *a* by the end of the summer [*Bayley et al.*, 2007].

[26] Evidence for water mediated control of trophic status was as strong as temperature mediated control. $P - PET_{cum}$ (growing season total) was negatively correlated to *med*(Chl *a*)$_{sat}$ (Table 1 and Figure 4b). Here we interpret $P - PET$ as an indicator of effective precipitation which factors in the effect of evapotranspiration on the overall water budget. $P - PET_{cum}$ might also contain built in radiation and temperature effects (i.e., drier years tend to have more sunlight and be warmer). The hydrologic threshold of $P - PET_{cum} = 0$ mm appeared to mark a distinction between consistently high *med*(Chl *a*)$_{sat}$ conditions when $P - PET_{cum} < 0$ mm to much lower *med*(Chl *a*)$_{sat}$ as $P - PET_{cum}$ increased beyond the threshold. This is consistent with the findings of *Sass and Creed* [2008], who reported that the $P - PET_{cum} = 0$ mm threshold marked the transition from a hydrologically disconnected landscape with isolated wetlands to hydrologically connected landscapes with connected wetlands. In the hydrologically connected landscape, the water depth of Utikuma Lake, a regional lake within the Utikuma Uplands (lake surface area $= 2.9 \times 10^4$ ha), increased by a significantly greater degree than expected from direct precipitation onto the lake [*Sass and Creed*, 2008] reflecting the contributions of runoff from ephemeral draws and lowlands that were not saturated during drier periods but became saturated runoff generating areas during wetter periods [*Devito et al.*, 2000, 2005b]. There was a marked difference in lake level response in Utikuma Lake when $P_{cum} > PET_{cum}$ as compared to lake level response when $P_{cum} < PET_{cum}$ (Figure 6). While our analysis focused on the functioning of the landscape as a whole, we would expect differences in the response of individual lakes to the regional $P - PET > 0$ mm climate signal. The differences will arise because of biophysical properties that control the movement and storage of water the regional climate signal into the lakes.

[27] Climatic regulation of surface hydrologic conditions that govern both lake level fluctuations and surface hydrologic connections between land and lakes may have important implications for the concentration of TP, which is the limiting nutrient to algal growth, and therefore on the interannual variation of Chl *a* within the lakes (Figure 7). During dry periods ($P < PET$), when lakes are generally isolated from surface contributing areas, we hypothesize that lakes function as buckets and TP is regulated by rising or falling water depths. When lake levels are higher TP is diluted, conversely, when lake levels are lower TP is concentrated. Support for this mechanism is given by *Noges et al.* [2003] who showed that as water depths drop, there is an increase in both the concentration of TP and algal biomass in a boreal lake. Similarly, *Markensten* [2006] reported dilution and/or flushing of Chl *a* during periods of high precipitation and discharge in several Swedish lakes monitored over a 30-year period. Other mechanisms that may reinforce the dilution versus concentration process are increased resuspension of bottom nutrients when lake levels are low [*Bengtsson and Hellstrom*, 1992; *Schoenberg and Oliver*, 1988] and the release of nutrients from exposed lake-beds during dry periods and subsequent rewetting [*Covich et al.*, 1997; *Ferone*, 2001]. The relative importance of these processes for our study lakes needs to be established by future field studies.

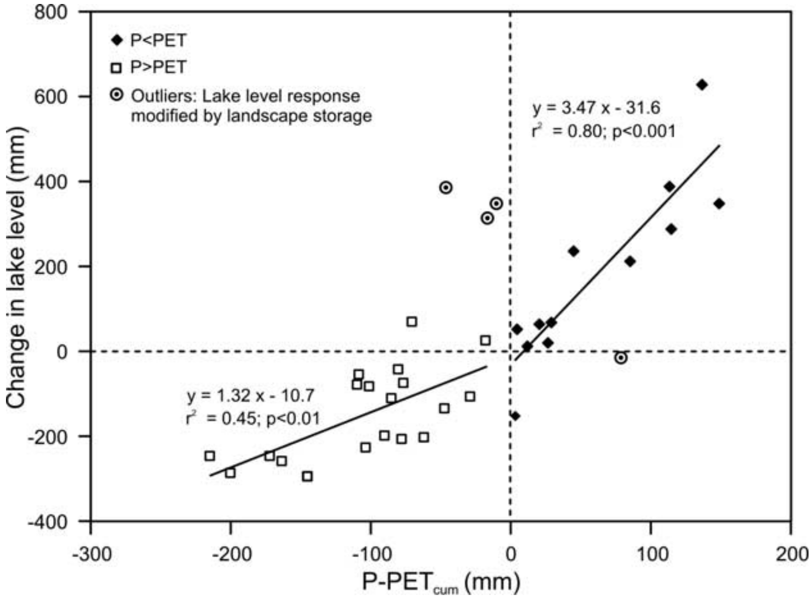

Figure 6. Lake level change measured at Utikuma Lake from the beginning to the end of the growing season as a function of growing season total of daily total precipitation minus daily total potential evapotranspiration ($P - PET_{cum}$). The two regression lines fit to the data show the enhanced response of lake level to climate input when $P - PET_{cum} > 0$ mm, suggesting increased input of water from the landscape. Modified from *Sass and Creed* [2008].

[28] During wet periods ($P \gg PET$), when lakes are generally more connected to surface contributing areas, we hypothesize that lakes collect and store an increasing amount of water which they receive from adjacent wetlands and upland areas contained within their catchments (Figure 7). In many lake systems around the world, increased water input from catchments leads to an influx of nutrients [e.g., *Dillon and Molot*, 2005] and a subsequent rise in lake trophic status. The mechanism responsible for this increase in nutrients is hydrologically regulated flushing, which occurs when a rising water table intersects nutrient rich surface soil layers, mobilizes the nutrients, and initiates lateral transfer of nutrients through surface and shallow subsurface water flow paths. Although event-based hydrologic flushing of phosphorus has been documented in lakes on the western Boreal Plains [e.g., *Evans et al.*, 2000; *Ferone*, 2001], at the timescale of our study, there was no evidence for the flushing mechanism. It appears that the increases in water volume coming from the catchment supersede the transfer of phosphorus into lakes (i.e., the concentration of phosphorus in water flowing into lakes is much lower than the concentration of phosphorus in the lakes).

[29] It is possible that both water supply mediated and water temperature mediated processes are important in explaining the inter-annual changes in trophic status. A weak correlation between T_{may} and $P - PET_{cum}$ (rho = -0.43, $p = 0.09$) suggested that the two climatic variables were possibly indicators of the same climate driver. Physically this makes sense as wetter years tend to be cooler. On the basis of our data set, it was difficult to say with certainty which physical processes ultimately control interannual changes in trophic status. However, the results of the regression tree suggested that the water mediated processes were stronger in influenci phic status.

[30] Although we hypothesized that climate controls on trophic status would be mediated through temperature and precipitation effects, we also tested for the potential effect of wind on the trophic signal measured in our lakes. Others have found wind to have a strong effect on the trophic status of especially shallow lakes, as wind increases turbulence in the water column, which may increase nutrient resuspension from bottom-sediments [*Bengtsson and Hellstrom*, 1992] and/or increase mixing of surface scums formed by cyanobacteria [*Paerl*, 1988]. We did not find any statistical evidence for wind effects on trophic status; however, this could be attributed to the limitation that the wind data came from a climate station located about 80 km from our study region.

5.2. Climatic Versus Biotic Control on Trophic Status

[31] A widely used management technique is to lower water depths to promote the growth of SAV to reduce concentrations of Chl *a* and improve water quality [*Coops and Hosper*, 2002]. This raises the question of why did *med*(Chl $a)_{sat}$ increase when water depth was lowered? On the basis of intensive investigation of individual lakes (lakes that are on average smaller and shallower than the lakes used in our satellite sampling), we know that SAV can grow well in shallow lakes on the Boreal Plain, even when the maximum water depth is only 0.5 m. We also know that this growth is associated with reduced concentrations of Chl *a* [*Bayley and Prather*, 2003; *Norlin et al.*, 2005]. However, in this study, *med*(Chl $a)_{sat}$ was significantly higher in extremely dry years (≈ 15 $\mu g\ L^{-1}$) than during extremely wet years (≈ 7 $\mu g\ L^{-1}$). As mentioned in section 3.2, the imagery used in our estimation of Chl *a* was not sensitive to SAV and therefore it is possible that high Chl *a* lakes also had high SAV. One explanation as to why *med*(Chl $a)_{sat}$ increased when water depth was lowered is that SAV grows

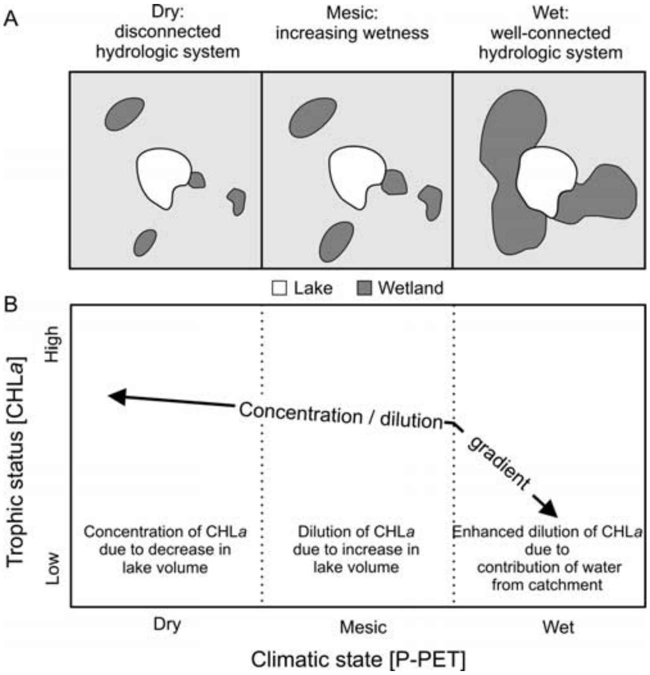

Figure 7. Conceptual model of how lake trophic status changes as a function of climate. Temporal (interannual) changes in trophic status are driven by climatic influence on lake volume. Trophic status, defined in terms of Chl *a*, decreases as a result of dilution because of increasing lake volume. Dilution of Chl *a* is enhanced during wet conditions when water contributions from the catchment increase because of increased surface connections between lakes and their contributing areas.

well but this growth is unable to "clear" the water when the concentration of TP rises. For example, *Bayley and Prather* [2003] found that in a synoptic survey of 148 boreal lakes, 12% of the lakes had high Chl *a* and dense SAV. Similarly, S. Bayley (unpublished data, 2003) found that in another synoptic survey of 79 boreal lakes, 14% of the lakes had high Chl *a* and dense SAV. It is possible that if given enough time, SAV would eventually "clear" up the lakes during those drier years when lake levels are low.

[32] We speculate that climatic control on lake water depths, especially in the extreme drought and extreme flood years, may be more important than other internal controls on Chl *a*. The effects of climate are often difficult to distinguish in individual lakes when so many abiotic and biotic processes may be operating (e.g., internal biotic processes, differential distribution of water and nutrients due to geologic and topographic differences). Only with a large database compiled over a number of years can we distinguish climatic controls on the trophic status of lakes. Part of the reason that the effects of climate are difficult to distinguish is that Chl *a* can change as a function of daily, monthly, seasonal or annual fluctuations of temperature, precipitation, and perhaps other climatic variables such as radiation and wind. The change in $med(\mathrm{Chl}\ a)_{\mathrm{sat}}$ from approximately 15 μg L^{-1} (during dry years) to approximately 7 μg L^{-1} (during wet years) in 76 lakes is significant despite the apparently small differences in $med(\mathrm{Chl}\ a)_{\mathrm{sat}}$. The fact that significant tions were observed between the long-term trophic state data set and climatic variables further highlights the importance of capturing the extremes in climatic conditions in a longer time series. Although our 20-year study period could be considered long enough to capture the extremes in climate conditions as well as the corresponding lake trophic status, there are longer climate cycles that could impart dynamics not fully captured by a 20-year period.

[33] While climate impacts seemed to be most pronounced during extremely dry or wet years, other factors such as topography, surficial geology and internal biotic factors were possibly more important during mesic years (in terms of $\mathrm{P} - \mathrm{PET}_{\mathrm{cum}}$) when water levels were not changing radically. We explored the role of biophysical landscape controls on trophic status in another paper [*Sass et al.*, 2008].

[34] Finally, we considered the extrapolation of the findings from this set of lakes to others in the boreal forest. The negative correlation between P − PET and Chl *a* may apply generally to boreal lakes experiencing subhumid climate and having hydrologic response units characterized by deep surficial deposits and minimal surface relief. A recent study analyzing the relation between climate and dissolved organic carbon measured in 7514 lakes from around the world indicated that there was a negative correlation between the two variables [*Sobek et al.*, 2007]. Therefore, it is possible that such inverse relations between indicators of climate and indicators of trophic status and nutrient status are more general, appearing only when we analyze data sets of large spatial extents or long temporal periods.

6. Conclusions

[35] Advances in remote sensing over the last two decades have opened up a new toolbox for the detection of hydroecological patterns over large spatial and long temporal scales. This has allowed the study of large expanses of the boreal forest which had formerly been unfeasible. In this paper we made use of an archived remote sensing and climatic data set to explore the influence of climate on the interannual variation in the trophic status of 76 lakes over a 20-year period on the subhumid part of the Boreal Plain. We found statistically significant relations between indicators of climate and of trophic status. Our results suggested that both temperature and precipitation mediated processes may effect trophic status. Higher spring temperatures were positively related to algal Chl *a* estimated from Landsat images at the end of summer. On the other hand, growing season effective precipitation (P − PET) was negatively correlated to algal Chl *a*. This suggested that Chl *a* and potentially the underlying phosphorus concentrations were diluted during wetter years. While these climate-trophic status relations were detected at the landscape scale, it is still to be determined how spatial differences in geology and topography might influence the temporal variation in trophic status of individual lakes.

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