

Spatial variability of climate and land-use effects on lakes of the northern Great Plains

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Abstract

Evaluation of the effects of climate change and human activities on lakes requires improved understanding of how stressors interact and the degree to which individual sentinel lakes represent broad spatial patterns of ecosystem response to disturbance. We surveyed modern water chemistry (major ions, conductivity, salinity, lake volume) and sediments (algal pigments, stable isotopes) in 21 lakes that surround Humboldt Lake, Saskatchewan, site of a 2,000-yr climate reconstruction, to quantify spatial synchrony (S , the mean among-lake correlation coefficient) of prairie lake response to climate variability, land use, and their interactions. Whole-lake mass balances of total dissolved substances constructed at each site revealed that evaporation of water controlled seasonal changes in salt content only in years with dry summers (2003), leading to widespread spatial coherence of ecosystems ($S = 0.78$). In contrast, variations in hydrologic inputs (precipitation, groundwater) and solute fluxes regulated salt balances of lakes during years with wet summers (2004, 2005) and substantially reduced lake synchrony ($S = 0.13$ – 0.58). Furthermore, >25% of sites exhibited increased nitrogen influx (as $\delta^{15}\text{N}$) and cyanobacterial production (as fossil pigments) between ca. 1920 and 2003, with particularly strong effects of land use recorded for northeastern sites, where evaporative forcing was greatest. Finally, principal component and canonical ordinations with redundancy analysis both explained ~50% of the variance in lake sensitivity to climate and land use and revealed that the effects of climate and land use interacted strongly, but that the unique effects of each factor remained identifiable in modern lake surveys.

The northern Great Plains of North America are projected to experience increased temperature, increased winter precipitation, and decreased summer precipitation because of global warming by the year 2030 (IPCC 2001). During the past 100 yr, this region has already been subject to intense multiyear droughts during the 1930s, 1980s, and 2000s (Sauchyn et al. 2003) that have adversely affected agricultural production, water quality and availability, and wetland health (Wheaton et al. 1992). However, paleocli-

mate reconstructions for the prairie region have revealed that drought is not only a common phenomenon, but that its intensity during the past millennia has often been more severe than that observed during the 20th century (Fritz et al. 2000; Laird et al. 2003).

Interannual variability in temperature and precipitation on the northern Prairies is influenced by air masses originating over the Pacific Ocean, Arctic, and Gulf of Mexico (Bryson and Hare 1974). Furthermore, climatic variability at decadal, centennial, and millennial scales appears to be affected by changes in atmosphere–ocean linkages, such as the Pacific Decadal Oscillation (PDO; Tian et al. 2006), El Niño–Southern Oscillation (ENSO; Brown et al. 2005), and North Atlantic Oscillation (NAO; Laird et al. 1996), systems which influence the occurrence of both droughts and floods (Shabbar et al. 1997). In general, these continental-scale forcing mechanisms are thought to synchronize variation in the physical and chemical properties of lakes within smaller regions such as the Prairies (Magnuson et al. 1990; Bonsal et al. 2006). However, there is an increasing recognition that variation in lake position within local hydrological landscapes can produce diverse responses of lakes to regional climatic events (e.g., Webster et al. 1996). Additionally, recent research suggests that changes in regional land use, especially agricultural development and urbanization, can alter or obscure lake response to climate variability (Hall et al. 1999; George et al. 2000; Bunting et al. 2007).

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Unfortunately, to date, few studies have quantified how lake sensitivity to climate, land use, and their interactions varies as a function of the geographic position of lakes or how these relationships change through time.

Climate variability can influence prairie lakes by altering the flux of energy and mass to and from lakes, often in a coupled manner. For example, elevated summer temperatures intensify stratification of lakes (Covitch et al. 1997), while increasing evaporative losses of water but not solutes (Webster et al. 1996). In topographically closed basins (no visible surface outflow), these changes lower lake volume and lead to increased ionic concentration in surface waters (Fritz 1990; Schindler et al. 1990). Similarly, changes in precipitation can either increase or decrease lake water salinity and volume depending on the seasonality of precipitation (summer, winter) and the degree to which water enters the lake directly, from surface inflow, or via groundwater (Evans and Prepas 1996; Remenda and Birks 1999; Winter 1999). Because of these multiple pathways, many of which vary as a function of catchment characteristics (Blenckner 2005), quantification of the precise effects of climatic events on lakes often benefits from the comparative use of mass balances (Crowe 1993; Webster et al. 1996), hydrologic or morphometric models (Stone and Fritz 2004), and multiyear monitoring studies (Winter and Rosenberry 1998; Conly and Van der Kamp 2001). Taken together, these studies suggest that changes in prairie lake volume and chemistry (salinity, ionic composition) are under complex multifactor control, with substantial variation possible even among lakes within relatively small geographic regions (e.g., Last 1992; Evans and Prepas 1996). Unfortunately, less is known of how such lake sensitivity to climate varies among years or in response to disturbance from human activities.

European settlement has altered the landscape of the northern Great Plains since ca. 1880, with the most substantial effects following the advent of mechanized agricultural practices (ca. 1920), development of widespread nutrient subsidies (ca. 1940s), and site-specific urbanization (Hall et al. 1999). As with climate effects on lakes, agricultural activities change surface and groundwater hydrology (loss of wetlands, modified groundwater recharge, lotic channelization) and mass flux to lakes (mineral turbidity, dissolved organic matter [DOM], nutrients, agrochemicals, major ions) (e.g., Euliss and Muchet 1996; Soranno et al. 1996), whereas urbanization increases both nutrient inputs and pollution with organic and inorganic toxins (Leavitt et al. 2006). In theory, such similarity of mechanism could make it difficult to distinguish among climatic and anthropogenic causes of variances in lakes. Fortunately, naturally high influx of phosphorus (P) from glacial tills and prairie soils (Klassen 1989) leads to conditions in which influx of nitrogen (N) regulates algal production in many Canadian prairie lakes (Hall et al. 1999; Leavitt et al. 2006). Because excess N from both urban (Savage et al. 2004) and agricultural sources (Anderson and Cabana 2005; Elliott and Brush 2006) has an elevated stable N isotope signature relative to background $\delta^{15}\text{N}$ signals during the past 100 yr (Rusak et al. 2004), it is possible to identify the unique effects of

anthropogenic activities on nutrient influx and lake production from an analysis of N isotopes in lake sediments (e.g., Bunting et al. 2007).

In this paper, we combined whole-lake mass balances of dissolved substances (salt) and water with paleolimnological analyses of algal production (fossil pigments) and N influx (stable isotopes) in 21 prairie lakes to investigate the interactive effects of climate and land use on lake chemistry. Specifically, mass balances were used to quantify temporal and spatial variability in lake response to seasonal and interannual climate variability (evaporation, hydrology), whereas ratios of $\delta^{15}\text{N}$ and algal pigment concentrations in modern and preagricultural sediments (pre-1920) were used to quantify spatial variation of lake response to changes in land use during the 20th century. Finally, principal components and redundancy analyses were used to determine how effects of climate and land use might interact on a landscape scale.

Materials and methods

Study area—Twenty-one lakes were selected from the northern Great Plains of southern Saskatchewan, Canada, to quantify spatial variability in lake sensitivity to climate and land use (Fig. 1; Table 1). This prairie region (49–53°N, 103–108°W) is characterized by a gradient from subhumid continental climate in the northeast to occasionally semiarid conditions in the southwest. Annual summer precipitation averages ~25 cm, with mean temperatures of 12–19°C during the ice-free season (Environment Canada climate normals 1971–2001), while potential evaporation usually exceeds precipitation by 40–60 cm yr⁻¹. Lakes were selected to lie both parallel and perpendicular to the predominant gradients of precipitation deficit, defined as total precipitation minus total potential evaporation (Fig. 1).

Vegetation within the northern Great Plains is composed mainly of agricultural crops (wheat, barley, alfalfa, canola) and mixed-grass pasture (cattle, pigs), whereas the northern limits include an aspen parkland transition. Originally, the region included a mixture of long-, mixed-, and short-grass prairie but was converted to grain agriculture during 1890–1906, with especially intense cultivation beginning in the 1920s and the advent of mechanized agricultural practices (Statistics Canada 1991).

All study lakes are topographically closed basins, with little lotic inflow and no visible outflow. Maximum lake depths vary from 1.3 to 30 m, surface areas from 0.5 to 60.7 km², and volumes from 1.4×10^6 to 5.3×10^8 m³, and most lakes exhibit very high indices of climatic exposure (~10⁶ m), defined as the ratio of lake area to mean depth (Magnuson et al. 1990). Average summer salinity measured as total dissolved substances (TDS) varies from fresh (0.4 g L⁻¹) to saline (50.7 g L⁻¹), dissolved N ranges from ~700 to ~8,000 µg L⁻¹, and dissolved P ranges from ~10 to ~600 µg L⁻¹. Further characteristics of the study lakes are presented in Table 1. Because of the loss of some samples, not all lakes were used in all analyses, although no fewer than 16 sites were included in most instances.

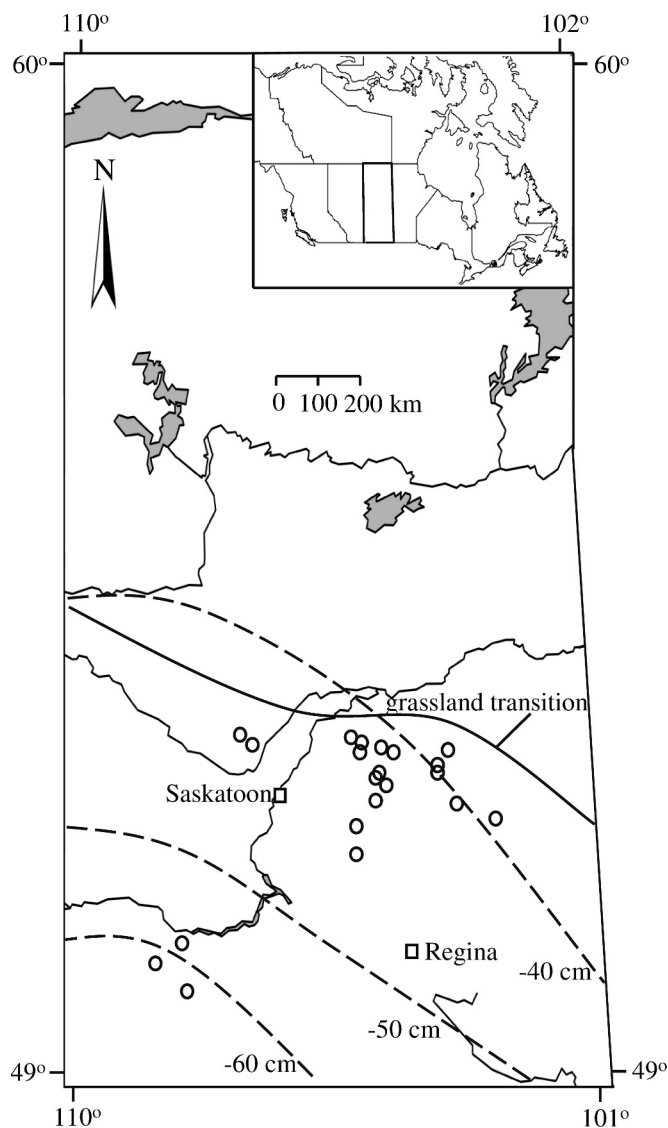


Fig. 1. Location of sampling sites in Saskatchewan, Canada, (open circles), and major cities (open squares). Solid line denotes grassland transition (GT). Dashed lines indicate isopleths of equal precipitation deficit, defined as total precipitation minus total potential evapotranspiration (cm yr^{-1}) (Laird et al. 1996). All lakes are located within endorheic drainage basins.

Physical and chemical analyses—The response of modern physical and chemical properties of each lake to seasonal climatic forcing was measured by visiting each site three times during the ice-free season, including spring (day of the year [DOY] ~ 120), summer (DOY ~ 200), and fall (DOY ~ 280) from 2003 to 2005. All lakes were sampled within a 2-week interval in any given season. Lakes were surveyed for water chemistry in summer 2003 with an integrating tube sampler deployed either throughout the water column ($Z_{\text{max}} < 5.0$ m) or within the uppermost 5.0 m ($Z_{\text{max}} > 5.0$ m). Water samples were filtered through 0.45- μm sterile membrane filters and analyzed for major ions at University of Alberta Water Chemistry Laboratory following standard procedures of Pfaff (1993) and Stainton et al. (1977). Analytes included sodium (Na^+), chloride

(Cl^-), calcium (Ca^{+2}), magnesium (Mg^{+2}), sulfate (SO_4^{-2}), calcium carbonate (CaCO_3), bicarbonate (HCO_3^-), and carbonate (CO_3^{-2}). In all years, salinity (g TDS L^{-1}) and conductivity ($\mu\text{S cm}^{-1}$) were determined at 1-m intervals for the entire water column with the use of a YSI model 85 probe. Overall, probe measurements of salinity during 2003 were highly correlated with the sum of measured ions ($r^2 = 0.884$, $p < 0.0001$); therefore, more highly depth-resolved probe measurements were used to construct salt mass balances (see below).

Lake nutrient status was determined on a subsample of integrated water collected during the summer of 2003. Water was filtered through a 0.45- μm sterile membrane filter before analysis for nitrite (NO_2^-), nitrate (NO_3^-), ammonium (NH_4^+), total Kjeldahl nitrogen (TKN), total organic carbon (TOC), soluble reactive phosphorous (SRP, orthophosphate), and total dissolved phosphorous (TDP) according to the standard methods of Stainton et al. (1977).

Lake response to climate—Seasonal changes in lake levels were measured with a line and surface level method modified from Mossa (1998). In each season and year, a cord was fastened to a permanent structure (e.g., tree, fence) located within 15 m of the lakeshore and was extended on a level plane to the edge of the water, at which point the vertical distance from water surface to plane was measured. Changes in these geometric relationships among seasons were used to estimate seasonal variation in lake level. To estimate lake volumes, bathymetric maps previously produced by Saskatchewan Environment Fisheries Branch and provided through Information Services Canada were digitized into the plotting program SURFER 8.0 (Golden Software 2003). Six lakes (Shannon, Lenore, Lewis Creek, Pellitier, Rabbit, Success) had not been mapped previously, so >100 soundings per lake were used to produce new bathymetric maps during either 2002 or 2003. In all cases, contour intervals were digitized with SURFER and were gridded by a triangulation-with-linear interpolation method (Golden Software 2003). Grid spacing of X and Y were equidistant for all lakes.

Seasonal changes in salt content and lake volume were estimated for each lake and year from digital bathymetric maps and field measurements to determine whether lakes exhibited synchronous variation in salinity. In each season, salinity (g TDS L^{-1}) was measured at the midpoint of each 1-m depth interval with a YSI model 85 probe and was multiplied by the volume of that layer to estimate total salt mass at a given depth. These salt masses were summed for all 1-m layers to estimate total salt content of the lake. Depth-weighted salt concentration (g TDS L^{-1}) in each season was calculated by dividing total salt content into total lake volume for the appropriate season. Spatial synchrony of seasonal changes in salinity was then estimated by standardizing sampling date to DOY 120 (spring), 200 (summer), and 280 (fall); Z -transforming annual time series of salinity for each lake; and calculating lake synchrony (S) following the methods of Patoine and Leavitt (2006). This method is numerically equivalent to estimating the mean Pearson correlation coefficient for Z -transformed seasonal time series of salinity in all pairs of

Table 1. Summary characteristics of study lakes. DOC, dissolved organic carbon. TKN, total Kjeldahl nitrogen.

Lake ID	Lake	Latitude (°N)	Longitude (°W)	Surface			Exposure index			TKN ($\mu\text{g L}^{-1}$)	TP ($\mu\text{g L}^{-1}$)	TKN: TP	DOC (mg L ⁻¹)	Cl (mg L ⁻¹)	SO ₄ (mg L ⁻¹)	Na (mg L ⁻¹)	K (mg L ⁻¹)	Ca (mg L ⁻¹)	Mg (mg L ⁻¹)
				Volume (m ³ ×10 ⁶)	area (km ²)	Elevation (m)	Z _{max} (m)	Salinity (g L ⁻¹)											
43	Antelope	50.28	108.40	62.9	13.8	700.9	5.2	2,661.5	10.7	4,062	250	16	68	524	12,478	3,670	265	14	1,650
11	Arthur	52.56	105.43	11.5	2.9	540.5	4.0	735.0	16	3,681	253	15	61	467	33,265	3,240	370	49	4,360
6	Charron	52.40	104.33	13.9	4.0	555.5	5.0	794.0	7	2,491	131	19	39	424	8,689	1,490	210	46	1,630
56	Clair	51.98	104.05	2.0	1.2	523.8	3.0	386.7	2.2	1,722	103	17	N/A	79	2,511	584	63	126	285
13	Deadmoose	52.31	105.16	74.6	10.9	538.5	29.9	364.5	19	2,607	62	42	41	7,136	14,673	5,950	303	48	1,900
54	Edouard	52.38	104.33	2.8	1.0	580.4	5.0	193.2	0.3	1,983	20	97	N/A	6	209	30	22	35	59
23	Fishing	51.83	103.50	175.5	32.1	529.4	19.5	1,644.6	2.2	1,187	16	76	19	64	2,366	344	76	98	406
20	Humboldt	52.15	105.10	70.5	19.1	543.5	6.0	3,183.3	1.5	1,474	111	13	21	176	1,271	199	64	104	240
55	Kipabiskau	52.56	104.20	19.4	5.2	521.9	8.0	653.8	0.4	742	9	81	N/A	8	201	26	11	47	50
10	Lenore	52.50	104.98	1.4	0.5	536.8	10.0	45.2	3	2,233	28	79	35	215	4,670	748	169	40	900
52	Lewis Creek	51.43	105.51	1.7	2.0	525.5	1.3	1,569.2	1.7	1,907	610	3	32	71	1,889	307	61	142	264
29	Manitou	51.75	105.50	40.1	12.8	492.9	4.3	2,981.4	50.7	6,337	437	15	159	19,009	49,690	16,500	905	48	10,950
9	Middle	52.56	105.16	8.2	5.9	533.9	4.0	1,470.0	33	8,009	324	25	143	2,760	51,587	9,990	768	25	9,450
44	Pellitier	49.98	107.93	9.7	2.9	825.0	8.5	345.9	0.4	696	9	76	10	11	115	46	16	23	78
18	Rabbit	52.60	107.00	9.1	4.6	504.3	4.9	944.9	5.6	2,214	57	39	36	157	7,296	1,250	134	33	1,230
17	Redberry	52.71	107.15	531.5	60.7	501.5	15.5	3,914.2	12.2	1,973	35	56	39	273	17,584	2,580	230	18	3,020
53	Shannon	52.63	105.43	2.6	1.0	548.9	7.3	142.7	2.4	1,465	40	37	23	51	2,936	271	110	59	640
41	Success	50.48	108.01	3.3	0.7	715.4	20.0	36.0	28	2,951	84	35	53	1,286	20,182	6,900	406	5	2,400
7	Wakaw	52.66	105.58	36.0	10.7	510.5	10.0	1,074.0	2.2	934	15	63	16	79	1,261	336	36	220	356
14	Waldsea	52.28	105.20	37.2	4.7	533.1	12.9	362.0	17.5	2,027	45	45	31	4,973	20,214	3,860	317	325	3,360
21	Wolverine	52.01	105.23	3.4	1.4	566.3	1.5	953.3	4.4	2,864	68	42	44	292	20,214	739	173	189	900

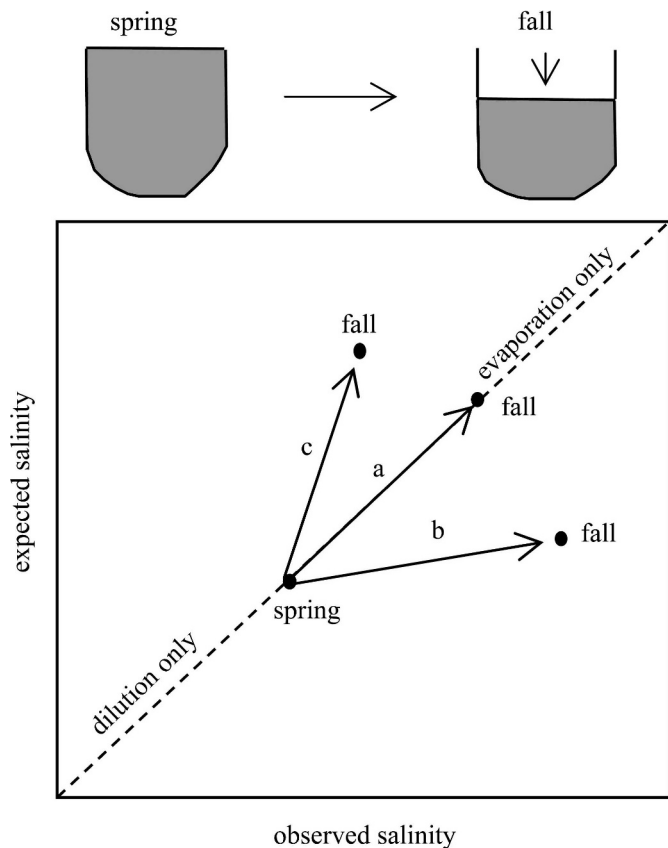


Fig. 2. Schematic diagram of an evaporation model to determine the mechanisms behind seasonal changes in depth-weighted lake water salinity. Expected salinity in fall is calculated by dividing the total mass of dissolved substances (salt) observed in the spring into the volume of lake water observed in fall. Expected salinity equals observed salinity in spring. Under conditions in which lake level declines and evaporation alone controls changes in salinity, observed and expected salinity will be equal and lie on a line of slope 1.0 (arrow a). In contrast, slopes > 1.0 (arrow b) indicate that observed salinity was lower than expected salinity because of unexpected inputs of water (or removal of salts), whereas slopes < 1.0 (arrow c) demonstrate observed salinity is higher than expected salinity, indicating preferential influx of dissolved substances or loss of water by nonevaporative pathways. Interpretations of mechanisms involved in salinity change must include consideration of direction of lake level change to account for potential dilution.

lakes. Strong spatial coherence of seasonal changes in salinity suggests that lakes vary in response to large-scale phenomena such as climate or land use (George et al. 2000; Patoine and Leavitt 2006) and that detailed analysis of individual sentinel ecosystems (e.g., paleoclimate reconstructions) can provide insight into broad-scale regulatory processes.

Digital bathymetric maps and field measurements of lake volume and salinity were also used to quantify the relative importance of evaporation and influx of water or salt as controls of temporal variability of lake water salinity (Fig. 2). In the first step, the observed depth-weighted salt concentration was estimated as above for each lake for both spring and fall periods. We then calculated the depth-

weighted salt concentration expected under conditions in which evaporation was the sole mechanism causing changes in salinity. We assumed that no evaporation had occurred during the initial sampling period and, therefore, that expected and observed salinity were equal in spring. In contrast, we assumed that salts within surface water evaporated during summer were dissolved into underlying lake water and, therefore, that expected salinity in fall could be calculated by dividing the total mass of salt measured in spring into the total volume of water observed in fall. If evaporation alone controlled changes in lake water salinity, then lake level should decline, whereas expected and observed fall salt concentrations would be equal. Under these conditions, seasonal changes in salinity would lie on the 1 : 1 line (slope = 1.0) on plots of expected versus observed salinity (Fig. 2a). In contrast, lakes that received more salt than water (e.g., hypersaline groundwater, dissolution of sedimentary salts, erosional influx) should exhibit slopes < 1.0 (Fig. 2b), whereas lakes that received more water than salt (dilute water inputs, in situ precipitation of salt) should exhibit slopes > 1.0 (Fig. 2c). Interpretation of slopes is more complicated in years during which lake levels increased from spring to fall, in that slopes of ~ 1.0 could also indicate near-perfect dilution of spring salt content with water alone. To address this issue, slopes were compared among years with dry (2003, 38.1 ± 6.8 mm rain month $^{-1}$) and wet summers (2004, 46.2 ± 6.4 ; 2005, 57.6 ± 12.9 mm rain month $^{-1}$).

Preliminary analysis revealed that the slopes calculated above were undefined numerically for lakes during years in which there was little seasonal change in observed salinity (i.e., slope denominator = ~ 0) and that these sites biased maps of lake response to climate (*see below*). Fortunately, this bias could be overcome with the use of either of two procedures. First, we eliminated any site in which slope was > 5.0 or < -5.0 (2–5 lakes yr $^{-1}$) and in which observed salinity varied < 0.5 g TDS L $^{-1}$ during the year. Alternatively, seasonal time series of both observed and expected salinity were first Z-transformed before slopes were estimated. Slopes calculated using these two procedures were highly correlated ($r = 0.790$, $p < 0.0001$) and were not significantly or substantially different (mean \pm SD, slope_{raw} = 0.45 ± 1.69 , slope_{ztransform} = 0.21 ± 1.42). However, because Z-transformation had no measurable effect on the identification of lakes experiencing purely evaporative forcing (i.e., slopes of 1.0 remained 1.0) but allowed us to retain all sites for mapping, we used the Z-transformation to determine spatial patterns of lake response to climate. Other potential transformations (e.g., log, square root, etc.) were deemed inappropriate because of difficulties handling null (0) or negative values.

Spatial patterns of the importance of evaporation in regulating seasonal changes in lake water salinity were estimated by the use of SURFER 8 to map the geographic distribution of slopes derived from the evaporation model (Fig. 2). Interpolations among lakes were calculated with a radial-basis gridding method and a multiquadratic kernel function with equidistant X and Y grid spacing (Golden Software 2003). We predicted that the importance of evaporation would follow regional patterns of precipitation

deficit (Fig. 1) and should be greatest in lakes of southwest Saskatchewan, where semiarid conditions can occur.

Lake response to land use—Lake response to changes in land use during the 20th century was estimated by quantifying changes in algal biomass (as fossil pigments) and nutrient influx (as stable N isotopes) in sediment cores from each site. Analysis of fossil carotenoids and chlorophylls allows accurate reconstruction of changes in production of most major algal groups, whereas N isotopic signatures are often a linear function of allochthonous N influx to the lake (e.g., Anderson and Cabana 2005; Leavitt et al. 2006; Bunting et al. 2007). Changes in inferred N flux and algal production in response to land use practices were estimated by comparing concentrations of fossil pigments and stable isotope ratios in modern (0–2 cm depth) samples with those deposited before agricultural intensification in this region (ca. 1920). Although changes in N cycling in prairie lakes also occur in response to climatic variability over several centuries (Rusak et al. 2004), sedimentary $\delta^{15}\text{N}$ signals exhibit minimal variability ($\pm 0.15\%$) since ca. 1900 in the absence of land use change (Rusak et al. 2004; Leavitt et al. 2006).

Short sediment cores (~40 cm length) were obtained from each survey lake with a 10-cm-diameter Glew gravity corer deployed over the deepest portion of each basin. Surficial sediments (0–2 cm) and those from the bottom of the cores (38–40 cm) were isolated, homogenized, and frozen until analysis for nitrogen isotopes ($\delta^{15}\text{N}$) and sedimentary pigments. We also analyzed activities of ^{137}Cs , total ^{210}Pb , and ^{214}Pb (a direct measure of background or supported ^{210}Pb) in the lowermost samples of all sediment cores according to the gamma spectrometric methods of Engstrom et al. (2006). Because it was impractical to determine precise chronologies for all 21 sites, we used activities of ^{137}Cs and excess (unsupported) ^{210}Pb to estimate whether bottom sediments were deposited before 1945 (no ^{137}Cs) or 1900 (no excess ^{210}Pb). These approximate dates were tested further at two sites where sediment cores were fully dated by ^{210}Pb and ^{14}C analyses (Laird et al. 2003). Although sedimentation rates differed among sites, our analysis revealed that sediment depths >35 cm were uniformly older than 1920, the approximate date of agricultural intensification in this region (Statistics Canada 1991).

Algal pigments from sediments of each lake were extracted, filtered, dried under pure N_2 gas, and quantified with an Agilent (Hewlett Packard) model 1100 high-performance liquid chromatograph (Leavitt and Hodgson 2001). Algal abundance was estimated as organic matter-specific fossil concentrations (nmol pigment g^{-1} organic matter) of compounds that represent the abundance of total algae (chlorophyll *a* [Chl *a*], β -carotene); the siliceous algae (fucoxanthin), mainly diatoms (diatoxanthin), cryptophytes (alloxanthin), total cyanobacteria (echinenone), and colonial *Nostocales* cyanobacteria (canthaxanthin); chlorophytes (Chl *b*); and a mixture of chlorophytes and cyanobacteria (lutein–zeaxanthin) (Leavitt and Hodgson 2001). Algal enrichment during the 20th century was calculated as a ratio of pigment concentrations in modern

and pre-1920 sediments. Because cyanobacteria are most closely associated with elevated production of lakes in this region (Vinebrooke et al. 1998; Patoine et al. 2006), our analysis focused on fossil indicators of total cyanobacteria (echinenone) and *Nostocales* cyanobacteria (canthaxanthin). These pigments were selected rather than aphanizopyll (N_2 -fixing cyanobacteria) or myxoxanthophyll (colonial cyanobacteria) because the former was not completely resolved from background substances in >30% of lakes and the latter was not present consistently in sedimentary records.

Nitrogen isotopic analyses ($\delta^{15}\text{N}$) were completed on modern (surface) and preagricultural (deep) sediment samples from each survey lake. Sediments were freeze dried, homogenized, and packed into tin capsules for combustion. Stable N isotope ratios were determined at the University of Regina's Environmental Quality Analysis Laboratory with a Thermoquest (F-MAT) Delta^{plus} XL isotope ratio mass spectrometer following the procedures of Savage et al. (2004). Changes in N influx during the 20th century were estimated as a ratio of modern $\delta^{15}\text{N}$ to preagricultural $\delta^{15}\text{N}$, with values >1 indicating increased influx of allochthonous N (Leavitt et al. 2006; Bunting et al. 2007). These ratios were compared qualitatively with algal enrichment ratios (*see above*) calculated with the use of echinenone (total cyanobacteria) and canthaxanthin (colonial cyanobacteria) to evaluate potential effects of biological N fixation on changes in the sedimentary isotope signature (Patoine et al. 2006). Spatial patterns of historical changes in sedimentary N isotopes and cyanobacterial production were quantified with SURFER 8 as described above. Such top to bottom comparisons are common in paleoecology (Smol 2002) and have been used successfully in other prairie lakes to evaluate lake sensitivity to climate (Vinebrooke et al. 1998). Although postdepositional degradation of fossil pigments might bias estimates of the degree to which algal biomass has increased (Leavitt and Hodgson 2001), potential sedimentary transformations are not spatially structured (e.g., Vinebrooke et al. 1998; Patoine and Leavitt 2006) and should not alter spatial patterns of land use effects on algal production.

To determine how the $\delta^{15}\text{N}$ signatures of lake sediments varied as a function of local soil characteristics, duplicate soil cores ~25 cm deep were collected from within each lake catchment and analyzed for N isotope content. To minimize the influence of agricultural practices on background isotopic signatures (e.g., tillage, fertilization), all soil cores were taken from within mature Aspen stands >40 yr old near each lake according to Anderson (1986). Surface soils (0–5 cm) were isolated, freeze dried (0.1 kPa), homogenized, and packed in tin capsules for isotopic analysis of $\delta^{15}\text{N}$ as above. Sedimentary and soil $\delta^{15}\text{N}$ values were compared to evaluate whether spatial variation in lake N isotopes reflected site-specific differences in background soil $\delta^{15}\text{N}$, independent of anthropogenic activities.

Climate–land use interactions—Multivariate statistics were used to quantify the complex and covarying effects of climate and land use on prairie lakes. Initially, principal components analysis (PCA) was used to quantify the degree

to which among-site variation in lake sensitivity to climate and land use could be explained by linear gradients of underlying, but unmeasured, environmental variables. Next, redundancy analysis (RDA) was conducted with instrumental records of climate and land use to determine whether this among-lake variability could be explained by linear combinations of measured environmental predictor variables. We inferred that RDA captured the main gradients of environmental variability if both PCA and RDA explained similar and substantial amounts of variance among lakes (Hall et al. 1999). Finally, comparison of predictor and response variables within RDA provided a preliminary measure of the degree to which the effects of lake sensitivity to climate and land use practices were confounded.

All response variables were log-transformed to normalize variance, centered, and standardized before PCA (mean = 0.0, SD = 1.0). Response variables included 20th century changes in key algal taxa (colonial cyanobacteria, total cyanobacteria, diatoms, cryptophytes, chlorophytes, total algae) expressed as modern:pre-1920 pigment concentration ratios (*see above*), as well as concomitant changes in inferred N flux as modern:pre-1920 $\delta^{15}\text{N}$ signatures. In addition, lake sensitivity to climate forcing was estimated as log-transformed standard deviations in lake salinity (not Z-transformed) and lake volume during 2003, the year with the driest summer. PCA ordinations were performed with CANOCO version 4 (ter Braak and Šmilauer 1998).

Redundancy analysis, a direct gradient ordination technique, was used to quantify the proportion of observed variation among lakes that was a linear function of measured land use and climatic variables. Lake response variables in RDA were the same as those used for PCA. In addition, environmental predictor variables (*see below*) related to climate and land use were log-transformed to normalize variance, centered, and standardized before analysis. Environmental variables were removed from the RDA if they were highly correlated with other predictor variables (i.e., variance inflation factors [VIF] $\gg 20$) and did not contribute significantly to the model with forward selection (Hall et al. 1999). Monte Carlo permutation tests with 999 iterations were used to determine significance of the first RDA axis. As a result of standardization, length of arrows in both PCA and RDA are not indicative of the absolute strength of correlations among predictor and response variables, although ordinations can still be interpreted with respect to basic correlations (positive, negative) and factor loading on the ordination axes.

Predictor variables used in RDA ordinations included metrics of both seasonal climatic variability and long-term land use practices. Specifically, climate variables included average ice-free air temperature ($^{\circ}\text{C}$), total annual precipitation as rain (mm), and snowpack (cm) accumulated from the previous winter (all data from Environment Canada weather stations located closest to each site), as well as estimates of gross annual evaporation (mm) (Agriculture and Agri-Food Canada, Regina, Saskatchewan), and direct measurements of lake area (km^2) and volume (10^6 m^3). All climate data were obtained for each

site during 2003, the year of strongest evaporative forcing (*see below*). Land use practices for each lake catchment were estimated from agricultural data obtained from Statistics Canada (2001) Agriculture Community Profiles Census Division data. Catchment-specific variables included the present density of cattle and pigs on farms (both as animals km^{-2}), total farm area (km^2), area of land with manure (km^2), and area of land with commercial fertilizer (km^2); all parameters known to have changed substantially since 1920 and to have influenced the water quality of prairie lakes (Hall et al. 1999). In addition, modern nutrient contents (total N, total P [TP]) of each lake and catchment soil $\delta^{15}\text{N}$ were used as predictor variables related to terrestrial inputs of nutrients. Finally, eigenvalues representing the Euclidean distance between lakes were calculated with the use of eigenvector maps on the basis of the geographic coordinates of each lake following Borcard and Legendre (2002), as modified by Griffith and Peres-Neto (2006). These eigenvectors allowed us to evaluate the potential importance of the geographic relationship among sites (spatial structure) without directly measuring specific underlying environmental gradients. However, although the resulting positive eigenvector maps were included in preliminary RDA ordinations, these spatial predictors had VIF $\gg 20$ (i.e., redundant with other measured predictor variables) and were removed from subsequent analyses.

Results

Lake response to climate—Lake levels declined from spring to fall at all sites except Deadmoose Lake in 2003, the year with the lowest mean summer precipitation ($38.1 \pm 6.8 \text{ mm month}^{-1}$). In contrast, lake levels increased at six sites in 2004 and 11 sites in 2005 (Fig. 3b), years with progressively wetter summers (46.2 ± 6.4 and $57.6 \pm 12.9 \text{ mm month}^{-1}$, respectively). Similarly, mean ($\pm\text{SD}$) declines varied among years, from $-0.39 \pm 0.34 \text{ m}$ in 2003 to $-0.18 \pm 0.29 \text{ m}$ and $+0.1 \pm 0.38 \text{ m}$ in 2004 and 2005, respectively, although no lake exhibited the same pattern of change in volume in all years.

Seasonal patterns of lake water salinity varied synchronously among lakes during dry 2003 (mean $\pm\text{SD}$, $S = 0.78 \pm 0.19$), but were significantly ($p < 0.0001$) and substantially less coherent during the wet years 2004 and 2005 (Fig. 3a). For example, 13 of 16 lakes exhibited coherent seasonal changes in Z-transformed salinity during 2003, a year with relatively little summer precipitation. In contrast, changes in salinity were substantially less coherent in 2004 ($S = 0.57 \pm 0.34$) and 2005 ($S = 0.13 \pm 0.32$), successive years with wet summers. Overall, mean lake-pair synchrony (S) exhibited a marginally significant negative relationship with mean summer rainfall ($r = -0.993$, $p = 0.077$) but was unrelated to changes in mean summer evaporation ($r = 0.252$, $p = 1.000$).

Intra-annual changes in lake salinity were driven mainly by evaporation in dry 2003, whereas seasonal variation in salt content was controlled by changes in flux of salt or water during wetter 2004 and 2005 (Fig. 3b). For example, slopes of plots of observed versus expected fall salinity

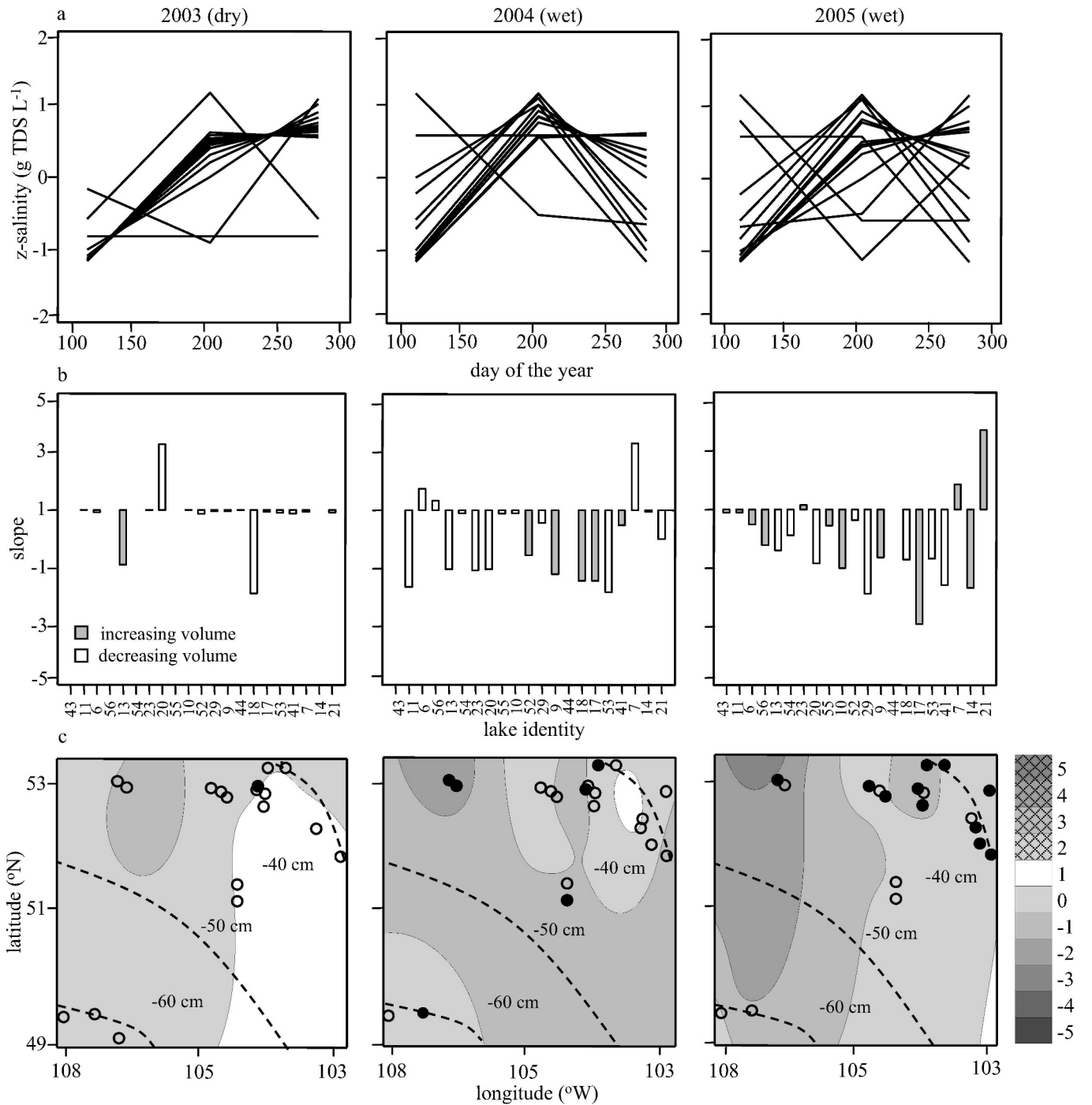
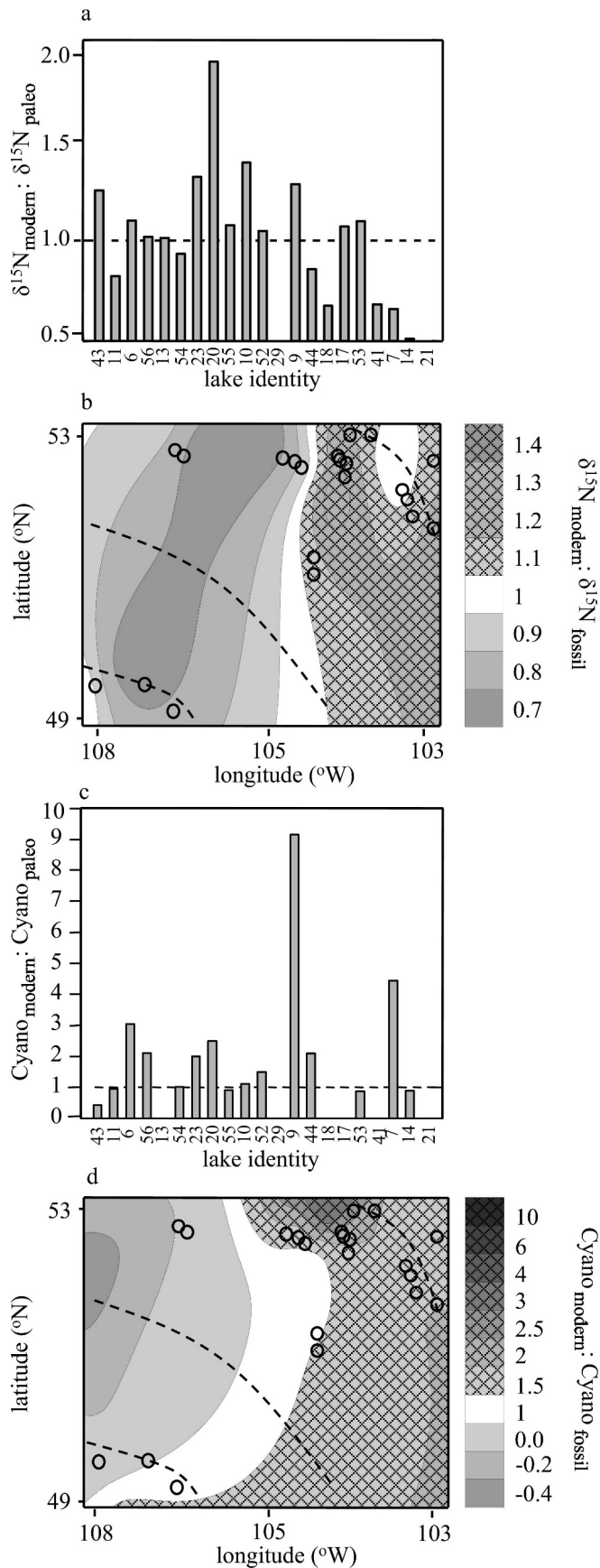


Fig. 3. (a) Seasonal changes in Z-transformed salinity (g TDS L⁻¹) among spring (DOY 120), summer (DOY 200), and fall (DOY 280) in years with dry (2003) and wet summers (2004, 2005). (b) Bar plots showing slope determined from salt mass balance model and Z-transformed seasonal time series of salinity for lakes with declining (open bars) or increasing (closed bars) volume from spring to fall. Slope of ~1.0 and declining lake levels indicate evaporative control of lake hydrology. Lake sequence is arbitrary but the same among years. (c) Spatial patterns of slopes derived from salt mass balance and Z-transformed seasonal time series. Surface interpolations were determined with a radial-basis model with a multiquadratic function calculated in SURFER 8. Dashed lines represent the precipitation deficit (i.e., total precipitation – potential evaporation, cm yr⁻¹). Lake levels either declined (open circles) or increased (closed circles) during the year.

(both Z-transformed) were characteristic of an evaporation-only model (slope ≈ 1.0, lake level decline) for 13 of 16 lakes in 2003. In contrast, most lakes exhibited negative slopes in 2004 (15 lakes) and 2005 (16 lakes), although the

absolute value of slopes and the direction of lake level change differed among years for individual lakes. Similar patterns were observed in analyses of untransformed salinities, with 10 of 14 lakes exhibiting slopes ~1.0 in



2003, but only 5 of 15 and 4 of 17 in 2004 and 2005, respectively (data not shown).

Lake sensitivity to climate was spatially structured regardless of year (Fig. 3c), with evaporative lakes (slope ≈ 1.0 , lake level decline) most common in the northeastern sector of the study region ($\sim 51\text{--}53^{\circ}\text{N}$, $103\text{--}104.5^{\circ}\text{W}$) and nonevaporative lakes most common in the west ($\sim 106\text{--}108^{\circ}\text{W}$). For example, although most lakes exhibited evaporative concentration in 2003, this pattern was particularly pronounced for lakes east of 104.5°W . Similarly, although changes in mass flux of salt or water regulated changes in lake water salinity during 2004 (i.e., negative slopes), lakes with the strongest evaporative signals (slope ≈ 1.0 , lake level decline) were congregated again in the northeast sector. In general, the northeastern location of evaporative lakes in 2003 and 2004 contrasts strongly with average gradients of precipitation deficit (precipitation – potential evaporation; Fig. 3c), which suggest that the strongest evaporative forcing should occur in the southwest region ($\sim 49^{\circ}\text{N}$, 108°W). However, although evaporative lakes were also occasionally present in the northeast during 2005, most regional lakes experienced increased lake level consistent with elevated summer rainfall in that region.

Lake response to land use—Stable isotope analyses suggested that lakes exhibited a wide range of nutrient enrichment during the 20th century, recorded as changes in $\delta^{15}\text{N}$ signatures of modern sediments relative to those deposited before ca. 1920 (Fig. 4a). For example, $\sim 25\%$ of sites recorded substantial historical increases in sedimentary $\delta^{15}\text{N}$ (i.e., $>50\%$ increase of $\delta^{15}\text{N}$), with the most substantial increase ($\sim 5\text{‰}$) occurring at Humboldt Lake, site of documented urban wastewater inputs (Rusak et al. 2004). In contrast, other sites showed either stable or declining ratios of sedimentary $\delta^{15}\text{N}$ signatures during the 20th century. Historical changes in sedimentary $\delta^{15}\text{N}$ were also structured in space (Fig. 4b), with elevated modern:historical $\delta^{15}\text{N}$ ratios in the relatively humid east and northeast regions and neutral (~ 1.0) or fractional ratios at western sites ($>105.5^{\circ}\text{W}$).

Stable N isotope ratios in lake sediments could have underestimated increases in N loadings to some lakes during the 20th century because of increases in cyanobacteria that fix atmospheric N of low $\delta^{15}\text{N}$ ($\sim 0\text{‰}$) (Patoine et al. 2006). For example, total cyanobacteria (as echinenone) increased two- to 10-fold in seven prairie lakes (Fig. 4c),

Fig. 4. (a) Bar plot of isotopic nitrogen signatures of modern to preagricultural sediment ratios ($\delta^{15}\text{N}_{\text{modern}} : \delta^{15}\text{N}_{\text{pre-1920}}$) in survey lakes. Dashed line indicates no historical enrichment of isotopic signatures. (b) Spatial patterns of sedimentary $\delta^{15}\text{N}_{\text{modern}} : \delta^{15}\text{N}_{\text{pre-1920}}$ ratios calculated with SURFER 8 as in Fig. 3. (c) Bar plot of modern:preagricultural ratios of total cyanobacterial abundance (as fossil echinenone). Dashed line indicates no historical enrichment of total cyanobacterial pigments. (d) Spatial patterns of cyanobacterial pigment enrichment determined as in Fig. 3. Negative ratios arise from SURFER 8 extrapolation beyond the lake survey and should not be interpreted.

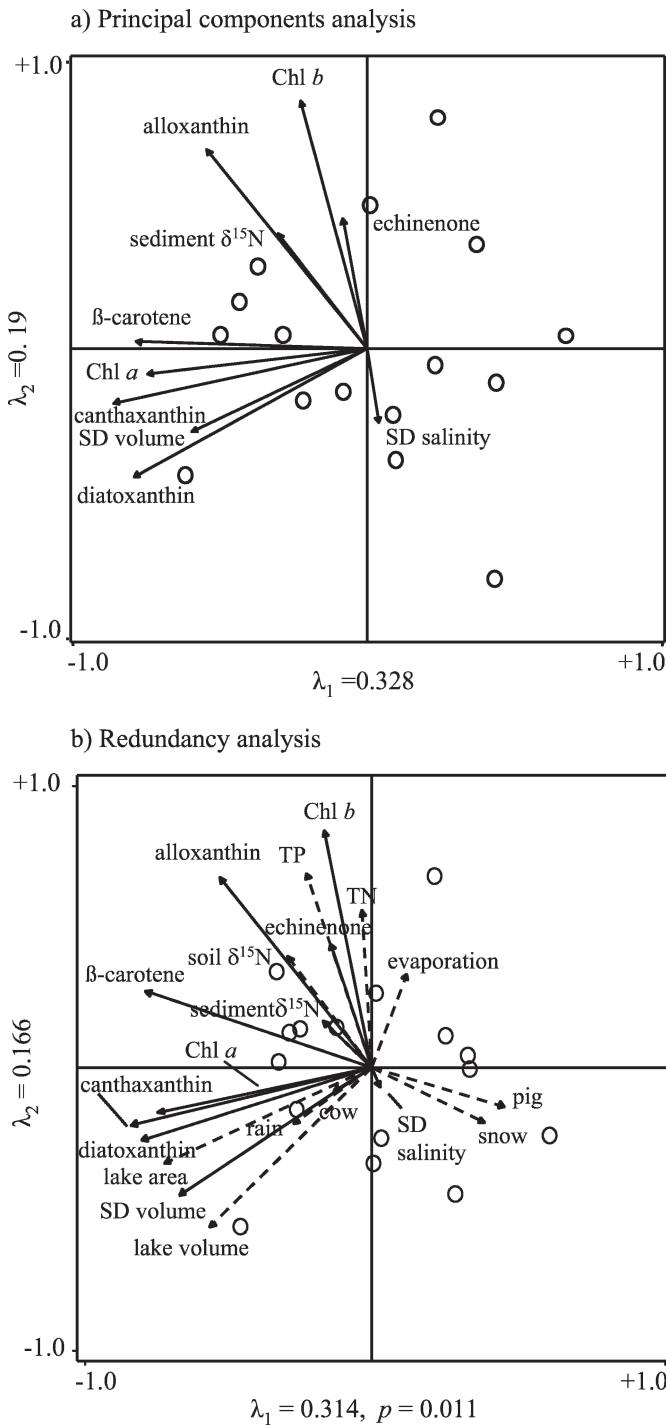


Fig. 5. (a) Principal components analysis (PCA) ordination diagram illustrating the relationship of lakes (open circles) and response variables (solid arrows) relative to first ($\lambda_1 = 0.328$) and second ($\lambda_2 = 0.19$) PC axes. All response variables were log-transformed and included seasonal standard deviations of lake water salinity and lake volume during 2003 and modern pre-agricultural sedimentary ratios of alloxanthin (cryptophytes), diatoxanthin (mainly diatoms), Chl *b* (chlorophytes), echinenone (total cyanobacteria), canthaxanthin (*Nostocales* cyanobacteria), Chl *a* (labile fossil, all algae) and β -carotene (stable fossil, all algae), and $\delta^{15}\text{N}$ (N influx). (b) Redundancy analysis (RDA) ordination diagram illustrating relationship between lakes (open

circles), response variables (solid arrows), and significant environmental predictors (dashed arrows) measured during 2003. Environmental predictors include present cattle density on farms (animals km^{-2}), surface soil $\delta^{15}\text{N}$, density of pigs on farms (animals km^{-2}), total rainfall (mm), total evapotranspiration (mm), lake surface area (km^2), total lake volume (m^3), and total snow pack (cm). Similar and high degrees of explained variance on the first two axes ($\sim 50\%$) in both PCA and RDA suggest lake variability in climate and land use sensitivity is structured along linear gradients and that RDA adequately captured these gradients.

whereas colonial *Nostocales* (as canthaxanthin), many of which fix nitrogen, increased 50–300% in 10 study lakes (data not shown). In general, increases in total cyanobacterial (Fig. 4d) exhibited similar spatial patterns to those observed with sedimentary N isotopes (Fig. 4b), with the most substantial increases recorded at eastern sites. In contrast, the abundance of *Nostocales* cyanobacteria generally declined since 1920 in northeastern lakes, while these algae increased most at western sites (data not shown).

Climate and land use interactions—Principal components analysis captured 51.8% of variance among lakes along the first ($\lambda_1 = 0.328$) and second ($\lambda_2 = 0.190$) ordination axes (Fig. 5a). PCA axis 1 was negatively correlated with seasonal deviations in lake volume, and historical changes in abundance of total algae (β -carotene, Chl *a*), *Nostocales* cyanobacteria (canthaxanthin), and diatoms (diatoxanthin). In contrast, the second axis was correlated negatively to seasonal deviations in lake water salinity and positively with historical increases in total cyanobacteria (echinenone), green algae (Chl *b*), cryptophytes (alloxanthin), and N influx ($\delta^{15}\text{N}$).

Redundancy analysis explained a similar (48.0%) and significant ($p = 0.005$) amount of variance, as did PCA on first ($\lambda_1 = 0.314$) and second ($\lambda_2 = 0.166$) axes (Fig. 5b). As in the PCA, RDA axis 1 was correlated negatively with historical changes in abundance of total algae (β -carotene, Chl *a*), *Nostocales* cyanobacteria (canthaxanthin), and diatoms (diatoxanthin) and with seasonal variability in lake volume. However, RDA further revealed that several response variables were significantly correlated ($p = 0.1$ to <0.01) with lake area and volume (canthaxanthin, seasonal change in lake level), cattle density on farms (Chl *a*, seasonal salinity change), and the N isotope signature of undisturbed catchment soils (seasonal salinity change, alloxanthin, Chl *b*). Furthermore, RDA axis 1 was positively correlated with the previous winter's snowpack depth and the density of pigs on modern farms. In contrast, RDA axis 2 was positively correlated with historical increases in the abundance of total cyanobacteria (echinenone), cryptophytes (alloxanthin), and green algae (Chl *b*), as well as several predictor variables, including lake nutrient status (TKN, TP) and, to a lesser extent, soil $\delta^{15}\text{N}$, whereas lake volume was negatively correlated with RDA axis 2. Together, these patterns suggest that modern climate and historical land use practices interact in complex

ways to regulate the chemical and biological properties of prairie lakes, but that the unique effects of each factor remained identifiable on a landscape basis.

Discussion

Use of salt mass balances revealed that the mechanism by which climate influences prairie lakes varies among years, with evaporative losses of water regulating seasonal variation in salinity during years with dry summers and nonevaporative mechanisms (changes in mass flux of water and salt) controlling variability of salt content in years with wet summers (Fig. 3b). Furthermore, evaporative and mass flux-based mechanisms appear to have different effects on the spatial synchrony of lakes, with elevated summer rain reducing coherence among sites (Fig. 3a). Unexpectedly, northeastern lakes that exhibited the most consistent evaporative forcing among years were also the sites with the greatest inferred increases in N influx from land (Fig. 4b) and cyanobacterial production (Fig. 4d), suggesting that lake sensitivity to climate variability and land use practices interact, at least on a landscape scale. Redundancy analysis confirmed these interactions by demonstrating, for example, that seasonal variability in lake water salinity was significantly correlated with background soil $\delta^{15}\text{N}$ ($p < 0.05$), water column N ($p < 0.01$), and, to a lesser extent, cattle density ($p < 0.1$), all indices of nutrient loading to lakes. However, despite these overlaps, variables related to both intra-annual climate variability and long-term land use practices were retained in RDA analyses (Fig. 5b), demonstrating that each exerted unique effects on the production and chemical composition of prairie lakes.

Climatic effects—The main finding of this study was that lake salinity varied synchronously over a large region (ca. 49–53°N, 103–108°W) because of evaporative loss of lake water during a dry summer. This finding is consistent with studies of spring ice melt that suggest regional synchrony can result from changes in mean air temperature over lakes and rivers (e.g., Magnuson et al. 2000; Bonsal et al. 2006) and with investigations of algal phenology that demonstrate high spatial coherence for taxa influenced by changes in lake stratification (George et al. 2000; McGowan et al. 2005). In all cases, spatial coherence among sites appears to result from increased transfer of energy to the lake surface, rather than changes in mass flux, and is consistent with observations that lakes with high exposure indices (Table 1) are especially sensitive to climatic variability (Magnuson et al. 1990; Patoine and Leavitt 2006) and that variability in prairie lake volume was significantly correlated with lake area ($r = 0.878$, $p < 0.01$; Fig. 5b). Although widespread changes in groundwater chemistry could also lead to synchronous variation in lake water salinity (Last 1999), our lakes are underlain by several discrete confined intertill and unconfined surficial aquifers (e.g., Dalmeny, Condie, Logan, Blucher, and Conquest aquifers), each with little lateral connection (Pupp et al. 1991; Van der Kamp and Hayashi 1998), suggesting that large-scale coherence from groundwater intrusion is unlikely. Furthermore,

analysis of salt mass balances revealed that groundwater inputs were limited (slope ≈ 1.0) in 13 of 16 lakes during 2003 (Fig. 3b) despite high lake synchrony (Fig. 3a). Taken together, these patterns suggest that spatial synchrony of seasonal changes in lake water salinity of prairie lakes arises mainly during dry summers.

Changes in mass flux, particularly of water, appeared to reduce seasonal synchrony of prairie lake chemistry. For example, mean pairwise synchrony declined from 0.78 ± 0.19 in 2003 to 0.57 ± 0.34 and 0.13 ± 0.32 in 2004 and 2005, respectively, a pattern that was linearly related to increased summer precipitation ($r = -0.993$, $p = 0.077$) but not to changes in potential evaporation ($r = 0.252$, $p = 1.000$). Similarly, analysis of salt mass balances in 2004 and 2005 (Fig. 3b) revealed that most lakes in both years exhibited substantial influence of hydrologic variability (slope = -1.0 to -2.0), either because of lake level increase or decline (Fig. 3b,c). These patterns are also consistent with the findings of Almendinger (1990) and Fritz et al. (2000), who suggested that differential inputs of groundwater caused century-scale asynchrony in chemistry of other closely spaced prairie lakes, and with those of Webster et al. (1996), who found that the chemical response of lakes to drought varied as a function of the relative importance of direct precipitation and groundwater fluxes. High spatial variability of groundwater effects might reflect the patchy geographic distribution of snow and summer precipitation (Walker et al. 1995; Quiring and Papakyriakou 2005), as well as the discontinuous nature of regional aquifers (Van der Kamp and Hayashi 1998) compared with spatial patterns of temperature variability (Whitfield et al. 2002).

Although based on only 3 years of analysis with 21 lakes, comparison among years suggests that synchrony in limnological time series might arise from the disproportionately strong effect of specific *coordinating events* rather than a consistent temporal response of lakes to climatic forcing. For example, both Rusak et al. (1999) and McGowan et al. (2005) noted that although time series of plankton abundance exhibited significant synchrony among regional lakes at the scale of a decade, annual coherence varied from $S = 0.0$ – 0.70 among individual years, at least in part because of the influence of specific ENSO events (e.g., 1997). Our mass balance studies refine this observation for lakes of the northern Great Plains by suggesting that lake coherence occurs only during years in which energy transfer (evaporation) is the predominant mechanism altering lake chemistry, whereas mass flux of water and dissolved substances leads to the spatially heterogeneous patterns of lake chemistry change seen in other surveys (e.g., Last 1992). Furthermore, we suggest that it is the absence of precipitation that maintains the importance of energy transfer as a coordinating event, consistent with prior observations that multiyear droughts have a disproportionately strong effect on prairie ecosystems (e.g., 1930s).

Spatial patterns of evaporative forcing did not follow long-term landscape gradients of precipitation deficit known for this region (Figs. 1, 3c). For example, salt mass balances calculated for 2003 and 2004 revealed that

seasonal changes in salinity of northeastern lakes ($>52^{\circ}\text{N}$, $<105^{\circ}\text{W}$) were controlled mainly by evaporation of lake water, despite their location in a relatively humid region of the study area. Similar lack of spatial congruence between lake chemistry and geographic gradients of climate features have also been reported by Gorham et al. (1983) and Last (1992), although those authors quantified variance in the species and quantity of dissolved salts rather than lake sensitivity to climate. In all cases, previous investigations identified groundwater composition as the principle factor influencing geographic gradients in lake chemistry. Unfortunately, although spatially structured variation in fluxes of salt and groundwater might also be responsible for geographic patterns in evaporative forcing observed in this study, detailed hydrologic monitoring at each site (e.g., Almendinger 1990) was beyond the scope of this analysis. Instead, we suggest that the lack of spatial congruence of measured (Fig. 3b) and expected (Fig. 1) evaporative forcing could result from differences in the temporal scale of sampling among studies (annual and decadal, respectively). Consistent with this view, we note that lake level changes in 2005 largely corresponded to long-term geographic gradients of precipitation in the prairie study region (i.e., more humid in northeast region).

Land use effects—Stable isotope analysis revealed that 25% of prairie lakes exhibited substantial increases in N influx during the 20th century, recorded as elevated $\delta^{15}\text{N}$ in modern sediments relative to those in preagricultural deposits (Fig. 4a). As shown elsewhere, sedimentary $\delta^{15}\text{N}$ increases as a linear function of agricultural intensity, particularly the mass of N added as fertilizer (Anderson and Cabana 2005; Elliot and Brush 2006; Bunting et al. 2007). Taken together, these studies suggest that it is the presence of N in excess of terrestrial requirements of plants and microbes that allow highly fractionating transformations (e.g., nitrification, denitrification, NH_3 volatilization) to enrich terrestrial N pools with ^{15}N . Consequently, although the N isotope signature can vary initially among individual N sources (e.g., synthetic fertilizer, manure) (Kendall 1998), $\delta^{15}\text{N}$ signatures consistently increase as a function of total N use by farms (Anderson and Cabana 2005; Elliot and Brush 2006; Bunting et al. 2007). Similar N isotopic enrichment also occurs when lakes receive urban wastewaters because secondary and tertiary sewage treatment processes also favor selective loss of ^{14}N via denitrification and NH_3 volatilization (reviewed in Leavitt et al. 2006). Consistent with this view, $\delta^{15}\text{N}$ ratios increased from $\sim 5\text{‰}$ to nearly 10‰ at Humbolt Lake, site of the sole documented urban wastewater influx (Rusak et al. 2004).

Presumptive effects of agriculture and urbanization on N influx to prairie lakes were greatest at northeastern sites (Fig. 4b) located at the boreal–grassland transition (Fig. 1) where soil $\delta^{15}\text{N}$ was highest (Fig. 5b). These same sites also experienced the greatest increase in abundance of total cyanobacteria (Fig. 4d), consistent with eutrophication of prairie surface waters by agricultural or urban runoff (Hall et al. 1999; Leavitt et al. 2006). Although close spatial correspondence of increases in total cyanobacterial production and N influx is consistent with lake eutrophication

by allochthonous N inputs (see Leavitt et al. 2006; Bunting et al. 2007), two lines of evidence suggest that P rather than N influx controlled water quality degradation since 1920 at the boreal–grassland transition. First, modern chemical analyses (Table 1) show that although mean ($\pm\text{SD}$) TP concentrations are presently great ($129 \pm 160 \mu\text{g P L}^{-1}$), so are TKN:TP mass ratios (42 ± 25), suggesting that P influx limited algal growth in most lakes. Second, concentrations of pigments from potentially N_2 -fixing cyanobacteria (canthaxanthin) decreased in most northeastern lake since ca. 1920 (data not shown), suggesting lesser requirements for N after the advent of agriculture. Instead, lake response to land use was greatest at the edge of the boreal forest transition, sites that also exhibited the greatest evaporative forcing of lake chemistry during dry years, as well as the greatest increase in lake level during wet years (Fig. 3c). As documented by Schindler et al. (1990, 1996), both evaporative concentration of autochthonous nutrients and increased delivery of allochthonous nutrients can increase algal production in lakes.

Climate and land use interactions—Both qualitative comparisons of spatial gradients (e.g., Fig. 3c compared with Fig. 4b, see above) and multivariate analyses (Fig. 5) demonstrated that lake sensitivity to climate and land use covaried on a landscape scale, although the mechanisms that underlie these changes were not always evident. For example, redundancy analysis explained $>30\%$ of variation among lakes on the first ordination axis and suggested that both historical changes in the abundance of many algal groups (diatoms, *Nostocales* cyanobacteria, total algae) and seasonal variability in lake volume were correlated with lake size, density of livestock on farms, and the N isotope signature of undisturbed catchment soils. Similar interactive effects of climate and land use on both algal abundance (Hall et al. 1999) and synchrony among lakes (Patoine and Leavitt 2006) have been recorded for other regional lakes ($\sim 50.4^{\circ}\text{N}$, $102\text{--}106^{\circ}\text{W}$), suggesting that few prairie sites record or experience unique effects of climate or land use alone. Instead, we suggest that variability enters lake ecosystems when climate and humans alter influx of mass or energy. Furthermore, because land use practices rarely alter energy inputs to lakes (cf., thermal pollution), we suggest that climate and land use interact mainly through changes in hydrology.

Comparison of multivariate analyses suggests that RDA captured all extant linear gradients of environmental variability. For example, because both PCA and RDA explained $\sim 50\%$ of the variance among lakes on the first two axes ($\sim 70\%$ on all axes), while producing very similar ordinations of response variables (5a,b, respectively), we infer that no further linear gradients of environmental change could explain variation in lake response to climate and land use. Consistent with this view, spatially explicit eigenvalues representing the Euclidean distance between lakes did not explain unique variation in lake properties ($\text{VIF} \gg 20$) and were not retained in the final RDA. Together, these patterns suggest that residual variance was either geographically unstructured or was not organized along linear orthogonal gradients.

Differences in timescale of variability between climate (seasonal, interannual) and land use effects (decadal, centennial) likely obscured complex, slow, or lagged interactions between forcing mechanisms (e.g., slow aquifer replenishment). Prior comparisons of prairie lake sensitivity to climate (Hall et al. 1999; Fritz et al. 2000) suggested that a large region must be surveyed to avoid bias associated with local groundwater anomalies and to capture extant climatic gradients (e.g., Fig. 1). Unfortunately, although our study region encompassed >100,000 km², such intensive sampling (ca. 60 lake-years) precluded longer term studies of climatic variability. Regardless, we believe that our analysis encompassed a substantial proportion of the full range of climatic variability exhibited during the 20th century because this region experienced a drought during ca. 2000–2003 that was as severe, though less spatially extensive, as that of the 1930s (Sauchyn et al. 2003; Bonsal and Wheaton 2005).

In conclusion, the use of salt mass balances suggested that climate exhibits two distinct pathways that influence prairie lakes. First, evaporation of water (a result of energy transfer) acts as a coordinating mechanism that induces spatial synchrony of regional lakes. In contrast, precipitation (mass transfer) reduces the geographic seasonal coherence of lakes, likely because of the patchy distribution of individual precipitation events (Walker et al. 1995; Quiring and Papakyriakou 2005) and high spatial variability in groundwater recharge (Van der Kamp and Hayashi 1998). Although climatic and anthropogenic forcing mechanisms can be either synergistic or antagonistic when a common pathway is disturbed (e.g., surface hydrology), future research is required to predict the outcome of complex interactions between energetic and mass flux pathways (e.g., warmer, wetter future scenarios). In this regard, we feel that an ecosystem's balance of mass and energy transfer could be particularly informative, particularly if they include a wide range of lakes, prolonged monitoring periods, and analyses of both specific ions and stable isotopes ($\delta^2\text{H}$, $\delta^{18}\text{O}$) to distinguish among summer and winter sources of water.

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