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Structuring features of lake districts: landscape controls on lake chemical responses to drought

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SUMMARY

1. Within a lake district of relatively homogeneous geomorphology, the responses of lakes to climate are influenced by the complexity of the hydrogeologic setting, position in the landscape, and lake-specific biological and physical features. We examined lake chemical responses to drought in surface water- and groundwater-dominated districts to address two general questions. (1) Are spatial patterns in chemical dynamics among lakes *uniform* and synchronous within a lake district, suggesting broad geomorphic controls; variable in a *spatially explicit* pattern, with synchrony related to landscape position, suggesting hydrologic flowpath controls; or *spatially unstructured* and asynchronous, suggesting overriding control by lake-specific factors? (2) Are lake responses to drought a simple function of precipitation quantity or are they dictated by more complex interactions among climate, unique lake features, and hydrologic setting?

2. Annual open-water means for epilimnetic concentrations of chloride, calcium, sulfate, ANC, DOC, total nitrogen, silica, total phosphorus, and chlorophyll *a* measured between 1982 and 1995 were assembled for lakes in the Red Lake and ELA districts of north-western Ontario, the Muskoka – Dorset district in south-central Ontario, and the Northern Highland district of Wisconsin. Within each district, we compared responses of lakes classified by landscape position into highland or lowland, depending on relative location within the local to regional hydrologic flow system. Synchrony, defined as a measure of the similarity in inter-annual dynamics among lakes within a district, was quantified as the Pearson product-moment correlation (*r*) between two lakes with observations paired by year. To determine if solute concentrations were directly related to interannual variations in precipitation quantity, we used regression analysis to fit district-wide slopes describing the relationship between each chemical variable and annual (June to May) and October to May (Oct–May) precipitation.

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3. Among lakes in each of the three Ontario districts, the pattern of chemical response to interannual shifts in precipitation was spatially uniform. In these surface water-dominated districts, solute concentrations were generally a simple function of precipitation. Conservative solutes, like calcium and chloride, tended to be more synchronous and were negatively related to precipitation. Solutes such as silica, total phosphorus, and chlorophyll *a*, which are influenced by in-lake processes, were less synchronous and relationships with precipitation tended to be positive or absent.

4. In the groundwater-dominated Northern Highland lakes of Wisconsin, we observed spatial structure in drought response, with lowland lakes more synchronous than highland lakes. However, there was no evidence for a direct relationship between any solute and precipitation. Instead, increases in the concentration of the conservative ion calcium during drought were not followed by a symmetrical return to pre-drought conditions when precipitation returned to normal or above-average values.

5. For calcium, time lags in recovery from drought appeared related to hydrologic features in a complex way. In the highland Crystal Lake, calcium concentrations tracked lake stage inversely, with a return to pre-drought concentrations and lake stage five years after the drought. This pattern suggests strong evaporative controls. In contrast, after five years of normal precipitation, calcium in the lowland Sparkling Lake had not returned to pre-drought conditions despite a rebound in lake stage. This result suggests that calcium concentrations in lowland lakes were controlled more by regional groundwater flowpaths, which track climatic signals more slowly.

6. Temporal dynamics driven by climate were most similar among lakes in districts that have a relatively simple hydrology, such as ELA. Where hydrologic setting was more complex, as in the groundwater-dominated Northern Highland of Wisconsin, the expression of climate signals in lakes showed lags and spatial patterns related to landscape position. In general, we expect that landscape and lake-specific factors become increasingly important in lake districts with more heterogeneous hydrogeology, topography or land use. These strong chemical responses to climate need to be considered when interpreting the responses of lakes to other regional disturbances.

Keywords: calcium, climate, groundwater, hydrology, lake–groundwater interactions, lakes, landscape position, long term research, Ontario, regionalisation, seepage, water chemistry, Wisconsin

Introduction

Regionalisation, the extrapolation from a few intensively studied sites to larger geographic areas, is of considerable interest to ecologists (Turner, Dale & Gardner, 1989) and has become more of a priority as we grapple with environmental issues that affect ecosystems at regional to global scales (Vitousek, 1994). For lakes, regionalisation schemes have generally relied on catchment and in-lake attributes to predict characteristics of unmonitored sites (Dillon & Kirchner, 1975; Rochelle et al., 1989). Recently, limnologists have developed a spatially explicit view of lake districts in which lake features and their dynamics are constrained by underlying geomorphic templates formed by forces such as glaciation (Magnuson & Kratz in press; Riera *et al.*, 2000). Landscape position, defined as spatial location along a local to regional hydrologic flowpath, potentially provides significant explanatory power for a wide range of morphometric, chemical and biologic attributes of lakes (Kratz *et al.*, 1997; Soranno *et al.*, 1999; Riera *et al.*, 2000).

Because this landscape perspective explicitly views lakes as hydrologically connected to their catchments and to each other, climate is assumed to be an important driver of temporal variability (Magnuson, Benson & Kratz, 1990; Webster *et al.*, 1996). Strong climatic events, such as drought, imposed over broad geographic areas, thus provide a particularly useful regional disturbance to explore relationships between landscape position and lake dynamics.

We propose that the pattern of lake chemical response to drought depends on hydrogeologic complexity within a lake district. Patterns will be either spatially uniform and synchronous, spatially structured with synchrony related to landscape position, or spatially unstructured and asynchronous (Fig. 1). In the first case, a uniform response to climate will occur in lake districts with a relatively simple hydrogeology. Spatially structured patterns will develop where landscape position influences the sources and fluxes of water and solutes between lakes and the surrounding landscape (Cheng & Anderson 1994; Webster *et al.*, 1996; Kratz *et al.*, 1997). Finally, unstructured patterns should occur where controls by lake-specific factors, such as morphometry, affect physical properties, internal cycling and water residence time, or where food web interactions are strong and override the effect of climate (Fee & Hecky, 1992; Fee *et al.*, 1996; Baines *et al.*, 2000).

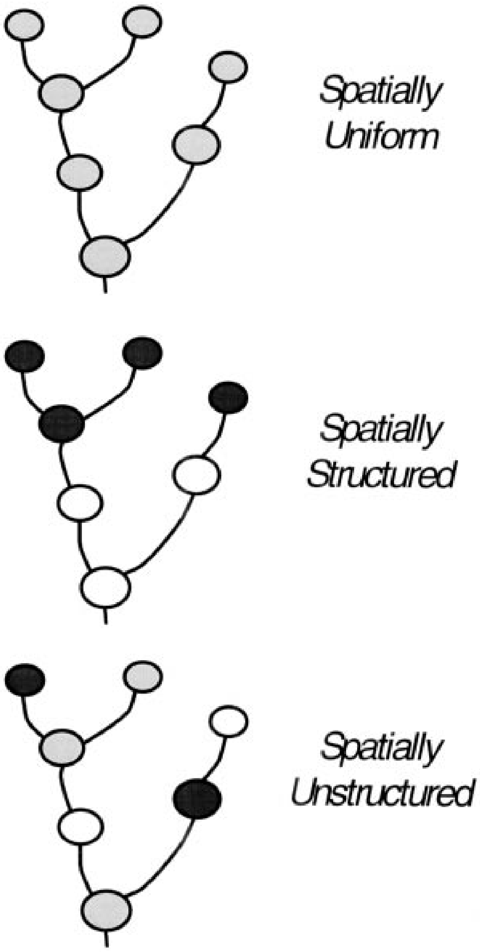

Fig. 1 Spatial patterns in the response to drought among neighboring lakes; solid lines indicate hydrologic connections, either through surface water or groundwater. Lakes with the same shading have synchronous dynamics.

We contrast spatial patterns in lake chemical response to drought in four lake districts in North America that differ in hydrologic setting despite sharing a geomorphic template shaped by common glacial forces. Our analysis takes advantage of long-term research programs in Ontario, Canada (the Experimental Lakes Area and the Dorset Research Centre) and Wisconsin, USA (the North Temperate Lakes Long-Term Ecological Research program). Effects of drought on these lakes have been well-studied and provide the basis for much of our current understanding of the potential effects of climate change on freshwater ecosystems in the region (Schindler *et al.*, 1990, Schindler *et al.*, 1996a; Schindler *et al.*, 1996b; Schindler, 1997; Webster, *et al.*, 1996; Dillon, Molot & Flutter, 1997; Magnuson *et al.*, 1997). We combine data from these districts to achieve a more synthetic understanding of how interactions between lakes and the landscape influence chemical responses to regional climate shifts.

We address two general questions in this paper. (1) Are spatial patterns in chemical dynamics among lakes *uniform* and synchronous within a lake district, suggesting broad geomorphic controls; variable in a *spatially explicit* pattern, with synchrony related to landscape position, suggesting hydrologic flowpath controls; or *spatially unstructured* and asynchronous, suggesting overriding control by lake-specific factors? (2) Are chemical dynamics of lakes in a district a simple and direct response to precipitation quantity or are they dictated by more complex interactions among climate, unique lake features, and hydrologic setting? Our results describe limits on the extrapolation of climate-related phenomena observed in a small number of lakes within and among lake districts, and demonstrate the role of hydrogeologic complexity in determining spatial patterns of climate response.

Methods

Lake districts

The Upper Great Lakes region encompasses several well-studied lake districts (Fig. 2, Table 1), containing high densities of relatively undisturbed lakes in forested catchments. We focus on four districts: the

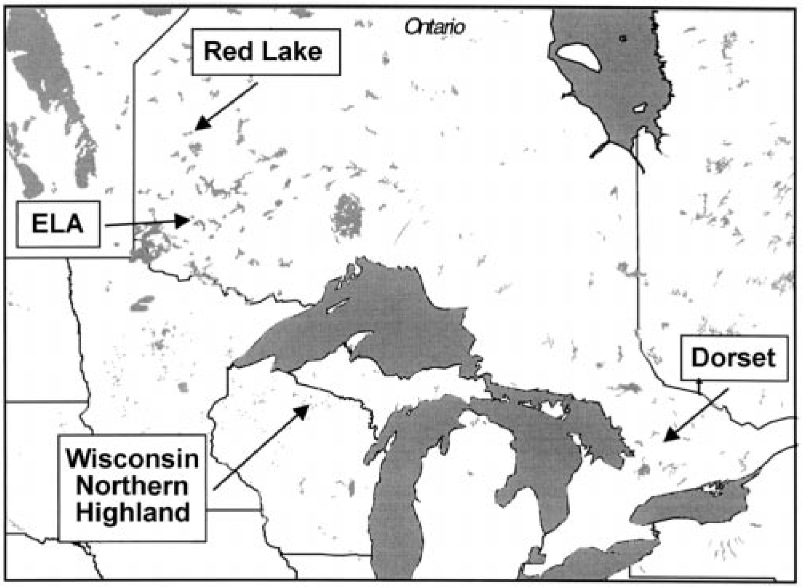

Fig. 2 Location of the four lake districts in Wisconsin and Ontario in the Upper Great Lakes Region.

Experimental Lakes Area (ELA) and Red Lake District, both in northwestern Ontario; the Dorset research lakes in the Muskoka District of south-central Ontario; and the LTER and EPA Regional Long-Term Monitoring lakes in the Northern Highland District of north-central Wisconsin. Most relevant here, are the high quality, internally consistent, long-term time series ranging from nearly one to three decades on multiple lakes in each district.

Much of the physiography of the upper Great Lakes region was shaped by glacial activity 10 000–12 000 years ago, which left behind a landscape containing high densities of lakes. The region has relatively low topographic relief, becoming moderately rugged locally in the North. Although all the districts are situated over the granitic bedrock of the Canadian Precambrian Shield, physiographic and hydrologic features differ. In the Ontario districts, glacial scouring exposed bedrock outcrops and deposited tills that are low in carbonates and typically < 1 metre depth, although till depths can extend to ~10 m in valley bottoms (Brunskill & Schindler, 1981; LaZerte & Dillon, 1984; Fee & Hecky, 1992). As a result, surface water is the dominant hydrologic linkage between the Ontario lakes, which tend to be drainage systems of relatively low ionic strength. Groundwater inputs are

Table 1 Characteristics of the four districts

Attribute	ELA	Red Lake	Dorset	Wisconsin
Lat/long	49° N / 93° W	51° N / 94° W	45° N / 79° W	46° N / 89° W
Lake names	H: L149, L224, L239, L373, L442	H: Green, Linge, Orange	H: Blue Chalk, Chub, Crosson, Dickie, Harp, Heney, Plastic, Red Chalk	H: Crystal, Morgan, Vandercook
	L: L164, L165, L240, L377, L938	L: Musclow, Sydney, Trout		L: Allequash, Big Muskellunge, Trout
Precipitation (mm)	669 *(488–838)*	623 *(373–718)*	1044 *(803–1185)*	831 *(621–1077)*
Evaporation (mm)	517 *(399–672)*	(na)	618 *(497–754)*	556 *(450–654)*
Hydrologic setting	Surface-water	Surface-water	Surface-water	Groundwater
Till depth (m)	1–10	1–10	1–10	~ 50
Other regional disturbances	Logging, Fire	Logging	Logging, cottaging, high acid deposition, road salting	Logging, cottaging, moderate acid deposition, road salting

H=highland lakes, L=lowland lakes; na=not available. Values for precipitation and evaporation are the mean (*range*) of calendar year totals from 1982 to 1995.

important only where till is deeper (Schindler *et al.*, 1976; Hinton, Schiff & English, 1993; Devito, Roulet & Hill, 1996). In contrast, lakes in northern Wisconsin are isolated from bedrock by thick glacial-fluvial deposits, which are low in carbonate minerals and upwards of 50 m thick (Okwueze, 1983). Groundwater is the dominant hydrologic feature linking lakes in this region (Magnuson *et al.*, 1990) and spatial patterns in lake attributes are dictated by interactions between lakes and groundwater (Kratz *et al.*, 1997). Precipitation and transient inputs of local groundwater flow dominate the hydrology of seepage lakes high in the landscape, which lack surface water inlets or outlets, and, thus, tend to be low in ionic strength (Anderson & Cheng, 1993; Wentz, Rose & Webster, 1995). Lowland lakes, including both seepage and drainage types, receive groundwater discharge from deeper regional flowpaths that have longer contact times for weathering reactions with minerals in the aquifer and thus, higher solute concentrations (Cheng & Anderson, 1994).

The catchments of the study lakes in the four districts are predominately forested, with boreal vegetation (spruce and jack pine) in the North replaced by mixed conifers and hardwoods in the South. Disturbance histories of the districts have in common widespread logging at the turn of the century. They differ in the extent of cottaging and road development (highest in Dorset and northern Wisconsin), recent major fires and local clear cutting (ELA), and acid deposition (highest at Dorset then becoming lower to the West).

The database was assembled from several long-term studies. The 10 ELA lakes include four well-studied lakes with records dating back prior to the 1970s (L239, L224, L240, and L373) which have been used as reference lakes for whole-lake experiments and as indicators of long-term natural variability (Hecky, Campbell & Rosenberg, 1994). The remaining six ELA lakes (L377, L442, L938, L164, L165, and L149) along with L373, comprise the ELA Lake Variation Study (ELVS), conducted between 1986 and 1993 (Campbell, 1993; McCullough & Campbell, 1993). The ELVS lakes were originally selected to represent the range of water residence times and extent of surrounding wetlands observed at ELA. The Red Lake district lakes (Green, Orange, Sydney, Musclow, Trout, and Linge) are located 150 km north of ELA. The lakes, part of the Northern Ontario Lake Size Series (NOLSS) study, vary primarily in surface area, with other attributes such as water residence time relatively constant (Fee *et al.*, 1989). The NOLSS and ELVS studies, both initiated in 1986, provide complementary gradients designed to better understand limnological variability as related to mappable metrics and standard meteorological data (Fee *et al.*, 1989). The eight Dorset lakes in the Muskoka District of south central Ontario (Blue Chalk, Chub, Crosson, Dickie, Harp, Heney, Plastic, and Red Chalk) were selected in the mid 1970s to represent a cottaging gradient in a series of headwater lakes (Dillon, Reid & Evans 1993). Later, these lakes were used to document effects of acid deposition (Dillon, Reid & deGrosbois, 1987). The Northern Highland lakes in Wisconsin include five of the seven Wisconsin NTL-LTER lakes (Allequash, Big Muskellunge, Crystal, Sparkling and Trout) all non-bog lakes located in the same ground-catchment (Magnuson *et al.*, 1990). In addition, we included data for Vandercook and Morgan lakes, in different flow systems 4 and 120 km from Trout Lake, respectively, which were monitored by the EPA Regional Long-Term Monitoring program (Webster & Brezonik, 1995). The Wisconsin lakes include two drainage (Trout and Allequash) and six seepage lakes, lacking surface inlets or outlets. The lakes represent the diversity in hydrologic type found in the district, from hydraulically mounded seepage lakes to groundwater flow-through lakes to drainage lakes located in regional groundwater discharge areas (Eilers *et al.*, 1983). In contrast, the Ontario lakes are all drainage lakes.

Lake database

Our analyses are based on open-water means (except for chlorophyll *a*, which is the June to August mean) of epilimnetic samples collected from 1982 to 1995. This period spanned a regional drought that occurred from roughly 1987–1990. ELA and Dorset sampling frequency was monthly. Red Lake samples were collected weekly from ice-out until stratification (early to mid-June) and every 3 weeks thereafter. Samples were collected at one metre for the ELA ELVS lakes, as integrated epilimnetic volumes for the remaining ELA lakes and the Red Lake District lakes (Fee *et al.*, 1989), and as integrated, hypsometrically weighted samples for the Dorset Lakes. For the Wisconsin lakes, sampling frequency was quarterly

Table 2. Chemical and physical attributes of highland (H) and lowland (L) lakes in the four districts (mean with range in italics)

Lake district	LP	N	Cl$^-$ (μeq L^{-1})	Ca^{2+} (μeq L^{-1})	SO$_4$$^{2-}$ (μeq L^{-1})	ANC (μeq L^{-1})	DOC (mg L^{-1})	TN (μg L^{-1})	SiO$_2$ (mg L^{-1})	TP (μg L^{-1})
ELA	H	5	12	138	67	158	6.0	350	1.9	7.2
			6.8–18.4	*94–161*	*42–109*	*84–226*	*3.1–9.3*	*215–697*	*0.3–5.2*	*5.3–11.7*
	L	5	9.3	130	66	136	8.0	347	2.3	9.3
			7.2–13.0	*111–168*	*50–95*	*101–211*	*5.1–11.4*	*264–421*	*1.8–2.9*	*7.2–11.3*
Red Lake	H	3	6.9	202	47	261	7.7	329	1.3	8.9
			5.6–7.7	*149–271*	*42–53*	*186–378*	*6.7–8.4*	*310–353*	*0.6–1.8*	*7.8–10.5*
	L	3	7.9	315	51	411	6.7	308	0.9	10.0
			6.0–8.9	*230–446*	*40–61*	*306–568*	*4.2–9.2*	*216–394*	*0.2–2.0*	*7.8–12.4*
Dorset	H	8	20	116	141	35	3.5	237	1.1	5.9
			9.8–46	*92–115*	*132–153*	*4.7–80*	*1.9–5.1*	*173–297*	*0.3–1.9*	*3.9–8.2*
Northern Highland Wisconsin	H	3	10.0	60	94	10.4	2.3	160*	0.04	5.2*
			7.2–12.8	*56–65*	*67–144*	*12–27*	*1.3–3.6*		*0.03–0.05*	
	L	4	40	481	68	650	3.7	285	7.0	10.4
			9.0–97	284–603	63–74	370–827	3.0–4.3	219–353	0.3–12.8	5.7–19.1

	LP	N	Chl *a* (μg L^{-1})	wrt (years)	Surf area (ha)	Z$_{max}$ (m)	WS:LK ratio	GW in (%)	Ups. Lks (#)
ELA	H	5	2.0	16.5	30	20.1	4.6	nd	0.4
			0.9–4.9	*7.3–25.0*	*16–54*	*4.0–30.4*	*2.0–9.1*		*0–1*
	L	5	2.2	1.0	26	9.7	247	nd	26
			1.1–3.3	*0.7–3.0*	*18–44*	*4.6–17.9*	*16–632*		*5–51*
Red Lake	H	3	2.7	11.5	321	24.3	3.2	nd	6
			1.9–3.5	*9.8–13.0*	*89–706*	*19.0–30.0*	*0.4–6.6*		*1–15*
	L	3	3.0	13.1	14219	55.9	8.3	nd	150†
			1.8–4.1	*7.5–22.3*	*2219–34690*	*45.7–73.2*	*0.4–8.1*		*100–200*
Dorset	H	8	3.0	2.3	52	23.1	5.7	nd	0
			1.7–4.9	*1.2–4.0*	*21–94*	*5.8–38*	*2.6–8.8*		*0–1*
Northern Highland Wisconsin	H	3	1.4‡	5.8	31	10.4	3.8	3	0
				2.6–10.4	*17–39*	*3.8–20.4*	*2.3–4.9*	*0–6*	*0–0*
	L	4	2.8	5.9	420	21.2	6.4	27	1.2
			1.4–5.7	0.5–10.8	81–1091	8.0–35.7	2.3–4.9	16–35	0–4

* TP and TN only available for one highland lake in Wisconsin.

† The number of upstream lakes for the lowland Red Lake district lakes are estimates.

‡ Chlorophyll data only available for Crystal Lake.

LP refers to landscape position; *n*=number of lakes; DOC=dissolved organic carbon; TN=total nitrogen; TP=total phosphorus. Chl *a*=chlorophyll *a*; wrt=water residence time; Z$_{max}$=maximum depth; WS:LK=catchment to lake area ratio; GW in=groundwater input; Ups. Lks= number of upstream lakes; nd=not determined.

(spring, summer and fall), and samples were collected at one metre from the Regional Long-Term Monitoring lakes and as hypsometrically-weighted samples from the LTER lakes. Additional samples were collected on a biweekly to monthly basis for total phosphorus, total nitrogen, dissolved organic carbon (DOC), chlorophyll *a* and silica for the LTER lakes; phosphorus, chlorophyll *a* and total nitrogen were not measured in the two Regional Long-Term Monitoring lakes. For all lakes, annual or summer means were calculated as straight averages, with no time weighting.

Analytical methods are documented in Fee *et al.* (1989), Stainton, Capel & Armstrong (1977), Ontario Ministry of the Environment (1983), and Morrison (1991). Outliers were identified by checking ion balances (which included organic anions), examining extreme outliers outside three times the inner 50% quartiles for each lake and solute, and visually inspecting data series. Annual means for each solute were then calculated from the censured data, with outliers removed. Morphometry, water residence time, and hydrologic data were from McCullough & Campbell (1993), Fee *et al.* (1989), Hutchinson et al. (1984), and Webster *et al.* (1996).

Our definition of landscape position as either highland or lowland is based on the relative position of a given lake within its local to regional hydrologic flow system (Kratz *et al.*, 1997). It is thus in between a catchment-scale definition and an elevation-based concept applicable in regions of strong topographic gradients. In Wisconsin, landscape position was assigned on the basis of the percent input from groundwater, with highland lakes receiving less than 10% of their water from groundwater (Table 2). For ELA and Red Lake district lakes, we based landscape position on the number of upstream lakes, with highland lakes having fewer than 2 and 15 upstream lakes, at ELA and Red Lake, respectively. Different criteria were used for ELA and Red Lake because we wanted a relative measure of landscape position within each district; the lowland Red Lake lakes had more than 100 upstream lakes necessitating a different splitting point (Table 2). The Dorset lakes were either headwater systems or were directly downstream from a headwater lake (Red Chalk Lake) and thus were all classified as highland lakes.

Precipitation data

Monthly precipitation totals were accumulated from daily observations collected at ELA and Dorset, and from daily records available from the National Climatic Data Center for Minocqua Dam, Wisconsin and the Canadian Climatic Center for Red Lake, Ontario. To determine whether lake chemistry in each district was responding to seasonal or longer scale climatic influences, two precipitation averaging periods were used as predictor variables. The October through May (Oct–May) total generally corresponds to the seasonal influence of the major recharge period occurring prior to the open water season. The June through May (annual) total is the precipitation accumulated prior to the majority of open-water measurements of a given year. This time scale better represents more extensive drought periods.

Synchrony

Synchrony, also referred to as temporal coherence, is a measure of the similarity in year-to-year patterns of variation between a lake pair (Magnuson *et al.*, 1990; Kratz *et al.*, 1998; Baines *et al.*, 2000). We quantified synchrony as the Pearson product-moment correlation coefficient *(r)* between two lakes, with observations paired by year. Synchrony at the district or landscape scale was estimated as the mean of the correlation coefficients calculated for all possible lake pairs. To determine if synchrony was related to landscape position within a lake district, we calculated means for lake pairs that were both highland lakes, both lowland lakes, or mixed pairs, which were highland by lowland crosses.

Regressions linking chemistry and drought

We used linear regression analysis to evaluate district-wide relationships between precipitation quantity (Oct–May and annual totals) and solute concentrations (annual open-water means from epilimnetic samples). Our goal in this analysis was not to quantify individual lake responses to climate drivers *per se*, but rather to determine whether groups of lakes within a district were responding directly and synchronously to a common climatic signal. The models produced intercepts for each lake and an overall slope, which represented the relationship between precipitation and a given solute for the lakes as a group. Slope estimates different from zero at $P < 0.10$ were considered significant. Chemical variables were log-transformed where necessary to ensure normality. In addition to district-wide analyses, similar regressions were performed on lakes grouped by landscape position (i.e. lowland or highland) in all districts except Dorset and grouped by mean water residence time for Wisconsin lakes. We were unable to group the ELA or Red Lake lakes by water residence time because this factor was confounded with landscape position; highland lakes had longer water residence times than did lowland lakes (Table 2).

Results

Patterns and synchrony in precipitation among lake districts

The 1987–90 drought was evident in lower precipitation at each site, particularly in 1988, although it was manifest in different pre- and post- drought patterns (Fig. 3). The drought was bracketed by higher-than-normal precipitation years in Wisconsin and ELA, while it was part of a more persistent pattern of decreasing precipitation across the decade at Dorset. The Oct–May time series were roughly similar to those for annual precipitation at Red Lake and Wisconsin. At Dorset, drought conditions were more frequently encountered during the study period with sharp declines in the Oct–May precipitation in 1982–83, 1987–88, and 1992–93, which are all El Niño years (Dillon *et al.*, 1997).

We calculated correlation coefficients between each site pair to determine if temporal patterns in precipitation were synchronous across the entire region. In general, annual precipitation totals were synchronous (mean r=0.52) with the Ontario districts more synchronous when paired with each other (r = 0.52–0.66) than with Wisconsin (r = 0.31–0.47). Synchrony in Oct–May precipitation was relatively high among the ELA, Red Lake and Wisconsin sites (r=0.49–0.66), but low when these sites were paired with Dorset (r < 0.11).

Patterns and synchrony in lake chemistry within lake districts

Among the four districts, differences between highland and lowland lakes in average lake solute concentrations were most pronounced in the Wisconsin Northern Highland lakes (Table 2). The concentrations of silica, calcium, ANC, and total nitrogen were up to two orders of magnitude higher in lowland compared to highland

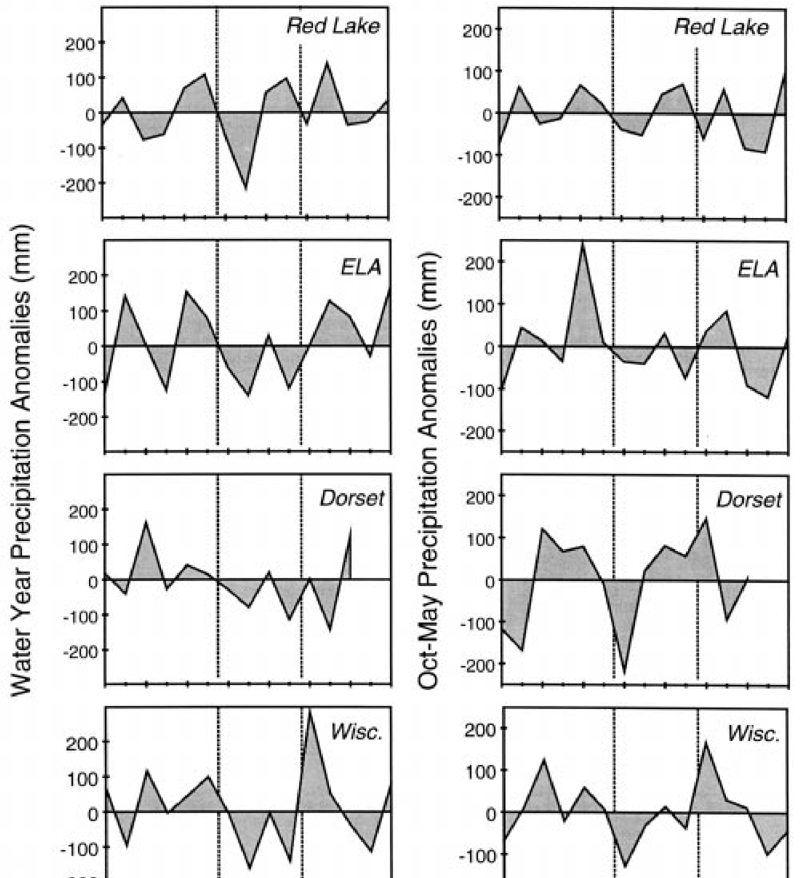

Fig. 3 Annual anomalies in annual (June-May) and Oct–May precipitation totals at monitoring stations in the four districts. Anomalies were calculated as the difference from the 1981–1995 mean. The nominal drought period is marked by dotted lines.

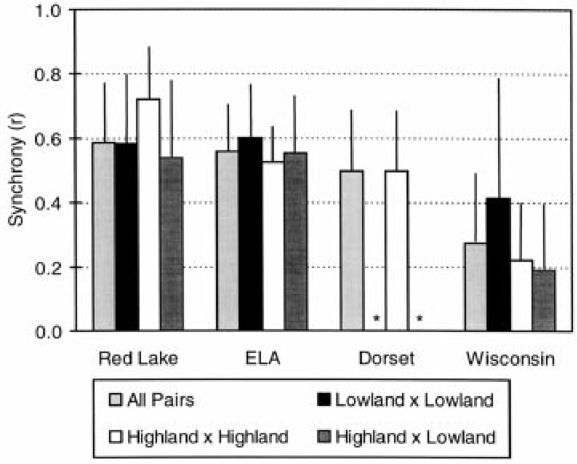

Fig. 4. Average synchrony *(r)* across all chemical variables for lake pairs within each district. In addition to the overall mean, we show means for pairs consisting of lowland by lowland lake crosses, highland by highland lake crosses, and mixed pairs consisting of highland by lowland lake crosses. The standard deviation is indicated by the error bar. A '*' indicates no data were available; the Dorset set does not include any lowland lakes.

lakes. Moreover, in all cases except for total nitrogen, these differences bracketed the entire range exhibited within the three Ontario districts. In the Red Lake district, calcium and ANC were somewhat higher in lowland lakes compared to highland lakes. At ELA, differences between highland and lowland lakes were minimal, despite major differences in morphometry and water residence time (Table 2).

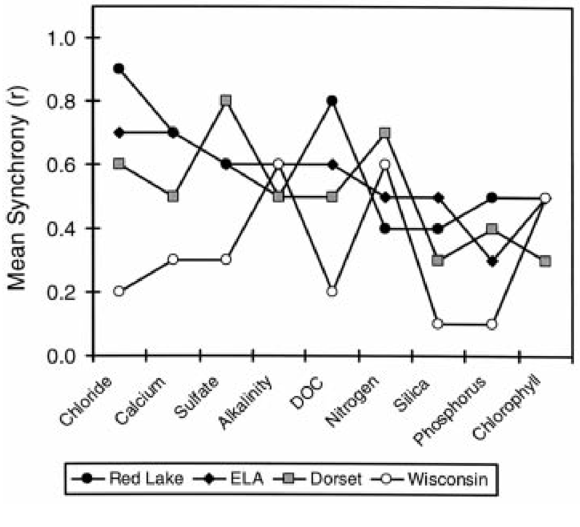

Fig. 5 Average synchrony *(r)* for all lake pairs in each district for each chemical variable, arranged from more to less conservative from left to right.

Consistent with the above results, mean synchrony for all chemical variables was higher within each of the Ontario lake districts than in Wisconsin (Fig. 4). This pattern held for the overall mean and for lake pairs grouped by landscape position (i.e. highland by highland, lowland by lowland, and highland by lowland crosses). In Wisconsin, only synchrony among lowland lake pairs approached that of the other districts. When we evaluated mean synchrony for each chemical variable, we observed a pattern of lower synchrony for less conservative solutes (Fig. 5). Again, the Wisconsin lakes were less synchronous and the relationship between synchrony and the relative conservative nature of the solutes was less apparent.

Relationships between lake chemistry and climate variables

We used regression analysis to evaluate the degree to which synchronous lake chemical behavior could be explained by a direct relationship with precipitation. Three patterns emerged from this analysis (Table 3). First, for the Ontario sites, precipitation tended to be negatively related to more conservative solutes (chloride, calcium, sulfate, and ANC), and positively related to less conservative solutes (DOC, total nitrogen, silica and total phosphorus). No relationship between precipitation and chlorophyll *a* was detected. Second, the chemical dynamics of the Wisconsin lakes as a group showed little correspondence to inter-annual variations in precipitation. The few slopes that were significant, were not strongly so. Finally, for the ELA and Dorset lakes, the regression slopes calculated between annual precipitation and concentrations of some solutes changed in significance or direction when Oct–May precipitation was substituted as the predictor variable. For the ELA lakes, annual precipitation better explained temporal patterns in the more conservative solutes while Oct–May precipitation better explained total nitrogen concentrations. For the Dorset lakes, the direction of slope reversed for calcium, sulfate and total nitrogen concentrations, from positive for Oct–May precipitation to negative or not significant (for total nitrogen) for annual precipitation.

To determine if the relationship between solute concentrations and precipitation varied with lake landscape position, we conducted separate regression analyses for highland and lowland lakes within each district. In general, relationships between lake chem-

Table 3 Mean synchrony *(r)* between all lake pairs in a district and results from regressions between precipitation variables (Oct–May and annual totals) and concentrations of eight solutes, ordered from more to less conservative. Significant slope estimates from the regression analyses are indicated by '+' for a positive and '–' for a negative slope estimate. One, two and three symbols indicate significance at P levels of 0.10, 0.01 and 0.001, respectively

	Synchrony	Chemical variables								
Lake district	Slope direction	Cl	Ca	SO_4	ANC	DOC	TN	SiO_2	TP	Chl*a*
ELA	*Mean r*	*0.749*	*0.691*	*0.645*	*0.561*	*0.633*	*0.491*	*0.520*	*0.267*	*0.457*
	Oct–May				– –	++	+++	+	+	
	Annual	– –	– – –	– – –	– – –	+++		+++		
Red Lake	*Mean r*	*0.915*	*0.674*	*0.648*	*0.539*	*0.768*	*0.426*	*0.352*	*0.476*	*0.468*
	Oct–May	– – –		–	–	+		+	–	
	Annual	– –			– –	+++	–		–	
Dorset	*Mean r*	*0.624*	*0.464*	*0.808*	*0.467*	*0.531*	*0.689*	*0.256*	*0.385*	*0.257*
Oct–May		+++	+++	–		+++	+			
	Annual	–	–	– –	–			+++	+	
Northern Highland	*Mean r*	*0.205*	*0.266*	*0.320*	*0.624*	*0.197*	*0.573*[a]	*0.088*	*0.139*[a]	*0.469*[a]
Wisconsin	Oct–May	–		+		+				
	Annual	–					–			

[a] TN, TP, and chlorophyll *a* were available for only one Wisconsin highland lake and all four lowland lakes.

istry and precipitation variables for highland and lowland groups did not differ from those determined for all lakes in a district shown in Table 3. Only a few contrasts between highland and lowland lakes of significance were noted. For ELA, regression slopes for total nitrogen and Oct–May precipitation were positive in the highland lakes ($P < 0.001$) but not the lowland lakes. For the Red Lake district, ANC was negatively related to precipitation variables in highland ($P < 0.10$ for annual and $P < 0.001$ for Oct–May precipitation), but not lowland lakes. Finally, in Wisconsin, regression slopes were positive and significant only for DOC in lowland lakes ($P < 0.01$ for annual and $P < 0.10$ for Oct–May precipitation) and for silica in highland lakes ($P < 0.10$).

Because water residence time is a lake-specific attribute that potentially influences responsiveness to drought, we also examined differences among Wisconsin lakes with long (> 7 years) and short (< 5 years) water residence times relative to the 4-year drought. Only regressions of DOC against Oct–May precipitation (positive slope) and total nitrogen against annual precipitation (negative slope) were significant at $P < 0.10$ for the group of lakes with long water residence time.

Calcium dynamics related to drought

Calcium, generally considered conservative in these lakes, provides a useful tracer of the effects of regional climatic shifts on hydrologic connections between lakes and the landscape (Webster *et al.*, 1996). Supplied by weathering and atmospheric deposition, calcium can be transported to lakes from the catchment via overland, surface and groundwater flowpaths. We focus on its dynamics to explore differences between the ELA and Wisconsin lake districts. Most strikingly, synchrony in calcium was high among ELA lakes (mean r= 0.69), suggesting a uniform response to climate. However, in Wisconsin only the lowland lake pairs were synchronous (mean r=0.89); mixed pairs (i.e., highland by lowland crosses) and highland lake pairs were asynchronous, both with mean r=0.00. This pattern suggests that dynamics were related to landscape position.

Despite differences in synchrony patterns among districts, calcium concentrations tended to increase during the four year drought (1987-90) at all sites (Fig. 6). However, even among the synchronous lowland lakes in Wisconsin, dynamics across the entire 12-year study period were not explained by interannual changes in precipitation as they were at ELA (Table 3). We compared temporal trajectories of calcium concentration plotted against annual precipitation, depicted as anomalies from the mean, for representative ELA (L239) and Wisconsin (Crystal and Sparkling) lakes. For L239, points generally fell along a negative-tending diagonal, moving between higher calcium concentrations in drier years (negative

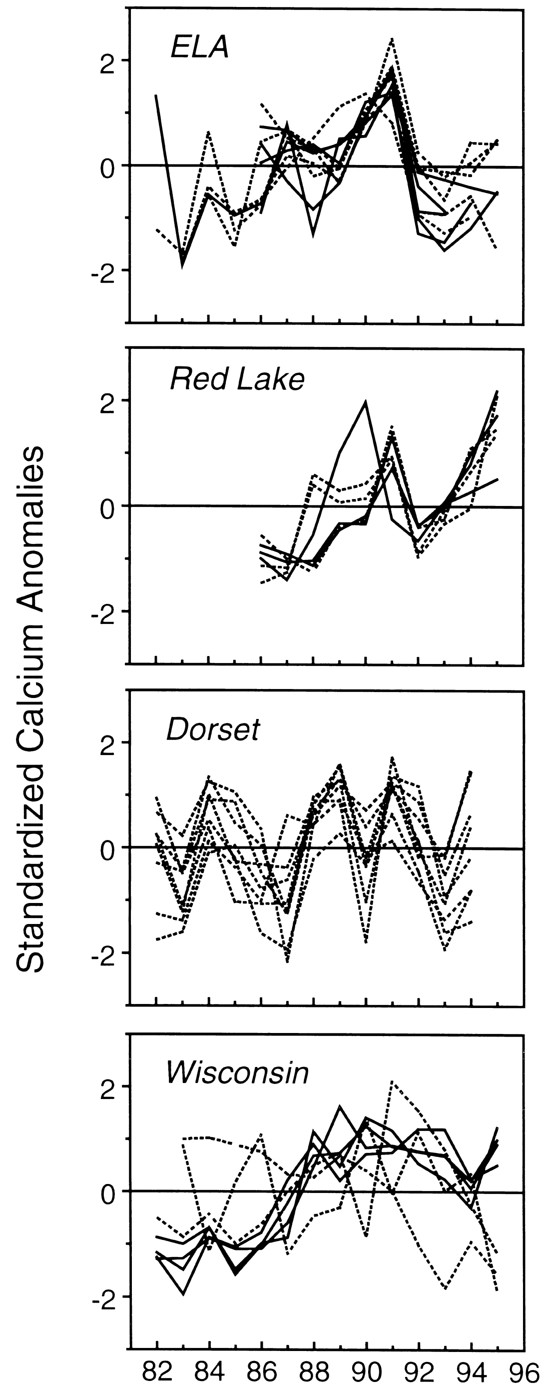

Fig. 6 Time series for calcium in highland (dotted) and lowland (solid) lakes in each district. Calcium concentrations were converted to standardized anomalies; each point for the time series of a given lake is expressed as (x_i – mean)/std dev, where the mean and standard deviation are calculated from the entire lake series.

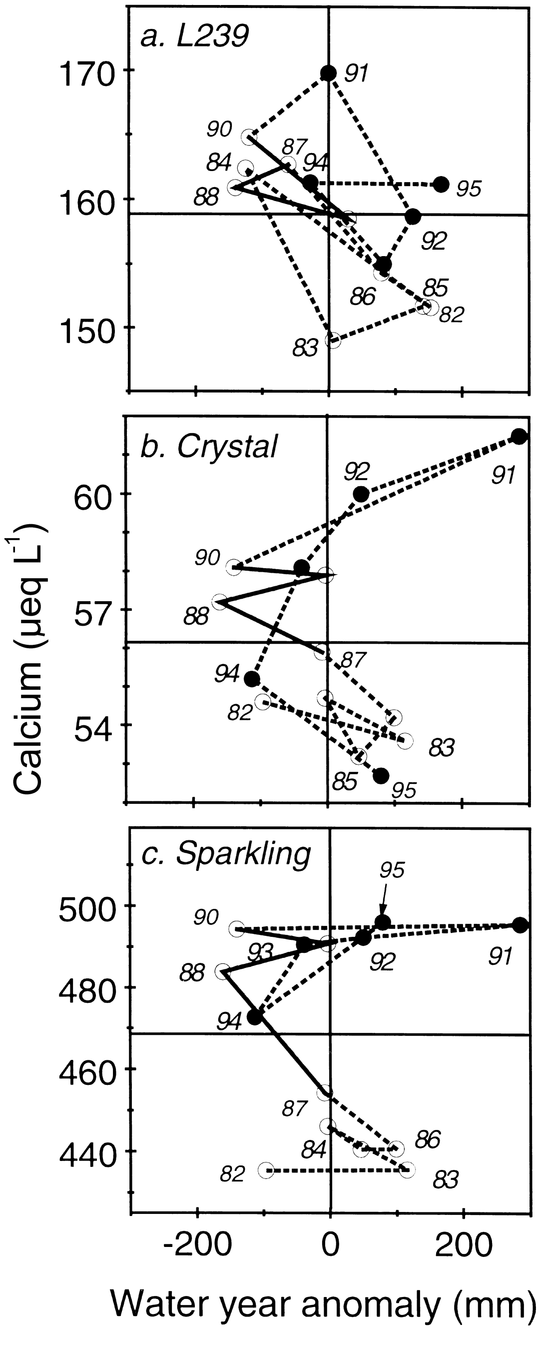

Fig. 7 Calcium concentration plotted against precipitation anomalies (i.e., difference from the long-term annual mean) for L239 at ELA (a), and for Crystal (b) and Sparkling (c), highland and lowland Wisconsin lakes, respectively. Trajectories were divided into three segments, pre-drought 1982–86 (dotted line, open markers), drought 1987–90 (solid line, open markers) and post-drought 1991–95 (dashed line, solid markers). The solid horizontal line references the mean calcium concentration for each lake.

precipitation anomalies), to lower concentrations in wetter years (Fig. 7a). Although the post-drought trajectory appeared elevated compared to the pre-drought period, the response of calcium to climate was generally direct, corresponding to the strong negative relationship between calcium and precipitation discussed earlier (Table 3).

Quite different temporal trajectories through the calcium and precipitation anomaly space were apparent for two Wisconsin lakes – the highland Crystal and the lowland Sparkling (Fig. 7 b, c). Trajectories of calcium through time were independent of precipitation anomalies, a result consistent with the lack of relationship with annual and seasonal precipitation variables (Table 3). In fact, the trajectory for Sparkling Lake suggests that calcium may have moved between two relatively stable states, with the drought triggering a jump to a higher concentration, which remained fairly constant despite an interannual fluctuation in annual precipitation of nearly 400 mm. Calcium concentrations in Crystal Lake were more dynamic than in Sparkling Lake (Fig. 7b), but still fluctuated independently of precipitation anomalies, and, in contrast to Sparkling, returned to pre-drought levels by 1995.

Discussion

We assessed the degree to which drought responses observed in individual or small groups of lakes could be extrapolated to other lakes within a district and among other districts in the glaciated Upper Great Lakes region. At the decadal time scale, we observed two spatial patterns in lake response to climate, based on the degree of synchronous behavior and strength of the relationships between chemical concentrations and precipitation. In the three districts dominated by surface-water flowpaths – ELA, Red Lake and Dorset – we observed high synchrony among lakes and strong relationships between solute concentrations and precipitation. Not only were the lakes remarkably similar in temporal patterns (Fig. 6), much of this variability appeared to be directly related to interannual fluctuations in precipitation (Table 3), suggesting a generally uniform and direct response to climate. In contrast, solute concentrations in the groundwater-dominated lakes in Wisconsin exhibited a non-uniform response, with weak relationships to interannual variation in precipitation, and lower synchrony. Further, highland and lowland Wisconsin lakes differed in both mean lake features (Table 2) and synchrony (Fig. 4). Synchrony among lowland lakes was generally high and approached levels observed for the Ontario districts, but synchrony among highland lakes was generally low (Fig. 4).

For the drainage lakes within the Ontario districts, the responses of solutes to climatic fluctuations reflect alterations in the water balance and external fluxes combined with resistance to in-lake loss processes (Schindler *et al*., 1970, Schindler *et al*., 1996a). During drier conditions, the water balance shifts, such that stream inputs decline and the difference between precipitation and evaporation becomes smaller. As a result, the decline in solute transport from the catchment to lakes via stream flow is countered by an effective increase in loading rate as lake water residence times become longer. For more conservative solutes, these hydrologic changes lead to increased concentrations (Schindler *et al*., 1990, 1996a; Schindler, 1997). This pattern is typical for calcium, which is not subject to calcite saturation in these low ionic strength lakes. Calcium accumulated in the water column during drier periods despite lower inputs from the catchment. Even sulfate, an ion subject to in-lake processing by sulfate reduction, increased during dry conditions. In contrast, longer residence times caused by drought conditions do not result in elevated concentrations of less conservative solutes like nitrogen, silica, and phosphorus because the combination of lower fluxes from catchments and rapid in-lake cycling produce lower concentrations (Schindler *et al*., 1996a; Magnuson *et al*., 1997).

At Dorset, we observed that the slope describing the relationship between solute concentrations and precipitation changed in direction when the precipitation predictor variable was totaled on an annual basis compared to the seasonal Oct–May period. In contrast to the generally negative relationships between more conservative solutes and annual precipitation described in the previous paragraph, calcium and sulfate concentrations were positively related to Oct–May precipitation. During dry summers in El Niño years at Dorset, as water levels decrease and wetlands become desiccated, reduced sulfur becomes oxidized to sulfate that can subsequently be flushed into downstream lakes during fall rains (LaZerte, 1993; Dillon *et al*., 1997; Devito, Hill & Dillon, 1999). This sulfate pulse is accompanied by hydrogen and calcium ions, consistent with our observations of positive relationships with Oct–May precipitation for both these ions. While Oct–May precipitation does not explicitly measure the dry summer conditions that lead to sulfur oxidation, it does reflect the subsequent flushing of accumulated ions into lakes, accounting for higher concentrations the following open water season. Further, this response is not strictly a snowmelt phenomenon but is an interaction between wetlands and runoff, initiated by dry summer conditions. Total nitrogen, also showing strong positive relationships with the Oct–May precipitation, but not the annual precipitation totals, may be linked to this wetland flushing mechanism. This climate-driven mechanism depends on another regional disturbance – atmospheric deposition history. A long history of high acid loading rates at Dorset has led to sulfur accumulation in wetlands. At ELA, while similar sulfate pulses from wetlands have been documented, the magnitude is substantially lower, because of historically lower rates of acid loading from the atmosphere (Bayley, Behr & Kelly, 1986).

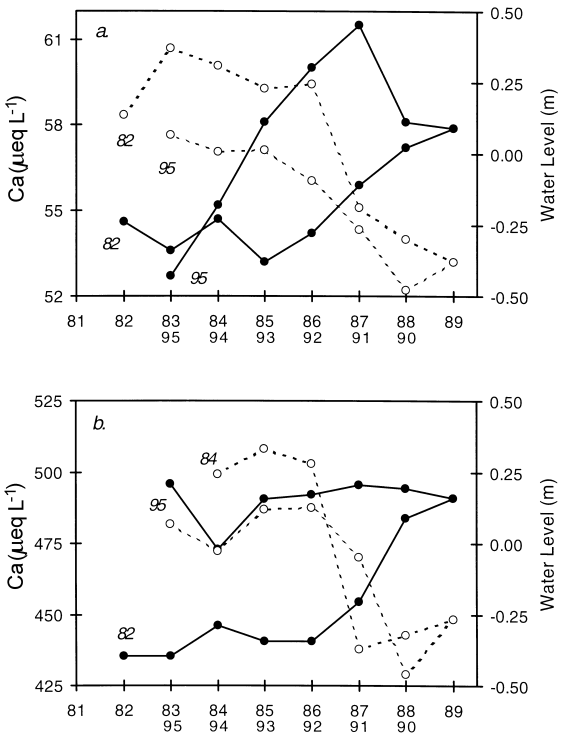

Fig. 8 Calcium concentration (solid line) and lake level anomalies (i.e., difference from the mean; dotted lines) plotted against time for Crystal (a) and Sparkling (b), highland and lowland Wisconsin lakes, respectively. Data are plotted through mid-drought 1987–1990, then in reverse time to overlay recovery with the pre-drought period.

Unlike the Ontario lakes, chemical dynamics of Wisconsin lakes over the 12 year study period were not directly or uniformly related to precipitation quantified at seasonal or annual time scales (Table 3). However, similar to the response of the Ontario lakes, during the four-year drought the concentrations of conservative ions like calcium increased in all lakes (Webster *et al.*, 1996). The temporal patterns for Wisconsin lakes (Fig. 6) suggest that recovery from drought followed a different trajectory from that followed as the climate changed from wetter to drier (Baines *et al.*, 2000). The decrease in precipitation over evaporation during drought influences these lakes through increased evaporative concentration, leading to declines in water level, particularly in seepage lakes, that recover slowly following drought. If the effect of drought was solely a function of hydraulic shifts related to evaporative concentration, temporal trajectories of calcium should be linked in a negative fashion with lake water level. As evaporative losses cause water levels to decline, calcium concentrations should increase. Indeed, Crystal Lake exhibited this pattern (Fig. 8a), suggesting that evaporative concentration and, therefore, water level influenced calcium concentrations during and after drought. In contrast, Sparkling Lake exhibited the pattern of two relatively stable states, irrespective of lake stage (Fig. 8b).

Because groundwater is the major source of calcium to the Wisconsin lakes, especially the lowland lakes, we propose that the nature of the interaction between lakes and groundwater flowpaths introduces lags in recovery from strong climate signals. Further, the difference between the temporal trajectories and the duration of lags in recovery experienced by Crystal and Sparkling lakes suggests that the stronger connection between lowland lakes and deeper, regional groundwater flowpaths produces longer time lags in chemical response to climate drivers. Although both are seepage lakes, groundwater inputs to the highland Crystal Lake vary from 9% in very wet periods to none during dry years, and the primary groundwater sources are transient local mounds which develop near the lake shore (Anderson & Cheng, 1993; Kenoyer & Anderson, 1989). Sparkling Lake, located lower in the flowpath, is more strongly connected to deeper regional groundwater flows, receiving more of its water from groundwater (25%) (Krabbenhoft *et al.*, 1994). Because regional flowpaths are longer, exposure time to weathering reactions is increased and, thus, concentrations of solutes like calcium, silica and ANC can be much higher than observed in groundwater from local sources (Kenoyer & Bowser, 1992; Wentz *et al.*, 1995). During drought, as local flowpaths reverse or diminish, groundwater from more stable regional flowpaths is thought to provide a larger proportion of the water input to lowland lakes (Webster *et al.*, 1996).

Originally we had expected that the relatively long water residence times characteristic of the Wisconsin seepage lakes (2.5–10 years) would make their chemistry less responsive to interannual changes in precipitation. Because drainage lakes often have shorter water residence times than seepage lakes in groundwater-dominated settings, we also expected that differences between groundwater- and surface water- dominated districts in chemical response to climate could, at least in part, be explained by water residence time. However, the range in water residence times for the Wisconsin lakes was actually less than that determined for the ELA lakes. Further, we found no substantive differences between lowland and highland lakes from ELA in either synchrony or climate responses, despite the shorter water residence times of the lowland lakes (Table 2). These results suggest that the lack of a direct response to climate by the Wisconsin lakes was not strictly a function of differences in water residence time among lakes but was related more generally to hydrologic setting.

The observed spatial patterns of lake response to climate support our contention that hydrologic complexity related to lake district geomorphology leads to fundamental differences in the nature of the response of lakes to drought (Fig. 9). Chemical responses of lakes to a common regional drought can be extrapolated within lakes at ELA and Red Lake, districts with hydrologic flowpaths dominated by surface water flows. Within these surface water-dominated districts, lakes exhibited high synchrony across a range of chemical solutes, and were directly responsive to changes in precipitation. Responses to drought can thus be considered spatially uniform (see Fig. 1). In contrast, drought response patterns in the groundwater-dominated Wisconsin lakes were spatially structured. Lowland lakes were synchronous but highland lakes were not. The lack of synchrony among highland lakes suggests a local scale of control, such as differing dynamics between lakes and transient local groundwater flow systems during drought (Anderson & Cheng, 1993; Cheng & Anderson, 1994), or the influence of other regional factors like acid deposition (Stoddard et al., 1999). Alternatively, the dynamics of these highland lakes may be driven by underlying gradients not identified in this paper. In the more complex hydrologic setting of the Northern Highland District of Wisconsin, groundwater acts as a capacitor, delaying the expression of climatic signals in lakes.

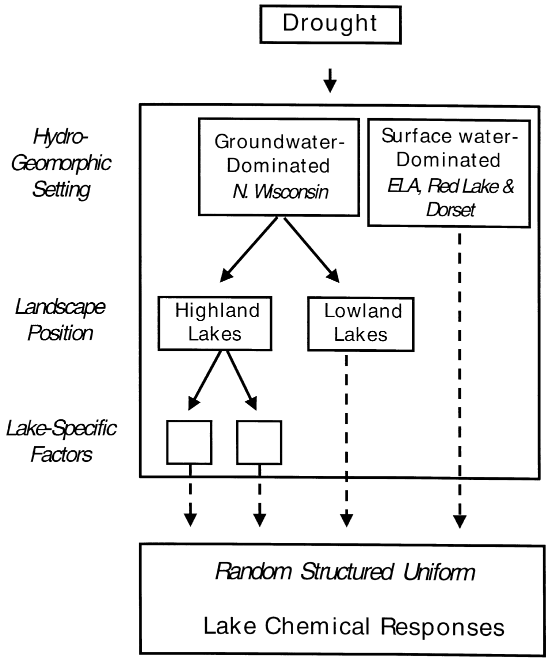

Fig. 9 Conceptual framework indicating spatial scale at which we observed synchronous temporal behavior in calcium among lakes from the Red Lake, ELA, Dorset, and Wisconsin sites. Open boxes were placed at the lake-specific level to suggest that for more biologically reactive chemical variables, we expect in-lake factors play a more important role in mediating lake dynamics.

We have developed a regionalisation framework (Fig. 9) based on lake assemblages in four lake districts in the upper Great Lakes region. In this region of low topographic relief, the ELA district in Ontario and the Northern Highland in Wisconsin provide strong contrasts in hydrologic complexity. In Wisconsin lakes, spatial patterns linked to lake–groundwater interactions, structure both mean chemical attributes and temporal dynamics. In contrast, the influence of landscape position on the dynamics of lakes in the ELA and Red Lake districts is limited by the predominance of shallow till over impervious bedrock. These sites may, however, be end-members in terms of complexity of hydrogeology among surface-dominated districts. For example, Soranno *et al*., 1999) found relatively strong spatial patterns across a wide range of surface-drained lakes in regions with thicker deposits of weatherable material coupled with either strong elevational or land-use gradients. Further, they found that annual synchrony was only related to landscape position (defined by position along a given lake chain) for weathering-related variables in lakes with long water residence times and significant spatial patterning.

A landscape perspective for lakes needs to incorporate the hydrologic complexity of regional and local groundwater flowpaths. As Winter (1999) points out, the effects of transient local flow systems make simple inferences about lake–groundwater interactions based solely on topographic position misleading. Such a perspective assumes that only position within the regional flow system, which more closely correlates with topography, is important. Our analyses emphasize the general need to consider interactions between lakes and both local and regional groundwater flowpaths. Similar patterns have been documented in other regions. For example in the groundwater-dominated prairie-wetland complexes in the Great Plains of the United States, heterogeneity related to local groundwater flowpaths establishes landscape patterns and causes lags in responses to drought similar to those we observed at the Wisconsin sites (Winter & Rosenberry, 1995; LaBaugh *et al*., 1996). Even in regions considered dominated by surface-water flow, heterogeneity in till thickness and physiography interact to influence local groundwater flowpaths. Examples include the temporal response of lakes to acid deposition (Stoddard *et al*., 1998) and the export of sulfur from valley bottom wetlands (Devito *et al*., 1999).

Our conclusions must be considered within the context of other district and regional scale disturbances, such as high rates of acid deposition, which can interact with climate in complicated ways (Schindler *et al*., 1996b; Yan *et al*., 1996). Despite differences among districts in the expression of drought signals by lakes across the landscape, however, we did observe strong chemical responses that are clearly related to climate. Interactions between regional features and climate must be considered when interpreting trends related to other environmental stresses, whether regional or local in scale.

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