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DISSOLVED ORGANIC CARBON AS AN INDICATOR OF THE SCALE OF WATERSHED INFLUENCE ON LAKES AND RIVERS

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Abstract. Land use and land cover can have a significant impact on water chemistry, but the spatial scales at which landscape attributes exert a detectable influence on aquatic systems are not well known. This study quantifies the extent of the landscape influence using the proportion of wetlands in the watershed measured at different distances to predict dissolved organic carbon (DOC) concentrations in Wisconsin lakes and rivers, and to determine whether the watershed influence varies with season or hydrologic type of lake. The proportion of wetlands in the total watershed often explained the most variability of DOC in lakes when stepwise regression was used. However, best-model techniques revealed that, for lakes, r^2 values often only differed 1–3% between models using the proportion of wetlands in the total watershed and models using only the proportion of wetlands in nearshore riparian areas (25–100 m). In rivers, the proportion of wetlands in the watershed always explained considerably more of the variability in DOC than did the proportion of wetlands in the nearshore riparian zone. The watershed influence also varied seasonally in rivers, as the proportion of the watershed covered by wetlands explained more of the variability in DOC in the fall than in the spring. Overall, the proportion of wetlands in the landscape explained much more of the variability of DOC concentrations in rivers than in lakes.

Key words: *dissolved organic carbon; land cover; land use; spatial scale; watersheds; wetlands; Wisconsin.*

Introduction

Land use and land cover changes can have significant impacts on freshwaters (Omernik 1977, Osborne and Wiley 1988, Soranno et al. 1996). The proportion of a particular type of land cover or land use within a watershed has been used to explain, predict, or model water chemistry (Osborne and Wiley 1988, Hunsaker and Levine 1995, Hurley et al. 1995, Watras et al. 1995, Johnes et al. 1996, Soranno et al. 1996, Johnson et al. 1997), algal abundances (Richards and Host 1994), aquatic invertebrate community composition (Barton 1996), and biotic integrity of fish communities (Allan et al. 1997). However, the spatial scale at which landscape attributes exert a detectable influence on aquatic systems is not well understood.

The importance of scale in ecology has been reiterated in a variety of forms (Allen and Hoekstra 1992, O'Neill 1996). Changes in scale can be measured both in terms of grain and extent. In this study, watershed characteristics (i.e., the composition and spatial arrangement of land cover types) are measured at different scales; that is, at different extents of the watershed from nearshore vegetation to the entire watershed. In this case, smaller landscape scales refer to nearshore areas (smaller extents) and larger landscape scales refers to larger areas (or extents). For the purposes of this discussion, scaling refers to relating watershed characteristics measured at different scales to changes in water chemistry variables (but see Patterson et al. 1984, Boyce and Chiocchio 1987, Mortimer 1987, Royer et al. 1987, Fee and Hecky 1992, Fee et al. 1996, and Ogihara et al. 1996 for other ways in which the importance of scale has been examined in freshwaters).

Scaling the relationship between landscape characteristics and water chemistry has yielded mixed results (Omernik et al. 1981, Wilkin and Jackson 1983, Cooper et al. 1987, Osborne and Wiley 1988, Sivertun et al. 1988, Hunsaker et al. 1992, Hunsaker and Levine 1995, Johnson et al. 1997). For example, streams in agricultural watersheds with riparian buffers are often less degraded than are those with no riparian vegetation (Debano and Schmidt 1990). This is particularly true in smaller watersheds (Schlosser and Karr 1981), a testament to the importance of vegetation at closer, smaller landscape scales. In contrast, Omernik et al. (1981) found that upland land uses were as important as were land uses near streams in larger watersheds. Thus, whether characteristics measured at the scale of the watershed vs. the nearshore area can best predict water chemistry variables remains an open question. This study quantifies the watershed influence (as proportion

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of and distance to wetlands) and evaluates its usefulness in explaining the variability of DOC concentrations in lakes and rivers.

DOC is of interest to ecologists as it can affect physical, chemical, and biological properties of freshwater systems. Through attenuation of solar radiation, DOC can provide UV-B protection to aquatic microflora and fauna (Morris et al. 1995, Schindler et al. 1996, Schindler and Curtis 1997) and depress primary productivity in lakes (Jackson and Hecky 1980). Reductions in DOC concentrations can increase lake transparency (Fee at al. 1996), causing deeper euphotic zones and thermoclines (Schindler et al. 1997). The fulvic and humic acids of DOC can influence the acid–base chemistry of freshwaters (Sullivan et al. 1989), affecting the cycling of metals such as copper, mercury, and aluminum (Campbell et al. 1992, Miskimmin et al. 1992, Driscoll et al. 1995), and thus influencing the amount of trace metals found in aquatic organisms (Stephenson and Mackie 1988). DOC can also support bacterial secondary production (Moran and Hodson 1990), influence the availability of some forms of phosphorus to phytoplankton (Steinberg and Muenster 1985), and alter sedimentation rates (Weilenmann et al. 1989).

Autochthonous DOC has several origins. Phytoplankton release a large portion of their photosynthate to the open waters as extracellular DOC (Nalewajko and Marin 1969). This colorless DOC is composed primarily of carbohydrates and amino acids that are rapidly metabolized by bacteria (Wright 1970). Aquatic macrophytes in the littoral zone can also secrete DOC in amounts comparable to that released by phytoplankton (Wetzel and Manny 1972, Wetzel 1990). However, decomposition of these labile, secreted compounds is often very rapid (48 h) (Steinberg and Muenster 1985), and they constitute only a small proportion of DOC in natural waters.

Allochthonous DOC can enter a system through precipitation, leaching, and decomposition. Highly productive wetlands can generate massive amounts of organic matter that enter lakes primarily in dissolved form (Kowalczewski 1978, Wetzel 1990, 1992). This tea-colored DOC is composed of fulvic and humic acids, products of the degradation of lignin and cellulose (Engstrom 1987). The majority of DOC in natural freshwaters can be composed of these colored, refractory, allochthonous compounds (Hesslein et al. 1980, Schindler et al. 1992, Wetzel 1992). True color, in particular, can provide a measure of the colored portion of DOC (Cuthbert and del Giorgio 1992). Thus, the concentration of DOC in lakes and rivers can provide a useful index of the watershed influence because it is primarily derived from surrounding wetlands.

We addressed three groups of questions regarding the landscape influence on DOC concentrations in lakes and rivers to link what is already known about watershed/DOC relationships to the scaling studies already in progress with nutrients. It was determined whether wetlands measured at small scales (near shore) or wetlands in the entire watershed were the best predictors of DOC concentrations in lakes and rivers. We are unaware of any other studies using DOC to assess the landscape influence at different scales.

To what extent does the landscape influence DOC in lakes? Does the entire watershed explain more of the variability in DOC than does the nearshore riparian zone?

Landscape parameters are strongly correlated with DOC, color, and total organic carbon (TOC) in lakes and streams, and include the drainage ratio (Schindler 1971, Gorham et al. 1986, Engstrom 1987, Rasmussen et al. 1989, Kortelainen 1993, Houle et al. 1995), slope (Rochelle et al. 1989), water residence time (Meili 1992), and percentage of the watershed covered by wetlands (Myllymaa 1985, Eckhardt and Moore 1990, Kortelainen 1993, Watras et al. 1995; P. J. Dillon and L. A. Molot, *unpublished manuscript*). Wetlands and wetland soils are often the source of much DOC input to lakes and streams (Hemond 1990, Dosskey and Bertsch 1994), even though they may occupy only a small percentage of the catchment area (Dosskey and Bertsch 1994, Hinton et al. 1998). However, it is not fully understood how proximity and positioning of landscape units such as wetlands influence the export and resulting concentrations of watershed inputs (Allan et al. 1993).

Does the extent of landscape influence vary in lakes of different hydrologic type?

Two hydrologic types of lakes were examined. Drainage lakes have an inlet and/or an outlet, and the major source of water is stream drainage. Seepage lakes do not have an inlet or an outlet, and the main water sources are precipitation, runoff, and groundwater. The drainage ratio (watershed area/lake area) of drainage lakes is often >10, while the drainage ratio for seepage lakes is often <10. If watershed size can be used as an indicator of hydrologic connectivity between a lake and the landscape, a higher drainage ratio might suggest greater hydrologic connectivity. Thus, differences in the watershed influence might be expected between drainage and seepage lakes.

Does the extent of landscape influence differ between lacustrine and riverine systems? Does the landscape influence vary seasonally?

While DOC is fairly stable both seasonally and annually in lakes (Wetzel 1983), particularly in the area of Wisconsin considered here (LTER–NTL 1998) (but see Dillon and Molot 1997, Schindler et al. 1997), the flux of DOC in rivers is often more variable in spring than fall (Hurley et al. 1995). In addition, the contribution of DOC from plant exudates and leaching from detritus is often many times higher in the summer and fall than in other seasons (Kaplan et al. 1980). We

TABLE 1. Characteristics of lakes sampled in fall 1984 and summer 1991 (mean ± 1 SE; N = number of lakes sampled).

Lake variable	Fall 1984 ($N = 64$)	Aug 1991 ($N = 55$)	Drainage lakes ($N = 44$)	Seepage lakes ($N = 66$)	Spring-fed lakes ($N = 9$)
DOC (mg/L)	5.6 ± 3.5	6.1 ± 2.9	6.0 ± 3.0	5.5 ± 3.4	7.2 ± 3.6
True color (PCU)	38.4 ± 36.2	···	···	···	···
Lake area (LA) (km^2)	0.4 ± 0.7	1.1 ± 1.4	1.5 ± 1.5	0.3 ± 0.5	0.5 ± 0.4
Lake volume units (km^3)	5.5 ± 9.1	19.3 ± 30.2	24.9 ± 32.1	4.1 ± 7.7	5.4 ± 3.7
Water residence time estimate	3.5 ± 1.1	4.2 ± 1.9	4.2 ± 1.9	3.6 ± 1.4	3.5 ± 1.2
Proportion of lake covered by emergent or floating macrophytes	0.13 ± 0.24	0.05 ± 0.09	0.06 ± 0.11	0.11 ± 0.23	0.08 ± 0.15
Number of drainage lakes	19	25	44	···	···
Number of seepage lakes	42	24	···	66	···
Number of spring-fed lakes	3	6	···	···	9
Area of total watershed (km^2) (WA)	7.3 ± 22.2	7.9 ± 10.8	18.0 ± 26.2	1.3 ± 1.2	2.8 ± 1.5
Drainage ratio (WA/LA)	12.9 ± 19.3	11.7 ± 23.6	22.4 ± 32.3	6.2 ± 4.0	8.0 ± 6.7
Proportion of total watershed in wetlands	0.16 ± 0.17	0.12 ± 0.09	0.18 ± 0.13	0.12 ± 0.15	0.12 ± 0.06
Proportion of terrestrial watershed in wetlands	0.17 ± 0.17	0.14 ± 0.11	0.20 ± 0.15	0.12 ± 0.14	0.13 ± 0.08

Note: DOC = dissolved organic carbon; PCU = platinum cobalt units.

investigated whether the proportion of wetlands in the entire watershed explained more of the variability in DOC concentrations than did the wetlands in the nearshore area and whether this relationship differed between the fall and spring.

METHODS

Site description

The topographic relief of the northern lakes site consists of gradual, small, rolling hills, rarely exceeding 50 m (Attig 1985), with a high density of seepage and drainage lakes. Soils are generally thin and sandy, with high hydraulic conductivity. Pleistocene glacial till, low in carbonates, sits atop the southernmost extension of the granitic Precambrian shield and explains the low concentration of base cations (Ca, Mg) in these lakes (Patterson 1989, Webster et al. 1993). In the rest of the state, sedimentary materials (particularly sandstone and dolomite) deposited by Paleozoic seas cover the granitic shield. While much of the state was glaciated, a sizable driftless area also occurs in southwestern Wisconsin.

Site selection

Diverse data sets, collected in different seasons, years, and hydrologic systems, were used to examine the landscape influence on DOC and true color. Two separate data sets were used to examine lakes (Table 1). The fall 1984 data set consisted of a subset of 64 lakes from Phase I of the U.S. Environmental Protection Agency's National Acid Precipitation Assessment Program (NAPAP) Eastern Lake Survey (ELS) (Overton et al. 1986). The ELS consisted of randomly selected lakes with a lake area >4 ha and conductance <1500 μS/cm (Linthurst et al. 1986). These lakes were sampled in October 1984 just after fall turnover, when spatial variation within the lakes was reduced. Additional special-interest lakes that were part of other long-term studies were also sampled in the ELS (Kanciruk et al. 1986, Landers et al. 1986, Overton et al. 1986). A different set of 55 lakes, centered around the Long Term Ecological Research–North Temperate Lakes (LTER–NTL) site at Trout Lake Station, were sampled in August 1991. These lakes were not randomly distributed, but rather chosen for their accessibility. Six lakes were common to both the fall 1984 and the summer 1991 data sets. In addition, a set of seven intensively sampled lakes of the LTER–NTL provided seasonal baseline data for DOC and color from 1984 through 1991. Summary statistics for lakes are provided in Table 1.

Seasonal DOC data were also collected to evaluate the landscape influence on rivers at 24 sites throughout Wisconsin. The rivers were sampled as part of previous work relating watershed characteristics to mercury levels in Wisconsin rivers by the University of Wisconsin Water Chemistry Department and by the Bureau of Research, Wisconsin Department of Natural Resources (WDNR) (Hurley et al. 1995). Sites were chosen to comply with criteria set forth by the National Water Quality Assessment Program of the U.S. Geological Survey (USGS). Secondary consideration was given to bedrock type and water table depth. Sites sampled in fall 1992 represented base flow levels, and sites sampled in spring 1993 represented peak flow levels (Hurley et al. 1995). Summary statistics for rivers are provided in Table 2.

TABLE 2. Watershed characteristics for Wisconsin rivers in this study (mean ± 1 SE; N = number of watersheds).

Characteristic	Value
Watershed area (km^2)	217.3 ± 163.8
Percentage wetlands in watershed	11.0 ± 13.5
Average DOC (mg/L)	10.0 ± 6.9
Spring DOC (mg/L)	9.4 ± 3.9
Fall DOC (mg/L)	10.6 ± 10.9
Agriculture and forest	$N = 8$
Agriculture only	$N = 6$
Agriculture and wetlands	$N = 1$
Wetlands and forest	$N = 9$
Agriculture and forest	$N = 8$

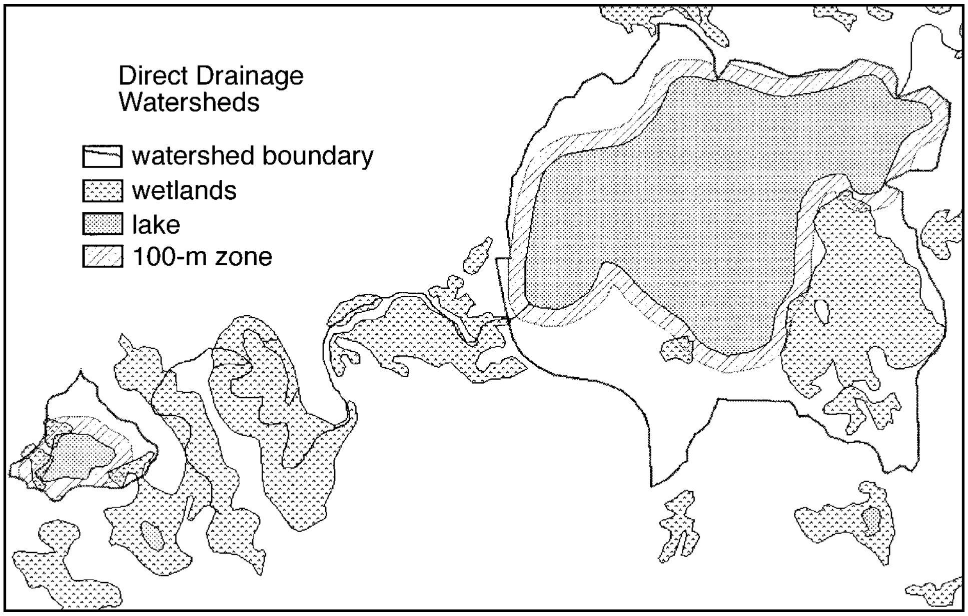

FIG. 1. Digitized watersheds using ARC/INFO to create buffer zones around lakes within the area of direct drainage only (i.e., the area of nonchannelized flow). The 100-m zone is shown for a seepage lake on the left (Kasomo Lake) and a larger drainage lake on the right (Lost Lake). These zones were merged with GIS wetlands data, and the proportion of wetlands within each zone (or scale) was calculated. For seepage lakes, the direct drainage area is also the total watershed area.

Water chemistry analysis

DOC was determined using infrared spectrophotometry in accordance with EPA Method 415.2 (modified) for the lakes sampled in fall 1984, and true color (measured in platinum cobalt units [PCU]) was determined using a Comparator model CO-1, EPA 110.2 (Hach, Loveland, Colorado, USA) (modified) (Linthurst et al. 1986). DOC in the LTER–NTL lakes was measured in summer 1991 using wet potassium persulfate digestion with a Corporation Model 700 TOC analyzer (O/I Analytical, College Station, Texas, USA). While DOC concentrations can fluctuate seasonally and interannually, 10 years of monthly data collected from seven lakes in the region by the LTER–NTL program suggest that this variability is minor relative to the variability among lakes (LTER–NTL 1998). Differences among methods may introduce some noise into our data set, but they are unlikely to affect the overall conclusions, as measured DOC concentrations in the six lakes sampled in both the fall and summer using different methods were very similar.

Water chemistry data for the selected Wisconsin rivers were obtained courtesy of the University of Wisconsin Water Chemistry Department and the Bureau of Research, WDNR. DOC samples were filtered through Whatman GF/F filters (nominal pore size 0.7 μm [Whatman Inc., Fairfield, New Jersey]) in an all-glass filtration unit. Carbon was determined on a Shimadzu Model TOC5000 high-temperature combustion carbon analyzer (Shimadzu Scientific Instruments, Inc., Columbia, Maryland, USA) (Hurley et al. 1995).

Spatial data

Lake area (LA) was obtained from digital hydrography layers (1:100 000). The proportion of each lake covered in floating or emergent macrophytes was also determined using Digital Wisconsin Wetlands Inventory Data (1:24 000) (WDNR 1991). Watershed area (WA) was determined from USGS topographic maps (1:24 000) using quality control recommendations of the Environmental Protection Agency and WDNR (Webster 1983), and then digitized. For drainage lakes, both the direct drainage and total watershed area were digitized (Figs. 1, 2). For seepage lakes, the direct drainage area was equivalent to the total watershed area. ARC/INFO (Environmental System Research Institute, Inc., Redlands, California, USA) was used to calculate the proportion of wetlands in the total watershed of each lake. Wetlands were defined in accordance with Wisconsin Wetlands Inventory Data (WDNR 1991). Measurements of wetlands in the total watershed for lakes included the proportion of wetlands within the total watershed boundary, including any lake area covered in floating or emergent macrophytes. The proportion of wetlands in the terrestrial watershed did not include floating or emergent macrophytes that fell within the lake boundary, and thus lake area was subtracted from the terrestrial watershed area measurements.

The proportion of wetlands at different scales for lakes was calculated within the area of direct drainage only. Zones of increasing distance from the lake shore, (''scales'') were created around each lake at 25, 50,

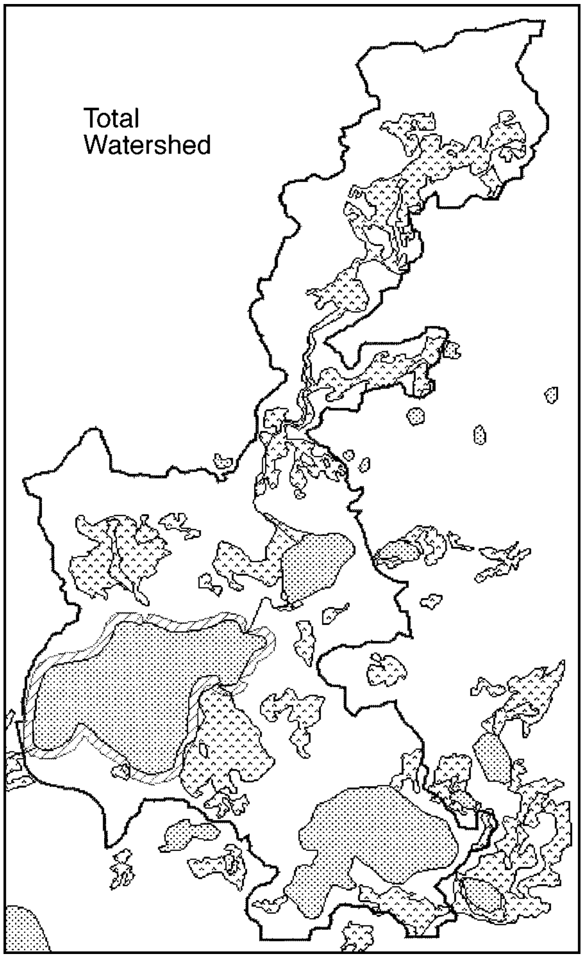

FIG. 2. A view of Lost Lake showing the entire upstream drainage area (including areas connected by channelized flow). Such areas were used to delineate the total watershed and to calculate the proportion of wetlands in the total watershed for drainage lakes.

100, 200, through 1500 m until the direct drainage watershed boundary was reached (see Figs. 1, 2). The concentric scales were overlain with digital wetlands data, and the proportion of wetlands in each zone was calculated. Each zone included any previous smaller zones, but not the area of the lake itself. For example, the proportion of wetlands at the 500-m scale is the proportion of wetlands in the area from the lakeshore out to 500 m around a given lake, but only within the direct drainage boundary. In the case of rivers, buffers of 200 m were created and compared to the wetlands in the entire watershed. The 200-m buffer was necessary due to the coarser resolution of the river wetlands data. These data were overlain with the USGS Land Use and Land Cover data set (1:250 000) to determine the proportion of wetlands at each scale. The coarser resolution of data used with rivers was necessary because of the larger area of the riverine watersheds.

Statistical analysis

Regression analysis was used to determine which of the following independent variables explained the most variability of DOC in lakes: the proportion of wetlands in the total watershed, proportion of wetlands in the terrestrial watershed, and proportion of wetlands measured at different scales. Each zone included the area of all smaller zones, and as such was highly correlated with previous zones. Thus, only one scale was used as an independent variable in any final regression model. The proportion of the lake area covered in emergent or floating vegetation and the drainage ratio (WA/LA) were also used as independent variables for lakes (Schindler 1971). In addition, the mean depth (in feet) was used as a surrogate for water residence time (WRT). Mean depth was obtained from Wisconsin Lakes (WDNR 1995). When mean depth was not available, it was estimated from maximum depth (in meters) using the relationship derived from those lakes where both maximum and mean depth were available: mean depth = $(4.649\,650 + [0.266\,618 \times \text{maximum depth}]) \times 0.3048$. When lakes were sorted by hydrologic type, only drainage and seepage lakes were examined. Spring lakes were not analyzed as a separate hydrologic category due to small sample size. The analysis was repeated using true color as the dependent variable only with the fall 1984 data set. For rivers, the proportion of wetlands in the watershed and the proportion of wetlands in the first 200 m of the watershed were used as potential independent variables. Due to non-normality of the proportional wetlands data, proportion (p) of wetlands was arcsine square-root transformed for all analyses.

Residual plots were used to detect heteroscedasticity (Draper and Smith 1981). As a result, DOC (measured in milligrams per litre) and true color (PCU) were transformed to $\log_{10}$(DOC) and $\log_{10}$(color), respectively. Stepwise regression was used to identify the scale that explained the most variability in DOC. Best-model techniques in SAS were used to identify other candidate models based on comparisons of r^2, adjusted r^2, $\sqrt{\text{MSE}}$, and Mallows' C_p statistics when other variables were included (e.g., WA, LA). SAS best-model techniques enable the evaluation of several ''best'' models (by comparing the above parameters) rather than just the one model selected by stepwise regression. The final regression models reported had the highest r^2, highest adjusted r^2, and lowest C_p statistics. All statistical analyses were conducted using SAS (SAS Institute 1989).

RESULTS

The proportion of wetlands in the total watershed explained the most variability in DOC when all lakes were examined using stepwise regression (Table 3). However, best-model techniques revealed minimal differences between r^2 values when either the proportion of wetlands in the total watershed or the first 50 m were

TABLE 3. Results of stepwise regression showing proportion of total variance in $\log_{10}$(DOC) explained by landscape predictors for lakes.

Season and hydrology	N	Independent variable	r^2	p	$\sqrt{\text{MSE}}$	C_p
Fall 1984 and Summer 1991	119	wetlands within total watershed	0.26	0.0001	0.1799	8.26
Drainage lakes	44	wetlands within total watershed	0.31	0.0001	0.1501	1.22
Seepage lakes	66	wetlands within 1000 m	0.27	0.0001	0.1907	10.8
Fall 1984	64	wetlands within terrestrial watershed	0.33	0.0001	0.1938	6.16
		drainage ratio (WA/LA)†	0.03, 0.36‡	0.0001	0.1903	4.75
Drainage lakes	19	wetlands within total watershed	0.38	0.0051	0.1778	−3.12
Seepage lakes	42	wetlands within 1500 m	0.32	0.0001	0.1832	12.05
Summer 1991	55	wetlands within 50 m	0.29	0.0001	0.1396	1.01
Drainage lakes	25	wetlands within 50 m	0.26	0.009	0.1271	7.40
		water residence time	0.08, 0.34‡	0.0102	0.1228	6.34
Seepage lakes	24	wetlands within 25 m	0.35	0.0021	0.1555	3.14

Notes: N = number of lakes sampled. The proportion of wetlands (p) at different distances within the watershed is arcsine square-root transformed.

† WA = watershed area; LA = lake area.

‡ The partial r^2 for the second variable is followed by the model r^2.

used as independent variables (Fig. 3). When separated by hydrologic type, larger scales again explained the most variability in DOC for drainage lakes (total watershed) and for seepage lakes (1000 m) (Table 3). When separated by season/year, the best predictors were wetlands measured at larger scales (total watershed) for lakes sampled in fall 1984 and smaller scales (50 m) for lakes sampled in summer 1991.

When both season and hydrologic type were analyzed separately, the most variability in DOC for fall 1984 drainage lakes was explained by the proportion of wetlands in the total watershed. DOC in seepage lakes sampled in fall 1984 was best predicted by wetlands measured at large scales of the landscape (1500 m) (Table 3). For drainage lakes sampled in summer 1991, nearshore wetlands (50 m) and WRT explained the most variability in DOC, while the amount of wetlands at near, small scales (25 m) was also the best predictor of DOC in summer 1991 seepage lakes.

The most statistically significant scale according to stepwise regression results, however, was not the only useful predictor of DOC concentrations. The relative variability in DOC explained by wetlands measured at different landscape scales was assessed by determining regression coefficients (r^2) for each scale independently, as well as for the total and terrestrial watersheds (Fig. 4). All season/years and hydrologic categories showed an increase in the proportion of the total variability explained by wetlands measured at small landscape scales (50–100 m). Only in the case of fall 1984 drainage lakes did the proportion wetlands in the total watershed explain a notable amount more of the variability in DOC than the nearshore riparian areas (25–100 m).

For all lakes sampled in fall 1984, the best predictor of true color was the proportion of wetlands in the total watershed. When analyzed by hydrologic type, true color in drainage lakes was best predicted by the proportion of the lake covered in floating or emergent macrophytes (Table 4). Wetlands measured at larger scales (1000 m) were also the best predictor of true color in seepage lakes in the fall.

In riverine systems, the proportion of wetlands in the entire watershed always explained the most variability in DOC, regardless of season. However, the proportion of wetlands in the watershed explained much more of the variance in the fall than in the spring (Table 5).

DISCUSSION

Two main approaches have been employed to study hydrologic and biogeochemical linkages between heterogeneous landscape units and how the spatial arrangement of those landscape units influences material transport within catchments (Allan et al. 1993). Traditional whole-catchment input–output biogeochemical studies often treat the catchment as a ‘‘black box’’ (Bormann and Likens 1967). Such studies ignore spatial heterogeneity within a watershed, despite the fact that a heterogeneous mix of vegetation and geomorphic units can cycle and transport materials at different rates and magnitudes (Knight and Fahey 1985, LaZerte 1989, Durand et al. 1991, Mulder et al. 1991, Allan et al. 1993). In the case of DOC, many factors such as soils, geology, topography, vegetation, and land use and management can influence loading and in-stream concentrations, but the individual effects of such factors can be hard to distinguish in whole-catchment studies (Nelson et al. 1993). The other main approach, studies involving detailed flow-path analyses or long-term hydrologic monitoring, must by necessity consider only a few watersheds (Nelson et al. 1993, Dillon and Molot 1997, Schiff et al. 1997, Schindler et al. 1997, Hinton et al. 1998). This study, however, uses a ‘‘gray box’’ approach (Allan et al. 1993), which provides a useful compromise between complete ‘‘black boxing’’ of an entire watershed and detailed flowpath analyses where few replicates are possible. Although this study does not directly measure fluxes, the scaling approach offers a useful way to examine some of the heteroge-

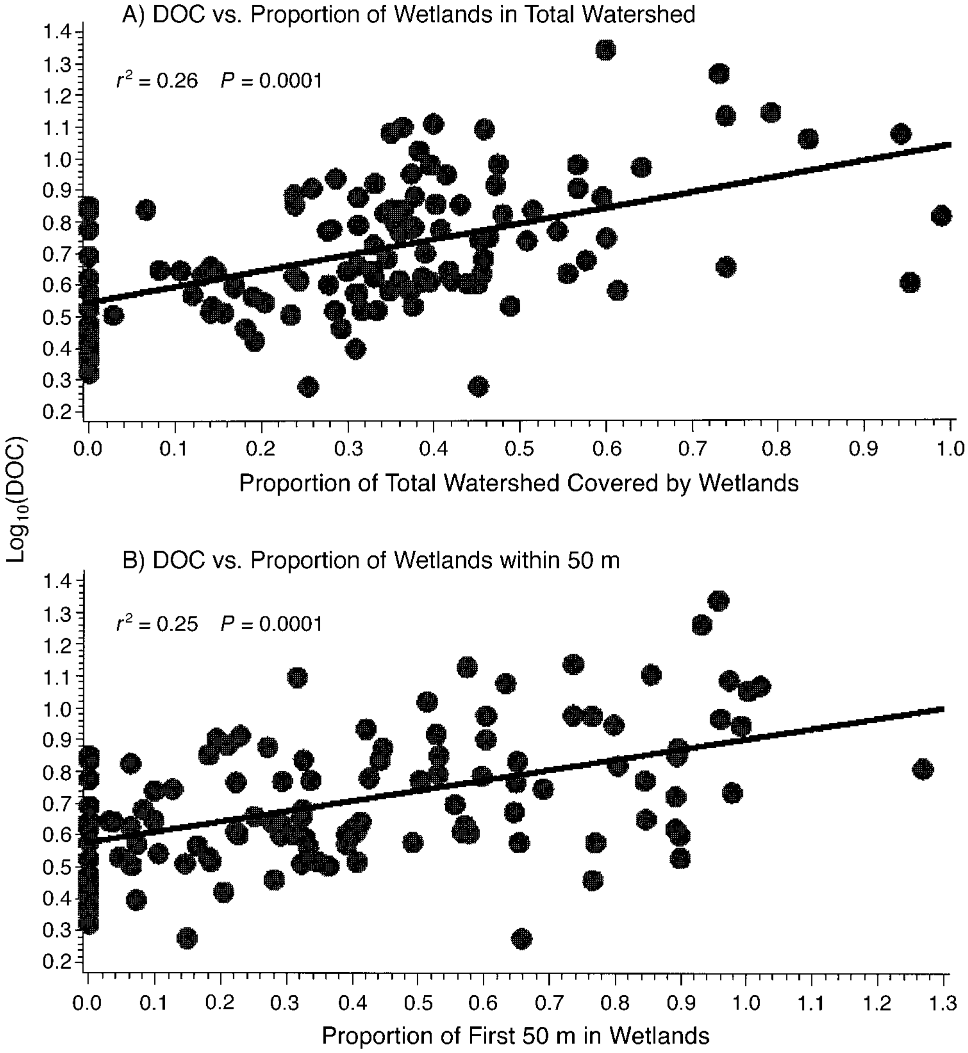

FIG. 3. Variability in DOC of all lakes explained by the proportion of wetlands at small (50-m) and large (total watershed) scales. The regression analysis used $\log_{10}$(DOC) and the arcsine square-root transformed value of the proportion of wetlands. (A) $\log_{10}(\mathrm{DOC}) = 0.489$(proportion wetlands in total watershed) $+ 0.547$; $\sqrt{\mathrm{MSE}} = 0.1799$. (B) $\log_{10}(\mathrm{DOC}) = 0.325$(proportion of wetlands in 50 m) $+ 0.580$; $\sqrt{\mathrm{MSE}} = 0.1803$.

neity of land cover types within the watershed while allowing increasing generality with a large sample size, and may suggest further hypotheses for detailed hydrologic work.

To what extent does the watershed influence DOC in lakes? Does the entire watershed explain more of the variability in DOC than does the nearshore riparian zone?

The proportion of wetlands in the watershed or the proportion within 50 m explained similar proportions of the variance in DOC when all lakes were examined together ($r^2 = 0.26$ and 0.25, respectively; see Fig. 3). Thus, increased landscape information (i.e., the proportion of wetlands measured at even larger scales of the landscape) did not necessarily lead to better predictability (higher r^2). This suggests that the topographic watershed may not always be the most useful and accurate way to define the contributing area for lakes (Soranno et al. 1996).

The topographic watershed also does not reflect the influence of groundwater, since the topigraphically defined watershed boundaries generally do not accurately reflect groundwater-contributing areas (Garrison et al. 1987). While scaling also fails to address groundwater dynamics, by focusing the area of the watershed under consideration it does have practical advantages. Scaling is more consistent and less subject to individual interpretation than is watershed delineation. This is exacerbated in regions with low relief, such as Wisconsin. Considering only a portion of the landscape can also simplify loading models (Soranno et al. 1996) and can

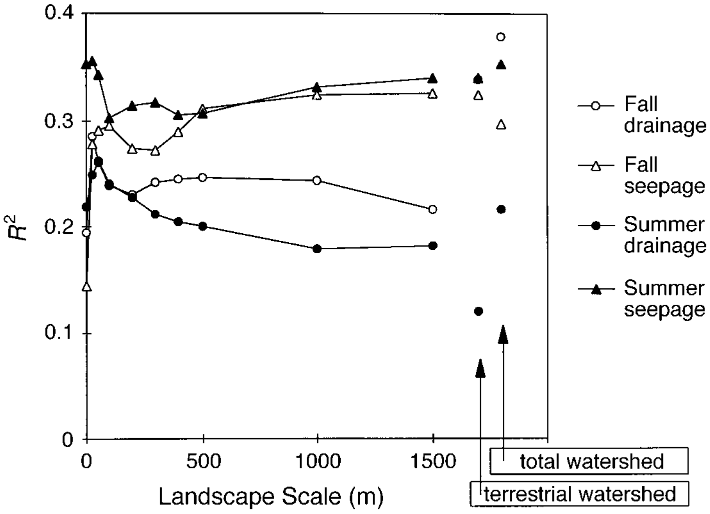

FIG. 4. Regression results at several spatial scales. Regression analysis was used to determine how much of the variability in DOC was explained by measuring the proportion of the watershed occupied by wetlands. The proportion of wetlands was measured at increasing distances from the edge of the lake until the total watershed area was reached (the terrestrial watershed is simply the proportion of wetlands in the total watershed minus the lake area). The variability in DOC (as measured by r^2 values) explained by measuring wetlands is shown versus the distance at which the wetlands were measured. Lakes are separated by hydrologic type as well as by the season in which they were sampled.

suggest where field calibrations for loading and export coefficients may be most useful.

Does the extent of watershed influence vary in lakes of different hydrologic type?

Regardless of whether or not lakes were separated seasonally, stepwise regression results suggested that the variability of DOC in drainage lakes was always best explained by the proportion of wetlands at slightly larger scales than was DOC in seepage lakes. However, the difference between drainage lakes and seepage lakes was relatively small (Fig. 4). Rather, a consistent increase in the amount of variability in DOC explained by wetlands measured at small nearshore scales (25–100 m) was suggested at all sampling dates in both drainage and seepage lakes. The nearshore area is also the location of the majority of the wetlands around these lakes (Fig. 5). Information at broader scales (i.e., the proportion of wetlands measured at even larger scales of the landscape) did not necessarily lead to better predictability (higher r^2). In fact, information at broader scales actually explained less of the variability in DOC in some cases. Only with drainage lakes sampled in fall 1984 did more watershed information appear useful, as the proportion of the variability of DOC explained by wetlands was clearly maximized by the proportion of wetlands in the watershed. However, the increase in explanatory power from wetlands measured at small scales, followed by a subsequent decrease, still occurred even in these lakes until the scale of the total watershed was reached. Thus, a strong influence of nearshore wetlands was demonstrated for drainage and seepage lakes at all sampling dates.

The predictability of DOC in drainage lakes using catchment variables was usually higher than in seepage lakes (Table 3). This finding is similar to that of Kortelainen (1993), who found that catchment variables such as latitude, WA/LA, and the proportion of the catchment in peatlands explained 55% of the variation in TOC in a set of 970 lakes. When separated by hydrologic type, 61% of the variation in TOC was explained by catchment variables for drainage lakes, 59% for headwater lakes, and 52% for closed lakes, but only 32% for seepage lakes (Kortelainen 1993).

How does the landscape influence differ between lacustrine and riverine systems? Does the landscape influence vary seasonally?

The proportion of wetlands in the total watershed always explained more of the variability of DOC in

TABLE 4. Stepwise regression models for true color in lakes showing proportion of total variance in $\log_{10}$(color) explained by landscape predictors for lakes by season and hydrologic type.

Season and hydrology	*N*	Independent variable	r^2	*p*	$\sqrt{\text{MSE}}$	C_p
Fall 1984	64	wetlands within 100 m	0.29	0.0001	0.3135	1.08
		drainage ration (WA/LA)†	0.03, 0.32‡	0.0001	0.3097	0.65
Drainage lakes	19	proportion of lakes covered in emergent/ floating macrophytes	0.34	0.0094	0.2756	−0.35
Seepage lakes	42	wetlands within 100 m	0.33	0.0001	0.3096	4.22

Notes: *N* = number of lakes sampled. The proportion of wetlands (*p*) at different distances within the watershed is arcsine square-root transformed.

† WA = watershed area; LA = lake area.

‡ The partial r^2 for the second variable is followed by the model r^2.

TABLE 5. Proportion of total variance in $\log_{10}$(DOC) explained by the percentage of wetlands in the watershed for rivers.

Season	N	Independent variable	r^2	p	$\sqrt{\text{MSE}}$	C_p
Fall and spring	24	wetlands within total watershed	0.57	0.0001	0.1950	5.13
Fall	24	wetlands within total watershed	0.69	0.0001	0.2762	−1.06
Spring	24	wetlands within total watershed	0.18	0.0390	0.1972	16.36

Notes: N = number of watersheds. The proportion of wetlands at different scales (p) is arcsine square-root transformed.

rivers than did the proportion of wetlands in the nearshore area. P. J. Dillon and L. A. Molot (*unpublished manuscript*) also found that the percentage of peatlands in the catchment explained much of the variance in models of long-term DOC and color export. In addition, a strong seasonal effect was detected in rivers in this study (Fig. 6). The proportion of wetlands in the watershed explained a large amount of the variance of fall DOC concentrations ($r^2 = 0.72$), but not of spring DOC concentrations.

Many studies have also reported a strong, often positive relationship between DOC and discharge (Mulholland and Watts 1982, Meyer and Tate 1983, Thurman 1985, Eckhardt and Moore 1990, Leenheer 1994), particularly during peak or rising flows (Meyer and Tate 1983, Hinton et al. 1997). However, stream DOC concentrations can also be inversely related to discharge (Hornberger et al. 1995) or completely independent of discharge (Hinton et al. 1997). Actual DOC concentration at a given level of discharge can also depend on the position in the hydrograph and the season (Schiff et al. 1997) and can be influenced by large storm events (Hinton et al. 1997).

In studying discharge related to storms, Hinton et al. (1997) found that 50% of the annual DOC export occurred during the wettest periods of the hydrologic regime. Particularly in small watersheds, storm events can contribute a substantial amount of DOC export (Grieve 1984, Hinton et al. 1997). However, amounts may also depend on the frequency of previous storms and drought (Schindler et al. 1992, Hinton et al. 1997). Hinton et al. (1998) suggested that higher DOC concentrations on the rising limbs of hydrographs indicate that flushing of organic sources at the wetland surface may be important during storms, while Schiff et al. (1997) found that most DOC entered during high-flow events via shallow, nearshore flowpaths within a few meters of the stream. Empirical relationships between DOC concentration and discharge may also change during storm events because DOC pathways and fluxes may be different during base-flow and storm-flow conditions, resulting in changes in both the quantity and quality of exported DOC (Jardine et al. 1990, Easthouse et al. 1992).

However, the utility of discharge or percentage of wetlands in a watershed to explain DOC concentrations may vary according to the dominant land cover in a watershed, interacting with seasonal and storm-driven effects. Eckhardt and Moore (1990) examined DOC concentrations in both wetland and ‘‘nonwetland’’ (<1% wetland) catchments. A significant positive relationship between DOC concentrations and discharge was demonstrated in nonwetland catchments. Conversely, in wetland catchments, discharge explained a very small proportion of the variability in DOC, but a strong positive relationship existed between DOC and the percentage of the watershed in wetlands. Fewer seasonal differences were apparent, however, as the DOC/discharge correlation was significant from spring through early winter ($r^2 = 0.26$–0.67) (Eckhardt and Moore 1990).

Seasonal regressions between DOC and discharge

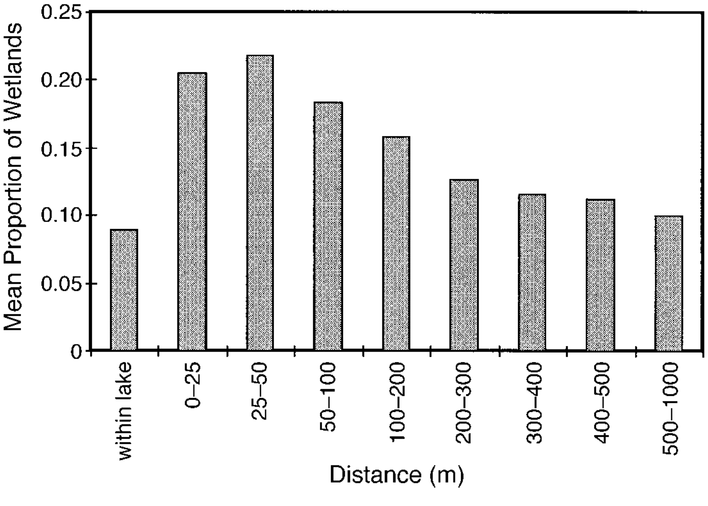

FIG. 5. The average proportion of each area covered in wetlands at different distances from lakes.

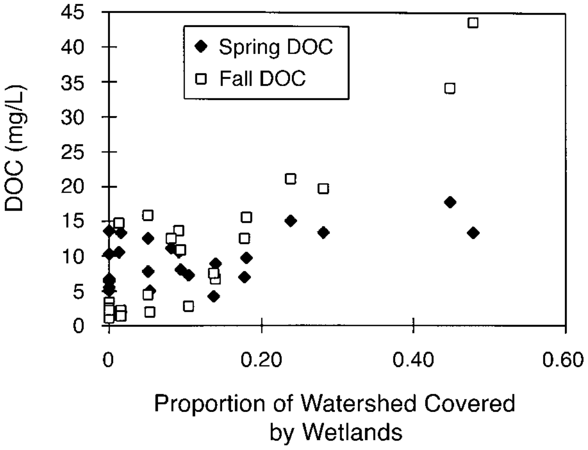

FIG. 6. Relationship between DOC and percentage of wetlands in the watershed for rivers during different seasons.

can be mediated by the dominant land cover. Hinton et al. (1997) found a significant seasonal relationship between DOC and stream discharge in subcatchments without wetlands, but an insignificant relationship in an areas with even small wetland areas. Hinton et al. (1998) also found a positive relationship between DOC and discharge in nonwetland soils, but found that leaching and flushing of wetlands soils at high discharges lead to lower DOC concentrations with successive storms. Hinton et al. (1997) found that export of DOC during stormflow was more important at upland terrestrial sites than at sites with wetlands. An explanation of this finding is that the relative increase in DOC export during storms is smaller in watersheds with wetlands (Hinton et al. 1997). Thus, land cover may also mediate the influence of season and storms on DOC/discharge relationships.

The above studies provide a context for the work presented here and suggest that, in nonwetland catchments, the variability in DOC is related to discharge, while in wetland-dominated catchments, variability in DOC can be explained by the percentage of wetlands in the catchment. Hinton et al. (1998) suggested that differences in DOC/discharge relationships between wetland and nonwetland catchments is related to flow path in nonwetland areas and to DOC production and leaching in ponded water in wetland-dominated catchments. The DOC/discharge relationship may thus be a result of increasing DOC with increasing discharge in uplands, but decreasing concentrations of DOC with discharge in wetland catchments due to dilution (Schiff et al. 1997). Hinton et al. (1998) found that even a small amount of wetlands in some catchments dominated DOC export during both base flow and storm flow. They suggested that ‘‘it would be pointless to relate DOC dynamics to hillslope flowpaths in such catchments’’ and that this dominant influence of wetlands over hillslopes is why correlations between wetland area and DOC export occur. Statistically, it is likely that percentage of wetlands explains more of the variability in DOC export or concentration in wetland catchments because of the truncated range of the independent variable in nonwetland catchments (e.g., if wetlands only occupy 1–10% of the watershed).

Finally, there were differences in the extent of watershed influence for rivers and drainage lakes. The proportion of wetlands in the landscape explained more of the variability in DOC of rivers ($r^2 = 0.69$) than in drainage lakes ($r^2 = 0.31$–0.38). In the spring, however, the proportion of wetlands in the catchment explained less of the variability in DOC in rivers ($r^2 = 0.25$) than in drainage lakes. These differences may be partially due to the confounding influence of water residence time (WRT) in the drainage lakes and all upstream lakes. Longer WRT can lead to increased mineralization of DOC (both biologically and photochemically) in lakes (Stumm and Morgan 1981); both empirical studies and mass balance studies have shown that DOC concentrations in lakes tend to decrease with increasing WRT (Curtis and Adams 1995) both within (Schindler et al. 1992) and among lakes (Rasmussen et al. 1989, Meili 1992) in humid regions. Lower values of water color have also been reported in lakes that receive a high proportion of water from upstream lakes (Rasmussen et al. 1989).

While we acknowledge that WRT can vary tremendously due to lake size, depth, precipitation, evaporation, drainage basin size, soil and rock permeability, and hydraulic conductivity (Wetzel 1990), adding an estimated term for WRT based on mean depth of the receiving lake explained an additional proportion of the variability (0.08) in some models. Thus, within-lake dynamics should be considered to better explain DOC concentrations in lakes. Unfortunately, the mechanisms of DOC loss, flocculation (Kepkay and Johnson 1989, Urban et al. 1990), microbial degradation (Tranvik 1989, Hessen 1992), and photolysis (Kieber et al. 1990, Vallentine and Zepp 1993) are not well quantified (Curtis and Adams 1995), and removal rates for DOC are most likely site specific and possibly source specific (Curtis and Adams 1995). However, even if WRT and DOC loss could be easily estimated for receiving lakes and all upstream lakes, DOC retention and loss may be less closely related to WRT when passing through upstream lakes than when derived directly from surrounding terrestrial catchments (Schindler et al. 1997).

CONCLUSIONS

Scaling research has yielded mixed empirical results, and few theoretical constructs exist to explain the similarities and differences in the broad-scale behavior of various substances in different hydrologic systems. Although what constitutes a lake, a reservoir, or a river may be debatable (Wetzel 1990), few ecologists work across such a large hydrologic gradient (see McDowell and Likens 1988, Leenheer 1994), and science has few ways to make comparisons across such systems. What

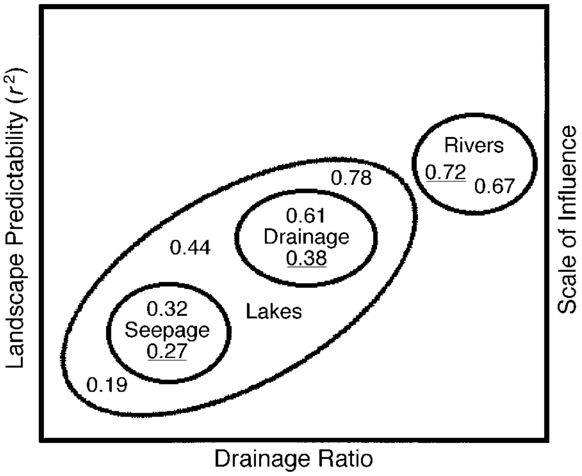

FIG. 7. A plot of the variability in DOC explained by simple landscape characteristics (the proportion of the watershed, or some other scale, in wetlands, the drainage ratio, latitude, or area of upstream lakes) may suggest that landscape predictability (r^2) may vary for seepage lakes, drainage lakes, and rivers. Data were compiled from Hope et al. (1996), P. J. Dillon and L. A. Molot (*unpublished manuscript*), Myllymaa (1985), and Eckhardt and Moore (1990). Data from this study are underlined and use the highest possible r^2 values from best-model techniques.

is needed is a transportable and testable framework to allow systematic comparisons of a variety of water chemistry variables in different systems.

For DOC, at least two interesting contrasts are evident. Along with the differing extent of the landscape influence for different hydrologic systems examined here, another may be the proportion of the variability in DOC that can be easily explained from simple landscape characteristics in different hydrologic systems. Fig. 7 suggests limits to the proportion of variability in DOC concentrations that can be explained by simple landscape characteristics across the continuum of rivers, drainage lakes, and seepage lakes. While we recognize the potential problems in using r^2 values from the literature (such as inappropriate or lack of data transformations or violations of regression assumptions), such values may certainly provide a rough indicator of our ability to predict a system property (e.g., DOC concentrations) from landscape characteristics. Such a comparative framework may also suggest additional hypotheses concerning the relative importance of in-lake vs. watershed influences in controlling DOC.

Developing such a framework is important in an immediate, practical sense, and may have urgent implications for long-term management as well. For example, measurements of local material transport rates from different land use types (Roseboom et al. 1982, Peterjohn and Correll 1984) are extremely critical. Unfortunately, these are costly, labor intensive, and simply not possible everywhere (Osborne and Wiley 1988), particularly in the developing world. Rapid and less expensive approaches are needed (Osborne and Wiley 1988) to compare, evaluate, and monitor aquatic systems.

A better understanding of the linkages between hydrologic flow paths and biogeochemical cycling is also important to develop empirical generalizations and predict the effects of global and regional environmental changes such as climate change, acid precipitation, and land use conversion (Allan et al. 1993). This is particularly true in the case of DOC. Global warming, drought, and acidification will most likely affect loading rates and the resulting concentrations of DOC in freshwaters (Schindler et al. 1997, Schindler and Curtis 1997). This is important, as it has been estimated that over 100 000 lakes in North America alone are naturally vulnerable to UV radiation because of limited DOC inputs (Schindler and Curtis 1997). DOC production in wetlands may be just as important as phosphorus management in addressing eutrophication problems, and the extent of wetlands in a watershed may be an often overlooked master variable driving lake productivity (Carpenter et al. 1998). A richer understanding of DOC dynamics, particularly in response to anthropogenic alterations, should thus be regarded as a high priority (Schindler et al. 1997).

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