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The Influence of Land Use on Lake Nutrients Varies with Watershed Transport Capacity

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ABSTRACT

Nutrient loading to lakes depends on both the availability of nutrients in a watershed and their potential for movement to a lake. Many studies have demonstrated that variation in watershed land use can translate to differences in lake water quality by affecting nutrient availability. There have been few attempts, however, to understand how loading to surface waters is affected by land use when there are differences in watershed transport capacity. We compared the relationship between land use/cover and lake nutrients in lakes draining watersheds that exhibited high and low transport capacity using a 5 year (2001–2005) dataset describing the chemistry of 101 lakes and reservoirs in a region of intensive agriculture. We measured watershed transport capacity by compositing the hydrologic, geologic, and topographic variables correlated with interannual variability in lake total nitrogen (TN) or phosphorus (TP) because the hydrologic permeability of watersheds amplifies downstream responses to rainfall events. Factors describing watershed transport capacity differed for TN and TP, consistent with differences in nutrient mobility and biogeochemistry. Partial least squares regression revealed that watershed transport capacity influenced the nature of the association between land use/cover and lake chemistry. In watersheds with low transport capacity, in-lake processes and near-shore land use/cover tended to be more influential, whereas, in watersheds with high transport capacity, land use/cover across the entire watershed was important for explaining lake chemistry. Thus, although land use is a key driver of nutrient loading to lakes, the extent to which it influences water quality can vary with watershed transport capacity.

Key words: agriculture; Iowa; landscape configuration; nitrogen; phosphorus; riparian areas; water chemistry.

INTRODUCTION

Understanding the influence of land use on water quality remains an important yet elusive goal for ecologists and resource managers alike. Although numerous studies have demonstrated an association between watershed land use and nitrogen (N) and phosphorus (P) loading to surface waters, relationships between land use and water quality are surprisingly variable at the scale of entire watersheds (Omernik 1977; Jones and others 2001; Allan 2004). Some of this variability may be due to inherent differences in the structure of watersheds that affect their ability to convey materials, that is, a watershed's transport capacity. Nutrient loading is a function of both the availability of nutrients in a watershed and their potential for movement to

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receiving waters (Lewis and Grimm 2007). After all, it is not whether nutrients exist in a watershed that matters to water quality, it is the rate at which they move to water that impairs aquatic ecosystems.

The hydrology, geology, soils, and topography of a watershed can all influence watershed transport (Dillon and Kirchner 1975; D'Arcy and Carignan 1997; Van Herpe and Troch 2000) and in so doing, may affect the extent to which land use impacts water chemistry. For example, Kleinman and others (2006) found that site hydrology, as modified by soil properties, interacted with rainfall intensity and landscape position to determine mass losses of N and P, leading to high temporal variation in in-lake nutrients. They concluded that it was the coincidence of high nutrient availability and high transport potential controlling nutrient loss from the soil, rather than either factor alone (Kleinman and others 2006). Similarly, Lewis and Grimm (2007) showed that the hydrologic responsiveness of catchments often varies and can determine N loading following a storm event. Although watershed size does not affect nutrient transport directly, it may alter the extent of land use impacts by modifying the spatial scale at which land use within a watershed contributes to water quality. Several studies indicate that near-shore land use tends to be more important in smaller watersheds than in larger watersheds, where the entire watershed often contributes to nutrient loading (Omernik and others 1981; Strayer and others 2003; Buck and others 2004). Hunsaker and Levine (1995) suggested that this could be due to differences in the amount of energy available to move water and materials, which arise when the percentage and location of land cover varies.

Lakes are strongly linked to their watersheds through the transport of materials carried by surface runoff (Müller and others 1998), and many studies have demonstrated that land use composition can affect nutrient loading to lakes by altering nutrient availability at this scale (Soranno and others 1996; Arbuckle and Downing 2001; Jones and others 2004). An important part of water quality restoration is, therefore, nutrient reduction from watershed inputs (Jeppesen and others 2005), although successful restoration often involves additional measures (Jeppesen and others 2007). Because reduction of watershed nutrient flux is an essential precursor to restoration, it is important to determine how watershed characteristics mediate the relationship between land use and lake water quality. Lake landscape position can be a key factor in understanding variability among lakes (Soranno and others 1999; Martin and Soranno 2006). In particular, lake order, which measures connections to streams by stream order (Riera and others 2000), can account for a considerable amount of variability in water chemistry (Martin and Soranno 2006). Artificial drainage can also affect hydrologic connectivity (David and others 1997) and may increase connectivity to the point that the impact of land use on lake water quality is more severe than in lakes draining less altered watersheds. These factors have only rarely been examined in the context of land use exports, however.

In our study, we used a suite of agriculturally dominated watersheds to investigate how the influence of land use on lake and reservoir water quality varies with watershed transport capacity. Specifically, we asked whether differences in transport capacity affect the relative importance of different land-use-related variables for explaining in-lake concentrations of N and P. Because watershed transport capacity cannot be measured directly, we used the temporal variability of lake nutrient concentrations as a proxy to infer conditions associated with transport (Figure 1). This approach is based on the assumption that variables that increase transport will enhance the interannual fluctuation of nutrient concentrations when nutrient availability (due to land use) is fixed and precipitation is the primary source of variability. Several studies have previously shown that precipitation is a key driver of nutrient fluxes in agricultural watersheds, where external inputs are the dominant form of loading (Correll and others 1999a; Correll and others 1999b).

We hypothesized that individual watershed characteristics integrate to govern watershed transport capacity. We thus identified individual variables positively correlated with interannual variability in total nitrogen (TN) or total phosphorus (TP) concentration and then composited the variables to classify the watersheds as high or low transport capacity (Figure 1). We used interannual variability as our measure of temporal flux rather than intra-annual variability because the latter measure would likely capture differences in nutrient availability as well as differences in watershed transport capacity owing to variation in the rate and timing of fertilizer applications and management practices that occur among watersheds. We then examined the relative importance of watershed characteristics for explaining maximum in-lake TN and TP concentrations for watersheds with high and low transport capacity (Figure 1). Although some of the same variables were used to stratify the watersheds and to explain in-lake nutrient concentrations, this approach is warranted

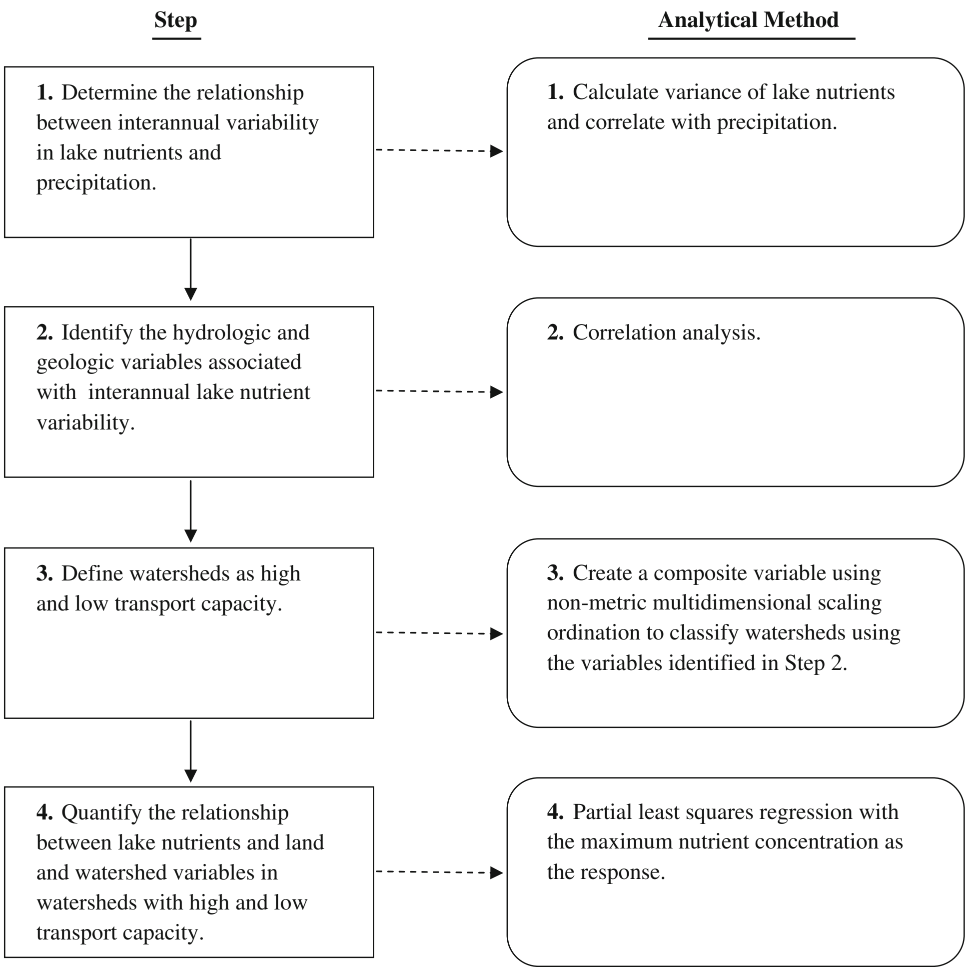

Figure 1. Conceptual diagram of the overall approach taken to evaluate how differences in watershed transport capacity influence the effect of land use on lake nutrients.

as a means of distinguishing differences in the role of land use among watersheds whose ability to convey materials may vary. Similar methods have proven effective elsewhere (Lewis and Grimm 2007). Additionally, the variables defining watershed transport capacity were correlated with the variance of log-transformed nutrient concentrations, after the effect of mean lake depth had been removed; thus, these variables were not associated with nutrient concentrations per se and can be considered as possible explanatory factors for the observed data.

Methods

Limnological Data

We sampled lake nutrients and temperature in 101 lakes three times during the ice-free season from 2001 to 2005 (spring–early summer, mid-summer, and late summer-fall). Most of these lakes (78%) were reservoirs, that is, dammed rivers. Others were natural basins (14%) or oxbows (8%). Lakes ranged in size from 5 to 1271 ha, and watersheds ranged in size from 14 to 50,587 ha. Field crews sampled at the deepest point in each lake basin, as determined by sonar and existing bathymetric maps. Field crews used temperature profile data to determine the depth or absence of the thermocline. An integrated column sampler was used to collect water from the upper mixed zone of the lake. If no thermocline was present, then field crews sampled the entire water column to a maximum depth of 2 m (mean depth of all lakes: 2.98 m ± 1.35 SD). Samples were transported to the laboratory under refrigeration. Total phosphorus samples were analyzed using the Murphy-Riley method in Standard Methods (Clesceri and others 1998) with turbidity correction. Total nitrogen samples were analyzed using the second derivative spectroscopy method (Crumpton and others 1992).

Watershed Data

Watershed boundaries for each of the 101 lakes were provided by the Iowa Department of Natural Resources (IDNR, www.igsb.uiowa.edu/nrgislibx) or were recreated when found to have significant errors. Boundaries were delineated using 10-m digital elevation models (DEMs) and digital raster graphics (DRGs, USGS, www.usgs.gov). The average slope of each watershed was also calculated.

Boundaries were used to summarize land use/cover, hydrology, soils, and surficial geology for each watershed. Land-use data were extracted from a 30-m resolution digital land cover map derived from 2002 satellite imagery (Landsat TM) and classified by the IDNR (/www.igsb.uiowa.edu/nrgislibx). We combined the 17 original land cover classes into five categories (open water, forest, grass, agriculture, and commercial (includes both industrial and residential land use)) and determined the percentage of the watershed area each occupied. We also characterized land use within a 100-m buffer of each lake, constrained by watershed boundaries.

The arrangement of agriculture within watersheds was further characterized as a percentage of watershed area weighted by its inverse distance (IDW) from the shoreline (Soranno and others 1996; King and others 2005). Following the methods of King and others (2007), we first calculated the distance of every pixel in the watershed to the shoreline using simple Euclidean distance. Each pixel of agriculture was then weighted by the inverse of its distance to the shoreline (1/distance) and summed for a distance-weighted pixel count for the entire watershed. The sum of the distance-weighted land-use pixels was divided by the sum of distance-weighted total land in the watershed to yield distance-weighted percentage agriculture (IDW-agriculture).

Hydrologic variables included stream length and percentage of land with a high probability of having artificial drainage within a watershed. Stream length was defined as the total length of arcs extracted by overlaying watershed boundaries on the Iowa Aquatic Gap Streams dataset (www.igsb.uiowa.edu/nrgislibx), which is based on an enhanced version of the 1:100,000 National Hydrography Dataset (NHD, www.usgs.gov). Lake order calculations as described by Riera and others (2000) were also based on this data set. We calculated the percentage of land with a high probability of having artificial drainage by spatially joining the Iowa Soil Properties and Interpretations Database (ISPAID, www.extension.iastate.edu) with the U.S. General Soil Map (STATSGO, http://www.soildatamart.nrcs.usda.gov) for Iowa and selecting for soils that would require tile drainage to achieve optimal agronomic yields or row crops (G. E. Miller, unpublished data). Criteria for selection included: a surface slope less than 5%, drainage that was moderately good to very poor, and subsoil with less than 40% clay content. These criteria also ensured that only arable lands were selected. We used the ISPAID and STATSGO datasets to characterize soil permeability and surficial geology (% alluvium, loess, till) within each watershed as well.

We calculated additional watershed variables based on other publicly available data. The number of confinement feeding operations (CFOs) within each watershed was determined from a dataset of CFOs registered with the state and available from the IDNR. Water residence time for each lake was based on total streamflow (Q (Schilling and Wolter 2005)). A list of all variables is shown in Table 1.

Data Analysis

To provide support for the assumption that the temporal fluctuation of nutrient concentrations can be used as a proxy for watershed transport capacity, we first examined the correlation between in-lake nutrient concentrations and precipitation patterns in watersheds with high and low interannual nutrient variability. We defined a watershed as having high nutrient variability if the average standard deviation of log-transformed (SDL) lake nutrient concentrations for TN or TP between 2001 and 2005 ranked in the top 10% of all watersheds; watersheds with low nutrient variability ranked in the bottom 10% of all watersheds for these metrics. We used the SDL rather than another metric for comparing variability because it corrects for mean-variance scaling and is robust to skewed distributions (McArdle and others 1990; Fraterrigo and Rusak 2008). We computed Spearman's rank correlation coefficients between spring in-lake nutrient concentrations (sampled during May) and total spring precipitation (March–May) for each individual lake over the 2001–2005 sampling period. We focused on the spring sampling period because the relationship between precipitation and nutrient flux tends to be the strongest in this season (Correll and others 1999b; Correll and others 1999a) and we wanted a conservative measure of the precipitation-nutrient association in watersheds exhibiting low nutrient variability. Correlations in the high and low variability groups were compared using ANOVA.

We determined the gradient of watershed transport capacity by first identifying the individual variables (from those listed in Table 1) associated with variability in lake nutrient concentration and then deriving a composite variable from them. Expecting that variables involved in nutrient

Table 1. Mean (±1 SE) Lake and Watershed Properties for High and Low Transport Capacity Watersheds with Respect to TN and TP

Property	Watershed transport capacity with respect to nutrients			
	N—High (N = 17)	N—Low (N = 22)	P—High (N = 13)	P—Low (N = 11)
Lake chemistry and morphometry				
Max. TN (mg/l)	6.04 (1.07)	2.55 (0.69)	–	–
Max. TP (μg/l)	–	–	220.6 (36.1)	121.0 (27.0)
WA: LA*	44.17 (9.38)	13.94 (4.55)	31.03 (6.20)	7.03 (1.66)
LA (ha)*	280 (83)	60 (16)	414 (91)	11 (2)
LV ($m^3 \times 10^{-3}$)*	8,556 (2,141)	1,250 (330)	12,269 (2,154)	270 (31)
Lake depth (m)	3.35 (0.39)	2.64 (0.29)	3.45 (0.50)	2.95 (0.50)
Land use/cover				
IDW Agriculture*	25 (3)	15 (3)	25 (4)	10 (3)
% Agriculture	56 (5)	26 (6)	58 (6)	20 (7)
% Commercial	5 (2)	13 (3)	3 (0)	11 (3)
% Grass	27 (3)	27 (3)	27 (5)	28 (4)
% Forest	7 (2)	13 (4)	6 (1)	17 (4)
% Ag-100*	7 (2)	7 (2)	8 (2)	6 (2)
% Comm-100*	10 (3)	20 (3)	11 (3)	16 (4)
% Forest-100*	47 (6)	30 (5)	44 (6)	36 (7)
% Grass-100*	37 (4)	43 (3)	38 (4)	43 (5)
% Tile drained	20 (6)	18 (4)	27 (7)	14 (5)
Feed Conf.*	0.76 (0.26)	0 (0)	0.85 (0.32)	0 (0)
Soils and parent material				
% Alluvium	13 (2)	17 (4)	10 (2)	16 (8)
% Till	22 (8)	18 (6)	31 (10)	6 (2)
% Loess	42 (7)	16 (5)	28 (8)	26 (9)
% HP soil*	0 (0)	6 (2)	1 (1)	5 (3)
% LP soil*	10 (4)	18 (5)	18 (7)	15 (8)
% MP soil*	77 (6)	52 (6)	66 (9)	52 (10)
Watershed morphometry and hydrology				
Total WA (ha)*	8,761 (3,006)	598 (150)	11,659 (3,625)	98 (21)
% Slope	6 (1)	4 (1)	4 (0)	4 (1)
Water res. time (y)	0.71 (0.17)	3.38 (0.91)	0.86 (0.21)	6.01 (2.10)
Stream len. (m)	50,960 (12,739)	458 (316)	68,126 (14,092)	0 (0)
Lake order <0*	0	22	0	10
Lake order >0*	17	0	13	1

TN = total nitrogen; TP = total phosphorus; LA = lake area; LV = lake volume; IDW = inverse distance-weighted agriculture; Ag-100 = agriculture within 100 m of lake; Comm-100 = commercial land within 100 m of lake; Forest-100 = forest within 100 m of lake; Grass-100 = grassland within 100 m of lake; Feed Conf. = number of feeding confinements; HP soil = high permeability soil; LP soil = low permeability soil; MP soil = moderate permeability soil; Total WA = total watershed area; Lake order <0 = number of lakes with lake order <0; Lake order >0 = number of lakes with lake order >0.
Values for TN and TP are based on the maximum values of these variables during 2001–2005.

transport would be positively correlated with in-lake variability of TN and TP, we calculated the interannual variance of the log-transformed nutrient data from 2001 to 2005. As with the SDL, taking the variance of log-transformed observations corrects for mean-variance scaling and skewed distributions (McArdle and others 1990; Fraterrigo and Rusak 2008). Because nutrient concentrations in shallow lakes can be intrinsically more variable due to wind mixing (Søndergaard and others 1992), we removed the effect of lake depth by regressing variance and mean lake depth. We then calculated Spearman's rank correlation coefficients to identify the variables significantly associated ($P < 0.05$) with the residuals. We created a composite variable from the variables associated with TP variance using non-metric multidimensional scaling (NMS) after computing a matrix of Bray-Curtis dissimilarities. Using the ''autopilot'' procedure in PC-Ord (v. 4.34, MjM Software), we performed 50 runs with the real data, each with a random starting configuration, and checked our solutions against those attained with randomized data to ensure a better-than-random solution.

Diagnostic (scree) plots suggested a two-dimensional solution was optimal. NMS was thus rerun, specifying two dimensions and the best starting configuration. The final stress for this solution was 4.37 (stress values <5 are considered very good (McCune and Grace, 2002)). Only one variable, lake order, was significantly related to TN variance, so NMS was not performed.

Using the NMS scores, we stratified the watersheds into groups with respect to TP transport. Watersheds were classified as having high or low transport capacity if they were at the ends of the transport capacity gradient, which were defined as approximately 10% of the data at either end of the continuum adjusted for natural break points. To distinguish high and low transport capacity with respect to TN, we classified watersheds by lake order alone. Watersheds with a lake order of 3 or above were classified as having high transport capacity, which corresponded to lakes whose outlets were third- or higher order streams. Watersheds with a lake order of less than -1 were classified as having low transport capacity because they were not connected to the surface drainage network by either permanent or temporary streams (Riera and others 2000).

We used partial least squares regression (PLS (Wold 1995)) to examine the relationship between TN or TP and the explanatory variables (Table 1) in watersheds with high and low transport capacity. PLS circumvents several problems associated with traditional multivariate analysis, specifically multicollinearity among predictor variables and a low number of observations relative to predictor variables (Wold and others 1984). It does so by projecting predictors onto orthogonal 'latent' components, which are then used as independent variables in a regression. The latent components in PLS are calculated to maximize the covariance between the response and predictors through the simultaneous decomposition of X and Y matrices or vectors. This approach makes PLS superior to other multivariate methods for examining the relationship between dependent and independent variables (Eriksson and others 1995).

We found the minimum number of latent components needed to obtain the best generalization for the prediction of new observations through a cross-validation procedure similar to bootstrapping (Wold 1978; Stone and Brooks 1990). The data were divided into five groups (typically, 5–10 groups are used depending on the number of observations), and a model was developed from the data with one of the groups omitted. The omitted group was used as a test set, and differences between actual and predicted Y-values of the test set were squared and summed to yield a partial PRESS (predictive residual sum of squares). The procedure was repeated until all groups had been omitted once. The values for the partial PRESSs were then summed giving a total PRESS, which equates to the predictive capability of a component of the PLS model. To aid in interpretability, the total PRESS was re-expressed as Q^2 by dividing the total PRESS by the sum of squares of the observed Y-values corrected for the mean (SS) and subtracting from 1 ($Q^2 = 1 - \mathrm{PRESS/SS}$, where $SS = \sum (y - \bar{y})^2$ (Eriksson and others 1995)). New components were added to the model if they were statistically significant, that is, when Q^2 was greater than 0.097, which corresponds to P less than 0.05 (Fridén and others 1994).

Two additional measures were calculated to indicate model validity and the relative influence of predictor variables. The measure R^2Y gives the proportion of variance in the response variable that is explained by the model and corresponds to the multiple correlation coefficient, R^2. It differs from Q^2 in that the computation of R^2Y does not require cross-validation and therefore does not yield a measure of the model's predictive ability. Variable importance in the projection (VIP) values quantifies the contribution of each predictor to explaining the variation in the response variables. VIP values greater than 1 are considered the most relevant, although this does not indicate the direction of influence (that is, positive or negative (Wold 1995; Johansson and Nilsson 2002)).

Prior to calculations, predictor variables were centered and scaled to unit variance to give all variables the same relative importance (Johansson and Nilsson 2002). Response variables were log-transformed to minimize deviations from normality. The PLS regressions were done with the software XLSTAT version 2006.5 (Addinsoft, Inc.), with lake order specified as a categorical variable.

Results

The mean standard deviation of log-transformed (SDL) TN and TP concentrations for all lakes between 2001 and 2005 was 0.33 and 0.45, respectively. Watersheds in the top 10% of these distributions had a mean SDL greater than 0.53 for TN and greater than 0.63 for TP and were classified as having high temporal variability. Watersheds in the bottom 10% of these distributions had a mean SDL less than 0.15 for TN and less than 0.24 for TP and were classified as having low temporal variability.

Correlations between spring precipitation and in-lake nutrient concentrations were stronger in watersheds with high variability than in those with low variability for both TN (mean ρ: high = 0.70, low = 0.30) and TP (mean ρ: high = 0.78, low = 0.45). For TN, the differences were statistically significant ($F = 3.93$, $P = 0.05$). For TP, however, the differences were not significant ($F = 2.30$, $P = 0.14$) due to the presence of a single outlier. Removing the outlier gave a statistically significant result ($F = 6.06$, $P = 0.02$).

We detected several factors that were positively correlated with the interannual variance of TP after removing the effect of mean lake depth. The factors included total watershed area ($\rho = 0.21$, $P < 0.04$), water residence time ($\rho = 0.28$, $P < 0.004$), the ratio of watershed area to lake area ($\rho = 0.20$, $P < 0.04$), stream length ($\rho = 0.24$, $P < 0.02$), percentage of watershed with tile drainage ($\rho = 0.38$, $P < 0.0001$), and the ratio of lake area to lake volume ($\rho = 0.19$, $P = 0.05$). Ordination of these variables with NMS resulted in a model explaining 75% (Axis 1 = 22%, Axis 2 = 53%) of the variation in watershed characteristics (Figure 2). Axis 1 was most closely associated with percent tile drainage ($r = 0.31$), whereas axis 2 was most closely associated with total area ($r = 0.52$) and stream length ($r = 0.62$). Only lake order was associated with TN variance ($\rho = 0.20$, $P < 0.05$), so NMS was not performed.

Using the ordination scores, we classified 13 watersheds as having high transport capacity and 11 watersheds as having low transport capacity with respect to TP. Ranking watersheds according to lake order resulted in 17 watersheds with high transport capacity and 22 watersheds with low transport capacity with respect to TN. Watersheds with high transport capacity were generally larger and better connected hydrologically than those with low transport capacity (Table 1), consistent with expectations about the factors influencing nutrient transport. There were no systematic differences in lake type, however. Eighty-two percent and 62% of the lakes in watersheds with high transport capacity were reservoirs (for TN and TP, respectively), whereas 64 and 100% of the lakes in watersheds with low transport capacity were reservoirs (for TN and TP, respectively).

All of the PLS-regression models were significant ($Q^2 > 0.097$) and explained a substantial amount of variation in lake nutrients ($R^2Y > 65\%$) with a single component (Table 2). Models from watersheds with high and low transport capacity did not differ systematically with respect to their predictive or explanatory power, although the model for TN

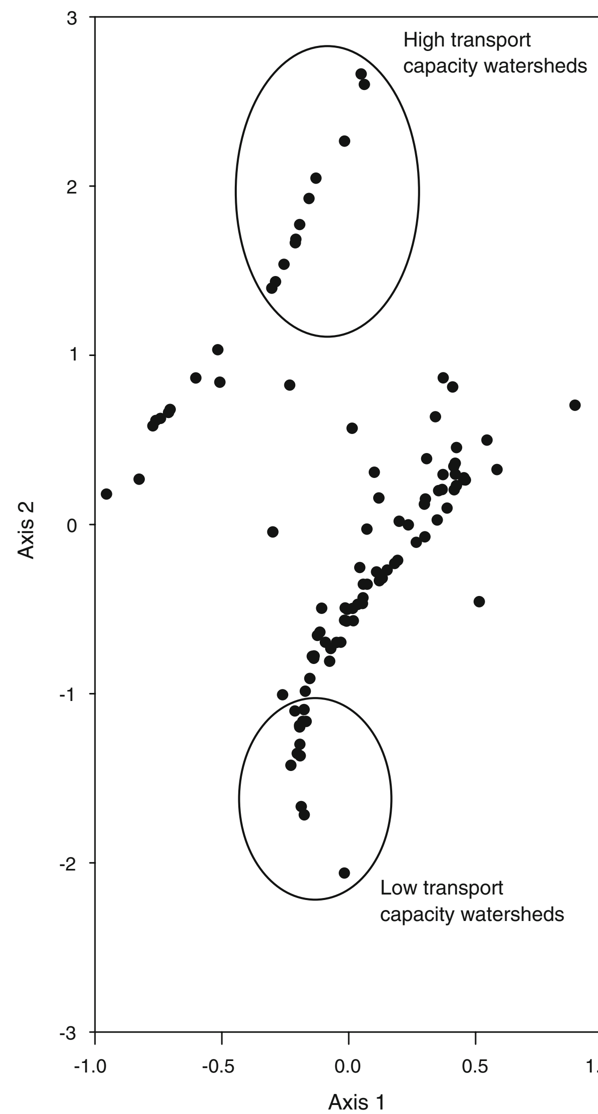

Figure 2. Non-metric multidimensional scaling (NMS) ordination to stratify watersheds by transport capacity with respect to TP. Relative to their axes scores, the top 10% of watersheds were classified as having high transport capacity, whereas the bottom 10% were classified as those with low transport capacity. NMS was not used to classify watersheds with respect to TN because lake order was the only variable associated with TN variance.

in watersheds with high transport capacity had almost twice the predictive power of the other models. In contrast, explanatory power was similar among all models.

Overlays of the VIP values in watersheds with high and low transport capacity suggested that the relative importance of the predictors differed with watershed transport capacity, and that patterns varied for TN and TP (Figure 2). In these figures, variables with high explanatory power for all

Table 2. Results of the PLS Analysis

Nutrient	Watershed transport capacity	Q^2	R^2Y
TN	Low (N = 17)	0.330	0.675
	High (N = 22)	0.627	0.787
TP	Low (N = 13)	0.374	0.805
	High (N = 11)	0.233	0.655

All models are based on one latent component. Q^2 indicates the predictive power of the model based on cross validation, whereas R^2Y indicates the explanatory power of the model and is analogous to the multiple correlation coefficient, R^2.

watersheds are displayed in the upper right quadrant, whereas those variables differing in explanatory power between watersheds with high and low transport capacity are found in the lower right and upper left quadrants. For example, agriculture and forest within 100 m of the shore, IDW-agriculture, and percent forest were considerably more important for explaining TN variability in watersheds with low transport capacity than in watersheds with high transport capacity, whereas percent grass and grass within 100 m of the shore were more important for explaining TN variability in watersheds with high transport capacity (Figure 2). Several variables were important for explaining variation in TN regardless of transport capacity, including percent tile drainage, agriculture, and glacial till.

There was less overlap between the explanatory variables for TP in watersheds with high and low transport capacity (Figure 2). Percent commercial cover was the only variable relevant for explaining TP in both types of watersheds. Agriculture-related variables (agriculture within 100 m of the shore, IDW-agriculture, percent agriculture, and percent tile drained), as well as commercial land within 100 m of the shore, were associated with TP variability in watersheds with low transport capacity but not in those with high transport capacity. Grass and forest within 100 m of shore were important only in watersheds with high transport capacity.

Evaluation of model parameters for variables with VIP values greater than 1 indicated general similarities in the direction of influence on water chemistry in watersheds with high and low transport capacity (Figure 3). For instance, in both types of watersheds percent tile drainage, percent agriculture, and percent till were positively related to in-lake TN concentration, whereas percent alluvium was negatively related to in-lake TN concentration (Figure 3). Likewise, percent commercial coverage had a similar overall effect on TP concentration regardless of watershed transport capacity and despite differences in the magnitude of the effect (Figure 3).

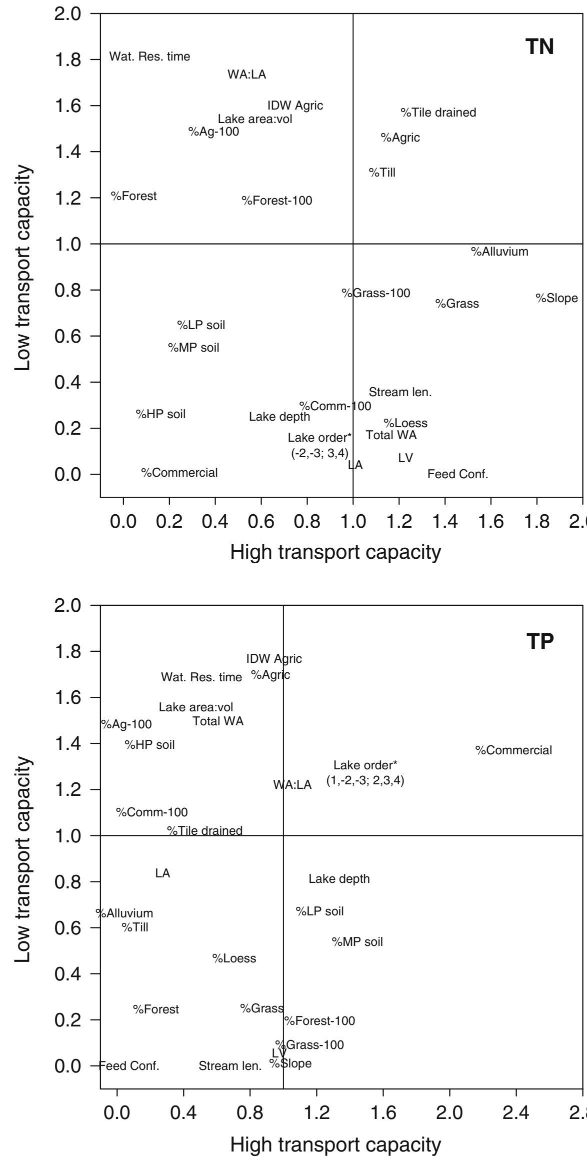

Figure 3. Overlay plots comparing the relative importance of different explanatory variables used in models predicting total nitrogen (TN) and total phosphorus (TP) in lakes with low and high transport capacity. Plotted on the x-axis are the variable importance in the projection values (VIPs) of explanatory variables in watersheds with high transport capacity. Plotted on the y-axis are the VIPs of explanatory variables in watersheds with low transport capacity. In general, only variables with importance values of 1.0 or greater are considered relevant. Thus, variables in the upper right quadrants of the graphs have high explanatory power in both types of watersheds, whereas variables in the bottom right quadrants of the graphs have high explanatory power only in watersheds with high transport capacity. Refer to Table 1 for label definitions. *The VIPs for the variable lake order are based on the mean of the VIPs calculated for each lake order class (lake order classes are shown in parentheses for low and high transport capacity watersheds, respectively).

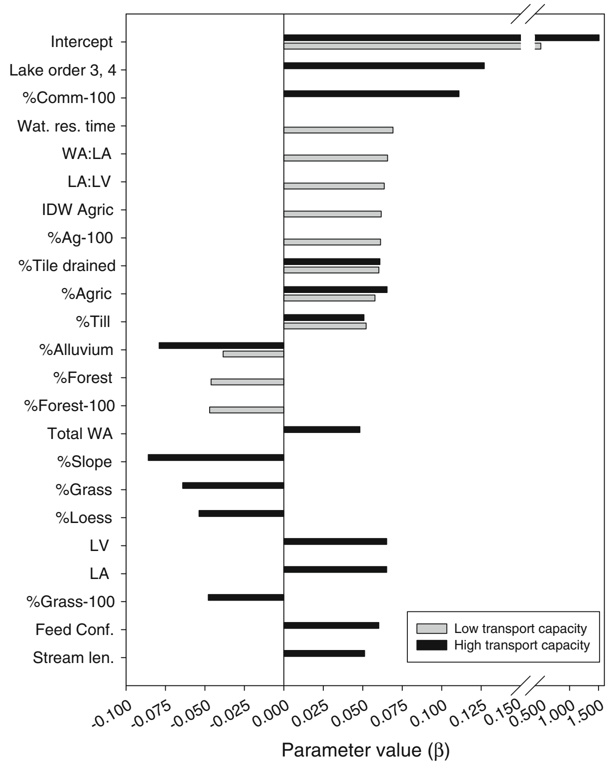

Figure 4. Model coefficients for predicting total nitrogen in lakes with low (N = 17) and high (N = 22) transport capacity. Only variables with relative importance values greater than 0.95 are included. Refer to Table 1 for label definitions.

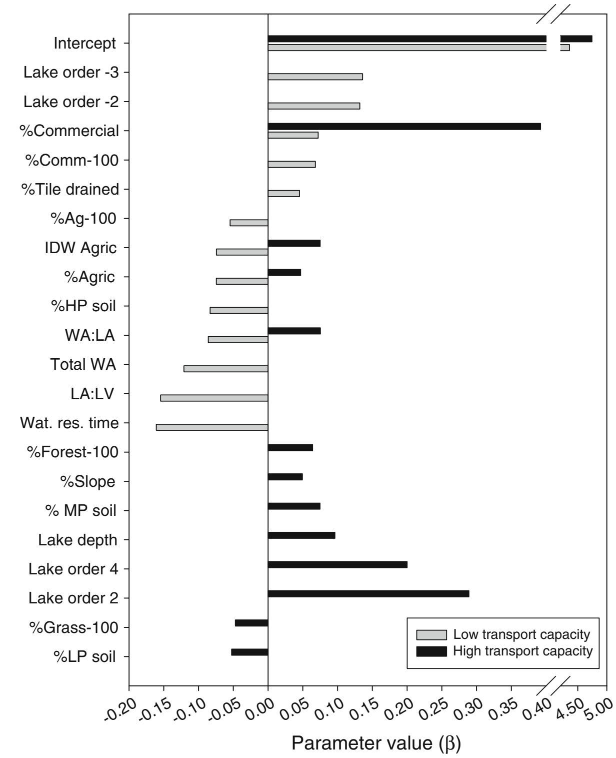

Figure 5. Model coefficients for predicting total phosphorus in lakes with low (N = 13) and high (N = 11) transport capacity. Only variables with relative importance values greater than 0.95 are included. Refer to Table 1 for label definitions.

In contrast, the direction of the effect of some variables depended on the nutrient being considered. Variables related to agriculture tended to have a positive influence on TN, but a negative influence on TP in watersheds with low transport capacity (Figures 4, 5). Percent of near-shore forest (riparian areas) had a positive effect on TP concentration, but a negative effect on TN concentration.

Discussion

Limnological theory suggests that in-lake nutrient concentrations are largely determined by external inputs (Reckhow and others 1980; Canfield and Bachmann 1981), and a growing number of empirical studies linking land-use composition and lake chemistry support this idea. Our results corroborate it as well; the amount of agriculture and commercial (developed) land in a watershed was a strong predictor of in-lake TN and TP concentration, respectively, regardless of watershed transport capacity. The relationship between agriculture and nitrogen concentrations in receiving waters has been widely reported and is presumably a result of the high loadings and low retention of nitrogenous fertilizers in cultivated fields (Howarth and others 1996; Johnson and others 1997; Jones and others 2001; Jones and others 2004; King and others 2005). The association between lake phosphorus concentration and commercial or urban land has also been documented previously (Omernik 1976; Osborne and Wiley 1988; Soranno and others 1996), but is less universal. For example, others have found that the amount of agriculture in a watershed best explains phosphorus concentrations (Jones and others 2001; Jones and others 2004). Developed lands, be they residential, commercial, or industrial, increase the abundance of impervious surfaces in a watershed, which promotes excessive runoff and reduces the potential of nutrient attenuation in these areas (Soranno and others 1996; Carpenter and others 1998). Sewage inputs can also be key sources of P in developed areas, especially in rural locations where septic systems act as point sources (Muscutt and Withers 1996).

In our study, there was also an association between the percentage of tile drainage in a watershed and within-in lake TN concentration at both levels of watershed transport capacity. Other studies have shown that tile drainage can account for much of the inorganic N lost from agricultural fields (David and others 1997; Tomer and others 2003). This occurs primarily during periods of high rainfall when tile drainage short-circuits other transport processes (Logan and others 1994; David and others 1997; Tomer and others 2003). Watersheds are thus rendered ''leaky'' irrespective of characteristics that may otherwise modulate their capacity for moving N. Accordingly, watershed transport capacity has little bearing on how tile drainage relates to the concentration of TN in lakes.

In contrast, there were differences in the relationship between tile drainage and in-lake TP concentration with watershed transport capacity. Tile drainage was an important factor for explaining TP in watersheds with low transport capacity but not in those with high transport capacity. Unlike N, a large proportion of the P delivered to surface waters arrives via runoff in either dissolved or particulate forms (Sharpley and Syers 1979), with inlets and sediments being additional sources of P in lakes (Reed-Andersen and others 2000). Tile drainage therefore has little effect on P loading to lakes supplied by overland flow (Sims and others 1998), a pattern consistent with our results for watersheds with high transport capacity. Because watersheds with low transport capacity are not well linked to their outlets by transport processes or hydrology, however, P delivery via overland flow should be limited in these watersheds. Artificial subsurface drainage may thus introduce a new source of P that can substantially influence lake concentrations. In this way, tile drainage alters how P is transferred between terrestrial and aquatic systems in watersheds that have low transport capacity but not in watersheds that have high transport capacity.

Watershed transport capacity affected the influence of other land-use/cover variables on lake nutrients, as well. One of the most striking differences was in the role of the spatial pattern of land use/cover in explaining lake chemistry. Near-shore agricultural and commercial lands, as well as distance-weighted agriculture, were strongly associated with TN and TP concentrations in watersheds with low transport capacity, but were unrelated to nutrient concentrations in watersheds with higher overall transport capacity. The greater relative importance of land-use spatial configuration in watersheds with low transport capacity compared to those with high transport capacity is consistent with expectations given broad-scale differences in nutrient movement potential. A watershed with high transport capacity is more permeable to nutrient sources located any distance from the outlet, as there is a set of integrated characteristics directing the flow of nutrients to the lake. As a result, nutrient flux is controlled at the watershed scale in watersheds with high transport capacity and near-shore sources are less influential. Watersheds with low transport capacity lack mechanisms for nutrient delivery at broad scales, however, making the proximity of a source area highly relevant for determining the potential of nutrient attenuation. As nutrients deriving in near-shore areas are less likely to attenuate before reaching a lake, they would contribute more heavily to a lake's nutrient concentration. Thus, although land away from receiving waters is generally thought to have less impact on nutrient concentrations (Osborne and Wiley 1988), watershed transport capacity seems to mediate this relationship in lakes.

Others have recognized that the relative importance of land cover for predicting water quality may change over time and space. Seasonal differences in hydrology have often been cited in explaining changes in relationships and predictive power (Johnson and others 1997; Gergel and others 1999; Gergel and others 2002). For example, Johnson and others (1997) found that relationships between land cover and stream water quality variables observed during the summer were absent during the autumn, when there was less of a hydrologic connection between the catchment and the rivers. Hydrology is woven into our definition of watershed transport capacity, which may explain why watersheds with different levels of transport capacity showed different associations with land use/cover. The spatial scale at which the influence of land use on water quality is assessed may also contribute to differences in the relationship between land cover and water quality. Several studies have now shown that different water quality variables respond to land use at different scales due to differences in their mobility (Allan and others 1997; Gergel and others 2002; Allan 2004), a pattern consistent with our results. From a mechanistic standpoint, variable-source area regulation of flushing from soils integrates these ideas (Creed and Band 1998). The concept of hydrologically sensitive areas (HSAs) is most relevant, however, because it pertains to the probability of pollutant transport risk. HSAs are defined as areas in a watershed especially prone to generating runoff and therefore potentially susceptible to transporting contaminants to perennial surface water bodies (Walter and others 2000). Managing watersheds in light of this concept requires that efforts be focused on those areas where HSAs coincide with land uses that potentially contribute pollutants.

Watershed size may affect how well land cover predicts water quality, too. Strayer and others (2003) found less predictability in smaller watersheds (1–10 km^2) and argued that this reflected the increasing importance of the spatial configuration of land use. Our low transport capacity watersheds tended to be smaller than our high transport capacity watersheds (Table 1), yet we did not find consistent differences in the predictability or explanatory power of our models (Table 2). In a study of agricultural catchments in New Zealand that focused on questions similar to those addressed in our study, Buck and others (2004) reported that upstream land use was more influential on the water quality of larger streams, whereas local land use and other factors were more important in smaller streams. They attributed these differences to the averaging out of local effects of heterogeneity at broader scales. Lakes may operate similarly, but for different reasons.

In general, watershed transport capacity tended to separate lakes into those most influenced by in-lake or near-shore processes versus those most influenced by processes occurring at the scale of the entire watershed. Variables such as water residence time (strongly related to the ratio of watershed area to lake area) and the ratio of lake area to volume had high explanatory power in watersheds with low transport capacity (Figure 2) and reflect control of nutrients via liberation through decomposition (TN) and sediment transport and retention (TP). Conversely, in watersheds with high transport capacity, stream length, lake order, soil and geologic characteristics, as well as slope—all measured at the watershed scale—were the most relevant variables. This suggests that lake nutrient concentration was a function of the factors that influenced nutrient movement across the landscape.

Still, not all the variables singled out in our analysis fit the proposed conceptual model or were straightforward to interpret. For example, we found a negative relationship between TP and agriculture in watersheds with low transport capacity, which runs contrary to expectations. As Johnson and others (1997) pointed out, however, agriculture in the midwestern US can be positively correlated with clay soils, which have high adsorption potential for P. If low transport capacity watersheds move water and materials more slowly than high transport capacity watersheds, then there would be a greater chance that particulate forms of P would be occluded in these areas. The negative relationship between low permeability soil (clays) and TP in watersheds with high transport capacity appears to parallel this phenomenon, but at the scale of the entire watershed. The positive relationship between forest and grass in near-shore riparian areas and TP in watersheds with high transport capacity was also unexpected. Yet riparian and grassy areas are often used for grazing and watering livestock in this region, and so may, in fact, be source areas for P. These relationships could also be artifacts due to covariance among these variables and other variables related to TP; however, the only variables associated with near-shore forest and grass were lake area and lake volume. Moreover, only lake volume was important for explaining TP. This demonstrates the complexity that may be inherent in linking water quality to land use that, while broadly categorized, depends upon individual human decisions concerning the details of land management.

Our findings have several implications. As has been previously recognized, N and P transport differs and thus management of landscapes to mitigate these nutrients must differ (Heathwaite and others 2000). Our work indicates that management decisions should be made in the context of the surrounding watershed as well, with an appreciation for the features that determine a watershed's capacity to transport water and materials. For example, data suggest that riparian buffers may be more effective for sequestering nutrients in watersheds with low transport capacity than in those with high transport capacity, and may have very little influence on water quality when landscapes are highly permeable. The spatial pattern of land cover has increasingly been recognized as an important factor in the nutrient fluxes of surface waters, but the conditions under which spatial configuration matters, has, until recently, been unknown (Gergel 2005; King and others 2005).

We sought to understand why the effect of landscape composition and configuration on lake chemistry varies across watersheds. To assess the factors driving the variation and to isolate potential differences in explanatory variables that might emerge, we focused on the extremes of transport capacity. Dichotomizing lakes and watersheds in this fashion is artificial—these systems are not binary—but this approach helped us to probe the variability in the relationship between land use/cover and lake water quality. We also recognize that using the temporal variability of lake nutrient concentrations to infer the conditions associated with transport capacity can be problematic. Internal loading contributes to nutrient fluxes in many shallow, eutrophic lakes (Søndergaard and others 1992; Søndergaard and others 1999, 2003; Spears and others 2007), but this is not the case in these lakes. Water columns are nearly always oxic, indicating the low likelihood of substantial internal loading in these ecosystems (Nürnberg and Peters 1984). Wind velocity, lake fetch, depth, and other morphometric and hypsometric variables have been found uncorrelated with nutrient concentrations, and daily analyses of wind-driven mixing show only slight changes over calm-to-windy cycles and return quickly to prior nutrient levels after winds decline (J. Downing, unpublished data). Moreover, several other studies on this suite of lakes, employing full nutrient mass balance measurements, indicate no large excess nutrient load that cannot be accounted for by external nutrient inputs (J. Downing unpublished data). Nutrient concentrations in tributaries are generally so high that internal loading makes up an amount of nutrient input that is insignificant compared to budget measurement error. Although some internal loading undoubtedly occurs in these lakes as in others (Søndergaard and others 2003), it generally appears insignificant compared to the extreme levels derived from external sources.

Aside from increasing our understanding of how terrestrial and aquatic systems are linked, such methodology may assist in devising management strategies for lakes that vary with respect to watershed characteristics.

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