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Stream nitrate uptake and transient storage over a gradient of geomorphic complexity, north-central Colorado, USA

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Abstract:

The understanding of nutrient uptake in streams is impeded by a limited understanding of how geomorphic setting and flow regime interact with biogeochemical processing. This study investigated these interactions as they relate to transient storage and nitrate uptake in small agricultural and urban streams. Sites were selected across a gradient of channel conditions and management modifications and included three 180-m long geomorphically distinct reaches on each of two streams in north-central Colorado. The agricultural stream has been subject to historically variable cattle-grazing practices, and the urban stream exhibits various levels of stabilisation and planform alteration. Reach-scale geomorphic complexity was characterised using highly detailed surveys of channel morphology, substrate, hydraulics and habitat units. Breakthrough-curve modelling of conservative bromide (Br^-) and nonconservative nitrate (NO_3^-) tracer injections characterised transient storage and nitrate uptake along each reach. Longitudinal roughness and flow depth were positively associated with transient storage, which was related to nitrate uptake, thus underscoring the importance of geomorphic influences on stream biogeochemical processes. In addition, changes in geomorphic characteristics due to temporal discharge variation led to complex responses in nitrate uptake. Copyright © 2011 John Wiley & Sons, Ltd.

KEY WORDS eco-hydrology; transient storage; nitrogen spiralling; fluvial geomorphology; solute transport modelling; land use

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INTRODUCTION

Land-use changes and altered hydrologic and sediment regimes have resulted in the widespread degradation and homogenisation of physical habitat in urban and agricultural streams (Jacobson *et al*., 2001; Allan, 2004). Land-use alterations often destabilise channels and degrade physical habitat prompting stream rehabilitation activities. Most rehabilitation projects construct static control features instead of restoring the dynamic processes that create a diverse habitat template (Bernhardt *et al*., 2005; Wohl *et al*., 2005). Concurrent with the growing interest in mitigating the effects of land-use change on streams, there has been continual scientific research on nutrient-uptake functions of small streams and their influence on downstream water quality, particularly nitrogen (N) enrichment (Peterson *et al*., 2001; Mulholland *et al*., 2008). According to a recent literature review, the greatest opportunity for nitrogen removal could exist in small streams carrying large loads of nutrients at low to moderate discharges (Craig *et al*., 2008). Well-functioning stream networks can, therefore, regulate the export of nutrients from the landscape and ameliorate the detrimental effects of eutrophication in downstream ecosystems (Alexander *et al*., 2000, 2007). However, little is known about the linkages between nutrient uptake and rehabilitation activities that attempt to create more complex habitat templates.

Altered streamflow and sediment regimes in agricultural and urban streams often lead to decreases in geomorphic complexity, herein defined as the multiscale assemblage of physical channel components, ranging from patch-scale physical characteristics to reach-scale channel form variation. This decrease in complexity occurs via planform straightening, channel enlargement, sediment aggradation, removal of woody debris and bank vegetation, or the armouring of naturally variable banks (Allan, 2004). Geomorphic complexity is a key influence in creating areas of transient storage within a channel, yet the linkages between this complexity and nutrient uptake are poorly understood. Of particular relevance to this study, geomorphic complexity can generate dead zones, blockages, backwater effects and complex hydraulics that all influence transient storage (Roberts *et al*., 2007).

Transient storage is the temporary retention of water in streams, including both in-channel areas (pools, eddies, and channel margins) and the porous boundaries of the streambed and banks, known as the hyporheic zone (Packman and Bencala, 2000). Geomorphic complexity influences the in-channel storage through increased channel roughness, the greater extent of backwater and the creation of more tortuous flow paths. Removal of in-stream wood and vegetation has been shown to decrease transient storage, whereas construction of flow baffles increases storage (Ensign and Doyle, 2005). Fluid exchange between the main channel and the hyporheic

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zone is a function of hydraulic pressures of the flowing stream, channel geomorphic complexity and the hydraulic conductivity of the streambed and banks (Tonina and Buffington, 2009). Specifically, the magnitude of vertical hydraulic pressure gradients has been shown to be positively correlated with both increasing average water–surface concavity and spacing between zones of flow upwelling and downwelling (Anderson *et al.*, 2005). Strong gradients of oxygen concentration and organic carbon availability, coupled with greater travel time through the microbially rich hyporheic zone, create the potential for high metabolic activity and can significantly influence nutrient dynamics (Mulholland and DeAngelis, 2000; O'Connor *et al.*, 2010).

The fraction of median travel time due to transient storage, then normalised to a 200-m reach, ${F_{\mathrm{med}}}^{200}$, is a robust metric of transient storage (Runkel, 2002). In a review of contemporary nutrient spiraling literature, ${F_{\mathrm{med}}}^{200}$ is negatively correlated with nutrient-uptake length (S_{w}), although the relationship between nutrient-uptake velocity (v_{f}) and ${F_{\mathrm{med}}}^{200}$ was not significant (Ensign and Doyle, 2006). Likewise, ${F_{\mathrm{med}}}^{200}$ is inversely related to S_{w} for denitrification in the second Lotic Intersite Nitrogen Experiment (LINX) II study (Mulholland *et al.*, 2009) but was not identified as a significant influence in a concurrent analysis of S_{w} of uptake (Hall *et al.*, 2009). These results suggest, albeit inconclusively, a linkage between nutrient uptake and transient storage, which we believe can be clarified with improved description of key geomorphic measures such as longitudinal variation. Nutrient-tracer studies have tended to characterise base-flow conditions on low-order streams to minimise nutrient release and simplify field studies, but complex interactions between the hydrologic setting and the nutrient uptake necessitate investigation at a wider range of flow conditions (Fisher *et al.*, 2004). A few studies have performed repeated tracer injections at the same site to examine the influence of discharge on transient storage (D'Angelo *et al.*, 1993; Wondzell, 2006) and nutrient uptake (Martí *et al.*, 1997; Valett *et al.*, 1997), with most favouring cross-stream comparisons. Our study aims to address these knowledge gaps by examining the influence of channel physical complexity, variable flow hydraulics, transient storage and geomorphic setting on nitrate uptake.

The objectives of the present study are threefold: (i) to explicitly define and compare multiple forms of geomorphic complexity in the study streams, (ii) to quantify the level of transient storage and nutrient uptake in six stream reaches across a gradient of geomorphic complexity and land-use influences and (iii) to identify the physical and hydraulic channel attributes that most directly influence hyporheic exchange and nutrient uptake. We address these objectives by testing the following hypotheses:

1. increased levels of geomorphic complexity, transient storage, reach-wide metabolic activity and/or organic carbon significantly increase nitrate uptake and
2. increased levels of various forms of geomorphic complexity result in significantly more transient storage.

These hypotheses reflect our understanding that local hydrologic, geomorphic and transient-storage characteristics comprise the physical template within which organisms process nutrients in streams.

METHODS

Study reach selection

Three 180-m reaches on each of two streams were chosen for their distinctive geomorphic setting and historical human modification. The agricultural stream, Sheep Creek, was subject to cattle-grazing practices, and the urban stream, Spring Creek, showed various levels of stabilisation and planform alteration (Table I). All segments were surveyed using a detailed protocol for characterising physical complexity in terms of habitat units with distinct combinations of geomorphic, substrate and hydraulic attributes. Study reaches were selected to exclude major changes in slope, geology, sediment or discharge.

Sheep Creek is located in a cattle-grazed mountainous location 80 km northwest of Fort Collins, Colorado (40°55'48″N, 105°38'16″W), within the Roosevelt National Forest at an elevation of 2530 m (Figure 1a). The riparian area was heavily grazed from the 1890s until 1956 when the U.S. Forest Service fenced sections to exclude cattle grazing along 2.5 km of the stream (Phillips *et al.*, 1999). The flow regime is snowmelt dominated and regulated by an upstream $4.6 \times 10^6\,\mathrm{m}^3$ reservoir that seasonally fills in the spring and drains via Sheep Creek in the late summer.

Spring Creek is located in the moderate-density urban setting of Fort Collins, Colorado (40°30'50″N, 105°4'7″W), at an elevation of 1500 m (Figure 1b). The upper segment of this watershed was truncated by the construction of Horsetooth Reservoir in 1949, and the existing watershed is largely composed of commercial and residential urban development. The use of the stream as a storm water corridor and the flashy urban flow regime (resulting in five major floods in the last 75 years) have led the city to straighten and stabilise significant portions of the streambed and banks for flood mitigation.

Three separate nutrient injection experiments at varying discharges were performed on each of the Spring Creek study reaches during the summer of 2007. The multiple injections, labelled X, Y and Z in Table I and throughout the following text, were designed to analyse the influence of discharge and geomorphic context on transient storage and nutrient uptake. An unexpected small flood passed through the corridor immediately after injection Y, scouring fines and organic matter from the substrate and flattening nonwoody bank vegetation.

Data collection

Stream classification. Each reach was first classified using the stream typology of Montgomery and Buffington

Table I. Summary of study reach settings and injections

Reach	Character	Channel type	Sinuosity	Slope	d_{50} (mm)	Injection code	Date of field visit	Flow rate, Q (L/s)	Successful BTC model
Sheep A	Nongrazed and largely incised within heavy brush and tree-lined banks, coarse substrate	Plane bed	1.08	1.5%	67	ShA_X	15 July 2007	108	Yes
Sheep B	Nongrazed and highly sinuous with grass and brush-lined banks, finer substrate	Pool riffle	1.91	0.7%	48	ShB_X	16 July 2007	88	No
Sheep C	Grazed with grass-lined banks, moderately incised, coarse substrate	Plane bed	1.24	1.2%	54	ShC_X	17 July 2007	102	Yes
Spring Creek Railroad	Straightened to allow grading of the adjacent property. Silty-clay bed with heavy grass lining the banks	Plane bed	1.01	0.2%	<2	SpR_X	28 June 2007	70	No
						SpR_Y	1 August 2007	17	Yes
						SpR_Z	8 August 2007	21	Yes
Spring Creek Stuart	Lateral and grade controlled with large grouted block bank protection with grouted boulder steps	Forced pool riffle	1.05	0.9%	35	SpS_X	26 June 2007	133	No
						SpS_Y	31 July 2007	46	Yes
						SpS_Z	9 August 2007	108	Yes
Spring Creek Edora	Set in a large city park, the most 'natural' of the three Spring Creek reaches	Pool riffle	1.16	0.4%	14	SpE_X	25 June 2007	157	No
						SpE_Y	30 July 2007	72	Yes
						SpE_Z	6 August 2007	152	Yes

(1997). Next, patch-scale variation was quantified by dividing the stream into unique patches of geomorphic, hydraulic and sediment characteristics. These patches (2–15 m^2 in area) spanned the width of the channel and often formed a repeating spatial pattern. All patch delineation and identification were performed by a single individual to eliminate interobserver variation.

Physical measurements. Each 178- to 191-m study reach was subdivided by 21 equally spaced transects. The cross-sectional geometry of each transect, the downstream width profile and the thalweg profile were surveyed with a total station. Cross sections were surveyed at least every 0.5 m across their width. Thalweg profile and channel width were surveyed at a longitudinal density less than 3 m downstream, also at breaks in curvature or slope.

The stream discharge was measured at two or more cross sections using greater than ten depth-averaged measurements with an electromagnetic velocimeter. The recorded discharge was taken to be the average of multiple discharge measurements falling within 10% of each other. Later, cross-sectional discharge measurements were compared with discharge calculations derived from conservative tracer data to obtain the best possible estimate. In addition, after each tracer injection, channel hydraulics were measured via flow depth and depth-averaged velocity at five points across each of the 21 cross sections. The substrate was quantified with a minimum 300-particle pebble count, composed of 100 measured particles per patch type using a gravelometer and sampling grid (Bunte and Abt, 2001a).

Tracer injection. Nitrate concentrations were targeted at four times that of ambient, and Br^- levels were targeted higher than 2 mg/l. All injection solutions were well mixed and below the solubility limits of the combined solutes. Tracers were injected at least 20 m upstream of the first transect and were mixed via riffles or flow constriction within that distance. A 60-min constant rate injection of an aqueous potassium nitrate ($\mathrm{KNO_3}$) and sodium bromide (NaBr) solution was dispensed into the stream using a Watson-Marlow Model 323S/D peristaltic pump (Watson-Marlow Inc., Wilmington, MA). Samples for constructing injectant breakthrough curves (BTCs) were collected via grab samples at the upstream and downstream ends of each reach. These 20-ml samples, filtered to 0.7 µm, were extracted at 2-min intervals for 10 min before and 130 min after the injection period for a total sampling time of 200 min.

Benthic organic matter collection. Benthic organic matter (BOM) on and within the uppermost 5 cm of substrate was collected at nine locations per reach, randomly selected both among repeating habitat units and across selected transects. Selected sampling locations were isolated by sinking a 0.262-m diameter cylinder into the substrate. Organic matter on the bed surface was removed before the upper 5 cm of the substrate was agitated to release BOM. We screened all BOM through a

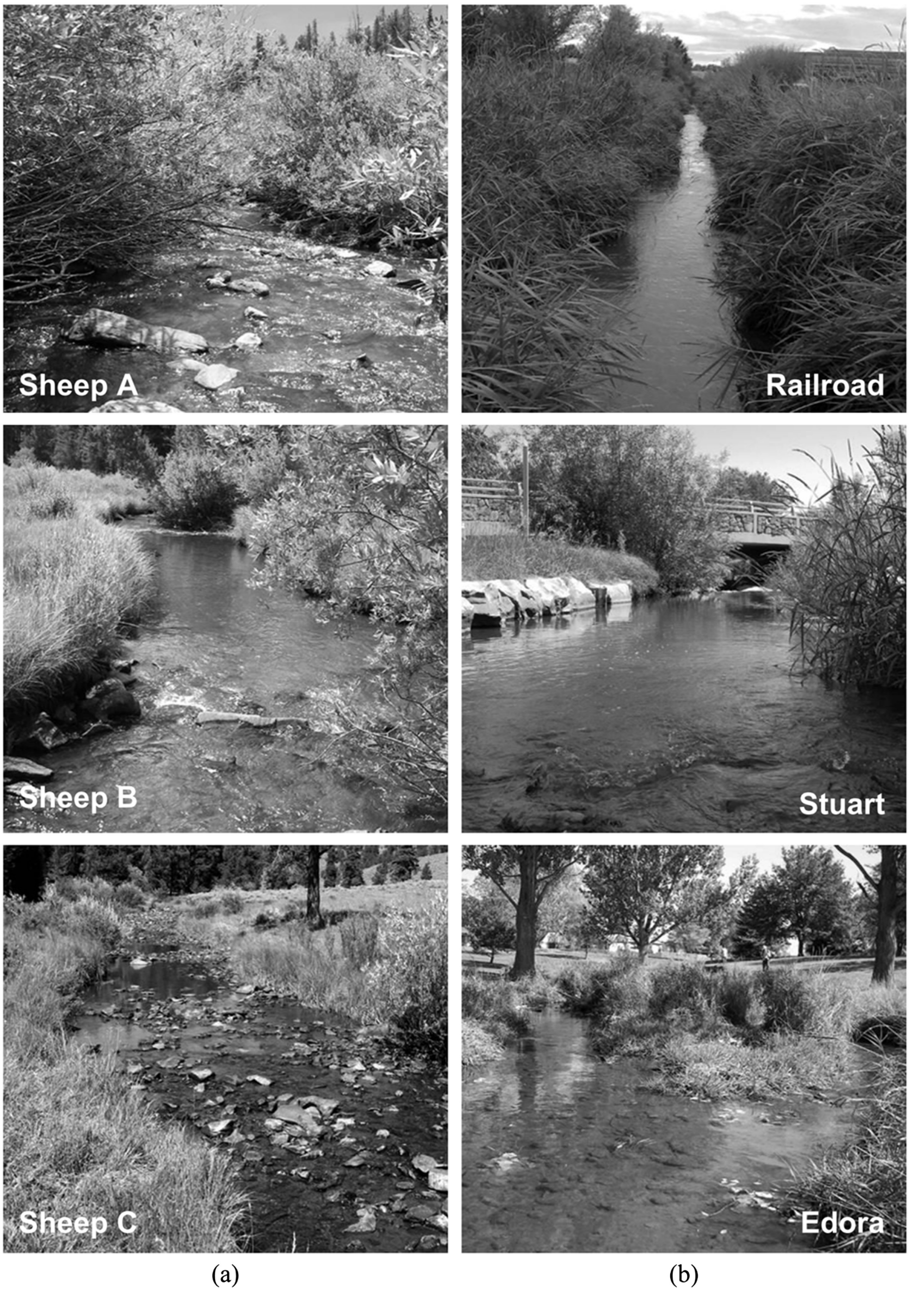

Figure 1. Representative photographs of (a) Sheep Creek—agricultural and (b) Spring Creek—urban reaches

500-μm sieve mounted over a sampling bucket, with the material retained on the sieve designated as coarse BOM (CBOM) and the portion suspended in the bucket as fine BOM (FBOM). The volume of the FBOM sample was recorded, and a representative subsample of FBOM was removed for laboratory analysis.

Metabolism. Data to model metabolic activity were measured with an In-Situ Troll 9000 Multi-parameter Probe (In-Situ Inc., Fort Collins, CO) equipped with optical dissolved oxygen, temperature and barometric pressure sensors. Probes were deployed immediately after the tracer injection and logged ambient conditions at 10-min intervals for 48 h. A vented cable was used to equalise the unit to atmospheric pressure, eliminating postprocessing pressure correction.

Data and sample analysis

Habitat units were linked to their representative geometric, sediment size and hydraulic parameters, and then reach-averaged geometric, hydraulic, and textural parameters were areally upscaled from the condition of each habitat unit to the average reach condition. Geomorphic complexity metrics based on the field data were adapted for unequally spaced survey points. Calculated metrics included longitudinal roughness, which is the average deviation of the thalweg elevation from a straight line approximation of the stream profile, relative submergence, calculated as the ratio of mean flow depth to 84th percentile grain size (for all geomorphic complexity metrics reported in this study, see Table II).

BOM samples were analysed for their ash-free dry mass content. FBOM samples were filtered through 1.6-μm

Table II. Variables included in transient-storage regression models

Variables	Abbreviations	Units	References/equations
Reynolds number	Re	–	Garcia (2008)
Specific stream power	ω	W/m^2	Garcia (2008)
Longitudinal roughness[a,b]	LR	–	$\mathrm{LR} = \frac{\sum_{i=1}^{n}\left[\left(z_{\mathrm{obs}} - z_p\right)_i \cdot I_{\mathrm{p}}\right]}{D}$
Width residual[a,c]	WR	–	$\mathrm{WR} = \frac{\sum_{i=1}^{n}\left[\left\lvert w_{w,i} - \bar{w}\right\rvert \cdot I_{\mathrm{p}}\right]}{\bar{w}}$
Average thalweg concavity[a,d]	AThC	–	$\mathrm{AThC} = \left(\sum_{i=1}^{n}\left\lvert\frac{d^2 z_i}{dx_i^2}\right\rvert \cdot I_{\mathrm{p}}\right)$
Sediment geometric coefficient of gradation	s_grad	–	Bunte and Abt (2001b)
Relative submergence[e]	R/d_{84}	–	Garcia (2008)

[a] Proportion of influence (I_{p}) is a measure from halfway between the point of interest (x_i) and the next point upstream (x_{i-1}) to halfway between the point of interest and the next point downstream (x_{i+1}) over the length of the reach (L), $I_{\mathrm{p}} = \frac{(x_i - x_{i-1})/2 + (x_{i+1} - x_i)/2}{L}$.

[b] z_{obs} = observed bed elevation; z_{p} = predicted bed elevation (from straight-line approximation); and D = hydraulic depth.

[c] $w_{w,i}$ = wetted width at ith point; $\bar{w}$ = reach average width.

[d] $\frac{d^2 z_i}{dx_i^2}$ = numerical approximation of the second derivative of the bed elevation from Chapra and Canale (1988).

[e] R/d_{84} = ratio of the hydraulic radius R to the 84th percentile stream bed sediment size d_{84}.

pore size, 9-cm diameter glass-fibre filters, dried at 100 °C for 12 h and oxidised in a muffle furnace at 500 °C for 6 h. CBOM samples, not requiring filtering, were similarly dried, weighed and combusted, following Clescerl *et al.* (1998). BTC samples were stored at a temperature lower than −15 °C from the day of collection until processing. Analysis for Br^- and $NO_3{}^-$ concentration was performed on a Metrohm Ion Analysis ion chromatograph (Metrohm, Herisau, Switzerland) following the U.S. Environmental Protection Agency Method 300.0 (USEPA, 1993). Quality assurance included 10% duplicate samples and recalibration of the instrument every 200 samples and/or when standards fell outside of the 10% accuracy limit. BTCs were later refined using a three-point moving median filter, minimising sampling noise and diminishing outlier effect while maintaining the shape of the BTC, including signal edges and stepwise discontinuities (Tukey, 1977).

BTC and metabolism modelling

A nutrient-uptake model incorporating transient storage, called one-dimensional transport with inflow and storage (OTIS) (Runkel, 1998, 2007), was selected over a previously used uptake length approach (Stream Solute Workshop, 1990) for its ability to more accurately model transport and nutrient kinetics (O'Connor *et al.*, 2010). The conservative tracer BTC is the source of the transient-storage variables: channel area (A), storage area (A_S), dispersion (D) and an exchange coefficient between the channel and the storage areas (α). Subsequently, holding the transient-storage conditions constant, OTIS then computes the first-order uptake coefficients for the main channel (λ) and the storage zone (λ_S) from the nonconservative tracer BTC.

UCODE, a computer code for universal inverse modelling, was used to optimise each OTIS model (Poeter and Hill, 1999). UCODE has been extensively used in groundwater modelling with MODFLOW and successfully used in conjunction with OTIS (Scott *et al.*, 2003; Briggs *et al.*, 2009). For this project, the optional double-dogleg trust-region approach outperformed the default modified Gauss–Newton method for model convergence and stability (Poeter *et al.*, 2005). To compare the results from this study to previous work, time series nutrient-uptake metrics were converted into steady-state values in accordance with Runkel (2007). The numerical stability, the parameter variance and the convergence of each OTIS model were scrutinised. BTCs from four of the 12 tracer injections were removed from subsequent analyses because of failure to meet stability, variance or convergence criteria.

Following the recommendations of Hanafi *et al.* (2007), cross-site parameter uncertainty was quantified with Monte Carlo simulations, including OTIS-UCODE parameters, transient-storage metrics and nutrient-uptake metrics. These simulations projected the normally distributed random variation of each parameter to computations of the fundamental equations for each metric more than 10 000 iterations.

The dimensionless transient-storage metric, $F_{\mathrm{med}}{}^{200}$, was selected over other transient-storage metrics as it includes stream velocity and exchange rate between the storage zones and the main channel. $F_{\mathrm{med}}{}^{200}$ relates the downstream velocity (u), A, A_S and exchange coefficient (α), normalised to a 200-m reach length (L):

$$F_{\mathrm{med}}{}^{200} \cong \left(1 - e^{-L\frac{\alpha}{u}}\right)\frac{A_S}{A + A_S} \qquad (1)$$

The Stream Metabolism Program was used to compute whole-stream metabolism, as represented by gross primary productivity (GPP) (Bales and Nardi, 2007). Model input data included stream discharge, dissolved oxygen concentration (measured at a single station continuously for 48 h), water temperature and barometric pressure.

Statistics

Principal component analysis (PCA) was used to assess the content and redundancy of physical and geomorphic variables (Jolliffe, 2002). The most informative variables were then compared across study reaches to examine variation in channel complexity. PCA axis scores were not used in subsequent analyses, but the information from the ordination was used to help select variables for inclusion in regression analyses of transient-storage and nutrient-uptake processes.

A multistep statistical process quantified associations among the independent channel measurements and the dependent transient-storage and nutrient-uptake parameters. First, the data set of complexity, substrate, channel, BOM, metabolism and hydraulic measures was reduced to a set of statistically independent variables using PCA and correlation analysis. Next, separate data sets were tiered on the basis of *a priori* knowledge of the influences of transient-storage and nutrient-uptake processes (Tables II and III, respectively). Each tiered variable set was then regressed against either the transient-storage or the nutrient-uptake metrics. The best subsets of multiple regression models with two variables or less were sorted by their adjusted R^2 value and subjected to meeting parameter and overall model significance ($P < 0.10$). Variables were also examined for consistent patterns of inclusion and influence direction in selecting the most significant and interpretable models. Logarithmic transformations were applied, which provided good adherence to the regression assumptions of linearity, homoscedasticity and independent and normally distributed residuals. Statistical analyses were performed using SAS 9.2 (2008, SAS Institute, Inc., Cary, NC).

RESULTS

Regression models

Transient storage and relative submergence were consistently significant predictors of nutrient uptake, and $F_{\mathrm{med}}{}^{200}$ was significantly related to both nutrient-uptake measures, S_{w} and v_{f} (Table IV). Relative submergence and longitudinal roughness were the strongest predictors of $F_{\mathrm{med}}{}^{200}$ ($P = 0.067$). Representative regression models were chosen from all significant models as indicators of the general trend of both transient storage and nutrient uptake. No significant regression models related GPP, NO_3^- concentration or any measures of BOM with either nutrient-uptake metric (S_{w} or v_{f}). Longitudinal roughness and relative submergence were the only geomorphic complexity metrics that was a significant predictor of $F_{\mathrm{med}}{}^{200}$ in the regression models. OTIS-UCODE parameter estimates and variance for the eight models passing numerical stability, parameter variance and convergence criteria are found in Table V.

Transient-storage and nutrient-uptake estimates

Monte Carlo simulations indicated significant differences ($P < 0.10$) in the transient-storage metric $F_{\mathrm{med}}{}^{200}$ between injections Y and Z at each Spring Creek reach (Figure 2a). $F_{\mathrm{med}}{}^{200}$ was significantly different among Y injections at Spring Creek, but no significant difference was found among the Z injections after the small flood and at a higher discharge. Sheep Creek $F_{\mathrm{med}}{}^{200}$ values were the lowest of all eight injections, although no significant difference was found between Sheep A and Sheep C reaches.

No apparent differences exist between land-use types for either reach-scale nutrient-uptake metric, although the intersite differences in v_{f} at Sheep Creek were similar in magnitude to intrasite differences before and after the high-discharge event on Spring Creek (Figure 2b). Values of v_{f} in this study are within the range of previous studies, but in the lower 25% (Figure 4). In individual injections on Spring Creek, v_{f} was significantly different ($P < 0.10$) between the Y and the Z injections at the Edora reach. Uptake velocities at sheep A and sheep C reaches were

Table III. Variables included in nutrient-uptake regression models

Variables	Abbreviations	Units	References
Gross primary production	GPP	g O^2/m^2/day	Bales and Nardi (2007)
Fraction of median travel time	$F_{\mathrm{med}}{}^{200}$	–	Runkel (2007)
Ratio of storage to channel area	A_s/A	–	Stream Solute Workshop (1990)
Total BOM	TBOM	g/m^2	Wallace *et al.* (2007)
Reynolds number	Re	–	Garcia (2008)
Relative submergence	R/d_{84}	–	Garcia (2008)
Ambient concentration of NO_3^--N	C_NO$_3$	mg/l	Stream Solute Workshop (1990)

Table IV. Representative regression models

Dependent variable	Sample model	Model P value	Adjusted R^2	β_1 P value	β_s P value
Fraction of median travel time, $F_{\mathrm{med}}{}^{200}$	$F_{\mathrm{med}}{}^{200} = 2.78(R/d_{84})^{1.15}\mathrm{LR}^{1.96}$	0.067	0.53	0.026	0.086
Uptake length, S_{w} (m)	$S_{\mathrm{w}} = 1.06 \times 10^3(F_{\mathrm{med}}{}^{200})^{-0.20}(R/d_{84})^{-0.23}$	0.007	0.81	0.053	0.050
Uptake velocity, v_{f} (m/s)	$v_{\mathrm{f}} = 6.65 \times 10^{-6}\mathrm{Re}^{0.85}(F_{\mathrm{med}}{}^{200})^{0.29}$	0.045	0.59	0.023	0.040
	$v_{\mathrm{f}} = 2.26 \times 10^{-7}\mathrm{Re}^{1.067}(R/d_{84})^{0.38}$	0.057	0.56	0.022	0.051

Table V. Summary of OTIS-UCODE output parameters, transient-storage, nutrient-uptake, BOM and metabolism metrics

Site Code	A (m^2)	A_S (m^2)	D (m^2/s)	α (1/s)	λ (1/s)	λ_S (1/s)	S_w (m)	v_f (mm/s)	FBOM (g/m^2)	CBOM (g/m^2)	GPP (g O^2/m^2/day)
ShA_X	4.39E − 01 (6.72E − 03)	1.88E − 01 (2.11E − 01)	1.23E + 00 (2.45E − 01)	5.19E − 05 (1.94E − 05)	1.27E − 04 (1.66E − 05)	−1.39E − 04 (1.22E − 04)	2.44E + 03 (1.50E + 04)	2.18E − 02 (7.31E − 01)	7.69	17.59	0.59
ShC_X	5.30E − 01 (5.39E − 03)	1.17E − 01 (1.05E − 01)	1.25E + 00 (1.14E − 01)	2.85E − 05 (9.56E − 06)	4.29E − 05 (1.81E − 05)	6.03E − 02 (1.54E + 01)	4.81E + 03 (1.88E + 05)	4.92E − 03 (4.00E − 03)	54.92	3.89	0.35
SpR_Y	1.42E − 01 (4.35E − 03)	5.68E − 02 (4.92E − 03)	1.34E − 01 (6.52E − 02)	4.76E − 04 (1.08E − 04)	1.22E − 04 (1.78E − 05)	1.36E − 04 (6.19E − 05)	7.07E + 02 (1.28E + 02)	1.63E − 02 (2.62E − 03)	119.69	48.17	0.09
SpR_Z	1.60E − 01[a]	3.15E − 02 (8.32E − 03)	8.36E − 01 (2.88E − 01)	2.49E − 04 (8.45E − 05)	1.19E − 04 (4.44E − 05)	−1.50E − 04 (1.26E − 04)	1.25E + 03 (5.68E + 04)	8.09E − 03 (4.31E − 03)	101.14	23.54	0.13
SpS_Y	6.40E − 01[a]	1.95E − 01 (7.47E − 03)	9.64E − 02 (3.58E − 02)	7.68E − 04 (9.26E − 05)	1.21E − 04 (2.81E − 05)	−2.23E − 04 (8.19E − 05)	3.86E + 02 (1.03E + 05)	8.93E − 03 (5.30E − 03)	561.00	119.70	0.64
SpS_Z	9.60E − 01[a]	1.49E − 01 (1.78E − 02)	4.21E − 01 (8.44E − 02)	2.73E − 04 (5.14E − 05)	7.32E − 05 (1.66E − 05)	−4.30E − 05 (1.11E − 04)	1.90E + 03 (1.82E + 04)	1.46E − 02 (4.96E − 03)	84.58	5.92	0.07
SpE_Y	5.51E − 01 (1.45E − 02)	1.05E − 01 (2.01E − 02)	3.89E − 01 (1.19E − 01)	1.33E − 04 (5.02E − 05)	−1.08E − 06 (1.67E − 05)	3.83E − 04 (2.49E − 04)	6.17E + 03 (3.06E + 05)	4.40E − 03 (3.41E − 03)	322.91	23.83	0.15
SpE_Z	6.69E − 01 (2.51E − 02)	2.14E − 01 (2.79E − 02)	2.72E − 01 (2.81E − 01)	4.55E − 04 (1.40E − 04)	8.81E − 05 (4.07E − 05)	1.95E − 04 (1.79E − 04)	1.74E + 03 (5.00E + 04)	2.22E − 02 (9.76E − 03)	102.25	10.73	0.14

Values are presented as mean and standard deviation (SD) for each metric.

[a] Transient-storage models for injections SpR_Z, SpS_Y and SpS_Z would not converge with all four variables; thus, the only term which is also a field-measured value, *A*, was fixed to the reach-averaged physical measurement.

significantly different ($P < 0.10$). With respect to S_w, SpR_Y was significantly different ($P < 0.10$) from ShA, SpE_Z and SpS_Z (Figure 2c).

Geomorphic complexity

Visual comparison of the levels and types of geomorphic complexity demonstrate variation among the six study reaches (Figure 3). The range of cross-sectional, longitudinal and planform variation is represented by the metrics of sinuosity, longitudinal roughness, width residual and average thalweg concavity. The engineered drop structures in the Stuart reach and a complex natural thalweg profile at Edora reach resulted in high measures of longitudinal roughness. With its pool-riffle morphology, sheep B reach had the greatest sinuosity. Sheep C reach was relatively prismatic for most of its length, but deep pools near the upstream and downstream ends and continual small-scale fluctuations in the thalweg profile yielded the highest average thalweg concavity.

BOM and metabolism

More BOM was found in the lower gradient, urban Spring Creek reaches than in the steeper, agricultural Sheep Creek reaches (Table V). The reach open to grazing (ShC) contained more reach-averaged FBOM and total BOM than the reach within a grazing enclosure (ShA), but it contained less CBOM. The Stuart reach, characterised by large backwater areas, had the highest level of BOM before the small flood. The flood that occurred between Spring Creek injections Y and Z reduced the amount of both FBOM and CBOM in all three reaches.

GPP was on average higher at the agricultural Sheep Creek reach than it was across the urban reaches of Spring Creek (Table V). In addition, the GPP of the nongrazed Sheep A reach, with dense, shrub-lined banks, was greater than the grazed and open canopy, Sheep C reach. Results from the stream metabolism modelling are reported as daily values of gross primary production because of data limitations of a single oxygen profile recorded at the time of each injection.

DISCUSSION

Influences on transient storage and nutrient uptake

Significant relationships between nutrient-uptake variables (both S_w and v_f) and transient storage support our first hypothesis and are consistent with previous findings that channel hydraulic characteristics are an important control on nitrogen uptake (Valett *et al.*, 1996; Haggard *et al.*, 2001; Claessens *et al.*, 2010). Reynolds number, essentially stream unit discharge, was the strongest predictor of v_f among the variables examined ($P < 0.025$ in both models) and, with the additional positive relationship between relative submergence and ${F_{med}}^{200}$, seems to reflect the influence of stream depth. This apparent relationship between flow depth and nutrient-uptake rate is consistent with the results of the earlier LINX study

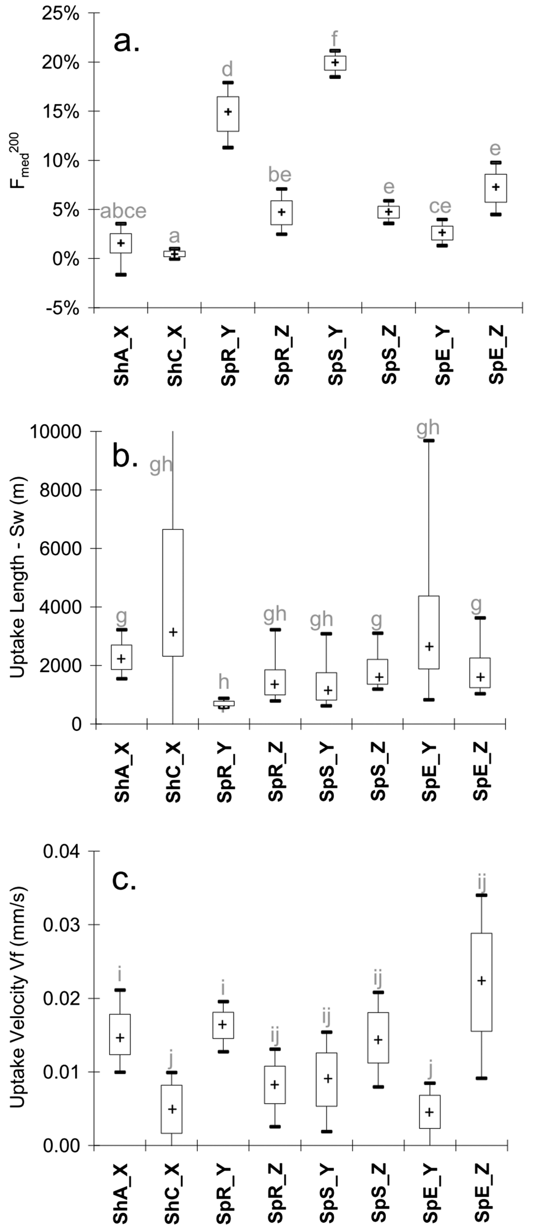

Figure 2. Distributions for transient-storage metric (a) F_{med}^{200} and nutrient-uptake metrics (b) S_w and (c) v_f across tracer injections. (Note: box plots display Monte Carlo simulation derived 10th, 25th, 50th, 75th and 90th percentiles, and letters above box plots represent significant groups; $\boldsymbol{P} < 0.10$.)

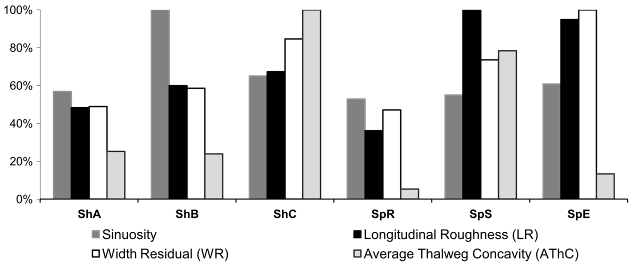

Figure 3. Relative geomorphic complexity across study reaches. (Note: all complexity metrics expressed as a percentage of the maximum reach value for the six study sites.)

(Peterson *et al.*, 2001). Subsequent studies focusing on urban and agricultural streams were inconclusive with respect to the relative influence of hydraulic and metabolic factors on nutrient uptake and removal. For example, the LINX II study identified F_{med}^{200} as a significant predictor of denitrification using structural modelling (Mulholland *et al.*, 2009). However, a companion article included F_{med}^{200} in most leading total uptake regression models, but not in multivariate structural equation models, which primarily favoured biochemical descriptors (Hall *et al.*, 2009). This study reinforces the influence of channel hydraulics and geomorphic context on nutrient-uptake processes.

Multiple studies have found significant positive relationships between v_f and GPP (Hall and Tank, 2003; Mulholland *et al.*, 2006, 2008) and an inverse relationship between v_f *and* ambient NO_3^- concentration (Payn *et al.*, 2005; O'Brien *et al.*, 2007; Mulholland *et al.*, 2008). Clearly, GPP and NO_3^- concentration are fundamentally linked to uptake, but neither was a significant predictor in this study. This could be due to the small sample size, hydraulic influences acting as surrogates for biochemical factors, limitations in the one-station modelling of GPP, or a narrow range of measured GPP (0.07–0.64 g O_2/m^2/day) and ambient NO_3^- concentrations (0.1–1.6 mg/l). Values of v_f and NO_3^- concentrations observed in this study were within the range of variability of both the LINX II study (Mulholland *et al.*, 2008) and a comprehensive data set of previous nutrient-uptake studies compiled by Tank *et al.* (2008) (Figure 4).

Our second hypothesis is supported by the statistical modelling, which indicates that longitudinal roughness and relative submergence are significant predictors of F_{med}^{200}. Previous work has suggested linkages between longitudinal roughness and transient-storage processes, including significant relationships between the mean storage time and a multimetric variable, including longitudinal roughness (Gooseff *et al.*, 2007) as well as vertical hydraulic gradients and average water–surface concavity (Anderson *et al.*, 2005). The inclusion of relative submergence in this relationship further supports the influence of backwater effects as a significant driver of transient storage (Hester and Doyle, 2008). Given this

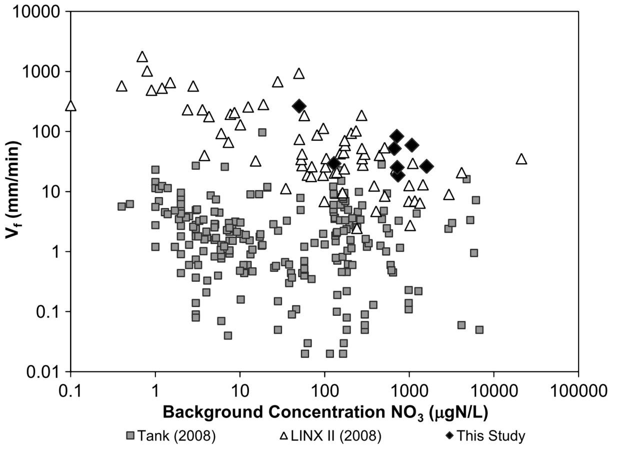

Figure 4. Comparison of v_f and NO_3^- concentration among this study, LINX II (Mulholland *et al.*, 2008) and a data set of previous uptake studies (Tank *et al.*, 2008).

DOI: 10.1002/hyp

connection between backwater and transient storage and the characteristics of the reaches within this study, it seems that in-stream storage may overshadow hyporheic storage. The three reaches on Spring Creek (comprising six of the eight injections included in the regression analysis) have limited potential for short-term hyporheic storage as they are underlain by clay-loam soils (Natural Resources Conservation Service (2009) and contain higher levels of substrate-clogging FBOM than any of the Sheep Creek reaches. Furthermore, in-channel storage is associated with dense vegetation within the channel margins at Railroad reach, backwater from drop structures at Stuart reach and the natural deep pools and eddies of Edora reach. Sheep A and Sheep C reaches had the lowest modelled transient-storage capacity in this study on the account of their plane-bed morphologies and high slopes. The advective nature of the Sheep Creek reaches combined with the lowest transient-storage levels provides additional evidence of the predominance of in-channel over hyporheic storage across our study sites.

Nutrient uptake does not seem to vary significantly between agricultural and urban sites in this study (Figure 5) and previous studies (Haggard *et al.*, 2001; Mulholland *et al.*, 2008). The highly altered urban Spring Creek reaches seem to support nutrient uptake comparable with the Sheep Creek reaches which could arguably, in the case of Sheep A, be considered more geomorphically 'naturalised' after passive rehabilitation via removal of grazing stressors. The natural recovery of Sheep A reach may be a factor in the greater value of v_f than in Sheep C reach, but when contrasted to both Sheep C reach and the urban Spring Creek reaches, Sheep A reach uptake is not substantially different.

Complex interactions with geomorphic context and discharge history

A complex interaction exists between unit discharge and F_{med}^{200} across the eight injections, related to the geomorphic context, hydrologic history and level of channel stabilisation of each reach (Figure 5). The inclusion of multiple sites along each study stream, exhibiting a variety of passive and structural restoration measures, allowed us to investigate a broader range of channel complexity and biogeochemical response than the selection of a single site at each stream. The agricultural reaches of Sheep Creek, which seem to be more geomorphically complex and plausibly have greater transient storage than the urban reaches of Spring Creek, were found to have lower transient storage. However, nutrient uptake on Sheep A and Sheep C reaches is not markedly different than the Spring Creek reaches, perhaps indicating a differing mechanism of uptake than Spring Creek. The uptake rates in Sheep Creek are possibly related to the moderate to high levels of GPP, which may have been spurred by a disproportionate increase in NO_3^- relative to background concentration as compared with the Spring Creek sites.

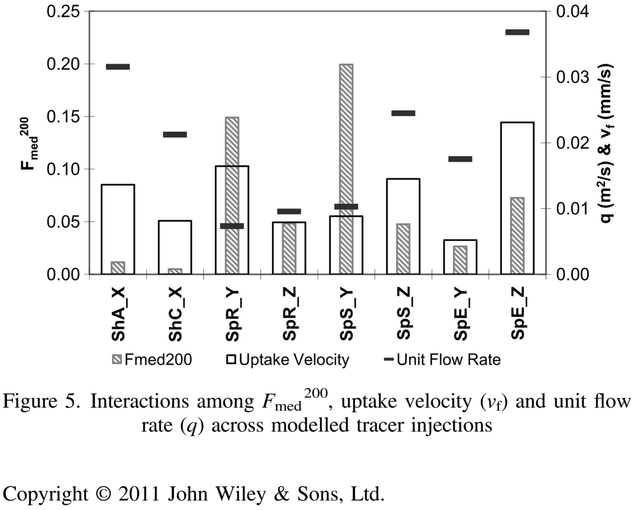

Figure 5. Interactions among F_{med}^{200}, uptake velocity (v_f) and unit flow rate (q) across modelled tracer injections

A limited number of studies have performed repeated tracer injections at the same site to examine the influence of discharge on transient storage (D'Angelo *et al.*, 1993; Martí *et al.*, 1997; Wondzell, 2006) and nutrient uptake (Valett *et al.*, 1997; Hall *et al.*, 2002; Simon *et al.*, 2005). Two tracer injections at each Spring Creek study reach, on either side of the small flood, enabled us to consider both the magnitude of the discharge at the time of injection and the effects of channel alteration due to the flood. Although no clear association was found between unit discharge and transient storage, distinctive relationships can be drawn between the effects of the flood on the physical channel template and the mode of transient storage. At the Railroad reach, transient storage decreased after the flood. Before the flood, transient storage was likely enhanced by extensive tall grasses standing in the channel margins, which caused eddying and zones of low velocity, but after the flood these grasses were largely flattened. Bed and bank stabilisation at the Stuart reach limited the effects of the flood on the channel, yet postflood transient storage decreased as the previously slow-moving backwater pools were transformed by the higher flow rates into advection zones. The Edora reach appeared to retain much of its in-channel storage after the flood, but fine sediment and organic matter were swept from the bed, possibly allowing the higher discharge during the second injection to drive more water into the hyporheic zone or channel margins, thus increasing overall transient storage. In-channel storage has generally shown more influence on nutrient uptake than hyporheic storage in previous studies (Gucker and Boechat, 2004; Ensign and Doyle, 2005; O'Connor *et al.*, 2010), but partitioning the two transient-storage zones (Salehin *et al.*, 2003; Briggs *et al.*, 2009) would be necessary to examine the distribution and influence of hyporheic and in-channel storage. Comprehensive results from the effects of this flood event are not presented here but will be described in a subsequent manuscript by the same authors.

At Sheep Creek, flow conditions are dictated by an upstream reservoir (Stednick and Fernald, 1999; Flenniken *et al.*, 2001). These antecedent flow conditions seem to alter channel morphology, thereby influencing the extent and duration of hyporheic storage. In the early spring, streamflow releases are minimal until the reservoir is filled, followed by a sharp peak of excess runoff in May. During mid-summer, a minimal discharge is maintained until downstream water rights are invoked, and the reservoir is drained at near-bankfull discharge for more than one month through our study reaches. The apparent effect of these multiple long-duration, high-discharge events is to flush away surface fines, to remove organic matter and to protect the remaining bed sediment. Flume experiments have demonstrated the same geomorphic response to discharge modification as extended duration releases of clear water and limited sediment supply both lead to an armoured bed surface (Hassan *et al*., 2006). This armoured surface has been found to limit the depth and duration of hyporheic exchange (Marion *et al*., 2008) and coupled with the high slopes and plane bed could further explain the minimal values of ${F_{\mathrm{med}}}^{200}$ compared with the Spring Creek sites.

Ecological processes are highly influenced by hydrogeomorphic interactions (Doyle *et al*., 2005; Alexander *et al*., 2009), as shown in the complex interplay between transient storage, NO_3^- uptake and unit discharge described earlier. For an understanding of nutrient-uptake processes to evolve, techniques must be developed to better account for complex physical–biologic interactions. Not only is the amount of discharge influential (Doyle, 2005), but so is the temporal sequencing of flow events and the geomorphic responses of the channel to those events. As such, the dynamic and context-specific nature of these processes represents a formidable challenge in the development of network-scale models of nitrogen flux.

Geomorphic complexity

We were able to quantify dominant forms of channel complexity at each site, with longitudinal roughness clearly identified as a significant predictor of transient storage across study sites. In contrast to previous work (Gooseff *et al*., 2007), land use was not the primary control on overall channel complexity among study sites. Longitudinal roughness characteristics were instead influenced by historical channel alterations, removal of grazing pressure, channel vegetation and geomorphic response to sequences of flow events. The resulting types and degrees of channel complexity fall on a gradient of persistence over time (e.g. longitudinal roughness being more persistent than substrate embeddedness, which is more persistent than herbaceous vegetation influences). Further research is required on how to express the temporal and spatial influence of geomorphic complexity components in upscaled models of nutrient uptake.

Clearly, multiple forms of complexity are important influences on stream ecosystem functions (Brooks *et al*., 2005; Sheldon and Thoms, 2006). As different forms of physical heterogeneity influence diverse ecological functions, the selection of geomorphic complexity metrics for stream surveys should focus on the scale and processes of interest. Detailed protocols, including the one developed in this study, provide a framework for measuring and applying a wide range of reach-scale geomorphic complexity metrics. Alternatively, experiments controlling discharge and geomorphic features could help further discern the interactions among geomorphic complexity, transient storage and nutrient uptake (e.g. Ensign and Doyle (2005)). Only through the development of mechanistic understanding of physical and geochemical processes will we be able to provide design guidance for enhanced nutrient processing through stream restoration.

CONCLUSIONS

Our results underscore the important influence of channel hydraulics and geomorphic context on complex variability in transient storage and nutrient processing. Geomorphic setting, including longitudinal roughness and deep tranquil flow, is associated with transient storage and multiple measures of nutrient uptake in urban and agricultural streams spanning a gradient of physical modification. These results were subjected to extensive uncertainty analysis of both the tracer BTCs and the resulting transient-storage and nutrient-uptake metrics. This study further reinforces the dependence of both nutrient processing and transient storage on current and antecedent flow conditions by demonstrating the influence of discharge variation via two injections in each of three reaches of an urban stream. In addition, the mode and extent of transient storage appears to change, depending on the combination of geomorphic characteristics and antecedent discharge sequence at each study site. The detailed geomorphic reach-scale characterisation developed in this study provides a methodology to explicitly quantify channel complexity and to improve the understanding of hydrogeomorphic drivers of nutrient spiraling processes. Finally, our results indicate that land use alone does not dictate the type and degree of geomorphic complexity, whereas influences such as historical alterations, bed and bank vegetation and dynamic geomorphic responses to flow regime have a more apparent impact.

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