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In-channel transient storage and associated nutrient retention: Evidence from experimental manipulations

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Abstract

We examined the effect of in-channel flow obstructions such as vegetation and coarse woody debris (CWD) on transient storage and nutrient uptake by using experimental channel manipulations. Transient storage and nutrient uptake were measured under existing conditions in a vegetated agricultural stream and a shaded blackwater stream, and measurements were repeated after removal of vegetation and CWD. Removal of vegetation and CWD decreased transient storage area (A_s) by 61% and 43% in the agricultural and blackwater streams, respectively, and decreased the portion of median travel time owing to transient storage (F_{med}) by 45% and 56%, respectively. Flow baffles were then added to create in-channel transient storage in both streams. Baffles increased A_s 227% and 119% for the agricultural and blackwater streams, respectively, and increased F_{med} 309% and 132%, respectively. Ammonium and PO_4 uptake for the blackwater stream, determined by using nutrient addition experiments and expressed as the mass transfer coefficient (V_f), decreased after CWD removal by 88% and 38%, respectively. Ammonium V_f in the blackwater stream increased 143-fold after baffles were installed, and PO_4 V_f increased from -1.7 to 53 mm min^{-1}. Nutrient uptake rates were not calculated for the agricultural stream because sediment disturbance inadvertently altered the sediment-water column nutrient equilibrium. Results from both streams demonstrate that in-channel transient storage, rather than hyporheic storage, can be a substantial portion of overall transient storage in streams. In-channel transient storage influenced nutrient uptake in a blackwater stream, although these results could not be corroborated with data from the agricultural stream.

Eutrophication of riverine and estuarine water caused by anthropogenic nutrient loads is a nationally recognized threat to water quality (Howarth et al. 2002). Management of this problem requires knowledge of the biogeochemical processes that modify nitrogen (N) and phosphorus (P) within river networks. Up to 70% of the nitrogen load of a watershed can be removed during passage through a stream network (Seitzinger et al. 2002). Headwater streams are an especially important location of nutrient uptake in a river network and attenuate inorganic nutrient loads delivered downstream (Alexander et al. 2000; Peterson et al. 2001). Better understanding of the processes governing the transformation of nutrients along a river continuum requires knowledge of how physical features of stream channels influence hydrology and biologic processes. Coupling the biology and geomorphology of riverine ecosystems requires addressing two critical issues: (1) how physical stream features influence the temporary retention of solutes (transient storage), and (2) how this transient storage affects the biotic and abiotic capability of the stream to transform nutrients.

Transient storage describes the temporary hydrologic retention of stream water apart from the main advection flow in the stream channel. This hydraulic storage increases the contact time of main-channel water with biogeochemically reactive sediments, and thus, increased transient storage is often presumed to increase nutrient retention in stream ecosystems (Valett et al. 1996). The predominant technique for estimating transient storage area and exchange in streams is to fit a one-dimensional hydrologic transport model to observed solute break-through curves from a conservative tracer injection. Several versions of this model are commonly used, but all incorporate advection, dispersion, and two additional parameters describing the lumped processes of surface and hyporheic storage zone size and exchange rate with the main channel (Runkel et al. 2003).

Transient storage can be a combination of hyporheic flow (within streambed sediments) and turbulent dead zones within the surface water, although most research to date has focused on hyporheic storage. Any flow obstruction in the stream (submerged vegetation, rocks, leaf packs, debris jams, etc.) contributes to channel roughness and subsequent flow resistance, thereby slowing the downstream passage of stream water. It is assumed that the proportion of storage in the hyporheic zone relative to the stream channel will be greater in higher gradient streams with associated pressure-head differentials and porous substrates (Harvey and Wagner 2000). Hyporheic flow exposes stream water to interstitial sediment pore water zones with lower redox potential, higher

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concentrations of organic carbon, and heterotrophic biofilms that may transform N and P between inorganic and organic forms. In contrast, in-channel storage only extends the contact time of water with surficial sediments and their associated biofilms, and thus, it is generally believed that the importance of hyporheic processes outweighs the nutrient removal functions of in-channel storage (Hall et al. 2002).

Surface transient storage zones comprised a greater percentage of the channel surface area in swampy and step-pool stream reaches and a lower percentage in meandering and run reaches in 12 tropical headwater streams (Gucker and Boechat 2004). The percentage of channel surface area composed of these dead zones was strongly correlated with ratio of storage zone area to channel area, and indicated the importance of surface-water dead zones to the total transient storage in the stream. Solute injection studies of Hubbard Brook (New Hampshire) streams have shown that side pools at the channel margin have a much longer turnover time than those in the main channel of the stream (Hall et al. 2002). However, the contribution of these side pools to total hydrologic retention in Hubbard Brook streams was not quantified. In-channel transient storage was attributed to the flow resistance caused by aquatic vegetation in an Arizona stream (Harvey et al. 2003). In laboratory experiments, flow obstructions (Hutchinson and Webster 1998) and bedforms (Packman et al. 2004) have been shown to induce hyporheic flow, but the contribution of these obstructions to in-channel storage through increased flow resistance was not examined. Algal biofilms were found to contribute greatly to transient storage when flumes with identical substrates were allowed to develop different densities of periphyton (Mulholland et al. 1994). Thus, in-channel transient storage mechanisms contributing to flow resistance (quantified as channel friction), dead-zones, and biofilm matrices are significant factors affecting hydrologic retention.

Other studies have used transient storage as an independent variable with which to relate nutrient uptake across a range of streams. In South American headwater streams, the extent of overall transient storage zone area and surface-water dead zones was highly correlated with nutrient uptake rates (Gucker and Boechat 2004). Investigations of hyporheic and in-channel nutrient uptake in a Canadian stream suggested that in-channel storage zones might have been the predominant location of nutrient uptake (Hill et al. 1998). Uptake length has historically been a more popular metric of describing nutrient spiraling, although these measurements are directly proportional to stream discharge and therefore do not provide effective comparison of nutrient affinity between streams or in a stream over time as velocity changes. Hence, studies that have found a correlation between uptake length and transient storage (see Valett et al. 1996; Marti et al. 1997) would not have been successful in making these connections had a metric of nutrient uptake been used that represents only the benthic demand for nutrients (i.e., mass transfer velocity, V_f) (Hall et al. 2002). Results of a cross-site comparison of 11 diverse stream types did not show a correlation between V_f and transient storage (Webster et al. 2003). Furthermore, results of an intersite comparison of 13 Hubbard Brook streams demonstrated that transient storage was not a useful predictor of nutrient uptake (Hall et al. 2002). Techniques have been developed to determine the percentage of nutrient uptake occurring within the transient storage zone (Mulholland et al. 1997; Thomas et al. 2003; McKnight et al. 2004). These studies report that of the total ecosystem nutrient uptake, 44–49% of NO_3 uptake and 43% of PO_4 uptake occurred while water resided in transient storage zones of several mountain streams, and 7–16% of ecosystem NO_3 uptake occurred in the transient storage zone of Antarctic melt water streams.

With the exception of Gucker and Boechat (2004), all of the studies reviewed above have lumped together hyporheic and in-channel storage because, at present, there is not an easy method to differentiate between the two locations of transient storage based on data from stream tracer studies (sensu Stream Solute Workshop 1990). Recent efforts by Gooseff et al. (2003) have explored the efficacy of simulation modeling to describe short and long-term hyporheic flowpaths by the residence time distribution used in the model, but they did not address the problem of differentiating in-channel and hyporheic flow. To better understand the functional relationship between nutrient uptake and storage area, determination of storage zone location (hyporheic vs. in-channel) is necessary (Harvey et al. 1996; Hall et al. 2002; Salehin et al. 2003).

Despite the usefulness of experimental manipulations in other limnological research, surprisingly few studies have attempted to experimentally manipulate stream channel features and examine the resultant changes in transient storage or nutrient retention. Removal of woody debris from a stream channel did not significantly alter N and P retention compared with a reference stream containing debris (Aumen et al. 1990). However, the study assumed that nutrient uptake in the two streams was equal, and nutrient uptake in the manipulated stream was not measured before debris removal to confirm this assumption. Exclusion of coarse woody debris (CWD) from two Coweeta (North Carolina, USA) streams was associated with decreased NH_4 and PO_4 retention relative to a reference stream (Webster et al. 2000). Direct comparison of the effects of litter on nutrient uptake was obscured by the use of uptake length as a metric of nutrient assimilation (as discussed by Hall et al. 2002) and the inherent assumptions involved in using a reference stream. Another deficiency of these studies is that they did not quantify the impact of debris on transient storage: removal of stream debris decreased not only microbial biomass but also the potential contact between stream water and microbes by removing flow obstructions that contribute to transient storage.

The present study evaluated reach-scale N and P uptake and hydrologic retention in a more tightly controlled experimental design than has previously been performed. Experimental manipulations of two contrasting stream channels allowed estimation of the effect of in-channel debris on transient storage and nutrient uptake. These findings were then corroborated in a second experiment in which in-channel transient storage zones were created to mimic the hydraulic effects of natural channel debris. Results conclusively demonstrate that hydraulic flow resistance owing to channel debris was the predominant site of hydrologic retention in two low-gradient streams. Nutrient uptake and surface-water transient storage were coupled in one stream, but these results could not be replicated in a second stream because of methodological difficulties.

Study sites—Two field sites were used for this study, both in the North Carolina coastal plain (35°N, 77°W). Snapping Turtle Canal is an artificially excavated and channelized drainage canal, draining a watershed of ~4 km^2 of soybeans. The stream channel is oriented east to west, with a slope of 0.0012. Stream depth and width were uniform throughout the study reach (~ 0.2 m and 3.4 m), and there was little variability in the bed topography. During the present study, the canal was unshaded for its entire length and contained a dense mat of slender pond weed (*Potamogeton pusillus*) along the channel bottom. The channel bed sediment was a coarse- to medium-grained sand overlaid with 5–10 cm of fine organic sediment; no woody debris or other channel obstructions existed along the study reach.

Slocum Creek is a channelized blackwater stream that drains a watershed of ~ 8 km^2 of pine plantation in the Croatan National Forest. The stream is heavily shaded by a riparian canopy of mixed hardwoods and conifers. The stream reach was incised into sandy sediment with a gradient of 0.0026. Stream depth and width were 0.5 m and 1.9 m at baseflow. There was no macrophyte vegetation along the stream reach studied. CWD accumulated into small jams, which in turn resulted in some bedform and flow variability, including deep (> 1 m) scour pools and associated backwaters. The two sites were similar in that they both had beds composed of sand/silt sediments, which limits the potential for hyporheic storage in comparison with gravel or cobble-bed streams. Further, both channels had a sinuosity of 1:1 and thus had limited complex flow patterns induced by geomorphic planform variability (e.g., helicoidal flow exchanges).

Methods

Solute injections—Short-term nutrient injections were performed with nitrogen (NH_4Cl), phosphorus (KH_2PO_4), and a conservative tracer (NaCl). A solution of ~230 g NaCl L^{-1} was mixed in the laboratory and amended with N and P in the field just before each injection. A peristaltic metering pump was used at stream-side to dispense ~200 mL min^{-1} into the center of the streams. Specific conductivity was monitored at the terminus of each stream reach by using a YSI 650 datalogger linked to a YSI 600 series sonde. Parameters were recorded at intervals of 1 min 12 s, corresponding to the input time step of the simulation model used for data analysis (0.02 h; see following).

Water sampling stations were located equidistantly along the stream reaches (stations A, B, and C, respectively), except in January when a fourth station (D) was added. In Snapping Turtle Canal, stations were located at 20 m, 35 m, and 50 m during the vegetation removal experiments and at 12 m, 23 m, 37 m, and 50 m during the baffle experiments. In Slocum Creek, stations were located at 33 m, 66 m, and 100 m during the debris removal experiments and at 15 m, 35 m, 55 m, and 75 m during the baffle experiments. Water column samples were collected in triplicate 50-mL polyethylene tubes before solute addition and three times after the conservative tracer reached a plateau concentration at the terminus of the reaches. Water sample collection was accompanied by specific conductivity measurements using a YSI 30 conductivity probe calibrated to an NaCl standard. Water samples were filtered through 0. 7-μm glass fiber filters at stream-side, frozen, and analyzed within 1 week of collection for NH_4, NO_3, and PO_4 on a Lachat QuikChem 8000 flow injection analyzer (Lachat).

Stream manipulation—Two experimental manipulations were performed in each stream: the first was a vegetation removal conducted in October 2003, and the second was a baffle addition in January 2004. On each date, two NH_4 and PO_4 additions were performed, one immediately before the manipulation (hereafter referred to as the control) and a second immediately after manipulation of the channel (hereafter referred to as the treatment). Identical solute concentrations and approximately the same injection rates were used in the control and treatment solute injections. In all cases, the pre- and postmanipulation solute injection experiments were conducted on the same day, with the treatment injection begun 1 h after the manipulation was finished (the length of time required for water column turbidity to return to predisturbance levels along the reach). This relatively short time between injections was necessitated by the unpredictable hydrology of the Snapping Turtle Canal. Wind-driven tides in the adjacent Pamlico Sound estuary rapidly alter hydrologic conditions in Snapping Turtle Canal, causing flow direction and discharge to change on the time-scale of minutes to hours. Although a longer hiatus between injections may have allowed stream sediments, microbial consortia, and macrophytes more time to equilibrate to changes induced by the manipulations, rapid fluctuations in flow velocity, discharge, depth, nutrient concentrations, and nutrient uptake rates would also have introduced unwanted variability between the treatment and control. Similar confounding variables in Slocum Creek were avoided as well by conducting injections on the same day.

The first manipulation (October 2003) consisted of removing macrophyte vegetation from the stream bed (in the case of Snapping Turtle Canal) and removing CWD from the stream (in the case of Slocum Creek). Before manipulation at Snapping Turtle Canal, ~90% of the channel bed was covered with submerged macrophytes. A 50-m reach of Snapping Turtle Canal was raked for ~ 3 min m^{-2}, and all raked vegetation was transferred out of the channel. This raking removed large quantities of the submerged macrophytes and also disturbed the channel bed to depth of 5 cm. Before manipulation at Slocum Creek, the volume of transient storage that was created by the CWD in the channel was visually estimated, although hydraulic storage created by fully submerged and thus unseen CWD was unknown. All CWD was removed from a 100-m section of the channel, with each piece of removed debris being measured after removal. The bed of the channel was raked to remove the smaller woody debris and detritus for ~ 1 min m^{-2}. To estimate the portion of vegetation or debris removed by using these methods, debris was collected from a 1-m^2 sample plot by using the methods described, and then all debris was

Fig. 1. Snapping Turtle Canal with baffles installed, January 2004.

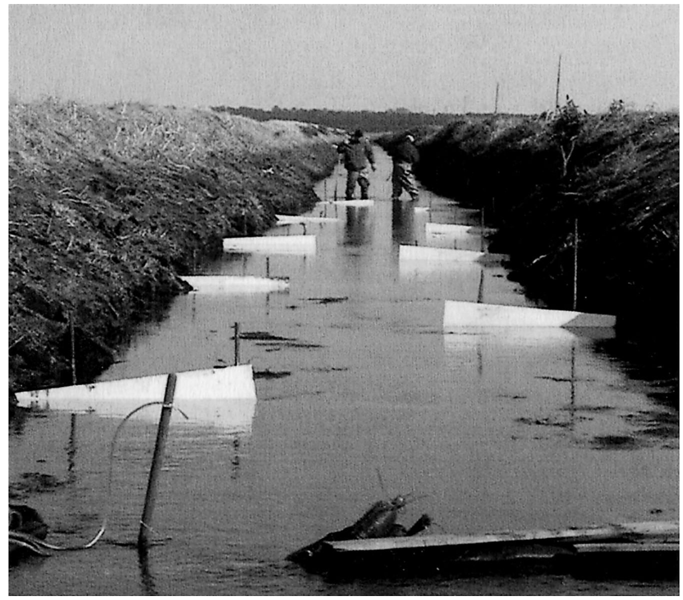

Fig. 2. Slocum Creek with baffles installed, January 2004.

collected from the sample plot (i.e., 100% vegetation or debris removal). Vegetation samples from Snapping Turtle Canal were dried, weighed, and combusted at 550°C for determination of ashfree dry mass. Woody debris and detritus raked from Slocum Creek was dried and weighed.

In the second manipulation (January 2004), nine plywood baffles sealed with exterior-grade latex paint were installed along the stream reach (50 m and 75 m of Snapping Turtle Canal and Slocum Creek) perpendicular to the flow. Vegetation coverage and CWD were substantial in Snapping Turtle Canal and Slocum Creek, respectively, but were not quantified. The baffles were placed against alternate banks and evenly spaced along the length of the channel to create a meandering flow (Figs. 1, 2). In addition, for the third baffle along the channel, located 7 m from the upstream end of the study reach, specific conductivity was measured at 30-s intervals in the dead-zone behind the baffle and in the main advection flow adjacent to the same baffle in Snapping Turtle Canal for the first 17 min of the injection. In Slocum Creek, flow velocity measurements were made with a handheld velocity probe along five lateral transects surrounding the location of a baffle before and after it was installed in the stream. Velocity was measured at a depth of 60% of the water column depth.

Solute transport and uptake calculation—The OTIS model (Runkel 1998) was used to determine the hydrologic parameters dispersion coefficient (D), channel cross-sectional area (A), channel storage zone cross-sectional area (A_s), and storage zone exchange coefficient (α). The parameter estimation option of OTIS (OTIS-P) was used for derivation of the model parameters that best fit the observed data (STARPAC) (Donaldson and Tryon 1990). Based on the specific conductivity measurements taken during water sample collection, lateral inflow was deemed to be an insignificant component of channel flow, and OTIS was run assuming no lateral inflow. Discharge was calculated by the dilution gauging method (Kilpatrick and Cobb 1985).

The cumulative effect of transient storage on reach-scale retention of water depends on A_s, α, and flow velocity in the main channel. The average residence time of water in transient storage zones (T_s, min) was calculated as

$$T_S = \frac{A_S}{\alpha \times A} \qquad (1)$$

(Harvey et al. 1996).

The average residence time of water in transient storage zones per length of stream channel (R_h, s m^{-1}) was calculated as

$$R_h = \frac{A_S}{Q} \qquad (2)$$

where Q is the volumetric flow rate of the stream (Morrice et al. 1997). These widely used metrics of transient storage neglect flow velocity and thus do not adequately describe the influence of transient storage along a stream reach (Runkel 2002). Therefore, the relative influence of the transient storage zone on hydraulic transport was determined by calculating the fraction of the median travel time attributable to the transient storage:

$$F_{\text{med}} \cong [1 - e^{-L(\alpha/u)}] \times \frac{A_s}{A + A_s} \qquad (3)$$

where L is stream reach length (m), and u is stream velocity (m s^{-1}) (Runkel 2002). Also, the F_{med} was calculated for a standardized distance of 200 m (F_{med}^{200}) to allow comparison of results with other stream ecosystems (Runkel 2002).

Nutrient uptake was analyzed following the method of the Stream Solute Workshop (1990). The N and P concentrations of samples collected during the injection were normalized by using the following formula:

Table 1. Hydrologic parameter and amount of nutrient concentration increase above ambient at site A in Snapping Turtle Canal and Slocum Creek.

Stream	Experiment	Discharge (L s^{-1})	Velocity (cm s^{-1})	F_{med} (%)	F_{med}^{200} (%)	Damkohler number	T_s (min)	R_h (s m^{-1})	ΔNH_4 (μg N L^{-1})	ΔPO_4 (μg P L^{-1})
Snapping Turtle Canal	control	22	4.0	1.19	4.47	0.1	210	10.4	—	—
	vegetation removed	19	4.0	0.65	2.46	0.2	91	4.7	—	—
	control	31	6.4	3.27	8.07	3.7	3.9	1.8	—	—
	flow baffles	26	4.6	10.1	17.6	4.4	5.1	4.9	—	—
Slocum Creek	control	77	17.1	22.8	24.7	10.1	1.3	1.9	87	32
	debris removed	78	17.5	10.0	13.7	6.1	1.9	1.1	85	29
	control	53	21.3	18.0	23.5	5.7	1.4	1.5	157	64
	flow baffles	53	21.2	23.8	27.2	7.5	1.1	1.8	131	57

$$C_n = \frac{C - C_b}{T - T_b} \quad (4)$$

where C_n (μg L^{-1}) is the normalized nutrient concentration, C is the observed concentration in stream, C_b is the background nutrient concentration, and T and T_b (μS cm^{-1}) are the observed and background tracer measurements. Assuming nutrient uptake is a first-order rate function of the concentration in the stream, the normalized nutrient concentrations at each sampling site ($C_n x$) can be modeled as

$$C_n x = C_n 0 \times e^{-K_c \times X} \quad (5)$$

where $C_n 0$ (μg L^{-1}) is the value of C_n at the injection site ($x = 0$), and K_c (m^{-1}) is the first-order uptake rate coefficient. K_c is estimated as the slope of the regression of ln ($C_n x$) versus distance x (because the slope of the regression is negative where nutrient uptake occurs, K_c is converted to a positive number by multiplying by -1). The uptake velocity, V_f (mm min^{-1}), is a vertical transfer velocity of nutrient from the water column to benthos and is calculated as

$$V_f = u \times h \times K_c \quad (6)$$

where h is channel depth. The mass transfer velocity was used to calculate the areal uptake rate of NH_4 and PO_4 (μg m^{-2} s^{-1}) during the injection as

$$U = V_f \times C_p \quad (7)$$

where C_p is the peak nutrient concentration entering the modeled stream reach (the average of all concentrations measured during the injection at the sampling site A). Areal uptake rate calculated by using the peak nutrient concentration is higher than the rate occurring at ambient nutrient concentration in the stream (Dodds et al. 2002). This is commonly accounted for by estimating the ambient uptake rate by substituting the background nutrient concentration for the peak value (C_p) in Eq. 7. The current study is not intended as a comparison of ambient uptake rates, hence Eq. 7 is used because it explicitly accounts for changes in nutrient concentrations and the inherent effect on U and V_f.

The standard error of K_c (the regression slope of the normalized nutrient data) was used to calculate V_f plus one standard error as

$$V_f^+ = u \times h \times K_c^+ \quad (8)$$

where K_c^+ is K_c plus one standard error. Next, V_f minus one standard error was calculated as

$$V_f^- = u \times h \times K_c^- \quad (9)$$

where K_c^- is K_c minus one standard error. The standard error imparted to U (U^+ and U^-) was calculated as

$$U^+ = V_f^+ \times C_p \quad \text{and} \quad (10)$$

$$U^- = V_f^- \times C_p \quad (11)$$

All nutrient data collected at each sampling point (instead of average values) were used for the linear regression to calculate K_c. Thus the standard error integrates the two potential sources of error: (1) analytical variance in the replicate samples and (2) environmental variability in nutrient uptake along the reach. The slopes of the normalized nutrient data regression in the control and treatment experiments were compared by using a one-tailed Student's t-test (α = 0.1). The hypotheses for the debris removal experiments were H_0: $slope_{(control)} \geq slope_{(treatment)}$, and H_A: $slope_{(control)} < slope_{(treatment)}$ (recall that the more negative the regression slope, the greater the nutrient uptake). Hypotheses for the baffle addition experiments were H_0: $slope_{(control)} \leq slope_{(treatment)}$, and H_A: $slope_{(control)} > slope_{(treatment)}$.

Results

Snapping Turtle Canal—Discharge in Snapping Turtle Canal ranged from 19 –31 L s^{-1}, with higher discharges in January than October (Table 1). Discharge and channel area were lower after vegetation removal (likely the result of increasing water stage in the adjoining estuary), and subsequently, flow velocity remained constant. Velocity did decrease after baffles were installed (a consequence of the larger channel area and lower discharge in the treatment solute injection) (Table 1). The solute break-through curves for the conservative tracer during control and treatment injections show a divergence as the concentration approaches plateau, indicative of a difference in A_s between the treatment and control (Fig. 3). Damkohler numbers (an index of the influence of transient storage on reach-scale advection transport) calculated for the Snapping Turtle Canal experiments ranged from 0.1 to 4.4 and were mostly within the range of values for which hydrologic parameter estimates were most reliable (Harvey and Wagner 2000) (Table 1).

Of the total macrophyte vegetation in Snapping Turtle Canal (40 kg organic matter), 40% (16 kg organic matter) was removed by raking. After removal of the vegetation, A_s de-

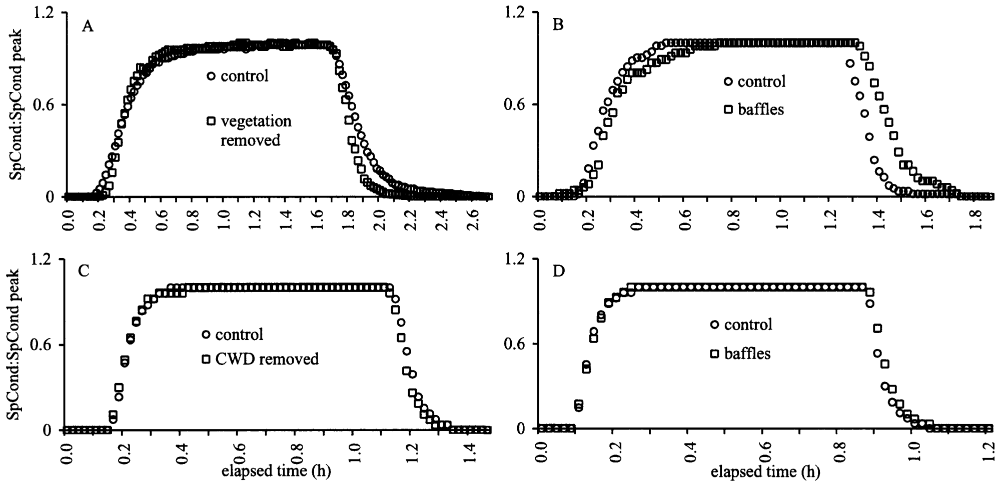

Fig. 3. NaCl break-through curves as measured by specific conductivity: (A) Snapping Turtle Canal vegetation removal experiment, (B) Snapping Turtle Canal baffle experiment, (C) Slocum Creek debris removal experiment, and (D) Slocum Creek baffle experiment.

creased by 61%, and α increased by only 1% (Fig. 4 ; Table 2). The fraction of the median travel time attributable to transient storage decreased 45% after vegetation removal (Table 1). The low F_{med} values calculated for Snapping Turtle Canal in these two solute injections (1.2% and 0.7%) indicated that transient storage had little influence over hydraulic transport, likely because of the very slow rate of transient storage exchange ($\alpha < 4.0 \times 10^{-5}$ s^{-1}).

Raking submerged aquatic vegetation from Snapping Turtle Canal caused noticeable sediment resuspension that required ~1 h to be flushed from the stream reach. Uprooting of vegetation and wading in the stream caused substantial disruption to the organic sediment profile of the channel bed. Similar effects were observed after baffles were installed in Snapping Turtle Canal as a result of wading in the stream. The resultant suspended sediment load in both manipulations likely blanketed the remaining periphyton community within the channel, altering the biochemical cycling of nutrients along the stream reach. The disturbance of the sediments may have altered their chemical equilibrium with the water column, possibly flushing sediment pore water with a high concentration of NH_4 or PO_4 into the water column. Consequently, the nutrient uptake values calculated from this experiment likely reflect substantial artifacts of the manipulation itself. Therefore, these experiments were deemed unsuccessful as a manipulation of channel features contributing to transient storage without concomitant disruption of the biogeochemical cycling of the stream reach. Nutrient concentrations and uptake metrics from both experiments in Snapping Turtle Canal are thus not presented.

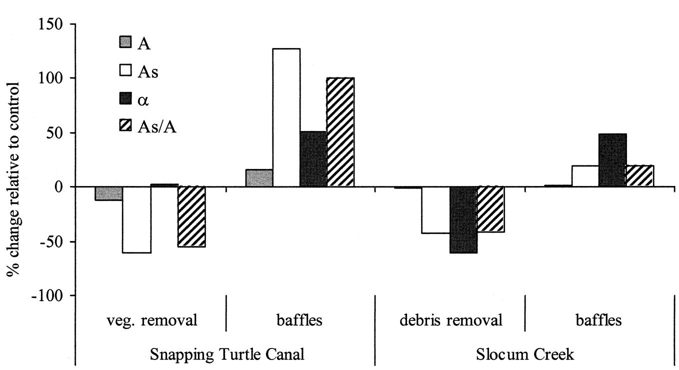

Fig. 4. Relative change in OTIS-P estimated hydrologic parameters between the control and treatment injections in Snapping Turtle Canal and Slocum Creek.

The total submerged surface area of the baffles installed in Snapping Turtle Canal was 1.9 m^2. Based on visual observation, the baffles created a total of 2.7 m^3 of transient storage in the stream reach, averaging 0.05 m^2 of visually observed A_s per linear length of stream channel. The model-derived estimate of A_s once baffles were installed was 0.07 m^2 per linear length of stream channel, or 217% greater than the A_s for the control injection (Fig. 4, Table 2). The α was increased from 4.9×10^{-5} s^{-1} to 7.4×10^{-5} s^{-1} by the introduction of baffles (Table 2). The baffles tripled the fraction of median travel time attributed to transient storage from 3.3% to 10.1% (Table 1).

The increase in tracer concentration at the beginning of the solute injection was much more rapid in the main advection flow than it was in the storage zone behind baffles. The dead zone behind the third baffle required 3.5 min longer than did the adjacent advection flow for the conservative tracer to be detected (Fig. 5). Once the tracer did enter the storage zone, a much longer period of time was needed to reach the plateau tracer concentration. Based on a linear extrapolation of the observed increase in tracer concentration behind the baffle, 20 min were required for the storage zone to be filled (i.e., to have complete replacement of ambient water with the injection water). The inverse of this time period is an empirically derived measure of α: 8.3×10^{-4} s^{-1} (recall that the model-derived estimate of α was 7.4×10^{-4} s^{-1}).

Slocum Creek—Slocum Creek discharge was higher in October (78 L s^{-1}) than January (53 L s^{-1}) (Table 1). There was a slight increase in flow velocity in Slocum Creek after

Table 2. Hydrologic parameter estimates (±SD) determined using OTIS-P.

Stream	Experiment	Dispersion (m^2 s^{-1})	Channel area (m^2)	Storage area (m^2)	Storage exchange (s^{-1})	A_s/A (%)
Snapping Turtle Canal	control	0.145±0.003	0.553±0.003	0.23±0.066	$3.3\times10^{-5}\pm4.0\times10^{-7}$	41.6
	vegetation removed	0.052±0.002	0.477±0.002	0.089±0.02	$3.4\times10^{-5}\pm5.0\times10^{-6}$	18.7
	control	0.096±0.023	0.488±0.023	0.056±0.022	$4.9\times10^{-4}\pm3.8\times10^{-4}$	11.5
	flow baffles	0.049±0.019	0.565±0.043	0.127±0.042	$7.4\times10^{-4}\pm4.9\times10^{-4}$	22.5
Slocum Creek	control	0.034±0.037	0.451±0.023	0.149±0.022	$4.3\times10^{-3}\pm1.3\times10^{-3}$	33
	debris removed	0.193±0.034	0.445±0.013	0.085±0.012	$1.7\times10^{-3}\pm4.7\times10^{-4}$	19.1
	control	0.067±0.094	0.248±0.004	0.079±0.003	$3.9\times10^{-3}\pm4.0\times10^{-4}$	31.9
	flow baffles	0.096±0.094	0.25±0.025	0.094±0.025	$5.8\times10^{-3}\pm3.0\times10^{-3}$	37.6

CWD was removed and a slight decrease in velocity after baffles were installed (Table 1). Approximately 4.1 m^3 of CWD were removed from Slocum Creek (134 individual pieces of CWD with diameter $>$ 5 cm, length $>$ 0.5 m), as well as 47% (9.1 kg dry mass) of the total mass of leaves and sticks that were present on the channel bed (19.5 kg dry mass). Based on visual estimates, there were 21 distinct CWD jams along the reach, creating a total of 11.0 m^3 of transient storage, or an A_s of 0.11 m^2 per linear length of stream channel. The model-derived estimate of A_s before CWD removal was 0.15 m^2 per linear length of stream channel (Table 2). Figure 3 shows the solute break-through curves measured at the downstream end of the experimental reaches. Damkohler numbers calculated for the Slocum Creek experiments ranged from 5.7 –10.1, indicating that the reach length was slightly longer than ideal, enhancing the uncertainty in the hydrologic parameters estimated (Table 1). Transient storage zone area decreased 43% after CWD removal (Fig. 4 ; Table 2). Also, α decreased 60% after debris was removed, and F_{med} decreased 56% (Fig. 4 ; Tables 1, 2).

Unlike Snapping Turtle Canal, there was not a thick deposit of fine organic matter overlying the sediments in Slocum Creek. Therefore, raking and wading in the stream did not cause substantial sediment resuspension, nor did wading in the stream cause notable deep disruption of the channel bed sediments. The lack of aquatic vegetation and compact sandy sediment allowed these manipulations to be performed without serious disruption of the hydrology or biogeochemistry of the stream. Uptake of NH_4 decreased from 3.3 mm min^{-1} (5.3 μg m^{-2} s^{-1}) in the control experiment to 0.4 mm min^{-1} (0.6 μg m^{-2} s^{-1}) once debris was removed (Fig. 6). Uptake of PO_4 decreased from 2.1 mm min^{-1} (1.3 μg m^{-2} s^{-1}) to 1.3 mm min^{-1} (0.8 μg m^{-2} s^{-1}) after debris removal (Fig. 6). The standard error of these uptake rates is large relative to the difference between treatments (Fig. 6), and the null hypothesis ($slope_{[control]} \geq slope_{[treatment]}$) was not rejected for either nutrient (NH_4: $t = -0.50$, $df = 13$; PO_4: $t = -0.08$, $df = 13$). Background NH_4 remained constant at 9 μg L^{-1} between the control and treatment injections, whereas PO_4 increased from 5 to 6 μg L^{-1} (Table 3). Background NO_3 increased from 10 to 28 μg L^{-1} after debris was removed. Peak nutrient concentrations of NH_4 and PO_4 decreased 2% and 5%, respectively, between the control and treatment injections (Tables 1, 3).

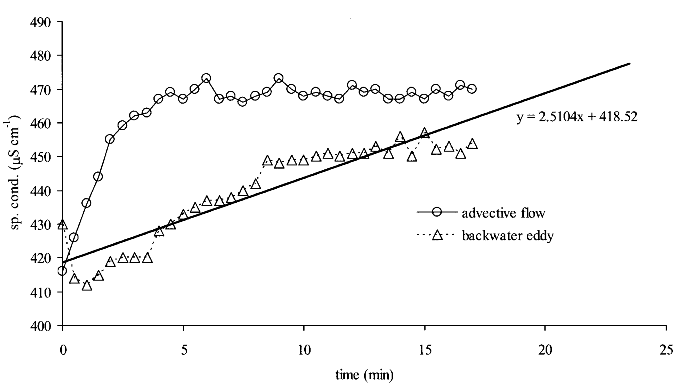

Fig. 5. Measurements of specific conductivity taken in the riffle beside flow baffle 3 and the backwater eddy behind the baffle in Snapping Turtle Canal, January 2004.

Similar to those at Snapping Turtle Canal, the cross-sectional area of the baffles installed in Slocum Creek totaled 1.9 m^2, and velocity measurements showed that the baffles had a measurable impact on the local velocity field (Fig. 7). The α estimated by the model showed that this form of storage had a higher exchange rate than was caused by CWD. Visual observation yielded an estimate of 3.3 m^3 of total storage zone volume for the stream reach, or an A_s of 0.044 m^2 per linear length of channel. The OTIS-P parameter estimates showed A_s increased from 0.079 to 0.094 m^2 per linear length of channel after baffles were installed (Table 2). The fraction of the median travel time attributable to transient storage increased 32% after baffles were installed (Table 1).

Ammonium uptake increased from 0.2 mm min^{-1} (0.4 μg m^{-2} s^{-1}) to 28.5 mm min^{-1} (70.3 μg m^{-2} s^{-1}) and PO_4 uptake increased from -1.7 mm min^{-1} (-2.0 μg m^{-2} s^{-1}) to 53.5 mm min^{-1} (55.2 μg m^{-2} s^{-1}) after baffles were installed in Slocum Creek (Fig. 6). This negative value of PO_4 V_f indicates that there was a net generation of PO_4 from the streambed during the injection, although this is not indicated by the background PO_4 values before the injection began (Table 3). Although potential error in these estimates was large, the range in error did not overlap for the control and treatment experiments. The null hypothesis ($slope_{[control]} \leq slope_{[treatment]}$) was rejected for both NH_4 ($t = 1.72$, $df = 12$) and PO_4 ($t = 2.10$, $df = 12$) in favor of H_A (nutrient uptake was more rapid after the addition of baffles to the stream). Background NH_4 decreased from 18 to 17 μg L^{-1} after baffles were installed, and background NO_3 remained at 12 μg L^{-1} during both injections (Table 3). Peak NH_4 and PO_4 concentrations

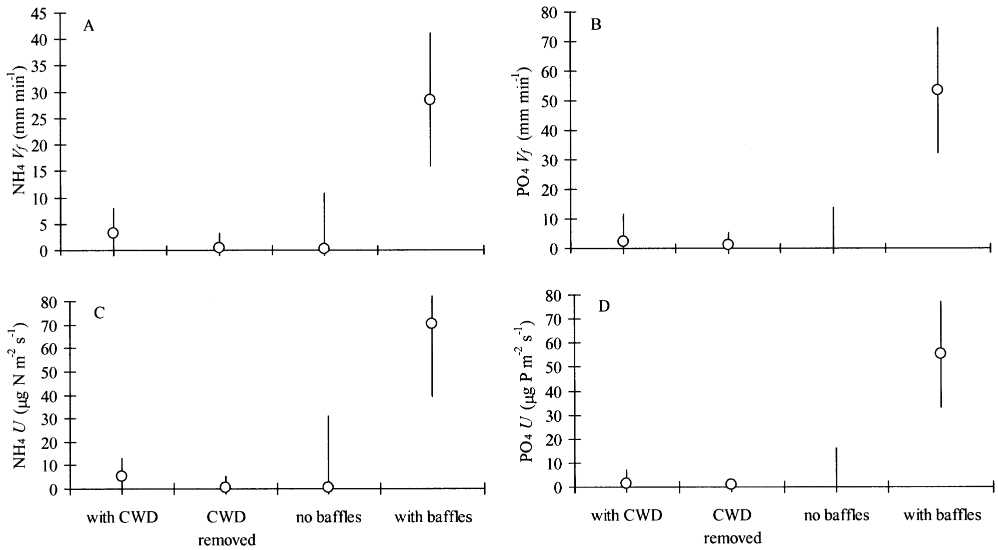

Fig. 6. Mass transfer velocities and areal uptake rates at enriched concentrations (±1 SE) of NH_4 and PO_4 in Slocum Creek manipulation experiments: (A) V_f NH_4, (B) V_f PO_4, (C) U NH_4, and (D) U PO_4.

decreased 15% and 11%, respectively, between the control and treatment injections (Tables 1, 3).

Discussion

Transient storage—Physical manipulations of stream channels in this study allowed estimation of the proportion of transient storage occurring within the channel by measuring transient storage parameters before and after debris was removed from the stream. Removal of vegetation from Snapping Turtle Canal demonstrated that in-channel storage accounts for ~100% of the total transient storage area, but in-channel storage had little effect on median travel time, as indicated by very low values of F_{med} before and after vegetation was removed. The relationship observed in Slocum Creek between reduction in CWD (>> 50%) and decrease in storage area (40%) showed that not all of the A_s can be accounted for by in-channel woody debris. A considerable decrease in α after debris removal showed the relative importance of a more slowly operating mechanism of storage in Slocum Creek.

The OTIS-P estimate of α was verified by actual measurement of the conservative tracer approaching equilibrium with an artificially created zone. The observed change in tracer concentration allowed calculation of an α of 8.3×10^{-4} s^{-1}, whereas the OTIS-P model predicted α to be 7.4×10^{-4} s^{-1}. The model prediction is expected to be slower than the observed value because the model integrates the effects of the turbulent storage with the much slower exchange through the vegetation (4.9×10^{-4} s^{-1} in the control injection). Furthermore, visual observations of storage zone size created by the baffles (0.05 m^2) supported the OTIS-P estimate of 0.07 m^2. The larger transient storage area estimated by OTIS-P can be attributed to the additional storage provided by macrophyte beds that was not visually observable (vegetation was abundant along the reach but not quantified). This verification of the OTIS-P simulation model by field-based observations (1) provided support that the dominant location of transient storage in this stream was either in mats of vegetation or behind baffles, and (2) demonstrated that visual estimates of in-channel storage can approximate those derived from simulation modeling when hyporheic transient storage is small.

The α values determined for Snapping Turtle Canal are similar to those in other streams. In an examination of an agricultural stream in Sweden, Salehin et al. (2003) estimated α of 6.1×10^{-4} s^{-1} in a heavily vegetated reach. Harvey et al. (2003) reported α values between 4.7×10^{-4}

Table 3. Background nutrient concentrations (μg L^{-1}) in Slocum Creek before experimental injections.

	Debris removal				Baffle construction			
	Control		Treatment		Control		Treatment	
Site	NH_4	PO_4	NH_4	PO_4	NH_4	PO_4	NH_4	PO_4
A	10	5	10	6	17	6	17	5
B	9	5	8	5	19	5	17	5
C	9	5	10	6	18	5	16	5
D	—	—	—	—	18	5	17	7
Reach average	10	5	9	6	18	5	17	6

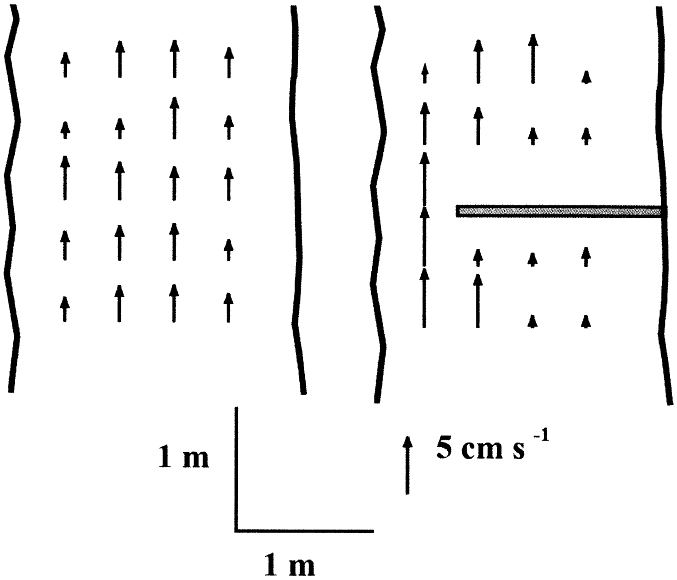

Fig. 7. Velocity flow fields measured with and without flow baffle in place at baffle 3 on Slocum Creek, January 2004. Note flow stagnation upstream and downstream of baffle and increase of velocity adjacent to baffle.

s^{-1} to 5.6×10^{-4} s^{-1} for a heavily vegetated stream reach in Arizona. Some of the highest α values in the literature are reported by Tank et al. (2000), whose estimate of α was 2.0×10^{-3} s^{-1} in Upper Ball Creek, North Carolina, and by Leanen and Bencala (2001), who reported an α of 1.9×10^{-3} s^{-1} for the South Yamhill River, Oregon. These values were similar to our lowest estimate of α for Slocum Creek, showing that Slocum Creek had a much higher rate of transient storage exchange than did other streams described in the literature. The values from Upper Ball Creek and the South Yamhill River may indicate the importance of hyporheic flow in these higher-gradient, porous-bed streams. The more rapid α estimates for Slocum Creek probably reflect the importance of relatively fast exchange of water within turbulent eddies combined with a smaller influence of hyporheic exchange.

The parameters A_s and α were integrated measures of all the hydrologic processes occurring along the reach. The ratio A_S:A indicated the extent of storage zone area relative to the open channel area, thus providing a metric for the physical capacity of the channel to retain water. However, A_S: A cannot indicate the actual location of the storage zone, that is, hyporheic versus in-channel. Although A_S: A for a stream reach may change with discharge and the extent of in-channel debris present, concomitant estimates of α can help identify the dominant mechanism of transient storage. For instance, Harvey et al. (2003) examined transient storage parameters over a 5-yr period at a single reach as the cover of macrophytes expanded into a stream channel. Their data showed little systematic change in α but showed a monotonic increase in A_S: A with time, which indicated consistency in the location of transient storage (submerged macrophyte beds), but a systematic increase in the overall capacity of this storage mechanism. If the fundamental mechanism for transient storage were to change over time (e.g., from macrophyte beds to hyporheic), then a change in α would occur unless the rate of exchange with the hyporheos happened to match the rate of exchange with macrophyte beds. Therefore, differences in α indicate changes in the physical processes contributing to transient storage, and they are especially useful when comparisons of the same stream reach are made over time.

By comparing the changes in α between the control and treatment experiments in the present study, it is possible to identify when the dominant location of transient storage at our sites changed. For instance, despite removing 40% of the vegetation in Snapping Turtle Canal, producing the commensurate 60% decrease in A_s, α in Snapping Turtle Canal remained virtually unchanged after vegetation was removed. This indicated that the dominant mechanism of transient storage (in-channel as opposed to hyporheic) did not change, although the volumetric capacity of this storage did change. In addition, the relationship between vegetation removed and the consequent decrease in A_s shows that all of the transient storage in Snapping Turtle Canal was likely owing to in-channel dead zones caused by vegetation. The placement of baffles in Snapping Turtle Canal, however, dramatically increased α and indicated that the predominant location of transient storage had shifted from within the macrophyte beds to within the dead zones behind the baffles. The α associated with the baffles obscured evidence of α associated with vegetation. Mixing of water in the dead zones behind the baffles occurred more rapidly than did the exchange within the submerged aquatic vegetation (Fig. 5 ; Table 1).

Median travel time was an effective metric for comparison of the control and treatment data because it put the net effect of transient storage on hydraulic transport in context of the travel time of water through the stream reach. Consideration of A_s and α alone does not necessarily indicate the importance of transient storage to overall hydrologic transport through the stream. In Snapping Turtle Canal, for example, the large size of the transient storage zone (A_s = 0.23 m^2) was not associated with a large F_{med} (1.2%). Transient storage exchange rate dictated the importance of transient storage to hydraulic transport by controlling the through-flow of stream water into transient storage zones. Although the range in A_s/A of both streams overlapped, α was one to two orders of magnitude higher in Slocum Creek, and subsequently, F_{med} in Slocum Creek was, on average, much higher.

Values of F_{med} normalized to a standard length (F_{med}^{200}) allow comparison of different streams and lengths of stream channel (Runkel, 2002). Values of F_{med}^{200} in tropical streams in South America ranged from ~12–95% and differed significantly based on stream morphotype (Gucker and Boechat 2004). Values of F_{med}^{200} in the coastal plain streams studied here ranged from 2.5–27% and were closest to the values of run reaches in the tropical streams. This is not surprising, given the similar sinuosity of the coastal plain streams studied here to those in South America.

The use of F_{med} was superior to other measures of transient storage such as the hydrologic retention factor (R_h) and transient storage zone residence time (T_s), which lead to different conclusions regarding the importance of transient storage. For example, removal of debris from Slocum Creek increased T_s from 1.3 min to 1.9 min, indicating an overall increase in the importance of transient storage despite decrease of 42% in A_s/A and a 56% decrease in F_{med}. Furthermore, T_s decreased from 1.4 to 1.1 min when baffles were installed in Slocum Creek, whereas R_h increased from 1.5 to 1.8 s m^{-1}. The decrease in T_s would suggest that the baffles had a negative influence on overall transient storage along the stream reach, whereas increased R_h suggests the opposite. If T_s and R_h had been used as the primary indicators of the importance of transient storage to water transport, these contradictory data would have confounded any conclusions on the effect of the baffles. The concomitant changes in A_s, A_s/A, and F_{med} observed in all the manipulation experiments of this study highlight the utility of using F_{med} as a metric of transient storage.

The manipulation experiments in Snapping Turtle Canal did not significantly interfere with measured transient storage parameters. Although hyporheic flowpaths and exchange rates may have been altered by the manipulations in Snapping Turtle Canal, the fine organic sediments probably restricted substantial hyporheic exchange and therefore did not contribute to the reach-scale transient storage measurements. Although stream velocity decreased between the control and baffle addition treatments, this change in stream advection velocity alone would have increased F_{med} from 3.3% to only 4.3% in the absence of transient storage. However, F_{med} increased from 3.3% to 10.1% after the manipulation, indicating that addition of baffles and associated transient storage (as opposed to reduced velocity) accounted for most of the observed increase in F_{med}. The hydraulic effects of raking the sandy sediments of Slocum Creek are unknown. Installation of flow baffles in Slocum Creek may have induced hyporheic exchange by creating a positive pressure differential between the upstream and downstream side of the baffle. However, diversion of surface water into the hyporheic zone would be expected to decrease the rate of transient storage exchange (relative to the predominant surficial turbulent processes as determined by CWD removal). The increase in exchange rate observed after baffles were installed indicated that any baffle-induced hyporheic exchange was overshadowed by water column processes.

Nutrient biogeochemistry—The present study provided direct examination of the relationship between in-channel hydraulic storage and nutrient retention in stream ecosystems. Nutrient data from the CWD experiment in Slocum Creek did not show a significant decrease in uptake rate after CWD was removed owing to the high variability in replicate samples. A real, although subtle, change in the uptake rate would have easily been masked by the large standard error in uptake measurements. Decreased NH_4 and PO_4 uptake after removal of CWD in Slocum Creek would presumably be a result of the loss of microbial biofilm surface area and the decreased hydrologic retention time attributable to transient storage. Addition of baffles to Slocum Creek significantly increased V_f and U and indicated that the additional 32% of median travel time added by the baffles greatly increased nutrient removal from the stream water. The baffle experiment demonstrated that nutrient uptake in this stream was controlled by in-stream transient storage.

Despite attempts to keep the level of nutrient addition constant between the control and treatment nutrient injections, there was a considerable decrease in peak NH_4 concentration (26 μg L^{-1}) during baffle addition to Slocum Creek. It is necessary to consider the effect of these differences in nutrient concentration on the measured uptake rates and subsequent comparison of the results from the manipulations. The decrease in peak NH_4 concentration would have been expected to decrease U relative to the control injection. Thus, the large increase in U would have been even greater had the peak concentration remained the same.

Our measurements of nutrient uptake using nutrient additions underestimated the ambient V_f and overestimated ambient U owing to the increase in stream-water nutrient concentrations, and therefore must be used with caution in comparisons with other streams (Dodds et al. 2002). Instead of attempting to extrapolate the observed data to ambient uptake rates, this analysis is based on using observed U values calculated by using Eq. 7, which reflect the effect of nutrient concentration in the stream and enable comparison between pre- and postmanipulation nutrient concentrations.

Disturbance to the streambed during these experiments was impossible to avoid. Raking of debris from the channel bottom of Slocum Creek disturbed not only the sediment but also the microbial community on and in the sediment. However, background NH_4 and PO_4 concentrations in Slocum Creek changed by only 1 μg L^{-1} after each manipulation, indicating that the chemical exchange between the sediment and water column was not significantly altered by the manipulations (Table 3). The physical characteristics of Slocum Creek (sandy substrate and lack of vegetation rooted in the sediment) allowed the manipulation experiments to be performed without substantial disturbance to the biogeochemistry of the stream.

The PO_4 V_f (53.5 mm min^{-1}) in Slocum Creek after baffles were installed is higher than almost all measurements reported in the literature. The PO_4 uptake measured in the control experiment was < 1 mm min^{-1}, although V_f derived from this nutrient enrichment approach would be expected to be lower than V_f under ambient nutrient concentrations. It is possible that the pressure gradient created by the baffles forced flow into the hyporheic zone, increased water-sediment contact within hyporheic zones, and enhanced PO_4 uptake. However, research in both a Mediterranean stream and an Antarctic stream found that PO_4 uptake in the hyporheic zone was minimal, and that most PO_4 uptake occurred in surficial sediments (Butterini and Sabater 1999; McKnight et al. 2004). Unfortunately, the mechanism of PO_4 uptake stimulated by flow baffles was not apparent from the data collected.

Raking vegetation from the channel in Snapping Turtle Canal provided an artificial analog to sediment disturbance after spates in this watershed. Channel bed sediments can be extensively reworked during storms, resulting in burial of channel vegetation in some reaches and scouring of sand and vegetation in others. Therefore, the observed reduction in transient storage during the vegetation removal experiment could also occur after storm events as well. This reduction in the influence of transient storage during periods of increased nutrient loads during storm events likely has ecological ramifications for the estuary located ~1.5 km downstream.

Very few studies of nutrient spiraling that use whole-stream nutrient injections report error in uptake rates (except see Hart et al. 1992). This study demonstrates that potential error is high, especially when using a small number of sampling sites (≤4) as is common (see Mulholland et al. 1997; Hall et al. 1998; McKnight et al. 2004). The standard method of calculating nutrient uptake through solute injections assumes that uptake operates as a first-order process and is longitudinally homogenous along a stream reach. However, nutrient uptake in streams is highly spatially variable (McClain et al. 2003). Thus, it is critical to consider the error imparted by environmental variability when discussing results of nutrient injection experiments. Calculation of the standard error in the normalized nutrient regression slope (K_c) was used in the present study and reflected both environmental variability and analytical variance. In addition, a Student's *t*-test was used to test hypotheses in the two sets of experimental manipulations.

Submerged aquatic vegetation accounted for most of the A_s in a highly vegetated stream, and woody debris and leaf litter were responsible for a significant proportion of A_s in a low-gradient blackwater stream. Understanding of the effect of transient storage on nutrient retention will be strengthened by future investigations documenting the proportion of total transient storage caused by in-channel storage. Stream channel manipulations were found to be an effective way to determine the portion of transient storage that is caused by in-channel flow obstructions. Removal of vegetation and debris from these streams decreased F_{med}, although the apparent decreases in V_f and U of inorganic N and P in Slocum Creek were not significant. Flow baffles resulted in increased F_{med} in both streams and concomitant increases in NH_4 and PO_4 uptake in the blackwater stream. The biogeochemical results from Slocum Creek were not able to be verified with data from the second stream, however. The combination of manipulative experiments (debris removal and baffling) illustrated that nutrient uptake in the blackwater stream not only is a function of biofilms on the channel debris but also depends on the exposure of stream water to this debris by temporary hydrologic storage in turbulent eddies. Although similar data have demonstrated this ecological interaction in laboratory flumes (Mulholland et al. 1994), the present study is the first to experimentally determine these interactions in natural stream ecosystems.

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