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Comparison of morphological and biological control of exchange with transient storage zones in a field-scale flume

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[1] To determine how differences in geomorphologic setting influence spatial heterogeneity in transport and uptake of limiting nutrients, we investigated reach-scale interactions between porous bed material textures, bed morphology, transient storage, and nutrient retention in a field-scale flume (84 m × 2.75 m). Conservative salt tracer and soluble reactive phosphorous additions were used to quantify effects of plane bed and alternate bar morphologies, and clean gravel versus sandy gravel bed texture on reach-scale nutrient retention and transient storage. We conducted experiments under light and dark conditions to clarify the role of benthic production on surface-subsurface hydrologic interactions and the relative influence of increasing biomass on nutrient uptake rates. Mean water residence time varied by a factor of 8 across treatments (4–32 min) and transient storage volume varied strongly with sediment texture. The exchange rate coefficient was greatly influenced by presence of alternate channel bars. Phosphorus uptake had the tendency to change with total volume of sediment-water interaction during dark conditions where periphyton abundance was low. However, under light conditions, periphyton growth clogged bed material pores and essentially eliminated exchange between the surface and subsurface. Uptake then was related to periphyton biomass accumulation rather than hydraulic or geomorphic parameters. The location and mechanism of stream nutrient retention may be more temporally and spatially dynamic than previously realized. Under clean bed conditions in streams (e.g., shaded riffles, streambeds following floods or in winter), nutrient uptake will be hyporheic dominated. Under high periphyton biomass conditions, nutrient uptake will be elevated in the surface sediments, minimal in the hyporheic, and thus benthic dominated.

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1. Introduction

[2] Humans have markedly altered the biogeochemical functioning and geomorphology of aquatic ecosystems through effects that include increased nutrient and sediment loading, stream channelization, and damming. Over the past three decades, many studies have emphasized the role of streams in retaining nutrients via biogeochemical transformations [*Ensign and Doyle*, 2006]. However, only recently has the potential interaction of geomorphology and biogeochemistry been explicitly considered [*Alexander et al.*, 2000; *Sweeney et al.*, 2004].

[3] Channelization, deforestation, and urbanization all have detrimental effects upon natural channel morphology, and there is a well established understanding of how channels physically respond to these types of disturbances [*Knighton*, 1998]. The impacts of these geomorphic disturbances on stream nutrient dynamics remain largely unknown, primarily because there is fundamentally poor understanding of how geomorphology influences nutrient dynamics in general. Such lack of understanding precludes the potential for using models to forecast channel changes on stream nutrient loads, and thus the application of stream restoration in efforts to improve water quality [*Palmer et al.*, 2005; *Alexander and Allen*, 2006; *Bukaveckas*, 2007].

[4] A critical issue then is if and how geomorphology, hydraulics, and hydrology can interact to affect stream biogeochemistry. There are several examples of how this may occur, and thus which mechanisms need to be quantified. One common example is the role of channel mor-

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Table 1. Experimental Conditions for Dark Runs

Injection	Texture	Topography	Discharge (L s^{-1})	Velocity (m s^{-1})	DaI	K ($\pm 1\ \sigma$) (cm s^{-1})	Days of Light
1	gravel	plane bed	17.6	0.03	0.43	3.2 (±2.4)	dark
2	gravel	alternate bars	13.0	0.02	0.18	3.2 (±2.4)	dark
3	sandy gravel	plane bed	14.0	0.03	0.47	0.26 (±0.11)	dark
4	sandy gravel	alternate bars	11.0	0.02	0.13	0.26 (±0.11)	dark

phology in determining hydrologic and biological connectivity to groundwater in the longitudinal, lateral and vertical directions [*Kondolf et al.*, 2006], as such surface-groundwater interactions are commonly associated with increased rates of biogeochemical cycling [*Valett et al.*, 1996]. Also, geomorphic variability can create areas of hydraulic variability, leading to alternative benthic substrate patches, which have inherently different biogeochemical characteristics [*Kemp and Dodds*, 2002]. More broadly, systematic geomorphic changes, whether natural or anthropogenic, can change multiple parameters simultaneously (e.g., shape, substrate size, benthic patches), and thus lead to widely varying biogeochemical responses [*Fisher et al.*, 1998, 2007; *Dent et al.*, 2002; *Orr et al.*, 2006].

[5] Previous studies linking geomorphology/hydrology to stream biogeochemistry have been through intersite or interreach comparisons [*Martí and Sabater*, 1996; *Peterson et al.*, 2001; *Wolheim et al.*, 2001; *Webster et al.*, 2003; *Dent et al.*, 2007]. In such studies, streams with different geomorphic or hydrologic characteristics are studied using identical techniques, and differences in biogeochemical processes are quantified and attributed to these physical differences. Alternatively, studies have leveraged management actions or disturbances to conduct predisturbance and postdisturbance studies, and thus link physical form to biogeochemical process [*Doyle et al.*, 2003; *Orr et al.*, 2006; *Bukaveckas*, 2007]. The limitation of using these types of approaches, particularly for studies of reach-scale nutrient retention, is that within-reach variability and changes through time may be significant, but poorly quantified.

[6] Comparatively fewer studies have used highly controlled experimental settings to examine physical and biogeochemical interactions in streams. In hydraulics and geomorphology, controlled experiments have served for decades as the backbone for building mechanistic understanding of fluvial processes and as the foundation from which predictive, numerical models were built. Those ecosystem studies that have used controlled experimental approaches have similarly provided important insights into specific mechanisms of stream biogeochemistry [*Kim et al.*, 1990; *Mulholland et al.*, 1994; *Battin et al.*, 2003]. However, these previous studies have occurred at temporal or spatial scales that make their results difficult to relate to their field study counterparts.

[7] Here we explicitly link stream geomorphology and hydrology to biogeochemistry using an indoor experimental flume whose flow and dimensions are comparable to first- and second-order streams on which many field-scale stream biogeochemistry studies have been conducted. This allowed us to use a simulated, yet realistic, stream setting where channel geometry, bed material, and hydrology could be both highly controlled and manipulated directly. We evaluated the effects of changing these physical attributes by quantifying their effect on nutrient retention, the short-term removal of nutrients from the water column by temporary removal (e.g., biotic uptake and sorption). Short-term retention alters the amount, form, and timing of downstream nutrient export and thus provides a particularly useful metric of whole-ecosystem function. Specifically we compared transient storage zone characteristics for two bed forms and two sediment textures with and without the presence of a periphyton mat. We were interested in determining the difference between a simple and more complex bed form with respect to the exchange rate coefficient, the size of the transient storage zone, and the water residence time in the flume overall.

[8] Most broadly, we sought to understand the specific mechanisms by which geomorphology could influence nutrient retention, a basic ecosystem-level process in streams. Specifically we addressed two questions: (1) How do these physical conditions control the nutrient dynamics of biotic and abiotic uptake? (2) How does periphyton accumulation and persistence control the location and rates of nutrient uptake? We hypothesized that more complex bed forms would increase the size of the transient storage area as well as increase exchange with this zone and thereby increase uptake. We also hypothesized that the addition of a growing periphyton mat would increase nutrient uptake through biotic assimilation, while decreasing the influence of transient storage zones on uptake.

2. Experimental Conditions

2.1. Main Channel Flume

[9] The experiments were conducted from April through October of 2006 at the University of Minnesota's St. Anthony Falls Laboratory on the Mississippi River near Minneapolis, MN. The experiments were run on the "main channel" flume, which is a straight, rectangular cross section, concrete research channel with a width of 2.75 m, depth of 1.8 m, test length of 55 m and a slope of 0.002 (m/m). The main channel is located below ground level, and under normal operating conditions there is only low light from overhead fluorescent fixtures. Average sediment depth for the series of experimental runs was 50 cm with some variability dependant upon the bed conditions. Water for the facility was supplied from the Mississippi River through a sluice-type adjustable head gate. An additional adjustable gate at the downstream end of the channel was used as a sharp crested weir to control the water surface elevation in the flume. Discharge was continuously monitored and held constant during each of the experimental runs.

[10] We used the main channel to test four different alternative bed/channel conditions with ambient light each once (dark runs) (Table 1), and then one bed/channel condition with elevated light conditions several times over a 24 d growth period (light run) (Table 2). The dark runs were used to quantify the effect of variable bed morphology

Table 2. Experimental Conditions for Light Runs

Injection	Texture	Topography	Discharge (L s^{-1})	Velocity (m s^{-1})	DaI	K ($\pm 1\ \sigma$) (cm s^{-1})	Days of Light
5	sandy gravel	alternate bars	11.5	0.40	0.32	0.44 (±0.6)	0
6	sandy gravel	alternate bars	4.8	0.25	0.81	-	3
7	sandy gravel	alternate bars	7.7	0.40	0.69	0.40 (±0.23)	6
8	sandy gravel	alternate bars	4.0	0.21	0.16	0.25 (±0.10)	16

and bed textures on transient storage and to measure nutrient retention in the flume due to heterotrophic organisms and abiotic sorption before adding periphyton. The light run was used to quantify the interactions between channel morphology, transient storage, and periphyton accumulation on nutrient retention. In each set of runs, we quantified nutrient retention using standard solute injection techniques [*Stream Solute Workshop*, 1990].

2.2. Dark Runs

[11] During the dark runs, two different bed textures (gravel and sandy gravel) and two different bed morphologies (plane bed and alternate bars) were used sequentially to differentiate between the influence of bed texture and morphology on transient storage and nutrient retention (Table 1). We started with a clean gravel bed channel and indoor, low-light conditions. The initial bed sediment was a well sorted gravel with D_{50} of 9 mm and $D_{100} < 32$ mm; all material in the gravel mixture was >2 mm. A bed load transporting flood was used to reset the bed and generate a hydraulically deposited alluvial sediment bed. During dark runs, the flow encompassed the entire width of the flume channel and the flume discharge was set well below the threshold of sediment motion for 2 d.

[12] Initially the bed topography was a plane bed, where the bed sediment depth was uniform and flow depth over the bed was relatively uniform at approximately 60 cm. Plane bed topography exhibited very little cross stream variation but 3–5 small amplitude (5 cm) sediment waves formed along the length of the test section. During the 2 d period, we ran a constant discharge of 17.6 l s^{-1} through the channel and measured soluble reactive phosphorus (SRP) uptake and transient storage via solute injections described below.

[13] Next, discharge was increased to initiate entrainment and transport conditions. A flow diversion (sandbag) was placed in the channel upstream of the test section to deflect initial flow into the left wall of the flume. This initial deflection created a series of alternate bars through the test reach which consisted of three well formed longitudinal bars with approximately 15–20 cm of relief. We reduced discharge to 13.0 L s^{-1} for 2 d, and again measured SRP uptake and transient storage (gravel bed, alternate bar, Table 1).

[14] We then mechanically mixed a commercial, fine grit safety sand into the gravel so that the second bed texture (sandy gravel bed) was created with 20% sand. The sandy gravel bed had a D_{50} of 7 mm and $D_{100} < 32$ mm, but the fine tail of the sediment grain size distribution was much finer than the gravel bed texture. Flow in the flume was increased to entrainment and transport conditions with the flow deflector removed, effectively washing out the alternate bars and returning to a plane bed condition. We then reduced flow below entrainment (14.0 L s^{-1}) for 2 d, and measured SRP uptake and transient storage (sandy-gravel plane bed condition, Table 1).

[15] Finally, we reinserted the flow deflector at the upstream end of the flume and increased discharge to create the alternate bar morphology. We then decreased flow below entrainment (11.0 L s^{-1}) for 2d, and measured SRP uptake and transient storage (sandy-gravel, alternate bar, Table 1).

2.3. Light Run and Periphyton Growth

[16] The second phase of the experiment consisted of constant bed morphology conditions with variable periphyton conditions. The bed was held constant as alternate channel bars with a sandy gravel bed for the light run. Through a trial period we found that periphyton growth was limited by light and phosphorus availability. To stimulate periphyton growth, we first used 18 high-power grow lights (Sun System V Econogrow mini, 400 W mercury halide bulbs) evenly spaced along the length of the flume, centered over the wetted channel at a height of 30 cm above the bed surface. The lights were set on timers to produce diel cycles of 16 h light, 8 h dark and algae naturally occurring in the Mississippi River source water colonized the bed. In addition, to allow light to penetrate to the bed surface below turbid Mississippi River water, flow depths were kept at 3 cm. This low flow depth resulted in large portions of the bars being exposed subaerially. A single sinuous water flow path resulted with a well defined thalweg and all of the channel bed exposed to light.

[17] Second, to alleviate the phosphorus limitation of periphyton growth, we used a continuous drip of KH_2PO_4 above the test reach to elevate the ambient SRP concentration to ~30 μg L^{-1} (±6 μg L^{-1} standard deviation). With the combination of light and SRP drip, during the 24 d of the light run, a thick cover of a diatom-dominated periphyton assemblage was produced under the lights. In the stretches of channel between lights there was less periphyton accumulation.

3. Methods

3.1. Overview of Approach

[18] We used reach-scale experimental releases of phosphorus and a conservative salt tracer to measure nutrient uptake under each of the combination of bed textures and bed morphologies as well as at intervals through the light run. Tracer data were used in the transport model OTIS-P [*Runkel*, 1998] to determine water flow and transient storage parameters. Bed permeability was measured in situ under each condition. During the light run biological parameters were measured to determine the amount of biomass accumulation and biological activity of this material that could contribute to nutrient uptake. A separate, lab-

based, assay was used to measure the abiotic component of phosphorus uptake.

3.2. Nutrient Uptake

[19] Net uptake of phosphorus was quantified by using short-term additions of NaCl as a conservative tracer in both dark and light runs, short-term additions of KH_2PO_4 in the dark runs, and ongoing KH_2PO_4 drip in the light run [*Stream Solute Workshop*, 1990; *Webster and Ehrman*, 1996]. Phosphorus was chosen as the study nutrient because available data for water chemistry in the Upper Mississippi revealed relatively high NO_3-N concentrations (0.5–2.0 mg/L), (USGS gauging station 05288500) indicating nitrogen is not limiting in this system. Paired NaCl/KH_2PO_4 injections were done for each of the four dark bed configurations then in the light run at days 1, 4, 12, 17, 19, and 24. Additional, NaCl-only, injections were done using the same set up on days 0, 1, 3, 6 and 16 of the light run to provide input data for the transport model (below).

[20] For each dark run injection, a solution of NaCl and KH_2PO_4 was pumped into the upstream end of the flume above the test reach using a peristaltic pump (Mityflex 4000). The concentration of NaCl in the solution was adjusted to elevate conductivity to approximately 1000 μS above background. The solute phosphorus concentration was adjusted with the goal of elevating the concentration 0.5 times the background to avoid overestimating uptake rates [*Mulholland et al.*, 2002]. The measured increases in SRP below the mixing zone were 20 to 180 μg PO_4-P L^{-1}, resulting in an increase of 5 to 66% above ambient (mean and median equal to 28%). In the light runs there was an ongoing phosphorus drip during the entire growth period that elevated the phosphorus concentration above background. Therefore it was not necessary to add additional KH_2PO_4 to the injection solution and phosphorus uptake was measured during six injections of NaCl alone using the same method as in the dark runs.

[21] Specific conductance was monitored at the upstream and downstream ends of the test reach with a Hydrolab datasonde (Hach DS5) recording at 1 or 2 min intervals beginning $\geq$20 min before each injection. The Hydrolab conductivity probes were calibrated to closely bracket the range of conductivity measured. Initial water samples were collected in triplicate at the top (0 or 10 m) and bottom (50 or 55 m) of the test reach and collected again after conservative-tracer steady state was achieved. Steady state was indicated by conductivity-curve plateau at the downstream conductivity probe and for each run final samples were collected $\sim$90 min after pumping began. Water samples were filtered at time of collection (0.45-μm glass-fiber filter) into 15 ml falcon tubes and frozen until processed. Phosphorus concentration was measured as SRP on an Autoanalyzer (Lachat Quikchem 8000).

[22] Conductivity measurements from the data sonde were compared with pump start and stop times and used to calculate water residence time in the test reach. Mean water retention time was calculated as minutes elapsed from pump start to a downstream conductivity reading of 1/2 the plateau value [*Webster and Ehrman*, 1996].

[23] Phosphorus concentration was corrected for dilution using the conservative tracer data [*Webster and Ehrman*, 1996]. Phosphorus uptake length (S_w; m) and uptake rate (U; μg m^{-2} min^{-1}) were calculated according to established protocol [*Stream Solute Workshop*, 1990; *Webster and Ehrman*, 1996]. Uptake rate was calculated using the equation:

$$U = \frac{C_b Q 60}{S_w w} \tag{1}$$

where C_b is the background concentration of SRP (μg m^{-3}), Q is discharge (m^3 s^{-1}), S_w is uptake length (m), w is the average stream width for the reach (m), and 60 is a unit conversion factor.

3.3. Transport Model

[24] The one-dimensional transport model OTIS can be used to simulate downstream transport of waterborne solutes using the assumption that solute concentration varies only in the longitudinal direction. OTIS is based on the advection–dispersion equation with terms added to account for transient storage and lateral inflow [*Runkel*, 1998, 2002] to estimate stream main-channel cross-sectional area (A), transient storage (A_s) and storage-zone exchange coefficient (α). A modified version, OTIS-P, uses a nonlinear regression model to automate parameter estimation. We used the metric A_s/A to characterize transient storage relative to channel area [*Runkel*, 1998] and the derived parameter F_{med} to describe the influence of transient storage on hydraulic transport

$$F_{med} \cong \left[1 - e^{-L(\alpha/u)}\right] \times \frac{A}{A + A_s} \tag{2}$$

where L is the reach length and u is the stream velocity [*Runkel*, 2002].

[25] A time-variable model was constructed in OTIS-P and was run against conductivity data recorded at the most downstream location at 1 min intervals throughout the injection period. Data from the upstream conductivity sonde were used as the upstream boundary condition for the reach. No adjustment for lateral input was needed in the concrete-walled flume. For each injection, multiple iterations of OTIS-P were run to determine the optimal set of estimated parameter values. All model runs converged to a solution and the Damkohler numbers (*DaI* in Tables 1 and 2), which ranged between 0.13 and 0.81, are well within the range of optimum parameter certainty [*Wagner and Harvey*, 1997].

3.4. AFDM and Chlorophyll *a*

[26] During the light run, periphyton was sampled from benthic substrate at 9 locations 4 times, 0, 10, 18 and 22 d after lights were turned on. For each sample a 10 cm^2 plastic tube was placed on the bed surface and all surface sediment was collected. Sediment was scrubbed thoroughly in deionized water to remove biofilm and the resulting slurry was filtered onto preashed glass fiber filters. Duplicate slurry samples were filtered to quantify ash free dry mass (AFDM) and all filters were stored below 0°C until analysis.

[27] Filters were placed in 15 ml acetone resistant centrifuge tubes and covered with 20 ml of a 90% acetone solution buffered with ammonium hydroxide following *Wetzel and Likens* [1991]. After 24 h refrigeration, absorbance was determined before (664 and 750 nm) and after

Table 3. Solute Transport Parameters for Dark Runs

	A_s/A		α (s^{-1})		F_{med} (%)		Mean Travel Time (min)	
	Plane Bed	Alternate Bars	Plane Bed	Alternate Bars	Plane Bed	Alternate Bars	Plane Bed	Alternate Bars
Gravel	0.28	1.76	0.00009	0.00010	1.99	7.08	18	19
Sandy gravel	0.26	1.34	0.00005	0.00005	1.88	7.49	31	31

acidification (665 and 750 nm) on a Beckman DU 640 spectrophotometer [*Steinman and Lamberti*, 1996]. Chlorophyll *a* is reported as per cm^2 surface area.

[28] AFDM determination was made by passing biofilm slurry through preashed 47 mm glass fiber filters. All filters were dried in a 100°C drying over for at least 24 h, weighed then ashed at 550°C for 5 h, cooled in a desiccator and reweighed [*American Public Health Association* (*APHA*), 1995].

3.5. Hydraulic Conductivity

[29] Vertical hydraulic conductivity (*K*) was measured at five cross-stream stations spaced every 10 m along the test reach using a 6.2 cm diameter falling head permeameter (Tables 1 and 2). A total of eight tests were conducted during the alternate bar clean gravel run and 20 tests under the alternate bar sandy gravel condition. In addition, hydraulic conductivity was measured during the light phase runs to track changes in permeability with periphyton abundance. After 14 d of growth four permeability tests were conducted directly under the lights and four were conducted at midpoints between lights to account for differences in periphyton densities with different light availability.

3.6. Metabolism and Respiration

[30] Whole-flume metabolism was calculated from upstream and downstream dissolved oxygen (DO) measurements as in the work of *Marzolf et al.* [1994] using the additional equation provided by *Young and Huryn* [1998]. Gas evasion from the flume water surface was measured using conservative SF_6 gas injections.

[31] A stock solution was created by bubbling SF_6 gas for 1 min at 5 L s^{-1} into a closed 50 L tank of river water into which 20 Kg NaCl had previously been dissolved. The salt and gas tracer solution was then injected into a well mixed area of the flume above the test reach at a constant rate of 600 ml/min. After 60 min, duplicate water samples were taken from the flume at 10 m intervals in the downstream direction using 25 ml amber glass vials fitted with septa caps. Headspace in the samples was generated with pure N_2 gas, allowed to equilibrate with the sample and then analyzed for SF_6 on a gas chromatograph (HP 5890 Series II). Specific conductance in the remaining sample water was measured to account for dilution. Evasion was calculated as in the work of *Hope et al.* [2001] following the methods of *Wanninkhof* [1992] and *Genereux and Hemond* [1992], using the dispersion coefficient of SF_6 from *King and Saltzman* [1995].

[32] Dissolved oxygen was continuously monitored at the upstream and downstream ends of the flume (meters 0, 55) for the duration of the experiment using two Hydrolab datasondes (Hach DS5) with semipermeable membrane DO probes. Very little photosynthesis was expected during the dark phase of the experiment due to low ambient light in the indoor facility. During the light experiments, no diel pattern in DO was observed while the grow lights cycled on and off. For these reasons, observed differences in dissolved oxygen from the upstream to downstream probe were assumed to be respiration in the test reach. Community respiration scaled to a 24 h period (CR_{24}) was calculated as the difference in upstream and downstream DO values adjusted for probe calibration and reaeration, then multiplied by the flume discharge for 24 h.

3.7. Abiotic Phosphorus Uptake

[33] The relative magnitude of abiotic uptake of SRP by the sandy-gravel sediment was determined by lab incubation of 1% formalin amended (killed) sediment with a comparison to intact (live) sediments. Formalin has been shown to be effective in inhibiting bacterial activity in sediment, especially for relatively short incubation periods [*Tuominen et al.*, 1994]. Two sets of 10 sediment samples were incubated in a 60 μg L^{-1} PO_4-P solution matching elevated concentrations in the flume, buffered with 50 mg L^{-1} $CaCl_2$ and 30 mg L^{-1} $NaCl_2$ to match natural stream water ionic strength [*Klotz*, 1988, 1991]. A 1:10 (g damp sediment: ml solution) ratio was used and samples were held at room temperature (22°C) and agitated at regular intervals and all were sampled after 24 h of incubation. A set of reagent blanks was carried through the procedure. For all samples aqueous and sediment phases were separated by filtration through a 0.45 micron glass fiber filter and SRP was determined using an autoanalyzer as described above.

4. Results

4.1. Bed Permeability and Tracer Results: Dark Runs

[34] In both bed textures (gravel, sandy gravel), alternate bar morphology elevated the transient storage area relative to the plane bed morphology (Table 3). However, in both bed morphologies, sandy gravel had lower hydraulic conductivity and a lower transient storage exchange coefficient (α) than gravel (Tables 1 and 2). The exchange rate coefficient (α) decreased by half with the addition of sand to the bed material and the mean residence time of water in the flume, as measured by half plateau of the conductivity breakthrough curve nearly doubled. The influence of transient storage on transport time, quantified by F_{med}, increased substantially from plane bed to alternate bar morphology under both bed textures.

4.2. Periphyton Growth

[35] Periphyton rapidly colonized the test reach of the flume after lights were installed and responded strongly to light availability. A colony-forming, river diatom (*Fragilaria spp.*) dominated mat developed over the 24 d growing period. Biomass was visibly denser in the 1 m × 1.5 m area directly under each light and tapered in the darker, interlight areas. When average chlorophyll values were calculated for

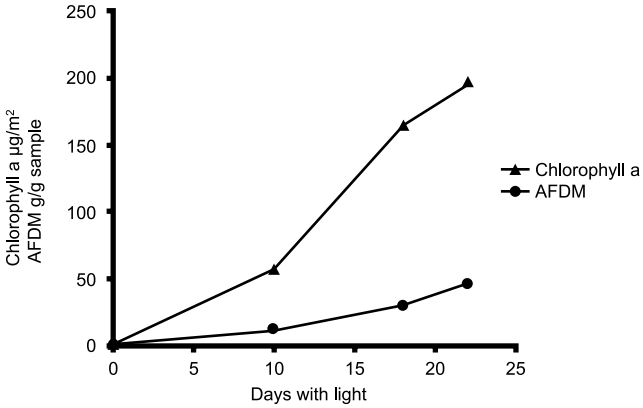

Figure 1. Benthic algal chlorophyll and ash free dry weight (AFDM) accumulation with days of light measured days 0, 10, 18, 22 of light run.

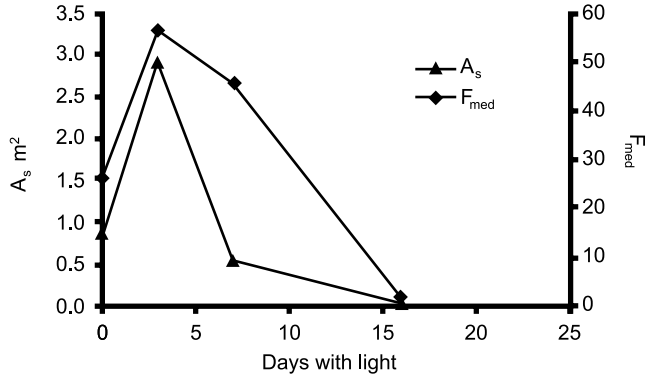

Figure 3. Volume of the transient storage zone, and F_{med} with days of light measured days 0, 3, 6, 16. The surface cross-sectional area (A) did not change over this time period.

periphyton cover in the entire channel, the amount of chlorophyll increased steeply when lights were added then the increase tapered at the end of the three week growing period (Figure 1).

4.3. Bed Permeability and Tracer Results: Light Run

[36] Bed permeability was measurably lower directly under the lights (K = 0.19 ± 0.04 SD cm s^{-1}) than in the shadowed area between lights (K = 0.27, standard deviation ± 0.09 SD cm s^{-1}). Permeability was higher in areas of low chlorophyll *a* concentrations and low AFDM on the benthic surface and lower in areas with high chlorophyll *a* and AFDM.

[37] The transient storage exchange coefficient values also varied inversely to periphyton accumulation: by 16 d after lights were turned on, α values dropped to near zero (Figure 2). Values of A_s increased during the first three days of light and periphyton growth, but then decreased after day 3. F_{med} followed this same general pattern (Figure 3).

4.4. Respiration and Metabolism

[38] Evasion values calculated from the SF_6 injections showed reaeration was negligible compared to the overall concentration of dissolved oxygen (<0.01%). Respiration, reflected in CR_{24} in the dark runs followed the same pattern as A_s/A, with highest values in the gravel alternate bar configuration and lowest in the sandy gravel plane bed configuration (Tables 3 and 4). In the light run CR_{24} (Figure 4) variability did not correspond to water temperature or nitrogen availability.

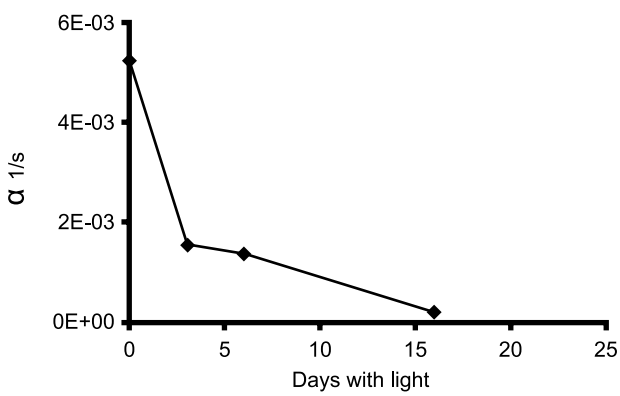

Figure 2. Exchange rate coefficient between main flow area and transient storage zone (α) with days of light measured days 0, 3, 6, 16 of light run. Transient storage here is dominated by hyporheic flow.

4.5. Phosphorus Uptake

4.5.1. Dark Run

[39] Phosphorus uptake was higher in clean gravel than sandy gravel for both bed configurations (Table 4). In fact, it was not possible to measure phosphorus uptake in sandy gravel because uptake rates were too low to change phosphorus concentrations along the length of the flume by a measureable amount. Higher phosphorus uptake rates corresponded to the treatments with higher exchange rate coefficients (i.e., high α values). But uptake rates were not different in treatments with larger A_s/A values than those with less storage area.

4.5.2. Light Run

[40] During the light run, phosphorus uptake was highest immediately after initiation of the light treatment, and tapered with time and accumulation of algal biomass, with the exception of higher uptake rates on day 19 (Figure 4). In the lab evaluations of abiotic uptake, live sediment treatment phosphorus concentrations decreased by an average of 23.4 ug PO_4-P L^{-1}, which was significantly higher than killed sediments average of 17.8 ug PO_4-P L^{-1} (t test, $p < 0.05$). If this ratio of biotic to abiotic uptake was maintained in the flume, approximately 24% of overall phosphorus retention was due to microbially mediated processes and the rest due to physical adsorption to sediment. However, phosphorus U values were showed the opposite pattern as

Table 4. Uptake Measurements for Dark Runs

	CR_{24} (g O_2 $Flume^{-1}$ d^{-1})		SRP Uptake (μg m^2 min^{-1})	
	Plane Bed	Alternate Bars	Plane Bed	Alternate Bars
Gravel	714	2867	59	69
Sandy gravel	109	1582	not measurable	not measurable

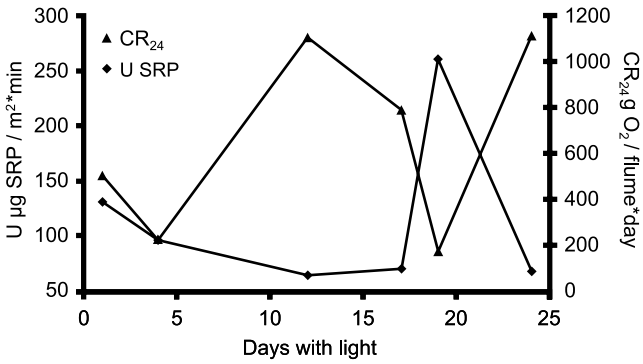

Figure 4. SRP uptake (U) with days of light paired with community respiration scaled to a 24 h period (CR_{24}) measured days 1, 4, 12, 17, 19, 24.

CR_{24} (Figure 4) suggesting there was a biotic influence on uptake.

5. Discussion

5.1. Geomorphic Influences of Transient Storage and Nutrient Uptake

[41] Transient storage measures were strongly influenced by the bed morphology we induced in the flume. The relative storage area, expressed by the ratio A_s/A increased approximately fivefold to sixfold with the change from plane bed to alternate bar morphology, whereas there was very little difference between gravel and sandy gravel runs. At the same time, the opposite response to bed morphology and bed texture was measured for the exchange coefficient (α). Exchange essentially did not change between bed morphologies but decreased by half in the sandy gravel texture when compared to the clean gravel texture. The influence of transient storage on transport time, quantified by F_{med}, increased substantially from plane bed to alternate bar morphology under both bed textures which confirms the above argument that transient storage has a larger relative effect on hydraulic transport when bed forms are present.

[42] While relative transient storage area increased with bar morphology, the total volume of water interacting with the storage zone was a function both of storage area and exchange rate. For example, in the alternate bar, clean gravel configuration the subsurface storage area could be relatively small compared to surface storage, but rapid exchange with the main flow water means a significant portion of the surface flow may pass through this part of the bed. This result is similar to observations from field settings where structure was added to streams increased the size of the transient storage zone [*Roberts et al.*, 2007]. The relationship is important to the overall control of biogeochemical processes, because sediment-water interactions can be a major determinant of nutrient retention in streams [*Mulholland and DeAngelis*, 2000].

[43] For the clean gravel runs, all of which were dark runs, phosphorus uptake was slightly higher in the alternate bar morphology than in the plane bed. Aerial uptake rate U was below the detectable threshold for our methods for both of the sandy gravel runs suggesting there was much less uptake with sand than in the clean gravel runs. Changes in bed texture and hydraulic conductivity had a stronger influence on nutrient uptake than addition of surface features, even though transient storage area and F_{med} were larger with alternate bar morphology. This suggests that the near surface hyporheic flow may be an important location for biogeochemical transformations [*Holmes et al.*, 1998; *McClain et al.*, 2003] in porous bed material where both biotic and abiotic mechanisms are active. The changes in abiotic parameters may have had a large influence on phosphorus uptake during the dark runs because the bed was fully mobilized between treatments, preventing significant biomass growth during the 2 d low-flow periods.

5.2. Biotic Influences on Transient Storage and Nutrient Uptake

[44] We observed that values of A_s and F_{med} increased initially at the same time as periphyton growth but then decreased after day 3 and eventually fell close to zero by day 16. *Battin et al.* [2003] observed similar trends in their stream side flumes. They suggest that the presence of biofilms and algal filaments increases the near bed transient storage area and reduces near bed velocities thereby leading to greater deposition of suspended sediments. We theorize that, as the biofilm mat becomes thicker and detritus clogs the interstices of the bed pores it eventually reduces hyporheic exchange and overall transient storage area (Figures 1, 2, and 3). A comparison of breakthrough curves during days 3, 6, and 16 of the light run clearly shows an increase in the mass of solute measured in the surface water by the downstream sonde over time. This increase corresponds with periphyton colonization of the bed, and suggests that as bed pore space is clogged, more solute is retained in the surface water instead of passing into the subsurface and leaving the flume as hyporheic flow. *Battin et al.* [2003] also show a decrease in A_s and exchange velocity after an initial peak, which corresponds with an overall reduction in biomass attributed to detachment and grazing. However, the decrease in transient storage area for the fully turbulent, "fast" runs (which most closely approximates our work) starts before the biomass decreases [*Battin et al.*, 2003, Figures 1d and 2a]. This observation and the fact that biomass continued to accumulate through our runs (Figure 1) suggests that pore clogging via biofilm growth and detrital accumulation may play a significant role in reducing hyporheic exchange over time.

[45] Owing to differences in water volume and travel time, dark and light runs should not be compared directly. However, change in phosphorus uptake over time was much greater during the light run than in comparisons between any of the dark runs; that is, periphyton changes were more important than channel morphology, sediment texture, and associated hydrologic changes for phosphorus uptake. Phosphorus uptake was high just after lights were turned on when biomass accumulation rate was high and there was biotic demand for phosphorus.

[46] Light run CR_{24} was on the order of values measured in streams with elevated nutrient levels [*Duff et al.*, 2008]. In the field, it has been shown that stream metabolism can have a strong influence on nutrient uptake rates [*Roberts and Mulholland*, 2007] but the expected relationship is increased uptake with increased metabolism, which is the opposite of what was seen the flume.

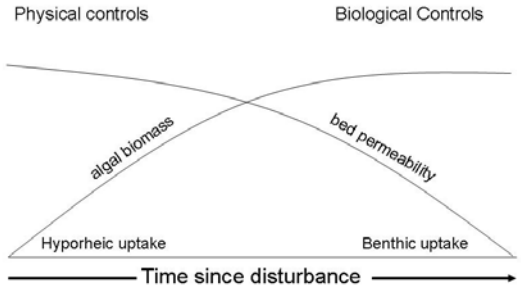

Figure 5. Conceptual model of the shift from physical to biological control of limiting nutrient uptake rates through a biological growing period following disturbance.

[47] It has been previously demonstrated that surface water-groundwater interaction and size of the hyporheic zone can increase uptake rate of limiting nutrients in streams where increasing water exchange with the hyporheic zone have more rapid nutrient cycling [*Lautz and Siegel*, 2007]. Additionally, flume studies designed to test the influence of algae on nutrient uptake have found that the growth of periphyton mats increased transient storage zones and slow water in comparison to those with limited periphyton growth. These studies demonstrate a close link between hydraulic characteristics and nutrient cycling rates [*Kim et al.*, 1990; *Mulholland et al.*, 1994; *Battin et al.*, 2003]. Applied to the field, this information shows the importance of including transient storage and biological growth in modeling stream nutrient retention [*Kim et al.*, 1992]. While these earlier experimental designs did not use a porous media substrate to model hyporheic flow or subsurface transient storage, their results support our own hypothesis that the initial increase in transient storage was due to periphyton related roughness, followed by a decrease, related to loss of hyporheic exchange due to pore clogging.

[48] We suggest that much of the transient storage in the flume was hyporheic flow during gravel dark runs and the beginning of the light run. However, there are methodological difficulties in separating the hyporheic and surface components of storage and we did not address this directly. The difference between gravel and sandy gravel exchange rate coefficients in the flume is consistent with a study of small, sand bed streams [*Stofleth et al.*, 2008] that found that water exchange with hyporheic storage zones accounted for <1% of total exchange with storage areas. In their stream, the addition of surface features did not increase the proportion of exchange with the subsurface. This supports our finding that small amount of hyporheic exchange is associated with sand bed channels and low phosphorus uptake. It suggests that hyporheic flow can be important in overall biogeochemical processing when bed material allows large exchange. This may not be the case in sand channels or clogged beds. Additionally, streambeds are often not uniformly homogenous and bed stratigraphy and armoring can significantly alter water flow paths and surface exchange [*Marion et al.*, 2008], potentially increasing or decreasing residence times [*Cardenas et al.*, 2004].

[49] The flume transient storage metrics approximated those of streams used in previous field measurements of transient storage and nutrient uptake. Compared to a compilation of 16 field studies of uptake [*Lautz and Siegel*, 2007], the flume A_s/A values were in the middle of the range for streams (0.26–1.76 compared to 0.01–128) as were F_{med} values (1.88–56.4% compared to 0.6–92.8%). Flume α values were similar to those streams for the dark runs only. At the beginning of the light run they were an order of magnitude higher than in the natural systems (52.3 * 10^{-4} s^{-1} versus the highest field measurement of 7.0 * 10^{-4} s^{-1}) and decreased to within the natural range by the end of the light run. The initial, very high, exchange rate coefficient was caused by a shallow water depth (~4 cm) compared to the deep substrate depth (~60 cm) and may have exaggerated the impact of bed clogging over the growing period compared to the average stream.

[50] Other studies have shown that fine material accumulation reduces hyporheic flow and exchange [e.g., *Rehg et al.*, 2005] and that this reduction can limit phosphorus uptake in streams [*Ryan et al.*, 2007]. Our experiments show periphyton growth alters the uptake and retention of biologically limiting nutrients and that periphyton growth itself can clog pores, as well enhance suspended sediment deposition. Also, our results demonstrate that it is possible for the decline in nutrient uptake caused by bed clogging to be offset by biological uptake if a biologically active agent such as periphyton is present.

[51] Sediment interstitial space can act as a nutrient sink [*Valett et al.*, 1994] although this capacity is limited by nutrient availability, which is a function of exchange rate and volume. Spatial variability in subsurface microbial activity has also been well documented in stream studies as well as the overall importance of discrete locations of high biological activity in stream nutrient budgets and function [*Grimm and Fisher*, 1984; *Valett et al.*, 1994; *Holmes et al.*, 1998]. Our results suggest a possible mechanism for temporal change in location of biogeochemically active areas (Figure 5) and a separation of the two main locations of nutrient uptake. Other work has referred to these areas as separate subsystems within the channel cross section [*Valett et al.*, 1996]. Here we consider that the contribution of specific benthic locations to overall biogeochemical transformations can vary in time. Specifically, high nutrient retention rates may occur in hyporheic areas at times when there is low periphyton or algal biomass accumulation, such as in a nongrowing season or immediately following bed-mobilizing floods. Over a growing season, or with time since a bed moving disturbance, or with addition of fine organic sediments, subsurface areas may become isolated from stream water source of nutrients and therefore become less important to overall nutrient budget as biomass, detrital material, and fine sediment accumulate.

[52] If periphyton growth is high enough, patches of surficial organic material could become the dominant mechanism of nutrient retention and essentially shift the location of rapid nutrient cycling from hyporheic to near surface habitats. This would also signal a shift from physical control of nutrient uptake mediated through hydrologic parameters and channel geometry, to biological control where benthic biomass accumulation, decomposition and trophic interactions become more important in determining reach-scale nutrient retention.

[53] The relation between flow regime, periphyton accumulation, bed porosity, and nutrient cycling is complex, and

there are almost certainly feedbacks between these factors. Sediment transporting flows, for example, essential clear the bed of accumulated periphyton and detritus while at the same time reconfigure the surface textural patterns and bed forms. This establishes the new habitat upon which future microbial and algal communities will develop. And those communities will, in turn, modify the physical habitat. The influence of flow dynamics on algal growth also has been documented on smaller scales [*Hondzo and Lyn*, 1999; *Hondzo and Wang*, 2002]. Other flume studies have shown biotic clogging also occurs within the bed related to labile carbon availability and preferential flow pathways in the bed [*Battin and Sengschmitt*, 1999a; *Kasahara and Hill*, 2006], which can be a function of bed surface features [*Cardenas and Wilson*, 2007; *Cardenas et al.*, 2008] and is likely to occur in natural rivers as well [*Battin and Sengschmitt*, 1999b]. Other inputs of organic matter to streams, such as leaf fall, can also complicate the relationship between transient storage and nutrient uptake because water storage parameters can be influenced through physical processes at the same time stream metabolism responds to increased carbon availability [*Argerich et al.*, 2008].

[54] More careful documentation of these interactions will improve our overall understanding of stream ecosystems, and potentially facilitate more process-based designs for restoration projects which promote favorable and sustainable ecosystem functions. Quantifying in-stream and hyporheic contributions to transient storage under different bed conditions (e.g., composition and morphology) can be used to develop predictive models for nutrient uptake under varying hydrologic conditions. Linking feedbacks between biological and physical components of this system will allow us to determine where and when morphologic drivers are most important and the circumstances where ecological and food web dynamics play a more important role.

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