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Nitrogen and phosphorus uptake in two Idaho (USA) headwater wilderness streams

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Abstract Nitrate and phosphate solutions were released into two reaches of two central Idaho streams to determine within- and between-stream variability in uptake lengths, uptake rates, and mass transfer coefficients. Physical and biotic stream characteristics and periphyton nitrate-uptake rates in recirculating chambers were measured to determine their influence on nutrient dynamics. Phosphate uptake length did not differ among the four reaches. There were no within-stream differences in nitrate uptake lengths but they did differ between the two streams. Long nitrate uptake lengths likely were due to instream concentrations above saturation but also may have been influenced by differences in active surface area and algal abundance. Nitrate and phosphate uptake lengths were longer, and uptake rates higher, than most other published values. However, mass transfer coefficients were comparable to measurements in other streams. Mass transfer coefficients may be a better parameter for temporal and spatial comparisons of instream nutrient dynamics, and for determining the underlying causes of variability in uptake length.

Key words Nitrogen · Phosphorus · Nutrient spiraling · Uptake rate and length · Stream nutrient cycling

Introduction

Nutrient dynamics in stream ecosystems often are described in terms of spiraling length (Webster and Patten 1979; Newbold et al. 1981, 1982, 1983); that is, the distance an element travels as it cycles through dissolved and organic forms. Total spiraling length is the sum of uptake length and turnover length. Uptake length and turnover length are functions of downstream transport and the transfer of nutrients from inorganic to organic form, and organic to inorganic form, respectively. Under base flow conditions uptake length appears to dominate total spiraling length (Newbold et al. 1981; Mulholland et al. 1985). Therefore, uptake length has been used as an indication of total spiraling length to describe stream nutrient dynamics (Munn and Meyer 1990; D'Angelo et al. 1991).

Uptake lengths have at least two implications in the study of stream ecosystems. First, the shorter the uptake length the more limiting the nutrient is likely to be and nutrient availability often limits other processes (Newbold et al. 1982), e.g., primary production and detrital processing (Elwood et al. 1981; Tank and Webster 1998). Second, uptake lengths are a measure of stream stability (Newbold et al. 1982; Minshall et al. 1983; D'Angelo and Webster 1991); that is, the retention of nutrients indicates maximum utilization of available resources.

The use of nutrient-uptake lengths to evaluate factors influencing nutrient dynamics requires knowledge of influencing factors (physical and biotic), the range of values expected, and their natural variability in streams. Uptake lengths are the result of both biotic and physical processes (Elwood et al. 1983; Minshall et al. 1983; Kim et al. 1992). Physically, uptake lengths are controlled by the interaction between downstream transport within the water column (nutrient flux) and the contact between the water column and active benthic compartments. Different substrata influence the interactive surface area available and the movement of water into interstitial spaces (Munn and Meyer 1988; Triska et al. 1989). This increased contact, in conjunction with biotic activity, can reduce uptake lengths (Munn and Meyer 1988, 1990).

Biotic nutrient uptake occurs through heterotrophic microbes in association with detrital organic matter, ranging in size from fine particles to logs, and by incorporation into algal biomass. Detrital uptake can be

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influenced by particle size (Mulholland et al. 1985; Corning et al. 1989; D'Angelo et al. 1991) and the nutrient status of the decomposing substrata and surrounding water (Gregory 1978). Algal uptake rates vary with nutrient availability, light (Tischner and Lorenzen 1979; Triska et al. 1983, 1989), water velocity (Whitford and Schumacher 1961; Humphrey and Stevenson 1992), community development (Triska et al. 1983; Mulholland et al. 1985, 1994; Grimm 1987), and temperature (Corning et al. 1989; D'Angelo et al. 1991; Garbisu et al. 1992). The relative importance of autotrophic versus heterotrophic uptake varies among streams. Phosphorus uptake lengths in low-order forested streams are strongly influenced by benthic organic matter (Newbold et al. 1983; Mulholland et al. 1985). However, algal uptake dominated nitrogen dynamics in a third-order Oregon stream (Triska et al. 1983) and has a strong influence on nitrogen retention in the desert Southwest (Grimm 1987).

The purpose of this study was to facilitate the use of uptake parameters as a means to evaluate factors influencing nutrient dynamics by obtaining comparable measurements of nitrogen and phosphorus uptake parameters in wilderness streams of the Intermountain Region of the Western United States. In addition, potential factors that could cause variability in these parameters within and among similar streams and among those reported elsewhere were investigated.

Methods

Uptake parameters were evaluated in two reaches within each of two separate streams, located in the Frank Church River of No Return Wilderness Area in central Idaho. These two streams were selected because while they are both of similar size and within the same ecoregion, drainage level differences in aspect, geology, and fire history have resulted in dissimilarities in solar radiation, hydrology, and water chemistry. These physical changes influence water temperatures, substratum size distribution, and primary production. Therefore, these two streams provided a means to evaluate the variability in uptake parameters within an ecoregion and investigate some of the physical and biotic factors that influence nutrient dynamics.

Reaches of approximately 300 m in length were located on two second-order streams, Pioneer Creek, of northern aspect, and Cliff Creek, a south-facing stream. The mouths of the streams are within a few hundred meters of each other and flow into Big Creek, a tributary to the Middle Fork of the Salmon River, located in Central Idaho (United States). Both streams are subject to similar climatic conditions. Most annual precipitation occurs as snowfall during winter (Finklin 1988), resulting in streams characterized by high spring and low summer discharge. Both streams drain similar-sized basins of 17 km^2 and 19 km^2 for Pioneer and Cliff, respectively.

The combination of southern aspect and a loss of forest cover in the upper portions of the drainage, due to a forest fire in 1988, give Cliff Creek more extreme variations in discharge with season. For example, discharge in Cliff Creek decreased from 891 l s^{-1} in April to 83 l s^{-1} at the time of this study in August compared to a decrease from 197 l s^{-1} to 88 l s^{-1} in Pioneer Creek.

The difference in aspect also results in slight differences in temperature, which ranged from 8.5 to 13°C and 7.4 to 12°C in Cliff and Pioneer Creeks, respectively, during the release experiment. Although similar in general climate and size, these two streams have distinct geologies. Cliff Creek flows over igneous rock of the Idaho Batholith whereas Pioneer Creek flows over metamorphic quartz. Geological differences, in addition to the previous fire, result in dissimilar stream water nutrient concentrations. At the time of this study, nitrate-N and phosphate-P concentrations were an order of magnitude higher in Cliff Creek than in Pioneer Creek (Table 1).

Short-term solute injections of nitrate and phosphate were used to determine uptake lengths. The solute injection method has been shown to increase estimates of uptake length due the disproportional relationship between uptake rate and concentration, and the remineralization of nutrients (Mulholland 1996). The use of radiotracers is preferable but was not suitable for use in a designated wilderness area. The potential errors associated with solute injections were minimized by limiting the duration of injections (90 min) and limiting the increase of nutrients above ambient levels during injections (1.6–5 times background). Short-term injections should reduce the errors associated with cellular release and remineralization of organically bound nutrients (Mulholland 1996). The use of nitrate also should reduce remineralization errors due to the additional nitrification required to convert ammonium to nitrate. The effects of disproportional uptake rates relative to concentrations can be minimized by reducing the difference between ambient nutrient concentrations and concentrations during the injection. The increase in injection concentrations was within the range reported in similar studies (Munn and Meyer 1990; D'Angelo and Webster 1991; Marti and Sabater 1996).

Benthic organisms preferentially take up ammonium over nitrate due to the inhibition of cellular transport and reduced energy associated with nitrate reduction. Ammonium has been shown to inhibit nitrate uptake by laboratory cultures of algae and bacteria (Tischner and Lorenzen 1979; Garbisu et al. 1992). Field studies also have supported the preferential uptake of ammonium (Stanley and Hobbie 1981; Grimm and Fisher 1986). However, nitrate was used in this study because concentrations were an order of magnitude greater than ammonium and, therefore, may more closely

Table 1 Mean stream width, depth, and velocity for the four study reaches, with discharge and background nutrient concentrations for Pioneer and Cliff Creeks

	Pioneer Creek		Cliff Creek	
	PR1	PR2	CR1	CR2
Mean width (m)	1.94	1.98	2.00	1.99
Mean depth (m)	0.157	0.177	0.175	0.170
Mean velocity (m s^{-1})	0.29	0.25	0.24	0.25
Discharge (l s^{-1})	88		83.3	
NO_3-N (mg l^{-1})	0.052		0.330	
NH_4-N (mg l^{-1})	0.005		0.010	
PO_4-P (mg l^{-1})	0.005		0.012	
Specific conductivity (μS cm^{-1})[a]	114.0		78.9	
Alkalinity (mg $CaCO_3$ l^{-1})[a]	50.62		35.44	

[a] Measured in July 1994

approximate total nitrogen dynamics. In addition, the influences of biotic and physical factors on nitrate uptake are expected to be comparable within these and among other streams.

On 2 August 1994, a solution of 11.02 g NO_3-N l^{-1}, 1.22 g PO_4-P l^{-1}, and 159.12 g Cl l^{-1}, was continuously dripped into the upstream end of the lower Pioneer reach (PR2) at a rate of 50 ml min^{-1} for 90 min, using a 12-V DC metering pump. Water samples were collected at seven transects below the injection point every 10 min throughout the injection. The first transect was separated from the injection point by a mixing zone caused by a small waterfall. The remaining six transects were located approximately 25, 75, 150, 200, 250, and 300 m below transect 1. Background nitrate-N, ammonium-N, phosphate-P, and chloride concentrations were determined from four water samples collected at 30-min intervals above the injection point. Water samples were returned to an adjacent field station, filtered (0.45 μm pore size), and preserved (phosphorus samples were frozen and nitrate samples acidified with 2 ml concentrated H_2SO_4 l^{-1} and frozen (APHA 1989). Nitrate-N was analyzed by the automated (Alpkem) cadmium reduction method, phosphate-P by the ascorbic acid method (Beckman DB-G Spectrophotometer), and chloride by ion-specific chromatography (APHA 1989).

The second reach in Pioneer Creek (PR1) was directly upstream of PR2. Approximately 2 h after the conclusion of the injection at PR2, identical injection procedures were used at PR1.

The following day, similar methods were used in the downstream (CR2) and upstream (CR1) reaches of Cliff Creek. For both reaches in Cliff Creek the injectate concentration was 30.89 g NO_3-N l^{-1}, 1.31 g PO_4-P l^{-1}, and 182.95 g Cl l^{-1}.

At 20-m intervals stream morphometry, flow type, dominant substrata, the presence of large woody debris, and debris dams, were evaluated following the injections. Stream morphometry was determined by measuring stream width and five water depths across the stream. Flow type was qualitatively described, as either pool, rapid, riffle, or run. The dominant substrata were qualitatively described as boulder, cobble, pebble, gravel, sand, or a combination of two or more of these size classes. All occurrences of large woody debris and debris dams were noted.

Periphyton biomass within each reach was evaluated by scraping 3.13 cm^2 of algae off of three stones between each transect. Periphyton samples were filtered in the field (pre-ashed Whatman GF/C), and filters were frozen and stored in the dark until analyzed for chlorophyll-*a* (chl-*a*) and ash free dry mass (AFDM) within 1 week following collection. Chl-*a* was determined by the methods outlined in APHA (1989) modified by using methanol as the extracting solvent. AFDM was determined gravimetrically (dried at 80°C for 48 h or longer, weighed, ashed at 450°C for at least 3 h, cooled to room temperature in a desiccator and reweighed) (APHA 1989).

Benthic organic matter (BOM) was collected by disrupting 932.8 cm^2 of the stream bed at five locations in each stream and collecting the dislodged organic matter in a Surber sampler (250 μm mesh). Organic matter samples were preserved in the field with 4% formalin, returned to the laboratory, and separated into coarse and fine fractions. Coarse particulate organic matter (CPOM) consisted of particles retained in a 1-mm sieve, and fine particulate organic matter (FPOM) consisted of the remainder of the sample. AFDM of the coarse and fine fractions was determined gravimetrically as described previously.

Nutrient releases in Pioneer Creek increased nitrate-N concentrations from 0.05 to 0.23 mg l^{-1} and phosphate-P concentrations from 0.005 to 0.025 mg l^{-1}. This 4.6- to 5-fold increase maintained background N:P ratios. Calculated uptake parameters were based on the assumption that nutrient uptake would remain proportional at plateau concentrations. That is, the mass transfer coefficient, v_i (v_i = uptake rate/concentration; Stream Solute Workshop 1990), at background concentrations was equal to v_i at plateau concentrations. Based on this assumption, uptake length (S_w) was calculated by regressing the natural log of observed/expected concentrations against distance downstream (Fig. 1). The negative reciprocal of this straight-line slope is uptake length in meters (Newbold et al. 1983; Stream Solute Workshop 1990; Hart et al. 1992). Expected concentrations at distance x were determined as the product of plateau concentrations at transect 1 and the portion of chloride remaining at x distance downstream [$C_x = C_0(Cl_x/Cl_0)$].

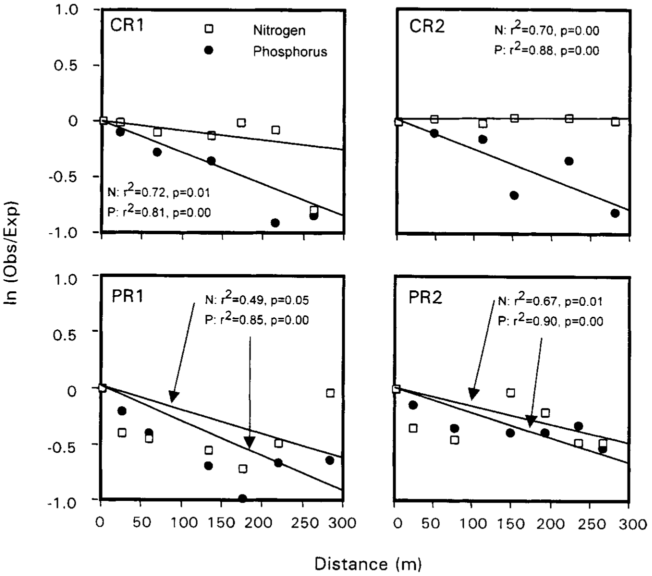

Fig. 1 Results from nutrient release experiments showing the similarity among all four phosphate slopes and the within-stream similarity and between-stream differences in nitrate removal

In Cliff Creek, injections increased nitrate-N concentrations from 0.33 to 0.52 mg NO_3-N l^{-1} and phosphate-P from 0.012 to 0.190 mg PO_4-P l^{-1} (1.6 times background). At these relatively high nutrient concentrations it was assumed that increases in nutrient concentrations would not result in increased uptake rates. That is, uptake would remain constant while concentrations increased. Uptake length, calculated at plateau observed/expected ratios, would therefore result in erroneously high values. To account for this, corrected observed concentrations were determined by subtracting the difference between observed and expected concentrations, at plateau, from background stream water concentrations. Expected concentrations were calculated by multiplying background stream water concentrations by the portion of chloride remaining at a given transect. These corrected observed and expected values were then used to determine S_w as above. Use of these corrected values should reflect uptake occurring at background concentrations.

The slopes of the regression equations, for each element independently and from all four reaches, were tested for significant differences by analysis of covariance (Zar 1984). If the slopes were not significantly different, a common regression coefficient was calculated, and uptake length was calculated from the common regression slope. Confidence intervals (CI) (95%) were determined for each slope.

The mass transfer coefficient, v_i, was calculated from the relationship to uptake length (Stream Solute Workshop 1990) where:

$$v_i = vd/S_w$$

and v = velocity (m s^{-1}), d = mean stream depth (m), S_w = uptake length (m), and v_i is in units of m s^{-1}. Uptake rate (mg m^{-2} s^{-1}) was calculated as v_i times background nutrient concentrations (mg m^{-3}). The mass transfer coefficient also equals uptake rate divided by nutrient concentration; therefore, in this study, we refer to v_i as uptake efficiency.

Periphyton nitrogen uptake rates were measured in recirculating chambers. Artificial substrata (unglazed ceramic tiles) were placed in Pioneer and Cliff Creeks on 2 July 1994. On 1 August 1994, the substrata, now colonized by algae, were placed within clear Plexiglas recirculating chambers. The chambers were filled with stream water (1.88 l total volume) and incubated for 4 h. Pre- and post-incubation water samples were used to determine nitrate uptake rates. Water samples were filtered, preserved, and analyzed as above. Nitrate uptake rates were calculated as the change in concentration times chamber volume and divided by substratum surface area.

Results

Substratum and flow types differed between the two streams. The predominant substratum type in Cliff Creek was boulder, which covered 42–46% of the stream bed. Boulders in combination with cobble described 80–85% of the stream bed surface area. In Pioneer Creek, boulders contributed only 14–18% of the total substratum, with the remainder evenly distributed among size classes equal to and smaller than cobbles. The smaller substratum size distribution in Pioneer increased the total surface area. Increases in total surface area due to particle size distribution were calculated based on spherical geometry, diameters of 25.6 cm for boulders, 6.4 cm for cobbles, 0.4 cm for pebbles and 0.2 cm for gravel, assuming that half of the substratum surface area was exposed. Based on these calculations, for every 1 m^2 of stream surface there was 31 m^2 of substratum surface area in Pioneer Creek and 26 m^2 of substratum surface area in Cliff Creek.

Pools occurred in higher proportion in the boulder-dominated Cliff than in Pioneer Creek, describing 17–22% and 6–10% of the flow types, respectively. Plunge pools were the commonest pool type, in both streams, and were not sites of high organic matter accumulation. Riffles were the predominant flow type in Cliff (60–63%) and rapids in Pioneer (53–55%). Based on the time for the chloride tracer to reach half of plateau concentrations at the downstream transect of each section, water velocities were 0.29 m s^{-1} for PR1, 0.28 m s^{-1} for PR2, 0.24 m s^{-1} for CR1, and 0.27 m s^{-1} for CR2.

Within Pioneer Creek, boulders and riffles were slightly more common in the upstream reach (PR1) with sand and pools occurring more often in the downstream reach (PR2). Within Cliff Creek, riffles and sand were common in CR1 and pools and gravel more abundant in CR2. Mean ratios of width to depth were slightly different among the four reaches; however, differences were not significant.

Chl-*a* values were significantly higher in Pioneer than Cliff Creek (*t*-test, $P = 0.001$, $n = 79$; Table 2). Differences in periphyton AFDM between the two streams were not significant (*t*-test, $P = 0.086$). There were no significant differences in periphyton chl-*a* or AFDM between the two sections of Pioneer Creek or the two sections of Cliff Creek. Within Cliff Creek, chl-*a* values were higher in the lower reach at 5.71 mg m^{-2} compared to 4.45 mg m^{-2} in the upper section. There were no significant differences in FPOM, CPOM, or total benthic organic matter between the two streams (*t*-test, $P > 0.88$ for all comparisons). Large woody debris (LWD) and debris dams were sparse in both streams.

Nitrate uptake length was significantly shorter in Pioneer than Cliff Creek ($P < 0.05$). Within-stream differences, however, were not significant. The uptake length of nitrate in Pioneer Creek, from the common regression, was 549 m, with a 95% confidence range of 279–1603 (Table 3). The large confidence range represents only extremely small differences in the slope of the regression line. Nitrate uptake length in Cliff Creek was 1839 m with a 95% confidence interval from 865 m to infinity. Uptake rates were higher in Cliff Creek (450 μg m^{-2} min^{-1}) than Pioneer Creek (255 μg m^{-2} min^{-1}). Although uptake rates were higher, uptake efficiency (v_i) was lower in Cliff than in Pioneer Creek, at values of 2.3 and 8.2×10^{-5} m s^{-1}, respectively.

There were no significant differences in phosphate uptake lengths between, or within, these two streams. Phosphate uptake length, from the common regression, was 370 m with a 95% confidence interval of 272–579 m. Uptake rates of phosphate were higher in Cliff Creek at 81 μg m^{-2} min^{-1} compared to 36 μg m^{-2} min^{-1} in Pioneer Creek. Uptake efficiency was similar at 11.3×10^{-5} m s^{-1} in Cliff Creek and 12.1×10^{-5} m s^{-1} in Pioneer.

Instream nitrogen-to-phosphorus ratios have been used to estimate potential nutrient limitation based on the relative requirements of autotrophic and heterotrophic communities for these two elements. Ratios of nitrate to phosphate uptake rates, derived from whole-stream releases, should estimate the relative element

Table 2 Values of biotic measurements of periphyton chlorophyll-*a* (*chl-a*), periphyton ash free dry mass (*AFDM*), coarse particulate organic matter (*CPOM*), fine particulate organic matter (*FPOM*), large woody debris (*LWD*), and debris dams

	Pioneer Creek		Cliff Creek	
	PR1	PR2	CR1	CR2
Periphyton				
Chl-*a* (mg m^{-2})	9.18		5.01	
AFDM (g m^{-2})	2.62		2.20	
Benthic organic matter				
CPOM (g m^{-2})	30.7		28.5	
FPOM (g m^{-2})	2.5		2.5	
Total (g m^{-2})	33.3		31.0	
LWD (count)	6	6	4	12
Debris dams (count)	1	6	1	0

Table 3 Uptake parameters from the two study streams (S_w uptake length, v_i mass transfer coefficient, U area-specific uptake rate)

Uptake parameter	Pioneer Value	95% CI	Cliff Value	95% CI
S_w (m)				
PO_4-P	370	272–579	370	272–579
NO_3-N	549	279–1603	1839	865-∞
U ($\mu g\ m^{-2}\ min^{-1}$)				
PO_4-P	36	23–50	81	52–111
NO_3-N	255	87–502	450	0–956
$v_i \times 10^{-5}$ ($m\ s^{-1}$)				
PO_4-P	12.1	7.8–16.5	11.3	7.2–15.4
NO_3-N	8.2	2.8–16.1	2.3	0–4.8
Uptake ratio				
NO_3-N:PO_4-P	15.5		12.2	

requirements at the stream ecosystem level. N:P uptake ratios were 15.5 in Pioneer Creek and 12.2 in Cliff Creek.

Periphyton mean nitrate uptake rates were higher in Pioneer Creek at 42.6 $\mu g\ m^{-2}\ min^{-1}$ compared to 19.7 $\mu g\ m^{-2}\ min^{-1}$ in Cliff Creek. Therefore, periphyton-nitrogen uptake rates were 17% of the total uptake rates in Pioneer but only 4.4% in Cliff Creek. Differences are even greater for mass transfer coefficients, with 13-fold greater values in Pioneer, at $1.2 \times 10^{-5}\ m\ s^{-1}$ to only $0.10 \times 10^{-5}\ m\ s^{-1}$ in Cliff Creek. Uptake efficiency was lower than the mean reach-level values for both streams.

Because between-stream phosphate uptake lengths were not significantly different and because physical habitat characteristics, flow types and substratum size were dissimilar, these characteristics probably had little influence on phosphorus dynamics in the two streams. Biotic components, LWD and debris dams, BOM, and periphyton AFDM were similar between the two streams and, therefore, could be responsible for similar phosphorus uptake lengths.

The large differences in nitrate uptake lengths allow comparison of the relative effects of substratum and flow types. Substratum-weighted nitrate uptake lengths were very different for the larger size classes, boulder and cobble. For example, habitat-specific uptake lengths for boulders were 140 and 808 m in Pioneer and Cliff Creeks, respectively. Conversely, substratum-weighted uptake lengths for the smaller particle sizes were similar at 249 and 175 m, for pebble and gravel combined. Flow-weighted uptake lengths for segments classified as runs were similar, while flow-weighted uptake lengths for segments classified as pools and riffles were dissimilar.

Discussion

These two streams are similar in their ability to retain phosphate, but nitrate is lost much more rapidly from Cliff Creek than Pioneer. If flow and substratum types were the cause of the differences in nitrate uptake lengths, then flow or substratum-weighted uptake lengths should be similar between the two streams. This suggests that pebble/gravel-sized substratum and runs influenced nitrate uptake lengths but boulder/cobble substratum and pools/riffle flow types did not. That is, nitrate uptake lengths were long in Cliff Creek due to the limited amount of substratum in the pebble/cobble size class and the small portion of the stream flowing as a run.

The greater surface area and periphyton biomass in Pioneer Creek may have increased nitrate retention in that stream. The smaller substratum size distribution in Pioneer Creek increased total surface area for periphyton attachment and periphyton chl-*a* values were higher in Pioneer Creek than in Cliff Creek. Periphyton nitrate uptake rates (standardized by area) were greater in Pioneer Creek. Therefore, it is possible that the greater surface area and higher algal component of the periphyton communities resulted in shorter uptake lengths of nitrate in Pioneer Creek. In addition, patches of bryophytes were common in Pioneer Creek and, while not excluded from periphyton sampling, bryophyte abundance was not directly quantified. Munn and Meyer (1990) attributed high nitrate retention on rock outcrops to moss communities; therefore, uptake by mosses also may have increased nitrogen retention in Pioneer Creek.

In addition to the potential biotic influence on nitrate retention in Pioneer Creek, the large differences in uptake lengths could have been the result of high concentrations in Cliff Creek. Nutrient uptake lengths are assumed to remain relatively stable until biotic uptake approaches saturation (Stream Solute Workshop 1990); at this point, uptake lengths should increase rapidly. Stream periphyton have been shown to be limited by nitrogen at concentrations below 0.10 $mg\ l^{-1}$ (Lohman et al. 1991) or 0.055 $mg\ l^{-1}$ (Grimm and Fisher 1986). Periphyton therefore should be saturated at concentrations above 0.10 $mg\ l^{-1}$. Saturation values for heterotrophic organisms are not known and may vary with the nutrient status of the detrital material. However, assuming similar whole-stream saturation values, Cliff Creek nitrogen concentrations were well above saturation prior to the injection (0.33 mg NO_3-N l^{-1}). This would account for the much lower values of v_i. If nitrogen uptake rates were saturated at some concentration near 0.10 mg l^{-1}, v_i would decrease rapidly as dissolved nitrogen concentrations increased above this value (Fig. 2). As v_i decreases, uptake lengths increase proportionately. Using the measured value of v_i in Cliff Creek, we can calculate what nitrate uptake lengths would be if stream water concentrations were at 0.10 mg NO_3-N l^{-1} (assumed saturation). Nitrate uptake lengths at this concentration would be 557 m, very close to the uptake length measured in Pioneer Creek (549 m) at stream water concentrations of 0.052 mg l^{-1}. From this we hypothesize that these two streams are saturated by nitrogen at concentrations between 0.05 and 0.10 mg l^{-1}, with dissolved concentrations in Pioneer Creek slightly below and in Cliff Creek substantially above saturation.

The similarity between nitrate uptake lengths measured in Pioneer and calculated for assumed saturation in Cliff suggests that, like phosphate, biotic similarities and not physical habitat differences, controlled nutrient retention. Periphyton biomass was slightly higher in Pioneer Creek than the upper reach of Cliff, but values in both streams were low. BOM biomass was the same in both streams and much higher than periphyton values. BOM has been shown to have a large influence on phosphorus retention in shaded deciduous forest streams (Mulholland et al. 1985; Newbold et al. 1983). The low portion of algal biomass to BOM and the small ratio of periphyton nitrate uptake to reach level values, suggest uptake is dominated by BOM in these streams as well. Large woody debris was sparse but occurred in similar quantities in Cliff and Pioneer Creeks. Although woody debris has been shown to be an active site for nitrogen and phosphorus uptake (Aumen et al. 1990; Munn and Meyer 1990), the slight differences would not be expected to exert a differential influence on nutrient dynamics in these two streams.

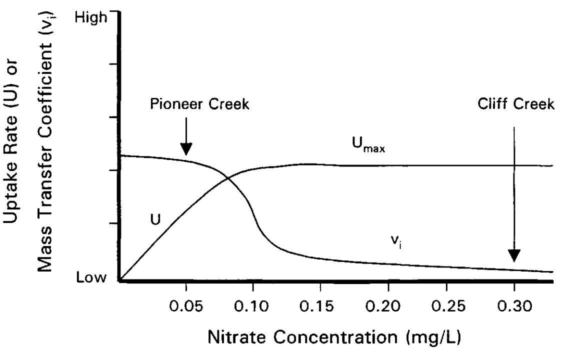

Fig. 2 Hypothetical relationship between nitrogen concentration (mg l^{-1}), uptake rate (U), and mass transfer coefficient (v_i). The initial slope of the uptake/concentration curve is less than one, so v_i decreases gradually. As uptake approaches saturation, v_i decreases rapidly, which would result in a rapid increase in uptake lengths. *Arrows* show instream nutrient concentrations in Pioneer and Cliff Creek and their relationship to the v_i curve. Enhanced nitrogen uptake, due, e.g., to light or temperature, would result in v_i values above this hypothetical line, and reduced uptake due to phosphorus or light limitation would result in values below the line

Instream phosphorus concentrations also were higher in Cliff Creek than Pioneer, at 0.012 and 0.005 mg l^{-1}, respectively. Following the same logic used above, increasing phosphorus concentrations should increase uptake length if v_i is reduced due to concentrations exceeding saturation. The thin periphyton communities observed in this study are likely to become saturated at phosphorus concentrations near 0.006 mg l^{-1} (Mulholland et al. 1990; Bothwell 1989). However, phosphorus uptake can continue above this concentration either as a result of diffusion limitation (Bothwell 1989; Mulholland et al. 1994), luxury uptake, or adsorption (Fig. 3), but not proportionally (Mulholland et al. 1990; Hart et al. 1992). If uptake continued above saturation, v_i would decrease slightly with concentrations increasing from 0.005 to 0.012 mg l^{-1} and uptake lengths would vary little. The similar mass-transfer coefficients measured in these two streams support this conclusion. The lower N:P uptake ratio in Cliff Creek compared to Pioneer also shows phosphorus uptake was proportionally greater in Cliff Creek.

While nutrient spiraling lengths provide a useful index for comparing total nutrient retention between streams, the strong effect of velocity and depth may obscure more subtle biotic and physical influences. Uptake lengths would be expected to increase with increasing discharge (Newbold et al. 1981; Hart et al. 1992), or water velocity (Meyer 1979; Bencala et al. 1993; D'Angelo and Webster 1991), and can be demonstrated by analysis of equations relating uptake length to velocity and depth, where uptake length, $S_w = (vd/v_i)$, and v = stream velocity, d = stream depth, and v_i = mass transfer coefficient (Stream Solute Workshop 1990). As can be seen if v_i remains constant, uptake length increases with the product of velocity and depth. Hart et al. (1992) suggested uptake lengths standardized by discharge would facilitate comparisons between streams with dissimilar flows. However, uptake

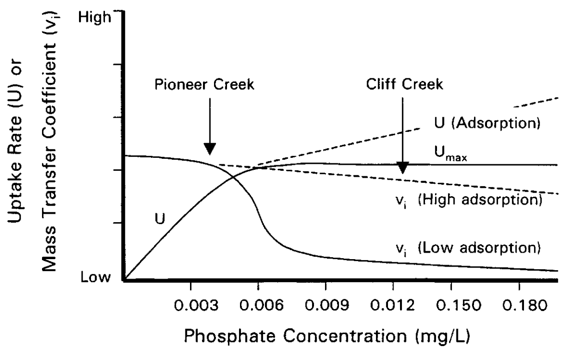

Fig. 3 Hypothetical relationship between phosphorus uptake rate (U), concentration (mg l^{-1}), and v_i. As concentration initially increases, v_i decreases gradually. Above phosphorus saturation concentrations, biotic uptake rates reach a maximum but abiotic uptake can continue. Under high abiotic adsorption v_i decreases gradually and under low abiotic adsorption v_i decreases rapidly

length standardized by discharge is equal to the product of nutrient concentration divided by uptake rate and stream width, or v_i^{-1} and width. Therefore, v_i is equal to the product of velocity and stream depth divided by uptake length. To reduce the variability associated with water velocity and stream depth and because elemental uptake rates vary with concentration, v_i may be a better parameter than uptake lengths or uptake rates for comparisons among streams, and for determining the underlying physical and biotic factors influencing nutrient retention.

The uptake length of nitrate in an Oregon stream with instream concentrations below saturation, was 42 m (Munn and Meyer 1990). This is considerably shorter than the nitrate uptake length of 549 m measured in Pioneer Creek with concentrations estimated to be at or slightly below saturation. However, the nitrogen mass transfer coefficient in the Oregon Stream (published uptake rate and concentration values), 9.9×10^{-5} m s^{-1}, was slightly higher than, but very comparable to the value of 8.2×10^{-5} m s^{-1} measured in Pioneer Creek. The slightly higher mass transfer coefficient for the Oregon stream relative to Pioneer Creek is consistent with the relationship outlined in Fig. 2; that is, more efficient uptake at lower concentrations. Similarly, the nitrate mass transfer coefficient of 1.2×10^{-5} m s^{-1} (estimated from published uptake rate and concentration) in a North Carolina stream limited by phosphorus (Munn and Meyer 1990) is very close to the 2.3×10^{-5} m s^{-1} measured in Cliff Creek where nitrogen uptake likely was saturated. Uptake lengths varied largely between these two streams at 689 m in the North Carolina stream and 1839 m in Cliff Creek. Therefore, the differences in nitrate uptake lengths between Pioneer Creek and the Oregon stream, and Cliff Creek and the North Carolina stream are primarily due to differences in water velocity and stream depth.

Nitrate uptake efficiency was slightly higher in Pioneer Creek and lower in Cliff Creek when compared with an undisturbed Mediterranean stream. Although nitrate uptake lengths were shorter (154–168 m) in this stream (La Solana) (Marti and Sabater 1996), mass transfer coefficients (4.13 and 3.79×10^{-5} m s^{-1}, estimated from uptake lengths and mean annual water velocity and depth) were between the values measured in these two Rocky mountain streams. The Mediterranean stream has been shown to be limited by phosphorus (Guasch et al. 1995) and mean annual instream nitrate-N concentrations are higher than Pioneer Creek. Therefore, mass transfer coefficients lower than those observed in Pioneer Creek are expected. Nitrate uptake in Cliff Creek and estimated in the Mediterranean stream (411–449 μg m^{-2} min^{-1}) were similar (and likely near saturation). Therefore, the differences in mass transfer coefficients are the result of instream water concentrations and are consistent with the hypothetical relationship shown in Fig. 2. Although nitrate mass transfer coefficients were similar, ammonium uptake efficiency was slightly higher in the Mediterranean stream (7.30 to 11.6×10^{-5} m s^{-1}) when compared with nitrate from either region.

Periphyton nitrate uptake efficiency was comparable with other studies but was considerably less than whole-stream values. The mass transfer coefficients for periphyton in a nitrogen-limited stream in the southwestern United States (3.6–4.0×10^{-5} m s^{-1}) (estimated from published nitrate uptake rate and concentration, experiment 3, Grimm and Fisher 1986). These values are higher than those measured for periphyton in Pioneer Creek and are probably due to differences in periphyton biomass as indicated by chl-*a* (roughly 40 mg m^{-2} compared to 9 mg m^{-2} in Pioneer Creek). The high periphyton mass transfer coefficient for the southwestern stream is roughly half of that measured in whole-stream studies, suggesting that nitrate uptake by detrital microbial activity is more efficient than uptake by periphyton communities. This supports the high nitrate retention associated with benthic organic matter accumulations reported previously (Aumen et al. 1990; Munn and Meyer 1990).

Phosphorus uptake lengths (370 m) for the Idaho streams were longer than most published values. Phosphorus uptake length measured using radiotracers ranged from 21 to 164 m in a small Tennessee stream (Mulholland et al. 1985, 1990). Uptake lengths from solute injection studies have generally been below 200 m (Hart et al. 1992; Mulholland et al. 1990; Munn and Meyer 1990; Marti and Sabater 1996). Comparisons of mass transfer coefficients, however, indicate that phosphate retention, during short-term injections, is greater in these two Idaho streams than most other previously investigated sites.

The high phosphate uptake efficiency in Pioneer and Cliff Creeks (11.3–12.1×10^{-5} m s^{-1}) is likely due to both biotic uptake and abiotic adsorption, with biotic uptake dominating in Pioneer Creek and abiotic adsorption controlling phosphate retention in Cliff Creek. Mass transfer coefficients, estimated from solute injections conducted by Mulholland et al. (1990), declined from 2.0×10^{-5} m s^{-1} to 0.69×10^{-5} m s^{-1} as phosphate-P concentrations increased from 12 to 163 μg l^{-1}. These authors hypothesized that as concentrations of phosphorus exceeded 5 μg l^{-1}, uptake due to adsorption continued but was not proportional to concentration changes. The estimated phosphate mass transfer coefficient for the nitrogen limited Oregon stream was similar to these low values at 0.18×10^{-5} m s^{-1} and abiotic sorption was found to be minimal at ambient phosphate-P concentrations (Munn and Meyer 1990). In contrast, while mass transfer coefficients showed a similar decline in an Australian stream with increasing injectate concentrations, abiotic adsorption was significant, and values were considerably higher (4.50–7.10×10^{-5} m s^{-1}) (Hart et al. 1992). High phosphate mass transfer coefficients (9.24–18.3×10^{-5} m s^{-1}) also were estimated from data presented for two Mediterranean streams (Marti and Sabater 1996). The authors postulated that, at least seasonally, co-precipitation with calcium carbonate might be the cause of high phosphate retention. The differences between the low and high mass transfer coefficients, therefore, may be due to differences in abiotic adsorption (Fig. 3). Based upon this premise, the high phosphate mass transfer coefficients measured in the two steams of this study likely are due to high abiotic adsorption; however, the low instream phosphate-P concentrations and higher N:P uptake ratios in Pioneer Creek suggest that biotic uptake may play a larger role in phosphate retention in comparison to Cliff Creek.

In conclusion, this study showed that while differences in substratum size distribution along with differences in periphyton biomass and nitrate uptake influenced retention, instream nitrate concentrations were the primary cause of differences in uptake lengths and mass transfer coefficients. The similarity in phosphate uptake lengths and mass transfer coefficients under widely divergent instream concentrations indicated that different processes controlled phosphorus dynamics. Comparisons with other studies suggest that abiotic adsorption may play a large role in phosphate retention. Further studies investigating the role of physicochemical processes in phosphorus dynamics are warranted. Mass transfer coefficients are a better parameter than uptake lengths for comparing streams that differ in water velocity, depth, and nutrient concentrations. Their inclusion in future analyses should further our understanding of the underlying factors affecting nutrient dynamics in stream ecosystems.

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