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N uptake as a function of concentration in streams

WALTER K. DODDS[1,15,16], AMANDA J. LÓPEZ[1], WILLIAM B. BOWDEN[2],
STAN GREGORY[3], NANCY B. GRIMM[4], STEPHEN K. HAMILTON[5],
ANNE E. HERSHEY[6], EUGENIA MARTÍ[7], WILLIAM H. MCDOWELL[8],
JUDY L. MEYER[9], DONNA MORRALL[10], PATRICK J. MULHOLLAND[11],
BRUCE J. PETERSON[12], JENNIFER L. TANK[13], H. MAURICE VALETT[14],
JACKSON R. WEBSTER[14], AND WILFRED WOLLHEIM[12]

[1]*Division of Biology, Ackert Hall, Kansas State University, Manhattan, Kansas 66506 USA*
[2]*Landcare Research, PO Box 69, Lincoln 8152, New Zealand*
[3]*Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331 USA*
[4]*Department of Zoology, Arizona State University, Tempe, Arizona 85287-1501 USA*
[5]*Kellogg Biological Station, 3700 E. Gull Lake Dr., Hickory Corners, Michigan 49060 USA*
[6]*Department of Biology, University of North Carolina Greensboro, Greensboro, North Carolina 27402 USA*
[7]*Centre d'Estudis Avancats deBlanes, Cami de Sta. Barabara s/n, 17300 Blances, Girona, Spain*
[8]*Department of Natural Resources, James Hall, University of New Hampshire,*
Durham, New Hampshire 03824 USA
[9]*Institute of Ecology, University of Georgia, Athens, Georgia 30602-2602 USA*
[10]*The Proctor and Gamble Company, Experimental Stream Facility, 1003 Route 50,*
Milford, Ohio 45150 USA
[11]*Environmental Science Division, Oak Ridge National Laboratory, P.O. Box 2008,*
Oak Ridge, Tennessee 37831-6036 USA
[12]*Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts 02543 USA*
[13]*Department of Biological Sciences, University of Notre Dame, Notre Dame, Indiana 46556-0396 USA*
[14]*Department of Biology, Virginia Polytechnic Institute and State University,*
Blacksburg, Virgina 24061 USA

Abstract. Detailed studies of stream N uptake were conducted in a prairie reach and gallery forest reach of Kings Creek on the Konza Prairie Biological Station. Nutrient uptake rates were measured with multiple short-term enrichments of NO_3^- and NH_4^+ at constant addition rates in the spring and summer of 1998. NH_4^+ uptake was also measured with $^{15}N\text{-}NH_4^+$ tracer additions and short-term unlabeled NH_4^+ additions at 12 stream sites across North America. Concurrent addition of a conservative tracer was used to account for dilution in all experiments. NH_4^+ uptake rate per unit area (U_t) was positively correlated to nutrient concentration across all sites ($r^2 = 0.41$, log–log relationship). Relationships between concentration and U_t were used to determine whether the uptake was nonlinear (i.e., kinetic uptake primarily limited by the biotic capacity of microorganisms to accumulate nutrients) or linear (e.g., limited by mass transport into stream biofilms). In all systems, U_t was lower at ambient concentrations than at elevated concentrations. Extrapolation from uptake measured from a series of increasing enrichments could be used to estimate ambient U_t. Linear extrapolation of U_t assuming the relationship passes through the origin and rates measured at 1 elevated nutrient concentration underestimated ambient U_t by ~3-fold. Uptake rates were saturated under some but not all conditions of enrichment; in some cases there was no saturation up to 50 μmol/L. The absolute concentration at which U_t was saturated in Kings Creek varied among reaches and nutrients. Uptake rates of NH_4^+ at ambient concentrations in all streams were higher than would be expected, assuming U_t does not saturate with increasing concentrations. At ambient nutrient concentrations in unpolluted streams, U_t is probably limited to some degree by the kinetic uptake capacity of stream biota. Mass transfer velocity from the water column is generally greater than would be expected given typical diffusion rates, underscoring the importance of advective transport. Given the short-term spikes in nutrient concentrations that can occur in streams (e.g., in response to storm events), U_t may not saturate, even at high concentrations.

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[15] E-mail address: wkdodds@ksu.edu

[16] Authors alphabetical after the 2nd author.

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Quantifying nutrient dynamics is central to understanding aquatic eutrophication and ecosystem function. Human activities often lead to short-term and long-term increased NO_3^-, NH_4^+, and PO_4^{3-} inputs to streams and groundwater. The impact of these nutrients on water quality and ecosystem function depends in large part on the pathways through which each cycles upon entering aquatic ecosystems. For example, if autotrophic uptake is a dominant pathway of nutrient retention, then undesirable algal blooms will often occur (Dodds and Welch 2000). If heterotrophic uptake is dominant, however, C degradation may be stimulated. Downstream transport of nutrients is important, as evidenced by the development of an anoxic zone that covers large areas in the coastal waters of the Gulf of Mexico (Rabalais et al. 1998) and toxic concentrations of NO_3^- in drinking water.

Small streams are key interfaces between terrestrial habitats and downstream receiving waters and can potentially regulate nutrient transport (e.g., Peterson et al. 2001). Nutrients can move from the water column into the benthos (uptake), or from the benthos into the water column (remineralization). The rate of remineralization should not respond quickly to short-term variations in water-column nutrient concentrations (Dodds 1993), so only uptake is considered in this paper. Characterizing benthic nutrient uptake as a function of variable in-stream nutrient concentrations is an important step in understanding how the stream benthic biota is linked to temporally and spatially variable nutrient concentrations in the water column.

At least 2 models can represent extremes on a possible continuum of the functional relationship between nutrient concentration in the water column and uptake rates by the benthos of the stream under the range of nutrient concentrations that typically occur in streams. At one end of the spectrum, uptake is linear and may be driven by hydrodynamic limitation of mass transport. Such linear uptake at moderate to low concentrations also could be related to abiotic sorption with low affinity and high saturation (i.e., low affinity uptake with a high half-saturation constant [K_s] will lead to apparently linear uptake until very high water-column nutrient concentrations are reached). However, if uptake rates are limited by mass transport alone, they are controlled by diffusion rates, which is characterized by Fick's first law:

$$J = D\frac{\delta C_n}{\delta z} \qquad [1]$$

where J is diffusion, D is the diffusion constant, and $\delta C_n/\delta z$ is the gradient in nutrient concentration (C), across distance (z) (Denny 1993). Molecular diffusion is very slow, so the diffusion flux can be thought of as controlled by the nutrient gradient across a stream-wide average diffusion boundary layer (Vogel 1994). If only mass transfer limits uptake, a linear relationship between nutrient concentration and uptake rate will result:

$$U_r = K_t C_n \qquad [2]$$

where U_t is uptake in units of mass per unit area benthos per unit time, C_n is the nutrient concentration, and K_t is an uptake constant that corresponds to D/dz in Fick's law, and is a function of the rate of advective transport. The relationship between uptake and concentration will hold constant over short time periods (i.e., K_t will remain constant) if discharge does not change.

At the other end of the continuum, U_t can be controlled by the biotic capacity of organisms or abiotic sites of adsorption to immobilize nutrients. At this end of the continuum, capacity is a nonlinear saturating model where kinetics rather than mass transfer dominate U_t. Michaelis–Menten uptake kinetics generally describe the relationship between U_t and C_n for individual cells or cell cultures and K_s values are usually close to 1 μmol/L for biotic uptake, ranging from 0.1–15 μmol/L (Brezonik 1994). Regardless of whether biotic capacity or abiotic sorption controls U_t, saturation is expected as concentration increases with this type of model, where U_t is represented by a maximum uptake rate (V_{max}).

It is unknown to what extent a linear model versus saturation kinetics models describe nutrient uptake in streams. If saturation kinetics occur, K_s values for U_t are not well known (except see Bothwell 1989, Mulholland et al. 1990). A prior study of NH_4^+ and NO_3^- uptake in a forested stream indicated that a linear model did not fit uptake rate as a function of nutrient concentrations (Mulholland et al. 2001). A model coupled with data from marine mesocosms suggested that there is a broad region where both uptake capacity and mass transfer limit U_t across solid–water boundaries (Sanford and Crawford 2000), but such an analysis has not been applied to streams to our knowledge.

Three interrelated measures are typically used to characterize nutrient uptake by the benthos in streams: 1) spiraling length, 2) uptake rate per unit benthos area (U_t), and 3) mass transfer velocity. Nutrient retention is a function of nutrient spiraling (Newbold et al. 1981) in streams. The most easily measured component of spiraling length is the uptake length (S_w), which describes the average distance traveled by a dissolved nutrient in the water column before being immobilized (Webster and Ehrman 1996). S_w is the main component of spiraling length (Newbold et al. 1981), making it a good index of nutrient retention (Kim et al. 1990). Though easily measured, S_w is not only a function of the uptake capacity of the benthos, but is also strongly influenced by discharge and water depth. S_w is therefore not the best parameter to compare across streams of different size when the relationship between uptake and nutrient concentration is of interest (Davis and Minshall 1999).

The mass transfer velocity (V_f, also referred to as the mass transfer coefficient by some investigators) can be thought of as the average velocity of a nutrient toward the benthos, and is independent of depth (Stream Solute Workshop 1990, Wollheim et al. 2001). We concentrate on U_t and V_f to highlight processes controlling the rate that nutrients move into the benthos. We used ^{15}N tracer additions and unlabeled short-term nutrient enrichments in a detailed assessment of U_t and V_f as a function of C_n. The study sites were prairie and gallery forest stream sites in Kansas and a cross-system comparison of 11 other streams across the United States as part of the Lotic Intersite Nitrogen eXperiment (LINX, Peterson et al. 2001).

We attempt to establish the general form of the relationship between U_t and C_n because this relationship is not well described for many streams. We test specific predictions that can be made relative to a linear model versus a model that assumes saturation of U_t. In a pure linear mass transfer model, U_t will be linearly related to concentration with no saturation. In this case, V_f should not be a function of concentration because any increase in concentration should lead to a proportional increase in U_t, so average nutrient velocity toward the benthos should remain constant. If only biotic capacity limits U_t, then U_t should saturate at low to moderate nutrient concentrations (i.e., <100 μmol/L). In this case, values for K_s should be comparable to those of single cells whose uptake is not constrained by transport. If U_t saturates, V_f will decrease with increasing nutrient concentration; average velocity of nutrient molecules decreases because benthic uptake moves a lower proportion of the molecules downward and out of the water column per unit time. In intermediate cases, where transport limitation or sorption with very high K_s values have an influence, K_s for U_t should be greater than expected for purely biotic uptake. However, at very high nutrient concentrations U_t is still expected to saturate.

Methods

Study sites

A prairie reach and a gallery forest reach of Kings Creek on the Konza Prairie Biological Station were used for detailed enrichment studies. Descriptions of the site's ecology (Gray and Dodds 1998), hydrology (Gray et al. 1998), geology (Oviatt 1998), and N cycling and transport (Dodds et al. 1996, 2000, Kemp and Dodds 2001) are available. The 100-m prairie reach in watershed N04D of Kings Creek was autotrophic, with relatively little leaf input. It initially had a high discharge (50 L/s) and high algal biomass (Dodds et al. 2000). As the stream dried in early summer, the study was moved downstream to the gallery forest site. The 75-m gallery forest reach was characterized by greater allochthonous inputs and lower light than the prairie reach. Discharge at each Kings Creek site for each date is reported in Table 1.

Experiments were conducted at 11 additional stream sites of approximately similar discharge and order as Kings Creek, in conjunction with the LINX study (Table 2). Most of these sites were relatively pristine. Only Eagle Creek and the East Fork Little Miami River had substan-

TABLE 1. Discharge, nutrient concentration at uppermost measurement site closest to the addition point, uptake length (S_w), uptake rate (U_t), and mass transfer velocity (V_f) for all nutrient additions at Kings Creek. SE for S_w in parentheses. See text for description of parameters.

Date (all 1998)	Site	Nutrient	Discharge (L/s)	Nutrient top conc. (μmol/L)	S_w (m)	U_t (μmol m^{-2} s^{-1})	V_f (m/h)
2 April	Prairie	NO_3^-	55	4	168 (38)	0.53	0.446
23 June	Prairie	NO_3^-	4	15	300 (41)	0.13	0.031
23 June	Prairie	NO_3^-	4	29	311 (61)	0.25	0.030
23 June	Prairie	NO_3^-	4	61	402 (62)	0.40	0.024
23 June	Prairie	NO_3^-	4	105	225 (47)	1.23	0.042
5 April	Prairie	NH_4^+	47	2	228 (34)	0.21	0.314
8 April	Prairie	^{15}N-NH_4^+	48	0.1	56 (22)	0.05	1.417
27 April	Prairie	^{15}N-NH_4^+	8	0.08	24 (4)	0.015	0.675
8 May	Prairie	NH_4^+	2	3	145 (17)	0.03	0.029
8 May	Prairie	NH_4^+	2	7	261 (26)	0.03	0.016
12 May	Prairie	^{15}N-NH_4^+	11	0.01	38 (5)	0.001	0.360
9 June	Prairie	NH_4^+	5	9	66 (9)	0.38	0.159
9 June	Prairie	NH_4^+	5	84	248 (65)	1.00	0.043
6 July	Gallery	NH_4^+	29	49	97 (5)	5.87	0.429
13 July	Gallery	NH_4^+	29	5	91 (7)	0.61	0.459
13 July	Gallery	NH_4^+	29	9	247 (80)	0.42	0.169
13 July	Gallery	NH_4^+	29	24	115 (25)	2.36	0.362

TABLE 2. Site characteristics for ^{15}N and unlabeled NH_4^+ additions.

Site	Biome	Discharge (L/s)	Average width (m)	NH_4^+ (μmol/L)	NO_3^- (μmol/L)	Reference
Upper Ball Creek, North Carolina	Deciduous forest	51.4	2.2	0.16	0.07	Tank et al. 2000
Walker Branch, Tennessee	Deciduous forest	9.8	2.2	0.19	1.11	Mulholland et al. 2000
Sycamore Creek, Arizona	Desert	70	7.1	0.14	1.20	
Bear Brook, New Hampshire	Deciduous forest	3.5	2.3	0.36	4.10	
Gallina Creek, New Mexico	Montane coniferous forest	4.2	2.1	0.37	0.54	
Quebrada Bisley, Puerto Rico	Tropical forest	17.9	1.8	0.33	10.07	Merriam et al. 2002
Eagle Creek, Michigan	Deciduous forest	208	4.9	1.28	2.06	Hamilton et al. 2001
Mack Creek, Oregon	Montane coniferous forest	55.8	7.3	0.21	3.88	
E1, Alaska	Tundra	20	1.3	0.10	2.55	Wollheim et al. 2001
Amity Creek, Michigan	Deciduous forest	71	2.2	0.48	0.62	
East Fork Little Miami River, Ohio	Deciduous forest	849	14.2	2.14	38.79	

tially elevated nutrient concentrations in the stream channel as a consequence of anthropogenic inputs. The sites were selected to maximize variation in type of biome, with discharge roughly similar across sites. Further descriptions of N cycling (Peterson et al. 2001) and metabolism (Mulholland et al. 2001) are published.

Unlabeled nutrient enrichments

We conducted multiple short-term elevated solute additions of $NaNO_3$ or NH_4Cl at Kings Creek from April to September 1998. Concentrations in the stream water were elevated by adding nutrients with a peristaltic pump to achieve specific solute release rates ranging from 2 to 38 mL/min, based on the discharge of the stream, the concentration of the stock solution, and a target nutrient increase. Water samples were collected at 3 downstream sampling points prior to the first addition on each date to determine background nutrient concentrations. Each solute addition was conducted at successively higher concentrations over the series of experiments conducted in 1 d.

A conservative solute tracer of NaBr or NaCl in solution with the nutrients was used to account for abiotic dilution caused by groundwater influx and to ensure that the solute addition had reached steady state (Stream Solute Workshop 1990). These additions also confirmed that the first sampling station was far enough downstream from the addition point to allow for complete mixing. The concentration of Br^- in the stream during the addition was monitored using ion-selective Br^- electrodes (Orion 290A) placed at sampling points midway and the furthest downstream from the addition point. Multiple calibration points and a 2nd-order polynomial fit were employed for the Br^- probe used at low concentrations to establish the standard curve. The maximum concentration of Br^- was ~0.1 µmol/L and Cl^- was ~0.5 µmol/L in the stream at plateau. The NaCl additions were assessed with standard conductivity probes. When ion concentrations had reached plateau downstream, water samples for nutrient analysis were collected from the center of the stream starting downstream and moving up to the enrichment site. Samples were transported back to the laboratory on ice. Ion additions probably did not interfere with abiotic exchange because they were done at low concentrations and we never documented increases in NO_3^- or NH_4^+ concentrations when only saline solutions were added.

Water samples were analyzed spectrophotometrically for $NO_3^- + NO_2^-$ (hereafter referred to as NO_3^-) following Cd reduction (Technicon 1973), and for NH_4^+ by the phenol hypochlorite method (APHA 1995). Bromide was analyzed in the laboratory using an ion-selective electrode. Care was taken to ensure stability of the electrode system (i.e., constant temperatures, standards made in stream water, and standardization before and after analyses of unknowns).

Stable isotope tracer additions of $^{15}NH_4^+$

NH_4^+ uptake at ambient concentration was also measured at all 12 sites. A solution of $^{15}NH_4Cl$ was released into the stream, and disappearance of $^{15}NH_4^+$ over distance was used to estimate U_t. The ^{15}N tracer approach was necessary because at ambient nutrient concentrations remineralization is comparable to uptake at the whole-stream level (Dodds 1993). Furthermore, at 2 of the sites (East Fork Little Miami River and Eagle Creek) no change of concentration downstream could be detected even with elevated NH_4^+ additions. When ^{15}N is used as a tracer in the water column, assuming insignificant rates of ^{15}N regeneration from the benthos, the rate of disappearance of $^{15}NH_4^+$ over distance allows calculation of U_t. We can assume insignificant regeneration of ^{15}N with short-term releases because remineralized N from the benthos has such a small amount of ^{15}N content, and estimates were made in the first day of ^{15}N release. Isotopic discrimination, a minor (~0.3%) component of uptake, was ignored. A solution of NH_4^+ enriched with ^{15}N (10 mol %) was released at each site, producing <1% increase in background NH_4^+ concentrations. Samples were collected and shipped on ice by overnight carrier to The Ecosystems Center at the Marine Biological Laboratory, Woods Hole, Massachusetts, where ^{15}N:^{14}N ratios in NH_4^+ were determined using a Finnigan Delta S mass spectrometer, following NH_4^+ diffusion under alkaline conditions (Holmes et al. 1998). ^{15}N results are reported as $\delta^{15}N$ (‰) values calculated using the following equation:

$$\delta^{15}N = \left[\left(\frac{R_{compartment}}{R_{std}}\right) - 1\right] \times 1000 \qquad [3]$$

where $R_{compartment}$ is the $^{15}N/^{14}N$ analyzed in the

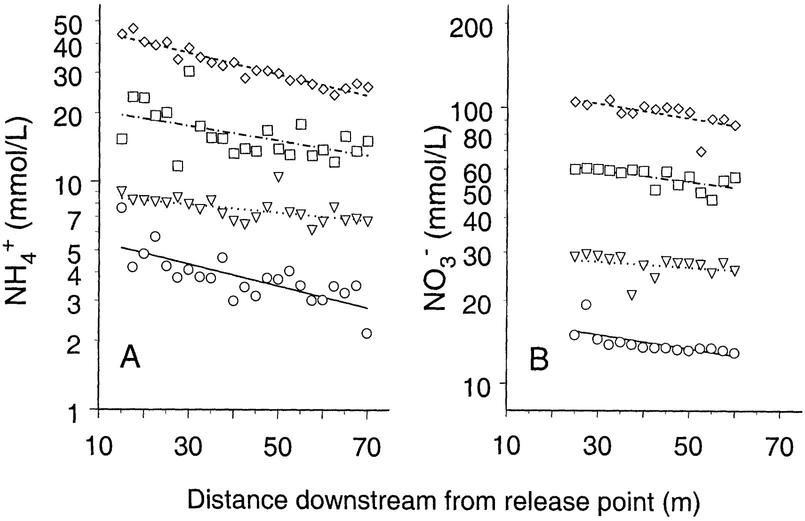

FIG. 1. Representative dilution-corrected concentrations of NH_4^+ in the gallery forest reach, 6 July 1998 (A) and NO_3^- in the prairie reach, 23 June 1998 (B) as a function of distance over a range of unlabeled nutrient-enrichment levels. Note log scale on y-axis.

sample and the N isotope standard is air (R_{std} = 0.003663).

Nutrient uptake calculations

S_w was calculated using linear regression of the natural log of nutrient concentration (or $\delta^{15}N$) corrected for dilution and background concentration versus distance. The slope of the line is uptake rate per unit distance (Webster and Ehrman 1996), and the inverse of the uptake rate (k_c) is the S_w. U_t is calculated using the following equation:

$$U_t = \frac{C_n}{S_w} \times \frac{Q}{w} \qquad [4]$$

where Q equals discharge, and w is average width.

Stream depth and wetted width were measured across 10 transects and averaged for the calculations of U_t. Plateau concentrations from the conservative solute tracer additions were used to calculate Q on each addition date using the following equation (Webster and Ehrman 1996):

$$Q = \frac{(C_I - C_b) \times Q_I}{(C_P - C_b)} \qquad [5]$$

where C_I is the concentration of NaBr addition solution, C_P is the plateau conservative solute concentration, Q_I is the addition rate, and C_b is the background concentration of conservative solute in the stream.

V_f was calculated from the equation (Newbold et al. 1981, Stream Solute Workshop 1990):

$$V_f = \frac{Q/w}{S_w} = \frac{U_t}{C_n} \qquad [6]$$

Results

Konza Prairie nutrient additions

Representative data demonstrate how nutrient concentrations tended to decrease downstream from nutrient-addition points (Fig. 1). The uptake rates were proportional to the slopes of the lines fit to the logarithmic plots. In all cases there was a significant amount of variance in the nutrient concentrations. In some cases, particularly at lower NH_4^+ concentrations, there was considerable variance inconsistent with sampling location (Fig. 1) longitudinally along the stream channel that could be caused by temporal or analytical variation. However, the regression analyses used to establish the lines all yielded significant slopes ($p < 0.05$).

These data and similar data not shown were used to calculate S_w values for each concentration used in the additions (Table 1). In general, S_w values were longer at higher nutrient concen-

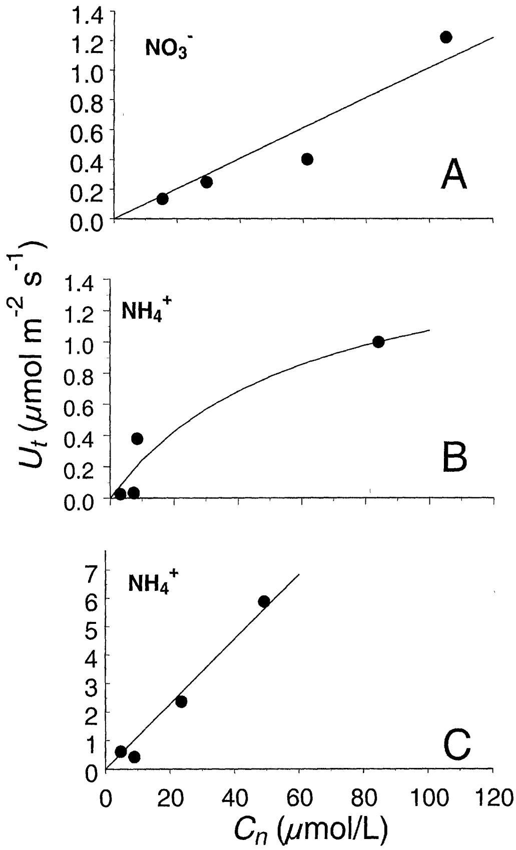

FIG. 2. Relationships of uptake rate (U_t) versus nutrient concentration (C_n) for (A) NO_3^- in the prairie reach, 23 June 1998, (B) NH_4^+ in the prairie reach, 8 May and 9 June 1998 combined, and (C) NH_4^+ in the gallery reach, 6 July 1998, with models for those relationships fit by regression (Table 3).

trations, and S_w values were longer for NO_3^- than NH_4^+ at the prairie site.

V_f values were variable across nutrients and across dates (Table 1). In general, values of V_f were higher in the gallery forest sites. In some cases there was a decrease in V_f with increasing concentration as is expected with kinetic uptake saturation (e.g., the addition of NH_4^+ on 8 May and 9 June), but in other cases there was no relationship with increasing concentration as expected with a linear mass-transfer model (e.g., NO_3^- additions on 23 June).

There was an increase in U_t as nutrient concentration increased for multiple additions at the 2 reaches on Kings Creek (Fig. 2). In all cases there must be no uptake at 0 nutrient concentration (i.e., no nutrient can leave the water column and enter the benthos if there is no nutrient in the water column), so these curves were fit with no intercept (forced through 0). The best-fit curves for these plots (Table 3) demonstrated that either a linear or a Michaelis–Menten model described a significant portion of the variance in these 3 cases. The best-fit curve was determined based upon the highest value for r^2. In 2 cases, nonlinear estimation fit the Michaelis–Menten model almost as well as a linear model, but V_{max} and K_s values were so great that the model was essentially a linear model at the concentrations of interest. The graph of U_t for NH_4^+ in the prairie (Fig. 2B) illustrates a potential case of kinetic uptake saturation (i.e., a potential Michaelis–Menten relationship), but omission of a single point would make a linear model fit the relationship with a comparable r^2. The calculated K_s concentration for U_t was 67 µmol/L.

TABLE 3. Modeled uptake rate (U_t) versus concentration for 3 additions, model parameters, and calculated ambient U_t for best model. See Table 1 and Fig. 2 for data and modeled curves. 1st order is the linear model, M–M is a Michaelis–Menten model. Both models were constrained to go through 0 uptake at 0 nutrient concentration. Ambient U_t is calculated for best-fit model. V_{max} = maximum uptake rate, K_s = half-saturation constant, V_f = mass transfer velocity, – = not applicable.

Site	Nutrient	Model	Constant (V_{max} or slope)	K_s (µmol/L)	r^2	Ambient conc. (µmol/L)	Ambient U_t (µmol m^{-2} s^{-1})	Ambient V_f (m/h)
Prairie	NO_3^-	1st order	0.01	–	0.95	4.10	0.042	0.036
		M–M	8.3×10^5	7.9×10^7	0.89	–	–	–
Prairie	NH_4^+	1st order	0.012	–	0.87	–	–	–
		M–M	1.73	61.3	0.91	0.62	0.017	0.099
Gallery	NH_4^+	1st order	0.11	–	0.98	2.35	0.268	0.410
		M–M	1.2×10^6	1.1×10^7	0.97	–	–	–

The graphs of the NO_3^- additions in the prairie reach (Fig. 2A) and the gallery forest NH_4^+ additions (Fig. 2C) show a linear (1st-order) relationship between U_t and concentration. Furthermore, for each doubling of nutrient concentration, there is an approximate doubling of U_t, as a mass transport model (Eqn 2) would predict.

Once the best-fit model (linear or Michaelis–Menten) had been determined for the 3 data sets in Fig. 2, ambient concentrations were used with the appropriate model to calculate the ambient U_t (Table 3). Ambient U_t values estimated this way were lower than those measured with any short-term nutrient enrichments from these data (Table 1), regardless of which model was used to describe U_t. Ambient values of V_f were greater than all V_f values for short-term unlabeled nutrient enrichments at Kings Creek for NO_3^-. In 2 sets of calculations using NH_4^+ data from the prairie and from the gallery forest, 1 of the lower short-term elevated additions had higher values of V_f than the value obtained by extrapolation to ambient concentration.

Tracer $^{15}NH_4^+$ additions

Using $^{15}NH_4^+$ as a tracer of uptake at ambient NH_4^+ concentrations, we observed that U_t values calculated from tracer additions were ~10 times lower than those estimated from nutrient additions at all 12 sites (Fig. 3). This discrepancy occurred even though we attempted to keep our enrichments as small as possible. Uptake measured with elevated nutrient enrichments does not account for remineralization (i.e., elevated additions measure net uptake, tracers measure gross uptake). The 10 times greater U_t measured with enrichments indicates that, with nutrient enrichments, net uptake ≈ gross uptake within ~10%. The assumptions behind this approximation are explored in the discussion.

Two sites, Eagle Creek and East Fork Little Miami River, had very long NH_4^+ S_w values. When unlabeled additions were attempted it was impossible to calculate U_t because there was no detectable decrease in total NH_4^+ concentration. Depletion of $^{15}NH_4^+$ down from the isotope addition point could be detected at these sites, and U_t at ambient NH_4^+ concentrations could be calculated (Hamilton et al. 2001, Donna Morrall, unpublished data).

The U_t values measured with $^{15}NH_4^+$ and unlabelled additions plotted across all sites demonstrated significant positive relationships between U_t and NH_4^+ concentration (Fig. 3A). Combining all of the U_t data yielded the following relationship:

$$\log_e(NH_4^+ U_t) = 0.251 + 0.212 \times \log_e(NH_4^+ \text{ concentration}), \quad r^2 = 0.41 \qquad [7]$$

with NH_4^+ U_t expressed in μmol m^{-2} s^{-1} and NH_4^+ concentration in μmol/L.

There was evidence for saturation of uptake in the plot of U_t against concentration across all sites. When the untransformed data (not on a log scale) were fit with linear and Michaelis–Menten relationships, the Michaelis–Menten relationship explained more of the variance (r^2 = 0.20 and 0.33 for linear and Michaelis–Menten curve fits, respectively). The 2-dimensional Kolmogorov–Smirnov test (Garvey et al. 1998) indicated that the data were bivariate ($p = 0.001$) and that a breakpoint occurred at 3.4 μmol/L NH_4^+. Piecewise regression analysis also suggested a breakpoint at 1.1 μmol/L NH_4^+, and the slope of the regression line above this point was significantly less than below. Fitting the data with 2 lines explained 76% of the variance. These 3 statistical approaches independently suggest some saturation occurs even when data across all sites are compared.

NH_4^+ V_f decreased with increasing nutrient concentration (Fig. 3B, $r^2 = 0.37$, $p < 0.0001$, linear regression of log-transformed data). When all sites with both unlabeled addition and tracer measurements were considered together, V_f was always lower with enrichment. The lower V_f values with tracer additions indicated some degree of uptake saturation at elevated concentrations occurred.

Discussion

Saturation of uptake

U_t generally increased for NH_4^+ and NO_3^- as stream nutrient concentrations in Kings Creek were increased during the unlabeled nutrient enrichments. U_t continued to increase up to very high concentrations in some cases in Kings Creek and at other sites (i.e., Konza, Fig. 2A and C; Sycamore Creek, Fig. 3). This finding suggests that there are cases where biotic saturation

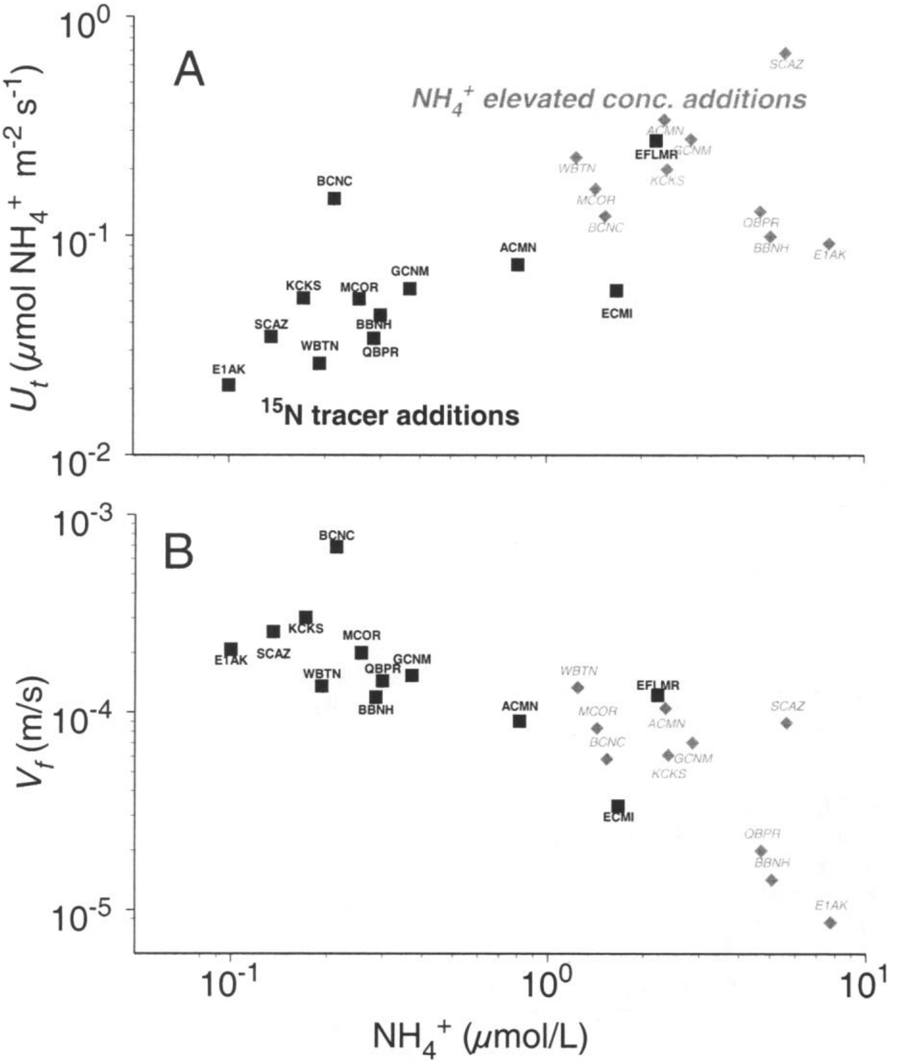

FIG. 3. Relationship between uptake rate, U_t (A) and mass transfer velocity V_f (B) and concentration of NH$_4^+$ for 12 stream sites as measured by an unlabeled enrichment of NH$_4^+$ or a tracer ^{15}NH$_4^+$ enrichment. WBTN = Walker Branch, Tennessee; BCNC = Ball Creek, North Carolina; SCAZ = Sycamore Creek, Arizona; BBNH = Bear Brook, New Hampshire; GCNM = Gallina Creek, New Mexico; QBPR = Quebrada Bisley, Puerto Rico; KCKS = Kings Creek, Kansas; MCOR = Mack Creek, Oregon, E1AK = E1, Alaska; ECMI = Eagle Creek, Michigan; EFLMR = experimental facility East Fork Little Miami River, Ohio; and ACMN = Amity Creek, Minnesota. Note log scales.

of uptake could not describe U_t as a function of C_n; K_s values of periphyton are generally <10 µmol/L (Borchardt 1996), and data in Fig. 2A, B, and C indicated K_s values likely exceed 60 µmol/L. If adsorption kinetics were important, uptake could eventually saturate, but only at higher concentrations than usually occur in the systems we studied. Some clear cases of saturation did occur.

At Eagle Creek, downstream nutrient flux was so high relative to uptake that U_t could be considered saturated regardless of how much nutrient was added, even though U_t at that stream was similar to the other sites under comparable C_n values (Hamilton et al. 2001), and a similar situation occurred in the East Fork Little Miami River. These sites had U_t values for NH_4^+ similar to those measured with NH_4^+ enrichments in more pristine sites. This result suggests that high U_t values can be maintained in systems with high nutrient loading, but that remineralization rates also increase leading to higher C_n values and downstream transport of dissolved nutrients.

Mass transport limitation of U_t (the linear model) is probably operating simultaneously with limitation of uptake kinetics by abiotic sorption and biotic capacity (Michaelis–Menten). Bothwell (1989) found an increase in periphyton biomass with increased PO_4^{3-} concentrations up to 0.9 μmol/L. When periphyton biomass was plotted against PO_4^{3-} concentrations (see fig. 7 in Bothwell 1989), the resulting curve could be broken into 3 sections. The 1st section (0–~0.03 μmol/L PO_4^{3-}) resembled Michaelis–Menten uptake kinetics. The 2nd section (~0.06–~0.9 μmol/L PO_4^{3-}) showed a linear response at these higher levels of nutrient enrichment. The final section exhibited complete saturation at concentrations >0.9 μmol/L PO_4^{3-}.

Mulholland et al. (1990) found that uptake of PO_4^{3-} in Walker Branch may be saturated at concentrations >0.16 μmol/L PO_4^{3-}. Mulholland et al. (1990) suggested that biological processes control uptake at low PO_4^{3-} concentrations (<0.16 μmol/L PO_4^{3-}), and physical/chemical adsorption dominated uptake when PO_4^{3-} concentrations were >0.16 μmol/L PO_4^{3-}. Thus, a combined model of biotic and abiotic limitation with potential hydrological effects applied to PO_4^{3-} uptake in Walker Branch.

Do biotic uptake or mass transfer dominate uptake?

The lack of saturation of U_t in some cases suggests the existence of a mass transfer component, high-saturation sorption kinetics, or dissimilatory processes such as nitrification and denitrification that may not saturate. We cannot rule out that such processes are in operation at least sometimes, although it is clear that assimilatory biotic uptake is important as well. More data are required on biotic conditions coupled with tracer measurements of U_t, and refined models including biotic uptake, abiotic uptake, and limitation by mass transfer rates (diffusion boundary layer effects) are necessary to understand uptake as a function of C_n across a wide variety of small streams. Our data support the predictions of Sanford and Crawford (2000), who suggested that simultaneous limitation of benthic nutrient uptake by biotic affinity and transport phenomena should operate under a broad range of conditions.

Our experiments cannot separate abiotic uptake (adsorption) from biotic uptake, but saturation of adsorption generally occurs at higher concentration than does saturation of biotic uptake (Mulholland et. al. 1990). Dissimilatory processes (denitrification and nitrification of NO_3^- and NH_4^+, respectively) may also have high K_s values. Nitrification rates at our study sites were 20 to 30% of total NH_4^+ U_t (Peterson et al. 2001). Denitrification at Kings Creek is <1% of NO_3^- uptake (Kemp 2001).

Mass transfer velocity

If there is hydrological limitation of V_f, it is overcome to some degree by channel characteristics, such as surface topography and advective transport into shallow subsurface channels. This advective transport can be demonstrated by a simple calculation that compares V_f in the diffusion boundary layer to values calculated for the water column. We will assume that the diffusion boundary layer (δz in eqn 1) is ~0.2 mm thick (Glud et al. 1994, Bott et al. 1997), and that the diffusion coefficient of ions through the layer (D) is 0.07 cm^2/h (CRC 1978). V_f then is D/dz, = 0.035 m/h, which is at least 1 order of magnitude less than most of the V_f values measured with tracers for all streams (Fig. 3B) and less than 15 of 20 values reported for Kings Creek (Tables 1, 3). We can rule out uptake in the water column (Dodds et al. 2000), which leaves benthic/hydrodynamic properties to explain how nutrients can move so quickly from the water column to the benthos.

The effective surface area for uptake must be at least several times greater than the actual streambed area given most of the calculated values for V_f. Flow through substrata with biofilms attached and flow through primary producers such as filamentous algae and bryophytes will increase the effective surface area of the stream bottom. It has been demonstrated that substantial flow occurs through filamentous algae (Dodds 1991). The effective increase in surface area for diffusion may be one reason filamentous algae are so successful in many streams.

The K_s values we were able to calculate for Konza additions were well above the K_s values that have been documented previously for microbial uptake of nutrients (Borchardt 1996). This result indicates some influence of mass transport limitation (no saturation expected at all) or low-affinity abiotic sorption processes (saturation only at very high concentrations). It is not possible to distinguish the effects of these 2 processes.

Using nutrient addition experiments

The relationship between distance from the addition and nutrient concentration was well characterized with 20 data points for each addition (e.g., Fig. 1). With this many sampling points we could identify outliers more easily than if samples had been taken with more coarse spatial resolution (e.g., every 10 m over a 60-m reach). The need for many sampling points was particularly relevant for the low-level nutrient additions where the limits of detection of colorimetric assays were being approached. Many other studies have used additions of this type to examine nutrient dynamics, but most used ~7 sampling stations (e.g., Newbold et al. 1981, Mulholland et al. 1990, Martí and Sabater 1996, Butturini and Sabater 1998, Davis and Minshall 1999). Depending upon which 7 points are chosen for each data series in Fig. 1, very different results are possible for each level of nutrient enrichment, particularly at low enrichments. The best 7 points to choose would be evenly spaced over the entire length of the reach. However, there were some outliers and these few points could still lead to errors even if points were taken over sufficiently long reaches. For future studies, we recommend ≥20 sampling stations in the reach where nutrients are decreasing.

Isotopic tracers are the only way to determine nutrient uptake at ambient concentrations. Many investigators are limited to short-term nutrient enrichments at levels well above ambient nutrient concentrations because of the difficulty and cost involved in ^{15}N tracer studies and the complications of using radioisotopes (^{33}P or ^{32}P) for P studies. Our data suggest that U_t values are substantially greater and V_f values are considerably less at increased nutrient levels than at ambient concentrations. However, by conducting additions at a series of increasing solute concentrations well below the saturation point, investigators can determine the best-fit relationship between C_n and U_t. This relationship can be used to extrapolate to ambient concentrations and establish possible stream responses to ambient levels of nutrients. We tested the possibility of such extrapolation by using the $^{15}NH_4^+$ and short-term pulsed addition data from 12 stream sites, and by comparing our extrapolations from nutrient-enrichment additions to ^{15}N addition at Kings Creek.

Estimating ambient uptake rates

For each of 10 sites in different biomes, we could calculate a U_t at elevated nutrient concentrations, and a ^{15}N tracer U_t determined at ambient concentrations. Gross uptake to the benthos must be 0 when ambient concentration in the water column is 0. Thus, there are 3 known points (0,0; ambient U_t and U_t with elevated NH_4^+ enrichments) to evaluate the applicability of the linear model (eqn 2). We used the line that passes through the origin, and the U_t measured at an elevated concentration for each stream to estimate an expected U_t at ambient concentrations given a linear model.

We assumed that gross uptake approximates net uptake at elevated concentrations. This approximation is based upon several assumptions. Remineralization is probably not influenced by short-term nutrient additions to the water column because remineralization is a heterotrophic process that depends upon quantity and stoichiometry of organic material, which is coupled to water-column C_n over longer time scales than the measurements we took of U_t at elevated nutrient concentrations. We also determined previously that remineralization rates were less than ambient U_t across the study sites (Peterson et al. 2001), so remineralization rates were <10% of uptake at elevated concentration. The idea that remineralization is approximately equal to ambient U_t is further supported by the observation that NH_4^+ varied little downstream from tracer release points. If ambient U_t exceeded remineralization, then concentrations would be expected to decrease downstream and vice versa.

If U_t follows a saturating curve, then this linear extrapolation using 2 points (U_t at elevated

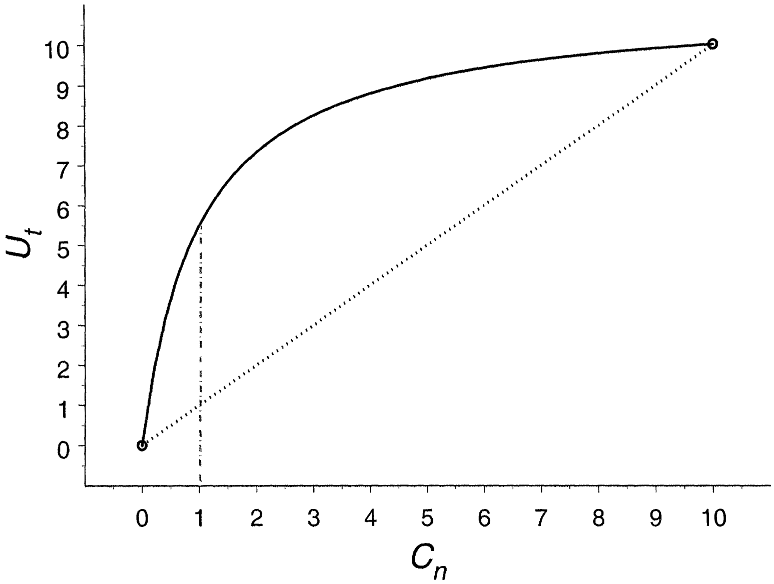

FIG. 4. A conceptual diagram of how estimation of uptake rate (U_t) at ambient nutrient concentration (C_n) using a single nutrient enrichment and extrapolation downward by a linear model through the origin will tend to underestimate actual uptake if a saturation model of uptake actually applies. Dashed vertical line illustrates how extrapolated uptake will be less than actual uptake if a linear model (dotted line) is used and a Michaelis–Menten model (dark line) actually applies.

nutrient concentration and 0) should underestimate ambient U_t (Fig. 4). When NH_4^+ U_t at ambient concentrations was estimated using the linear model, U_t was underestimated in all but Amity Creek. Uptake was substantially underestimated at E1 in Alaska, but a very high elevated NH_4^+ addition was used for this site. Removing E1, the average ratio of measured to expected U_t was 3.1 (Fig. 5, SE = 0.7, paired difference t-test, $p = 0.00005$).

Thus, we have 2 general methods that can be used to estimate NH_4^+ U_t at ambient concentrations in the absence of isotopic tracer data, and these methods were tested across biomes. The 1st is a simple relationship between U_t of NH_4^+ and water-column nutrient concentration (Fig. 3). This simple log–log relationship has considerable variance, but it encompasses systems from a wide variety of biomes. The fact that 41% of the variance in U_t of NH_4^+ can be ascribed to a single factor, NH_4^+ concentration in the water column, could be viewed as surprising in light of all the other factors that could alter U_t (e.g., heterotrophic versus autotrophic uptake, temperature, discharge, microbial biomass, light for primary producers, organic C supply for heterotrophic microorganisms, grazing). However, this relationship only constrains expected U_t at an individual instream concentration to within about an order of magnitude. The 2nd method to estimate the U_t at ambient concentrations is to use a linear extrapolation from a short-term unlabeled addition, and to multiply that rate by 3 (i.e., observed ambient U_t was 3.1 times higher than that calculated from unlabeled additions as discussed in the previous paragraph), which also entails considerable uncertainty. Neither method is as accurate as isotopic tracer techniques, but both are easier and more cost effective. It is not known how well such techniques will work for NO_3^- and PO_4^{3-} uptake.

A 3rd alternative for estimating NH_4^+ uptake at ambient concentrations was tested with the more detailed additions in Kings Creek. In this instance, the series of NH_4^+ enrichments in Kings Creek were used to create a Michaelis–Menten model of NH_4^+ U_t (Fig. 2B) that could be compared to the tracer measurement of U_t at ambient concentration (Table 2). The ^{15}N tracer and nonlinear estimates of U_t were 0.1 and 0.17 $\mu mol\ m^{-2}\ s^{-1}$, respectively. This result suggests that extrapolation of U_t from a series of increased-concentration nutrient additions may provide a better estimate than extrapolating

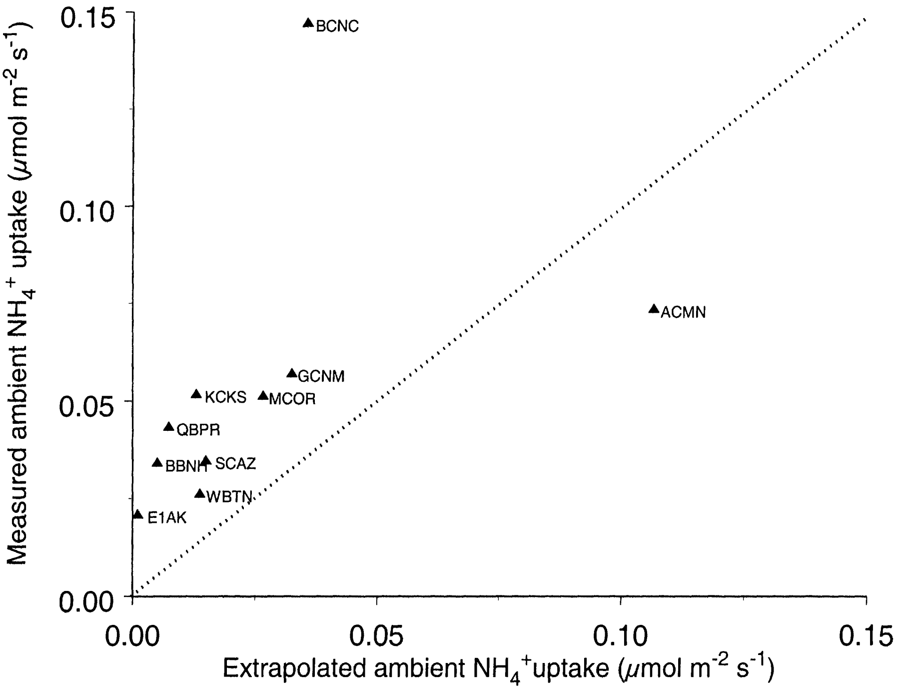

FIG. 5. Observed (using ^{15}N tracer) versus calculated NH_4^+ uptake rate (U_t) at ambient NH_4^+ concentration for 10 stream sites using observed data plotted in Fig. 4 and U_t calculated with a linear model from the elevated nutrient-enrichment experiments. Site acronyms as in Fig. 3. See text for a description of calculation methods.

from a single nutrient addition and using a linear model. We have demonstrated that values of U_t for NO_3^- and NH_4^+ cannot be effectively estimated with a single short-term addition using our data from Kings Creek, and the same result has been demonstrated for NH_4^+ in 11 other streams.

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