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Estimation of stream nutrient uptake from nutrient addition experiments

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Abstract

Nutrient uptake in streams is often quantified by determining nutrient uptake length. However, current methods for measuring nutrient uptake length are often impractical, expensive, or demonstrably incorrect. We have developed a new method to estimate ambient nutrient uptake lengths using field experiments involving several levels of nutrient addition. Data analysis involves plotting nutrient addition uptake lengths versus added concentration and extrapolating to the negative ambient concentration. This method is relatively easy, inexpensive, and based on sound theoretical development. It is more accurate than the commonly used method involving a single nutrient addition. The utility of the method is supported by field studies directly comparing our new method with isotopic tracer methods for determining uptake lengths of phosphorus, ammonium, and nitrate. Our method also provides parameters for comparing potential nutrient limitation among streams.

Nutrient uptake is a central ecosystem function of streams. Uptake by the stream biota largely controls retention of nutrients, and nutrient uptake is a potential control of rates of autotrophic and heterotrophic metabolism. As a fundamental ecosystem process, nutrient uptake is related to both basic ecological research and management issues concerning transport of nutrients by streams.

Human activities have had a profound effect on the cycling of nutrients in both terrestrial and aquatic ecosystems (e.g., Vitousek et al. 1997). The significance of streams as nutrient vectors from terrestrial catchments to receiving bodies of water (Peterson et al. 2001) is growing as increased deposition has exceeded the capacity of many terrestrial ecosystems to transform nutrients to immobile (insoluble) forms. However, in addition to being nutrient vectors, significant transformation and retention of nutrients may occur within streams themselves. Consequently, studies of stream capacity to transform and retain dissolved nutrients are important to understanding the impact and possible remediation of human activity on global nutrient cycles. For example, Peterson et al. (2001) used ^{15}N to measure uptake of inorganic nitrogen in small streams throughout North America. Their results indicated that small streams are important sites of nitrogen retention, and they suggested that small stream management may reduce nitrogen loading to downstream rivers, lakes, estuaries, and oceans.

In streams, nutrients are continually transformed from dissolved inorganic forms to particulate organic and eventually back to dissolved inorganic as they are transported downstream. This coupling of nutrient cycling and downstream transport was described as spiraling (Webster and Patten 1979). Subsequently, Newbold et al. (1981) and Elwood et al. (1983) developed metrics to describe stream nutrient spiraling. Spiraling length is the average downstream distance each nutrient atom travels as it completes a cycle from inorganic to organic and back to inorganic. Usually the majority of spiraling length is uptake length, the average distance a nutrient atom travels in dissolved inorganic form before it is immobilized by either biotic or abiotic processes (Ball and Hooper 1963; Stream Solute Workshop 1990; Newbold 1992). In addition to extensive use in studies of relatively undisturbed streams (e.g., Webster et al. 2003), nutrient uptake length has been used to measure stream response to forest and riparian management (Webster et al. 1991; D'Angelo and Webster 1991; Sabater et al. 2000; Valett et al. 2002), waste water treatment plant effluent (Haggard et al. 2001), and dam removal (Doyle et al. 2003). Accurate, convenient, and inexpensive

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measurements of nutrient uptake length are needed to assess stream ecosystem function as well as to allow for comparisons of response to management actions.

Several methods have been developed to measure nutrient uptake length in streams. The use of ^{32}P (and ^{33}P) tracer has been an extremely informative tool in stream ecology since it was first used in the Sturgeon River by Ball and Hooper (1963). Elwood and others used radioactive phosphorus as a tracer to measure uptake of phosphorus in Walker Branch, TN (Elwood and Nelson 1972; Newbold et al. 1983; Mulholland et al. 1985), and similar studies of phosphorus have been conducted at a few other sites (e.g., Gregory 1978; Hart et al. 1991; Mulholland et al.1997). However, health and safety concerns have made it impractical to use radioisotopes in most streams. Recently, the use of stable isotope tracers, particularly ^{15}N, has become a powerful tool for studying in-stream nutrient processes (e.g., Peterson et al. 1997), but the high cost of isotopically enriched material and analysis by mass spectrometry limit the use of this technology. An alternative method is to raise the in-stream nutrient concentration above ambient conditions and use the downstream disappearance of added nutrient to quantify uptake length (Webster and Ehrman 1996). This method is simple, fairly inexpensive, and widely used (e.g., Munn and Meyer 1990; Webster et al. 1991; Hart et al. 1991, 1992; Webster et al. 2000). However, studies by Mulholland and others have demonstrated that this method clearly overestimates uptake lengths of both phosphorus (Mulholland et al. 1990) and nitrogen (Mulholland et al. 2002).

Our objective in this paper is to describe the theoretical background for a simple and low cost method for determining nutrient uptake length under ambient conditions without radioactive or stable isotopes. We also provide experimental data from other studies to assess the effectiveness of this approach. We show that this new approach provides a more accurate and theoretically sound determination of nutrient uptake length in streams than the commonly used approach involving a single nutrient addition and analysis of the longitudinal rate of decline of the added nutrient.

Theoretical considerations—In a stream with steady-state channel nutrient concentration, nutrient inputs and outputs must be equal. Inputs include fluxes from benthic storage (mineralization) and external inputs (e.g., groundwater). Outputs include uptake of nutrients moving from the channel water to benthic storage or, occasionally, to external compartments (tree root uptake or degassing to the atmosphere). The mechanisms of uptake may be a combination of many biological and physical processes such as microbial assimilation and sediment sorption. As long as the downstream flux of nutrients is constant with time and distance, input must be equal to uptake ($I_{AMB} = U_{AMB}$, Fig. 1A). Under these conditions, uptake length (S_w) is

$$S_W = \frac{QC_{AMB}}{wU_{AMB}} \quad (1)$$

where Q is discharge, w is average stream width, and C_{AMB} is the ambient nutrient concentration of the stream (Newbold et al. 1981). Though ambient conditions are frequently termed "background," the term "ambient" is used in this paper for consistency.

The relationship between uptake and concentration of a limiting nutrient generally shows an asymptotic approach to a maximum and is frequently described using the Michaelis-Menten equation, which was originally used to model enzyme kinetics and frequently used to characterize kinetics of mixed microbial assemblages (e.g., Dodds et al. 1991):

$$U = \frac{U_{MAX}C}{C_{HALF} + C} \quad (2)$$

where U is uptake, C is water column nutrient concentration, U_{MAX} is the maximum uptake capacity of the stream, and C_{HALF} is the concentration at which half the maximum uptake is realized (e.g., Mulholland et al. 2002). The maximum uptake and half concentration values for a given nutrient and stream are measures of the potential for the nutrient to limit biological activity in the stream, depending on the ambient concentration of the nutrient.

Combining Eq. 1 and Eq. 2 for ambient (i.e., background) conditions ($C = C_{AMB}$ and $U = U_{AMB}$), ambient uptake length is:

$$S_W = \frac{QC_{AMB}}{w\left(\frac{U_{MAX}C_{AMB}}{C_{HALF} + C_{AMB}}\right)} \quad (3)$$

Isotopic tracer studies—The objective of isotope tracer studies is to label the nutrients of a stream without increasing ambient concentration. Uptake is assessed by adding a very small amount of labeled material to the water column and then measuring the decline of that label downstream (Fig. 1B). The validity of isotope tracer results depends on several approximations. First, during these isotope tracer studies, the overall nutrient concentration is not significantly changed, and the stream is not disturbed from steady state. Second, any input fluxes in the reach have a similar isotopic signature to that of the stream ambient concentration. Third, the introduced isotope must fully mix with the naturally occurring isotope. Finally, there is no mineralization of the assimilated isotopic tracer. If benthic storage is labeled for more than a few hours, mineralization will ultimately have the same isotopic signature as the upstream water column. Therefore, isotope studies are generally performed over short time periods to minimize mineralization of the isotopic tracer. If these four approximations are reasonable, the isotopic tracer technique will give an uptake length equal to the ambient uptake length, that is, the uptake length at ambient nutrient concentration in the water column (S_W).

Nutrient addition studies—Uptake length has also been measured by artificially elevating nutrient concentration for a short period. Uptake rate per unit length is measured as the downstream decrease of nutrient concentration (Fig. 1C).

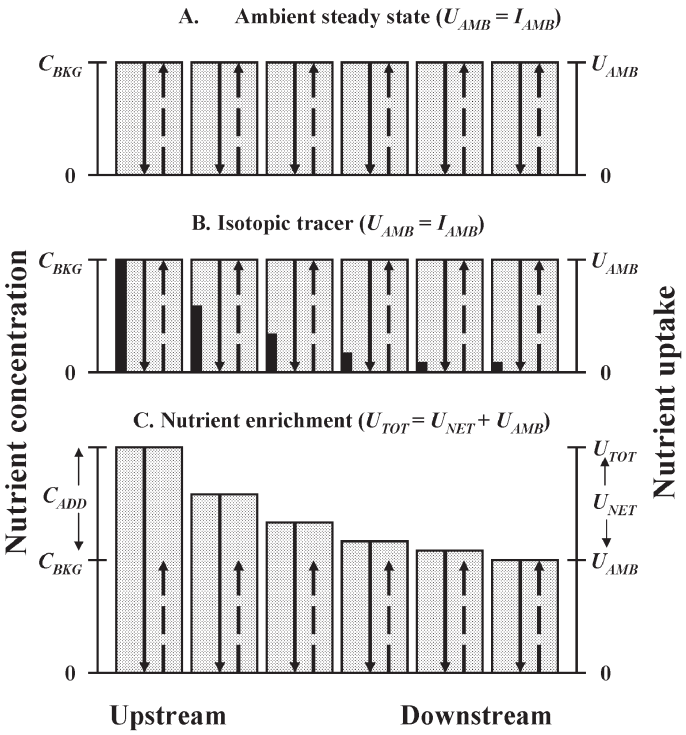

Fig. 1. Conceptual diagram of uptake length measurement. Symbols are defined in the text. Bars indicate nutrient concentrations at sequential downstream points, solid arrows indicate uptake fluxes, and dashed arrows indicate input fluxes. (A) Stream at steady state. Uptake fluxes are balanced with input fluxes and nutrient concentrations remain constant along the reach. (B) Isotopic tracers (black bars) added to mark the ambient concentration and measure ambient uptake length. The black isotope tracer bars should actually be several orders of magnitude smaller than illustrated. Ambient concentrations are not changed significantly by the isotope tracer addition and the stream is still at steady state. (C) Stream steady state altered with a nutrient addition and net uptake length measured from the downstream return to ambient values. Uptake increases above ambient values when the nutrient concentration is increased above ambient values.

Uptake length is then the inverse of this uptake rate. However, the uptake rate measured in this manner is not the ambient uptake rate. An elevation in stream nutrient concentration may cause an increase in uptake, depending on the functional relationship between uptake rate and concentration (e.g., Eq. 2). There is also no way to distinguish the added nutrient from ambient input fluxes. Therefore, the observed uptake is also a function of the input nutrient flux to the reach. The observed uptake in a nutrient addition experiment is the difference between the overall uptake flux in the stream (U_{TOT}) and the input flux (I_{AMB}), which we call net uptake (U_{NET}):

$$U_{NET} = U_{TOT} - I_{AMB}. \quad (4)$$

It is probably reasonable to assume mineralization and other inputs are not affected by increased nutrient concentrations on the time scales of most stream addition experiments (several hours), so U_{AMB} can be substituted for I_{AMB} in Eq. 4:

$$U_{NET} = U_{TOT} - U_{AMB}. \quad (5)$$

Then, U_{AMB} can be represented as a Michaelis-Menten function of the ambient nutrient concentration and U_{TOT} as a Michaelis-Menten function of total nutrient concentration, that is, added concentration (C_{ADD}) plus C_{AMB} (Mulholland et al. 2002):

$$U_{NET} = \frac{U_{MAX}\left(C_{AMB} + C_{ADD}\right)}{C_{HALF} + \left(C_{AMB} + C_{ADD}\right)} - \frac{U_{MAX}C_{AMB}}{C_{HALF} + C_{AMB}}. \quad (6)$$

The uptake length observed in addition experiments ($S_{W(ADD)}$) can then be expressed as a function of net uptake and the nutrient concentration added to the stream using Eq. 1:

$$S_{W(ADD)} = \frac{QC_{ADD}}{w\left(\frac{U_{MAX}\left(C_{AMB} + C_{ADD}\right)}{C_{HALF} + \left(C_{AMB} + C_{ADD}\right)} - \frac{U_{MAX}C_{AMB}}{C_{HALF} + C_{AMB}}\right)}. \quad (7)$$

The differences in uptake lengths observed by the two experimental methods (isotopic tracers versus nutrient addition) directly result from manipulations of in-stream nutrient concentration and the asymptotic, nonlinear response of physical, chemical, and biological uptake. This is the root of the consistent overestimation of ambient uptake length by addition experiments (Mulholland et al. 1990, 2002).

Net uptake length versus ambient uptake length—Mulholland et al. (2002) showed that for nutrient addition studies at multiple enrichment levels, both the theoretical and modeled net uptake lengths lie on a straight line (Fig. 2). The equation for this line can be derived from Eq. 7:

$$S_{W(ADD)} = \frac{Q\left(C_{HALF} + C_{AMB}\right)^2}{wU_{MAX}C_{HALF}} + C_{ADD}\left[\frac{Q\left(C_{HALF} + C_{AMB}\right)}{wU_{MAX}C_{HALF}}\right] \quad C_{ADD} \neq 0 \quad (8)$$

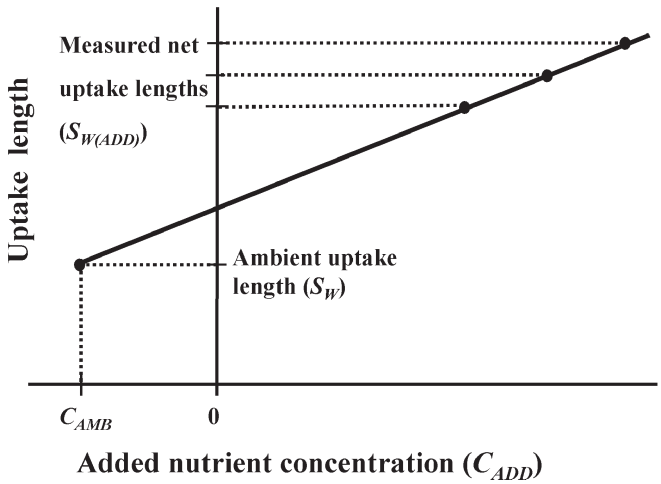

Fig. 2. Theoretical plot of uptake length versus added nutrient concentration for a series of nutrient additions.

Table 1. Results of simulations of nutrient uptake in streams*

Ambient concentration ($\mu g\ L^{-1}$)	Extrapolated uptake length (m)	Theoretical uptake length (m)	Extrapolated U_{MAX} ($\mu g\ m^{-2}\ s^{-1}$)	Extrapolated C_{HALF} ($\mu g\ L^{-1}$)
2	15.8	14.7	5.0	22.0
10	21.5	20	4.9	21.8
40	41.8	40	4.9	21.0

*Extrapolated uptake length was calculated by regressing addition measured net uptake length ($S_{W(ADD)}$) versus added nutrient (C_{ADD}) and extrapolating to negative ambient concentration. Theoretical uptake lengths were calculated directly from the parameters used in the model (Eq. 1). Extrapolated Michaelis-Menten parameters were calculated as described in the text. Actual U_{MAX} used in the model was 5 $\mu g\ m^{-2}\ s^{-1}$ and C_{HALF} was 20 $\mu g\ L^{-1}$.

The discontinuity in Eq. 8 when $C_{ADD} = 0$ is due to division by zero in Eq. 7. This implies that it is impossible to measure net uptake length without some change in concentration.

One method for estimating ambient uptake from nutrient addition studies has been to extrapolate uptake length measurements from multiple-level injections to the y-intercept ($C_{ADD} = 0$) using a linear relationship between uptake and nutrient concentration (Dodds et al. 2002). However, this method has been shown to overestimate ambient uptake length (Mulholland et al. 2002) and underestimate uptake rate (Dodds et al. 2002). Because Eq. 8 is linear, there must be some added concentration (C_{ADD}) at which net uptake length equals the ambient uptake length ($S_{W(ADD)} = S_W$). The expressions for net uptake length (Eq. 7) and ambient uptake length (Eq. 3) are equal when the added concentration is equal to negative ambient concentration ($C_{ADD} = -C_{AMB}$). This suggests that ambient uptake length can be estimated by extrapolating a series of linear net uptake lengths to the negative ambient concentration (Fig. 2).

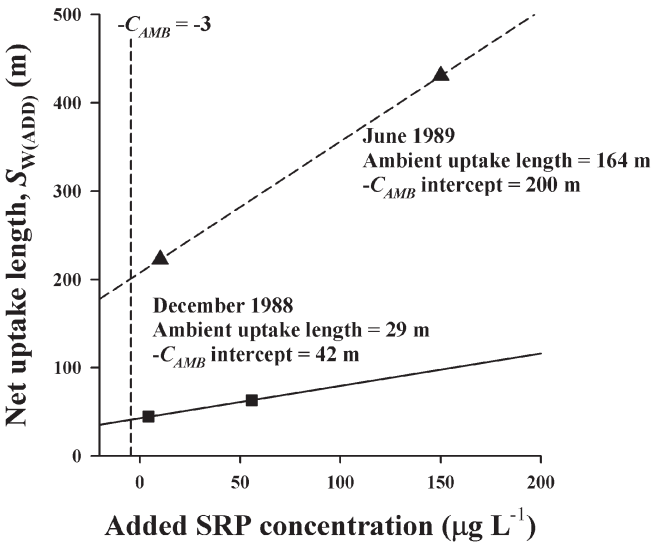

Fig. 3. Results of extrapolation using data from phosphate (SRP) releases on Walker Branch, TN (Mulholland et al. 1990). Net uptake lengths were calculated from two-level additions in December 1988 and June 1989. Ambient uptake lengths were determined by radioactive isotopic tracer releases of $^{33}PO_4$. SRP concentrations are the geometric mean of the study reach samples corrected for ambient concentrations. The dotted line is drawn at the negative ambient SRP concentration.

The logical implication of negative nutrient addition is a nutrient removal study. "Uptake length" for negative addition would be a measure of the stream capacity to recover ambient concentrations downstream from artificially lowered upstream levels. A nutrient removal study is probably impractical, but our derivation provides a theoretically sound method for estimating ambient uptake length from nutrient addition experiments.

Materials and procedures

Procedures for nutrient addition experiments were described in detail by Webster and Ehrman (1996). In general, a concentrated solution of nutrient and conservative solute (such as chloride) is delivered to a stream at a constant rate for several hours until nutrient and conservative solute reach constant concentrations. Water samples are then collected at various points downstream and analyzed for nutrient and conservative solute concentration. The natural logarithm of the added nutrient concentration (nutrient concentration corrected for ambient conditions and dilution) is then regressed against distance. The negative inverse of the slope of this line is the net uptake length ($S_{W(ADD)}$). This procedure is followed for several higher enrichment levels under similar stream conditions. The measured values of net uptake length are then regressed against the added nutrient concentration, and the line is extrapolated to negative ambient nutrient concentration where the y value is then the estimated value of S_W (Fig. 2).

A simpler technique is a single addition over a sufficiently long reach so sub-reaches can be analyzed as separate experiments with different enrichment levels. However, the validity of this approach requires a long, uniform reach where there is a constant relationship between uptake and concentration.

Assessment

Simulation—A computer model was used to test the validity of the theoretical analysis presented above. The model was written in C++ to simulate active solute transport under advective and dispersive conditions. Crank-Nicholson finite difference approximations were used to solve the partial differential equation:

$$\frac{\partial C}{\partial t} = E\frac{\partial^2 C}{\partial x^2} - u\frac{\partial C}{\partial x} - U_V \quad (9)$$

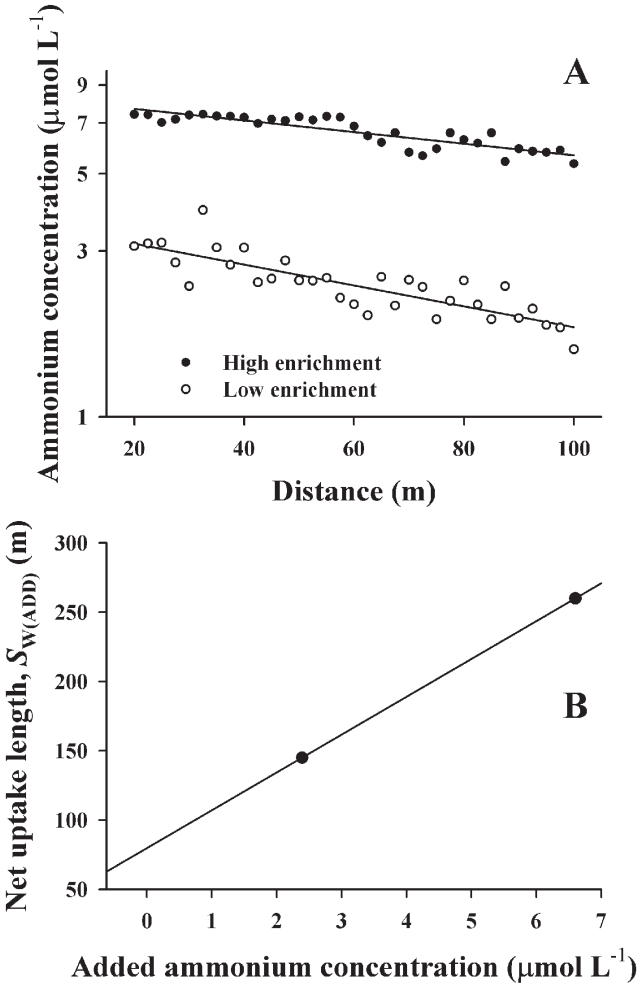

Fig. 4. Results of two-level ammonium addition (A) and extrapolation (B) using data from Kings Creek, KS (Dodds et al. 2002). Uptake lengths were calculated for each level of addition and plotted against the geometric mean of the study reach ammonium concentration corrected for ambient concentrations. In B, the y axis is drawn at the negative ambient ammonium concentration.

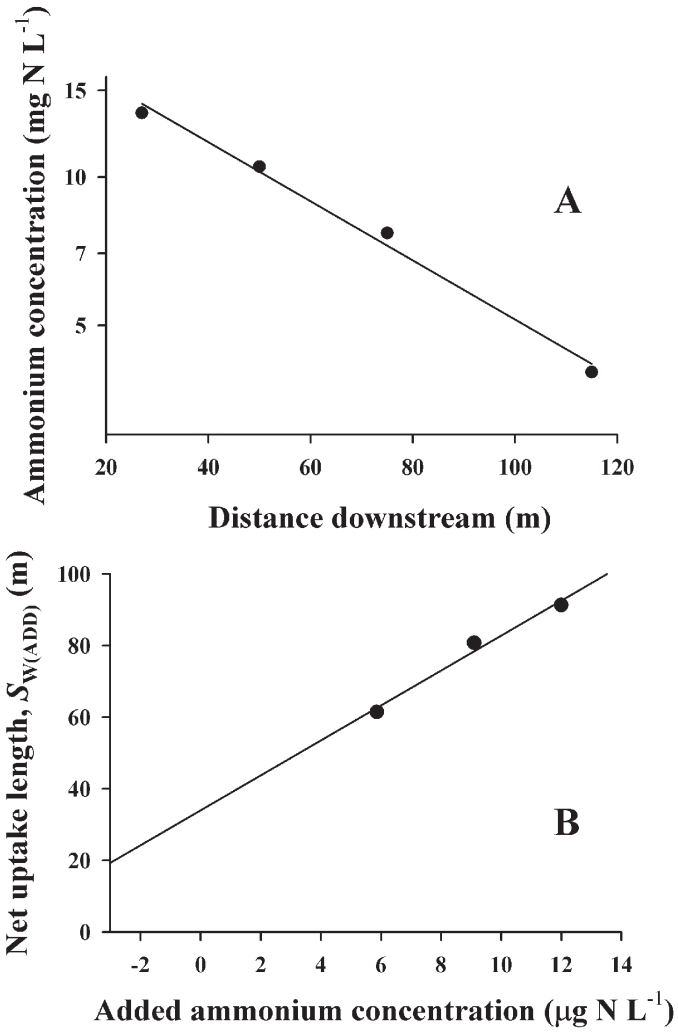

Fig. 5. Results of ammonium addition (A) and extrapolation (B) using data from Ball Creek, NC (Tank et al. 2000). Uptake lengths were calculated from the three sub-reaches during the single addition. Ammonium-N concentrations in B are the geometric mean of each sub-reach data set corrected for ambient concentrations. In B, the y axis is drawn at the negative ambient ammonium concentration.

where C is the nutrient concentration in the channel (mass per volume), t is time, x is distance downstream, E is a dispersion coefficient, u is mean velocity, and U_V is the uptake by volume. Uptake was modeled using a volumetric version of Eq. 6 with C_{HALF} = 20 μg L^{-1} and U_{MAX} = 5 μg m^{-2} s^{-1}.

A nutrient addition step function was applied as an upstream model input (boundary condition), and the model was run over enough time to reach constant concentrations. The simulation was repeated for multiple values of enrichment, and uptake length was calculated from the change in nutrient concentration with distance downstream. The regression-extrapolation method described above was used to estimate ambient uptake for the modeled stream and compared to the theoretical ambient uptake calculated from the values of C_{AMB}, C_{HALF}, and U_{MAX} used as model parameters.

The simulated stream had a discharge of 10 L s^{-1}, an average width of 3 m, an average depth of 10 cm, and a dispersion coefficient of 0.5 m^2 s^{-1}. Simulations were run at ambient levels of 2, 10, and 40 μg L^{-1}. Additions were modeled at added concentrations of 20, 40, 60, and 80 μg L^{-1}. We simulated the concentration of added nutrients with distance downstream to the point where added nutrient had been reduced to 50% of the upstream value.

When plotting and regressing simulated uptake length data, we plotted measured or simulated uptake length versus the geometric mean of the nutrient concentration over the reach. The theoretical uptake length calculated from Eq. 8 corresponds to the instantaneous uptake at any point in the reach. However, modeled or empirical uptake lengths correspond to an average

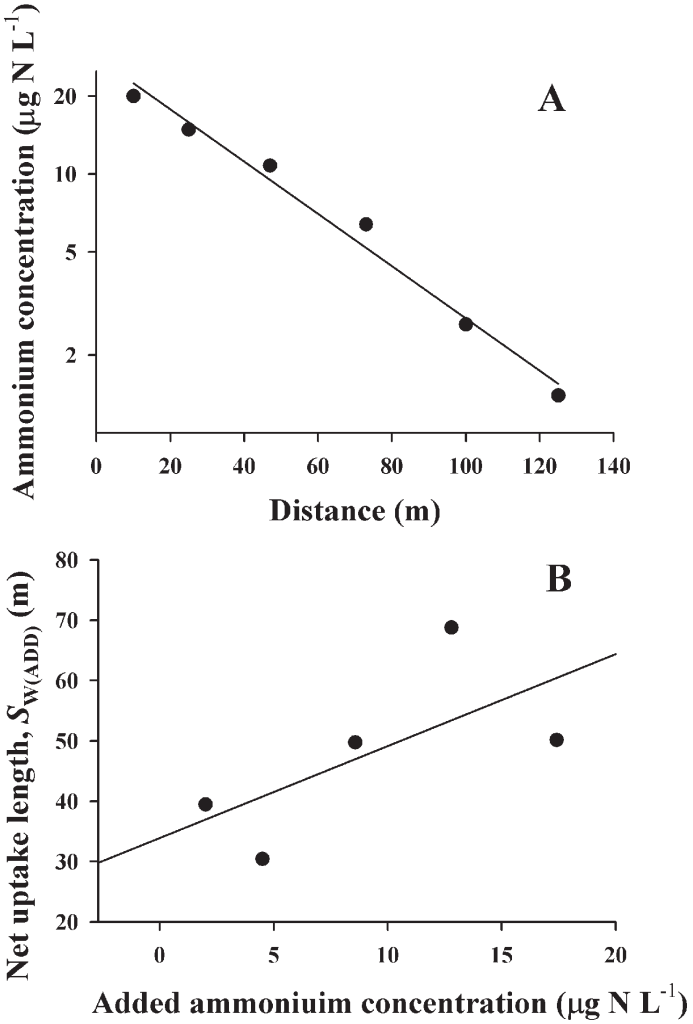

Fig. 6. Results of ammonium addition (A) and extrapolation (B) using data from Walker Branch, TN (Mulholland et al. 2000). Uptake lengths were calculated from the five sub-reaches during the single addition. Ammonium-N concentrations in B are the geometric mean of each sub-reach data set corrected for ambient concentrations. In B, the y axis is drawn at the negative ambient ammonium concentration.

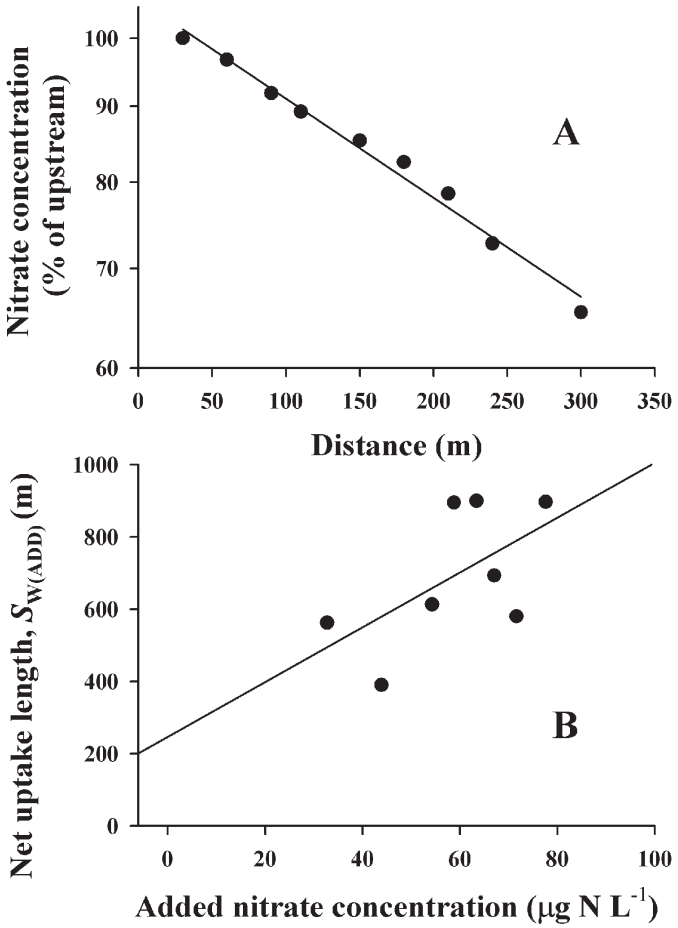

Fig. 7. Results of nitrate addition (A) and extrapolation (B) using data from Hugh White Creek, NC (Webster, Valett, and B. Niederlehner, unpublished data). Uptake lengths were calculated from the eight sub-reaches during the single addition. Nitrate-N concentrations in B are the geometric mean of each sub-reach data set corrected for ambient concentrations. In B, the y axis is drawn at the negative ambient nitrate concentration.

over a finite reach over which the added nutrient concentration is declining. Because nutrient concentration is declining approximately exponentially, the geometric mean is appropriate.

From these simulations, the extrapolation method was a good estimator of theoretical ambient uptake lengths (Table 1). Calculated uptake lengths were slightly greater than theoretical values, but we were able to estimate the theoretical ambient uptake length to within 7.5%.

Empirical assessment—There are a growing number of studies where nutrient uptake has been measured by both isotopic tracers and by addition, which we can use for empirical assessment of our technique. Mulholland et al. (1990) conducted two sets of $^{33}PO_4$ and phosphate addition releases in Walker Branch, TN. The releases occurred on consecutive days in December 1988 and on the same day in June 1989. In December, they measured net uptake lengths of 45 m at low enrichment and 67 m at high enrichment. When we extrapolated the regression line to the negative ambient phosphorus concentration (Fig. 3), we estimated an ambient uptake length of 42 m compared to their value measured with ^{33}P of 29 m. Similar analysis of the June data, where they measured net uptake length of 222 m at low enrichment and 455 m at high enrichment, produced a $-C_{AMB}$ intercept of 200 m compared to the ^{33}P-measured ambient uptake length of 164 m (Fig. 3). In this example, our extrapolation technique was not much better at estimating ambient uptake length than was net uptake length measured with very low enrichment.

As part of the Lotic Intersite Nitrogen Experiment (LINX) project, $^{15}NH_4$ was used as an isotopic tracer to measure ammonium uptake, and at each site net, ammonium uptake length was also measured with a single or multiple levels of ammonium enrichment (Peterson et al. 2001; Webster et al.

Table 2. Comparisons of uptake lengths determined from single nutrient additions, extrapolation from multiple additions, and isotope studies*

Stream	Data source	Nutrient	Discharge (L s^{-1})	C_{AMB} (µg L^{-1})	S_W from single nutrient addition (m)	S_W from extrapolation (m)	S_W from isotope (m)	Uptake (µg N m^{-2} s^{-1})	C_{HALF} (µg N L^{-1})	U_{MAX} (µg N m^{-2} s^{-1})	C_{AMB}/C_{HALF}
Walker Branch, TN, Dec 1988	Mulholland et al. (1990)	SRP	2.7	3	45 (low addition) 67 (high addition)	42	29				
Walker Branch, TN, Jun 1989	Mulholland et al. (1990)	SRP	9.4	3	222 (low addition) 455 (high addition)	200	164				
Kings Creek, KS	Dodds et al. (2000, 2002)	NH_4-N	2	8.7	145 (low addition) 260 (high addition)	62	38	0.16	32	0.36	0.27
Ball Creek, NC	Tank et al. (2000)	NH_4-N	43	3.0	65	22	28	2.17	6	1.88	0.42
Walker Branch, TN	Mulholland et al. (2000)	NH_4-N	9.6	2.7	45	30	23	0.28	14	1.53	0.19
Hugh White Creek, NC	Webster et al. (unpubl. data unref.)	NO_3-N	14.4	6	652	201	268				

*For the three ammonium uptake studies, we also show uptake and Michaelis-Menten parameters calculated from the multiple-addition extrapolations.

2003). At Kings Creek, KS, ammonium was enriched to two levels (Fig. 4A). For the higher level, $S_{W(ADD)}$ was 260 m, and for the lower enrichment, $S_{W(ADD)}$ was 145 m. Plotting these values versus C_{ADD} and extrapolating to a negative ambient ammonium concentration of 0.62 µmol L^{-1}, we calculated S_W of 62 m compared to 38 m estimated by a $^{15}NH_4$ tracer experiment (Dodds et al. 2000, 2002). For two of the LINX sites, the enrichment was over a sufficiently long reach that we were able to use consecutive pairs of sample collection points as sub-reaches for different enrichment levels. For Ball Creek, NC (Tank et al. 2000), $S_{W(ADD)}$ was estimated at 65 m over the entire reach (Fig. 5A). Using extrapolation to the negative ambient ammonium concentration, we estimated S_W at 22 m compared to $^{15}NH_4$-measured S_W of 28 m (Fig. 5B). At the other site, Walker Branch, TN (Mulholland et al. 2000), $S_{W(ADD)}$ was 45 m (Fig. 6A). From their data, we extrapolated (Fig. 6B) to S_W of 30 m compared to $^{15}NH_4$-measured S_W of 23 m. In each of these three examples of ammonium uptake, extrapolation gave a much better estimate of ambient uptake than did the addition method.

Nitrate uptake has been measured by both addition and isotopic tracers in Hugh White Creek, NC. A net nitrate uptake length of 652 m was measured by addition in May 2003 (Fig. 7A) (Webster et al. unpubl. data unref.). Extrapolation using downstream sub-reaches from this one addition experiment gave an estimate of S_W of 201 m (Fig. 7B). When uptake was measured 3 days later with ^{15}N, S_W was 268 m. Nitrate uptake length was also measured with ^{15}N tracer in this same stream reach in May 2000 (Valett et al. unpubl. data unref.) as 125 m at a much lower discharge.

Comments and recommendations

Using modeled data, extrapolation of net uptake length to $-C_{AMB}$ provided a close approximation of ambient uptake length. In addition, the cited empirical studies suggest this estimation method may be more useful than previous analyses of field data (Table 2). However, we have been involved with a number of other studies where the use of a long reach as a series of multiple enrichments did not work well because of variability along the reach. For example, the data from Kings Creek (Fig. 4A) clearly indicate variable uptake over the 100-m reach. Thus, the ideal way to apply the extrapolation approach for estimating ambient uptake length is to conduct multiple experiments under the same conditions over the same reach.

The slope and zero intercept of the regression line relating $S_{W(ADD)}$ to C_{ADD} can also be used to estimate Michaelis-Menten nutrient uptake parameters. If the expressions for slope and intercept in Eq. 8 are set equal to the regression determined values, these two equations can be solved simultaneously for the two unknowns, U_{MAX} and C_{HALF}. These whole stream Michaelis-

Menten parameters can potentially be used to characterize nutrient limitation of steams. For example, the ammonium half saturation concentrations were 6 μg L^{-1} for Ball Creek, 14 μg L^{-1} for Walker Branch, and 32 μg L^{-1} for Kings Creek (Table 2), suggesting that organisms in Ball Creek had more efficient ammonium uptake at lower ammonium concentration than did organisms in the other two streams. Based on the ratio of C_{AMB} to C_{HALF}, uptake in Ball Creek was closer to being limited by ammonium availability, but because of the very high U_{MAX}, ammonium uptake in Ball Creek, was nearly ten times as great as in the other two streams. These observations are probably overextended given the single measurements in each stream, but they illustrate the types of comparisons that might be possible from replicated studies. Appropriate replication has not been possible with current tracer techniques.

Ambient nutrient levels were very low in all of our cited empirical examples (Table 2), thus approximation of S_W by $S_{W(ADD)}$ measured at low C_{ADD} does not cause major error (Mulholland et al. 2002). At higher ambient nutrient levels, the extrapolation method may be more useful. Streams are not simply nutrient conduits, and the ability to efficiently and inexpensively measure nutrient spiraling parameters of streams is an important tool in understanding how nutrients are modified as they are transferred from terrestrial to freshwater and eventually to marine ecosystems.

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