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10, 6671–6693, 2013

**Solute specific
scaling of inorganic
nitrogen**

R. O. Hall Jr. et al.

Solute specific scaling of inorganic nitrogen and phosphorus uptake in streams

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Received: 4 April 2013 – Accepted: 4 April 2013 – Published: 10 April 2013

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Published by Copernicus Publications on behalf of the European Geosciences Union.

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Abstract

Stream ecosystem processes such as nutrient cycling may vary with stream position in the watershed. Using a scaling approach, we examined the relationship between stream size and nutrient uptake length, which represents the mean distance that a dissolved solute travels prior to removal from the water column. Ammonium uptake length increased proportionally with stream size measured as specific discharge (discharge/stream width) with a scaling exponent = 1.01. In contrast, the scaling exponent for nitrate (NO_3^-) was 1.19 and for soluble reactive phosphorus (SRP) was 1.35, suggesting that uptake lengths for these nutrients increased more rapidly than increases in specific discharge. Additionally, the ratio of nitrogen (N) uptake length to SRP uptake length declined with stream size; there was lower demand for SRP relative to N as stream size increased. Ammonium and NO_3^- uptake velocity positively related with stream metabolism, while SRP did not. Finally, we related the scaling of uptake length and specific discharge to that of stream length using Hack's law and downstream hydraulic geometry. Ammonium uptake length increased less than proportionally with distance from the headwaters, suggesting a strong role for larger streams and rivers in regulating nutrient transport.

1 Introduction

One of the most elegant applications of the ecosystem concept (O'Neill, 2001) has been to define the boundary or edge of an ecosystem and quantify the functioning (e.g. material cycling or energy flow) within this spatially explicit unit, as did Bormann and Likens (1967) for a small watershed. When ecosystems are well bounded (Post et al., 2007), we predict that as they change size, attributes will change concurrently. For example, dissolved solute concentrations in streams vary with the size of the drainage basin (Likens and Buso, 2006). Further, position in a watershed can determine chemical attributes of lakes (Kratz et al., 1997; Soranno et al., 1999). Despite these patterns,

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there are few quantitative relationships linking ecosystem processes and, for example, position in a drainage network. (Ensign and Doyle, 2006). Here we use an allometric scaling approach applied to stream ecosystems to examine how nutrient uptake rates in streams vary as a function of system size measured as specific discharge and position in the watershed.

Streams and rivers are well bounded laterally by their banks, but are open longitudinally. Because of this property, ecologists have developed a scale-independent means of measuring nutrient cycling: uptake length, which is the average distance a nutrient molecule travels before being removed from the water column via biotic processes (Newbold et al., 1981; Webster and Patten, 1979). Uptake length is estimated from the inverse of a first-order uptake rate of nutrients experimentally added to the water column of a stream (Newbold et al., 1981). This metric is scale independent in the sense that the length of stream chosen should not influence the value of the measured uptake length. However stream discharge and width will strongly regulate how far nutrients will travel (Tank et al., 2008). The nutrient spiraling approach combines both hydrologic and biologic controls on nutrient uptake in flowing waters and also quantifies the degree to which upstream reaches are functionally linked to downstream reaches or other ecosystem types, e.g. a lake (Arp and Baker, 2007). For example, if streams and rivers have short uptake lengths, on the order 10–100s of meters, then nutrient transport downstream may be mitigated (Mulholland et al., 2008). The role of small streams in removing dissolved nutrients has been well studied, with > 970 nutrient uptake experiments (Ensign and Doyle, 2006; Tank et al., 2008).

Nearly all nutrient uptake experiments have been conducted in small streams (Tank et al., 2008). Considering how nutrient uptake scales with stream discharge allows initial evaluation of the degree to which large streams and rivers may regulate downstream transport of nutrients. Given a lack of empirical data, researchers have conservatively assumed that nutrient demand is constant throughout a river network (Wollheim et al., 2006). Using a meta-analysis of previously published data, here we examine how nutrient uptake scales with stream specific discharge to both test the

assumption of constancy by Wollheim et al. (2006) and to begin to predict how larger lotic ecosystems might function.

Although there are much data on how streams cycle either nitrogen (N) or phosphorus (P), fewer studies examine how these elements cycle together. Cross et al. (2005) posited that elemental concentrations of benthic organisms will drive uptake of N relative to P, and if elemental composition were to change then it would alter the ratio of N vs. P uptake. Also, while the processes that remove inorganic N are mainly biotic and include a combination of assimilatory and dissimilatory processes, those that remove inorganic P have an additional abiotic component driven by sorption/desorption processes, including a significant role of suspended particles. Therefore, we hypothesized that N and P uptake could be decoupled, and as such the stoichiometry of nutrient demand may vary along a river network. Therefore we predicted that N removal would be in part a function of rates of carbon metabolism, whereas P uptake would be independent of metabolism.

Here we compare the demand for inorganic N (as ammonium, NH_4^+ and nitrate NO_3^-) and inorganic P (as soluble reactive phosphorus, SRP) by scaling nutrient uptake length as a function of specific discharge using previously published data on nutrient uptake. Given these scaling relationships between specific discharge and nutrient uptake length, we use scaling rules from fluvial geomorphology and hydrology (Dodds and Rothman, 2000; Leopold and Maddock, 1953; Rigon et al., 1996) to predict how nutrient uptake length changes along a river continuum.

2 Methods

2.1 Scaling nutrient uptake length from existing studies

We first relate uptake length, S_w , with specific discharge, Q/w , where Q is stream discharge ($\text{m}^3 \text{min}^{-1}$) and w is average wetted stream width (m). We choose this metric because it enables calculating uptake velocity v_f (m min^{-1}), a stream size-independent

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measure of nutrient demand (Stream Solute Workshop, 1990), which can be interpreted as biotic demand relative to nutrient concentration and is calculated as:

$$v_f = \frac{Q/w}{S_w} \quad (1)$$

We then test how specific discharge relates to nutrient uptake by scaling uptake length as a function of specific discharge. Rearranging Eq. (1):

$$S_w = \frac{Q/w}{v_f} \quad (2)$$

suggests that S_w will increase as Q/w increases while v_f will decrease with higher biological demand (v_f). Thus we propose a null model that if v_f is constant along a gradient of increasing Q/w , this will result in a scaling prediction of $S_w \propto (Q/w)^1$. In other words, given constant biological demand relative to concentration (measured as v_f) across a range of Q/w , S_w should increase at the same rate as Q/w and have a scaling exponent of 1. Using a meta-analysis of nutrient uptake experiments, we tested how much scaling exponents differed from 1 for each of the 3 solutes.

We gathered literature data on nutrient uptake in streams from recent reviews on nutrient spiraling in streams and rivers (Ensign and Doyle, 2006; Tank et al., 2008) plus other studies published after these two meta-analyses (Supplement). In addition we used unpublished data from a stream in Idaho (B. J. Koch, unpublished data), a stream in Venezuela (A. S. Flecker et al., unpublished data) and one in Yellowstone National Park (Tronstad et al., unpublished data), several streams in New Zealand (J. L. Tank, unpublished data) and an urban stream in Laramie, WY, (R. O. Hall, unpublished data) for a total of 969 separate nutrient uptake experiments. We included streams which authors identified as being located in areas of intense human activity such as agricultural and urban streams, but we analyzed these data separately from less altered streams. Most streams in the dataset were relatively small, reflecting the predominance of research carried out in small streams; 90 % of streams in this data set had discharge

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between 2–700 L s^{-1} with a median of 35 L s^{-1} . We also collated data on open-channel rates of gross primary production (GPP) and ecosystem respiration (ER) if they were measured in conjunction with the nutrient uptake experiments (Supplement). When individual streams included multiple measurements, using R package *plyr* (Wickham, 2011), we averaged Q/w and S_w to avoid bias toward streams with many measurements. Our dataset includes nutrient additions using three different solutes: NH_4^+ , NO_3^- and SRP.

For the scaling regressions we calculated slopes and their 95 % confidence intervals using standardized major axis (SMA) regression package (S)MATR in R (R Development Core Team, 2011). SMA regression minimizes variation in both x and y variables and thus better describes their relationship when the value of the slope is of biological interest in a symmetrical relationship (Warton et al., 2006). We also tested whether scaling relationships differed between reference and altered streams by testing if they shared a common slope and intercept (Warton et al., 2006). To relate metabolism with nutrient uptake we used ordinary least-squares regression.

2.2 Scaling nutrient uptake with stream length

Using the scaling coefficients calculated for NH_4^+ , NO_3^- , and SRP, we then estimated how uptake length will scale downstream from headwaters to a larger river (Vannote et al., 1980). We used stream length to define position in the watershed so that we could compare metrics having the same unit of length. We predict that nutrient uptake length (S_w) will scale as a function of specific discharge (Q/w) as

$$S_w \propto \left(\frac{Q}{w}\right)^a \quad (3)$$

where a is the scaling exponent measured in the above analysis. We relate stream width to discharge based on the power-law representation of stream hydraulic

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geometry:

$$w \propto Q^b \quad (4)$$

Combining Eq. (3) and Eq. (4), uptake length relates with Q as

$$Q \propto S_w^{\frac{1}{(1-b)a}} \quad (5)$$

5 Next we scaled discharge as a function of stream length from the headwaters. Hack's law states that the length of a stream from headwaters to the end of a watershed (L) will scale with drainage area (A) as

$$L \propto A^h \quad (6)$$

10 It is typically assumed that discharge (Q) scales with watershed area isometrically, but empirical work has demonstrated that

$$Q \propto A^c \quad (7)$$

(Galster, 2007). Substituting $Q^{1/c}$ for A and solving gives:

$$L^{\frac{c}{h}} \propto Q \quad (8)$$

Combining Eq. (5) and Eq. (8) and solving for S_w gives

$$15 S_w \propto L^{\frac{(1-b)ac}{h}} \quad (9)$$

The variables a , b , c , and h are not known with certainty, therefore we used a Monte Carlo approach to evaluate the expression

$$m = \frac{(1-b)ac}{h} \quad (10)$$

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For a , we assumed a normal distribution with mean as the estimate of the SMA regression slope and standard deviation as the standard error (se) of the regression for S_w for all 3 solutes versus Q/w in reference streams only (see results). We used a channel width exponent, b based on a meta analysis of downstream (as opposed to at-a-station) hydraulic geometry of channels (Singh, 2003). Often these data are collected at bankfull discharge, but there is variation in discharge regime among specific studies such that these data are calculated from a wide range of Q (Park, 1977). We used 38 estimates of worldwide rivers from Singh (2003); the mean was 0.47 and standard deviation was 0.13 and the distribution of b included the exponent derived from streams in our dataset (0.39). Hack's constant, h , was drawn from studies from 13 rivers (Rigon et al., 1996). For c we used data from 4 river networks with $c \sim 0.8$ (Galster, 2007); this value of $c < 1$ likely because of unequal distribution of rainfall in the headwaters areas of rivers (Galster, 2007). For b , h , and c , rather than assuming a distribution we randomly drew values from the range of values collected from the literature; we evaluated m 10 000 times and used the median and 5 % and 95 % quantiles to report variation on possible values.

3 Results

Ammonium uptake scaled isometrically with specific discharge (Q/w). The relationship had an SMA slope of 1.01 and a confidence interval including 1 (Fig. 1, Table 1), demonstrating that as Q/w increased, ammonium uptake increased at the same rate. Slopes of NH_4^+ uptake versus Q/w using data from human-altered streams were not different than those for reference streams, but the intercept was higher ($p = 0.0014$) showing that for equivalent Q/w , human-altered streams had longer uptake length, i.e., nutrients traveled farther.

Nitrate uptake length scaled with Q/w with a slope = 1.19, and the relationship included more variation compared to NH_4^+ (Fig. 1, Table 1). In contrast, the confidence interval for the slope did not include 1, suggesting that as Q/w increased, streams were

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less retentive of NO_3^- . Similar to the results for NH_4^+ , the slopes did not differ between reference and human-altered streams ($p = 0.65$), but the intercept for human-altered streams was higher ($p = 0.0001$) by 0.42, suggesting that uptake lengths averaged 2.6 ($10^{0.42}$) times longer in human-altered streams.

Soluble reactive phosphorus scaled with Q/w with a slope of 1.28, similar to NO_3^- , but the relationship for SRP had much less variation and smaller confidence intervals compared to the other two solutes (Fig. 1, Table 1). For SRP, human-altered streams shared the same regression slope ($p = 0.55$) and intercept ($p = 0.72$) as reference streams; however, there were fewer data for SRP uptake in human-altered streams compared to those for inorganic N species (Table 1).

Many streams had uptake length estimates for > 1 solute, either for both NH_4^+ and SRP, or both NO_3^- and SRP, thus we compared the ratio of inorganic N uptake length to SRP uptake lengths across a range of stream sizes. The ratio of $\log_{10} \text{NH}_4^+$ to SRP uptake length declined with increasing $\log_{10} (Q/w)$ indicating that as Q/w increased, the demand for NH_4^+ relative to SRP increased (Fig. 2). Nitrate showed the same pattern, with the ratio of $\log_{10} \text{NO}_3^-$ to SRP declining with increasing $\log_{10}(Q/w)$ (Fig. 2).

Reach-scale metabolism, reflecting carbon cycling, predicted NH_4^+ and NO_3^- but not SRP. Ammonium and NO_3^- uptake, expressed as uptake velocities (v_f), were positively related with \log_{10} total metabolism (GPP + ER) (Fig. 3), demonstrating that biological demand for carbon drove inorganic N uptake from stream water. In contrast, SRP uptake was unrelated to metabolism suggesting some other process regulated its uptake (Fig. 3).

The scaling exponent between distance from the headwaters (length) versus uptake length (Eq. 10), varied strongly because width (w) included variance in geomorphic scaling parameters b , based on hydraulic geometry (Table 1, Fig. 4). For NH_4^+ median $m_{\text{NH}_4} = 0.79$ with 5–95% confidence range of 0.47–1.19 (Fig. 4). Variation in b (scaling width as a function of Q) drove much of this variation because this parameter can vary strongly among river networks (Park, 1977; Singh, 2003). A median parameter estimate of 0.8 ($S_w \propto L^{0.80}$) suggested that uptake length of NH_4^+ will increase more slowly

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as one moves from the headwaters downstream (Fig. 5). Nitrate and SRP scaling exponents were larger, (median of $m_{\text{NO}_3} = 0.93$, 5–95 % confidence range 0.58 to 1.39 and median of $m_{\text{SRP}} = 1.06$, 5–95 % confidence range 0.66 to 1.59) (Fig. 4). These values suggest that uptake lengths of NO_3^- and SRP will increase at the same rate as downstream distance from the headwaters (Fig. 5).

4 Discussion

4.1 Differential uptake of NH_4^+ , NO_3^- and SRP

We have provided a scaling framework to examine how an ecosystem process such as nutrient uptake can vary as a function of stream size (measured as Q/w) and as distance increases downstream from the headwaters. Nutrient uptake lengths scaled differently with specific discharge such that NH_4^+ uptake scaled isometrically with Q/w , while demand for NO_3^- and SRP were less than that predicted by Q/w alone. Other ecosystem processes can also vary in a downstream direction. For example, nutrient export from forested watersheds can depend on the size of the watershed (Likens and Buso, 2006) and degree of allochthony may depend on river size (Vannote et al., 1980). Using a scaling framework provides a mechanism for quantifying how uptake length varies with specific discharge (Q/w), and allows us to link nutrient cycling with stream geomorphology along a stream network. In addition, because nutrient uptake experiments have been carried out in many streams, we were able to provide a constrained estimate of the scaling exponents.

Human alteration of streams (e.g. conversion to urban or agricultural land use) influenced scaling of both NH_4^+ and NO_3^- , not by changing the slope of the relationship, but by increasing the value of the y intercept. Thus human altered streams have proportionally longer uptake lengths, but similar scaling relationships with specific discharge. These results are consistent with research showing that streams in human-altered landscapes export more nutrients (Royer et al., 2006). However, the relationship is not

always straightforward; in a study of 69 streams, the effect of human land use was to simultaneously increase $\text{NO}_3^- S_w$ due to high NO_3^- concentrations, while simultaneously shortening S_w via augmented rates of photosynthesis (Hall et al., 2009b). However, using all 198 of the streams in this dataset demonstrated a consistent pattern of longer NO_3^- uptake lengths in human-altered streams.

Because streams and rivers are characterized by the unidirectional flow of water, the relationship between Q/w and relative N and P demand could be a result of upstream processing (Vannote et al., 1980), which could alter the stoichiometry of nutrients transported downstream (Schade et al., 2005). Additionally, attributes of stream morphology may directly affect nutrient cycling at a local scale, e.g. increased light availability in a larger (i.e. wider) stream may increase metabolic demand for N (Hall et al., 2009b). Nevertheless, the cycling of NH_4^+ , NO_3^- , and SRP must be partially decoupled; different processes drive the uptake of individual solutes as reflected in the differential scaling of NH_4^+ , NO_3^- , and SRP uptake length with stream size. Two examples of this solute-specific scaling include the abiotic sorption of SRP to particles not seen in “leaky” solutes like NO_3^- , and the gaseous loss of NO_3^- via denitrification that would not directly influence NH_4^+ .

Abiotic sorption and desorption by fine particles in the water column and benthos may control SRP uptake (Meyer, 1979). Despite the role of these abiotic factors, biota can quickly assimilate phosphorus as shown from $^{32}\text{P}\text{-PO}_4$ tracer studies (Newbold et al., 1983). Given that sorption/desorption with mineral particles can control SRP concentrations (Froelich, 1988), changes in mineral characteristics and/or the degree of P sorption may drive the pattern of reduced demand for SRP as stream size increases, and this effect may be more pronounced in streams with high fine sediment loads. It has been suggested that increased equilibrium SRP concentration would increase SRP uptake lengths given constant biological demand (Mulholland et al., 1990). Although NH_4^+ can also sorb to mineral surfaces, empirical studies show a consistent positive relationship between uptake velocity and stream metabolism (Hall and Tank, 2003; Newbold et al., 2006) suggesting that biological demand controls variation in

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NH_4^+ uptake. Regionally, SRP uptake can correlate with metabolism (Newbold et al., 2006), demonstrating that biological demand can be important, but the lack of a relationship between SRP v_f and metabolism found with our data analysis suggests that processes such as abiotic sorption more strongly regulate SRP uptake over a broad range of stream types and sizes.

Another explanation for the differences in scaling between SRP and DIN may be due to denitrification rates in streams (Alexander et al., 2000; Mulholland et al., 2008). If some fraction of N load is permanently lost from a stream via denitrification, then NH_4^+ and NO_3^- may have higher demand relative to SRP, in large streams. We see this pattern for NH_4^+ , but not NO_3^- . The scaling exponent of NO_3^- uptake length versus Q/w was similar to that of SRP showing no difference in demand with increasing Q/w . However, there was much more variability in the relationship between NO_3^- and Q/w compared to that for NH_4^+ . We suggest that this variability results from highly variable NO_3^- concentrations, which can vary by $> 10^5$, and that this variation in concentration strongly regulates S_w (Hall et al., 2009b). In a study that examined the joint effects of Q/w and NO_3^- concentration in 69 streams across the US collected using common methods executed in relatively small streams, NO_3^- scaled with Q/w with a coefficient < 1 showing higher demand for nitrate in larger streams (Hall et al., 2009b).

4.2 Scaling uptake length with stream distance downstream from headwaters

Our simple scaling model showed that uptake length of all 3 solutes scaled with distance from headwaters with exponent near 1, suggesting that larger streams and rivers have the potential to remove nutrients. This finding is the same as the assumption of constant v_f across a range of stream size (Wollheim et al., 2006). Constant v_f implies that larger rivers could strongly contribute to nutrient uptake within a river network (Wollheim et al., 2006). Empirical data for the Ipswich watershed supports this model (Wollheim et al., 2008). Ensign and Doyle (2006) showed that the number of nutrient spirals in a stream length or a particular stream order was more or less constant with

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increasing stream order, suggesting that larger streams are reactive for nutrients. By showing that S_w scaled isometrically with stream size (Q/w), our model implies that S_w will scale allometrically with stream length, i.e. S_w increases more slowly than does distance downstream from headwaters (Figs. 4 and 5). This finding suggests that large streams and rivers may remove as much or more nutrients than the well-studied small streams. Even if $a > 1$ as we found for NO_3^- and SRP, S_w will scale isometrically with river length suggesting that large streams can remove as much dissolved phosphorus as small ones. We also noted increased variation in the scaling exponent, m , but we emphasize that this variation does not represent uncertainty in the average estimate of m , but rather absolute variation in the scaling of hydraulic geometry among watersheds. Thus predictions for any one watershed should quantify the downstream hydraulic geometry of rivers in that watershed as first suggested by Wollheim et al. (2008).

Alexander et al. (2000) demonstrated that most inorganic N retention occurred in small streams, largely because v_f decreases with river depth (Wollheim et al., 2006). This finding is opposite of ours and we suggest two reasons that might explain contrasting results. First, by necessity, Alexander et al. (2000) measured net removal of dissolved nitrogen (based on mass balance) and not gross uptake rates like those that are measured using nutrient addition experiments that we analyze here. Second, Alexander et al. used much larger streams than those here. The smallest size class of streams in Alexander et al. (2000) were 0.4 m deep (they used depth as a stream size metric, Q/w was unavailable), which are deeper than all but 4 of the streams in our study. Much larger streams and rivers likely function differently as we note below.

Although we showed how nutrient uptake scaled across a range of stream sizes, these scaling exponents should not be extrapolated to large rivers without further empirical data collection (Tank et al., 2008). Although our analysis included a range of streams that varied 30 000-fold in discharge, we still lack data from rivers. The largest stream in our analysis, Lower Kuparuk River, Alaska ($18 \text{ m}^3 \text{ s}^{-1}$) is about 100-fold smaller than the median discharge of river basins in North America ($1930 \text{ m}^3 \text{ s}^{-1}$ Allan and Benke, 2005). Median stream discharge in our data set was $0.035 \text{ m}^3 \text{ s}^{-1}$ reflecting

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the emphasis, and historical focus that ecologists have placed on small streams, both because they are important with regard to their potential for nutrient uptake and transformation (Mulholland et al., 2008), and also because it is far more tractable experimentally to measure nutrient uptake in small streams than large rivers (Tank et al., 2008). We suggest that scaling relationships for small streams will not necessarily hold for rivers because of the addition of potamoplankton, higher sediment loads, larger floodplains, and human-altered hydrology, e.g. dams. Thus, the processes that control nutrient uptake in streams, i.e. uptake dominated by benthic biofilms, (Tank et al., 2000), or hyporheic storage (Hall et al., 2009a) may not apply to rivers that may have fundamentally different patterns of nutrient cycling. Data for reach-scale nutrient cycling rates in rivers await further investigation.

Supplementary material related to this article is available online at:

<http://www.biogeosciences-discuss.net/10/6671/2013/>

[bgd-10-6671-2013-supplement.zip](#).

Acknowledgements. Thanks to Ben Koch, Lusha Tronstad, and Alex Flecker for providing unpublished data on ammonium uptake. Denis Newbold inspired our scaling approach. Discussions with Carlos Martinez del Rio and Carl Legleiter improved the paper. This research was supported by the NSF grants DEB 01-11410, DEB 01-32983, and EAR 04-05934.

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Table 1. Parameters and statistics from standardized major axis regressions of \log_{10} uptake length (S_w) vs. \log_{10} specific discharge (Q/w). CI is confidence interval, n is sample size, r^2 is goodness of fit.

Solute	Land use	slope	95 % CI	intercept	95 % CI	n	r^2
NH ₄ ⁺	reference	1.01	0.90, 1.14	2.41	2.32, 2.48	111	0.57
	altered	1.20	0.94, 1.54	2.65	2.52, 2.79	35	0.49
NO ₃ ⁻	reference	1.19	1.01, 1.40	2.92	2.79, 3.06	133	0.13
	altered	1.12	0.90, 1.39	3.34	3.15, 3.53	65	0.24
SRP	reference	1.35	1.18, 1.53	2.55	2.46, 2.66	102	0.57
	altered	1.13	0.63, 2.03	2.67	2.31, 3.03	12	0.15

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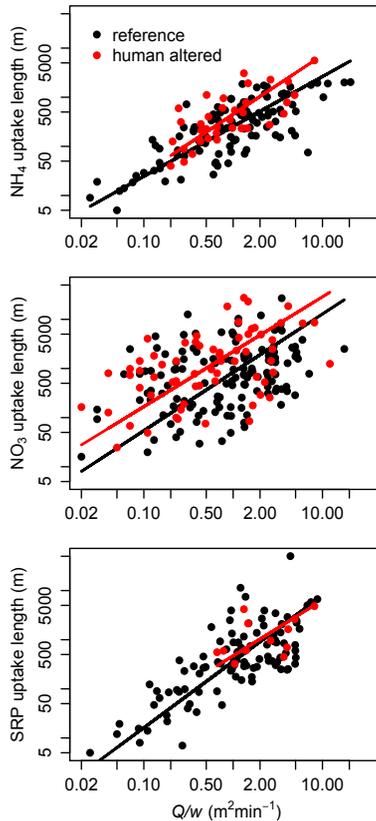


Fig. 1. Nutrient uptake length scaled isometrically for ammonium (S_{w-NH_4}) and allometrically for nitrate (S_{w-NO_3}) and soluble reactive phosphorus (S_{w-SRP}) as a function of stream specific discharge (Q/w). Points are data from individual streams and lines are standardized major axis regression lines fit through the data. Red points are streams with substantial human land use alteration in the watershed. Black points are reference streams. Parameters for regression equations are in Table 1.

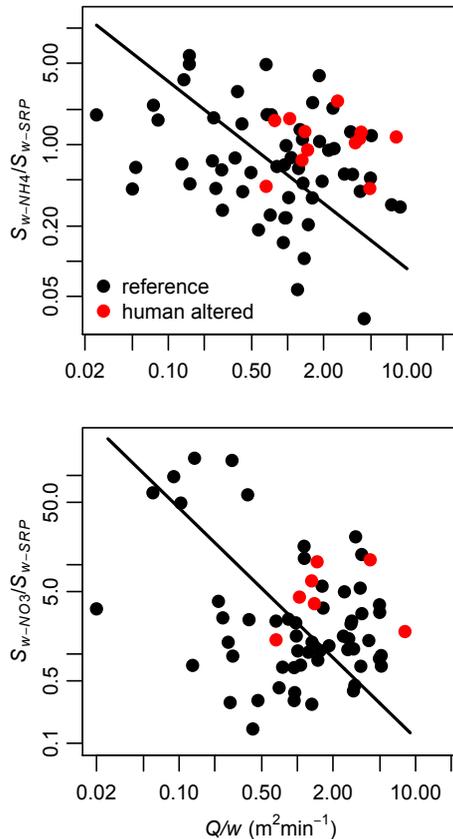


Fig. 2. Ratio of ammonium uptake length (S_{W-NH_4}) and nitrate uptake length (S_{W-NO_3}) to soluble reactive phosphorus uptake length (S_{W-SRP}) declined with specific discharge (Q/w) where measured in the same stream. Lines are ordinary least squares, $\log_{10}(S_{W-NH_4}/S_{W-SRP}) = -0.25\log_{10}(Q/w) - 0.20$ ($n = 57$, $p = 0.017$, $r^2 = 0.082$) and $\log_{10}(S_{W-NO_3}/S_{W-SRP}) = -0.43\log_{10}(Q/w) + 0.34$ ($n = 57$, $p = 0.011$, $r^2 = 0.094$).

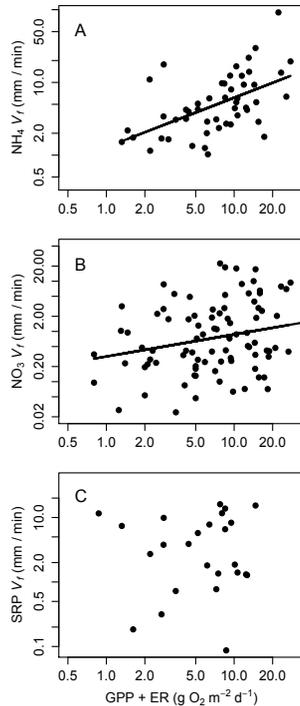


Fig. 3. \log_{10} ammonium (NH_4^+) and nitrate (NO_3^-) uptake velocity (v_f) were positively related to \log_{10} total metabolism (gross primary production + ecosystem respiration, units $\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) (**A** and **B**) while \log_{10} soluble reactive phosphorus (SRP) uptake velocity was unrelated to \log_{10} total metabolism (**C**) ($p = 0.89$, $n = 25$). Line between \log_{10} total metabolism and \log_{10} $\text{NH}_4^+ v_f$ is ordinary least-squares regression $\log_{10}(v_f) = 0.68 \log_{10}(\text{total metabolism}) - 0.11$ ($r^2 = 0.27$, $p < 0.001$, $n = 50$). Line for NO_3^- is $\log_{10}(v_f) = 0.44 \log_{10}(\text{total metabolism}) - 0.50$ ($r^2 = 0.04$, $p = 0.03$, $n = 89$).

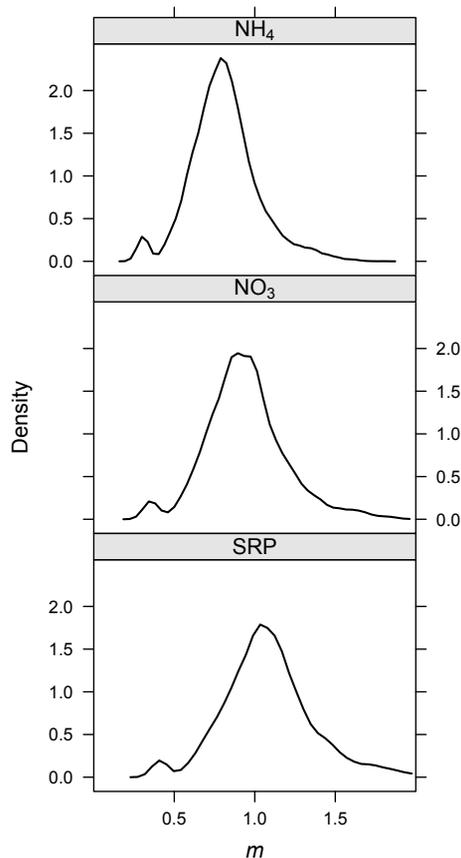


Fig. 4. Distribution of the scaling exponent, m , which relates uptake length of the 3 nutrients with distance from the headwaters. Lines are kernel densities based on a distribution of 10 000 estimates of m given uncertainty in parameters used to derive m (Eq. 10, in text).

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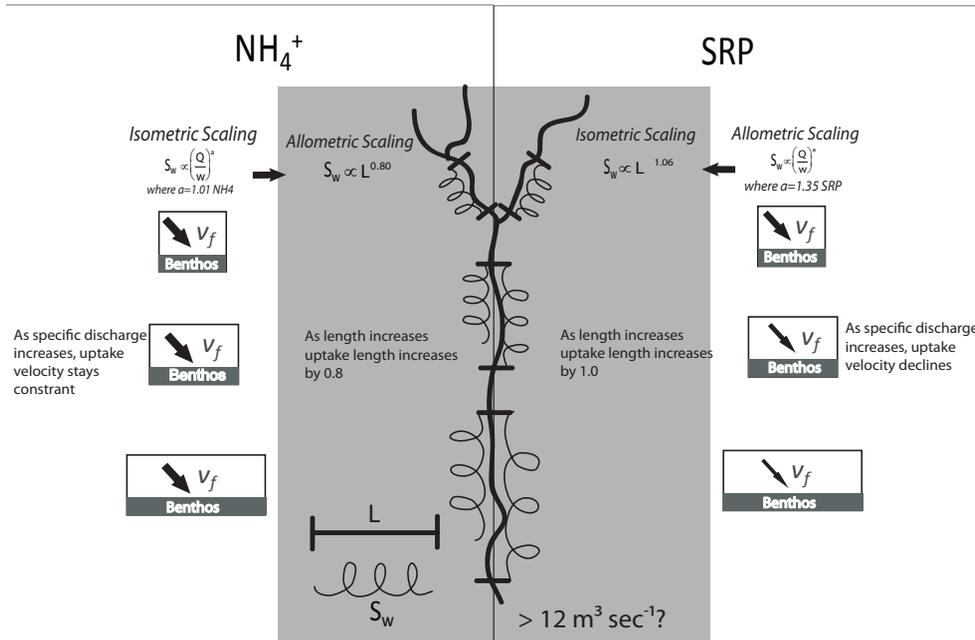


Fig. 5. Conceptual model demonstrates the relationships between scaling of uptake length (S_w) with stream size (measured as specific discharge, Q/w) and stream length (L) for ammonium (NH_4^+) and soluble reactive phosphorus (SRP). v_i is uptake velocity, the demand for nutrients relative to concentration.