Scaling of Physical Constraints at the Root-Soil Interface to Macroscopic Patterns of Nutrient Retention in Ecosystems

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Abstract: Nutrient limitation in terrestrial ecosystems is often accompanied with maintaining a nearly closed vegetation-soil nutrient cycle. The ability to retain nutrients in an ecosystem requires the capacity of the plant-soil system to draw down nutrient levels in soils effectually such that export concentrations in soil solutions remain low. Here we address the physical constraints of plant nutrient uptake that may be limited by the diffusive movement of nutrients in soils, by the uptake at the root/mycorrhizal surface, and from interactions with soil water flow. We derive an analytical framework of soil nutrient transport and uptake and predict levels of plant available nutrient concentration and residence time. Our results, which we evaluate for nitrogen, show that the physical environment permits plants to lower soil solute concentration substantially. Our analysis confirms that plant uptake capacities in soils are considerable, such that water movement in soils is generally too small to significantly erode dissolved plant-available nitrogen. Inorganic nitrogen concentrations in headwater streams are congruent with the prediction of our theoretical framework. Our framework offers a physical-based parameterization of nutrient uptake in ecosystem models and has the potential to serve as an important tool toward scaling biogeochemical cycles from individual roots to landscapes.

Keywords: nitrogen retention, biogeochemistry, plant nutrient uptake, ecosystem modeling, root function, plant-soil system.

Introduction

The ability of organisms to counteract the physical forces that limit resources essential for growth and reproduction is a defining feature of biological evolution and biogeochemical cycling (Vitousek and Howarth 1991). Organisms have evolved elaborate means of maintaining nearly constant levels of cell-bound nutrients in the face of strong abiotic forces (i.e., desiccation, leaching) that can lethally concentrate or strip these nutrients away. At all scales of biological organization, high internal demand by organisms is associated with small losses of bioavailable nutrients from system boundaries over cellular to ecosystem scales. At the ecosystem scale, nutrient loss is viewed as an indicator of the ecosystem’s nutrient status, where small losses of bioavailable nutrients indicate scarcity of that particular nutrient (e.g., Vitousek and Reiners 1975; Hedin et al. 1995). For terrestrial ecosystems, the underlying assumption is that nutrient deficiency within the plant-soil system leads to an effective drawdown of that nutrient in soils and thus minimal ecosystem losses. Similarly, the concept of relative “openness” of nutrient cycles is used to characterize nutrient retention, where small losses compared to internal (i.e. plant-soil) cycling rates represent an almost closed system.

A critical loss pathway is nutrient leaching from soils. Stream sampling of nutrients has been widely used as a convenient way to assess this integrated loss and nutrient status on a larger scale (landscape or ecosystem scale; Bormann and Likens 1967). For example, analyses of nitrogen (N) in streams that drain forested ecosystems reveal much larger exports of bioavailable nitrate under conditions of chronically high levels of anthropogenic N deposition (Aber et al. 2002; Perakis and Hedin 2002). The higher nitrate concentration in streams is thought of as the consequence of N saturation where N supply to plants exceeds demands and thus leads to excess N in the ecosystem. Similarly, larger ecosystem N losses in tropical compared to unpolluted temperate biomes (Vitousek and Reiners 1975; Brookshire et al. 2012) has been attributed to N saturation of biological demand in tropical systems compared to N limitation in temperate forests.

The concept of nutrient retention inherently depends on system boundaries and timescales. Within the plant-soil system, nutrients occur in pools that vary greatly in their characteristic turnover times ranging from quick (plant available) to slow (refractory soil organic matter). This hierarchical arrangement allows for fast-adjusting parts of the internal cycle to readily approach quasi-steady...
state conditions even if ecosystem-level nutrient fluxes are far from long-term steady state (input = output; Menge et al. 2009). For example, net N immobilization (retention) by soil microbes equilibrates rapidly, thus effectively re-supplying plant demand (Stark and Hart 1997). The notion of a biologically retentive ecosystem under limiting conditions therefore requires strong plant control over nutrients in soils, defining an almost closed system with respect to the N cycle (Brookshire et al. 2012): Consider that the amount of N transferred by litter production in mixed and deciduous temperate forests is \( \sim \)61 kg N ha\(^{-1}\) year\(^{-1}\) (Cleveland et al. 2013) which passes through the soil system mineral phases (ammonium and nitrate); for biomass N to be maintained, plant uptake must recoup this turnover loss. This plant-soil N flux contrasts with losses from soil ammonium and nitrate pools at much smaller rates (typically <1 kg N ha\(^{-1}\) year\(^{-1}\)).

However, given that water is both the carrier and loss vector for plant nutrients, it is not straightforward how biological sinks can overcome the tendency for water to leach nutrients away. In order to minimize such losses plants must effectually draw down soil nutrient concentrations. Recognizing this strong biological sink of available nutrients, most ecosystem models either allow plants and microbes to take up all of the mineral nutrients, if limited, or prescribe coefficients such that plant uptake rates are orders of magnitude stronger than those for leaching (Raich et al. 1991; Rastetter et al. 1997; Thornton et al. 2007; Gerber et al. 2010). All such models essentially assign or derive plant uptake rates phenomenologically, not mechanistically, for example by inverse determination using observed spatial patterns in hydrologic nutrient inputs and outputs (Brookshire et al. 2011).

On the other hand, numerical and analytical models of soil solute dynamics have provided mechanistic insight into solute movement at the scale of the soil-root interface (Nye and Tinker 1977). These models take into account the diffusion of nutrients in soils, uptake at the root surface, and in some instances, root growth (Silberbush and Barber 1983; Barber 1995; Leadley et al. 1997; Tinker and Nye 2000; Roose et al. 2001; Comerford et al. 2006). In many cases, these root-level models have been evaluated using fixed initial conditions and have focused on plant nutrient acquisition. Here we build on these existing modeling concepts designed to address plant nutrition (often referred to as the Nye and Tinker approach). Instead of focusing on plant nutrient acquisition, we attempt to model nutrient concentrations within natural soils and to predict the propensity for ecosystem loss via leaching pathways. We focus our analysis on nitrogen. Our analytical framework represents an effort to integrate the mechanics of solute transport and root uptake kinetics operating at the scale of root-water boundaries, with the macroscopic dynamics of nutrient cycling operating at the level of ecosystems and landscapes.

A central step in our analysis is to simplify these earlier models to allow for analytical evaluation and ask the following general question: What are the relative sink strengths of plant acquisition versus hydrologic leaching in controlling N concentration in soils and losses to deeper soil layers and streams? Specifically, we ask whether first principles of solute movement and observed data of root exploitation are sufficient to account for the observed drawdown of nutrients and whether increased water throughput interferes with the biological transport and uptake of nutrients within soils. We use our mechanistic framework of solute transport to scale plant uptake kinetics up to the ecosystem level to inform biogeochemical models. Finally, we evaluate data on root properties, ecosystem N input, and stream losses from ecological research sites representing major biomes to ask if mechanisms operating at the scale of the root-water interface can explain macroscopic patterns in hydrologic nutrient loss from ecosystems characterized by herbaceous or woody dominated vegetation.

**Methods**

**Model Development**

We build on the Nye and Tinker approach (Nye and Tinker 1977; Tinker and Nye 2000) and consider a straight root hair with the length \( dz \) that resides in the center of a cylinder of soil of radius \( R \) (fig. 1). The surrounding cylinder reflects the space that the root can influence. A simple production, diffusion, loss, and uptake of mineral nutrients can be applied and modified from Nye and Tinker (1977) as

\[
\frac{\partial C_l}{\partial t} = \kappa f \left( \frac{\partial^2 C_l}{\partial x^2} + \frac{1}{x} \frac{\partial C_l}{\partial x} \right) + m - lC_p, \tag{1}
\]

where \( x \) is the distance from the center of the root (units m), \( C_l \) the bulk concentration of nutrients (kg m\(^{-3}\)), \( C_p \) the concentration in soil solutes, \( m \) the mineralization rate (kg m\(^{-3}\) s\(^{-1}\)), \( \kappa \) the diffusion constant (m\(^2\) s\(^{-1}\)), \( l \) a loss rate that is proportional to the concentration (here we focus on leaching, but this term can equally apply to gas loss), \( f \) the fraction of the soil volume filled with water, and \( f \) denotes impedance that accounts for the tortuous transport pathways imposed by the soil matrix. The expanded diffusion equation (first term of eq. [1] on the right-hand side) results from its transformation into polar coordinates for parsimony with the framework’s cylindrical geometry. A central premise in this framework is that net mineralization, \( m \), equals the amount of nutrients...
available after microbial demand has been satisfied; that is, microbial uptake is assumed to be far more efficient than any other sink (Jackson et al. 1989).

We assume that only nutrients in the dissolved phase can be transported through diffusion, leached, and taken up. The relationship between total mineral nutrient concentration and the concentration in soil solution is given by (VanRees et al. 1990):

$$C_i = (\theta + b) \times C_{ip}, \quad (2)$$

where $b$ is the buffer factor that takes into account sorption/desorption, and $C_{ip}$ the total mineral nutrient concentration in soils.

In order to keep a simple, tractable system, we assume steady state of the plant-available nutrient pool by setting

$$\frac{dC_i}{dt} = 0. \quad (3)$$

This assumption implies that the temporal variability in sources (mineralization) and sink strength (plant uptake, leaching) occur on a longer timescale than the residence time of the nutrient in soils. We will address this assumption in the “Discussion” section.

The system requires two boundary conditions which we obtain from specifying the nutrient fluxes at the outermost cylinder wall (distance $R$) and the nutrient uptake at the root surface. We prohibit a nutrient flux across the outer wall as diffusion and uptake will lead to a maximum concentration at distance $R$ (i.e., there is zero gradient between two neighboring cylinders). Plant uptake at the root surface is often parameterized as a Michaelis-Menten process with

$$U(r) = \frac{V_{\text{max}} \theta C_i(r)}{k_m + C_i(r)}, \quad (4)$$

where $U(r)$ is the plant uptake at the root surface, $V_{\text{max}}$ describes the maximum uptake rate based on kinetic constraints and $k_m$ is the half-saturation constant in which a low $k_m$ represents a high affinity for the substrate. Term $\theta$ restricts nutrient uptake to the fraction of root surface in contact with soil water. Under nutrient-limiting conditions (i.e., $C_i \rightarrow 0$), the equation above can be approximated with

$$U(r) = \frac{V_{\text{max}}}{k_m} \theta C_i(r) = p \theta C_i(r), \quad (5)$$

where $p$ is the plant uptake coefficient under limiting conditions, assuming that plants operate at the maximum rate possible (inset, fig. 2). Details on solving the differential equation under consideration of the boundary conditions are given in appendix A (apps. A, B are available online). While the solution yields concentration as a function of distance $x_i$, we are primarily interested in the mean solute concentration across the entire cylinder, which is

$$\bar{C}_i = \frac{m}{l} \left[ 1 - \frac{2\theta pq_1}{(R^2 - r^2)(Rk)\theta pq_2 + lq_1} \right]$$

$$= \tau_i m, \quad (6)$$

where $\overline{C}_i$ is the mean concentration. It can easily be seen that $\bar{C}_i$ is a modifier with which the mean solute concentrations scale to $m$ (second expression, eq. [6]). Further, the terms

$$q_1 = I_1 \left[ \frac{l}{f_{q_1}} R K_0 \left( \frac{l}{f_{q_1}} R \right) - I_1 \right], \quad (7)$$

$$q_2 = I_1 \left[ \frac{l}{f_{q_2}} R K_0 \left( \frac{l}{f_{q_2}} R \right) - I_1 \right], \quad (8)$$

in equation (6) are combinations of the modified Bessel functions, with $L_i(x)$ and, $I_i(x)$ denoting modified Bessel functions of the first kind and $K_i(x)$ and $K_i(x)$ modified Bessel functions of the second kind. Note that within this framework the buffering of nutrients (buffer factor $b$) from sorption to soil surfaces has no effect on soil solute con-
Figure 2: Root uptake rate constants for ammonium and nitrate, based on literature value for mycorrhizae, grass, shrub, and tree plant functional types. We calculated concentration dependent optimal rates occurring under low nutrient supply compared to demand (inset) simplifying the two-parameter Michaelis-Menten model. We grouped uptake rate constants based on plant functional types. Error bars denote standard deviation across plant functional types. We converted uptake rates from a per mass basis (left), to the physically more meaningful uptake rates per root surface area (right).

Concentration. In absence of a leaching loss, the mean concentration becomes

\[
\overline{C_i} = m \left[ \frac{4R^4[\log(R^2/r^2) - (3/2)] + R^2r^2 - r^4}{16\beta k (R^2 - r^2)} \right] + \frac{(R^2 - r^2)}{2\theta p}
\]

\[= \tau_{i,\text{m}}
\]

Parameter Estimations and Data

For our analysis we use root and soil parameters as listed in table B1 (app. B). With respect to root properties, the critical parameters are root diameter, root length per mass, and root density (weight per root volume), for which we apply data from Jackson et al. (1997). These parameters are distinct for grass versus woody plants, with almost an order of magnitude difference in \(r\) and length per mass. The tortuosity (\(f\)) and water-filled pore space are assumed to be that of a soil near saturation (e.g., Leadley et al. 1997) since we are interested in retention versus hydrologic losses.

We approximate the average radius of influence \(R\) for a given soil column of height \(h\), such that the cylinders fill out the soil column:

\[h = \pi R^2 \text{length},\]

where "length" is the root length per meter square of soil surface, and \(h\) the depth of the active soil. Note that this equation omits the fact that packing root cylinders is creating a small amount of empty space that is not exploited by roots. Further, we use

\[\text{length} = \sigma \times M_r,\]

where \(\sigma\) is the specific root length (root length per root mass) and \(M_r\) the root mass in a given soil volume. Specific root length and root radius are related by

\[\frac{1}{j} = \frac{1}{r^2},\]

where \(\rho\) is the density of roots (mass per volume).

Parameters for plant uptake rates \(V_m, p\) are usually reported on a per mass basis, which we recalculate into a per area from

\[\left(V_m, p\right)_{\text{area}} = \frac{(V_m, p)_{\text{mass}}}{2\pi \sigma r}.\]
to come by. We did not conduct a systematic search but entered alternatively “$V_{\text{max}}$” and “$k_m$” in combination with “root” and “nitrogen” into Google Scholar. From there we then searched recursively through papers following the most promising references. Reported uptake rate constants are variable, and their values have been assessed for different purposes. We grouped the literature values into tree (Kamminga–Van Wijk and Prins 1993; Rothstein et al. 2000; Zerihun and Bassirirad 2001), shrub (Koch et al. 1991), grass (Bloom and Chapin 1981), and mycorrhizae (Jongbloed et al. 1991; Pérez-Tienda et al. 2012) classes. We present values of $p$ for roots and mycorrhizae in figure 2: despite the large variability in the published rates, we find the reported values for grass, shrub, and tree roots approximately converge if we convert the rates to the physically more meaningful rate of per unit surface area. A notable exception are mycorrhizal uptake rates per area, which in our summary of the data display a distinctly lower (order of magnitude) uptake capacity than plant roots. In our modeling experiment we use the geometric mean across the plant functional types and nutrient types as our root uptake parameters (table B1).

In order to predict landscape-scale nutrient uptake we take advantage of data from five long-term ecological research (LTER) sites. We selected sites where we could find information on necessary data, which are information on root morphology, mineralization, and stream N concentrations (table B2). The selection includes Andrews Forest, Coweeta, Hubbard Brook, Konza Prairie, and Luquillo LTERs.

**Results**

**Predictions of N Concentrations**

Our analytical solutions for $C_r$, show that at steady state the nutrient concentration in bulk soil and in soil solution scales directly to the amount of mineralization. It follows that concentration can be expressed per unit mineralization. We first investigate the concentration of nutrients under the assumption that there are no losses from solute transport ($I = 0$). Our framework leads to two distinct and additive terms that set nutrient concentrations, namely, a diffusion-driven term (first term inside the brace of eq. [9]) and an uptake-driven (second term) term. When applying our model using parameters of grass and tree root morphology, we obtain similar concentrations if we consider diffusion only versus the combined diffusion/uptake mechanism (fig. 3). Neglecting the uptake term (i.e., not accounting for the limitation of nutrient uptake at the root surface by assuming $p \to \infty$) reduces the overall concentration only by a small amount. This suggests efficient removal once dissolved N molecules arrive at the root surface, and thus the overall uptake efficiency of plants is mainly set by diffusion.

Our results follow the expectation that higher root mass allows for a better exploitation of the soil space and therefore a reduction in solute concentration (fig. 3). For each 100 kg N ha$^{-1}$ year$^{-1}$ mineralization into 30 cm of soil we obtain concentrations on the order of about 50–150 µg N L$^{-1}$ for root masses in the range of 0.2–0.5 kg m$^{-2}$ in forests. For a given mineralization rate and root mass, the calculated concentrations are much smaller in grass ecosystems, as smaller root diameters and root density in grasses (Jackson et al. 1997) allow for a more effective exploitation of the soil.

For a given root mass, a decrease in root radius (i.e., increase in specific root length; see eq. [12]), enhances drawdown of nutrients: halving the root radius reduces the concentration by a factor of four (fig. 4). Diffusion-limited uptake, that is, assuming high efficiencies, $p$, at the root surface, leads to a negative log-log relationship between the resulting concentration and root diameter. This makes sense: the smaller the root diameter, the larger the soil exploitation per unit mass and thus shorter diffusive
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Figure 4: Nutrient concentration as a function of tissue (root and hyphae) radii \( r \), with a total mass of 280 g in 30-cm-deep soils. Shown is the normalized concentration (per unit \( m \)). The black line indicates the result based on our default parameter set (table B1, available online), with the uptake coefficient for N at the root surface set to 250 m year\(^{-1}\). The effect of the range in affinities across all tree and grass roots are shown by the shaded grey area. The gray solid line represents the concentration if uptake was solely limited by diffusion; that is, the roots and hyphae would be able to draw down nutrients to zero at the root surface \( (p \rightarrow \infty) \). The circle with the error bar represents the concentration from mean and range in uptake coefficient \( (p) \) as reported for mycorrhizae. Dotted lines represent the average root diameter for tree (right) and grasses (left), respectively. The dependence on uptake coefficients increases as root radii become smaller: black line versus gray line.

Transport distances. We further find that as soil is increasingly exploited by roots (decreasing \( r \) while keeping root mass constant), root uptake coefficients become more and more influential in the potential draw down of solute concentration. If uptake coefficients per unit tissue surface for mycorrhizae were similar to those of tree roots, our framework suggests that mycorrhizae would be 10,000 times more efficient than roots per unit mass (fig. 4), since fungal hyphae diameter are a few micrometers (Ba˚a˚th and So¨derstro¨m 1979; Dighton and Coleman 1992). However, the limited data we found suggests weaker coefficients (smaller \( p \); fig. 2) for mycorrhizae on a per area basis. If we take into account the weaker uptake coefficient in hyphae compared to plants (fig. 4, circle) we obtain about a 10-fold increase in efficiency for the same biomass, still suggesting advantages by uptake through mycorrhizal interactions. However, we can expect that turnover rates are considerably faster for hyphae (a few days; Staddon et al. 2003) than for fine roots (months to several years; Joslin et al. 2006; Gaudinski et al. 2010); thus, the pay-off per unit carbon use may be similar, but we lack sufficient data to evaluate this possibility.

Both figures 3 and 4 present soil solute concentrations for a given amount of mineralization that have the unit of “time.” In our framework, the resulting variable can be viewed as an actualized residence time \( \tau \), since it represents the reservoir size (i.e., concentration) divided by the flux (i.e., mineralization). Consider the system

\[
\frac{dC_i}{dt} = m - U,
\]

where \( U \) is plant uptake. Similar to the uptake efficiency at the root surface, we derive a macroscopic uptake rate constant \( k_p \), where

\[
U = k_p \times C_i
\]

is a sink that is proportional to the concentration. This system represents a strong internal cycle (closed system) where all N mineralized is being taken up by plants. At steady state we have

\[
C_\tau = \frac{m}{k_p} = \tau m,
\]

or, if we are interested in the residence time of the total mineral pool

\[
C_t = \frac{m}{k_p (\theta + b)} = \tau m,
\]

where \( \tau_\tau \) and \( \tau_\theta \) represent a residence time between mineralization and uptake of dissolved or total available N, respectively. In this closed-system mineralization uptake framework, \( \tau_\tau \) is the same as our \( \tau_{0,0} \) (in absence of leaching; eq. [9]), or the concentration per unit mineralization (figs. 3 and 4); and the “macroscopic” plant uptake rate constant, \( k_p \), is the inverse of the residence time. It is important to note that buffering soil solution via sorption processes increases the residence time of the total mineral nutrient content \( C_t \) and weakens the apparent capacity of plants to take up nutrients (eqq. [2], [16], and [17]) but has no effect on \( C_t \) in our framework.

Our approach has now led to an expression of a nutrient residence time and to macroscopic formulation of plant uptake under nutrient limiting conditions, which in turn is based on properties that affect nutrient movement and root exploitation. The macroscopic expression of equation (15) is frequently used in ecosystem models; our results therefore provide a bottom-up, mechanistic constraint of that parameter.
Effects of Water Percolation and Drainage

We have yet to evaluate whether our approach, which was derived from Nye and Tinker’s (1977) mathematical treatment of small-scale soil solute dynamics (millimeters and below), can be used to scale up to the ecosystem level (~30-cm soil column to watershed scale). In doing so, it becomes critical to address interactions with water percolation. We next introduce interactions with soil water into our framework and consider a suite of increasingly complex ecological and environmental scenarios.

We start off with the case of a strong internal cycle which we assumed in order to derive our plant uptake rate constant (case 1; see eq. [15]). In this case the concentration is exclusively set by the internal cycle and the amount lost from the ecosystem would simply be the product of the drainage rate ($u_d$, in units m s$^{-1}$) and the solute concentration (fig. 5). This simple relationship holds if dilution is irrelevant, and rates of export are much smaller than rates of mineralization (i.e., essentially a closed cycle). Total plant uptake is calculated as the product of the drainage rate ($u_d$) and the solute concentration (fig. 5). This simple relationship holds if dilution is irrelevant, and rates of export are much smaller than rates of mineralization (i.e., essentially a closed cycle). Total plant uptake is calculated as the product of the drainage rate ($u_d$) and the solute concentration (fig. 5).

With increasing drainage rates ($u_d$), dilution may no longer be neglected, and therefore we should consider the effect of water movement on the concentration. Our case 2 employs a macroscopic dynamics as used in many ecosystem models:

$$\frac{dC_i}{dt} = m - k_p C_i - \frac{u_p}{h} C_p,$$

where $u_p$ is the actual water velocity in soils. When scaling up to the active horizon, $u_p$ needs to be modified to account for the tortuosity and the volume through which water is able to move, hence, we have

$$u_p = \frac{f}{\theta} u_d.$$

The steady state solution for equation (18) is then

$$C_i = \frac{m}{k_p + \left(\frac{u_p}{h}\right)}.$$

We can see now the effect of the percolation rate on the concentration for case 1 in the limit $u_p/h \rightarrow 0$.

Both case 1 (closed system approximation) and case 2 (ecosystem models) assume independence of soil water percolation on the macroscopic plant uptake rate constant $k_p$. However, our analytical solution of the diffusion-uptake-loss dynamics equation (eq. [6]) suggests a different, and more complicated, relationship if there is a time-equivalent sink for N other than plant roots.

Our case 3 therefore considers possible interactions with leaching, where we use $k_p$ as derived from the concentration per mineralization (eq. [6]). We define a loss rate $l$ with $l = u_p/h$, where $l$ approximates a turnover of soil water. Loosely, this assumption of $l$ would apply to situations with homogenous mineralization around a vertical root that extends over the entire active soil, and where the probability of hydrological export is uniformly distributed in the soil volume. Although case 3 does now take into account the interactive effect of leaching, such ideal conditions are rarely present in natural soils, hence $l$ should be chosen such that it better reflects the physical conditions of the soil.

In our case 4 we select $l$ to reflect the physical characteristics of solute transport. The challenge is to find a sensible length scale over which we expect diffusion and advective transport to interact. This length scale is likely affected by the characteristic length over which solute transport shifts from diffusion to advection, as represented by the Peclet number ($Pe$):

$$Pe = \frac{u_p L}{\theta k}$$

where $L$ is the length scale under consideration. If $Pe \ll 1$, diffusive transport is dominant, but diffusion becomes

Figure 5: Concentration and ecosystem nutrient loss as a function of drainage/percolation rate. The individual cases denote different and increasingly complex ways of incorporating interactions of soil solute dynamics with percolation, as explained in the text. Concentration and ecosystem loss do differ but only marginally across the different cases, while all cases highlight strong retention capacity with minimal loss.
irrelevant when $Pe$ greatly exceeds 1. Therefore, we expect that water advection should interfere significantly with the diffusive transport (and thus plant uptake) if $L \geq \frac{f_{k}\kappa u_{x}}{u_{x}}$.

In soils, we may translate the characteristic scale into a length over which the concentration gradient toward the roots, as established by diffusion and uptake, is washed out by advective transport. Given our parameters and a drainage rate of 9 mm day$^{-1}$—which is thought to be an upper limit of infiltration in organic soils (Sitch et al. 2003)—we obtain a maximum critical length $L$ of approximately 3 mm. This critical length is in the vicinity of the average distance between roots, and we therefore might expect effects of water movement on root uptake. On the other hand, the critical length is considerably smaller than the volume of the active soil, therefore, a hydrologic loss over this scale does not constitute an ecosystem loss but rather an internal redistribution from one location to another in the soil. In order to account for such internal transport we stipulate that the hydrologic loss from one root segment with length $L$ constitutes a homogenous input into the next segment (i.e., into another cylinder with length $L$). The resulting concentration is the solution of

$$C_i = (m + IC_i)_{\text{r}_i}, \quad (22)$$

where $(m + IC_i)$ are the inputs (due to mineralization in the current root segment and the advective leakage from an identical root segment upstream; see also eq. [6]).

We further test effects of advective transport in our case 5, where we perform a numerical integration of a simple advection diffusion scheme. We assume in this case that water percolates perpendicular to roots in a constant advective flow (i.e., that roots are positioned parallel to the soil surface). This differs from the previous case 4 in that we take into account root-scale concentration gradients, such that the advective input is no longer a homogenous source. The two-dimensional differential equations, boundary conditions, assumptions, and simplifications for the numerical treatment are presented in appendix A.

For all five cases we then calculated N concentration and N loss rates (fig. 5). The concentrations and hydrologic loss rate change little with increasing complexity and the solutions for cases 2–5 are close to the closed system approximation (case 1). The comparison of the different cases highlights the strong internal control (i.e., plant uptake) on concentrations. We find only a small tendency toward dilution in all cases, and interestingly, we observe a slightly more retentive behavior of the ecosystem in case 4. The explanation is that the homogenous input from advection (eq. [22]) leads to an increase in concentrations close to the root surface and thus increases plant uptake.

Our analytical and numerical results also confirm a strong retention and internal drawdown of nutrients despite limitation by diffusive transport through soils; in fact, soil percolations at 9 mm/day (3.285 m/year) allow 97% of nutrients mineralized to be captured by roots, with a 3% loss by soil water percolating below the rooting zone (fig. 5). Therefore, assuming the simplified rendering of physical features we prescribe here, our results suggest that water percolation does little to affect soil solute concentrations. More critically, the increasing complexity of soil water interaction alters the outcome of our initial formulation of plant uptake and water losses only marginally. We acknowledge that our formulation of soil water interaction is extremely simplified, and future work should take into account the heterogeneity of soil water flow. Despite these simplifications, our physical and mechanistic-based analysis supports the notion of strong plant control ecosystem retention under N-limited conditions.

### Integration with Ecosystem Models

As shown in equations (18)–(20), our approach can be used to parameterize macroscopic root N uptake, in larger-scale ecosystem models and that holds in the presence of a competing hydrologic loss. However, a complicated expression is not desired, particularly in cases where there are large uncertainties and inhomogeneities with respect to the underlying parameters ($\theta$, $f$, $p$, $a$) and variables (root mass, active soil depth). Here, we make the following simplifying assumptions to arrive at a root uptake parameterization for potential use in ecosystem models: First, the uptake rate constant $p$ is likely negligible compared to the limitation by diffusion (fig. 3). Second, we can safely assume that the soil volume is much larger than the root volume, thus $R^2 \gg r^2$. Third, we neglect direct interactions between diffusive movement and soil percolation (cases 3–5 above). Applying these simplifications to equation (9), combining the result with equations (10) and (11) (which relate $R$ with root biomass and specific root length), and solving for $k_r$ (eqq. [16], [17]) yields

$$k_r = \frac{2\pi \sigma \kappa' M}{h[\log (h/\pi M, \sigma r^2) - (3/2)]^7}, \quad (23)$$

with $\kappa' = \kappa f$ or $\kappa' = \kappa f/(\theta + b)$ if operated on the dissolved or total mineral nutrients in soils, respectively.

We next confront the predictions of our framework against available data of N leachate concentration from LTER sites. By making use of the small-watershed approach (Bormann and Likens 1967), we estimate the macroscopic plant uptake rate constants ($k_r$) based on bottom-up and top-down approaches. We first solve $k_r$ using our ecosystem level top-down approach (Brookshire et al. 2011) via a simple watershed hydrometric N mass balance parameterized with data on stream N and soil N mineralization:
\[ \frac{dN}{dt} = I + M - k_p N - k_i N, \quad (24) \]

where \( I \) is an external mineral N source (atmospheric deposition) and, \( k_p \) and \( k_i \) uptake and leaching rates (as operated on the total available content). Term \( M \) is the mineralization integrated over the active soil volume, and \( N \) is the plant available soil \( N \) integrated over the soil volume (kg m\(^{-2}\)). Given the short residence time of available \( N \) in soils (and our large \( k_p \) values; fig. 3), we can safely assume steady state conditions (Brookshire et al. 2011) and approximate a quasi-closed system

\[ N = \frac{I + M}{k_p + k_i} \approx \frac{I + M}{k_p}. \quad (25) \]

The last term on the right-hand side signifies that internal sink strength is a much larger term than leaching losses, as found in figure 5 (see also Brookshire et al. 2011, 2012). The solute concentration \( C \) is obtained by dividing \( N \) with the soil volume \( h \). Knowing rates of mineralization, \( N \) deposition and stream concentration thus allows us to estimate a phenomenological \( k_p \).

The bottom-up approach is the framework presented here, where \( k_p \) depends on the diffusive transport of nutrients from the soil environment to the root surfaces (eq. [25]).

We show in figure 6 the comparison of the calculated \( k_p \) from the bottom up (model parameterized with root data) and the top down (phenomenological model parameterized with \( M, I \) and stream \( N \) data of combined ammonium and nitrate concentrations and solving eq. [25] for \( k_p \)). The uptake rate constant based on the bottom-up approach using independent measures of root exploitation and diffusion is congruent with the top-down inference across a large spread of \( k_p \) values within these LTER sites. Importantly, we find that inclusion of the atmospheric deposition flux contributes insignificantly to our estimates of \( k_p \), as we have previously shown (Brookshire et al. 2012). We do not provide formal uncertainty ranges in figure 6, as they are considerable: stream concentrations vary considerably over time and root properties are notoriously difficult to measure and vary temporally and spatially in soils. Similar difficulties arise with the estimation of net mineralization. A back-of-the-envelope calculation (using quadratic error propagation of log-transformed expressions) suggests that 33% uncertainty associated with each variable translates into an error factor of \( \sim 2 \) for \( k_p \) based on the top-down approach and \( \sim 3 \) based on the bottom-up approach. This large range of uncertainty highlights the need to establish and maintain routine biogeochemical measurements in soils. Despite such uncertainties, our framework that takes into account the physics of movement of nutrients in soils can be brought into agreement with observations at watershed levels.

**Discussion**

We motivate our analysis with the notion that in unpolluted, N-limited ecosystems, the large flux discrepancy between detrital nutrient turnover and mineral nutrient losses from the plant-soil system defines a nearly closed nutrient cycle. Our results confirm that such high retention requires plant uptake to be competitively dominant relative to hydrologic leaching. Our approach based on plants being responsible for \( N \) retention agrees with the classic pattern of large increases in mineral \( N \) losses from small watersheds triggered by forest clearing (removal of the plant sink) followed by strong reductions in losses during forest regrowth (Bormann and Likens 1967).

Populating our model with data for average root exploitation and root uptake coefficients, we find that diffusion is a rate limiting step for plant \( N \) nutrition. Root
densities, which we derived from a global data set and from individual watersheds, suggest short residence times (small concentration per unit mineralization) of mineral N in soils, resulting in a turnover of the total mineral (sorbed and dissolved) N pool on the order of a day or less as found earlier (Raynaud and Leadley 2004). The short residence time is critical for our model evaluation, since we solved the framework using a steady state assumption. The residence time of mineral N we obtained is much smaller than the timescale of root growth, variability in soil temperature, and in many cases also variability in soil moisture; as a consequence, diffusion gradients and resulting average concentrations closely track the temporal evolution of these boundary conditions. In other words, due to fast adjustment and short residence time, antecedent levels of soil nutrients have little influence on current concentrations (Yanai 1994). Such independence of initial conditions, while generally valid for the scope of modeling ecosystem-scale nutrient cycles is not always realistic. For example, soil moisture may change rapidly during rewetting following rain, which in turn can trigger a host of biogeochemical processes (Cabrera 1993; D’Odorico et al. 2003; Manzoni et al. 2004) such as pulses in mineralization via hydrologic reconnection of previously isolated soil pockets. Similar mechanisms may occur during rapid spring snowmelt events (Likens and Bormann 1972) and may be achieved efficiently with an existing and relatively simple root network. The residence time of the total mineral pool depends on the buffer factor. While nitrate typically is not sorbed to soil surfaces, ammonium and phosphate are. The residence time of the total concentration \( C \) scales with \( \theta (\theta + b) \) and therefore increases by a factor of \( \sim 10 \) for ammonium (Matschonat and Matzner 1995) compared to nitrate. The sorption of phosphate to mineral soils is even stronger, and the extension of our framework to phosphorus (P) nutrition may not be justified, since the estimated residence time will be on the order of several months (Raynaud and Leadley 2005). However, P tends to be more readily mineralized from organic matter than N owing to relatively weaker C-O-P ester bonds compared to stronger covalent C-N bonds (Vitousek and Howarth 1991), and this has been shown to have strong transient effects on the relative severity of N versus P limitation in terrestrial ecosystems (Menge et al. 2012). Therefore, it is possible that strong P buffering via sorption to iron oxides in soils could be ameliorated by enhanced supply particularly if plants acquire P directly from organic layers, a phenomenon we did not consider in our model.

The different residence times of N versus P have further important implications for plant nutrition strategies: given the relatively fast movement of N in soils, plant uptake may be achieved efficiently with an existing and relatively static root network. In contrast, the long residence times of phosphate may require more adaptive exploitation of soils. P can be hydrolyzed locally through exudates (e.g., phosphatase), thus allowing growing roots or hyphae to exploit sites of strong sorption tendency (Raynaud et al. 2008) and substantially increase phosphate intake since the combined concentration of sorbed and dissolved nutrients increases faster with distance from the tissue surface for a strongly sorbed nutrient compared to a nutrient that exists primarily in the dissolved phase. Our results for residence time distributions (and by extension total nutrient concentration) confirm that an active rooting strategy should be advantageous for strongly sorbed nutrients (Raynaud and Leadley 2004). This is consistent with the prediction that mycorrhizal association and the relative abundance of fibrous cluster roots should increase with soil age as P pools decline (Lambers et al. 2008).

We included the possibility of mycorrhizal symbiosis in our framework. We find that in contrast to roots, the uptake coefficient at the tissue surface is the rate-limiting step of nutrient intake in mycorrhizae, rendering diffusion rates less relevant. Uncertainties in the parameter with respect to mycorrhizal nutrient uptake remain large. For example, we cannot infer a clear advantage of mycorrhizal uptake under steady state conditions: that is, given the spread in parameters, a static root network may be equally efficient as a static mycorrhizal network if considered on the basis of nutrient acquired per unit carbon expense (i.e. tissue turnover; fig. 4). However, nutrient acquisition via fungal symbiosis would be expected to provide an advantage when accessing a previously unexploited N source (depletion of a sorbed pool or reaction to hotspots) because of lower upfront costs. Nutrient acquisition strategies is an area of active research (Pregitzer 2002; Hodge 2004; Lambers et al. 2008), and have previously been addressed with diffusion-uptake models (Silberbush and Barber 1983; Leadley et al. 1997; Roose et al. 2001; Comerford et al. 2006). Our model can serve to provide further mechanistic foundation for future analysis of the ecology of plant nutrition pathways, with respect to resource allocation, competition (Raynaud et al. 2008; Dybzinski et al. 2011), isotopic fractionation (Högberg 1997), and the evolution of plant-mycorrhizal interactions (Brunn et al. 2002).

At the scale of the active soil, our analysis confirms the notion of a high N retention capacity if N is limiting. We subjected our framework to various cases with different complexity of interactions between hydrologic leaching and plant uptake, starting from a quasi-closed system to a numerical model where advection may interfere with nutrient uptake. Across the different cases presented here, there is little difference in solute concentrations, which are in turn only marginally affected by the strength of hydro-
logic transport. Our model supports the notion of strong biologic controls on levels of mineral N in soils (Perakis and Hedin 2002), where concentrations are primarily set by rates of mineralization and the efficiency of plant uptake. Even at high drainage rates we find that only a sparsely small fraction of mineralized N is leached away from soils. By extension, we conclude that plant nutrient uptake via advective flow (passive nutrient uptake during water intake) is minor under N-limited conditions and would not lead to a marked drawdown in soil nutrient concentrations because these are set by diffusion.

Admittedly, we have adopted a very simplified view of soil and watershed hydrology. Our analysis was designed to investigate the role of nutrient uptake versus advective flow and ignores other aspects of root function and interactions with water. For example, roots and individual plants may be located in hotspots of water availability, particularly in water-limited systems, or may exhibit variable tolerances and adaptations to soil moisture conditions (Farrir et al. 2013). Soil moisture is also well known to influence rates of nutrient mineralization in soils (Pastor and Post 1986; Parton et al. 1987). Further, our analysis does not treat preferential flowpaths which may lead to locally fast movement of soil water at rates much higher than we considered here (Beven and Germann 1982). However, microbes tend to thrive best on capillary fringes (Holden and Fierer 2005) and are more abundant in micropores than macropores (Ranjard and Richaume 2001). Therefore we expect sites of high advective (i.e., macropore) flow to be zones of reduced mineralization and lowered potential for nutrient leaching losses. Isotopic evidence suggests the existence of tightly bound pools of water in soils from which plants feed and which scarcely mix with the mobile water that ultimately drains into streams (Brooks et al. 2010). While our approach is well suited to treat biogeochemistry within such a relatively stagnant water pool, our framework also offers a simple, mechanistic, and tractable way forward towards testing the relative importance of spatial and temporal heterogeneities in hydrologic conditions. Our framework may be unsuitable to predict losses N from agricultural systems: for example, pulses of N in soils from fertilizer create highly enriched and transient conditions where nitrogen supply exceeds plant demand. Further, fertilizer application can bypass the soil matrix by surface runoff or macropore flow such that the solute flux out of the soil is not entirely representative of the soil matrix. A recent review highlights the need to address interactions of soil water movement and plant nutrition in agricultural systems (Hopmans and Bristow 2002).

Finally, at the scale of the watershed, our bottom-up model agrees with the top-down derivation, offering the intriguing possibility that under N limitation, levels of nutrient concentrations in streams are to a first approximation the product of the strength of plant uptake (if nutrient limited) and rates of mineralization. Though we consider only a small number of sites in our comparison, we sought to contrast a wide range of climates and biomes (tropical vs. temperate, forests vs. grasslands). We were constrained in our analysis at the watershed level to sites containing all relevant data. Further, we necessarily relied on indirect data, such as biome-specific root morphology, or model-derived rates of mineralization (table B2) to make site-specific comparisons. These sources of uncertainty as well as others outlined above (differential flowpaths, sorption disequilibria, spatial heterogeneity) are expected to imprint on the concentration of mineral N in streams and will contribute to differences in bottom-up versus top-down estimates of the internal sink strength ($k^p$; fig. 6) at any location. Most importantly, our framework applies to the case of N limitation only, as a partial uptake by plants would leave residual N and thus increase soil concentrations. Our up-scaled sink strength is directly related to root properties and root exploitation. We suggest that future analysis should include the mycorrhizal contribution to plant uptake as plants in these sites maintain mycorrhizal symbiosis. Given our strong relationship between top-down and bottom-up analyses, our framework offers a quantitative baseline against which watershed biogeochemistry can be evaluated.

**Conclusion**

We have derived a solution for plant nutrient uptake that unifies bottom-up physical mechanisms of solute movement in soils and kinetics of nutrient acquisition with the macroscopic processes of nutrient cycling and loss in ecosystems. Our analysis of the relationship between root uptake and water flow underscores the primacy of diffusive transport and indicates that, under nutrient-limited conditions, advective flow is a vanishingly small sink compared to active plant N acquisition. Our findings provide a new simple and analytically tractable formulation for plant nutrient uptake in ecosystem models and place new constraints on our understanding of watershed level patterns of nutrient loss.

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**Literature Cited**


