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Emergence and Maintenance of Nutrient Limitation over Multiple Timescales in Terrestrial Ecosystems

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abstract: Nutrient availability often limits primary production, yet the processes governing the dynamics of nutrient limitation are poorly understood. In particular, plant-available (e.g., nitrate) versus plant-unavailable (e.g., dissolved organic nitrogen) nutrient losses may have qualitatively different impacts on nutrient limitation. We examine processes controlling equilibrium and transient nutrient dynamics at three separate timescales in a model of a nutrient cycling through plants and soil. When the only losses are from the plant-available nutrient pool, nutrient limitation at a long-term equilibrium is impossible under a wide class of conditions. However, plant biomass will appear to level off on a timescale controlled by plant nutrient turnover (years in grasslands, decades to centuries in forests), even though it can grow slowly forever. Primary production can be nutrient limited in the long-term when there are losses of plant-unavailable nutrients or when the mineralization flux saturates with increasing detrital mass. The long timescale required for soil nutrient buildup is set by the plant-unavailable loss rate (centuries to millennia). The short timescale (hours to days) at which available nutrients in the soil equilibrate in the model is controlled by biotic uptake. These insights into processes controlling different timescales in terrestrial ecosystems can help guide empirical and experimental studies.

Keywords: nitrogen limitation, model, forest, grassland, quasi equilibrium, dissolved organic nitrogen.

Introduction

The idea that a nutrient can limit primary production has been a fixture of ecology since at least 1840, when von Liebig (1840) suggested that the nutrient in shortest supply relative to plant demand limits plant growth. Myriad fertilization studies in agricultural and natural ecosystems since that time have revealed that nutrients can limit primary production, but most of these studies have considered only a single point in time. The dynamics of nutrient limitation through succession in natural ecosystems have been studied only more recently, and the interplay between nutrient losses and nutrient limitation through time has been a subject of increasing interest in the past few decades (e.g., Vitousek and Reiners 1975; Gorham et al. 1979; Hedin et al. 1995, 2003; Vitousek et al. 1998). Understanding nutrient limitation is now more important than ever, because human activities are altering nutrient conditions worldwide (Vitousek et al. 1997*a*, 1997*b*; Smil 2000). Nutrient-limited ecosystems will respond to increases in the availability of the limiting nutrient by removing it (and atmospheric CO_2) from circulation, mitigating global changes, whereas ecosystems that are not nutrient limited do not have this buffering capacity.

Until relatively recently, losses of plant-available nutrients (e.g., nitrate or phosphate) were the only losses considered in studies of nutrient limitation and balances in terrestrial ecosystems (e.g., Vitousek and Reiners 1975; Gorham et al. 1979). As an example of this traditional view, Vitousek and Reiners (1975) posited that nutrient losses in terrestrial ecosystems are linked to succession: when plants are actively growing, they assimilate and retain the nutrient that is most limiting to them, effectively preventing losses of that nutrient. Because there are always nutrient inputs from the atmosphere and/or from weathering, preventing losses would result in a buildup of this nutrient in the ecosystem as it is retained in the biomass (like a slow trickle of water into a bucket). As succession proceeds, this nutrient buildup continues until supply exceeds demand, at which point the nutrient no longer limits production, inorganic nutrients accumulate, and the bucket overflows (fig. 1*A* in Vitousek and Reiners 1975). Thus, according to the traditional view, a nutrient can limit primary production during succession but cannot do so indefinitely in the absence of a disturbance.

Nitrogen (N) loss data from forests in the northeastern United States reveal much higher nitrate losses in unlogged (old-growth) forests than in logged (successional) forests,

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which seems to support the traditional view (Vitousek and Reiners 1975). However, data from unpolluted old-growth ecosystems reveal very low losses of (Hedin et al. 1995; Perakis and Hedin 2002) and a high capacity for retention of (Perakis and Hedin 2001; Perakis et al. 2005) plant-available nutrients, suggesting that a nutrient (in this case, N) can limit primary production indefinitely. These data, although by no means conclusive, call into question whether the traditional view captures all the relevant nutrient dynamics.

In 1995, Hedin and colleagues described a new hypothesis—the leaky-bucket hypothesis—that accounts for the low losses of plant-available nutrients in old-growth ecosystems. This hypothesis states that, whereas losses of plant-available forms of a nutrient cannot maintain nutrient limitation in old-growth ecosystems, losses of plant-unavailable forms (e.g., dissolved organic forms of N [DON] or phosphorus [P; DOP]) of that nutrient can (Hedin et al. 1995). The idea was that losses of plant-unavailable forms are independent of biological demand ("demand independent") and act as an unavoidable leak in the system that, over time, could limit the availability of that nutrient, and thus limit primary production, even at steady state. This differs from losses of plant-available forms, which are demand dependent because plants take up available forms when they need them, preventing losses. Hedin and colleagues provided a mechanism for the unavoidable loss on the basis of their data from old-growth forest streams in Chile: DON, which is lost from ecosystems via leaching from the soil into streams, constituted the vast majority (~95%) of hydrological N losses from the system. Losses of nitrate and ammonium—the plant-available forms of N—were miniscule, indicating that plants continued to assimilate as much N as possible and that N continued to limit production in these old-growth ecosystems. Further research has revealed that DON losses are ubiquitous in forest ecosystems, ranging from 0.2 to 7 kg N ha^{-1} $year^{-1}$ (Perakis and Hedin 2002; Hedin et al. 2003; Houlton et al. 2006).

In addition to DON, other chronic losses may also be demand independent, such as temporal asynchrony in nutrient supply versus demand, soil erosion, occlusion (Vitousek 2004), or potentially, N gas losses (Houlton et al. 2006; but see Hedin et al. 2003). However, in this article we focus on the distinction between demand-dependent versus demand-independent nutrient losses in general, rather than specific loss vectors.

The topic of nutrient limitation at successional steady state is an intriguing one, but it covers a small part of successional nutrient dynamics. The concept of steady state (which we consider to be synonymous with equilibrium) depends on the processes considered, and processes in terrestrial ecosystems occur at many different timescales (Levin 1992; Hedin et al. 2003; Vitousek 2004). For example, microbe growth is much faster than plant growth, which in turn is much faster than nutrient release from rock weathering. Considering only the soil microbial community, steady state may be reached in a matter of days, whereas it takes years to decades or more for nutrients in plants to equilibrate. Although such differences in timescale in terrestrial ecosystems are well known, their effects on nutrient dynamics through the course of succession have only recently been probed (Baisden and Amundson 2003; Vitousek 2004). Understanding nutrient dynamics at multiple timescales is key to understanding nutrient cycles in a global-change world, and it remains an open challenge that is particularly amenable to mathematical models.

Here we examine steady-state and transient nutrient dynamics at three timescales in a model that includes nutrient pools in plants and the soil, with the soil pool divided into plant-unavailable (e.g., large organic molecules) and plant-available (e.g., inorganic or small organic molecules) nutrients. Our model includes nutrient-limited plant growth, turnover to the soil, net mineralization, abiotic inputs of the available form, and losses of both the available and the unavailable forms. In this framework, we ask the following questions: (1) Under what conditions can chronic losses of an available nutrient maintain limitation by this nutrient at equilibrium? (2) Under what conditions can chronic losses of an unavailable nutrient, with or without losses of the available form, maintain nutrient limitation at equilibrium? (3) What are the dynamics of the limiting nutrient at three timescales—those of the available nutrient in the soil (short), plant biomass (medium), and soil organic matter (long)—and how do these depend on the different types of nutrient loss?

Although our model is general in the sense that it contains no assumptions that are specific to one particular nutrient (similar to DeAngelis 1992), and thus it might be applied to other nutrients up to the longest timescale we consider (millennia), we hereafter focus on N, one of the most important elements in ecosystems and one that often limits primary production (Chapin 1980; Vitousek and Howarth 1991). That N could be the sole limiting resource early in primary succession is easy to understand (at least in mesic sites), because there is little N in most rocks (but relatively plentiful amounts of P, calcium, potassium, and other nutrients), plenty of available light, and a rapidly growing plant community. Because there are always atmospheric N inputs, however, as well as the possibility of biologically controlled N inputs (from biological N fixation [BNF]), sustained limitation by N through an old-growth system is perhaps the most intriguing nutrient limitation phenomenon (Vitousek and Howarth 1991; Vitousek and Field 1999; Rastetter et al. 2001; Vitousek et al. 2002; Menge et al. 2008). For these reasons, and because there are many N-related data, we use N cycling data to parameterize our model, and we often refer to the limiting nutrient as N.

Model Description, Analysis, and Simulations

Following other ecosystem models (e.g., DeAngelis 1992; Vitousek et al. 1998), our model includes plant N (B for "biomass," synonymous here with "plant"), plant-unavailable soil N (D for "detritus," synonymous with "organic" and "unavailable"), and plant-available N (A for "available," such as nitrate, ammonium, and small organic molecules), all in mass N area^{-1} (fig. 1). We use "unavailable" and "organic" interchangeably, as well as "available" and "inorganic," even though plants can access some organic molecules (e.g., Näsholm et al. 1998). Because we are concerned with single-nutrient limitation, we consider only one resource. Our model satisfies the equations

$$\frac{dB}{dt} = B(g(A) - \mu), \tag{1}$$

$$\frac{dD}{dt} = \mu B - m(D) - \phi(D), \tag{2}$$

$$\frac{dA}{dt} = I + m(D) - k(A) - Bg(A). \tag{3}$$

The growth function g depends only on A, so relative plant growth can be limited only by available N (as in consumer-resource theory, e.g., Tilman 1982). This differs from some models (e.g., Clark et al. 2005) where relative plant growth depends on plant biomass. Allowing $(1/B)(dB/dt)$ to be a function of B, that is, allowing relative growth or mortality to be directly density dependent, implicitly introduces other limitations, but we are interested in modeling single limitation. Plant N is transferred to organic N at the rate μ. Soil organic N is mineralized to available N (as defined by the function $m(D)$) and is lost as $\phi(D)$. There are abiotic inputs of available N (I), losses of available N ($k(A)$), and plant uptake ($Bg(A)$). All parameters are assumed to be positive unless otherwise stated, and the functions $g(A)$, $m(D)$, $\phi(D)$, and $k(A)$ are assumed to intersect the origin and increase monotonically. At present, we leave the growth, mineralization, and loss functions unspecified to show that some results do not depend on specific functional forms.

Inputs and losses are the abiotic inputs, available losses, and unavailable losses $((dB/dt) + (dD/dt) + (dA/dt) = I - k(A) - \phi(D))$. Abiotic inputs in the model represent atmospheric deposition (wet and dry deposition, cloud and fog inputs of available forms) and weathering inputs from bedrock for rock-derived nutrients (e.g., P). The major nutrient input excluded by this model is BNF, which is specific to one nutrient (N) and which we treat elsewhere (Menge et al. 2008). We interpret available losses as anything leaving the available pool, including leaching through the soil and (for N) gas losses through denitrification, nitrification, or ammonium volatilization. A major set of fluxes omitted by this model are those due to disturbances, because we are primarily interested in the dynamics of an ecosystem in the absence of disturbance. We will, however, discuss how disturbance would affect our results.

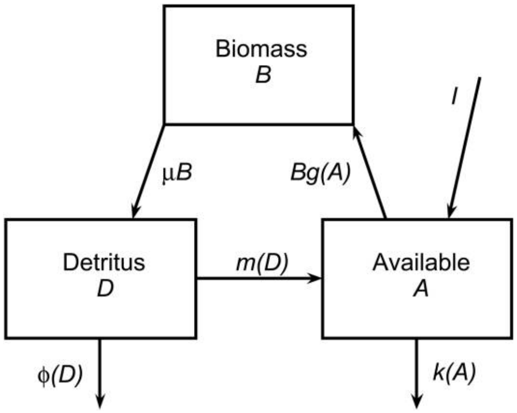

Figure 1: Model system described in equations (1)–(3). Boxes are the nutrient pools in the system: living plant biomass (B), plant-unavailable soil nutrients (D), and plant-available soil nutrients (A). Within-system fluxes include plant uptake ($Bg(A)$), turnover (μB), and net mineralization ($m(D)$). The fluxes into and out of the model ecosystem are an abiotic input to the available pool (I), losses of plant-unavailable nutrients ($\phi(D)$), and losses of plant-available nutrients ($k(A)$). The general functions $g(A)$, $m(D)$, $\phi(D)$, and $k(A)$, which we assume intersect the point (0, 0) and increase monotonically, are shown in the diagram. Some of our analyses are performed with the general functions, but when necessary we use linear (in the text) or saturating (in "Saturating Functions" in the appendix in the online edition of the *American Naturalist*) functions.

We analyze this model in two ways. First, we look for stable, steady-state solutions of equations (1)–(3) in different scenarios (available losses and/or unavailable losses). If a finite, locally stable equilibrium exists, it is possible for the plant population to be limited by one nutrient at steady state. This does not guarantee that a plant population will be limited by that nutrient, because no other resources are included in the model and some other resource may cap growth below the limit allowed by the availability of the nutrient, but we are interested in determining which mechanisms can allow a plant population to be limited by a single nutrient. Alternatively, if no such equilibrium exists and the plant pool increases forever, a

Table 1: Parameter definitions, units, and values for the model simulations

Parameter	Definition	Units	Grassland	Forest
g	N uptake rate	kg N^{-1} ha year^{-1}	4.0	.15
μ	Biomass N turnover rate	year^{-1}	1.0	.019
m	Net N mineralization rate	year^{-1}	.0091	.0076
ϕ	Unavailable N loss rate	year^{-1}	.0027	.00089
I	Abiotic N input flux	kg N ha^{-1} year^{-1}	15	2.0
k	Available N loss rate	year^{-1}	1.0	1.0

Note: Grassland parameter values for m, ϕ, and I are from Baisden et al. (2002) and Baisden and Amundson (2003). Other grassland parameter values come from assuming annual turnover (μ), the same $\overline{A}$ as forest (g), or the same loss rate as forest (k). Forest parameter values come from Hedin et al. (1995), Perakis and Hedin (2001), Vann et al. (2002), and Perakis et al. (2005). N = nitrogen.

single nutrient cannot limit primary production. We do not explicitly include another resource, but our interpretation of this perpetual growth is that some other resource (e.g., light, space, or water) or factor (e.g., top-down control) must ultimately limit plant production in the absence of disturbance. A final alternative is that plant N is capped but total ecosystem N increases forever, in which case a nutrient can limit plant production indefinitely but not total N accumulation.

Second, we assume that the three components of the system change on different timescales (aka return times; DeAngelis 1992), and we investigate the transient and quasi-equilibrium dynamics at each timescale. Quasi equilibria—states that do not change appreciably on the timescale of interest—are useful for understanding systems with different timescales because they reduce the complexity of the system, often permitting further insight (e.g., Ludwig et al. 1978).

At the shortest timescale, we assume that available N in the soil changes so rapidly that it comes to a quasi equilibrium instantaneously relative to changes in biomass N or soil organic N. On the intermediate timescale, we look at changes in plant N, assuming that available N keeps pace instantaneously with plant N and that soil organic N changes so slowly that it is relatively constant. On the longest timescale, we examine the dynamics of soil organic N, assuming that both available N and plant N keep pace instantaneously.

The assumption of separate timescales is generally supported by the literature. Tracer studies with ^{15}N show that nitrate and ammonium are taken up very rapidly in N-poor ecosystems (hours to days in grasslands and forests; Jackson et al. 1989; Schimel et al. 1989; Zak et al. 1990; Perakis and Hedin 2001; Providoli et al. 2006). In grasslands, it seems reasonable that the timescale of biomass N is short (a year to a decade) relative to that of soil organic N (decades to centuries; Brenner et al. 2001). In forests, total biomass takes longer to equilibrate, but because leaves and fine roots often contain more N than wood does (Binkley et al. 1992), it is reasonable that the timescales of plant N (years to decades or perhaps centuries, assuming that plant N is proportional to leaf area index; Uhl and Jordan 1984; Aber and Melillo 1991; Kashian et al. 2005) and soil organic N (centuries to millennia; Crews et al. 1995; Richardson et al. 2004) are separate.

We subject our model ecosystem (with linear functions) to two perturbations to reveal the three timescales and the accuracy of our quasi-equilibrium approximations. Starting from equilibrium, we numerically solve equations (1)–(3) (using MATLAB 7.4.0, R2007a's ode45), first stopping at 0.001 years (approximately half a day) to fertilize with 30 kg of available N ha^{-1}. Second, we simulate a disturbance that causes N loss (e.g., fire) at 0.1 years (~1 month), setting biomass and detritus N levels to 5% and 50%, respectively, of their predisturbance values. We run this system for 10,000 years for both grassland and forest parameters.

We also simulate the model with different rates of organic N loss to illustrate the effect of this loss rate on plant N dynamics. Using the N loss disturbance as our starting condition, we run the model without perturbation for 1,000 years, showing the first 10 years (grassland) or 100 years (forest) on a yearly scale and the rest on a century scale.

Grassland parameters come from the youngest site on a well-studied chronosequence of annual grasslands in the San Joaquin Valley, California (see Baisden et al. 2002 for site descriptions). Forest parameters come from well-studied, unpolluted, mixed angiosperm-conifer forests on the Isla de Chiloé, Chile (see Hedin et al. 1995; Vann et al. 2002 for site descriptions), which have more N in wood than most forests, thereby allowing a conservative test of timescale separation. Parameter values are presented in table 1.

Results

Equilibrium Analysis

We examine two cases of N loss in our model ecosystem. The first case permits only losses of available forms of N (traditional view, $\phi(D) = 0$ and $k(A) > 0$), whereas the second case permits losses of both available and unavailable forms of N (leaky-bucket hypothesis, $\phi(D) > 0$ and $k(A) > 0$). For both cases, there is a trivial equilibrium where plant and soil organic N masses are both equal to 0, but we do not consider this trivial equilibrium in our analysis.

Traditional View: Losses of Available N Only. Under what conditions can losses of available N alone sustain N limitation at equilibrium? From equations (2) and (3), the equilibrium plant N value when $\phi(D) = 0$ is

$$\overline{B} = \frac{I - k(\overline{A})}{g(\overline{A}) - \mu}, \tag{4}$$

where a bar denotes the equilibrium value of a variable. For plant N to be at equilibrium, N uptake must equal turnover ($g(\overline{A}^*) = \mu$, from eq. [1]), so $\overline{B}$ in equation (4) is undefined. For the ecosystem to be at steady state, inputs must equal losses ($I = k(\overline{A}^\dagger)$), so the numerator of equation (4) is also 0. The value of the available N pool that equilibrates plant growth ($\overline{A}^*$) is not the same as the value that causes inputs to equal losses ($\overline{A}^\dagger$). Therefore, if $\overline{A}^* < \overline{A}^\dagger$, plant biomass ($B$) grows to infinity (linearly when time is large), whereas if $\overline{A}^* > \overline{A}^\dagger$, plant biomass shrinks to 0. Although shrinkage is possible, we hereafter ignore it, assuming that plants can inhabit the site. Because we have not yet specified functional forms for plant N uptake or available N losses, the result that plants can grow forever holds for any uptake and loss functions subject to the conditions above.

This result agrees with those of other studies (e.g., fig. 3.4 in DeAngelis 1992), and it supports part of both the traditional view and the leaky-bucket hypotheses: losses of available N alone cannot maintain a long-term N-limited steady state of the full ecosystem under a wide range of conditions. Importantly, it is not necessary for plants to take up all available N (as in some models, e.g., Vitousek et al. 1998; Vitousek and Field 1999; Vitousek 2004) to overcome N limitation: in this model there are available N losses ($k(A) > 0$), but plants can still grow without bound.

One main assumption on which this result depends is that the mineralization function $m(D)$ does not saturate. When it does, there is still no equilibrium of the full ecosystem, but in the long term the subsystem with plants and plant-available nutrients approaches an asymptote (as we show in the quasi-equilibrium analysis below), thereby sustaining N limitation and capping plant biomass.

Leaky-Bucket Hypothesis: Losses of Unavailable N or Both. When losses of unavailable nutrients are included, stable equilibria are possible whenever (1) plants can inhabit the ecosystem and (2) organic losses can exceed the difference between inputs and steady-state inorganic losses (see "Conditions under Which Organic Nitrogen Losses Allow a Positive Equilibrium" in the appendix in the online edition of the *American Naturalist*). When such an equilibrium exists, it is locally stable, given our assumptions about $g(A)$, $m(D)$, $\phi(D)$, and $k(A)$ (see "Local Stability Analysis" in the appendix). This confirms the second part of the leaky-bucket hypothesis: losses of unavailable N can maintain N limitation at equilibrium under a wide range of conditions. This remains true even if plants take up all available N ($k = 0$, as in Vitousek et al. 1998; Vitousek and Field 1999).

Quasi-Equilibrium Analysis

In this subsection, we take advantage of the natural timescale separation in terrestrial ecosystems to simplify our model. At each timescale—available soil N (hours to days), plant N (years to centuries), and soil organic N (centuries to millennia)—we assume that slow variables are constant and fast variables have quasi-equilibrated. To examine the three timescales of the system (eqq. [1]–[3]), we specify linear functions for growth and inorganic loss, ($g(A) = gA$ and $k(A) = kA$, as in Menge et al. 2008), which are decent approximations of saturating functions when A is small. In "Saturating Functions" in the appendix, we show that the qualitative results are identical with saturating functions.

Short Timescale. From equation (3), with linear $k(A)$ and $g(A)$ and treating B and D as constants, the exact and approximate (see "Assumptions about Flux Magnitudes" in the appendix) quasi equilibria ($\hat{A}$) and short-timescale solutions are

$$\hat{A} = \frac{I + m(D)}{k + gB}, \tag{5}$$

$$\hat{A} \approx \frac{m(D)}{gB}, \tag{6}$$

$$A(t) = \hat{A} + \left(A(0) - \hat{A}\right)e^{-(k+gB)t}, \tag{7}$$

where $A(t)$ is the value of A at time t. The function $A(t)$ starts at $A(0)$ and approaches $\hat{A}$ asymptotically. The rate at which it approaches $\hat{A}$ (i.e., the timescale) is controlled by the exponent (DeAngelis 1992), $k + gB$. When plant uptake of available N is much greater than losses of available N ("Assumptions about Flux Magnitudes"), equation (7) says that the time it takes for soil available N to approach its equilibrium is controlled almost exclusively by plant N uptake, gB. The function $\phi(D)$ does not appear in equations (5)–(7), so unavailable N losses have no effect on the quasi-equilibrium value of soil available N. Furthermore, soil available N will equilibrate on its timescale (hours to days) independent of whether there are organic losses.

Intermediate Timescale. Substituting equation (5) into equation (1) and setting $dB/dt = 0$ yields the quasi equilibrium of plant N mass ($\hat{B}$). Using equation (6), equation (1) can be solved to yield plant N at time t as a function of soil organic N (see "Differential Equations from Timescale Analysis" in the appendix). These are

$$\hat{B} = \frac{I + m(D)}{\mu} - \frac{k}{g}, \tag{8}$$

$$B(t) \approx \hat{B} + \left(B(0) - \hat{B}\right)e^{-\mu t}. \tag{9}$$

Plugging equation (8) into equation (5) reveals that $\hat{A}$ is controlled by plant parameters ($\hat{A} = \mu/g$) beyond short timescales, as in classical consumer-resource theory (Tilman 1982). In equation (8), $\hat{B}$ is finite regardless of the value of $\phi(D)$, provided that $m(D)$ is finite. Therefore, when the plant N timescale is shorter than the soil organic N timescale, plant N approaches the quasi equilibrium $\hat{B}$ at the plant turnover rate (μ; see "Eigenvalue Calculations" in the appendix), regardless of whether there are organic N losses. In annual grasslands, μ is approximately uniform across tissue types and typically has a value of 1 year^{-1} or faster. In forests, μ is composed of litterfall and mortality rates (years to centuries), but it is dominated by whichever N pool (foliar or stem) is larger. In forests where there is more N in foliage than in stems, the timescale of plant biomass N is on the same order as litterfall.

Long Timescale. Because total N in the full model grows indefinitely without organic losses, and the short and intermediate timescales reach quasi equilibria, detritus N (and thus, total N) must grow indefinitely on the long timescale when there are no organic N losses. This can be illustrated with a linear soil organic N loss function ($\phi(D) = \phi D$) (which we use for the remainder of "Results"), which gives the equilibrium value of soil organic N ($\overline{D}$) and D at time t (from eq. [2]) on the long timescale,

$$\overline{D} = \frac{I - (k\mu/g)}{\phi}, \tag{10}$$

$$D(t) = \overline{D} + \left(D(0) - \overline{D}\right)e^{-\phi t}. \tag{11}$$

When $\phi = 0$, soil organic N is undefined at equilibrium (see also "Saturating Functions" and "Differential Equations from Timescale Analysis"). If $m(D)$ does not saturate, $\hat{B}$ also grows without bound (eq. [8]), but if $m(D)$ does saturate, $\hat{B}$, and thus $\overline{B}$, is bounded. When soil organic N is lost, D goes from $D(0)$ to $\overline{D}$ at a timescale controlled by the organic N loss rate, ϕ. However, linearization around the equilibrium shows that the true return rate for the longest timescale is closer to $\mu\phi/(\mu + m)$, and ϕ is the approximation when $\mu \gg m$ (see "Eigenvalue Calculations" for links between timescales and eigenvalues of the linearization matrix).

Simulations

Three Separate Timescales. The three timescales of the model are apparent in our first simulations, which show plant N (B), detritus N (D), and available N (A) in the grassland (fig. 2) and forest (fig. 3), with time on a logarithmic scale. The full system (eqq. [1]–[3], with functions and parameters listed in table 1) is in solid black in each figure, starting at equilibrium (*dotted lines*). Timescale approximations (eqq. [7], [9], [11]) are thick dashed lines, and quasi equilibria (eqq. [5], [8]) are dashed-dotted lines.

At 0.001 years, we fertilize with 30 kg available N ha^{-1}, which is rapidly taken up by plants, revealing the shortest timescale. The available N pool quasi-equilibrates within a few days (figs. 2*C*, 3*C*). When the forest takes up the pulse of N fertilizer (fig. 3*A*), biomass N stays relatively constant because the plant N pool is large relative to the fertilizer pulse, supporting our assumption of constant plant N mass on the short timescale. In the grassland, the biomass N increase is more apparent (fig. 2*A*) because the plant N stock is smaller than it is in the forest. The short-timescale approximation of available N, equation (7) (figs. 2*C*, 3*C*, *thick dashed lines*), fits the full system excellently for the forest (diverging by <0.2 kg N ha^{-1} from the full simulation; fig. 3*C*) and still fits quite well for the grassland (diverging by <2 kg N ha^{-1}; fig. 2*C*).

To reveal the intermediate timescale, we simulate a disturbance (such as fire) at 0.1 years, removing 95% of plant N (figs. 2*A*, 3*A*) and 50% of detritus N (figs. 2*B*, 3*B*). With the biomass crash, available N uptake decreases, so available N increases (figs. 2*C*, 3*C*). In the grassland, plants quasi-equilibrate in a few years (fig. 2*A*). Although plants remove N from the detritus pool (by way of the available pool) to fuel their growth, the detritus N pool is much larger than the plant N pool, so it remains effectively constant over the intermediate timescale (fig. 2*B*). The intermediate-timescale approximation of grassland biomass N, equation (9), is indistinguishable from the full system approximation, differing by <2 kg N ha^{-1}.

In the forest, it takes much longer for plants to regrow to their quasi equilibrium (~200 years; fig. 3*A*) because

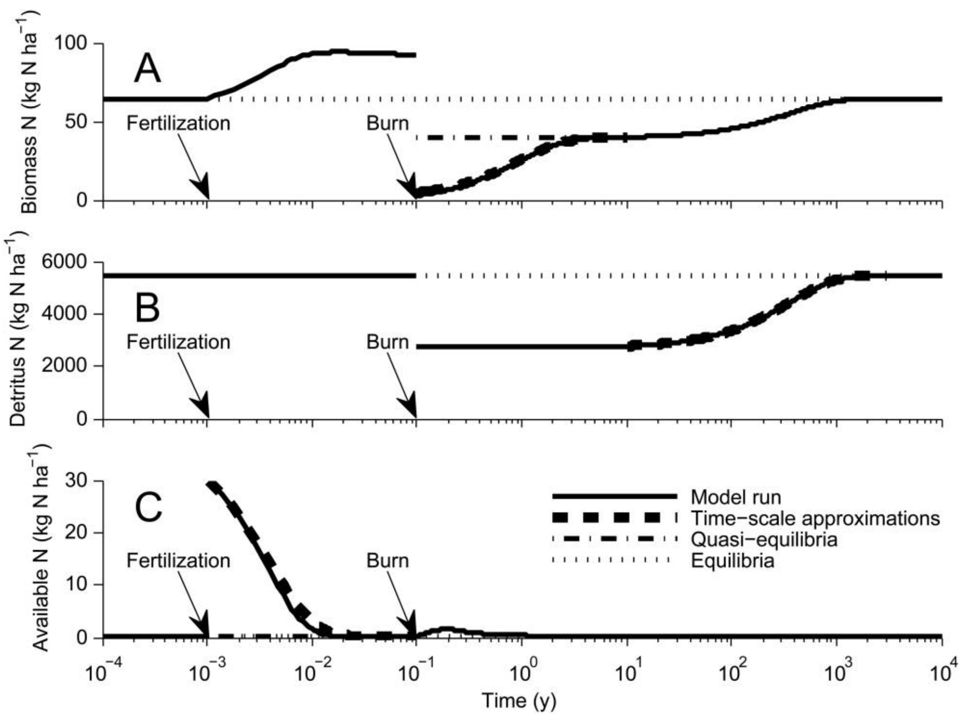

Figure 2: Three timescales of the model grassland with time on a logarithmic scale. The numerically integrated system (eqq. [1]–[3] with linear functions, using grassland parameter values in table 1) is represented by solid lines, equilibria by dotted lines, quasi equilibria by dashed-dotted lines, and timescale approximations by thick dashed lines. Stocks of (*A*) biomass N, (*B*) available nitrogen (N), and (*C*) detritus N are shown. The system starts at equilibrium, and then at 0.001 years we fertilize with 30 kg available N ha^{-1} to illustrate the short timescale. The quasi equilibrium (eq. [5], the same here as the equilibrium) and timescale approximation (eq. [7]) for available N are shown from 0.001 to 0.1 years in *C*. At 0.1 years, 95% of biomass and 50% of detritus N are removed to simulate a disturbance such as fire and reveal the intermediate timescale (plant regrowth). From 0.1 to 10 years, the quasi equilibria (eq. [8]) and timescale approximation (eq. [9]) of biomass N are shown in *A*. Starting at 10 years, when plant biomass has approached its quasi equilibrium, the long timescale begins, and the timescale approximation of detritus N (eq. [11]) is shown in *B*. The long timescale constitutes rebuilding total N stocks. Equilibria are shown at all times.

much of the plant N is locked up in stems and thus turns over slowly (table 1). Because the plant N pool is on the same order of magnitude as detritus N in the forest, the transfer of N from detritus to plants makes an appreciable dent in the detritus N pool (fig. 3*B*). Therefore, the assumption of constant detritus N on the intermediate timescale is not as good in the forest, as reflected by the divergence (~80 kg N ha^{-1}) of the plant N approximation (eq. [9]; thick dashed lines in fig. 3*A*) from the true value (solid lines in fig. 3*A*). However, this difference is only a maximum of 20% off from the true value.

Losses of N from this disturbance are substantial, and the rebuilding of total N constitutes the longest timescale. Starting at 10 years (grassland) or 200 years (forest), organic N begins to increase noticeably, and it nears its equilibrium after ~2,000 years (grassland; fig. 2*B*) or ~7,000 years (forest; fig. 3*B*). Available N and plant N track the changes in organic N almost instantaneously. The long-timescale approximation (eq. [11]; thick dashed lines in figures) starts at 10 years (grassland; fig. 2*B*) or 200 years (forest; fig. 3*B*). The approximation for the grassland is nearly perfect, diverging by <10 kg N ha^{-1} (<1% divergence), whereas the approximation for the forest diverges by <150 kg N ha^{-1} (<10% divergence). This divergence in the forest simulation stems from the breakdown of the assumption that $\mu \gg m$ in the forest (table 1; "Eigenvalue Calculations").

Effect of Organic Losses. Our final simulations display the effects of organic N losses on grassland (fig. 4*A*) and forest (fig. 4*B*) biomass N on intermediate and long timescales. We run the full system with four organic N loss rates ($\phi_1 = 0$, $\phi_2 = \phi_{\max}/4$, $\phi_3 = \phi_{\max}/2$, and $\phi_4 = \phi_{\max}$ years^{-1}, where $\phi_{\max}$ is the ϕ value for each ecosystem from table 1), starting directly after the disturbance. In the grassland, plant N increases rapidly in the first few years and then levels off on the yearly timescale. At 10 years, plant N is indistinguishable for the four ϕ values. In contrast,

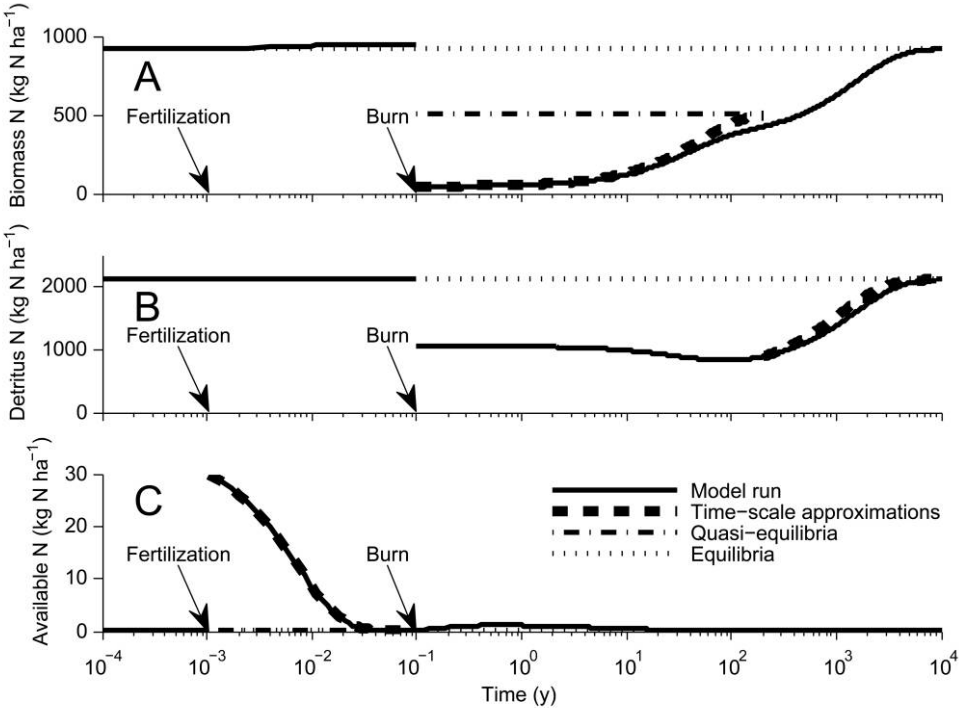

Figure 3: Three timescales of the model forest, with time on a logarithmic scale. The only differences from figure 2 are that forest parameters (table 1) are used and that the cutoff between the intermediate and long timescales is 200 years instead of 10 years.

the differing organic loss rates are quite important on the long timescale (after the vertical line). With $\phi_{\max}$, the system approaches equilibrium at 1,000 years, whereas for $\phi_{\max}/2$ and $\phi_{\max}/4$, plant N will grow appreciably for millennia, and for $\phi = 0$, plant N will grow linearly forever. In the long term, N limitation cannot be maintained when $\phi = 0$ (when $m(D)$ is linear), but on the timescale of years to centuries, N could limit plant growth and appear to cap plant biomass, even without organic N losses. In the forest, the story is similar, except it takes decades for plant N to appear to saturate, and thus we display the timescale break at 100 years (when plant N values are still nearly indistinguishable).

Discussion

Answers to the first two questions posed in "Introduction" are clear. First, under a large class of conditions, chronic losses of plant-available forms of a nutrient alone cannot maintain limitation by that nutrient at a long-term equilibrium, supporting part of both the traditional (Vitousek and Reiners 1975) and the leaky-bucket (Hedin et al. 1995) hypotheses. This is apparent from equation (4), which shows that plants can grow indefinitely when there are losses of available forms only (and therefore it implies that some other factor, such as light, must ultimately limit plant production in this scenario). This result is robust to a large class of functions for plant uptake, mineralization, and available nutrient loss, with a key exception.

When net mineralization is a saturating function of detritus N, plant biomass approaches an asymptote, so long-term nutrient limitation to plants occurs despite the continual accumulation of soil organic N. A saturating mineralization function is no less plausible than a linear form, and it could result from many mechanisms, such as decomposition being limited by something other than substrate (e.g., grazing) or a simple inability to process a large amount of detritus (sensu handling time). This would result in detritus accumulation and burial. Unfortunately, experiments testing the functional form are lacking, so we cannot rule out or fully embrace this mechanism. However, although it does not imply a loss in the same sense as DON leaching because the N is still physically in the ecosystem, saturating mineralization is similar to losses of unavailable N from the plants' perspective. As detritus N increases, proportionately less N is mineralized and thus proportionately more N is effectively lost to plants.

Second, losses of a plant-unavailable form of a nutrient can maintain limitation by that nutrient at an equilibrium of the full ecosystem under a large class of conditions,

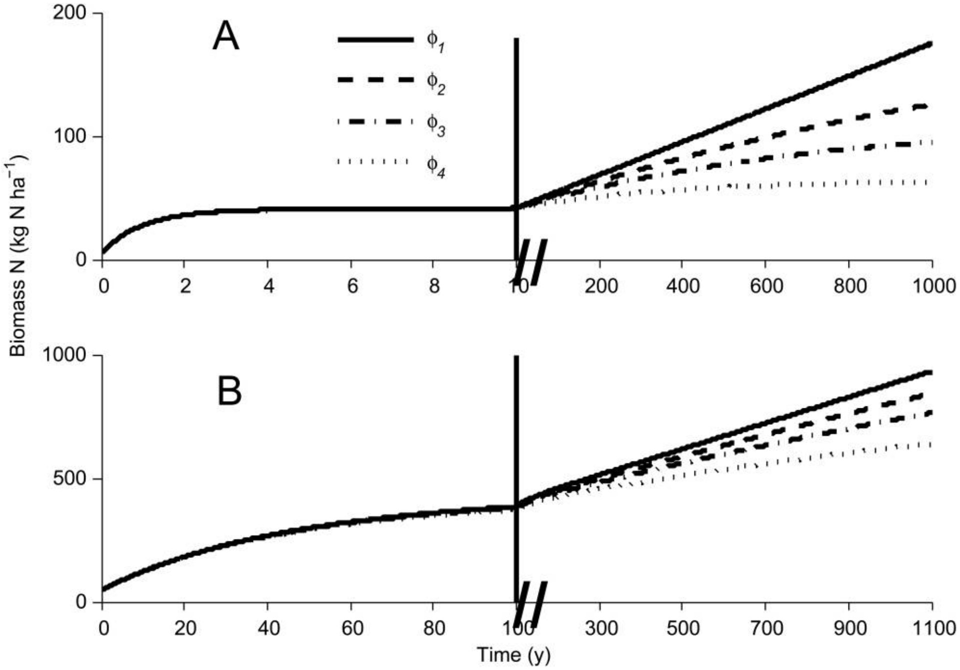

Figure 4: Effect of organic nitrogen (N) losses on (*A*) grassland and (*B*) forest biomass N over medium and long timescales. Starting the full model from right after the disturbance, biomass N stocks are shown on two timescales, for (*A*) the first 10 years or (*B*) 100 years and the following 1,000 years, both of which have a linear scale. Each separate run differs in the loss rate of unavailable N: $\phi_1 = 0$, $\phi_2 = \phi_{\max}/4$, $\phi_3 = \phi_{\max}/2$, and $\phi_4 = \phi_{\max}$ year^{-1}, where $\phi_{\max}$ is the value listed for the respective ecosystem type in table 1. All other parameters are as in table 1 for each ecosystem type. Note that when $\phi = 0$, N cannot limit plant growth at equilibrium.

confirming the second part of the leaky-bucket hypothesis and generalizing previous simulation studies (Vitousek et al. 1998; Vitousek and Field 1999). Specifically, organic losses can maintain nutrient limitation when two conditions are met: (1) plants can inhabit the ecosystem and (2) the organic loss flux can exceed a threshold set by the difference between inputs and steady-state inorganic losses when the detritus pool is sufficiently large. The first condition is true in any environment we are considering. The second condition is more interesting, and it highlights the importance of the relationship between the detritus N pool and organic N loss fluxes. The most straightforward relationship is that a constant fraction of the detritus N pool is lost per unit time (as in the linear function we use), in which case a stable, single-nutrient-limited equilibrium exists. However, many nonlinear relationships also allow for such an equilibrium. The only relationships that would violate the second condition (and render sustained N limitation impossible) are those that specify that organic N losses saturate below $I - k(\overline{A})$ as the detritus N pool grows. Although we feel that these are less likely than proportional relationships, studies examining the relationship between the soil organic N pool size and organic N loss fluxes are needed.

The fact that a loss from either the detritus or the biomass pool (or both) must be included to allow an equilibrium to exist has been recognized in many nutrient cycle models (e.g., DeAngelis 1992; DeAngelis et al. 1995; Daufresne and Hedin 2005; Ballantyne et al. 2008). However, to our knowledge, only one other model similar to ours has considered this result in light of the leaky-bucket hypothesis. Vitousek et al. (1998) used difference equation simulations to show that nutrient limitation could not be maintained when plants take up all available nutrients (i.e., losses of the limiting nutrient are 0), but first-order losses of plant-unavailable soil nutrients could maintain nutrient limitation indefinitely. Our results agree with this study, but they generalize it to a much larger class of models.

Taken together, our equilibrium results shed light on the importance of biotic control on nutrient losses in nutrient limitation in very old ecosystems. When plants have a chance to assimilate the nutrient that limits their growth before it is lost, they will not be limited by that nutrient indefinitely, which supports the traditional view. Importantly, they do not have to assimilate every molecule (as in Vitousek et al. 1998; Vitousek and Field 1999). In contrast, when there are losses from a pool that plants cannot control or from a continual accumulation of detritus N that cannot be broken down, a nutrient can limit primary production indefinitely.

Although a lack of biotic control on nutrient losses can maintain nutrient limitation, biotic control on nutrient inputs may counteract this effect (Vitousek and Howarth 1991; Vitousek and Field 1999; Rastetter et al. 2001; Vitousek et al. 2002; Menge et al. 2008). For example, BNF is under biotic control and can be a large N input. The model we present here omits BNF, but we have shown elsewhere that adding BNF to the model used in this study (using linear functions and assuming that N fixers have access to the same available N pool as nonfixers) changes the condition that renders equilibrium N limitation possible from organic N losses exceeding 0 to organic N losses exceeding BNF inputs. This would make sustained N limitation harder to explain, although physiological and ecological trade-offs with BNF could select against N fixers (Menge et al. 2008).

The answer to our third question (about nutrient dynamics at different timescales) is less concise because there is a rich array of dynamics in even this simple model ecosystem. For the most part, our assumptions of complete timescale separation are justified (figs. 2, 3). The available form of the nutrient is taken up very quickly after the fertilization, on the order of days (figs. 2*C*, 3*C*). After the disturbance, plants regrow and approach their quasi equilibrium in a matter of years in the grassland (fig. 2*A*) or decades to centuries in the forest (fig. 3*A*). On the longest timescale, the unavailable form of the nutrient increases slowly, approaching its equilibrium on the order of centuries to millennia (figs. 2*B*, 3*B*), and it is tracked by nutrient stocks in the biomass (figs. 2*A*, 3*A*).

This separation means that our analyses can help us understand the dynamics of the system, but it does not mean that the components of the different timescales are independent of one another. In fact, they depend heavily on each other. For example, at the fast timescale, the quasi equilibrium of available N in the soil depends on both the detritus and the plant N pools (eq. [5]).

Each of the timescales is controlled by the loss rate from the nutrient pool of interest. Plant uptake controls the short timescale (eq. [7]), plant turnover controls the intermediate timescale (eq. [9]), and organic losses control the long timescale (eq. [11]). Because plants have evolved in a competitive environment where nutrients are often in short supply, it makes sense that uptake from the available pool is rapid. Nutrient uptake helps a plant and hurts its competitors, so it should be under strong selection.

Plant turnover controls the intermediate timescale, as presented in figures 2*A* and 3*A*. The turnover rate is high in grasslands (table 1; fig. 2*A*) because all plant stocks (leaves, roots, reproductive structures) turn over quickly, whereas it is lower in forests (table 1; fig. 3*A*) because some nutrients are locked up in slower pools. A more realistic forest model would include at least two plant nutrient pools—one for rapid-turnover pools (foliage and fine roots) and one for slower pools (wood, stems, and coarse roots)—which would make the timescale approximations fit better.

The organic N loss rate controls the longest timescale, but it has a negligible effect at shorter timescales. The quasi equilibria of available N (eq. [5]) and plant N (eq. [8]) do not depend on the organic loss rate (ϕ), but the equilibrium plant and detritus pool sizes and the longest timescale do (eq. [8] when $D = \overline{D}$; eqq. [10], [11]; fig. 4). This result agrees with a study by Rastetter et al. (2005), who used the multiple element limitation (MEL) model to show that, when carbon (C) and N colimit plant growth, DON losses have a larger effect on the amount of C and N stored at long timescales (>60 years) than plant-available N losses do. Importantly, they found that the functional form of DON loss was also important to the magnitudes of C storage. Their interpretation of these results, similar to ours, is that the degree of plant control on nutrient loss is the key distinction. Our model shows that this result does not depend on the complexities of the MEL model (which includes many aspects that our model omits, such as stoichiometric differences, multiple element limitation, and many more pools), and it makes explicit the effect of the parameters on the equilibrium values and timescales (albeit for a simpler, and thus less realistic, model than the MEL model).

Together, these studies indicate that studies of organic loss rates in intact, old-growth ecosystems are crucial to understanding nutrient limitation over timescales of centuries to millennia. For example, Hedin et al. (2003) use their DON loss data to calculate when N sufficiency sets in across a long-term soil chronosequence in Hawaii. Empirical studies quantifying the relationship between soil organic nutrient pools and organic loss fluxes (i.e., the form of the function $\phi(D)$ and its parameters) will go a long way toward understanding nutrient limitation at long timescales. Our work shows that low-saturating loss functions cannot allow for a nutrient-limited equilibrium, and it shows exactly how the parameters of $\phi(D)$ affect the sizes of pool and timescales given certain assumptions about the shape of $\phi(D)$. The work of Rastetter et al. (2005) shows substantial effects of the functional form of $\phi(D)$ on C storage. Given the importance of these different outcomes (nutrient limitation vs. no nutrient limitation, C storage capacity, and the rate of C storage) on issues of global change, understanding the shape of $\phi(D)$ is important.

These multiple-timescale dynamics also have important implications for nutrient limitation at shorter timescales, particularly in experimental studies. In grasslands, plant

N appears to saturate at its quasi equilibrium (figs. 2*A*, 4), well before it reaches equilibrium, and it even appears to saturate when it will never equilibrate (when $\phi = 0$; fig. 4, *solid line*). With even a small amount of noise in the system (whether experimental error or true noise due to something like climate variability), the values of plant N at 10 years and 50 years would be indistinguishable. Furthermore, the values of plant biomass for the four different organic loss rates, even at 50 years, would be indistinguishable. Therefore, on the timescale of any typical experiment (less than a few decades), differences in organic losses have little to no effect on experimental results (as long as the treatments start at the same state).

Along with BNF, which we discuss above, our model omits other biogeochemical processes, trophic levels, and timescales (such as extremely rapid microbial activity [Jackson et al. 1989; Schimel et al. 1989; Zak et al. 1990; Perakis and Hedin 2001; Providoli et al. 2006] and slow geological processes [Walker and Syers 1976; Hedin et al. 2003; Vitousek 2004]). Furthermore, we do not explicitly treat disturbances such as fire, storms, or landslides in the analytical model, but these can remove nutrients or transfer plant biomass to the soil (Uhl and Jordan 1984; Yanai 1998; Houlton et al. 2003; Burns and Murdoch 2005; DeLuca and Sala 2006; Gray and Dighton 2006). An illustration of this effect is displayed in figures 2 and 3 when a disturbance removes plant and soil N; these large N losses take centuries to millennia to replenish. In many real ecosystems, disturbances occur on much shorter return intervals and thus could easily maintain nutrient limitation indefinitely, even without chronic losses (as in Vitousek et al. 1998; Vitousek and Field 1999; Vitousek 2004) or burial of organic nutrients.

Even without disturbance, our model shows that nutrient limitation can be maintained for a long time, with or without losses of plant-unavailable nutrients. On timescales of years (for grasslands) to centuries (for forests), biomass N can approach a quasi equilibrium that would be indistinguishable from a true equilibrium in a real ecosystem, even when nutrient limitation at steady state is impossible.

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Appendix from D. N. L. Menge et al., “Emergence and Maintenance of Nutrient Limitation over Multiple Timescales in Terrestrial Ecosystems”

(Am. Nat., vol. 173, no. 2, p. 164)

Supporting Analyses, Conditions, Equations, and Assumptions

Conditions under Which Organic Nitrogen Losses Allow a Positive Equilibrium

From setting $dB/dt = 0$ in equation (1), $\overline{A}$ is positive whenever

$$\lim_{A\to\infty} g(A) > \mu, \tag{A1}$$

that is, whenever plants with access to plenty of nutrients grow enough to overcome losses from plant turnover. The steady-state condition from equation (2) is $\overline{B} = (m(\overline{D}) + \phi(\overline{D}))/\mu$, so $\overline{B}$ is positive whenever $\overline{D}$ is positive. Finally, the steady-state condition for the whole system is $I - k(\overline{A}) - \phi(\overline{D}) = 0$, so $\overline{D}$ is positive whenever $I > k(\overline{A})$ and

$$\lim_{D\to\infty} \phi(D) > I - k(\overline{A}). \tag{A2}$$

When there are losses of organic nitrogen (N; $\phi(D) > 0$), $\overline{A}$ is set by $g(\overline{A}) = \mu$, corresponding to $\overline{A}^*$ in “Equilibrium Analysis, Traditional View” in “Results.” Therefore, nutrient inputs exceed abiotic losses at equilibrium ($I > k(\overline{A})$) whenever plants can inhabit the site without organic losses ($\overline{A}^* < \overline{A}^\dagger$). Assuming that this is true, condition (A2) says that $\overline{D}$ is positive when organic nutrient losses can exceed the difference between inputs and steady-state inorganic losses.

Local Stability Analysis

Local stability of the internal equilibrium of equations (1)–(3) is given by the Jacobian matrix of this system, evaluated at equilibrium, which is

$$\begin{bmatrix} 0 & 0 & \overline{B}g'(\overline{A}) \\ \mu & -(m'(\overline{D}) + \phi'(\overline{D})) & 0 \\ -g(\overline{A}) & m'(\overline{D}) & -(k'(\overline{A}) + \overline{B}g'(\overline{A})) \end{bmatrix}, \tag{A3}$$

where a prime indicates a derivative. As long as the equilibrium is positive and finite, and under the assumptions we made about the functions in the text, matrix (A3) satisfies the Routh-Hurwitz conditions for all eigenvalues having a negative real part (trace < 0, trace × sum of principal minors < determinant, determinant < 0), guaranteeing local stability of the equilibrium (for details of this analysis, see May 1973). Because this analysis did not depend on specific functional forms of $g(A)$, $m(D)$, $\phi(D)$, or $k(A)$, it holds for any such functions that intersect the origin and increase monotonically, such as the familiar linear, Michaelis-Menten, or logistic forms.

Saturating Functions

In this article, we use linear functions for $g(A)$, $k(A)$, $m(D)$, and $\phi(D)$ when a specific functional form is necessary. Many fluxes in nature (particularly biologically controlled ones) are saturating functions of their arguments, and the linear functions we used in the text are decent approximations of saturating fluxes when the arguments are small. However, D in particular can become large, so we now examine how explicitly treating the functions as saturating affects the results of the timescale analysis (note that the equilibrium analysis, including the linearization analysis around equilibrium in “Local Stability Analysis” and “Eigenvalue Calculations,” is independent of functional form, hence our focus on the timescale analysis here).

At the short timescale, let $k(A) = kA/(K_k + A)$ and $g(A) = gA/(K_g + A)$. The value for the quasi equilibrium of available soil N is now

$$\hat{A} = \frac{Y - \sqrt{X}}{2[I + m(D) - (k + Bg)]}, \tag{A4}$$

$$X = Y^2 + 4(I + m(D))K_k K_g[k + Bg - (I + m(D))], \tag{A5}$$

$$Y = kK_g + BgK_k - (K_k + K_g)(I + m(D)). \tag{A6}$$

Only the branch of $\hat{A}$ listed in equation (A4) is positive because $k + Bg > I + m(D)$ when $dA/dt = 0$ and $K_k, K_g > 0$. Unlike the linear case, an explicit solution for $A(t)$ is not possible with saturating functions, but $\hat{A}$ is globally stable on its timescale, so the behavior is qualitatively identical to the linear case.

At the intermediate timescale, the quasi-equilibrium value for plant N is now

$$\hat{B} = \frac{I + m(D)}{\mu} - \frac{(g - \mu)kK_g}{g[\mu K_g + (g - \mu)K_k]}, \tag{A7}$$

which, similar to the text, is finite whenever $m(D)$ is finite. As well, $\hat{B}$ is globally stable on its timescale, as in the linear case.

At the long timescale, the differential equation for soil organic N (assuming that $A = \hat{A}$ and $B = \hat{B}$) is now

$$\frac{dD}{dt} = \left\{I - \frac{(g - \mu)kK_g}{g[\mu K_g + (g - \mu)K_k]}\right\} - \phi(D), \tag{A8}$$

regardless of the functional form of $m(D)$. Note that this is very similar to equation (A14), with the only difference found in the constant term. Therefore, if $\phi(D)$ is linear, the solution of equation (A8) is equation (11). However, if $\phi(D) = \phi D/(K_\phi + D)$,

$$\overline{D} = \frac{K_\phi(I - [(g - \mu)kK_g]/\{g[\mu K_g + (g - \mu)K_k]\})}{\phi - (I - [(g - \mu)kK_g]/\{g[\mu K_g + (g - \mu)K_k]\})}, \tag{A9}$$

and there is no simple solution for $D(t)$. However, like $\hat{A}$ and $\hat{B}$, $\overline{D}$ is globally stable on its timescale, yielding the same qualitative behavior as the linear case. The only qualitative difference with saturating functions is the change noted in the main text: when $m(D)$ saturates and $\phi(D) = 0$, plant N does not grow without bounds, but soil organic N still does on the long timescale.

Assumptions about Flux Magnitudes

The mineralization fluxes of N ($m(D)$) are typically on the order of 10–100 kg N ha^{-1} year^{-1} (Bormann et al. 1977; Vann et al. 2002). This is much greater than abiotic N inputs (I) in unpolluted ecosystems, which are on the order of 0.1–1 kg N ha^{-1} year^{-1} (Hedin et al. 1995). Polluted systems can receive atmospheric N inputs on the order of 10–100 kg N ha^{-1} year^{-1} (Chapin et al. 2002). Plant N uptake ($Bg(A)$) is typically on an order similar to N mineralization, 10–100 kg N ha^{-1} year^{-1} (Bormann et al. 1977; Whittaker et al. 1979; Binkley et al. 1992; Perakis and Hedin 2001; Vann et al. 2002), and is typically greater than losses of plant-available N ($k(A)$), which are on the order of 0.1–10 kg N ha^{-1} year^{-1} (Bormann et al. 1977; Whittaker et al. 1979; Binkley et al. 1992; Hedin et al. 2003) in pristine ecosystems.

When mineralization fluxes are much greater than abiotic inputs ($m(D) \gg I$) and the plant N uptake rate is much greater than the available N loss rate ($g \gg k$), or when $k = 0$, equation (8) reduces to

$$\hat{B} \approx \frac{m(D)}{\mu}. \tag{A10}$$

Thus, the approximate plant biomass N quasi equilibrium is the ratio of the mineralization flux (which is a function of the soil organic N pool size) and the biomass turnover rate.

Differential Equations from Timescale Analysis

On the short timescale, the differential equation for the available N pool is

$$\frac{dA}{dt} = I + m(D) - k(A) - Bg(A), \tag{A11}$$

where B and D are constants. When $k(A)$ and $g(A)$ are linear functions, dA/dt can be solved to obtain equation (7).

On the intermediate timescale, the differential equation for plant N is

$$\frac{dB}{dt} = B\left[g\left(\frac{I + m(D)}{k + gB}\right) - \mu\right], \tag{A12}$$

where D is a constant. Under the assumptions detailed in “Assumptions about Flux Magnitudes” (i.e., using eq. [6] instead of eq. [5]), and when $g(A)$ is linear,

$$\frac{dB}{dt} \approx I + m(D) - \mu B. \tag{A13}$$

Equation (A13) can be solved, and the solution is equation (9).

The differential equation for the long timescale (soil organic N), assuming that A is given by equation (5) and B by equation (8), is

$$\frac{dD}{dt} = \left(I - k\frac{\mu}{g}\right) - \phi D. \tag{A14}$$

When $\phi = 0$, soil organic N grows linearly over time (as long as $I > k(\mu/g)$; otherwise, it shrinks). From equation (8), $\hat{B}$ is a function of D, so on the long timescale, plant N grows over time proportional to $m(D)$.

Eigenvalue Calculations

The Jacobian matrix (in “Local Stability Analysis”) gives the characteristic equation

$$\lambda^3 + (m' + \phi' + k' + \overline{B}g')\lambda^2 + \left[\overline{B}g(\overline{A})g' + (m' + \phi')(k' + \overline{B}g')\right]\lambda + \left(\overline{B}g(\overline{A})g'\phi'\right) = 0, \tag{A15}$$

where f' is shorthand for the derivative of the function f with respect to its argument, evaluated at the internal equilibrium; $\overline{B}$ indicates the equilibrium value of B; and the λ values are the eigenvalues of the Jacobian matrix. “Local Stability Analysis” shows that all eigenvalues have a negative real part, guaranteeing local stability. The magnitudes of the roots of equation (A15) control the three timescales near equilibrium: λ_1, the dominant eigenvalue, controls the long timescale; λ_2 controls the intermediate timescale; and λ_3 controls the short timescale.

When λ_1 is very small (i.e., when the longest timescale is very long), the cubic and quadratic terms in equation (A15) can be ignored, so

$$\lambda_1 \approx \frac{-\overline{B}g(\overline{A})g'\phi'}{\overline{B}g(\overline{A})g' + (m' + \phi')(k' + \overline{B}g')}. \tag{A16}$$

At equilibrium, $g(\bar{A}) = \mu$, and using the flux magnitude assumptions in “Assumptions about Flux Magnitudes” ($m' \gg \phi'$ and $\bar{B}g' \gg k'$),

$$\lambda_1 \approx \frac{-\mu\phi'}{\mu + m'}. \tag{A17}$$

Therefore, the assumption of the separation between the B and the D timescales (with B being faster) is equivalent to assuming that $\mu \gg m'$, which simplifies equation (A17) to $\lambda_1 \approx -\phi'$. For the parameters in table 1, these assumptions are met for the grassland, but the separation is not as clear for the forest, hence the divergence in the long timescale approximation from the numerical integration in figure 3.

The approximate values of λ_2 and λ_3 can be found by recognizing that the intercept in equation (A15) is approximately 0 (because $\phi' \approx 0$) and by factoring out λ_1. Thus,

$$\lambda_2 \approx \frac{1}{2}\left\{-(m' + \phi' + k' + \bar{B}g') + \sqrt{[(m' + \phi') - (k' + \bar{B}g')]^2 - 4\bar{B}\mu g'}\right\}, \tag{A18}$$

$$\lambda_3 \approx \frac{1}{2}\left\{-(m' + \phi' + k' + \bar{B}g') - \sqrt{[(m' + \phi') - (k' + \bar{B}g')]^2 - 4\bar{B}\mu g'}\right\}. \tag{A19}$$

These are different from the timescales shown in equations (7) and (9), and the necessary assumptions to simplify them to those timescales reveal the parameter assumptions that correspond to the separation of timescales. For λ_2, assuming that $\bar{B}g' + k' \gg m' + \phi'$ and $\bar{B}g' \gg k'$ (as in “Assumptions about Flux Magnitudes”) yields

$$\lambda_2 \approx \frac{1}{2}\left[-\bar{B}g' + \sqrt{(\bar{B}g')^2 - 4\bar{B}g'\mu}\right]. \tag{A20}$$

Assuming that $\bar{B}g' \gg \mu$, and by Taylor expanding around μ (ignoring higher-order terms),

$$\lambda_2 \approx -\mu, \tag{A21}$$

which is the timescale presented in equation (9). Assuming that $\bar{B}g' + k' \gg m' + \phi'$ is approximately equivalent to assuming that $\bar{A} \ll \bar{D}$, and assuming that $\bar{B}g' \gg \mu$ is approximately equivalent to assuming that $\bar{A} \ll \bar{B}$, both of which are generally true in all forests and grasslands.

For λ_3, assuming that $\bar{B}g' + k' \gg m' + \phi'$ and $\bar{B}g' \gg 1$ yields

$$\lambda_3 \approx -(k' + \bar{B}g'), \tag{A22}$$

which differs from the timescale in equation (7) only in that it is evaluated at equilibrium. Assuming that $\bar{B}g' \gg 1$ is equivalent to assuming that the residence time of an available nutrient molecule is much less than 1 year, which is generally true for all forests and grasslands.