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Nitrogen fixation and the mass balances of carbon and nitrogen in ecosystems

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Abstract. Ecosystems with high rates of nitrogen fixation often have high loss rates through leaching or possibly denitrification. However, there is no formal theoretical context to examine why this should be the case nor of how nitrogen accumulates in such open systems. Here, we propose a simple model coupling nitrogen inputs and losses to carbon inputs and losses. The nitrogen balance of this model system depends on plant (nitrogen fixer) growth rate, its carrying capacity, N fixed/C fixed, residence time of nitrogen and carbon in biomass, litter decay rate, litter N/C, and fractional loss rate of mineralized nitrogen. The model predicts the requirements for equilibrium in a nitrogen-fixing system, and the conditions on nitrogen fixation and losses in order for the system to accumulate nitrogen and carbon. In particular, the accumulation of nitrogen and carbon in a nitrogen-fixing system depend on an interaction between residence time in vegetation and litter decay rate in soil. To reflect a possible increased uptake of soil nitrogen and decreased respiratory cost of symbiotic nitrogen fixers, the model was then modified so that fixation rate decreased and growth rate increased as nitrogen capital accumulated. These modifications had only small effects on carbon and nitrogen accumulation. This suggests that switching from uptake of atmospheric nitrogen to mineral soil nitrogen as nitrogen capital accumulates simply results in a trade-off between energetic limitations and soil nitrogen limitations to carbon and nitrogen accumulation. Experimental tests of the model are suggested.

Introduction

One hundred kg nitrogen or more can enter a hectare of an ecosystem per year through nitrogen fixation (Carlson & Dawson 1985; Boring et al. 1988; Binkley & Giardina 1997). Consequently, nitrogen fixation by autotrophs can be an important mechanism of nitrogen accumulation in ecosystems (Boring et al. 1988; Sprent & Sprent 1990), and an important management tool for restoring degraded ecosystems (National Research Council 1979; Boring et al. 1988; Hibbs et al. 1994; Binkley & Giardina 1997).

There are some indications that systems of high nitrogen fixation may also have high losses of nitrogen through leaching (Binkley et al. 1992; Compton 1994). Denitrification can also be high in some nitrogen-fixing systems (Davidson et al. 1990; Struwe & Kjoller 1991), although this is not always the case (Binkley et al. 1992).

Although the accumulation of nitrogen in a nitrogen-fixing system cannot continue unbounded, the exact nature of the coupling between nitrogen fixation and nitrogen outputs remains obscure. For an ecosystem to achieve equilibrium, nitrogen fixation must eventually be self-arresting or other pathways such as leaching or denitrification must provide means for nitrogen to exit the system. And yet, these pathways must not grow instantaneously with the growth of the nitrogen fixation pathway, otherwise the system will never begin to accumulate nitrogen. What are the relationships between nitrogen inputs and outputs in an nitrogen-fixing system? Under what conditions does the system accumulate or lose nitrogen, and what conditions are required for equilibrium?

The purpose of this paper is to propose a logical and biologically reasonable mathematical framework coupling nitrogen inputs via nitrogen fixation with nitrogen outputs and the carbon balance of ecosystems. This framework captures the essence of the problem in a simple manner so that characteristics of a nitrogen-fixing system can be described with a minimum number of variables. We then examine the properties of this mathematical framework, beginning with equilibrial solutions, in the hopes that they may shed some insight on the biology. Even though most ecosystems are not at equilibrium, it is important to first seek equilibrial solutions because once they are found, the conditions for nonequilibrium behavior can also be specified. In this simple model, a nonequilibrium system is one with a net accumulation or loss of nitrogen. The model allows for nitrogen accumulation because of delays in the flow of nitrogen between components of the system. Finally, the model explicitly couples the flow of nitrogen to that of carbon through the ecosystem.

We will not provide here any empirical tests of the model simply because there are no studies in which the input/output balances of nitrogen-fixing ecosystems are fully quantified. We believe that a dynamical model in which these couplings are explicitly described may assist in focusing research and designing experiments on the nature of mass balances of carbon and nitrogen in nitrogen-fixing systems. We conclude by suggesting some experimental approaches that evaluate model predictions and quantify the mechanisms responsible for accumulation of nitrogen and carbon in nitrogen-fixing ecosystems.

Model development and analysis

Because we wish to couple the nitrogen balance of a system with that of energy, we will begin by deriving an equation for the mass balance of carbon in the system, then later transform this into a coupled equation for nitrogen. The change in ecosystem carbon storage (C_E) is given by the mass balance equation:

$$\frac{dC_E}{dt} = \frac{dC_V}{dt} + \frac{dC_S}{dt} \tag{1}$$

where C_V is vegetation carbon and C_S is soil carbon. We will now expand each of the terms on the right hand side to conform to the standard mass balance equation:

$$\frac{dC}{dt} = I_C - O_C \tag{2}$$

where I is input and O is output. Let us begin with the mass balance of carbon in vegetation. Photosynthesis (ps) is the mechanism of carbon input to vegetation, and respiration (rs) and litterfall (l) are the outputs. We assume that labile carbon allocated to symbiotic nitrogen fixers or to root exudates is part of respiratory loss because it is rapidly oxidized. The differential equation for the change in vegetation carbon becomes:

$$\frac{dC_V}{dt} = (ps - rs - l)C \tag{3}$$

The units of ps, rs, and l are C inputs or loss rates per unit C in biomass per unit time. Assuming the vegetation has both photosynthesizing organs (leaves) and non-photosynthesizing organs that only respire (wood and or roots), then as the vegetation grows, the proportion of carbon in respiring organs will increase. Therefore, the photosynthesis rate will decline and the respiration rate will increase:

$$ps = p_0 - pC \tag{4a}$$

$$re = r_0 + rC \tag{4a}$$

where p_0 and r_0 are the initial per capita rates of photosynthesis and respiration per unit time and p and r are the rates by which photosynthesis and respiration change with increases in C. Linear increases and declines, respectively in per capita respiration and photosynthesis rates are the simplest descriptions of changes in these rates with increased proportion of non-photosynthetic tissues; in the real world, the functions are likely more complex – such as allometric functions against biomass. However, if the real world functions can be transformed into linear relationships with vegetation carbon, the qualitative behaviors of this model will not change (for example, allometric functions can be transformed into Equation 4 by taking the logarithms of ps, rs, and C).

Substituting Equations 4a and 4b into Equation 3 and gathering terms, we obtain:

$$\frac{dC_V}{dt} = [(p_0 - r_0) - (p + r)C - l]C \tag{5}$$

As C increases, $dC_V/dt \to 0$. At this point, $C^* = K$, or carrying capacity, is reached. Setting Equation 5 equal to zero and solving for C^*:

$$C^* = K = \frac{p_0 - r_0 - l}{p + r} \tag{6}$$

Now define $p_0 - r_0 = g$, or the initial net growth rate before litterfall, and substitute into Equation 6, yielding:

$$K = \frac{g - l}{p + r} \tag{7}$$

or

$$p + r = \frac{g - l}{K} \tag{8}$$

Equations 7 and 8 allows us to transform Equation 5 to:

$$\frac{dC_V}{dt} = \left(g - \frac{(g - l)}{K}C\right)C - lC = gC\left(\frac{K - C + (lC/g)}{K}\right) - lC \tag{9}$$

This is the familiar logistic growth equation derived in the standard manner (von Bertalanffy 1968; Gotelli 1995) except with two outputs (rs and l) instead of the usual one output due to death, and the output from the vegetation in litter maintained separately from that in respiration.

Similarly, the mass balance of soil carbon equals the inputs of litter carbon from vegetation minus the per capita loss due to decay (κ), or:

$$\frac{dC_S}{dt} = lC - \kappa lC \tag{10}$$

Substituting Equations (9) and (10) into Equation (1), and (for simplicity) dropping subscripts on C, we obtain:

$$\frac{dC}{dt} = gC\left(\frac{K - C + lC/g}{K}\right) - \kappa lC \tag{11}$$

The fraction of carbon in vegetation transferred to litter (l) is simply the inverse of the residence time of carbon in vegetation ($l = 1/R$), so Equation (11) becomes:

$$\frac{dC}{dt} = gC\left(\frac{K - C + C/gR}{K}\right) - \frac{\kappa}{R}C \tag{12a}$$

which is our final dynamical equation for ecosystem carbon dynamics.

We now couple an equation for the dynamics of nitrogen to Equation 12a. For simplicity and to focus the problem, we will assume that all inputs are by fixation and that the only vegetation is a nitrogen fixer. We will also not discriminate between different pathways of nitrogen output. We will begin by assuming constant growth rate (g in Equation 12a) and fixation rate. We will then modify the model to allow fixation and growth rates to vary with nitrogen accumulation. We will consider how the model can be expanded to incorporate alternative pathways of nitrogen outputs later.

It is reasonable to begin by assuming that there is a proportional relationship (f) between nitrogen fixed and carbon fixed, that the plant biomass has a fixed N/C ratio (η), and that some proportion of nitrogen (d) released from decaying litter is lost from the ecosystem via leaching or denitrification. This allows us to derive a dynamical equation for nitrogen that can be coupled to the previous dynamical equation for carbon (Equation 12a):

$$\frac{dN}{dt} = fgC\left(\frac{K - C + C/gR}{K}\right) - \frac{d\eta\kappa C}{R} \tag{12b}$$

Equations 12a and 12b simultaneously describe the mass balances of carbon and nitrogen in a nitrogen-fixing system. Decomposition processes in this model ecosystem essentially distill off carbon while retaining some of the nitrogen. In real ecosystems, this process results in the well-known increase in N/C ratio of organic matter during decay.

Because the amount of N in the biomass is equivalent to fC, we can replace this term in the differential equation for nitrogen by N. This substitution allows us to determine the relationships between equilibrial carbon and nitrogen in the whole plant-soil system and all of the other controlling factors by setting both equations to 0 and solving simultaneously, yielding:

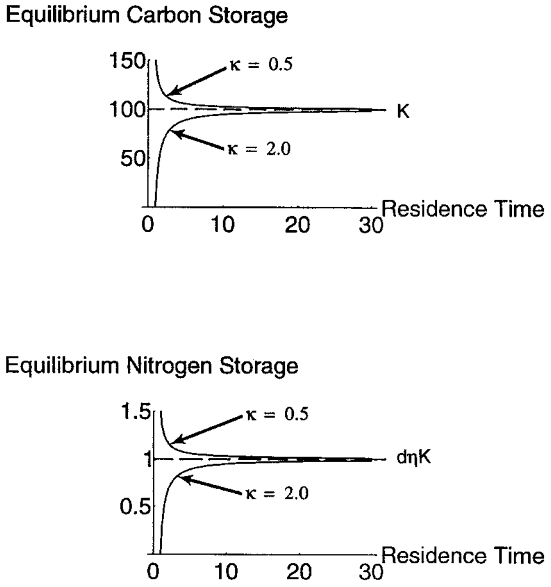

Figure 1. Effects of residence time (R) and decay rate (κ) on equilibrium ecosystem carbon and nitrogen storage as predicted from Equation 13.

$$\begin{cases} C^* = K\left[\frac{gR-\kappa}{gR-1}\right] \\ N^* = d\eta K\left[\frac{gR-\kappa}{gR-1}\right] \end{cases} \tag{13}$$

Obviously, increasing carrying capacity for vegetation increases both N^* and C^*. As residence time increases, $C^* \to K$ because the limit of $(gR-\kappa)/(gR-1)$ equals 1 as $R \to \infty$. The effect of increasing residence time (R) on equilibrium carbon storage (C^*) depends on the decay rate (κ). To demonstrate this, we plot numerical solutions (Figure 1) of Equation 13 for R ranging from 1 to 30 for the following parameter values:

$$K = 100;\ g = 2.0;\ d = 0.1;\ \eta = 0.1;\ \kappa = 0.5 \text{ and } 2.0$$

These parameter values are not intended to mimic any particular system. Nonetheless, they are reasonable order-of-magnitude estimates of these parameters in nitrogen-fixing forests for carbon and nitrogen in units of Mg ha^{-1} (Sprent & Sprent 1990; Hibbs et al. 1994, Binkley & Giardina 1997) and for the variation in decay rates from cool temperate regions to the tropics (Olson 1963). We will assume for the purpose of these numerical solutions a value of 0.1 for η (the N/C ratio of plant material) which is within the reported range of 6–12 g carbon fixed/g nitrogen fixed for nitrogen-fixing plants (Marschner

1995). The model currently does not mimic translocation of nitrogen out of tissues before litterfall: the process of translocation is subsumed within the residence time term. Adding retranslocation terms and distinguishing between different plant issues would not qualitatively change our conclusions and would therefore needlessly complicate the mathematics for now.

Equation 13 predicts that if $\kappa > 1$, C^* approaches K from below as $R \to \infty$ (Figure 1). Therefore, when decay rate is rapid, equilibrium carbon storage increases when the carbon resides for a long time in vegetation rather than being transferred to soil. However, if $\kappa < 1$, C^* approaches K from above as $R \to \infty$ (Figure 1). Therefore, when decay is slow, equilibrium carbon storage increases when the carbon resides in vegetation for a short time. In this case, the carbon is quickly transferred to soil where it accumulates as peat. This allows the ecosystem to store more carbon than simply that in vegetation at carrying capacity. The first situation would obtain in warm climates (i.e., the upland tropics), and the second in cold climates or waterlogged soils conducive to peat formation (i.e., the tundra or boreal regions or certain tropical peatlands; Olson 1963).

Similar considerations apply to N^*. As $R \to \infty$, $N^* \to d\eta K$. The effect of residence time on equilibrium nitrogen storage depends on decay rate in the same manner as it does for carbon (Figure 1). Now, consider what happens as N^* is increased by an increase in fixation rate, or decreased by additional outputs due to disturbances. Equation 13 predicts that for the new equilibrium N^* to be maintained, carrying capacity (K), loss rate (d), or plant N/C ratio (η) must also increase or decrease, depending on whether N^* increases or decreases, respectively.

At equilibrium, $N^* = f^*C^*$, where f^* is the equilibrium nitrogen fixation rate per unit carbon fixed. Substituting this for N^* in Equation 12b and solving for f^*, we obtain the required relationships between per capita fixation rate, f, and per capita loss rate, d, to maintain the system at equilibrium for all values of the other parameters and for a given amount of carbon in biomass at equilibrium:

$$f^* = d\left[\frac{\eta K}{C^*}\right]\left[\frac{gR - \kappa}{gR - 1}\right] \tag{14}$$

Higher f^* requires higher nitrogen loss rate, d, in order to maintain the system at equilibrium. Such high loss rates in nitrogen-fixing systems near equilibrium compared with non-fixing systems of similar age on similar soil types and in similar climates is exactly what is observed (Binkley et al. 1992). More specifically, the fixation rate is directly proportional to loss rate, the proportionality being determine by the relationships between all other terms within the brackets. Consideration of these terms shows that the fixation rate required to maintain equilibrium decreases with equilibrium ecosystem carbon pool, C^* and increases with plant N/C ratio, η. Thus, nitrogen fixers with high nitrogen concentration in litter must have a high fixation rate to maintain the system at equilibrium to offset losses through decay of litter with high nitrogen concentration.

Species differences in f^* and C^* also influence nitrogen loss rates. With a higher C^*, a lower f^* is required to maintain an equilibrium nitrogen pool. Alternatively, if two species have the same f^* but different C^* due to differences in g, R, κ or K (Equation 5a), then leaching or denitrification rates should be greater in the system with greater C^* to maintain equilibrium.

The relationship between f^* and net ecosystem production is also specified by Equation 14. The term $(gR - \kappa)$ in the numerator expresses the instantaneous net carbon balance of the system (net ecosystem production). As net ecosystem production increases due to either faster growth rate, longer residence time, or slower decay rate, then total losses will also increase for a given value of d, and the nitrogen fixation rate must also be high to maintain equilibrium. Thus, high productivity in nitrogen-fixing ecosystems comprised of perennial woody species with long residence times of nutrients in tissues must be accompanied by high fixation rates and high loss rates at equilibrium (Binkley et al. 1992).

We can now specify the fixation and loss rates required for nitrogen accumulation (non-equilibrium) in terms of all other variables. Nitrogen will accumulate when inputs are greater than outputs, or when the first term on the right hand side of Equation 12b is greater than the second term:

$$fgC\left(\frac{K - C + \frac{C}{gR}}{K}\right) > \frac{d\eta\kappa C}{R} \tag{15}$$

Solving for f and d we obtain the following conditions for nitrogen accumulation:

$$\begin{cases} f \;>\; \frac{d\kappa\eta K}{C+gR(K-C)} \\ \qquad \text{or} \\ d \;<\; \frac{f[C+gR(K-C)]}{\kappa\eta K} \end{cases} \tag{16}$$

As carbon accumulates, $K - C$ becomes smaller, and per capita fixation rate (f) must either be very large initially or must increase in order for nitrogen accumulation to continue. Furthermore, increases in the decay rate (κ) and N/C ratio of plants (η) also require that f increase proportionally for the system to accumulate nitrogen. Conversely, increasing decay rate, plant N/C

ratio, or carrying capacity require that nitrogen loss rate (d) decrease for nitrogen accumulation to continue. In other words, nitrogen-fixing systems with high decay rate and higher N/C ratio in plants need to retain nitrogen more effectively (have a lower d) to accumulate nitrogen.

If f is initially very large, then as C increases, f could decrease and still maintain the inequality required by Equation 16. There is some experimental evidence that as soil nitrogen increases, fixation rate declines and a greater proportion of nitrogen uptake is met by mineralized soil nitrogen (Marschner 1995; MacDicken 1994). The hypothesis for an increased preference for soil mineral nitrogen as nitrogen capital accumulates is that symbiotic nitrogen fixers, such as *Rhizobia* and *Frankia*, impose large energetic costs on the plants compared with uptake of soil nitrogen (Marschner 1995; MacDicken 1994). Because it would presumably be energetically more efficient to obtain mineral soil nitrogen rather than support symbionts to obtain atmospheric nitrogen, switching to soil nitrogen would presumably increase growth rate (g) by proportionally decreasing respiratory costs.

However, a decrease in f is not absolutely required by this inequality, and fixation rates sometimes remain high as soil nitrogen increases (Parrotta et al. 1996; Binkley et al. 1992; Binkley et al. 1994; Binkley & Giardina 1997). In one of the most thorough experiments with nitrogen fixation in tree plantations, Parrotta et al. (1996) labelled a soil in Puerto Rico with ^{15}N, and then examined rates of nitrogen fixation by *Casuarina equisetifolia* (J.R.&G.) Forst. and *Leucaena leucocephala* (Lam.) de Wit. Initially, *Leucaena* and *Casuarina* obtained almost all their nitrogen from fixation. Although the supply of soil inorganic nitrogen increased as a result of nitrogen fixation from yr 1 to yr 3.5, *Leucaena* and *Casuarina* continued to fix between 40% and 60% of their nitrogen supply at age 3.5 yr. However, this declining relative reliance on nitrogen fixation resulted from an overall increase in the rate of nitrogen use; the absolute rate of nitrogen fixation remained about 70 kg ha^{-1} yr^{-1}. In addition, Binkley et al (1992) and Compton (1994) have shown that red alder (*Alnus rubra* Bong.) maintains high rates of nitrogen fixation throughout stand maturation. In reviewing the literature, Binkley et al. (1994) and Binkley and Giardina (1997) find no conclusive evidence that increasing soil nitrogen always suppresses nitrogen fixation in forests.

Other changes in ecosystem processes during stand maturation have additional complicating consequences for carbon and nitrogen accumulation. For ecosystems with perennial, woody species, decay rates would decrease as the stand matured because the amount of slowly decaying wood of high lignin content would also increase. This would not only contribute to decreasing the overall decay rate, but would also require a longer residence time (R) in the vegetation to produce the woody tissue in the first place. We have seen previously that the interaction between residence time and decay rate partly determines carbon and nitrogen storage at equilibrium. Thus, the effect of decreasing fixation rate and increasing net growth rate on carbon and nitrogen accumulation may also be modified by concurrent increases in residence time and decreases in decay rates as the stand matured.

Therefore, to examine the consequences of such a hypothesized shift in sources of nitrogen for plant growth concurrent with increased residence time and decreased decay rates, we modified Equation 12 by assuming that the growth rate (g) increases and fixation rate (f) decreases linearly with increasing nitrogen capital, yielding the following expanded model:

$$\left\{\begin{aligned} \frac{dC}{dt} &= (\gamma_0 + \gamma N)\left[\frac{K - C + C/(\gamma_0 + \gamma N)R}{K}\right] - \frac{\kappa}{R}C \\ \frac{dN}{dt} &= (\phi_0 - \phi N)(\gamma_0 + \gamma N)C\left[\frac{K - C + C/(\gamma_0 + \gamma N)R}{K}\right] - \frac{d\eta\kappa C}{R} \end{aligned}\right. \tag{17}$$

In this expanded model, net growth is initially γ_0 (equal to g in Equation 1), when ecosystem nitrogen capital is zero. It then increases linearly at a rate γ as nitrogen capital accumulates. Likewise, fixation rate is initially ϕ_0 (equal to f in Equation 12) when ecosystem nitrogen capital is zero. It then declines linearly at rate ϕ as nitrogen capital accumulates. Strictly speaking, these changes in f and g would depend on the soil nitrogen pool alone (i.e., $(1 - d)\eta\kappa C/R$), not total ecosystem nitrogen capital. However, as the soil nitrogen pool would increase in proportion to the total ecosystem capital, having g and f depend on N does not qualitatively change the behavior of the model and makes the mathematics simpler.

There is virtually no data available to suggest how to modify the model further to make R and κ time dependent; furthermore, inserting additional functions for R and κ into Equation 17 would make a model so complex that it would be difficult to determine which processes controlled its behavior. Even without these additional refinements, analytical (symbolic) solutions for equilibrium nitrogen and carbon capital were unwieldy and not easily interpretable.

We therefore numerically simulated the accumulation of ecosystem carbon and nitrogen over time using fourth order Runge – Kutta techniques (Wolfram 1991) with the following values for the new parameters:

$$f = \phi_0 = 0.1,\ \phi = 0.01,\ g = \gamma_0 = 2.0,\ \gamma = 0.1$$

and values for the other parameters as before. Our assumed value of 0.1 for f or ϕ_0 (in units of g N/g C) is within the previously noted range of 6 to 12 g C/g N fixed (Marschner 1995). To test the effects of different residence times and decay rates on carbon and nitrogen accumulation, we also ran the

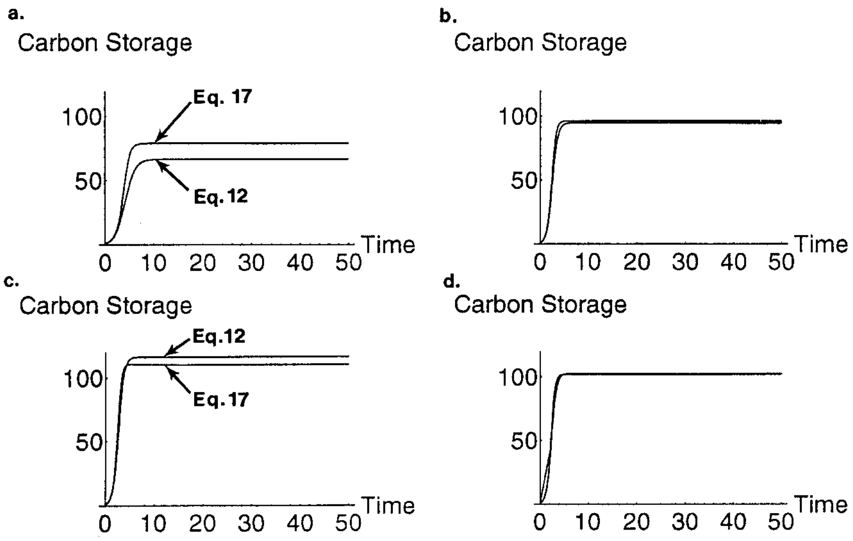

Figure 2. Effects of constant fixation rate and growth rate (Equation 12) on carbon accumulation compared with having fixation and growth rates depend on nitrogen capital (Equation 17). Nitrogen accumulation dynamics are qualitatively similar. (a) $R = 2$, $\kappa = 2$; (b) $R = 10$, $\kappa = 2$; (c) $R = 2$, $\kappa = 0.5$; d. $R = 10$, $\kappa = 0.5$.

simulations for $R = 2$ and 10 and $\kappa = 0.5$ and 2. Thus, we have a computer "experiment" which entails the following treatments in a factorial design: (1) fixation rate (f) constant or declining with increases in ecosystem nitrogen capital; (2) net per capita growth rate (g) constant or increasing with increasing ecosystem nitrogen capital; (3) long or short residence time (R); (4) fast or slow decay rate (κ).

Having fixation rate and growth rate depend linearly on nitrogen capital had little effect on the time course of carbon accumulation or on equilibrium carbon storage, except when residence time was low and decay rate was high (Figure 2). Even then, only equilibrium carbon storage was affected; the rate of approach to equilibrium was not markedly affected by the modifications introduced in Equation 17. The dynamics of nitrogen accumulation were qualitatively similar to those of carbon.

These relatively minor sensitivities of carbon and nitrogen accumulation to the modifications introduced in Equation 17 are surprising results. They may depend on the assumptions of a linear decline in nitrogen fixation and a linear increase in growth of nitrogen fixers as nitrogen capital accumulates. Note that the assumed rate of increase in growth rate with accumulation of nitrogen capital (γ) is an order of magnitude greater than the corresponding assumed decrease in fixation rate (ϕ), and so these results are not a fortuitous consequence of coincidentally equal increases and decreases in g and f with increasing nitrogen capital. More complex relationships between g or f and N may yield different results, but there is insufficient experimental evidence to propose more complex functions as alternatives to Equation 17.

These results suggest that switching from uptake of atmospheric nitrogen to mineral soil nitrogen as nitrogen capital accumulates simply results in a trade-off between energetic limitations and soil nitrogen limitations to carbon and nitrogen accumulation, particularly when accompanied by increasing residence time and decreasing decay rates as more wood and woody litter is produced (Figure 2d).

Discussion and suggested experiments

This model can be considered a first approximation of nitrogen and carbon balances in nitrogen-fixing ecosystems. The model in its present form does not take into account complex interactions in mixed species stands through competition between nitrogen fixers and non-fixers (Binkley 1992). These can be incorporated by deriving different growth and decay functions for different species, including competitive interactions of the effect of growth of each species on the others. These competitive interactions must themselves be constrained by the availability of nitrogen within the system and its input by fixation. The model also does not take into account the different residence times of carbon and nitrogen in different tissues and different decay rates of different types of litter and root exudates. These can be incorporated by partitioning g, R, η and κ into separate functions for each tissue. Finally, the model does not distinguish between different output pathways and their controlling factors. However, alternative output pathways for nitrogen can be incorporated into the model by modifying or expanding the fractional loss rate, d, to include multiple pathways such as simultaneous leaching and denitrification. For example, if there are two alternative pathways, d would be apportioned among the two with S the fraction of d lost by one pathway, and $(1-S)$ the fraction lost through the other. The output term is now expanded to a sum of losses through these two pathways in the proportions S and $(1-S)$.

Nonetheless, despite the need for further expansion, the model makes several predictions regarding the factors responsible for nitrogen accumulation in nitrogen-fixing systems. To experimentally test the model predictions, all inputs and outputs of nitrogen should be measured in nitrogen-fixing ecosystems, along with additional characteristics such as residence time, decay rate, fixation rate, and N/C ratio of biomass and litter. Such a complete analysis of the nitrogen budget of an nitrogen-fixing system has not to our knowledge been attempted, although some studies provide nearly complete budgets (e.g., Binkley et al. 1992; Parrotta et al. 1994, 1996).

Most of the model parameters are life history traits by which species differ, including per capita growth rate (g), residence time (R), decay rate of litter (κ), and N/C ratio of litter (η). The relative importance of each life history trait to ecosystem nitrogen accumulation can be determined with comparative studies of monocultures composed of different species chosen so that these life history traits vary in a factorial design. If complete budgets of these monocultures are determined, then the nitrogen balance of an ecosystem and its equilibrium carbon and nitrogen contents could be quantitatively related to these life history characteristics. For example, woody perennials, such as alder, have a higher R and would have a greater K than annual plants, such as peas. Equation 12a and 12b then predict that, when grown under similar conditions, the nitrogen accumulation rate should be higher in ecosystems composed of woody perennials than in ecosystems composed of annual plants. Therefore, the best way to accumulate nitrogen in a system is to have a perennial woody nitrogen fixer with large R, and allow it a high K. This maximizes nitrogen retained in the biomass and minimizes nitrogen lost by leaching and/or denitrification, particularly if decay rates are high. Again, the magnitude of R sets the time scale for these experiments.

One of the more surprising conclusions of these model analyses that bears further experimental work is that energetic limitations may be traded off for soil nitrogen limitations during stand maturation, and a switch from reliance on atmospheric nitrogen fixation to uptake of soil nitrogen may have minor consequences for carbon accumulation (Figure 2). This is supported by some data on energetic costs of nitrogen fixation vs. reduction of soil nitrate. For example, the carbon cost of nitrogen fixation of 6 to 12 g C/g N fixed assumed throughout this paper is of the same order of magnitude as approximately 3 g C/g N for reduction of nitrate (Marschner 1995). A rate of fixation of 150 kg nitrogen ha^{-1} yr^{-1} might have a carbon cost of about 1000–2000 kg carbon ha^{-1} yr^{-1}, compared with 500 kg carbon ha^{-1} yr^{-1} for assimilatory reduction of nitrate. The actual cost of nitrate utilization may differ, depending on cost of maintaining root systems, or the proportion of nitrate reduction carried out with excess reductant in leaves. In any case, a shift from relying on nitrogen fixation to nitrate utilization may reduce the carbon cost of nitrogen acquisition and assimilation, but the carbon cost would still be substantial. This is an area that would benefit from more detailed experimental approaches, including long-term, whole ecosystem ^{15}N tracer experiments (Silvester 1983; Reporter 1985; Caldwell & Virginia 1991; Binkley & Giardina 1997). The results reported here also suggest that these differences in carbon costs of nitrogen acquisition need to be assessed in the context of other concurrent changes in decomposition rates and residence time in live vegetation. The time scale for these long-term experiments should be at least of the order R, the residence time of nitrogen in live biomass.

Other factors may also limit g or f for a given species. One possibility might be limitation by another nutrient – such as phosphorus (P) or molybdenum (Mo) – by water potential, or by soil pH (Sprent & Sprent 1990). For example, we predict that fertilizing a nitrogen-fixing system with phosphorus or molybdenum would initially increase nitrogen accumulation by increasing either g or f or both, but that eventually outputs should also increase with time lag on the order of R. Such a fertilizer experiment will require simultaneous measurements not only of increased growth and nitrogen fixation rates, but also of leaching or denitrification; the experiment must last at least as long as R years. An interesting complication would be changes in phosphorus or molybdenum availability or soil pH during stand development and their effect on ecosystem carbon and nitrogen balances. Recently, Giardina et al. (1995) have shown that nitrogen fixation increases phosphorus availability in soils. If this results in a decrease in phosphorus limitations as nitrogen-fixing stands mature, then losses of nitrogen should increase with increased phosphorus availability during stand maturation with time lag R.

Although there are no empirical studies that provide a complete test of this model, we can compare model predictions with measured responses of nitrogen-fixing ecosystems to perturbations of nitrogen and carbon capital and budgets. For example, several studies indicate that harvesting nitrogen-fixing red alder stands leads to 10-fold reductions in rates of nitrogen leaching losses, delayed by 3–5 yr after harvesting (Bigger & Cole 1983; Van Miegroet et al. 1990). Our model predicts the observed decline in leaching loss (d) with cessation of fixation rate (f). It also predicts the observed delay in this decline which corresponds to residence time of nitrogen in woody alder litter.

In all these predictions and analyses, the residence time of carbon in biomass sets the time scale over which nitrogen and carbon accumulation experiments must be performed. It also determines the length of time between increased nitrogen inputs and when increased outputs would be detectable leaching below the rooting zone or emitted in gaseous form from the soil. Finally, in conjunction with the decay rate of litter in soils, R determines the time course of carbon and nitrogen accumulation in the ecosystem as well as their equilibria.

The analysis presented here may prove to be a valuable heuristic tool in designing experiments on the input/output nitrogen budgets of ecosystems. Although input/output studies have lost some of their appeal since the IBP Programme during the 1960s and early 1970s, the formal analysis presented here suggests that many questions remain unanswered.

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