



## **Ecosystem constraints to symbiotic nitrogen fixers: a simple model and its implications**

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**Abstract.** The widespread occurrence of *N* limitation to net primary production (NPP) and other ecosystem processes, despite the ubiquitous occurrence of *N*-fixing symbioses, remains a significant puzzle in terrestrial ecology. We describe a simple simulation model for an ecosystem containing a generic nonfixer and a symbiotic *N* fixer, based on: (1) a higher cost for *N* acquisition by *N* fixers than nonfixers; (2) growth of fixers and fixation of *N* only when low *N* availability limits the growth of nonfixers, and other resources are available; and (3) losses of fixed *N* from the system only when the quantity of available *N* exceeds plant and microbial demands. Despite the disadvantages faced by the *N* fixer under these conditions, *N* fixation and loss adjust *N* availability close to the availability of other resources, and biomass and NPP in this simple model can be substantially but only transiently *N* limited. We then modify the model by adding: (1) losses of *N* in forms other than excess available *N* (e.g., dissolved organic *N*, trace gases produced by nitrification); and (2) constraints to the growth and activity of *N* fixers imposed by differential effects of shading, *P* limitation, and grazing. The combination of these processes is sufficient to describe an open system, with input from both precipitation and *N* fixation, that is nevertheless strongly *N*-limited at equilibrium. This model is useful for exploring causes and consequences of constraints to *N* fixation, and hence of *N* limitation, and we believe it will also be useful for evaluating how *N* fixation and limitation interact with elevated *CO*<sub>2</sub> and other components of global environmental change.

### **Introduction**

The supply of nitrogen often limits the growth of plants, the composition of communities, the productivity of ecosystems, and other population, community, and ecosystem processes. Fertilization experiments suggest that added *N* enhances productivity in many or most intensive agricultural systems, temperate forests, temperate and tropical grasslands, boreal forests, and arctic/alpine tundras (Shaver & Chapin 1980; Miller 1981; Lee et al. 1983; Van Bremen & de Wit 1983; Hunt et al. 1988; Bonan 1990; Bowman et

al. 1993; Magill et al. 1997). Correlative studies also show a tight connection between *N* mineralization and forest productivity (Reich et al. 1997), and ecosystem models suggest *N* limitation is widespread (McGuire et al. 1992; Parton et al. 1993). Perhaps the most compelling evidence for the importance of *N* limitation is the tens of billions of dollars that humanity spends annually on *N* fertilizer.

However, despite all of the sustained scientific effort that has gone into analyzing the cycle of *N*, there are no generally accepted answers to the questions: Why does *N* supply limit productivity in so many natural and managed ecosystems? *N*-fixers should have a substantial competitive advantage in *N*-limited systems, and as a byproduct of their activity they should increase the quantity and availability of *N* in the system as a whole. Why don't they do so? In a world where biological *N*-fixation is ubiquitous, how can *N* limitation be widespread? What keeps *N* fixers from adding sufficient *N* to terrestrial ecosystems to bring the supply of *N* more or less into equilibrium with other potentially limiting resources?

One credible set of answers is that in the long term, *N* fixation does adjust *N* supply close to the availability of other resources (Schimel et al. 1997). In this case, *N* limitation would be a transient and/or marginal phenomenon – as indeed we know it is in most temperate lakes. Outside of frequently and intensely disturbed systems that are actively maintained in a transient state, such as annual crops or fire-dominated areas (Seastedt et al. 1991), *N* limitation might be more apparent than real, more proximate than ultimate. Alternatively, there are a number of mechanisms that could prevent *N* fixers from responding to even profound *N* limitation, and could thereby maintain *N* limitation in the long term. These mechanisms include energetic constraints to growth of or colonization by *N* fixers, disproportionate *P* (or other element) limitation to fixers as opposed to nonfixers, and disproportionately high rates of herbivory on fixers as opposed to nonfixers (Vitousek & Howarth 1991).

Determining whether *N* limitation is transient or sustained, marginal or substantial, is fundamental to our understanding of the biogeochemistry of terrestrial ecosystems (Vitousek & Howarth 1991). It also represents a major uncertainty in our ability to predict the responses of terrestrial ecosystems to components of global environmental change. For example, humanity has greatly increased the fixation of *N*, and its deposition to terrestrial ecosystems (Galloway et al. 1995; Vitousek et al. 1997a). Where that fixed *N* reaches *N*-limited systems, it can alter their composition, dynamics and *C* storage profoundly (Berendse et al. 1993; Schimel et al. 1996; Howarth et al. 1996; Nixon et al. 1996); where recipient systems are not *N*-limited, or *N* limitation

is marginal and/or short-lived, its consequences are smaller and less certain (Matson et al., this volume).

Another example – much of the uncertainty about long-term ecosystem responses to elevated atmospheric  $CO_2$  is related to  $N$  limitation. The stimulation of plant growth by elevated  $CO_2$  in short-term experiments is highly variable, but median increases are 30–40% (Poorter 1993; Poorter et al. 1996; Curtis 1996; Koch & Mooney 1996), substantially above the 5–10% increases in long-term NPP predicted by biogeochemical models (VEMAP 1995; Melillo et al. 1996).  $N$  limitation exerts profound constraints to  $CO_2$  responses in most biogeochemical models (McMurtrie & Comins 1996; Rastetter et al. 1997), even though the empirical evidence for decreased  $CO_2$  sensitivity under  $N$  limitation is mixed. Idso and Idso (1994) and Lloyd and Farquhar (1996) found no consistent effect of nutrient status on response to elevated  $CO_2$ , though a number of experiments tie the low sensitivity of particular plants or ecosystems to nutrient effects (e.g. Larigauderie et al. 1988; Diaz et al. 1993; Oechel et al. 1994; Leadley & Körner 1996).

What accounts for this contrast in results and perspective? One component involves species characteristics; species from nutrient-poor sites show small sensitivity to either nutrient (Chapin 1980; Chapin et al. 1986; Field et al. 1992) or  $CO_2$  additions (Poorter 1993; Poorter et al. 1996; Hunt et al. 1991, 1993). Another component involves time scale. Most growth experiments last from less than one to a few years, while in the biogeochemistry models, the important feedbacks involving nutrient limitation emerge only after several years, or even several decades, of  $CO_2$  exposure (McMurtrie & Comins 1996).  $N$  limitation gradually intensifies with the immobilization of  $N$  in plant biomass, litter, and soil organic matter, even where growth at elevated  $CO_2$  has no depressive effect on tissue decomposability (O'Neill & Norby 1996; Franck et al. 1996).

Alternatively, it is possible that in the medium to long term, increased  $CO_2$  could stimulate  $N$  fixation on land, making any  $N$  constraint on plant response to increased  $CO_2$  a transient phenomenon (Gifford 1992). The growth response to elevated  $CO_2$  appears to be somewhat larger in legumes than in other species (Hunt et al. 1991, 1993; Poorter 1993), and elevated  $CO_2$  often enhances symbiotic fixation under controlled conditions – usually as a consequence of increased legume growth, rather than increased  $N$  fixation per unit of legume biomass (Phillips et al. 1976; Finn & Brun 1982; Norby 1987; Arnone & Gordon 1990; Thomas et al. 1991; Ryle et al. 1992). What are the factors that regulate changes in  $N$  fixation under elevated  $CO_2$ ? Will the stimulation of fixation by planted, weeded, tended, often fertilized  $N$  fixers observed in experiments carry over to increased rates of  $N$  fixation in natural ecosystems?

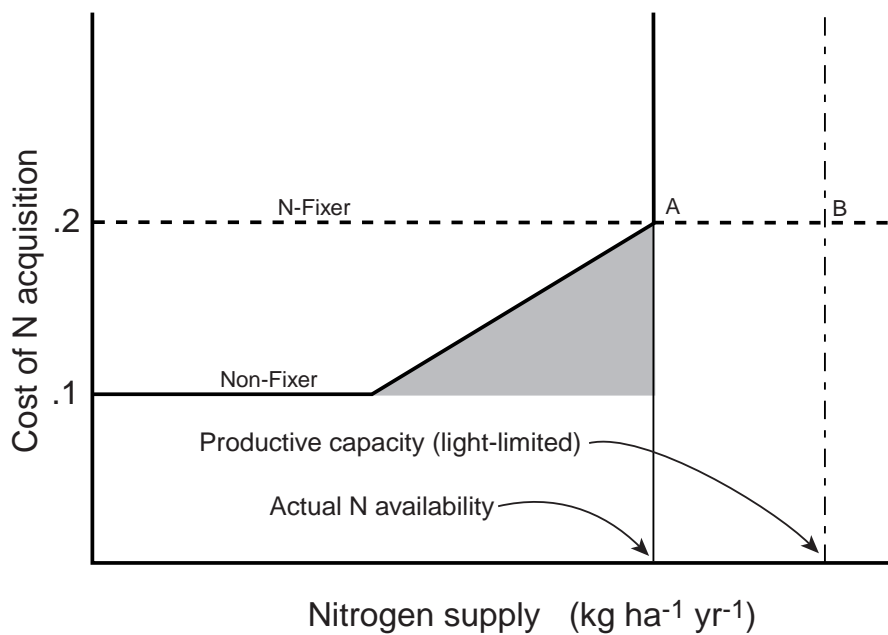
In this paper, we develop a conceptual model for the regulation of symbiotic  $N$  fixation in terrestrial ecosystems. We then use this model and a set of simple simulations to evaluate several mechanisms that could constrain rates of  $N$  fixation, and could thereby allow  $N$  limitation to persist indefinitely. Finally, we explore how these mechanisms could interact with components of human-caused global environmental change.

### **A conceptual model**

The basic assumptions of our model include: (1) The energetic cost of acquiring  $N$  through biological fixation exceeds the cost of acquiring  $N$  from the soil, whenever there is more than a trace of available  $N$  in the soil; (2) Symbiotic  $N$  fixers require and maintain higher concentrations of  $N$  and  $P$  in their tissue than do nonfixers; and (3) Symbiotic  $N$  fixers only acquire  $N$  through fixation, rather than obtaining it from the soil. The first two of these are readily supported (Pate 1986; Gutschick 1987; Smith 1992; McKey 1994). The last is not correct – symbiotic fixers can and do take  $N$  from soil, when it is available – but it simplifies the model substantially. More importantly, our purpose is to evaluate the controls of  $N$  fixation and the plant growth supported by it, not to model the growth of legumes per se (at least not yet).

We begin development of the conceptual model by assuming that for a nonfixer, the cost of acquiring soil  $N$  is a function of  $N$  availability, as illustrated in Figure 1. The  $x$ -axis represents the total quantity of  $N$  that could be available in soil annually (net  $N$  mineralization, inputs via precipitation, any other sources of available  $N$ ); the quantity of  $N$  that actually becomes available in a particular system is indicated by point  $A$  on the figure. Some of this available  $N$  can be acquired at a relatively low (and fixed) energetic cost, one that reflects the enzymatic machinery involved in  $N$  uptake and transport. However, after half of the available  $N$  has been taken up, obtaining the remainder requires increasing investment in roots, or carriers, or other mechanisms by which  $N$  can be obtained from dilute concentrations in soil. Costs increase to the point where essentially all of the available  $N$  in soil has been taken up; after that point, further investment in acquiring soil  $N$  is unrewarding. We model the cost function as increasing linearly, although in fact it probably increases exponentially.

In contrast, we assume that the cost to a symbiotic  $N$  fixer of acquiring a unit of  $N_2$  is constant, independent of the quantity of  $N$  fixed (Figure 1). We assume that the two cost functions cross at point  $A$ , where essentially all of the fixed  $N$  in the soil has been utilized. To the left of that point, nonfixers have a lower cost for  $N$  acquisition than fixers and can (we assume) outcom-



*Figure 1.* A conceptual model for the costs of  $N$  acquisition by nonfixers and  $N$  fixers. The  $x$ -axis represents  $N$  availability, as quantity of  $N$ /area (e.g.  $\text{kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ ). Any particular ecosystem will have a light-limited productive capacity, and a level of  $N$  availability required to support that productivity ( $B$ ); any system will also have an actual level of  $N$  availability ( $A$ ), which in this example is below the productive capacity. The dark solid line represents the cost of  $N$  acquisition by a nonfixer; we assume that  $N$  acquisition is relatively inexpensive when a large quantity of available  $N$  remains in the system, but the cost increases as a greater proportion of the available  $N$  is utilized. As the available  $N$  in the system approaches full utilization, the cost increases very steeply. In contrast,  $N$  fixers (dark dashed line) have a relatively high but constant cost of  $N$  acquisition. In this particular example, some light would remain unutilized after all of the available  $N$  had been taken up ( $A$ ), and  $N$  fixers could use that light to grow, fix  $N$ , and (ultimately) increase the  $N$  availability in the system towards  $B$ . The shaded area under the nonfixer's cost curve represents energy that could be allocated for purposes other than  $N$  acquisition, if more  $N$  were available.

pete them, while to the right of point  $A$ , fixers can obtain  $N$  and nonfixers cannot. Finally, we assume that there is a productive capacity for each site, set by the availability of resources other than  $N$ . Initially, we will use light as that ultimate resource. Point  $B$  (Figure 1) then corresponds to the quantity of available  $N$  that would be required to support nonfixers at this maximum (light-limited) level of productivity.

Given this simple formulation, the availability of  $N$  in an ecosystem should adjust to that of other limiting resources. If point  $A$  is to the left of  $B$  as in Figure 1, then symbiotic  $N$  fixers should grow, fix  $N$ , and gradually increase  $N$  supply until its availability is equivalent to  $B$ , and fixers no

longer have an advantage. At this point,  $N$  supply could still limit production of nonfixers, in that large additions of  $N$  would allow plants to reallocate some of the resources that they had used to acquire  $N$ . However, only energy equivalent to the shaded area in Figure 1 would be available for reallocation, so any increase in production would be marginal.

### Simulation

Based on the conceptual model in Figure 1, we put together a simple simulation of production and  $N$  cycling in an ecosystem containing a nonfixer and a symbiotic  $N$ -fixer. Nitrogen availability is calculated as the sum of net  $N$  mineralization,  $N$  inputs in precipitation or fertilizer, and any carryover from the previous year. The potential  $N$  uptake by nonfixing plants is set to 100 units of  $N$  (say 100 kg/ha/yr), corresponding to a maximum potential NPP of 5000 units of  $C$  (minus the  $C$  costs of  $N$  acquisition). If more than 100 units of  $N$  are available, the quantity in excess of 100 units is not taken up; if less than 100 units are available, all are taken up by nonfixers. Production of the nonfixers (NPPNF) is then calculated as

$$\text{NPPNF} = CN_{\text{nf}} * N_{\text{uptake}} * (1 - \text{costNF}), \quad (1)$$

where  $CN_{\text{nf}}$  is the  $C/N$  ratio (uncorrected for cost of  $N$  uptake) of nonfixers,  $N_{\text{uptake}}$  is uptake of  $N$  by nonfixers, and  $\text{costNF}$  is the  $C$  expended in acquiring  $N$ .  $\text{costNF}$  is determined using the function in Figure 1, in which the cost is 0.1 up to half of total  $N$  availability, then increases linearly to 0.2 for the last increment of available  $N$ .

Production by symbiotic  $N$  fixers (NPPfix) is then calculated as

$$\text{NPPfix} = 5000 * (1 - \text{fixCOST}) * (4500 - \text{NPPNF})/4500, \quad (2)$$

where  $\text{fixCOST}$  is the cost of fixing  $N$  (which we set equal to 0.3, calculated as 0.2 per unit of  $N$ , in terms comparable to nonfixers, multiplied by 1.5 to account for the greater  $N$  concentration in fixers). The potential productivity (independent of the cost of acquiring  $N$ ) is 5000; the light available for growth by fixers, after nonfixers have taken what they can, is proportional to  $(4500 - \text{NPPNF})/4500$ , 4500 being the maximum NPP of nonfixers that can be realized in practice. In effect, this formulation gives nonfixers priority for light in proportion to the soil  $N$  they can acquire. If there is still light available after nonfixers have taken what they can, then  $N$  fixers can grow (and fix  $N$ ). Water and other resources could be treated similarly.

The production of litter  $C$  and  $N$  by fixers and nonfixers (independently) is set to 10% annually of the  $C$  and  $N$  in plant biomass. The rate of decomposition is set to 5% of soil  $C$  per year, and net  $N$  mineralization ( $N_{\min}$ ) is calculated as

$$N_{\min} = \text{soil}N - \text{soil}C/CN_{\text{crit}}, \quad (3)$$

where  $\text{soil}N$  and  $\text{soil}C$  are the quantities of organic  $N$  and  $C$  (respectively) in soil, and  $CN_{\text{crit}}$  is the critical ratio of  $C$  to  $N$ , above which  $N$  is immobilized by microbes and below which  $N$  is mineralized.

The simulation maintains mass balance of  $C$  and  $N$  in plants, soils, and the system as a whole; it also constrains potential production and  $N$  uptake by fixers and nonfixers when their initial biomass is low. We include a relatively low rate of input of fixed  $N$  in precipitation (2 units per year), one designed to represent unpolluted regions. In this formulation, outputs of  $N$  occur only when  $N$  remains in the available pool after all biological demands are met. A complete listing of the simulation in MATLAB (including the extensions described in subsequent sections) is available from the authors at <http://jasper.stanford.edu/chrisweb/flab/flab.html>.

### Initial results

We used this simple model to simulate the development of an ecosystem on a new substrate, one that starts with no organic  $C$  or  $N$  in soil. Initially, very low levels of  $N$  are available in soil; consequently the growth of nonfixers is limited by  $N$ , light is available, and  $N$  fixers dominate the site and add substantial quantities of  $N$  to the system (Figures 2a, 3a). As this fixed  $N$  enters the soil, rates of  $N$  mineralization eventually increase, and nonfixers colonize, grow, and ultimately use almost all the available light, replacing the fixers. Similar patterns of species replacement are observed in the field during primary successions in which symbiotic  $N$  fixers are present (Walker & Syers 1976; Van Cleve et al. 1991; Chapin et al. 1994). Approximately 150 years into the simulation, the system reaches equilibrium levels of production, biomass,  $N$  mineralization, etc;  $N$  fixers are then very sparse in the system. Nevertheless,  $N$  remains limiting to nonfixers, if only marginally. We simulate additions of  $N$  to the equilibrium system by adding 50 units of inorganic  $N$  a year for a 20-year period beginning in year 300, and find a small increase in biomass of nonfixers that reflects their lower cost of acquiring  $N$  when its availability is high (Figures 1, 3a).

We also evaluated ecosystem development without  $N$  fixers, forcing the system to draw upon inputs of fixed  $N$  from the atmosphere. Under these

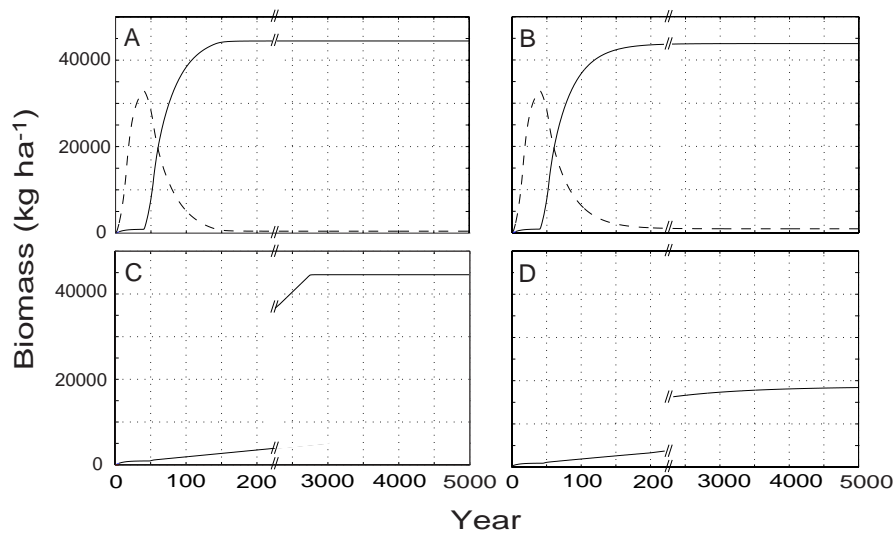
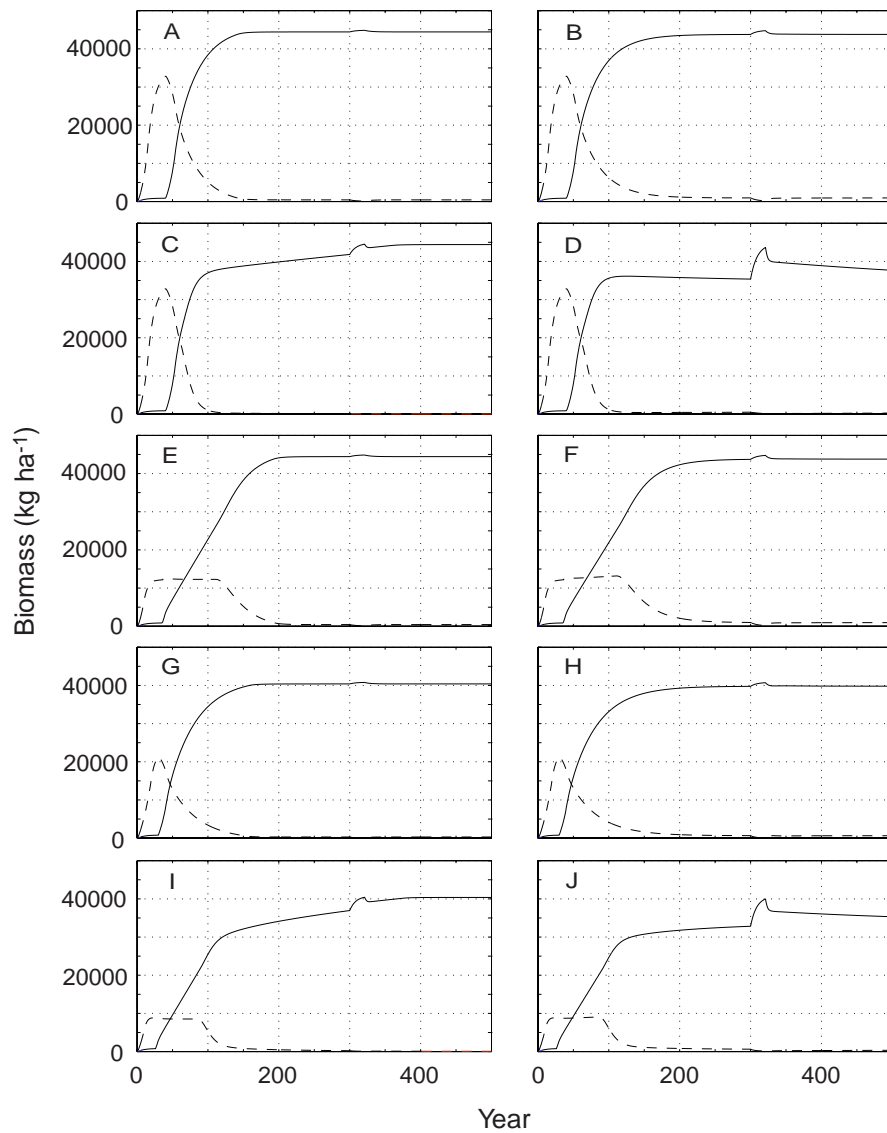


Figure 2. Simulated biomass of nonfixers (solid lines) and  $N$  fixers (dashed lines) through long-term ecosystem development on a site that begins with no  $C$ ,  $N$ , or available  $P$  in soil. The panels evaluate combinations of the presence or absence of  $N$  fixers and differing pathways of  $N$  loss. Those on top (a, b) include  $N$  fixers while those on the bottom (c, d) exclude them; those on the left (a, c) include only losses of  $N$  from the pool of available  $N$  that remains in the soil after plant and microbial uptake, while those on the right (b, d) also include losses of 5% of mineralized  $N$ . Note the change in scale on the  $x$ -axes.

conditions, the system eventually reaches the same equilibrium level of production, etc. – as indeed it must, as long as there are any  $N$  inputs, and only available  $N$  in excess of biological requirements is lost. However, it takes much longer to reach that equilibrium (2700 versus 150 years) (Figure 2c). Moreover, if we simulate  $N$  losses occurring by pathways other than removal of excess available  $N$ , by removing 5% of mineralized  $N$  annually, then in the absence of  $N$  fixers the system equilibrates at a lower biomass, productivity,  $N$  mineralization, etc., as observed in the simpler model of Vitousek et al. (1998) (Figure 2d). In practice, leaching of dissolved organic  $N$  and emissions of  $N$  trace gases produced during nitrification (though not denitrification) could represent losses that are independent of the existence of excess available  $N$  (Hedin et al. 1995; Parton et al. 1996). Without  $N$  fixers, such  $N$  losses can allow substantial  $N$  limitation to persist at equilibrium (Vitousek et al. 1998).

Finally, we evaluated the consequences of a 5% loss of mineralized  $N$  in the presence of  $N$  fixers. In this scenario, fixers remain within the system at equilibrium, though at a relatively low level (Figure 2b, 3b). Their activity is sufficient to offset losses of  $N$ , and (together with atmospheric inputs), to





*Figure 3.* Simulated biomass of nonfixers (solid lines) and fixers (dashed lines); the panels evaluate combinations of pathways of  $N$  loss and constraints on  $N$  fixers. Those on the left (a, c, e, g, i) include losses of  $N$  only from the pool of available  $N$  that remains in the soil after microbial and plant uptake; the panels on the right (b, d, f, h, j) also include losses of 5% of mineralized  $N$ . After 300 y, 50 units of  $N$ /year are added for 20 years, to evaluate the strength of  $N$  limitation. (a, b) The basic model, as outlined in the text. (c, d) Inclusion of a shade limitation to the colonization and growth of  $N$  fixers. (e, f) Inclusion of phosphorus limitation.  $P$  supply can constrain both nonfixers and fixers, but  $N$  fixers require more  $P$  and so are more severely constrained. (g, h) Inclusion of grazing, which removes 1% of the biomass of nonfixers and 5% of the biomass of  $N$  fixers annually. (i, j) The combination of all three constraints to the growth of  $N$  fixers.

maintain the system at the same equilibrium biomass as occurs when only  $N$  in excess of biological requirements is lost (Figure 2a, 3a).

Together, these initial simulations show that despite our rather strong assumptions about the poor competitive ability of fixers versus nonfixers (e.g., nonfixers have absolute priority for available  $N$  in the soil, nonfixers use available light in direct proportion to that available  $N$ ),  $N$  fixation is still sufficient to adjust levels of available  $N$  close to those of other limiting resources (in this case light). We believe that this model yields a reasonable representation of a system in which  $N$  limitation can be substantial but transient, or sustained but marginal. If the model were also a reasonable representation of the world,  $N$  limitation could affect the transient but not the equilibrium responses of ecosystems to regional and global change.

We now turn to mechanisms that could further constrain  $N$  fixers in comparison to nonfixers, and thereby extend the time over which  $N$  is limiting or even sustain substantial  $N$  limitation at equilibrium. We first add these constraints one at a time, evaluating both the conditions in which only excess  $N$  is lost, and those in which 5% of mineralized  $N$  (plus any excess  $N$ ) is lost. For each case, we simulate a 500-year course of ecosystem development, starting with no organic  $C$  or  $N$  in soil, and we apply a 20-year pulse of elevated  $N$  inputs at year 300 to evaluate the extent of  $N$  limitation.

### Energy limitation

Energy limitation could affect the growth and persistence of  $N$  fixers because their operational cost for  $N$  acquisition is high, and/or because the high cost of  $N$  fixation makes it difficult for fixers to become established and grow through the understory of a closed canopy system (Gutschick 1987). The former mechanism already is embedded in our model (Figure 1). For the latter, the cost of  $N$  fixation could in effect decrease the shade tolerance of  $N$  fixers, suppressing their ability to fix  $N$  in low-light environments where nonfixers would still be able to persist and grow.  $N$  fixers that had already reached the canopy might be able to grow and fix  $N$ , but  $N$  fixers in the understory would be unable to reach the canopy.

We simulated the influence of shade in a closed-canopy system by calculating a potential shade-limited NPP of the  $N$  fixer (potshNPPfix) as a function of the biomass of the nonfixers in the system (NFBiomass)

$$\text{potshNPPfix} = 5000 * (1 - \text{fixCOST}) * \left( 1 - \frac{1.00025^{\text{NFBiomass}}}{100 + 1.00025^{\text{NFBiomass}}} \right), \quad (4)$$

where  $\text{fixCOST}$  is the cost to  $N$  fixers for acquiring  $N$ . The term on the right provides a logistic function that takes on values between 0 and 1. This function has little effect when biomass is  $< 15,000$  units, but it suppresses the NPP of fixers almost completely when biomass approaches 35,000 units. The potential NPP from Equation (2) is compared with that from Equation (4) each year, and the lesser of the two is used.

The results of including shading (as simulated here) into the model are summarized in Figures 3(c) and 3(d), for the cases in which only excess  $N$  is lost and in which 5% of mineralized  $N$  is lost, respectively. This shading function constrains  $N$  fixers substantially as nonfixer biomass exceeds 30,000 units, shortening and reducing the pulse of  $N$  that fixers add to developing systems. Consequently, when the fixers decline,  $N$  remains strongly limiting to nonfixers. Where only excess  $N$  is lost, inputs of  $N$  in precipitation gradually reduce that limitation (Figure 3(c)). However, the combination of  $N$  losses proportional to mineralization and suppression of  $N$  fixers by shading (Figure 3(d)) yields an open system in which substantial  $N$  limitation can be sustained indefinitely.

### Phosphorus limitation

The availability of  $P$  can constrain rates of  $N$  fixation; this is the most important control of fixation in most temperate lakes (Schindler 1977), and there are clear examples wherein  $P$  additions stimulate  $N$  fixation in terrestrial ecosystems as well (Smith 1992; Crews 1993). Low  $P$  availability could limit fixers disproportionately because they have a greater requirement for  $P$  than do nonfixers (Pate 1986).

To simulate the effects of  $P$  supply on the growth and persistence of  $N$  fixers, we assumed that while the  $N:P$  ratio of fixers and nonfixers is the same, fixers require more of both  $P$  and  $N$  than nonfixers. We developed a simple  $P$  cycling and limitation module, in which the quantity of available  $P$  in soil is calculated as  $P$  mineralization plus  $P$  inputs from weathering plus turnover of labile inorganic  $P$  plus carryover from previous years plus fertilizer inputs. We assume that because nonfixers require less  $P$  (and thereby can produce more biomass per unit of  $P$  taken up), they can outcompete fixers for low levels in soil (ultimately if not immediately). Accordingly, the model gives nonfixers priority over fixers for uptake of available  $P$  (as for light).

In the implementation of this model, the uptake of  $N$  by nonfixers is calculated as described above, but it is now considered to represent a potential  $N$  uptake. We then calculate how much  $P$  would be required to match that uptake of  $N$  (given plant  $N:P$  ratios); if at least that much  $P$  is present in the available pool of  $P$  ( $\text{minP}$ ), the matching quantity of  $P$  is taken up. If

less  $P$  is available, then the entire  $\text{min}P$  pool is taken up, and  $N$  uptake is constrained to the level determined by  $P$  uptake. NPP of the nonfixers is then calculated as in Equation (1).

We calculate the potential production by fixers, as it is constrained by  $P$  supply ( $\text{potPNPPfix}$ ), as

$$\text{potPNPPfix} = \text{min}P * C P f, \quad (5)$$

where  $\text{min}P$  is now the quantity of available  $P$  remaining after uptake by nonfixers, and  $C P f$  is the carbon to phosphorus ratio of fixers. This potential production is compared to that calculated by Equation (2) above, and the smaller of the two potential productivities is used.

The production of litter  $P$  is set to 10% of biomass  $P$ , in parallel with  $C$  and  $N$ , and  $P$  mineralization is calculated analogously to  $N$  mineralization (Equation (3)). To account for the much lower mobility of  $P$  than  $N$ , we assume that only 10% of the available  $P$  remaining in the soil after biological demands are met can be lost from the system annually. This loss could represent leaching of inorganic  $P$ , or it could represent the formation of occluded  $P$  (cf Walker & Syers 1976). Twenty percent of the available  $P$  remaining after uptake is carried over to the next year, and 70% goes into a labile inorganic pool with a turnover time of 10 years. We assume  $P$  inputs via weathering to be 2 units/year, with a brief pulse of more rapid weathering in the initial stage of soil development.

The simulated consequences of  $P$  limitation are summarized in Figures 3(e) and 3(f). Pathways of  $N$  loss have little effect on the responses of biomass or other ecosystem characteristics to  $P$  limitation. Compared to the simple model (Figures 3(a, b)), a low supply of  $P$  strongly constrains the growth of  $N$  fixers early in ecosystem development, extends the period over which fixers are active by about 60 years, and delays equilibrium biomass in the system as a whole by about 50 years. Early in development, the production of nonfixers is limited by  $N$ , while that of fixers is limited by  $P$ . Additions of  $N$  would stimulate production by nonfixers, up to the point where they too would become  $P$ -limited. Additions of  $P$  would stimulate  $N$  fixers, which in turn would add  $N$  and stimulate nonfixers, bringing the whole system to equilibrium more rapidly. In this case, what appears as  $N$  limitation (to nonfixers) could actually be  $P$  limitation in disguise (Vitousek & Howarth 1991).

Later in development, sufficient  $P$  has weathered from the substrate so that  $P$  no longer constrains  $N$  fixation (in this model). However, this simulation only considers losses of excess available  $P$ , the inorganic  $P$  that remains after biological demands are met. The combination of a much lower rate of  $P$  weathering in very old soils (Walker & Syers 1976; Crews et al. 1995;

Newman 1995; Vitousek et al. 1997b) with losses of  $P$  via other pathways (such as leaching of dissolved organic  $P$ ) could in practice cause  $P$  limitation to  $N$  fixation in old as well as very young soils.

A low supply of elements other than  $P$  could also constrain  $N$  fixation, if  $N$  fixers require more of a particular element than do nonfixers. Molybdenum and iron are perhaps the most interesting of these other elements; both are necessary to the functioning of the nitrogenase enzyme, and  $Mo$  in particular is not even required by nonfixers that use ammonium as their sole  $N$  source. There is some evidence from both marine and terrestrial ecosystems that additions of  $Mo$  sometimes can stimulate rates of  $N$  fixation (Howarth & Cole 1985; Silvester 1989).

### Control by grazing

The growth of many grazing animals is limited by access to protein more than it is by access to energy.  $N$  fixers are systematically richer in protein than nonfixers, and are often preferred by both vertebrate and invertebrate herbivores (Hulme 1994, 1996). Selective grazing on  $N$  fixers could suppress  $N$  fixation and thereby keep  $N$  availability from equilibrating with the supply of other resources, as Ritchie and Tilman (1995) demonstrated in old-fields and savannas at Cedar Creek, Minnesota. Alternatively,  $N$  fixers could maintain more chemical defenses against grazers than nonfixers, reducing losses to grazing at the expense of effectively raising the cost of  $N$  fixation.

We simulated the effects of grazing by defining a fraction of the nonfixers' biomass that is consumed annually (grazefrac). We established a higher grazing pressure on  $N$  fixers using a multiple of this fraction. For the runs here, we set grazing on the nonfixers at 1% and grazing on fixers at 5%. We assume that all of the  $N$  and  $P$ , and half of the  $C$ , in grazed plant tissue is transferred to the soil organic pool; the remainder of the  $C$  is respired by grazers.

The effects of differential grazing on fixers versus nonfixers are summarized in Figures 3(g) and 3(h); pathways of  $N$  loss have little effect on responses to grazing. Relative to the control case (Figures 2(a, b)), grazing reduces the peak biomass of  $N$  fixers by about 35%; it thereby delays the whole system's approach to equilibrium by about 20 years. The equilibrium biomass of the nonfixer is reduced slightly by the direct effects of grazing. More interestingly, because grazers return material with lower  $C:N$  and  $C:P$  ratios to the soil than does litterfall, grazing causes substantial net mineralization of  $N$  from soil organic matter, and consequently increased growth of the nonfixer, to begin almost 10 years earlier than in the control case.

### The combined model

Results for the complete model, including the effects of shading, phosphorus, and grazing, are summarized in Figures 3(i) and 3(j). All three constraints contribute to simulated biomass dynamics during long-term ecosystem development. Given our set of parameters, *P* limitation and grazing interact to reduce the biomass of the *N* fixer in young systems by more than two-fold, in comparison with the control case. After about 125 years, suppression of *N* fixers by shading becomes the dominant effect, shaping the biomass of fixers directly, and that of nonfixers through consequent *N* limitation. The approach to equilibrium is much slower where *P* and grazing reduce the early pulse of *N* fixation (compare Figures 3(c) and 3(d) with Figures 3(i) and 3(j)), but ultimately the equilibrium biomass of fixers and nonfixers is set by shading. Where only excess *N* is lost from ecosystems (Figure 3(i)), sustained inputs of fixed *N* from precipitation drive a gradual increase in *N* capital that eventually offsets all but marginal *N* limitation. However, where *N* can also be lost by other pathways (Figure 3(j)), NPP and biomass can be constrained substantially by *N* supply, indefinitely.

We can also use the combined model to evaluate other ecosystem-level processes. Net primary production (NPP) varies similarly to biomass (Figures 4(a, b)); indeed, except for grazing, biomass is directly proportional to the 10-year running mean of NPP. Nitrogen fixation (Figures 4(c, d)) is scaled directly to the NPP of *N* fixers, through their fixed *C:N* ratio. The net mineralization of *N* and *P* lag early in ecosystem development (Figures 4(e, f)), as a consequence of microbial immobilization during the processing of litter that has *C:N* and *C:P* ratios well above the critical values for mineralization. After that early lag, *N* mineralization is the major cause of variation in the biomass and production of nonfixers. The decrease in net mineralization associated with *N* fertilization at 300 years represents a transient increase in immobilization in response to increased inputs of litter with fixed *C:N* and *C:P* ratios. To the extent that the inherent decomposability of litter increases and/or *C:nutrient* ratios decrease following fertilization, real systems might not experience this reduced net mineralization. There is mixed evidence concerning the effects of fertilization on litter decomposability, and good evidence that fertilization with *N* or *P* generally decreases *C:N* or *C:P* ratios in litter (Berg & Tamm 1991; Prescott et al. 1993; O'Connell 1994).

### Effects of fire

The constraints to *N* fixation modeled above effectively confine the growth of *N* fixers to early stages of soil and ecosystem development. Are these

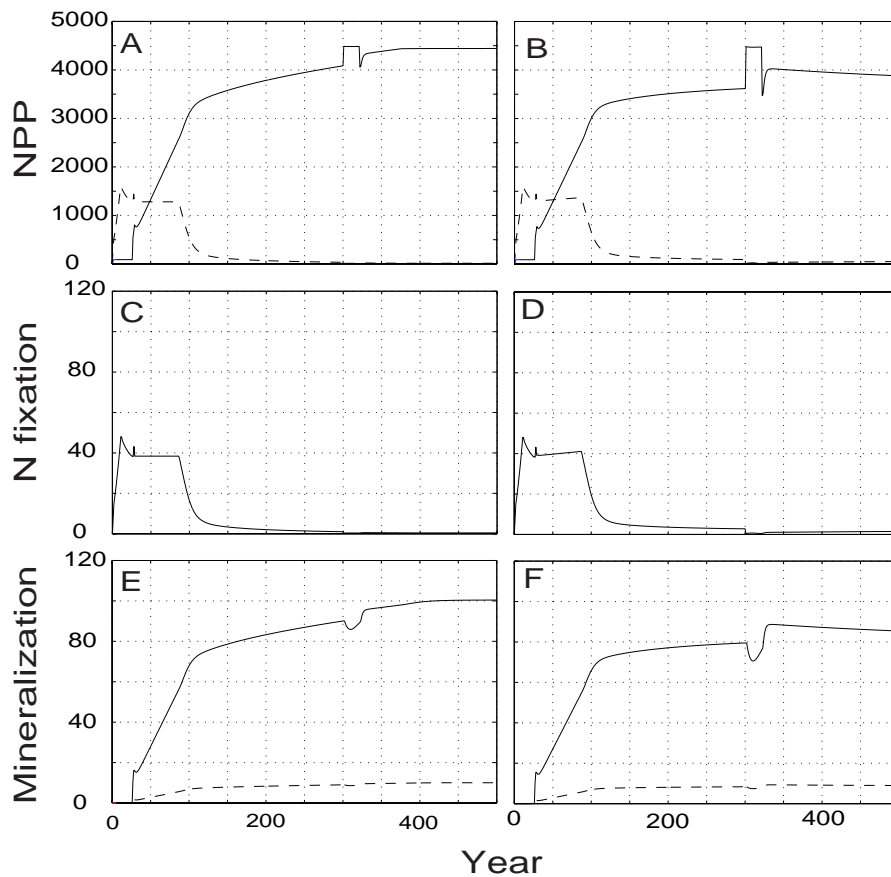


Figure 4. Rates of other ecosystem processes simulated using the combined model from Figures 3(i) and (j), with alternative pathways of  $N$  losses as in Figure 3. (a, b) Net primary production (NPP) of nonfixers (solid lines) and fixers (dashed line). (c, d) Rates of  $N$  fixation. (e, f) Net mineralization of  $N$  (solid lines) and  $P$  (dashed lines).

constraints so severe that  $N$  fixers are excluded under any reasonable circumstances? We evaluated this question (and the temporal dynamics of the model) by simulating the effects of fire on  $N$  fixers and nonfixers. We assume that fire volatilizes all of the  $C$  and  $N$  contained in fixers and nonfixers; all of the  $P$  returns to soil. These assumptions overstate the contrast between  $N$  and  $P$  – in practice, some plant  $N$  is retained within systems and some  $P$  is volatilized (Ojima et al. 1994; Kauffman et al. 1994) – but they do capture an important difference between  $N$  and  $P$ , and they are readily modified.

All fire simulations were carried out using the combined model (Figure 3(j)), including  $N$  losses by pathways other than excess available  $N$ , except that we evaluated the consequences of including versus excluding

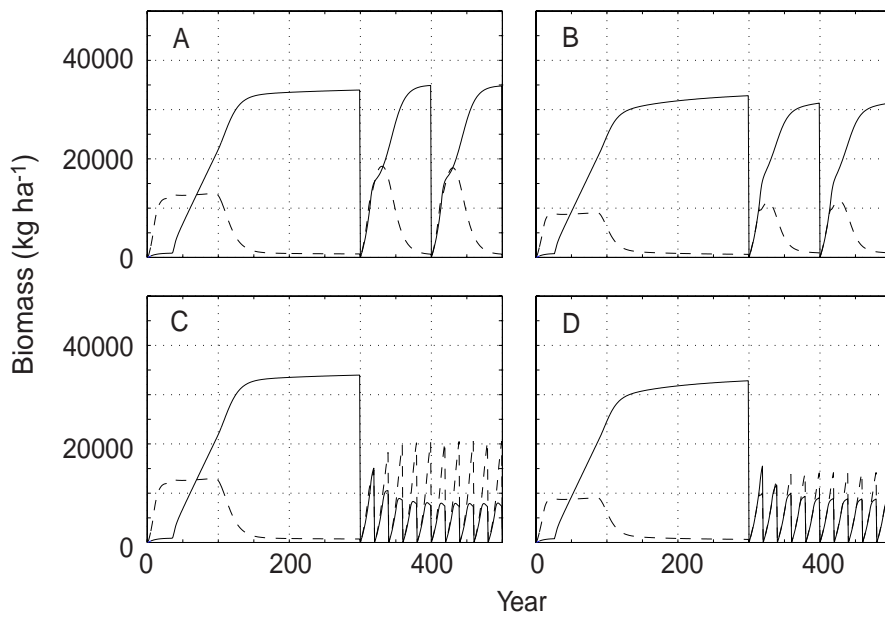


Figure 5. Effects of simulated fire on the biomass of nonfixers (solid lines) and fixers (dashed lines), in the combined model with (b, d) and without (a, c) grazing, using levels of 1% on nonfixers and 5% on  $N$  fixers. (a, b) A 100-year fire return interval, beginning after 300 y. (c, d) A 20-year fire return interval.

grazing. We tested two fire frequencies – fires every 20 versus every 100 years, in both cases initiating fire after 300 years of ecosystem development. In the model, the first fire has the effect of removing nonfixers, and so allowing colonization by fixers; it also temporarily removes shade limitation and enhances  $P$  availability. Fixers respond with a pulse of growth and activity (Figure 5). With a fire-return interval of 100 years or more, nonfixers eventually replace  $N$  fixers; the pulse of fixers following fire is briefer and smaller than that occurring at the beginning of ecosystem development, because substantial fixed  $N$  remains in the soil after fire. With these long fire-return intervals, fixers add sufficient  $N$  to sites to replace that lost during and after fire; subsequent fires give rise to the same dynamics as the first one (Figures 5(a, b)).

Despite the loss of fixed  $N$  from biomass, fire causes a large but brief pulse of net  $N$  mineralization (not shown). This increase is a consequence of the reduction in litter inputs after a fire, leading to decreased immobilization of  $N$  and an increase in net mineralization. The combination of reduced plant uptake and decreased immobilization further causes a large but brief increase in losses of ‘excess’ available  $N$  from the system following fire (not shown), in addition to that lost during fire. The magnitude of this simulated pulse



of available  $N$  suggests that the model probably overestimates  $N$  fixation immediately following a fire, at least when the fire-return interval is long; in practice, fixers may grow but their fixation of  $N$  is likely to be repressed in the presence of so much available  $N$ .

With more frequent fires, the quantity of  $N$  fixed between fires is insufficient to replace the  $N$  lost during and following fire (Figures 5(c, d)). The first fire causes a large pulse of net  $N$  mineralization, with consequent rapid growth of the nonfixer. However, losses of  $N$  are greater than inputs over the first 20-year cycle, and so the pulse of  $N$  grows smaller and  $N$  becomes more limiting following the second and subsequent fires. As a consequence,  $N$  fixers come to dominate NPP and biomass in the short interval between fires.

Differential grazing on  $N$  fixers substantially constrains their biomass and activity following fire. With long fire-return intervals, grazing substantially reduces the magnitude and duration of the post-fire pulse, and thereby sustains  $N$  limitation during post-fire succession (Figure 5(b)). With short fire-return intervals, fixers remain more abundant than nonfixers, but grazing reduces their peak biomass substantially (Figure 5(d)).

### Effects of elevated $CO_2$

Increasing concentrations of  $CO_2$  could have multiple effects on the production and biomass of  $N$  fixers and on constraints to their activity, as these are modeled here. Most of the direct effects should reduce constraints to  $N$  fixation, but several indirect effects could reinforce them. Predicting how these direct and indirect effects will work on balance will require determination of accurate coefficients, not just reasonable mechanisms, for the processes that constrain  $N$  fixation. However, we believe that it is useful to simulate some of the direct effects of increasing  $CO_2$  in an exploratory way.

We modeled the consequences of an increase in  $CO_2$  (say a doubling) by: (1) increasing the  $C:N$  ratio of nonfixers by a factor of 1.25, thereby increasing their potential NPP; (2) increasing the potential NPP of fixers by 1.5, to simulate a greater productive capacity under elevated  $CO_2$ ; (3) decreasing the cost of  $N$  acquisition by fixers by 1.5; and (4) shifting to the right the curve describing the effect of shading by nonfixers on growth of fixers, by dividing the coefficients in Equation (4) by 1.5.

We implemented these changes to the combined model, including  $N$  losses equal to 5% of net mineralization (Figure 3(j)), by introducing the effect of elevated  $CO_2$  200 years into the run (Figure 6). The NPP and biomass of nonfixers responds immediately to elevated  $CO_2$ , as a consequence of their increased  $C:N$  ratios (as is observed in many growth experiments).

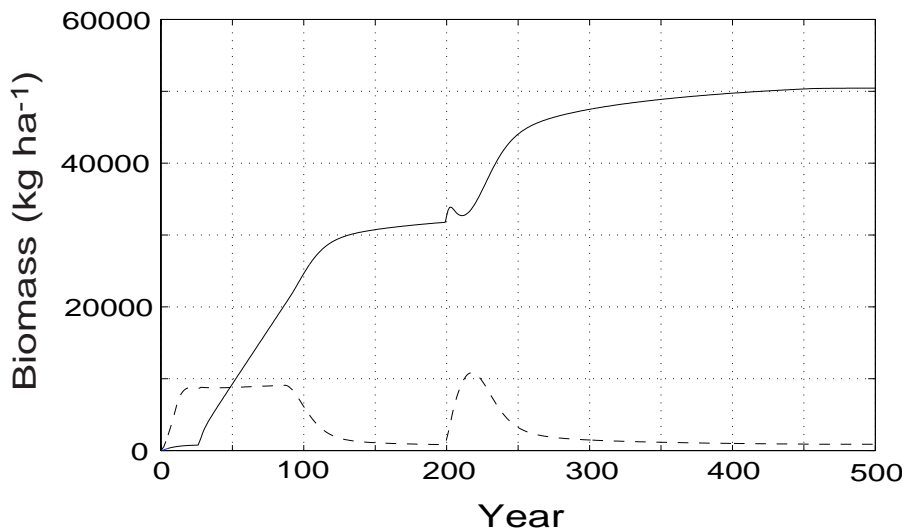


Figure 6. Effects of an instantaneous increase in  $CO_2$  at 200 y, on biomass of nonfixers (solid lines) and  $N$  fixers (dashed lines), using the conditions in Figure 3(j) as a base. Effects of increased  $CO_2$  on the fixers are simulated by decreasing the fixer's costs of  $N$  acquisition, shifting the curve describing effects of shading, and increasing potential NPP by a factor of 1.5; the potential NPP of nonfixers is increased by raising their  $C:N$  ratio by a factor of 1.25. Added  $CO_2$  stimulates the growth of nonfixers immediately, but this response decays as  $N$  is immobilized in litter with a higher  $C:N$  ratio.  $N$  fixers respond more slowly, but ultimately they increase  $N$  supply in the system as a whole, and drive a substantial increase in production, biomass, and  $C$  storage in soil.

However, the initial positive response declines over decades as a result of increased immobilization of  $N$  by higher  $C:N$  litter – just as is predicted by most ecosystem models (cf. McMurtrie & Comins 1996). More importantly,  $N$  fixers then respond gradually with a substantial pulse of growth and  $N$  fixation (Figure 6). Over more than a century, this pulse adds enough fixed  $N$  to increase the NPP and biomass of nonfixers by more than 40%; soil  $C$  and  $N$  also are increased. Under the particular conditions we evaluated, the most important reason for the  $N$ -fixers' response is the shift in the shade-limitation function, which can be related directly to the increased quantum yield of photosynthesis with increased  $CO_2$ .

We believe that Figure 6 represents the most likely direction of response to the direct effects of  $CO_2$ ; understanding the details and the magnitude of those responses will require additional work. However, increased  $CO_2$  also has indirect effects, and some of these may suppress the growth of  $N$  fixers. For example, the  $C:N$  ratios of  $N$  fixers may increase less than those of nonfixers, and grazers' relative preference for  $N$  fixers consequently may be reinforced. Also, increased  $CO_2$  may lead to a denser canopy of nonfixers, offsetting

any increased shade tolerance of the fixers. We believe that evaluating both the direct and the indirect effects of elevated  $CO_2$  on all of the mechanisms simulated here would be rewarding.

## Conclusions

The model described herein demonstrates that it is possible to simulate an ecosystem that contains active symbiotic  $N$  fixers and that receives fixed  $N$  in precipitation, and yet remains substantially  $N$ -limited at equilibrium. The necessary conditions are (1) that some  $N$  is lost from the system even when  $N$  is not available in excess of biological requirements; and (2) that some process(es) limit the growth of  $N$  fixers to a greater extent than that of nonfixers, over and above simple priority in access to resources. A number of ecosystem models incorporate the first condition. For example, Century simulates  $N$  trace gas emissions as a constant fraction of gross  $N$  mineralization (Parton et al. 1996); the multiple element limitation model (MEL) simulates relatively large losses of available  $N$  even when it is strongly limiting to plant and microbial activity (Rastetter et al. 1997). For the second condition, while mechanisms that could enhance or constrain  $N$  fixers have been discussed (cf. Vitousek & Howarth 1991), they are not widely incorporated into ecosystem models. Century generally makes overall  $N$  input a function of precipitation, although it can make use of  $N:P$  ratios (Parton et al. 1993); Rastetter et al. (1997) evaluated MEL with precipitation inputs only versus essentially unlimited  $N$  inputs, as a means to determine the potential effects of  $N$  fixation, but did not evaluate controls or constraints on  $N$  fixation.

In this analysis, we show that simple formulations of the differential effects of shading, limitation by  $P$ , and grazing all could suppress the growth of  $N$  fixers relative to nonfixers, and so could reinforce  $N$  limitation. We believe that this model provides a framework for evaluating constraints to  $N$  fixation, and so for analyzing the causes, nature, and consequences of  $N$  limitation in terrestrial ecosystems. Further, we think that the combined model, including some losses of  $N$  in proportion to mineralization (Figure 3(j)), is a reasonable representation of the mechanisms and dynamics (if not process rates and magnitudes) that are important in driving  $N$  limitation in mesic-to-wet, temperate and boreal forest ecosystems. Tropical forests appear to function quite differently, both in being relatively enriched in  $N$  (Martinelli et al. this volume) and in supporting relatively abundant legumes in closed-canopy forests (cf. McKey 1994).

To the extent that this model incorporates mechanisms that cause  $N$  limitation, it also provides a framework for suggesting how  $N$  fixation and limitation are likely to interact with components of human-caused global

environmental change. Where the mechanisms simulated here (and/or others) combine to constrain *N* fixation in temperate and boreal forests, anthropogenic inputs of *N* have the potential to alter the growth of and *C* storage in those forests profoundly. Similarly, the direct effects of increased *CO*<sub>2</sub> on *N* fixers could increase long-term forest production and *C* storage substantially, where they are not offset by indirect effects that suppress *N* fixation.

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