



A model analysis of N and P limitation on carbon accumulation in Amazonian secondary forest after alternate land-use abandonment

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Abstract. Productivity and carbon (C) storage in many mature tropical forests are considered phosphorus (P) limited because of advanced soil weathering. However, disturbance can shift limitation away from P and toward nitrogen (N) because of disproportionately large N losses associated with its mobility relative to P in ecosystems. This shift was illustrated by model analyses in which large disturbances including timber extraction and slash-burn were simulated in a P-limited tropical forest. Re-accumulation of ecosystem C during secondary forest growth was initially N-limited, but long term limitation reverted to P. Mechanisms controlling shifts between N and P limitation included: (1) N volatility during slash combustion produced ash that increased soil solution P more than N, (2) a wide N:P ratio in residual fuel and belowground necromass relative to soil organic matter (SOM) N:P produced a simultaneous P sink and N source during decomposition, (3) a supplemental (to aerosol deposition) external N source via biological N fixation. Redistribution of N and P from low C:nutrient SOM to high C:nutrient vegetation was the most important factor contributing to the resilience of ecosystem C accumulation during secondary growth. Resilience was diminished when multiple harvest and re-growth cycles depleted SOM. Phosphorus losses in particular resulted in long-term reductions of C storage capacity because of slow re-supply rates via deposition and the absence of other external sources. Sensitivity analyses limiting the depth of microbially active SOM in soil profiles further illustrated the importance of elements stored in SOM to ecosystem resilience, pointing to a need for better knowledge on the functioning of deeply buried SOM.

Introduction

Tropical forests are among the most important ecosystems in the global carbon (C) budget, occupying $\sim 2200 \times 10^6$ ha (Melillo et al. 1993) and accounting for 20%–25% of the estimated 2300 Pg (10^{15} g) C stored in soils and vegetation globally (Brown and Lugo 1982; Schlesinger 1997; Dixon et al. 1994). Land cover and land-use changes could be altering C budgets in these tropical environments significantly. Associated with the practice of forest conversion to alternate land-use is an export of C and nutrients from the ecosystem. Subsequent abandonment of the alternate land-use is common, and throughout Amazonia has resulted in the formation of expanses of regenerating secondary growth (Lucas et al. 1996). The ability

of these aggrading ecosystems to re-accumulate and store C will have implications for atmospheric CO₂ concentration and associated global climate change. Both the rate of C accumulation and the capacity for C storage are linked to a supply of nutrients, including nitrogen (N) and phosphorus (P), which can limit vegetation growth. However, the re-accumulation of these nutrients, once lost, may require thousands of years.

We use the Multiple-Element-Limitation (MEL) model to examine how ecosystem N and P stocks, characteristics of N and P cycles, and the assumption of either N or P limitation might constrain the re-accumulation of C in a tropical forest site subjected to tree harvests, slash combustion, and pasture conversion. Our examination is based on a well-studied site in the Brazilian Amazon with highly weathered soils that are typically P-limited. In this representative ecosystem the removal of biomass C and nutrients via harvest, combustion, and grazing disturbances could severely limit secondary forest growth, productivity, and the potential for C sequestration in both soils and vegetation. Because re-supply rates of nutrient capital by deposition are slow and because there are virtually no primary minerals remaining in such highly weathered soils, secondary forest growth depends on the redistribution of pre-existing nutrients (Markewitz et al. 2001), e.g. those contained within soil organic matter (SOM), and internal processes that augment external supply rates, e.g. symbiotic N fixation. Nutrient constraints on secondary forest growth may occur because of differential losses of N and P corresponding with disturbance. Our model analysis highlights how ecosystem N and P losses limit C re-accumulation in secondary forest growth following single and multiple disturbances or land-use conversion to cattle pasture with subsequent abandonment.

In mature tropical forests, vegetation requirements for N and P are largely satisfied by within-ecosystem recycling mechanisms (Jordan and Herrera 1981; Vitousek and Sanford 1986; Proctor 1987; Bruijnzeel 1991). It is generally thought that decomposition of organic matter is the most important mechanism in supplying plant available forms of both N (Matson and Vitousek 1987; Bowden 1986) and P (McGill and Cole 1981; Smeck 1985; Walbridge et al. 1991; Tiessen et al. 1994). Nutrient accumulation during forest aggradation depends on supply rates from external sources relative to their loss rates, and the entrainment of these elements within ecosystem cycles. External sources of N and P may include mineral weathering, deposition, and for N, biological fixation (Walker and Syers 1976; Vitousek and Sanford 1986; Bormann and Sidle 1990; Vitousek and Howarth 1991). Losses may occur via occlusion, leaching, and for N, volatilization (Walker and Syers 1976; Qualls and Haines 1991; Riley and Vitousek 1995; Crews et al. 1995; Hall and Matson 1999).

If the mature forest remains undisturbed the rates of N and P fluxes out of the system will approach their rates of supply from external sources as the forest itself approaches a steady state. However, N and P losses accompanying biomass removal or combustion can be large, and proportional N losses often exceed those of P because of differences in volatility and mobility (Buschbacher et al. 1988; Kauffman et al. 1995; Mackensen et al. 1996; Kauffman et al. 1998). Consequently, N rather than P, could limit secondary forest growth (Ewel 1986). The re-supply and re-en-

trainment of nutrients into ecosystem cycles could require decadal time scales or longer, and the system could exhibit a reduced capacity to support secondary vegetation growth unless otherwise compensated by a redistribution of nutrients from within the ecosystem.

In the following model analyses we describe how C accumulation in a forest ecosystem subjected to timber removals, slash combustion, and pasture conversion might be limited by either N or P as a consequence of the differences in N and P loss and accumulation rates. Further, we examine how N additions via symbiotic fixation and N and P redistribution within the ecosystem during secondary forest growth partially compensate for losses that occurred as a consequence of these land-use conversion practices. The analyses are extended to account for the impact of the multiple harvest rotations and cattle grazing on further losses of nutrient capital and the requirement for long-term re-accumulations from outside of the system in the absence of sources other than those accounted for by deposition. It is our goal to assess the resilience of the model system to land-use conversion manipulations with respect to C storage.

Methods

Description of the MEL model

The MEL model (Figure 1, Appendix 1) has been previously applied to examine (1) element limitation and vegetation acclimation to changes in resource supply (Rastetter and Shaver 1992), (2) recycling of elements through soil (Rastetter et al. 1997), (3) interactions among competing species (Herbert et al. 1999), and the energetic cost of N fixation in N limited systems (Rastetter et al. 2001). The model accounts for C and one nutrient element, either N or P, cycling among plant, soil organic matter, and inorganic pools, which are linked through plant and microbial processes (Rastetter et al. 1997).

The present application of the model includes a modification that accommodates a simple representation of the abiotic exchange of inorganic nutrient elements between solution (E_S) and inorganic labile (E_L) forms. Element exchange between these forms is represented as:

$$E_L = \frac{E_{MAX}\beta_{EO}E_S}{E_{MAX} + \beta_{EO}E_S}$$

where E_{MAX} is the maximum mass of an inorganic element that can be held on adsorption sites and β_{EO} is the initial slope of the function (i.e. when all adsorption sites are available). The modification is particularly important in approximating P dynamics between available solution forms and labile forms, which may become slowly available. In this representation the amount of solution P in the soil at any given time (extractable by resin exchange) is a function of labile P pools (Figure 2).

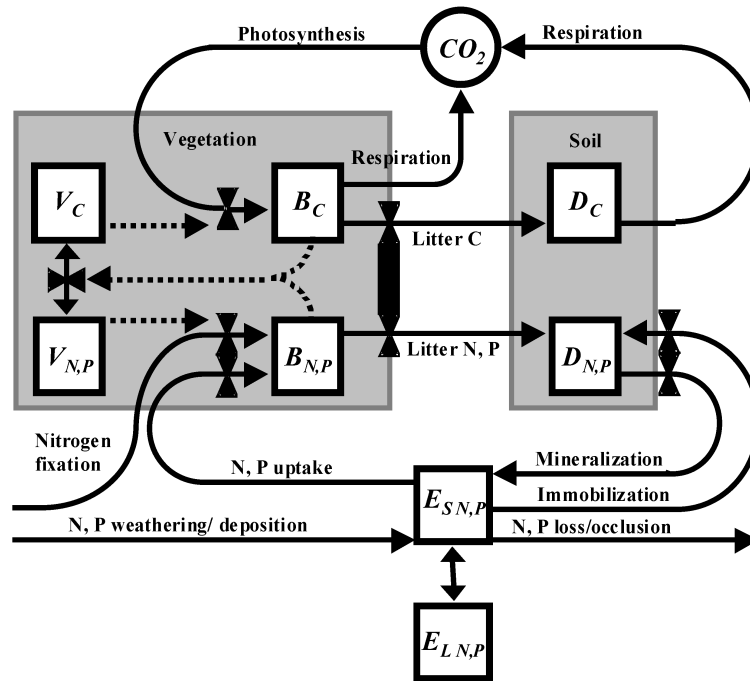


Figure 1. The Multi-Element Limitation (MEL) Model applied to C, N and P cycles in a terrestrial ecosystem. Elements are cycled among vegetation, SOM, and inorganic pools and are linked through the vegetation and microbial processes. As presented, solution inorganic nutrient pools are in equilibrium with labile inorganic pools. Solid arrows indicate material fluxes, and dotted arrows indicate the transfer of information used to calculate those fluxes.

In the present analyses we include in the labile P pool forms that are extractable with bicarbonate, NaOH, and dilute HCl, fully understanding that NaOH and dilute HCl extracts may become available only on decadal time scales (Mattingly 1975; Hedley et al. 1982; Smeck 1985; Cross and Schlesinger 1995).

A key property of the model is that the vegetation acclimates to changes in resource supply or plant resource requirements via continuous optimization of effort allocated toward the acquisition of C and another limiting element, i.e. N or P (V_C , V_N or V_P in Figure 1), so as to maintain a balanced element ratio (Rastetter and Shaver 1992; Rastetter et al. 1997). Uptake effort is a representation of the sum of all internal resources allocated toward the acquisition of an external resource, assumed strongly correlated with leaf area and fine root length.

MEL is a two-element model and it was not possible to analyze the three-element C, N, and P interactions simultaneously in one C-N-P simulation. Instead, the following analyses relied on paired model simulations for C-N and C-P cycles, which were analyzed separately and compared. The paired simulations were parameterized to have identical C pools and fluxes with associated C:N or C:P ratios characteristic to those of the modeled ecosystem in a pre-disturbance steady state.

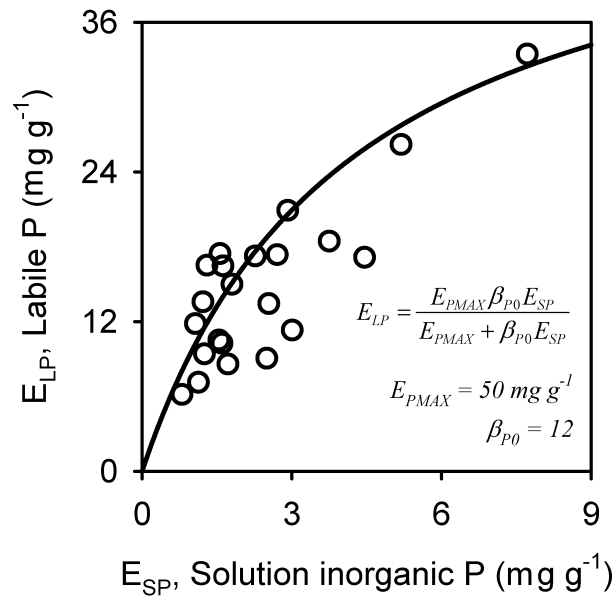


Figure 2. Relationship between solution inorganic P (E_{SP}) and labile P (E_{LP}), as defined in the model description. The line represents a model prediction fitted to data from Garcia-Montiel et al. (2000). Shaping parameters E_{MAX} and β_{EO} are in Appendix 2.

These paired simulations are henceforth referenced individually as either N-limited or P-limited.

Simulations

Modeled pools and fluxes of C, N, and P approximate those of a mature tropical rainforest in eastern Amazonia, including SOM and labile element pools to a soil profile depth of 200 cm (Appendix 2). Wherever possible data from a well-studied site near Paragominas, Brazilian State of Pará, were used to establish initial state variables and model parameters (Buschbacher et al. 1988; Uhl et al. 1988; Nepstad 1989; Nepstad et al. 1994; Davidson and Trumbore 1995; Nepstad et al. 2001). Model parameter estimates (Appendix 3) were made with an assumption that the system is P limited and could support as much as 10% more vegetation biomass in the absence of P limitation. Soil solution nutrient concentrations were based on measured values (Markewitz et al. 2002). The relationship between soil solution and labile P pools (Figure 2) was based on data describing P in different soil fractions from a forest-to-pasture conversion chronosequence in the Brazilian State of Rondônia (Garcia-Montiel et al. 2000).

Three forest conversion and land-use scenarios were simulated, including: (1) a harvest of wood biomass followed by slash burn and abandonment to secondary growth, (2) three wood harvest rotations, each with a slash burn followed by 20 years of re-growth, and (3) a wood harvest followed by slash burn and conversion

to alternate land-uses including eight or 20 years of either cattle grazing or crop production followed by abandonment. Element losses associated with pasture preparation, grazing, or cultivation are based on published values (Uhl et al. 1988; Buschbacher et al. 1988; Beck and Sanchez 1986; Kauffman et al. 1995, 1998; Dias-Filho et al. 2001). Element losses in multiple wood harvests were based on the pasture preparation assumptions, a standard wood production interval, harvest, and site preparation for the next wood crop, either natural or plantation, by slash-burn. No fertilizers are considered.

Assumptions in harvests, combustion, grazing, and cropping

Harvests removed 47.5% of C, N, and P bound in aboveground wood biomass (Table 1). These harvests assume that 70% of the aboveground wood in trees having stems ≥ 20 cm DBH was removed in the first harvest rotation, and are based on published stem diameter and biomass distribution data from the Paragominas site (Nepstad 1989). A C:biomass ratio of 0.5 was assumed for stem wood. Wood C:N and C:P (Appendix 3) were from Markewitz et al. (2002). The remaining fraction of aboveground biomass is left in place as slash. In multiple harvest simulations biomass removals were based on the formula applied in the initial harvest (47.5% of C, N, and P in aboveground wood). The interval between multiple harvests was 20 years, based on time required for the current annual wood biomass increment to decline below mean annual increment in secondary growth simulations (Evans 1982).

Post-harvest burn of slash, surface litter, and fine root mat, associated C, N, and P losses by oxidation and volatilization (Table 1), were based on data from seven sites located in Pará and Rondônia (Kauffman et al. 1995, 1998). A near complete loss of living vegetation was assumed, while unburned slash, buried roots and ash remained on site and in place. Assumptions applied to C, N, and P redistribution were (1) N and P content of ash were in biologically available inorganic form, and (2) residual unburned slash and buried roots became part of the detritus pool. We did not account for biomass conversion to recalcitrant C forms including charcoal. Slash additions to the aggregate detritus-SOM pool effectively increased soil C, N, and P, and widened SOM C:N and C:P. Because vegetation and post-burn necromass N:P are wide relative to SOM (Table 2), additions also widened SOM N:P. Ash additions of N and P immediately increased inorganic nutrient supply, some of which was adsorbed into labile pools (Table 3), as described by the element exchange equation and parameters in Appendix 2.

Grazing was simulated as annual conversions of live biomass to detritus and did not account for other grazing impacts. Annual conversions were random in quantity but constrained to maintain vegetation within $10\text{--}50 \text{ T C ha}^{-1}$ for 20 years, reflecting reports from pastures in the region (Uhl and Kauffman 1990; Houghton et al. 1991; Fearnside 1996). Nutrient exports associated with grazing were 0.5 kg P and $7.0 \text{ kg N ha}^{-1}\text{yr}^{-1}$, based on export in meat (Dias-Filho et al. 2001). Crop harvest were similar to grazing simulations but with higher nutrient export rates, $\sim 1.5 \text{ kg P ha}^{-1}\text{yr}^{-1}$ and $\sim 30 \text{ kg N ha}^{-1}\text{yr}^{-1}$, based on crop P exports (Beck and

Table 1. Loss and redistribution of C, N and P associated with timber harvest and burning of remaining slash. The harvest assumes the removal of 70% of the aboveground wood in trees with stem size classes greater than 20 cm dbh.

Initial pre-disturbance element stocks (g m ⁻²)	C	N	P
Vegetation	14971	171	5.64
Leaves ¹	376	14.5	0.90
Wood in stems < 20 cm DBH ²	4132	40.5	1.03
Wood in stems ≥ 20 cm DBH ²	8702	83.9	2.17
Fine root mat ²	110	5.0	0.31
Belowground ²	1651	25.7	1.11
Soil organic matter and litter			
Surface litter ³	568	24.4	0.5
SOM 200 cm depth ³	14842	1333	83.29
SOM 20 cm depth ³	4135	380.3	24.27
Loss and redistribution in first harvest and burn (g m⁻²)			
Wood harvested	-6091	-59.7	-1.57
Post-harvest fuel (slash, surface litter, root mat)	7797	110.0	3.46
Fuel oxidized or volatilized	-3898	-68.1	-2.25
Redistribution of remaining post-burn materials			
Aboveground necromass	3898	41.9	1.21
Belowground necromass	1551	23.2	0.98
Ash	78.0	3.8	1.62
Total losses from site	-9912	-123.9	-2.20
% Loss and redistribution			
Wood harvested ⁴	-47.5	-47.5	-47.5
Oxidation + volatilization loss from pre-burn fuel	-48.8	-58.4	-18.2
Pre-burn fuel converted to post-burn ash	1.0	3.5	47.0
Fuel remaining post-burn	49.9	38.1	34.9
Belowground biomass remaining as necromass	100	100	100

¹ Unpublished data M. Williams and D. Herbert. ² Nepstad (1989) and Trumbore et al. (1995). ³ Markewitz et al. (2002). ⁴ Harvested wood ~ 41%, 35%, and 28% of total biomass C, N and P respectively. Varies slightly in multiple harvests because of stand allometry effects on biomass distribution.

Sanchez 1986) and an assumed N:P = 20. Simulations allowed vegetation to accumulate to 13 T C ha⁻¹ (post-slash burn) prior to imposing grazing or crop harvests. Grazing/harvests were simulated for either 8 or 20 years, and then abandoned to secondary growth.

Re-accumulations of ecosystem C were modeled relative to redistribution, recycling, and re-supply rates of P and N following land-use conversion. Our analyses of the biogeochemical controls on secondary growth were restricted to a single limiting nutrient element, either P or N, with the assumption that supply rates of other nutrients were not limiting.

Table 2. Simulated C:N, C:P, and N:P ratios of dominant ecosystem pools, and N:P ratios characteristic to uptake processes at steady state. Element uptake ratios in vegetation differ from the vegetation element ratios because of differences in nutrient concentrations in tissues with rapid turnover rates (leaves and fine roots) and those with slow turnover rates (wood). An increase in nutrient content of post-burn slash relative to initial vegetation is a result of timber removal (wide C:nutrient ratios). Values for post-burn necromass are for the first harvest rotation.

Pool or flux	C:N	C:P	N:P
Vegetation	87.5	2654	30.3
Post-burn necromass	83.7	2499	29.9
Soil organic matter	11.4	184	16.2
Vegetation uptake			22.0
Microbial uptake			15.4

Table 3. Change in soil solution and labile N and P immediately after harvest and slash burn in simulations. Δ is a fractional change from the pre-disturbance forest reference. Differences after three harvests associated with active SOM depth are the result of feedbacks by SOM derived N and P on secondary growth and quantities of third-harvest slash. Solution and labile pools are defined in the model description.

Harvests	Active SOM depth (cm)	P limiting simulations				P occluding simulations			
		Solution (g m ⁻²)	Δ	Labile (g m ⁻²)	Δ	Solution (g m ⁻²)	Δ	Labile (g m ⁻²)	Δ
Forest	20–200	0.53	–	2.77	–	0.53	–	2.77	–
1	20–200	1.24	2.3	3.69	1.3	0.83	1.6	3.29	1.2
3	20	1.09	2.0	3.57	1.3	0.72	1.3	3.12	1.1
3	200	2.46	4.6	4.20	1.5	1.44	2.7	3.82	1.4
		N limiting simulations				N fixing simulations			
Forest	20–200	3.90	–	1.78	–	3.90	–	1.78	–
1	20–200	6.67	1.7	2.86	1.6	6.67	1.7	2.86	1.6
3	20	3.40	0.9	1.57	0.9	5.04	1.3	2.25	1.3
3	200	7.61	2	3.20	1.8	10.15	2.6	4.05	2.3

Sensitivity analyses

Sensitivity analyses were designed to assess the impact of N and P sources, sinks, and redistributions on vegetation re-growth and ecosystem C storage potential. These variations on the initial simulations account for N fixation, permanent occlusion of P made available during slash burns, and a restriction on the soil depth to which SOM is active. The maximum rate of N fixation allowed was ~ 5 g N m⁻² yr⁻¹, a value near the upper limit reported from a summary of tropical evergreen forests (Cleveland et al. 1999). N fixation in closed canopy forest was < 0.04 g N m⁻² yr⁻¹ reflecting resource optimization theory (light versus N limitation) as discussed in Rastetter et al. (2001). P occlusion assumed 50% loss of post-burn ash P resulting from irreversible transformations, transport to deeper soil horizons, or off site. The assumption limits the maximum quantity of P occluded (0.81

g m⁻² soil, see Table 1) by a 20 cm mineral soil profile (bulk density = 1.2 g cm⁻³, Nepstad (1989)) to 3.2 µg P g⁻¹ soil, a quantity easily realized in clay soils (Fox and Kamprath 1970; Bohn et al. 1985). Restrictions on SOM C, N, and P from a soil depth of 200 cm to 20 cm were based on SOM measured at Paragominas (Markewitz et al. (2002), also see Table 1). The rationale for a sensitivity analysis on active SOM depth is based on evidence that forest soils can be highly stratified with respect to microbial mediation of biogeochemical processes (Wood et al. 1984; Walbridge et al. 1991). The extent to which deep SOM P and N have been stabilized is unknown, as is the extent to which a change in land-use might destabilize deep or recalcitrant SOM.

Analysis of nutrient sources, redistribution, and carbon storage

The accumulation of C in a nutrient limited ecosystem is constrained by the characteristics of nutrient cycles (Shaver et al. 1992; McKane et al. 1997). Carbon storage will increase if: (1) ecosystem nutrient stocks increase, (2) C:nutrient ratios of ecosystem components increase or if (3) nutrients are redistributed from low C:nutrient components to high C:nutrient components (Schimel 1990; Shaver et al. 1992; Rastetter and Shaver 1992; McKane et al. 1995). We applied an analysis derived by Rastetter et al. (1992) designed to examine these three factors and their interactions. The contribution from the first factor is calculated as:

$$\Delta C_{\Delta C} = \Delta n q_{Ei} \quad (1)$$

$\Delta C_{\Delta n}$ is the change in C associated with a change in nutrients, Δn is the change in nutrients, q_{Ei} is the initial ecosystem C:nutrient ratio. The second factor is calculated as:

$$\Delta C q_B = B n_i \Delta q_B \quad (2)$$

$$\Delta C q_D = D n_i \Delta q_D$$

$\Delta C q_B$ and $\Delta C q_D$ are changes in C associated with changes in C:nutrient ratios of vegetation and SOM respectively, $B n_i$ and $D n_i$ are initial nutrient contents of vegetation and SOM, and Δq_B and Δq_D are the change in C:nutrient ratios of vegetation and SOM. The third factor is calculated as:

$$\Delta C_{redistribution} = (q_{Bi} - q_{Di})(\Delta B n D n_i - \Delta D n B n_i)/n_i \quad (3)$$

$\Delta C_{redistribution}$ is the change in C associated with nutrient redistribution between SOM and vegetation, $\Delta B n$ and $\Delta D n$ are the changes in vegetation and SOM nutrients, and n_i is the initial amount of nutrient in the ecosystem. Finally, the interaction among the factors is calculated as:

$$\Delta C_{interaction} = \Delta B n \Delta q_B + \Delta D n \Delta q_D \quad (4)$$

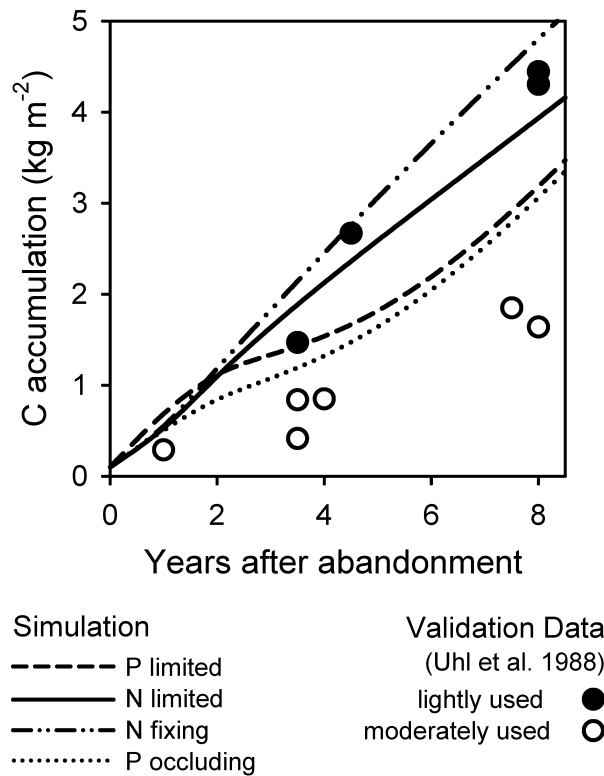


Figure 3. Validation of model parameters. Lines represent simulated vegetation re-growth after a single harvest and burn for N limited and P limited scenarios with 200 cm active SOM depth. Symbols represent secondary growth measured by Uhl et al. (1988) in abandoned pastures.

$\Delta C_{\text{interaction}}$ is the change in C associated with interaction of all three factors. The sum of equations (1)–(4) is the total change in ecosystem C.

Results and Discussion

Rates of vegetation re-growth (aboveground and belowground) in single harvest and slash burn simulations were comparable to those of empirically measured secondary vegetation growth (aboveground only) in abandoned cattle pastures near Paragominas (Figure 3). The sites had been identified as having a history of light to moderate use after conversion from forest (Uhl et al. 1988), and similar to the model ecosystem the sites were considered to be P limited (Buschbacher et al. 1988).

Early limitation by N and P on vegetation re-growth

Early re-growth of vegetation was characterized by a pattern in which N limited rates of C accumulation for one to five years after a slash-burn and P limited rates thereafter (Figure 4). An exception was evident in P occlusion simulations. The effect was a smaller P increase in post-burn soil solution relative to that observed in paired N simulations (Table 3). This difference, although small, was enough to shift limitation toward P, but only in the first harvest rotation. Otherwise post-burn solution P increases were characteristically large relative to N. The pattern suggests a relationship between initial changes in solution nutrient concentrations and which nutrient, N or P, is likely to control early vegetation re-growth rate. Furthermore, simulations illustrated that the manner in which N and P are lost from or redistribution within an ecosystem might control early differences in C accumulation.

Relative increases of N versus P in soil solution do not completely explain nutrient controls on initial rates of the vegetation re-growth. The strength of competing nutrient sinks must also be considered, illustrated here by fluxes of N and P into and out of the aggregate SOM pool via immobilization and mineralization processes (Figure 5). Mineralization and immobilization rates were influenced by additions of unburned slash and belowground necromass to the aggregate detritus-SOM pool. Wide C:nutrient ratios of necromass (Table 2) effectively diluted nutrient concentrations in detritus-SOM. Dilution created a nutrient sink, the result of microbial processes that increased N or P immobilization in the early stages of decomposition (Figure 5). In MEL model simulations the nutrient sink created by microbial immobilization is in direct and simultaneous competition with vegetation nutrient uptake.

The strength of detritus-SOM as a P sink versus N sink was dependent on the extent of nutrient dilution. Biogeochemically, it is useful to examine these paired simulations with respect to pool C:N:P, and particularly how N:P changed with additions of post-burn necromass. The change in N:P is a measure of dilution or enrichment of N relative to P after biomass removal, combustion, and redistribution. For example, residual unburned slash plus belowground necromass N:P is 29.9 but SOM N:P is 16.2 (Table 2). Clearly, necromass additions to detritus-SOM will dilute P more than N. The consequence is that initial necromass decomposition will immobilize more P than N and detritus-SOM will function as a simultaneous P sink and N source (Figure 5A and 5E). Increased immobilization of P relative to N was instrumental in promoting the early shift from N-limited to P-limited secondary vegetation growth, but within a few years a switch to net P mineralization from detritus-SOM (Figure 5) relaxed the P-limited phase and secondary growth became co-limited by N and P (Figure 4).

Multiple harvests affected both magnitude and duration of early nutrient limitation. Disproportionately large N losses relative to P losses were assumed in slash combustion so it is not surprising that after multiple harvests secondary growth was constrained more by N than by P (Figure 4A and 4C). Two additional constraints affected N limits on secondary growth. First, declines in pre-harvest biomass (Table 4) associated with site nutrient losses (Figure 6) led to decreased quantities of

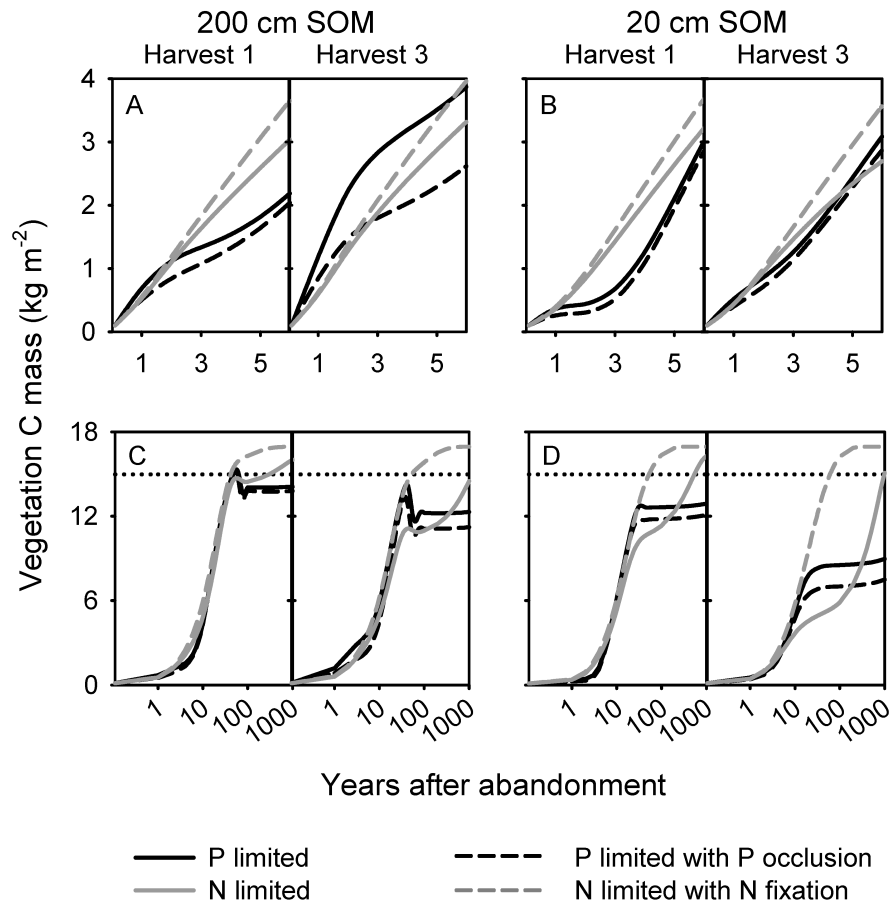


Figure 4. Re-accumulation of vegetation C in secondary growth. Panels on the left are 200 cm SOM simulations and panels on the right are 20 cm SOM simulations. The right half of each panel represents multiple harvests. Upper panels emphasize the first six years. Lower panels emphasize the longer trends. Declines in vegetation C after an initial peak are caused by feedbacks associated with quantity and quality of litter.

slash in later harvests. The result was smaller nutrient dilutions in detritus-SOM with each rotation. Because slash dilutes SOM P more than N (Table 2) smaller additions decreased sink strength more for P than N (Figure 5A). Second, relative increases in solution P were greater than increases in solution N (Table 3). The increase in solution nutrients after a single harvest was the direct result of post-burn ash deposits. While necromass decomposition in the first harvest initially immobilized nutrients, particularly P, the switch to net mineralization within three years increased the supply of available forms, especially P, prior to subsequent rotations (Figure 5).

Simulations limiting SOM elements to quantities in a 20 cm soil profile (Table 1) required a three-fold increase in turnover of detritus-SOM elements to meet steady

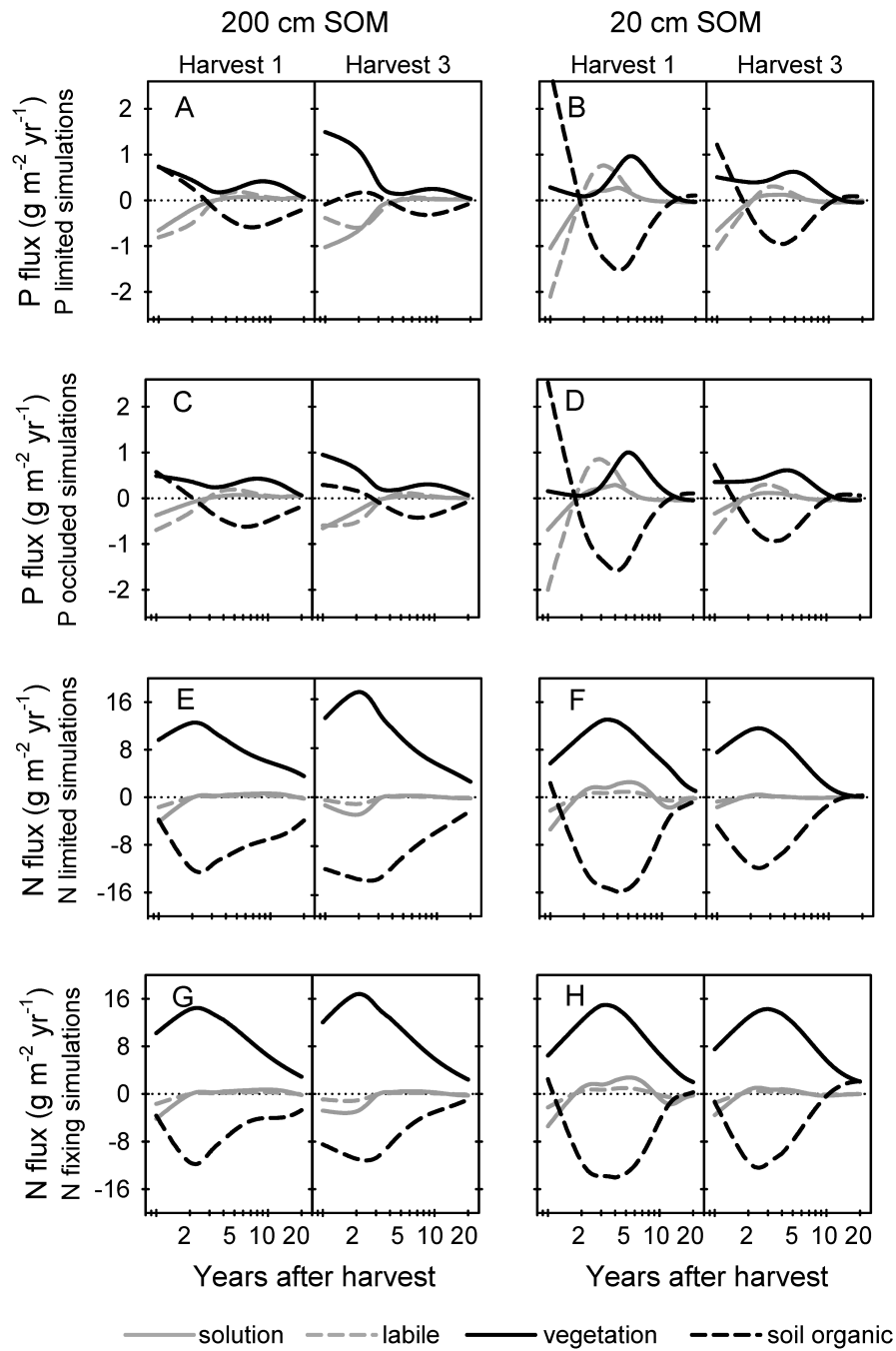


Figure 5. N and P fluxes into and out of soil solution, labile, and organic pools, and uptake by vegetation during re-growth. Plot lines above the zero-reference indicate fluxes into the represented pool (uptake or sink). Plot lines below the zero-reference indicate fluxes out of the represented pool (source). Panels on the left are 200 cm SOM simulations and panels on the right are 20 cm SOM simulations. The right half of each panel represents multiple harvests.

Table 4. Change in ecosystem C at 20 years after single and multiple harvests. Change (%) is relative to pre-disturbance C.

Harvests	Active SOM depth (cm)	P limiting simulations			P occluding simulations		
		% change in C storage			% change in C storage		
		SOM	vegetation	ecosystem	SOM	vegetation	ecosystem
1	200	-17.4	-33.9	-25.5	-18.2	-34.5	-26.3
1	20	-16.7	-28.2	-25.4	-17.8	-30.6	-18.8
3	200	-18.6	-29.5	-24.0	-21.7	-36.3	-28.9
3	20	-24.7	-47.9	-42.3	-29.3	-57.0	-27.8
		N limiting simulations			N fixing simulations		
1	200	-18.8	-38.4	-28.5	-15.4	-30.3	-22.8
1	20	-24.7	-40.9	-37.0	-19.7	-30.5	-27.9
3	200	-27.8	-43.6	-35.6	-21.4	-30.2	-25.7
3	20	-42.5	-69.6	-63.1	-24.6	-36.2	-33.5

state vegetation N and P requirements. Limited element stocks and increased SOM dynamics resulted in early onset of secondary growth nutrient limitation, especially for P (Figure 4). Two characteristics of these simulations influenced the earlier onset of P limitation. First, necromass additions (wide N:P) had a larger nutrient dilution effect on the smaller pre-disturbance SOM stocks (narrow N:P), which magnified the effect of P immobilization in the detritus-SOM pool. Consequently, the impact of residual necromass on P immobilization increased the strength of the P sink (Figure 5B). Second, large annual fluxes of P per unit SOM into solution via mineralization, associated with high SOM turnover, accelerated the depletion of SOM P.

Multiple harvests on the 20 cm soil profile produced smaller nutrient losses than on the unrestricted 200 cm profile (Figure 6). However, losses represented a greater proportion of total ecosystem nutrients. This proportionately large loss combined with the initially smaller pool of organic nutrients available for mineralization led to declines in vegetation C storage even when N fixation contributed to N inputs (Table 4), and feedbacks on SOM C via NPP led to larger declines in ecosystem C storage relative to simulations with 200 cm of SOM.

Long-term limitation by N and P on vegetation re-growth

Over time scales of 50 to 100 years and in the absence of symbiotic N fixation, N was generally as limiting or more limiting than P to secondary growth (Figure 4C and 4D). Longer-term limitation by N was a consequence of the magnitude of N losses relative to P losses during each harvest rotation (Table 1). Multiple harvest produced declines in total ecosystem N greater than 20%, approaching 50% when active SOM was restricted by soil depth (Figure 6). Moderate rates of symbiotic N fixation shifted secondary vegetation growth toward P limitation.

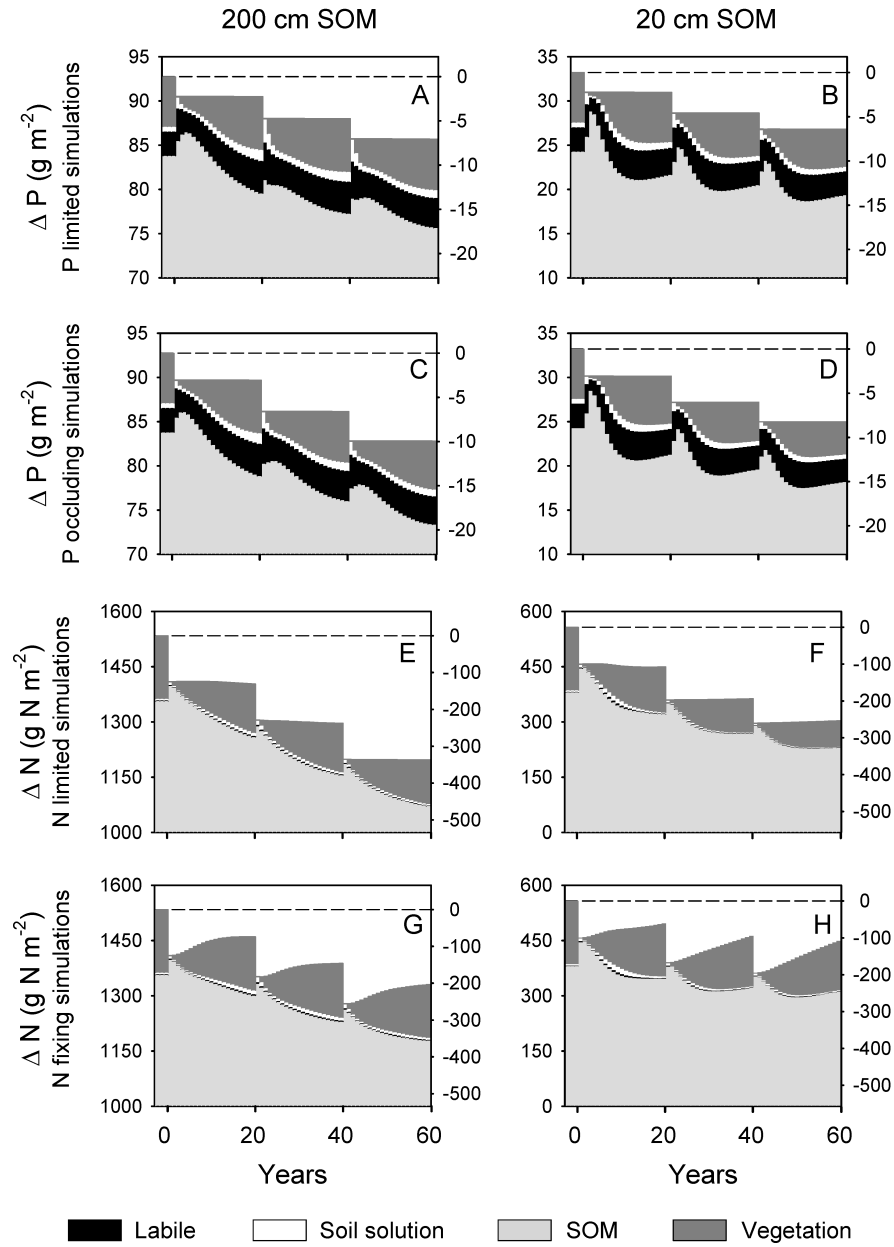


Figure 6. Redistribution and loss of ecosystem N and P. Bars before year 0 indicate N and P quantities and distributions in the pre-disturbance forest. Years 0, 20, and 40 are harvest years. Left Y axis labels represent quantities in the ecosystem. Right Y axis labels represent losses from the ecosystem. Organization of panels as in Figure 5.

On time scales approaching 1000 years N deposition was sufficient for vegetation C to re-accumulate to pre-disturbance levels. Deposition was negligible toward replacement of P, and vegetation C accumulation required longer time-scales.

In summary, secondary vegetation growth was characterized by an early N-limited phase, magnified by increased exports with multiple disturbances, but shortened in duration by moderate rates of symbiotic N fixation. The N-limited phase was followed by a P-limited phase, the result of net P immobilization in the detritus-SOM pool. This early P-limited phase was relieved by a shift from net immobilization to net mineralization of P when N:P of decomposing necromass had narrowed sufficiently. Long-term P limitation was the consequence of disturbance-caused P exports, the replacement of which requires thousands of years in the absence of a primary mineral P source.

Nutrient sources, redistribution, and carbon storage

In all simulations the aggregate detritus-SOM pool was identified as the most important source of nutrients supporting re-accumulations of ecosystem C during the first 100 years (Figure 7). Redistributions of N and P from SOM with narrow C:nutrient to vegetation with comparably wide C:nutrient allowed gains in ecosystem C. The cost was a depletion of SOM nutrients (Figure 6), which can lead to declines in ecosystem resilience, especially after multiple disturbances (Table 5). However, even after multiple disturbances redistributions of nutrients from SOM to vegetation remained critical to ecosystem C re-accumulation (Figure 7). Notably, narrow N:P of SOM relative to vegetation (Table 2) meant that SOM could play a larger role as a nutrient source in P-limited simulations relative to N-limited simulations.

By comparison with the importance of SOM as a nutrient source, and in the absence of N fixation, C accumulations associated with new input of either N or P were minimal. Small C accumulations that appear to be associated with new P input largely reflects movement of P out of labile pools as solution P declines (Figure 7A and 7B). This effect was magnified when active SOM was restricted by depth. However, the contribution to C accumulation was all but eliminated when P occlusion limited redistribution from post-burn ash to soil solution and labile pools (Figure 7C and 7D).

Long-term changes in ecosystem carbon storage

In the absence of symbiotic N fixation, simulations assume that the only source of nutrient input to the ecosystem is by deposition (Appendix 2). Consequently, centennial to millennial time scales will be required for re-accumulation and re-entrainment of nutrients after any substantive loss. Accordingly, simulations indicate that 100 years after abandonment to secondary growth there remains a reduction in ecosystem C storage capacity approaching 25% when systems were subjected to multiple harvests (Table 5). This reduction in C storage capacity can exceed 50% if mineralization of N or P from SOM is restricted by soil depth. By comparison,

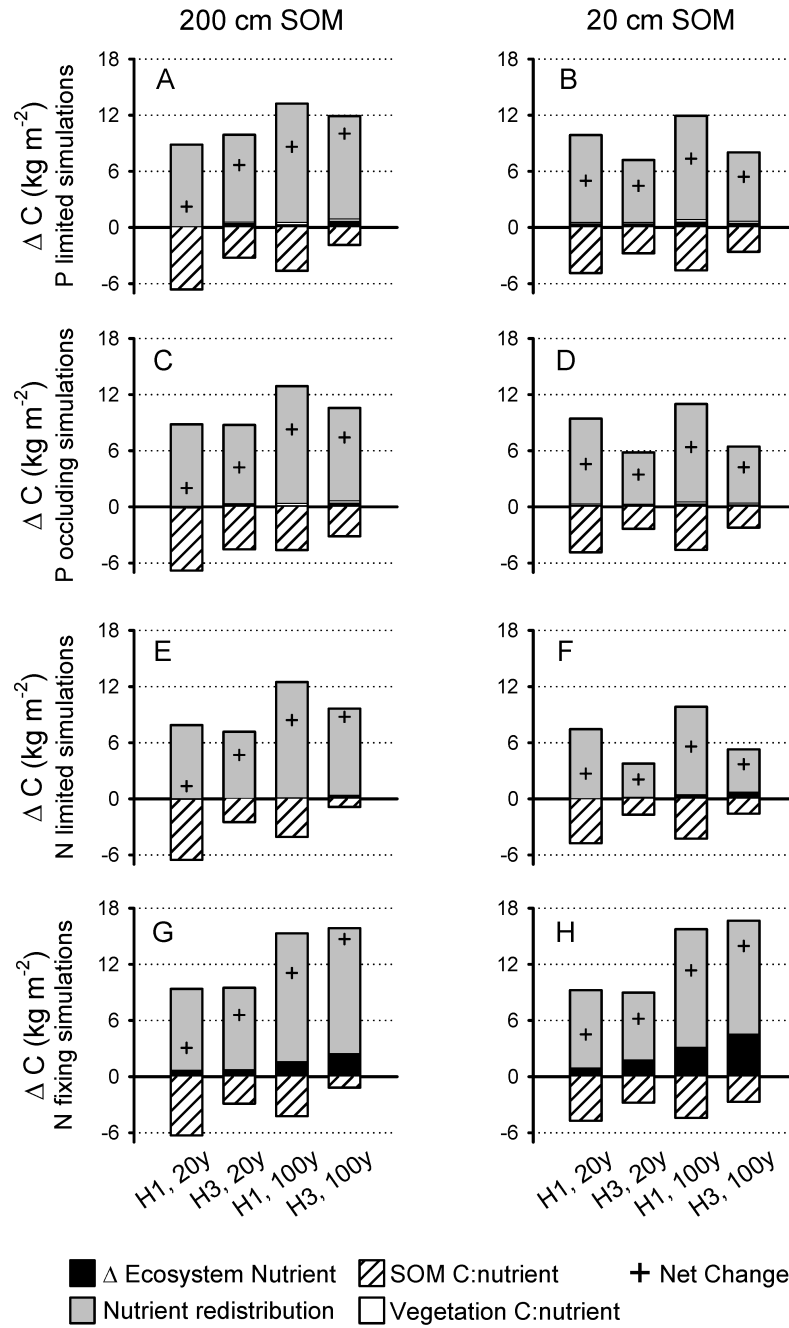


Figure 7. Changes in ecosystem C storage (ΔC) during vegetation re-growth. Carbon gains and losses are partitioned by nutrient source and redistribution within the ecosystem at 20 years (20 y) and 100 years (100 y) after one harvest (H1) and after three harvests (H3). Bars stacked above the x-axis represent C gains, bars stacked below the x-axis represent C losses, and + is the net change. Component definitions and calculations are detailed in methods. Interactions were dominated by nutrient redistribution and are not plotted. Organization of panels as in Figure 5.

Table 5. Long-term changes (100 years) in ecosystem C. Change (%) is relative to C distribution in the pre-disturbance forest. Net C gains in N fixing simulations were caused by removal of P limitation from the model system initially parameterized with an assumption of P limitation.

harvests	active SOM depth (cm)	P limiting simulations			P occluding simulations		
		% change in C storage			% change in C storage		
		SOM	vegetation	ecosystem	SOM	vegetation	ecosystem
1	200	-2.9	-6.2	-4.5	-3.7	-7.7	-5.7
1	20	-6.5	-15.4	-13.3	-8.9	-21.0	-18.1
3	200	-7.8	-18.3	-13.0	-11.7	-25.9	-18.4
3	20	-19.2	-42.8	-37.1	-24.7	-52.9	-46.1
		N limiting simulations			N fixing simulations		
1	200	-6.9	-3.5	-5.2	-1.5	8.8	3.6
1	20	-16.3	-24.3	-22.4	-0.5	9.2	6.9
3	200	-17.7	-26.7	-22.1	-3.7	5.7	0.9
3	20	-35.7	-60.8	-54.8	-1.0	8.3	6.1

simulations with symbiotic N fixation as an additional N source accumulated C to pre-disturbance levels (with small SOM reductions) within 100 years (Table 5). However, the rate of N fixation can be limited by other elements (Eisle et al. 1989; Chapin et al. 1991; Smith 1992). A depleted P supply would likely affect N fixation rate during P-limited phases, and this was not considered in simulations.

Grazing and cropping effects

Grazing and cropping analyses were restricted to N limited - N fixing, and non-occluded P limited scenarios. Grazing for 8 to 20 years produced only small additional P losses after the initial wood harvest and slash-burn losses (Figure 8A), and losses depleted ecosystem C storage capacity by $\sim 5\%$ in the long term. However, the small additional loss of P is important when soil depth for SOM activity is restricted. This restriction on organic P stocks available for mineralization led to long-term reductions in ecosystem C storage that could exceed 20%, depending on grazing duration (Figure 8B). Increased rates of P export in crop simulations produced further long-term P losses and a decline in C storage capacity approaching 40% (Figure 8C and 8D). Overall N losses did not exceed the initial land-use conversion losses because of additions via symbiotic fixation and deposition (Figure 8E–H). Additions were adequate to restore N stocks within 100 years. C stocks generally returned to pre-disturbance levels within 50 years because of N redistribution from SOM, exceeding pre-disturbance C stocks within 100 years because of new N additions and the lack of P as a secondarily limiting element.

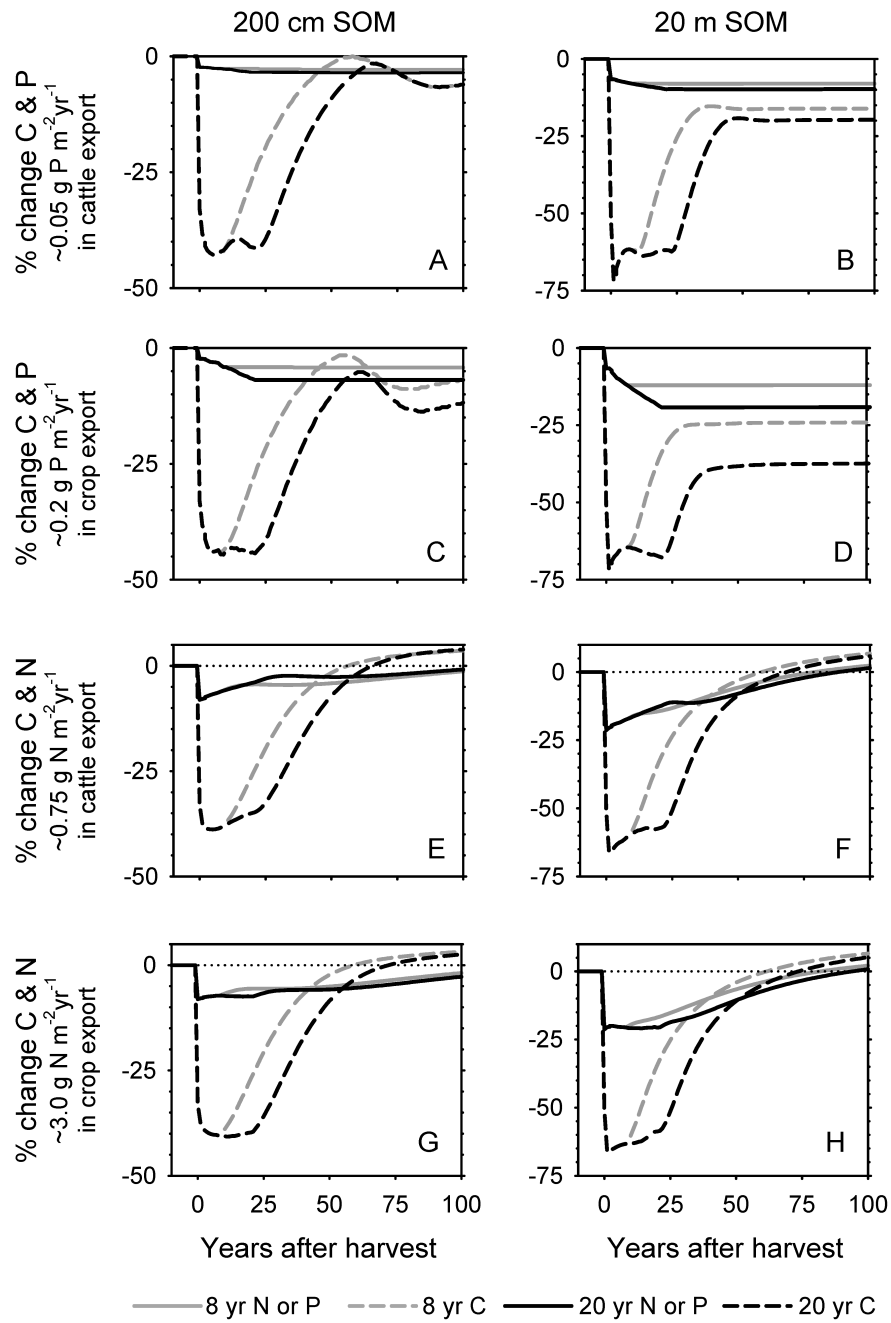


Figure 8. Changes in ecosystem C, N, and P after forest conversion and 8 and 20 years of cattle grazing or crop production. P-limited simulations (A through D) export $\sim 0.05 \text{ g P m}^{-2} \text{ yr}^{-1}$ in A and B, and $\sim 0.2 \text{ g P m}^{-2} \text{ yr}^{-1}$ in C and D. N-limited simulations (E through H) include the N fixation assumption and export $\sim 0.75 \text{ g N m}^{-2} \text{ yr}^{-1}$ in E and F, and $\sim 3 \text{ g N m}^{-2} \text{ yr}^{-1}$ in G and H. Panels on the left are 200 cm SOM simulations and panels on the right are 20 cm SOM simulations.

Conclusions

Carbon storage and accumulation processes are P-limited in the site studied. We hypothesize that disturbance-caused ecosystem N losses, which are large relative to P losses, will push C storage and accumulation toward N limitation. The duration of this N-limited phase depends on rates of new N input and re-entrainment within the ecosystem cycle. In the short term, biological N-fixation is likely an important mechanism in post-disturbance resilience because N deposition alone is not sufficient to compensate for disturbance-caused N losses. On longer time scales the site must revert to P-limitation because substantial external P sources are absent and small disturbance-caused ecosystem P losses ($2\text{--}3\text{ g m}^{-2}$) can reduce C storage potential on millennial time-scales.

Simulations suggest that N and P stored in SOM over millennial time-scales, can buffer disturbance-caused nutrient losses. The mechanism may impart resilience in C storage capacity through redistributions of N and P from narrow C:nutrient SOM to wide C:nutrient vegetation. Wide vegetation N:P relative to SOM N:P suggests that nutrient redistributions could effectively diminish post-disturbance P limitation. However, N and P mineralization rates from deeply buried SOM are generally unknown, as is uptake from this pool by vegetation. Microbial mediation of soil biogeochemical processes can be highly stratified, associated with plant root distributions (Wood et al. 1984; Walbridge et al. 1991). Relationships between concentrations of labile C from plant root exudates and microbial extra-cellular phosphatases indicate acute stratification of SOM P transformations (McGill and Cole 1981; Lee et al. 1990). Nonetheless, there is little data to support assumptions on activity or stability of deeply buried SOM. Sensitivity analyses illustrate that empirical investigations into SOM activity throughout soil profiles will improve confidence in knowledge of nutrient controls on C accumulation in secondary forest growth.

The mechanism most frequently cited as an explanation for P-limited productivity on old tropical soils is occlusion of biologically available inorganic P by iron and aluminum oxides (Uehara and Gillman 1981; Herbert and Fownes 1995). In our model, occluded P is permanently lost from the ecosystem. Therefore, in our sensitivity analyses with P occlusion, we predict low resilience in ecosystem C storage capacity. However, studies on forest-to-pasture conversion in Brazil indicate declines in occluded P fractions and increases in organic P fractions, suggesting redistribution of P from occluded to organic fractions after land-use conversions (Garcia-Montiel et al. 2000; Townsend et al. 2002). The mechanism for this redistribution remains poorly understood. Because of aggrading secondary vegetation in our model analyses, we predict a similar P redistribution, but with the redistribution being from SOM to vegetation.

The following mechanisms may explain differences between empirical and model analyses. (1) In the forest-to-pasture conversion studies changes in soil profiles below 10 cm were not measured and may contribute to changes in the upper 10 cm. (2) Conversion from high biomass forest to low biomass pasture results in smaller quantities of P and N bound in vegetation, and associated changes from

slow to rapid turnover biomass with vegetation type may explain increased SOM in the upper soil profile (Townsend et al. 2002; Herbert et al. 1999). (3) Occluded P fractions may not be permanently lost from the ecosystem (Garcia-Montiel et al. 2000).

We rely on assessments of potentially available nutrient stocks and new inputs to understand post-disturbance resilience of ecosystem functions such as C accumulation and storage or the viability of alternate land-use such as timber extraction and agriculture. Model simulations illustrate the importance of nutrients stored in SOM given generally small aerosol deposition rates. SOM is particularly important as a source of P for which there is no biological vector to the ecosystem. Future empirical research should focus on the stability and activity of deeply buried SOM and its role as a source of nutrients to aggrading vegetation.

Acknowledgements

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Appendix 1

Table A1. Model equations, variables, and parameters with notation for the nitrogen cycle.

(1)	$\frac{dE_N}{dt}=R_{Ne}+R_{Nm}-L_{Ne}-U_{Nm}-U_{Nv}$		
(2)	$\frac{dB_C}{dt}=U_{Cv}-R_{Cv}-L_{Cv}$	(3)	$\frac{dB_N}{dt}=U_{Nv}-L_{Nv}$
(4)	$\frac{dD_C}{dt}=L_{Cv}-R_{Cm}$	(5)	$\frac{dD_N}{dt}=L_{Nv}+U_{Nm}-R_{Nm}$
(6)	$\frac{dV_C}{dt}=-aV_C \quad : \quad \text{if } A>0 = -aV_N \quad : \quad \text{if } A<0$	(7)	$\frac{dV_N}{dt}=-\frac{dV_C}{dt}$
(8)	$B_A=\frac{B_{Amax}cB_C}{B_{Amax}+cB_C}$	(9)	$q=\frac{B_Cq_{\min}q_{\max}}{B_Aq_{\max}+(B_C-B_A)q_{\min}}$
(10)	$S_L=b_LV_CB_A$	(11)	$S_R=b_RV_NB_A$
(12)	$G_C=\frac{g_CE_C}{(k_C+E_C)}$	(13)	$G_N=\frac{g_NE_N}{(k_N+E_N)}$
(14)	$U_{Cv}=G_CI_0(1-e^{-k_S L_C})$	(15)	$U_{Nv}=G_N(1-e^{-k^S_N S_R})$
(16)	$r_{Nup}=\frac{G_Cb_Lk_I}{G_Nb_Rk^S_N}e^{k^S_N S_R-k^S_N L_C}$	(17)	$U_{Nfix}=\frac{g_{Nfix}S_R(r_{Nup}-r_{Nfix})}{k_{Nfix}+(r_{Nup}-r_{Nfix})};\text{if } r_{Nup}>r_{Nfix}=0;\text{otherwise}$

Table A1. Continued

(18)	$L_{Cv} = m_A B_A + m_W (B_C - B_A)$	(19)	$L_{Nv} = \frac{qB_N}{B_C} \left[\frac{m_A}{q_A} B_A + \frac{m_W}{q_W} (B_C - B_A) \right]$
(20)	$R_{Cv} = r_A B_A + r_W (B_C - B_A)$	(21)	$A = \ln \left(\frac{B_C}{qB_N} \right) + h \left(\frac{1}{B_C} \frac{dB_C}{dt} - \frac{1}{B_N} \frac{dB_N}{dt} \right)$
(22)	$L_{Ne} = \beta_{Ne} F_S$	(23)	$E_N = E_S + E_L$
(24)	$E_L = \frac{E_{MAX} \beta_{E0} E_S}{E_{MAX} + \beta_{E0} E_S}$	(25)	$\theta = \frac{\epsilon_N \phi}{\epsilon_C}$
(26)	$U_{Nm} = \frac{\psi \alpha_N D_C^2 E_N}{\theta D_N (\kappa_{Nm} + E_N)}$	(27)	$M_N = \psi D_N + U_{Nm}$
(28)	$\Lambda_C = \frac{\epsilon_C \theta M_N}{\psi D_C + \theta M_N}$	(29)	$\Lambda_N = \frac{\epsilon_N \psi D_C}{\psi D_C + \theta M_N}$
(30)	$R_{Cm} = \psi D_C (1 - \Lambda_C)$	(31)	$R_{Nm} = M_N (1 - \Lambda_N)$
A	acclimation potential	q_{max}	maximum plant C:N (g g ⁻¹)
a	acclimation rate (yr ⁻¹)	q_{min}	minimum plant C:N (g g ⁻¹)
B_A	active-tissue C in plants (g m ⁻²)	q_W	woody-tissue litter C:N (g g ⁻¹)
B_{Amax}	maximum B_A (g C m ⁻²)	r_A	active-tissue respiration rate (yr ⁻¹)
B_C	C in plant biomass (g m ⁻²)	R_{Cm}	microbial respiration (g C m ⁻² yr ⁻¹)
b_L	leaf area per unit C (m ² g ⁻¹)	R_{Cv}	plant respiration (g C m ⁻² yr ⁻¹)
B_N	N in plant biomass (g m ⁻²)	R_{Ne}	external N supply (g m ⁻² yr ⁻¹)
b_R	root length per unit C (m g ⁻¹)	R_{Nm}	N mineralization (g m ⁻² yr ⁻¹)
c	allometric parameter	r_{Nfix}	cost of N fixation (g C g ⁻¹ N)

Table A1. Continued

D_C	C in soil detritus (g m^{-2})	r_{Nup}	cost of N uptake ($\text{g C g}^{-1} \text{N}$)
D_N	N in soil detritus (g m^{-2})	r_w	woody-tissue respiration rate (yr^{-1})
E_C	CO_2 concentration (ml m^{-3})	S_L	leaf area ($\text{m}^2 \text{m}^{-2}$)
E_{MAX}	soil adsorption capacity for N (g m^{-2})	S_R	root length (m m^{-2})
E_S	soil solution inorganic N (g m^{-2})	t	time (yr)
E_L	soil labile inorganic N (g m^{-2})	U_{Cv}	gross photosynthesis ($\text{g C m}^{-2} \text{yr}^{-1}$)
g_C	canopy-level quantum yield (g C GJ^{-1})	U_{Nm}	microbial N uptake ($\text{g m}^{-2} \text{yr}^{-1}$)
G_C	substrate-corrected g_C ($\text{g C m}^{-2} \text{yr}^{-1}$)	U_{Nv}	plant N uptake ($\text{g m}^{-2} \text{yr}^{-1}$)
g_N	maximum plant N uptake ($\text{g m}^{-2} \text{yr}^{-1}$)	V_C	plant C uptake effort
G_N	substrate-corrected g_N ($\text{g N m}^{-2} \text{yr}^{-1}$)	V_N	plant N uptake effort
g_{Nfix}	N fixation constant ($\text{g}^2 \text{N g}^{-1} \text{C m}^{-2} \text{yr}^{-1}$)	α_N	microbial N uptake ($\text{g g}^{-1} \text{C}$)
h	acclimation damping (yr)	β_{CD}	organic C loss (yr^{-1})
I_0	above-canopy irradiance ($\text{GJ m}^{-2} \text{yr}^{-1}$)	β_{EO}	initial slope of soil inorganic N adsorption isotherm
k_C	$1/2$ -saturation for CO_2 (ml m^{-3})	β_{Ne}	inorganic N loss ($\text{g}^1 - \gamma \text{ m}^{-2} + 2 \gamma \text{ yr}^{-1}$)
k_I	light extinction ($\text{m}^2 \text{m}^{-2}$)	γ	inorganic N loss exponent
k_N	plant $1/2$ -saturation for N (g m^{-2})	ϵ_C	maximum microbial C efficiency
k_S	soil resource extinction ($\text{m}^2 \text{m}^{-1}$)	ϵ_N	maximum microbial N efficiency
L_{CD}	organic C leaching ($\text{g m}^{-2} \text{yr}^{-1}$)	η	leached organic C:N (g g^{-1})
L_{Cv}	litter C loss ($\text{g m}^{-2} \text{yr}^{-1}$)	θ	C:N microbial consumption (g g^{-1})
L_{ND}	organic N leaching ($\text{g m}^{-2} \text{yr}^{-1}$)	κ_{Nm}	microbial N $1/2$ -saturation (g m^{-2})
L_{Ne}	inorganic N leaching ($\text{g m}^{-2} \text{yr}^{-1}$)	Λ_C	microbial C efficiency
L_{Nv}	litter N loss ($\text{g m}^{-2} \text{yr}^{-1}$)	Λ_N	microbial N efficiency
m_A	active-tissue litter loss rate (yr^{-1})	M_N	microbial N consumption ($\text{g m}^{-2} \text{yr}^{-1}$)
m_W	woody-tissue litter loss rate (yr^{-1})	ϕ	C:N microbial byproducts (g g^{-1})
q	plant optimal C:N (g g^{-1})	ψ	decomposition rate (yr^{-1})
q_A	active-tissues litter C:N (g g^{-1})		

Appendix 2

Table A2. Assumed steady-state conditions for an old-growth eastern Amazonian forest

Variables	Value	Reference
B_C	14971	Nepstad (1989) and Jipp et al. (1998)
B_N	171	Leaf C:N = 26, C:P = 416 (M. Williams and D. Herbert unpublished data) assuming 22.3% N resorbed (Smith et al. 1998) and 70% P resorbed (Herbert and Fownes 1999) during senescence. Fine root C:N = 22.0 (Trumbore et al. 1995). Fine root N:P assumed same as leaf N:P = 16. Wood C:N = 102, wood N:P = 38 (Markewitz et al. 2002).
B_P	5.64	
D_C	15410	Values for upper 200 cm soil (Markewitz et al. 2002).
D_N	1357	
D_P	83.79	
E_{S-N}	3.9023	
E_{S-P}	0.5325	
E_{L-N}	1.7781	Assumed large N adsorption capacity ($N_{MAX} = 20$, $\beta_{EO-N} = 0.5$)
E_{L-P}	2.7733	Fitted to data from Garcia-Montiel et al. (2000) ($P_{MAX} = 4.9$, $\beta_{EO-P} = 12$)
E_C	350	Approximate 1990 atmospheric CO ₂ , Keeling and Whorf (1994).
V_C	0.5	Assumption that uptake effort is approximately equally divided between light interception and nutrient acquisition in the mature forest.
V_N	0.5	
V_P	0.5	
B_A	752	Nepstad (1989) and Trumbore et al. (1995)
U_{Cv}	2437	Assumed 2.21 times L_{Cv}
R_{Cv}	1329	$U_{Cv} - L_{Cv}$, steady-state assumption.
L_{Cv}	1108	Annual production: leaves = 293 g m ⁻² , twigs = 108 g m ⁻² , misc = 77 g m ⁻² (Markewitz et al. 2002). Fine root mass = 381 g m ⁻² (Nepstad 1989) 100% turnover of roots annually (Trumbore et al. 1995). Assumed 55 year turnover time for bole wood and coarse roots.
U_{Nv}	31.87	L_{Nv} steady-state assumption
U_{Pv}	1.447	L_{Pv} steady-state assumption
L_{Nv}	31.87	Leaf and misc litterfall N = 11.06, P = 0.273 (Markewitz et al. 2002). Fine root litter N = 17.32, P = 1.082 assuming no resorption. Wood, coarse root, and twig litter N = 3.49, P = 0.092 assuming no resorption.
L_{Pv}	1.447	
q_N	87.6	B_C/B_N steady-state assumption
q_P	2654	B_C/B_P steady-state assumption
R_{Ne}	0.56	Annual deposition (Bruijnzeel 1991; Williams et al. 1997).
R_{Pe}	0.0036	
L_{Ne}	0.56	R_{Ne} steady-state assumption
L_{Pe}	0.0036	R_{Pe} steady-state assumption
R_{Cm}	1108	L_{Cv} steady-state assumption
U_{Nfix}	< 0.04	symbiotic N fixation assumed near 0 in mature forest (Rastetter et al. 2001)
U_{Nm}	111.6	$\sim 3.5 * U_{Nv}$ = ratio of microbial to plant uptake (Nadelhoffer et al. 1999)
U_{Pm}	7.267	ϕ_N : ϕ_P assumption from Appendix 3 (Brady 1974; Hunt et al. 1991)
R_{Nm}	144.1	$U_{Nm} + U_{Nv}$ steady-state assumption
R_{Pm}	8.714	$U_{Pm} + U_{Pv}$ steady-state assumption

Appendix 3

Table A3. Parameter estimates for an old-growth eastern Amazonian forest

Parameter	Value	Reference
a	1	sets acclimation time to ~ 1 yr (Rastetter et al. 1997)
B_{Amax}	836	from Eq.8 with c and steady-state values for B_C and B_N
b_L	0.02	1/50 g C m ⁻² leaf
b_R	40	40 m g ⁻¹ C (Jackson et al. 1997)
c	0.5	Calibrated (see Rastetter et al. (2001))
g_C	134.55	from Eqs. 10, 12, and 14
g_N	6.089	from Eqs. 11, 13, and 15
g_P	4.538	
g_{Nfix}	3×10^{-6}	Sets peak N fixation rate ~ 5 g N m ⁻² yr ⁻¹ (Cleveland et al. 1999)
h	3	Sufficient to dampen oscillations in acclimation (Rastetter et al. 1997)
k_C	355	Sets GPP increase to 33% with $2 \times CO_2$ (McMurtrie and Wang 1993)
k_I	0.5	(Jarvis and Leverenz 1983)
k_N	0.8	$= 0.015 \text{ mol m}^{-3} \times 0.346 \text{ m H}_2\text{O} \times 14 \text{ g N mol}^{-1} \times (1 + \text{soil buffer slope})$, buffer slope ~ 10 (Williams and Yanai 1996)
k_P	10.74	$= 0.005 \text{ mol m}^{-3} \times 0.346 \text{ m H}_2\text{O} \times 31 \text{ g P mol}^{-1} \times (1 + \text{soil buffer slope})$, buffer slope ~ 200 (Williams and Yanai 1996)
k_S	1.6×10^{-4}	Cross sectional area of root influence / soil depth (2 m), assumes radius of root influence = 10 mm (Williams and Yanai 1996)
m_A	1	Assumes 1 year turnover for leaves (M. Williams pers. comm) and fine roots (Trumbore et al. 1995)
m_W	0.025	Assumes 40 turnover for wood
q_{AN}	26.5	Leaf litter C:N = 33.4 and C:P = 1356 (Markewitz et al. 2002; Smith et al. 1998). Fine root litter C:N = 22 (Trumbore et al. 1995). Assumes fine root N:P = 16 (Redfield 1958) and no N or P resorption.
q_{AP}	554.8	
q_{WN}	102	Markewitz et al. (2002)
q_{WP}	3876	
r_A	1.295	Assumption that $GPP = 2.2 \times NPP$ and wood respiration \sim wood NPP
r_W	0.025	
r_{Nfix}	9.12	12 glucose direct cost + 10.8 glucose construction and maintenance cost $\times 0.4$ g C g ⁻¹ glucose (Gutschick 1981)
α_N	0.0756	Solve equations 24, 27, and 29 simultaneously
α_P	0.0032	
β_{Ne}	0.1435	L_{Ne}/E_N , steady-state assumption
β_{Pe}	0.0068	L_{Pe}/E_P , steady-state assumption
ϵ_C	0.6	Hunt et al. (1991)
ϵ_N	0.8714	Solve equations 24, 27, and 29 simultaneously.
ϵ_P	0.8714	Assumption that $\epsilon_P = \epsilon_N$
κ_{Nm}	3.456	N uptake half saturation constant of 714 $\mu\text{M L}^{-1}$ (Hunt et al. 1991)
κ_{Pm}	0.097	Based on E. coli P uptake half saturation constant of 9.025 $\mu\text{M L}^{-1}$ (Mitchell and Chamberlin 1978)
ϕ_N	6	\sim microbial + fungal C:N and C:P ratios (Brady 1974; Hunt et al. 1991)
ϕ_P	86.9	
ψ	0.0148	Solve equations 24, 27, and 29 simultaneously

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