

Effects of global change on carbon storage in tropical forests of South America

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Abstract. We used a process-based model of ecosystem biogeochemistry (MBL-GEM) to evaluate the effects of global change on carbon (C) storage in mature tropical forest ecosystems in the Amazon Basin of Brazil. We first derived a single parameterization of the model that was consistent with all the C stock and turnover data from three intensively studied sites within the Amazon Basin that differed in temperature, rainfall, and cloudiness. The range in temperature, soil moisture, and photosynthetically active radiation (PAR) among these sites is about as large as the anticipated changes in these variables in the tropics under CO₂-induced climate change. We then tested the parameterized model by predicting C stocks along a 2400-km transect in the Amazon Basin. Comparison of predicted and measured vegetation and soil C stocks along this transect suggests that the model provides a reasonable approximation of how climatic and hydrologic factors regulate present-day C stocks within the Amazon Basin. Finally, we used the model to predict and analyze changes in ecosystem C stocks under projected changes in atmospheric CO₂ and climate. The central hypothesis of this exercise is that changes in ecosystem C storage in response to climate and CO₂ will interact strongly with changes in other element cycles, particularly the nitrogen (N) and phosphorus (P) cycles. We conclude that C storage will increase in Amazonian forests as a result of (1) redistribution of nutrients from soil (with low C:nutrient ratios) to vegetation (with high C:nutrient ratios), (2) increases in the C:nutrient ratio of vegetation and soil, and (3) increased sequestration of external nutrient inputs by the ecosystem. Our analyses suggest that C:nutrient interactions will constrain increases in C storage to a maximum of 63 Mg/ha during the next 200 years, or about 16% above present-day stocks. However, it is impossible to predict how much smaller the actual increase in C storage will be until more is known about the controls on soil P availability. On the basis of these analyses, we identify several topics for further research in the moist tropics that must be addressed to resolve these uncertainties.

Introduction

Tropical forests occupy ~2200 x 10⁶ ha or ~17% of the terrestrial biosphere [Melillo *et al.*, 1993] and are among the most important terrestrial ecosystems in the global C budget. About 20 to 25% of the estimated 2300 Pg (10¹⁵ g) of C in

terrestrial vegetation and soils is in tropical forests [Brown and Lugo, 1982; Schlesinger, 1991; Dixon *et al.*, 1994]. In their undisturbed state these forests account for a disproportionate ~40% of the total exchange of CO₂ between the terrestrial biosphere and the atmosphere [Melillo *et al.*, 1993]. Because of their large C reserves and their high rate of metabolism, tropical forests exert a major influence on the C balance of the atmosphere.

Despite their importance to the global C cycle, the responses of tropical forests to global warming have received relatively little attention. While projected temperature changes for the tropics are small (2° to 4°C) relative to mid- and high-latitude regions (2° to 10°C) [Mitchell *et al.*, 1990], tropical ecosystems

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may be particularly sensitive to small changes in temperature because the rates of many metabolic processes increase exponentially as temperature increases. Therefore small absolute temperature changes can have large proportional effects on metabolic rates at high temperatures. As a result, tropical ecosystems may dominate early responses of the biosphere to global warming [Townsend *et al.*, 1992]. In addition to responses to changing temperature, tropical forests may also have important responses to changes in cloudiness [Melillo *et al.*, 1993], soil moisture [Raich *et al.*, 1991], and atmospheric CO₂ [Körner and Arnone, 1992]. All of these factors are likely to change in tropical regions [Hansen *et al.*, 1981] and, as a result, tropical forests may play an increasingly important role in the interaction between the biosphere and global climate.

In this paper we use the Marine Biological Laboratory's General Ecosystem Model (MBL-GEM) [Rastetter *et al.*, 1991] to analyze potential changes in C storage of the forested part of the Amazon Basin during the next 200 years in response to predicted changes in atmospheric CO₂ and climate. Our analysis is based on MBL-GEM calibrated to soil and vegetation data for several sites along a 2400-km transect through the Amazon Basin. The climatic regimes along this transect [Raich *et al.*, 1991] differ by as much as the changes predicted for the Amazon Basin during the next 100 years [Hansen *et al.*, 1981; Hansen *et al.*, 1984] and therefore provide a useful means of constraining the model. We restrict our analysis to mature tropical forest ecosystems and do not consider the effects of changes in land use on C storage. We recognize that changes in land use have had and will have a major impact on C storage in the Amazon Basin [Houghton *et al.*, 1987, 1991], but we feel that a basic understanding of the processes controlling C storage in relatively undisturbed ecosystems must be established before more comprehensive estimates of changes in C storage can be made.

A primary focus of our analysis is to consider the implications of the predicted changes in the C cycle of tropical forest for the cycling of other elements such as N and P. It is important to understand these implications for other elements in order to evaluate the validity of the predicted changes in C. Changes in the C balance of most terrestrial ecosystems are widely believed to be tightly constrained by the cycles of other elements [e.g., Chapin *et al.*, 1980; Bolin and Cook, 1983; Melillo and Gosz, 1983; Billings *et al.*, 1984; Pastor and Post, 1986; Vitousek *et al.*, 1988; Raich *et al.*, 1991; Rastetter *et al.*, 1991; McGuire *et al.*, 1993; Melillo *et al.*, 1993]. Using MBL-GEM, we have developed a method for partitioning these C-nutrient interactions into the following three principal components: (1) the net sequestration or loss of nutrients by the ecosystem, (2) changes in the C to nutrient ratios of ecosystem components, and (3) the movement of nutrients among components that differ in their C:nutrient ratios [Schimel, 1990; Shaver *et al.*, 1992; Rastetter *et al.*, 1992]; (R. B. McKane *et al.*, Analysis of the effects of climate change on carbon storage in arctic tundra, submitted to *Ecology*, hereinafter referred to as R. B. McKane *et al.*, 1995). From these analyses we conclude that C storage is probably more constrained by the N and P cycles than MBL-GEM predicts, and thus the MBL-GEM predictions represent an upper limit to changes in C storage. This exercise serves to highlight those areas where further research is needed to better understand and predict the response of moist tropical forests to global change.

Study Area

The Legal Amazon Basin of Brazil has been defined by law to include the entire states of Acre, Amapa, Amazonas, Para, Rondonia, Roraima, plus parts of Mato Grosso, Maranhao, and Tocantins. It comprises an area of $\sim 500 \times 10^6$ ha of which $\sim 80\%$ is forest, $\sim 18\%$ is cerrado (shrubland and savanna), and $\sim 2\%$ is water [Raich *et al.*, 1991]. The forested area of the Amazon Basin is the largest contiguous expanse of tropical forest in the world.

This study focuses on tropical evergreen forest which accounts for over 90% of the total forested area in the Amazon Basin [Raich *et al.*, 1991]. This forest type typically occurs where mean annual temperature is greater than 22°C, mean annual precipitation is greater than 1500 mm, and the dry season is less than 4 months/yr. These closed-canopy forests are composed of a large number of broad-leaved evergreen tree species and have three or four tree strata. The canopy is 30-60 m high with scattered trees emergent to 100 m [National Academy of Science, 1982].

Three soil types, yellow latosols (Latosolos Amarelo Distróficos), red-yellow latosols (Latosolos Vermelho-Amarelo Distróficos) and red-yellow podzolics (Podzóficos Vermelho-Amarelo Distróficos) make up 60% of the total area of the Amazon Basin. The remainder of the area is made up of 25 additional mapped soil types [Moraes *et al.*, 1995].

Model Description

The Marine Biological Laboratory's General Ecosystem Model is a process-based, lumped-parameter model describing the interactions between C and N in terrestrial ecosystems (Figure 1). The model's structure is described in detail by Rastetter *et al.*, [1991]. It is intended to be generally applicable to most terrestrial ecosystems. We have used the model in the past to analyze the responses of arctic tundra and temperate deciduous forest to changes in CO₂ concentration, temperature, N inputs, irradiance, and soil moisture [Rastetter *et al.*, 1991, 1992]; (R. B. McKane *et al.*, 1995).

The MBL-GEM simulates, at the stand level, photosynthesis and N uptake by plants, allocation of C and N to foliage, stems, and fine roots, respiration in these tissues, turnover of biomass through litterfall, and decomposition of litter and soil organic matter. The model simulates responses to changes in atmospheric CO₂, temperature, soil moisture, irradiance, and inorganic N inputs to the ecosystem. Carbon dioxide is lost from the ecosystem through plant and soil respiration. Inorganic N losses are assumed to be proportional to inorganic N concentrations in soil. The model calculates all changes on a monthly time step. To be consistent with the time step, monthly averages are used for all climate drivers.

A major feature of the model is that vegetation acclimates to changes in the environment to maintain a nutritional balance between C and N. Thus environmental changes that stimulate photosynthesis (e.g., increased CO₂ or higher irradiance) result in an increase in allocation of C and N to fine roots, thereby stimulating N uptake. Similarly, environmental changes that stimulate N uptake (e.g., high inorganic N levels) increase allocation of C and N to foliage, thereby stimulating C uptake.

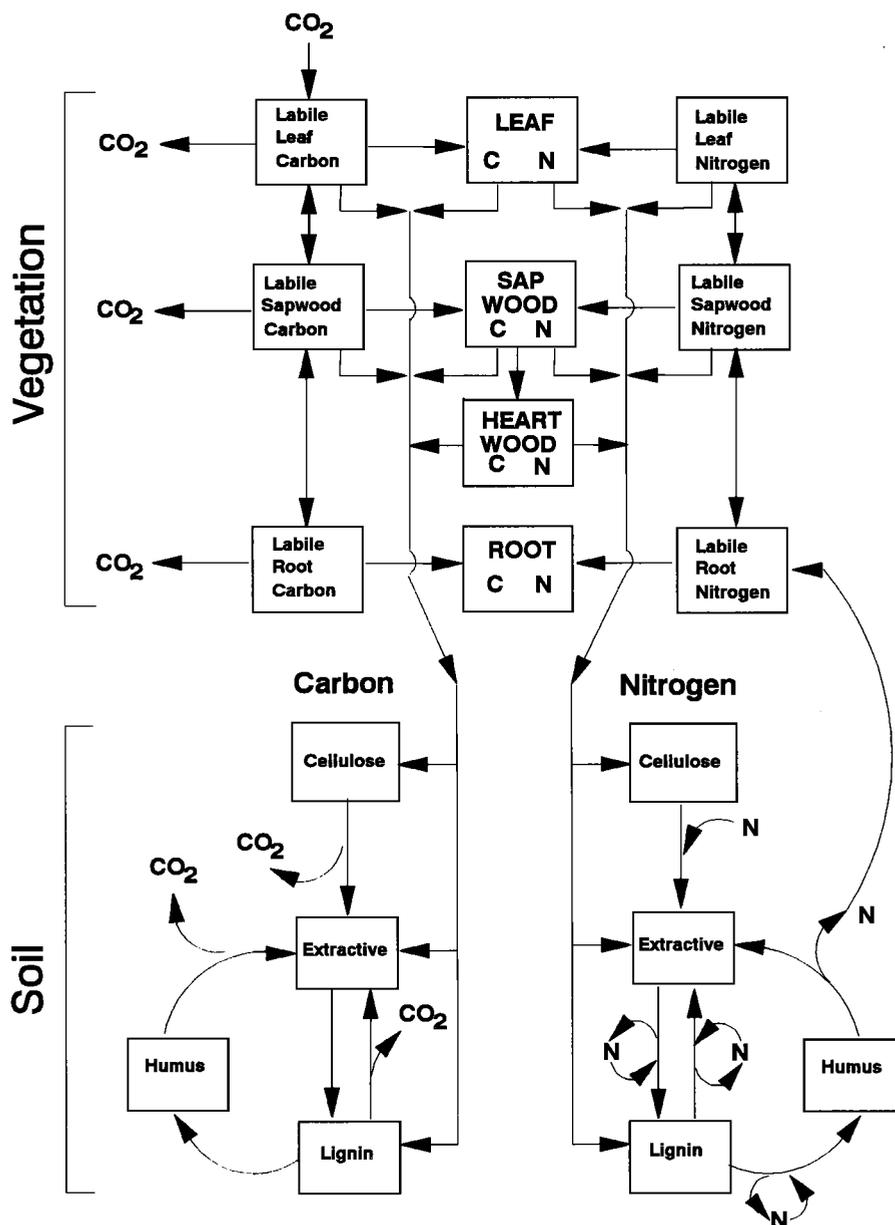


Figure 1. Schematic diagram of MBL-GEM, a general model of C and N cycles within terrestrial ecosystems. Equations for the model processes are given by *Rastetter et al.* [1991].

Model Calibration and Testing

Our goal in calibrating MBL-GEM for tropical evergreen forest was to derive a single parameter set that encompassed the response of tropical forests throughout the Amazon Basin to changes in temperature, soil moisture, light, nutrients, and atmospheric CO_2 . A single parameter set ensures that simulated changes in C stocks across the Amazon Basin are due entirely to differences in the environmental drivers, not to differences in parameters used to simulate different sites. Establishing a parameter set responsive to all of the environmental drivers enables long-term projections to be made of the responses of all forests within the Amazon Basin to changes in climate and CO_2 .

Thus our calibration procedure aims to integrate and scale up physiological and stand-level data to a regional scale so that basin-wide responses can be considered. After describing our calibration procedure and testing the model by predicting regional differences in C storage within the Amazon Basin, we use the model to predict changes in C storage in Amazonian Forests during the next 200 years.

Calibration Procedure

We distinguish between two types of parameters in our model: "rate parameters" and "shape parameters." Rate parameters usually have units that include inverse time (e.g., grams carbon per square meter per year ($\text{g C m}^{-2} \text{yr}^{-1}$), see Table

A1, footnote "c" for exceptions) and there is only one rate parameter for each process in our model. Shape parameters usually do not include units of time and there can be many such parameters describing how a process responds to various environmental factors like light, soil moisture, temperature, or N availability. To illustrate the distinction, consider the two parameters in the Michaelis-Menten function, which is widely used to describe metabolic processes:

$$R = R_m S / (k + S),$$

where R is the rate of the process, S is the concentration of some substrate used in the process, and R_m and k are parameters. We would specify R_m as the rate parameter for this process because it influences the magnitude of R everywhere along the domain of S (it also has units that include inverse time). The parameter k , on the other hand, only influences R at low concentrations of S , but strongly influences the shape of the response of R to changes in S . We would therefore identify k as a shape parameter.

This distinction between rate parameters and shape parameters is important because their values are determined differently in our application of MBL-GEM. To determine the value of the rate parameter for a particular process, an initial guess at the values of the shape parameters must be made. This initial guess can be based on fine-scale data for individual processes or on prior experience with the model applied to similar ecosystems. Also, to determine the rate parameter, a value for all the relevant environmental variables (e.g., temperature, light, and soil moisture), state variables (Table A1), and the rate of the process itself must be specified. From this information the value of the rate parameter can be calculated by an algebraic manipulation of the process equation. We refer to this calculation as a "back calculation" of the rate parameter because it involves an algebraic inversion of the process equation. For example, the rate parameter in the Michaelis-Menten equation can be back calculated as $R_m = R(k + S)/S$.

The procedure described above was used to back calculate all the rate parameters for plant processes. However, the rate parameters for most of the soil processes have been found to be general across a wide range of environments and litter qualities (M. Ryan, unpublished, 1989) and therefore do not need to be back calculated. On the other hand, data to partition soil organic matter and litter among the various organic matter classes used in the model is not available for many sites. We therefore used the known rate parameters and the litter input rates to back calculate the amounts of C and N in the various organic matter classes. This procedure is identical to that for the rate parameters except that the amount of C or N ends up on the left side of the inverted process equation rather than the rate parameter.

Shape parameters are determined by a more traditional "trial and error" iterative calibration procedure. The objective of the shape parameter calibration is to fine tune the response functions in the model to the environmental variables (e.g., light, soil moisture, and temperature). For example, three shape parameters must be calibrated to control how photosynthesis changes with temperature. This calibration requires data from several sites that differ in their environmental conditions. The iterative calibration procedure is as follows: (1) an initial guess at the shape parameters is made, (2) the rate parameters are

back calculated for a "primary" calibration site, (3) the model is run to equilibrium with the resulting parameter set for several "secondary" calibration sites with environments that differ from the primary calibration site, (4) shape parameters are adjusted to improve the fit at the secondary calibration sites, and (5) the rate parameters are back calculated again for the primary calibration site. This iterative procedure is continued until a single parameter set is found that adequately fits the data from both primary and secondary sites. The labile C and N in foliage, stem, and fine roots at the primary calibration site were treated as calibrated shape parameters rather than state variables because it was impossible to specify them from available data (because they are state variables, their value obviously changes as the model equilibrates to conditions at the secondary calibration sites).

Our primary calibration site was a mature tropical evergreen forest at the Ducke Forest near Manaus, Brazil (2°56' S, 59°57' W) which has been described in detail with respect to C and nutrient stocks and fluxes in vegetation and soil [Klinge and Rodrigues, 1968, 1973; Klinge, 1976]. From these data we specified 17 of the 23 state variables in the model, including the standing stocks of C and N for leaves, sapwood, heartwood, and fine roots; the total amounts of C and N in soil organic matter plus litter; and the amount of inorganic soil N (the remaining six-state variables describe labile C and N in foliage, stem, and fine roots and were calibrated as discussed above). Because we assume a year-to-year equilibrium, only a subset of five-plant process rates needed to be specified for the Manaus site: Gross primary production (GPP), net primary production (NPP) for foliage, stem and fine roots, and the total N uptake rate by vegetation (referenced parameters in Table A1). The rest of the process rates were inferred directly from this subset ("back calculated" parameters in Table A1). For example, at equilibrium total annual litterfall must be equivalent to the NPP for each tissue. Similarly, total respiration from the vegetation must equal the GPP minus the sum of the NPP for all the tissues. Because growth respiration is proportional to NPP, metabolic respiration can be calculated as total respiration minus growth respiration.

Our secondary calibration sites included two other mature tropical evergreen forests in the Amazon Basin. One site is near San Carlos, Venezuela (1°56'N, 67°03'W) and has been described in detail with respect to C and nutrient stocks and fluxes in vegetation and soil [Jordan and Uhl, 1978; Jordan et al., 1982; Jordan, 1985]. The other "site" is a 3° latitude x 2° longitude area (8°30'S to 11°30'S, 51°W to 53°W) in the Brazilian state of Mato Grosso, which was extensively sampled for timber volume and soil C as part of the Radar da Amazônia (RADAM) Brazil project [Moraes et al., 1995; D. Skole, unpublished data, 1994]. We have adjusted the RADAM data to account for C in vegetation and soil not measured in that survey (Figure 4, legend). The Manaus, San Carlos, and Mato Grosso calibration sites form a 2400-km transect running northwest to southeast through the Amazon Basin (Figure 2).

In addition to representing different geographic regions, the Manaus, San Carlos and Mato Grosso sites represent the full range of climatic and soil moisture regimes found within the Amazon Basin [Raich et al., 1991]. Compared to Manaus, the San Carlos site has almost the same mean annual temperature, but is cloudier (36% less irradiance) and does not have a dry season. Soil moisture at this site remains near field capacity

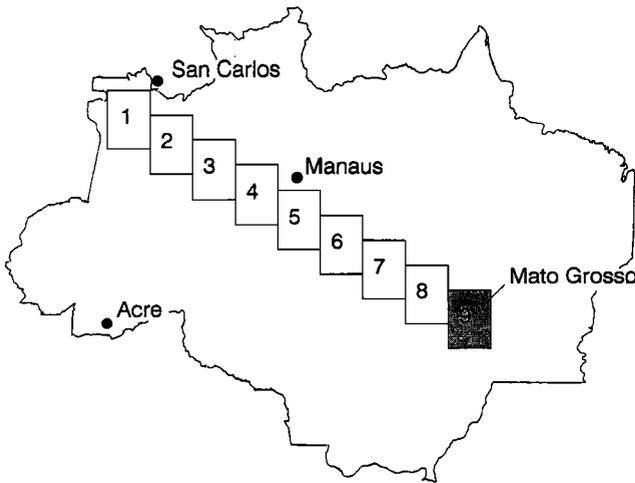


Figure 2. The Legal Amazon Basin showing the locations of the sites from which data were used in this study. Forests at the San Carlos [Jordan and Uhl, 1978; Jordan et al., 1982; Jordan, 1985], Manaus [Klinge and Rodrigues, 1968, 1973; Klinge et al., 1976], and Acre [Brown et al., 1992] sites have been intensively studied. The nine numbered cells are 3° latitude x 2° longitude and have been described by the Radar da Amazônia (RADAM) vegetation and soil surveys [Moraes et al., 1995; D. Skole et al., unpublished data, 1994].

(~62% of saturation) throughout the year. The Mato Grosso site, on the other hand, has wet and dry seasons similar to Manaus and receives similar irradiance, but is almost 4°C cooler (Table 1). Calibration of the model's shape parameters ("calibrated" parameters in Table A1 and Figure A1) to these three sites therefore constrains the model for a relatively wide range of temperature, irradiance, and soil moisture.

Table 2 can be used to assess how well the calibrated model simulated C stocks and fluxes for the Manaus, San Carlos, and Mato Grosso sites. Because all three simulations used the same parameter values (Table A1 and Figure A1), any simulated differences in C stocks and fluxes among sites are due entirely to differences in the environmental drivers (Table 1). The Manaus and San Carlos sites have been studied most extensively and are the only sites for which net primary production (NPP) data were available. Relative to Manaus, San Carlos has 13% lower NPP, 27% lower vegetation C, and 27% lower soil C. The model predicts the San Carlos values to be 15%, 24%, and 7% lower, respectively. The Mato Grosso site has 43% lower vegetation C and 11% lower soil C than Manaus. The model predicts the Mato Grosso values to be 35% and 12% lower, respectively. These results suggest that the model provides an adequate description of the differences among these sites.

**Testing the Calibrated Model:
Simulated versus Measured C Stocks Along
a 2400-km Amazon Transect**

To assess the general applicability of the parameterized model to Amazon forests, we ran the model for nine other sites that were not used to calibrate the model. We will refer to these nine sites as validation [from Rykiel, 1994] sites, although

Table 1. Monthly Values of Temperature, Photosynthetically Active Radiation (PAR), and Soil Moisture for the Three Tropical Evergreen Forest Sites.

	J	F	M	A	M	J	J	A	S	O	N	D	Annual Mean
Temperature, °C ^a													
Manaus	26.0	25.9	25.9	26.0	26.2	26.4	26.5	27.2	27.6	27.5	27.2	26.7	26.6
San Carlos	26.4	26.7	26.9	26.3	26.1	25.6	25.4	25.9	26.6	26.7	26.9	26.5	26.3
Mato Grosso	23.5	23.5	23.4	23.2	22.6	21.7	21.5	22.6	23.2	23.2	23.4	23.5	22.9
Acre	26.1	25.1	25.2	25.2	24.6	23.4	23.5	24.9	26.0	26.2	26.3	26.1	25.2
PAR, mol m ⁻² mo ⁻¹ ^a													
Manaus	843	843	829	783	833	889	979	1080	1177	1228	1093	960	961
San Carlos	731	702	653	583	547	514	502	565	621	650	661	682	618
Mato Grosso	725	759	770	748	876	982	1135	1149	1139	1067	969	849	931
Acre	573	615	629	622	726	822	963	962	939	863	780	678	764
Soil Moisture, % Saturation ^b													
Manaus	63.7	63.7	63.7	63.8	63.5	61.3	53.7	43.4	41.8	43.9	52.0	63.3	56.5
San Carlos	61.8	61.8	61.8	61.9	61.9	61.9	61.9	61.9	61.8	61.8	61.8	61.8	61.8
Mato Grosso	62.8	62.8	62.8	62.6	58.4	51.9	45.3	42.8	48.0	56.6	62.4	62.7	56.6
Acre	62.8	62.9	62.8	62.7	61.4	54.7	45.2	40.6	42.5	50.0	62.5	62.8	55.9

Forest sites used to calibrate MBL-GEM (Ducke Forest near Manaus, Brazil; San Carlos, Venezuela; and Mato Grosso, Brazil) and for a fourth site (Acre, Brazil) used for model validation.

^aTemperature and PAR are from a global data set described by Raich et al. [1991] that has a spatial resolution of 0.5° x 0.5°.

^bSoil moisture was determined with a water balance model [Vorosmarty et al., 1989] that uses climate, elevation, soils, and vegetation data from the global data set. All of the data in Table 1 represent long-term averages.

Table 2. Measured versus. MBL-GEM Predicted Carbon Fluxes and Stocks for Tropical Forests.

Site	Mean Annual Values of the Monthly Environmental Drivers in Table 1						
	Temperature, °C	Soil Moisture, % Saturation	PAR, mol m ⁻² yr ⁻¹	NPP, Mg C ha ⁻¹ mo ⁻¹	Vegetation C ^s , Mg/ha	Soil C ^s , Mg/ha	
Manaus, Brazil Measured and predicted	26.6	56.5	961	11.0	262	150	
San Carlos, Venezuela Measured Predicted	26.3	61.8	618	9.6 9.4	190 200	109 140	
Mato Grosso, Brazil Measured Predicted	22.9	56.6	931	No data 6.8	149 171	133 132	
Acre, Brazil Measured Predicted	25.2	55.9	764	No data 8.4	204 202	No data 132	

Carbon fluxes and stocks measured at at Ducke Forest near Manaus, Brazil (2°56'S, 59°57'W; Klinge [1976], Klinge and Rodrigues [1968, 1973]). San Carlos, Venezuela (1°56'N, 67°03'W; Jordan and Uhl [1978]; Jordan et al. [1982]; Jordan et al. [1985]). In the Brazilian states of Mato Grosso (8°30'S to 11°30'S, 51°W to 53°W; Moraes et al. [1995]; D. Skole unpublished data) and Acre (10°45' S, 68°45' W; Brown et al. [1992]). The locations of the sites are shown in Figure 2. The Manaus, San Carlos, and Mato Grosso site data were used for model calibration. The Acre site data were used for model validation (see "Model calibration and testing"). All of the predicted values were generated by driving the same parameter set of the model (Table A1 and Figure A1) with the environmental conditions specific to each site (Table 1).

^aThe measured soil and vegetation C stocks for the Mato Grosso site have been adjusted as described in Figure 4 to account for portions of those stocks not measured by the RADAM survey. Soil carbon stocks are to a depth of 1 m.

validation of any complex biogeochemical model is not possible in a strict sense [Oreskes *et al.*, 1994]. One of the validation sites was a primary tropical evergreen forest in the state of Acre, Brazil, for which vegetation biomass has been described [Figure 2; Brown *et al.*, 1992]. The Acre site is 1.4°C cooler than the Manaus site, receives 20% less irradiance, and has similar wet and dry seasons and corresponding soil moistures (Table 1). When the parameterized model was run with the environmental drivers set to simulate the Acre site, the model closely simulated the decrease in vegetation C relative to Manaus (-22% measured, -23% simulated) and suggests decreases in NPP (-24%) and soil C (-12%; Table 2).

The other eight validation sites are 3° latitude x 2° longitude cells that form a northwest to southeast transect through Brazil from 1.5°N, 69°W in the state of Amazonas to 10°15'S, 53°W in the states of Para and Mato Grosso (transect cells 1 to 8 in Figure 2). The Mato Grosso calibration site is transect cell 9 at the extreme southeast end of the transect. Like transect cell 9, mean soil and vegetation C stocks for each of the eight transect cells used for model validation are based on samples collected by the RADAM Brazil project [Morales *et al.*, 1995; D. Skole unpublished data, 1994]. These data were adjusted in the same way as transect cell 9 to account for C in vegetation and soil not measured by the RADAM survey (Figure 4, legend). Measured vegetation C in the middle of the transect (229 to 262 Mg/ha for cells 2 to 7) was significantly higher ($P < .05$) than stocks at the southeast end of the transect (168 and 149 Mg/ha for cells 8 and 9, respectively; Figure 4a). Measured soil C ranged from ~100 Mg/ha in the middle of the transect to > 125 Mg/ha on the northeast and southwest ends (Figure 4b). However, because of the large variances within transect cells, none of the measured differences in mean soil C were significantly different among transect cells ($P > .05$).

We ran the model with temperature, soil moisture, and photosynthetically active radiation (PAR) set to simulate transect cells 1 to 8, respectively (Figure 3). The model closely predicted vegetation C stocks along the transect (Figure 4a); in no case were predicted vegetation stocks significantly different ($P > .05$) from measured stocks (see Figure 4 legend). Thus the simulated results for the transect and Acre sites indicate that the model provides a reasonable approximation of how climatic and hydrologic factors regulate vegetation C stocks within the Amazon Basin. Separate runs of the model (not shown) to simulate the effect of temperature, soil moisture, or PAR alone indicated that vegetation C was most sensitive to changes in temperature. The model results therefore provide an explanation for the regional differences in measured vegetation C, that is, vegetation C was highest at warm locations and lowest at cooler locations (Figures 3 and 4a).

The model tended to overestimate soil C near the middle of the transect (Figure 4b) with predicted stocks at transect cells 3 and 5 being significantly higher ($P > .05$) than measured stocks. This overestimation is due to our calibration of the model to the Manaus site. Manaus is just outside of cell 5 (Figure 2) but has about ~40 Mg/ha more soil C even though the two sites have virtually identical climates (Table 1 and Figure 3). Because differences in soil C predicted by the model can only arise from differences in climate used to drive the model, it is impossible for the model to predict the difference between Manaus and cell 5. The difference between Manaus and cell 5 may be the result

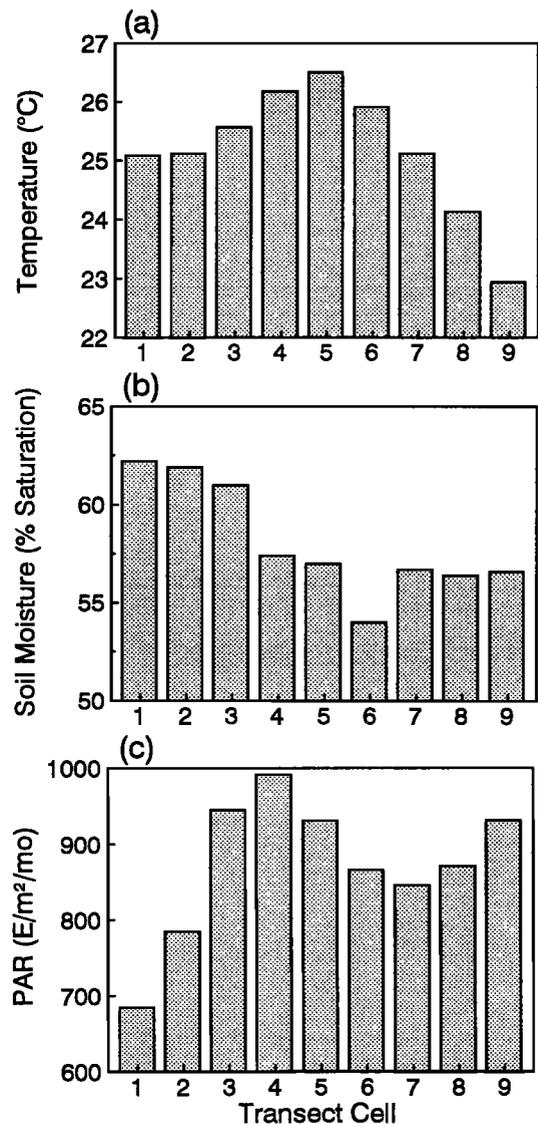


Figure 3. Average annual temperature, soil moisture, and photosynthetically active radiation (PAR) for the nine transect cells shown in Figure 1. Data are derived from Raich *et al.* [1991] and Vorosmarty *et al.* [1989]. Monthly averages for each transect cell (not shown) were used to drive MBL-GEM to simulate vegetation and soil C stocks (Figure 3).

of differences in soil properties (e.g., clay content) not considered in the model. Nevertheless, the model was able to predict soil C stocks in 7 of the 9 cells and vegetation C stocks in all of the cells and at Acre. We therefore feel confident in using our model to make first-order projections of changes in ecosystem C stocks.

Responses of Tropical Forests to Predicted Changes in Atmospheric CO₂ and Climate

Predicted Changes in Atmospheric CO₂ and Climate

In this section we use MBL-GEM to predict and analyze changes in C storage in tropical forests of the Amazon Basin in

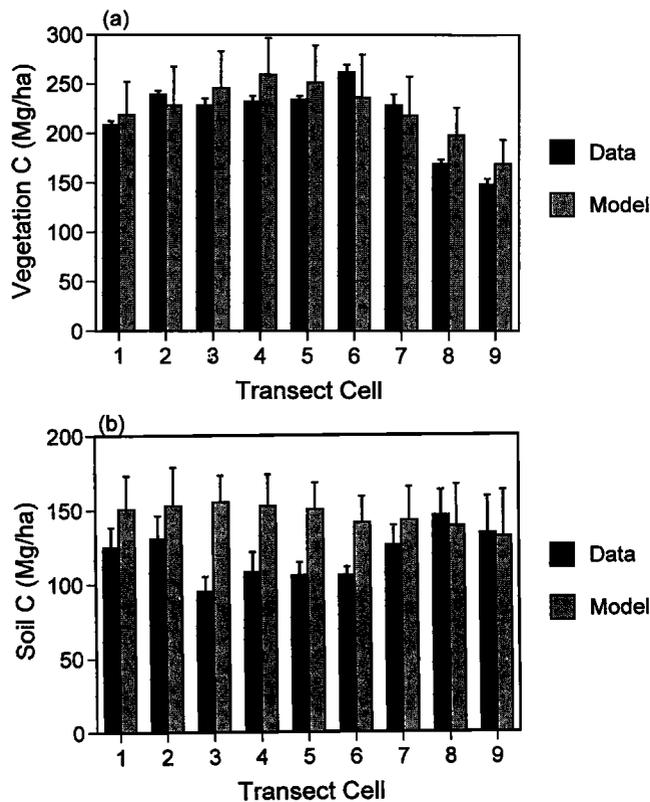


Figure 4. Measured versus MBL-GEM predicted C stocks in (a) vegetation and (b) soil to a depth of 1 m for the nine transect cells shown in Figure 1. Measured data are based on the RADAM soil and vegetation surveys [Morales *et al.*, 1995; D. Skole unpublished data, 1994]. To correct for differences between sampling methods used in the RADAM surveys and those used at the Manaus site [Klinge, 1976], the RADAM data were adjusted as follows. RADAM vegetation data for were multiplied by 1.54 to adjust C estimates based on timber volume to reflect total vegetation C. RADAM soil C data are for mineral soil only and were multiplied by 1.16, which brings the RADAM measurements nearest to the Manaus site (three locations within 0.5° of latitude and longitude) in agreement with the total soil C (mineral soil plus surface detritus) measured at the Manaus site. Error bars on corrected measured data indicate standard errors; these errors were used to test whether measured stocks were significantly different among transect cells. To test whether predicted and measured stocks for each transect cell were significantly different, we performed a *t* test after recalculating the standard error to include the systematic error associated with our derivation of the factors used to correct the measured soil and vegetation C stocks. These error bars are shown on the predicted stocks and were calculated as

$$\sigma_c = C ((\sigma_R/R)^2 + (\sigma_X/X)^2)^{1/2},$$

where *C* is corrected measured soil or vegetation C stocks, *R* is uncorrected measured C stocks for the RADAM samples nearest to the Manaus site, σ_R is the standard deviation associated with *R*, which we assumed to be approximate to the standard deviation of the uncorrected RADAM C stocks for transect cell 5 (the cell nearest to the Manaus site), *X* is uncorrected measured C stocks for cell 5, σ_X = standard error of *X*.

response to a simulated doubling of atmospheric CO₂ and associated changes in climate (Table 3). Temperature, rainfall, and irradiance (cloudiness) under doubled CO₂ were derived from the Goddard Institute of Space Studies (GISS) general circulation model [Hansen *et al.*, 1981; Hansen *et al.*, 1984]. Soil moisture was predicted with a continental-scale model of water balance using GISS-predicted climate [Vorosmarty *et al.*, 1989]. Time series to drive the model were generated by linearly changing CO₂ and each of these climatic variables from their present-day value to their predicted future value over a 100-year period, the time estimated for atmospheric CO₂ to double assuming that CO₂ emissions increase under a "business-as-usual" scenario [Houghton *et al.*, 1990]. We then held the year 100 values of CO₂ and climate constant for an additional 100 years to examine the adjustment of tropical forests to the predicted changes (Figures 5a - 5d). The time series for each climate variable included predicted seasonal (monthly) changes in the data.

Annual average temperature in the Amazon Basin is predicted to increase by about 4°C under doubled CO₂, which is about the same magnitude as the present-day range in temperature along the transect (Table 3 and Figure 3a). Soil moisture is predicted to decrease only slightly from its present-day value near field capacity. Except for cell 8, PAR is predicted to increase everywhere along the transect because of a decrease in cloudiness. The predicted decrease in cloudiness is much greater at the northwest end of the transect (cells 1 and 2), where PAR is predicted to increase by about 22%. At the southeast end of the transect (cells 8 and 9), the predicted change in PAR is only about ± 5 percent.

Constraints on C Storage Because of C-Nutrient Interactions

A key assumption of our analysis is that changes in C storage in response to climate and CO₂ will interact strongly with changes in other element cycles. These interactions arise because the production and accumulation of organic matter require both C and nutrients, especially P and N, and there are limits to the allowable C:nutrient ratios within tissues, organisms, and communities [Melillo and Gosz, 1983; Vitousek *et al.*, 1988; Schimel, 1990; Shaver *et al.*, 1992; Rastetter *et al.*, 1992].

Obviously, the C-nutrient interactions of most interest are those involving the nutrients that are most limiting. Although we are aware of no fertilizer studies describing nutrient limitations in mature tropical forests, P is often assumed to be the most important nutrient limiting primary production in the moist tropics [Sanchez *et al.*, 1982; see also Cuevas and Medina, 1986, 1988]. For oxisols and ultisols, which include almost two thirds of the soils in the moist tropics, evidence suggesting P limitation includes relatively high C/P ratios in biomass, high rates of P retranslocation from senescing foliage [Vitousek and Sanford, 1986], and low levels of available soil P associated with acidic conditions favoring formation of sparingly soluble Fe and Al phosphates [Uehara and Gillman, 1981].

Unfortunately, far less is known about P cycling than N cycling in forests. However, there are clear similarities between the two. We have therefore taken a three-step approach to examining the interactions between the C, N, and P cycles in

Table 3. Changes in Mean Annual Temperature, Soil Moisture, and Photosynthetically Active Radiation (PAR) Predicted by the the Goddard Institute of Space Studies (GISS) General Circulation Model

Amazon Transect Cell	Δ Temperature, °C	Δ Soil Moisture, % Saturation	Δ PAR, mol m ⁻² mo ⁻¹
1	+3.7 (25.1)	-0.1 (62.2)	+141 (685)
2	+3.8 (25.1)	-0.2 (61.9)	+173 (785)
3	+3.7 (25.6)	-1.5 (61.0)	+130 (945)
4	+3.6 (26.2)	-0.7 (57.4)	+79 (992)
5	+3.7 (26.5)	-0.5 (57.0)	+51 (931)
6	+3.9 (25.9)	-0.4 (54.0)	+17 (866)
7	+4.0 (25.1)	-0.2 (56.7)	+5 (846)
8	+4.1 (24.1)	-0.7 (56.4)	-5 (871)
9	+3.9 (22.9)	-0.5 (56.6)	+6 (931)

Model based on an increase of atmospheric CO₂ from 350 to 700 ppm (contemporary values are in parentheses). The Amazon transect cells refer to the locations shown in Figure 2.

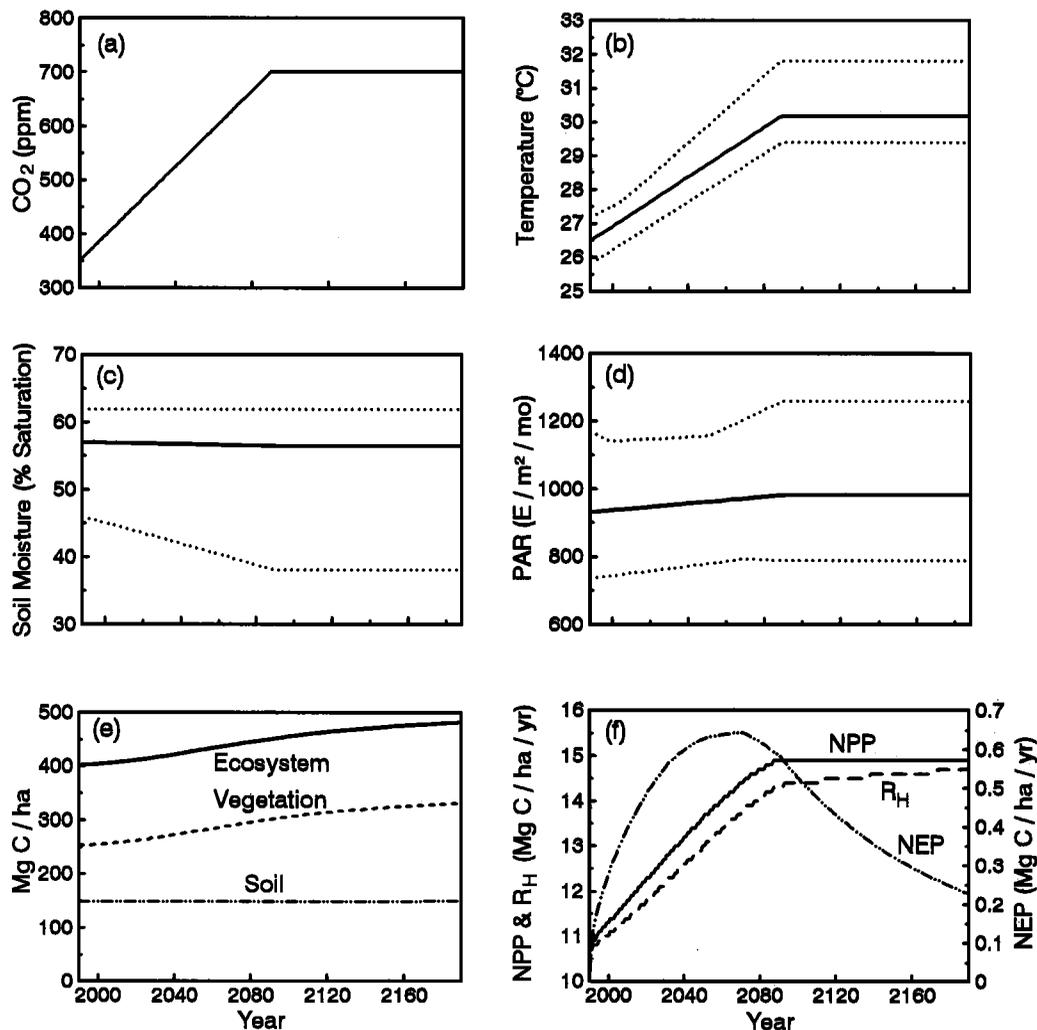


Figure 5. Changes in (a) CO₂, (b) temperature, (c) soil moisture, and (d) photosynthetically active radiation (PAR) predicted by the GISS general circulation model for transect cell 5. Dotted lines in (b) through (d) enclose the annual maximum and minimum values. MBL-GEM predicted changes under the GISS predicted climate for (e) C stocks (solid line is total-ecosystem C, dashed line is vegetation C, and chained line is soil C, and (f) C turnover for transect cell 5 (solid line is net primary production (NPP), dashed line is soil respiration (R_H), and chained line is net ecosystem production (NEP)).

tropical forests. First, we use MBL-GEM (a C- and N-based model) to examine constraints on C cycling when the N cycle is "open," for example, when there is a large input of N to the ecosystem from N fixation and atmospheric deposition. Second, we rerun MBL-GEM with no external input of N to examine constraints on C cycling when the N cycle is "closed." These first two analyses illustrate the potential implications for the wide range of N inputs reported for Amazonian forests. Finally, based on C-N-P stoichiometry and what is known about differences in N and P cycling, we make a final assessment of the limitation on C storage by P. That is, given the stoichiometry of C, N, and P interactions in tropical forests, how reasonable are MBL-GEM's predictions? We present our analysis as a heuristic exercise intended to highlight those areas where further research is needed to better understand and predict the response of tropical forests to global change.

Step 1: How Does C Storage Change When The N Cycle Is Open?

To examine changes in C storage when the N cycle is open, we ran the model for each transect cell with the predicted changes in CO₂ and climate (Table 3) and a total external input of N of 4 g m⁻² yr⁻¹. This external N input includes levels of N fixation (~2 g m⁻² yr⁻¹) and atmospheric deposition (~2 g m⁻² yr⁻¹) that are at the high ends of the ranges reported for the major soil types in the Amazon Basin [Vitousek and Sanford, 1986] (for this exercise we assume atmospheric deposition includes aerosol inputs equal to the N content of rainfall reported for Brazil). Our discussion focuses on changes in net primary production (NPP) and soil respiration and on several aspects of C-N interactions that contributed to the MBL-GEM predicted changes in C storage.

Changes in net primary production. During the first 100 years of the GISS climate scenario, while CO₂ and the climate variables were being ramped to their predicted future values, predicted NPP for all transect cells increased at a slowly accelerating rate. From years 100 to 200, when CO₂ and climate were held constant, NPP stopped increasing, but remained at elevated rates (Figure 5f). After 200 years, predicted NPP had increased along the transect by 2 to 4.5 Mg C ha⁻¹ yr⁻¹, or by 25 to 58% above initial values (Figure 6a).

To determine the cause of these predicted increases in NPP, we also ran simulations in which CO₂ and each climatic variable were varied individually (Figure 6a). The increase under the combined scenario ("all" in Figure 6) reflects a synergistic effect of the individual variables in transect cells 1 through 7; neither the effects of the individual variables alone nor their sum can account for the magnitude of the increase in NPP under the combined scenario in these cells. This synergism in cells 1 through 7 arises because of a colimitation of NPP in the model by CO₂ and N. An increase in CO₂ alone only increases NPP by about 5% because there is not enough N to support higher growth rates. An increase in temperature alone increases NPP by about 10% after 30 years (not shown), but this increase cannot be the direct effect of temperature on photosynthesis because the initial temperatures in these cells were very close to optimum for photosynthesis (Figure A1a). Rather, the predicted increase in NPP with temperature is an indirect effect of the

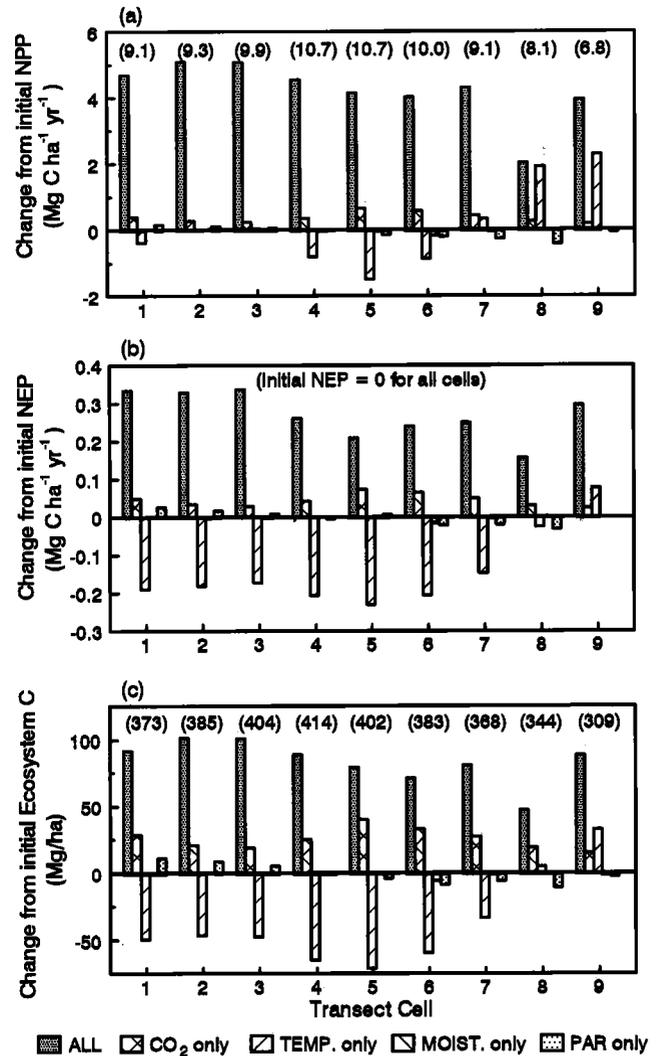


Figure 6. MBL-GEM predicted changes in (a) ecosystem net primary production (NPP) and (b) total ecosystem C stocks under elevated CO₂ and the associated changes in climate predicted by the GISS general circulation model. Bars indicate changes in response to all variables simultaneously and to CO₂, temperature, soil moisture, and photosynthetically active radiation (PAR) alone. Changes represent the difference between year 200 and year 0 of the simulations. Initial values of NPP, NEP, and ecosystem C for each transect cell are shown in parentheses above the bars.

stimulation of N turnover in the soils and the subsequent increase in N availability to vegetation. However, after 30 years, respiration associated with higher vegetation biomass reverses the increase in NPP in cells 1 through 7 (not shown), and NPP subsequently declines to a value about 3% lower, on average, than its initial value. When both CO₂ and temperature are increased in these cells, so that both C and N become more readily available to the vegetation, NPP is stimulated by about 40%. The increase in PAR at the northwest end of the transect (cells 1 and 2) increases predicted NPP by an additional 5%.

The predicted response of NPP in cells 8 and 9 does not show the same level of synergism obvious along the rest of the

transect. Initial temperatures in these cells were lower than those along the rest of the transect (Table 3) and were therefore farther from the optimum for photosynthesis (Figure 1Aa). Thus an increase in temperature in these cells stimulated both photosynthesis and soil N turnover. Consequently, most of the effect on NPP can be explained by the increases in temperature alone (Figure 6a). Nevertheless, the independent effects of the four environmental variables do not sum to their combined effect on NPP.

The predicted increase in NPP for cell 8 is less than half that for the rest of the cells (Figure 6a) because PAR decreased as temperature increased (Table 3). When PAR decreases, leaves at the bottom of the canopy can respire more C than they fix, resulting in a negative C balance for these leaves. This condition is exacerbated by increasing temperatures. Leaves with a negative C balance represent an unnecessary cost to the vegetation and are shed [Nobel *et al.*, 1993; Schoettle and Smith, 1991]. In cell 8, after about 40 years of the GISS scenario, the temperature was high enough, the PAR low enough, and the canopy thick enough that the model predicted a loss of leaf mass. That is, the canopy became strongly light limited and NPP responded only weakly to further changes in other resources like CO₂ and N.

Changes in ecosystem C storage. Like NPP, soil respiration increased under the combined GISS climate scenario, but increases in NPP always slightly exceeded increases in soil respiration. Thus the overall effect of predicted changes in NPP and soil respiration was to increase the rate of C sequestration, or net ecosystem production (NEP = NPP - soil respiration), in all transect cells. NEP increased during the first 100 years of the GISS scenario and remained positive, but declined slowly during the second 100 years when climate was held constant (Figure 5f). At year 200, NEP ranged from 0.16 Mg C ha⁻¹ yr⁻¹ for cell 7 to about 0.34 Mg C ha⁻¹ yr⁻¹ for cells 1, 2, and 3 (Figure 6b). These increases in NEP represent an annual increase of about 0.1% in ecosystem C stocks.

The cumulative effect of predicted changes in NEP after 200 years was to increase ecosystem C stocks in the transect cells by 47 to 102 Mg C/ha (Figure 6c), or by about 14 to 26% over initial stocks. In comparison, present-day C stocks at our three calibration sites average 330 Mg C/ha and differ by as much as 130 Mg C/ha (Table 2). In calibrating MBL-GEM, we assumed that these present-day differences in C stocks are due to differences in climate. The magnitude of climate change associated with elevated CO₂ is comparable to the differences in climate among the calibration sites. Thus the model's predicted responses in C storage do not seem unreasonable.

As with NPP, there was a strong synergism among the four environmental factors in their combined effect on ecosystem C stocks (Figure 6c). Again, the major effects were those of CO₂ on productivity and temperature on the turnover of soil organic matter. Increases in CO₂ stimulated C storage in all cells, but generally accounted for less than 50% of the storage under the combined scenario. Increased temperature alone substantially decreased C stocks in cells 1 through 7 because of its stimulation of soil respiration. The large loss of soil C in these cells is consistent with the analysis of Townsend *et al.*, [1992], who predicted that even small changes in temperature in the tropics could result in large losses of soil C because decomposition in these ecosystems is poised relatively high on

an exponentially increasing temperature response curve. However, this loss of C is more than compensated by increases in NPP due to the synergistic effects of temperature-induced increases in soil N turnover and CO₂-induced increases in photosynthesis. This result is consistent with the model predictions of Melillo *et al.*, [1995], who used the Terrestrial Ecosystem Model (TEM) to study the effects of climate and CO₂ concentration change in a global-scale factorial experiment.

In cells 8 and 9, increased temperature alone stimulated C storage because of its direct stimulation of photosynthesis in these relatively cool locations and because of its indirect stimulation of NPP through an increase in the turnover of soil N. However, when combined with even a small decrease in PAR in cell 8, the increase in temperature contributed to the loss of part of the canopy and a small decrease in the rate of C accumulation.

Virtually all of the predicted increase in total ecosystem C stocks in the combined GISS scenario was associated with an increase in vegetation (mostly wood) biomass. There was little, if any, predicted change in soil C (Figure 7). Nevertheless, the response of soils to changes in climate was very important to the overall response of these ecosystems. The relatively constant soil C stocks were the result of a balance between higher litter input rates (associated with higher NPP) and faster turnover rates of soil organic matter (associated with higher temperatures). It was this higher turnover of soil organic matter that supplied the N necessary to maintain the high NPP and high C stocks in vegetation. Thus the predicted responses in these ecosystems are a result of the strong feedback between soil and vegetation.

Carbon-nutrient interactions. Our analysis assumes that the C storage potential of terrestrial ecosystems is constrained by nutrient cycles. In particular, because the production and accumulation of organic matter require both C and nutrients, ecosystems can only increase C storage by (1) accumulating new nutrients from external sources, (2) increasing the C:nutrient ratios of their components, or (3) redistributing nutrients from components with low C:nutrient ratios (e.g., soils) to components with high C:nutrient ratios (e.g., vegetation, especially wood).

We quantified changes in ecosystem C stocks associated with these three factors using equations derived by Rastetter *et al.*, [1992]. This method of partitioning changes in C stocks is a purely mathematical means of describing the independent contributions of the three factors. The calculated contributions of the three factors (plus an interactive term) can be added to calculate the total change in ecosystem C. The method does not imply any underlying change in particular processes or the particular path by which nutrients come to be allocated to various ecosystem components.

The change in C stocks associated with the accumulation of nutrients from outside the ecosystem or with losses of nutrients from the ecosystem is calculated assuming (1) the C:nutrient ratios of both vegetation and soil did not change, and (2) that vegetation and soil gained or lost nutrients in the same proportion. Because of this second assumption, any disproportionate gain (or loss) of nutrient between vegetation and soil is viewed first as a gain (or loss) of nutrient by the ecosystem as a whole and then as a redistribution of that nutrient between vegetation and soil (see (3) for redistribution). Thus

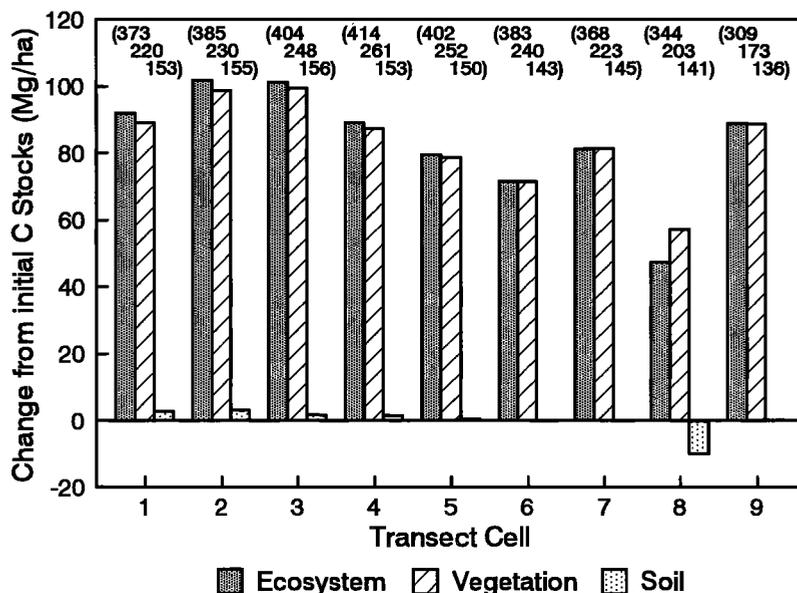


Figure 7. MBL-GEM predicted changes in C stocks in the whole ecosystem and in vegetation and soils under elevated CO₂ and the associated changes in climate predicted by the GISS general circulation model. All changes are indicated by bars and are the difference between year 200 and year 0 of the simulations. Initial values of ecosystem, vegetation, and soil C stocks for each transect cell are shown in parentheses above the bars.

$$\Delta C_{Nin} = \Delta N_T \Psi_T(0), \quad (1)$$

where ΔC_{Nin} is the change in ecosystem C stocks associated with a change in the amount of nutrient in the ecosystem, ΔN_T is the change in the amount of nutrient in the ecosystem, and $\Psi_T(0)$ is the initial C:nutrient ratio of the ecosystem.

The change in ecosystem C stocks associated with a change in the C:nutrient ratios of vegetation and soil is calculated assuming that the amounts of nutrient in vegetation and soil did not change. Thus

$$\Delta C_{VC:N} = N_V(0) \Delta \Psi_V, \quad (2a)$$

$$\Delta C_{SC:N} = N_S(0) \Delta \Psi_S, \quad (2b)$$

where $\Delta C_{VC:N}$ and $\Delta C_{SC:N}$ are the changes in ecosystem C stocks associated with changes in the C:nutrient ratio of vegetation and soil, respectively, $N_V(0)$ and $N_S(0)$ are the initial amounts of nutrient in vegetation and soil, respectively, and $\Delta \Psi_V$ and $\Delta \Psi_S$ are the changes in C:nutrient ratios of vegetation and soil, respectively.

The change in ecosystem C stocks associated with a redistribution of nutrient between vegetation and soil is calculated assuming (1) the total amount of nutrient in the ecosystem remained constant, and (2) the C:nutrient ratios of vegetation and soil remained constant. Thus

$$\Delta C_{redis} = \{ \Psi_V(0) - \Psi_S(0) \} \{ \Delta N_V N_S(0) - \Delta N_S N_V(0) \} / N_T(0), \quad (3)$$

where ΔC_{redis} is the change in the ecosystem C stocks associated with the redistribution of nutrient between vegetation and soil, ΔN_V and ΔN_S are the changes in vegetation and soil nutrient stocks, $N_V(0)$ and $N_S(0)$ are the initial amounts of nutrient in vegetation and soil, $\Psi_V(0)$ and $\Psi_S(0)$ are the initial C:nutrient

ratios of vegetation and soil, and $N_T(0)$ is the initial amount of nutrient in the ecosystem.

The interactions among these three factors can also result in an additional change in the ecosystem C stocks. This interaction was quantified as,

$$\Delta C_{inter} = \Delta N_V \Delta \Psi_V + \Delta N_S \Delta \Psi_S, \quad (4)$$

where ΔC_{inter} is the change in ecosystem C stocks associated with the interaction of the three factors represented in equations (1) - (3), and the other terms in the equation are as defined above. Algebraic manipulation reveals that the sum of (1) - (4) accounts for the total change in ecosystem C stocks [Rastetter *et al.*, 1992].

Using (1) - (4), we analyzed how these three factors of C-nutrient interactions regulated the predicted increases in ecosystem C storage described in the previous section. In each of the transect cells, most of the predicted increase in C stocks can be attributed to a redistribution of N from soils (with C:N ratios near 16) to vegetation (with C:N ratios between 80 and 110; Figure 8). This redistribution of N from soils to vegetation accounted for about two-thirds of the increase in C storage and is the result of warmer temperatures stimulating the decomposition (respiration) of soil organic matter and the release and subsequent uptake of soil N into vegetation. The redistribution of N between soils and vegetation has also been suggested as an important factor in the response of temperate and arctic ecosystems to changes in temperature (R. B. McKane *et al.*, 1995); [Rastetter *et al.*, 1992; Rastetter *et al.*, in press].

The next most important factor regulating C storage along the transect is the sequestration of N from outside the ecosystem (Figure 8). In our simulations, the input rate of N to the ecosystem does not change from present-day inputs, thus the

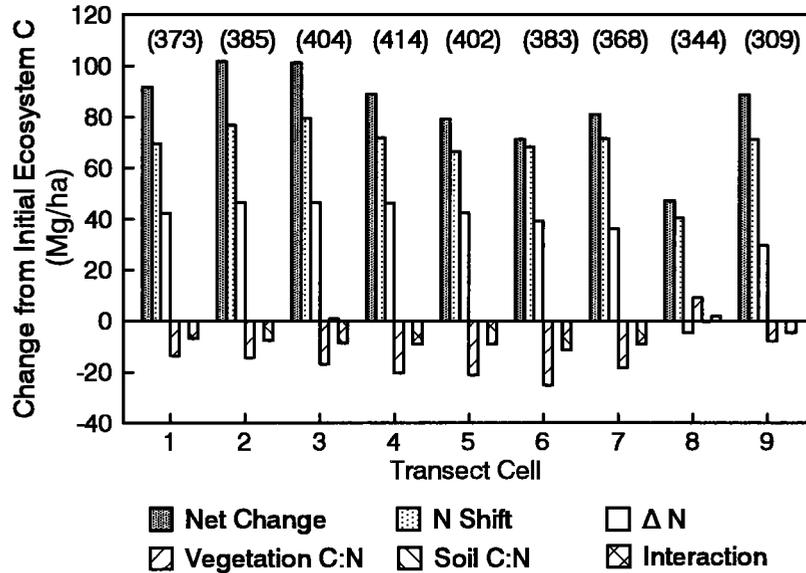


Figure 8. MBL-GEM predicted changes in total ecosystem C stocks under elevated CO_2 and associated changes in climate that can be attributed to various factors of the interaction between C and N. "Net Change" is the total change in ecosystem C stocks due to all factors combined. "N Redistribution" is the change in ecosystem C stocks that can be attributed to a redistribution of N between vegetation (with high C:N ratios) and soils (with low C:N ratios). " ΔN " is the change in ecosystem C stocks that can be attributed to changes in the total amount of N in the ecosystem. "Vegetation C:N" is the change in ecosystem C stocks that can be attributed to changes in the C:N ratio of vegetation. "Soil C:N" is the change in ecosystem C stocks that can be attributed to changes in the C:N ratio of soils. "Interaction" represents changes in C stocks associated with the interaction of all the factors. All changes are indicated by bars and are the difference between year 200 and year 0 of the simulations. The initial value of ecosystem C for each transect cell is shown in parentheses above the bars.

increase in N sequestration over the 200-year period is the result of more efficient N retention by the ecosystem. As NPP and litter inputs to soils increase, the demand for N by plants and soil microbes increases and less N is available to be lost from the ecosystem. Consequently, as productivity was stimulated by changes in CO_2 and climate, more N was retained by the ecosystem, which made it possible to accumulate biomass (C) in the vegetation. This mechanism generally contributed to about one third of the predicted increases in ecosystem C stocks. Cell 8 is the one location on the transect where this mechanism did not play an important role. Cell 8 became light-limited after about 40 years and therefore could not utilize additional N. Increases in N in cell 8 during the first 40 years were almost entirely lost from the ecosystem over the subsequent 60 years, resulting in only a small net gain by year 200.

The last of the C-N interactions that is important to the predicted changes in C storage under the GISS climate scenario is the decrease in vegetation C:N ratios (Figure 8). A change in vegetation C:N ratios can arise from changes in the C:N ratios of individual tissues or from changes in the relative contributions of woody versus nonwoody tissues to the total biomass. Under the GISS scenario, MBL-GEM predicts that both these factors will have an effect on C storage. In most of the transect cells, the model predicts that the amount of C stored in vegetation per unit N declined, resulting in a negative contribution of the vegetation C:N ratio to the net change in C stocks (Figure 8). This decline in vegetation C:N ratios is in part the result of greater C losses associated with higher respiration at high temperatures.

Predicted changes in the C:N ratio of soils were unimportant in all nine transect cells (Figure 8). The C:N ratio of soils can be changed by changing the relative amount of young, high C:N material in the soil. However, the high rate of decomposition in these ecosystems very rapidly reduces the C:N ratio of new litter to a uniformly low value, even under current climate. In contrast, arctic ecosystems have very slowly decomposing organic matter and relatively high soil C:N ratios. If arctic soils are warmed or drained, the C:N ratio can decrease substantially and result in significant C losses from the ecosystem (R. B. McKane et al., 1995); [Rastetter et al., 1995].

Changes in C:N ratios, N sequestration, and the redistribution of N from soils to vegetation can also interact with one another and contribute to the overall C budget of the ecosystem. For example, the sequestration of new N had a much larger effect on C storage because that new N was sequestered preferentially in vegetation rather than being sequestered proportionally in both soils and vegetation. Similarly, the redistribution of N from soils to vegetation had a much smaller effect on total C storage because the C:N ratio of vegetation simultaneously declined. These two opposing processes counteracted one another, resulting in only a small contribution of the interactive term to the net change in C stocks (Figure 8).

Step 2: How Does C Storage Change When the N Cycle is Closed?

For the second step of our analysis we reran MBL-GEM under the same atmospheric CO_2 and climate change scenario

(Figure 5a-5d) as the first step, except that we closed the N cycle by turning off external N inputs to the ecosystem. The closure of the N cycle did not affect the internal N cycling rate because we assumed an initial equilibrium condition in which N inputs exactly equal N losses. Thus in the previous simulation there was an initial loss of N that matched the $4 \text{ g N m}^{-2} \text{ yr}^{-1}$ input (but diverged once the ecosystem was perturbed). By closing the N cycle, we turned off both the input and loss but left the internal cycle unchanged. A closed N cycle scenario is more analogous to the P cycle because external inputs of P to tropical forests are extremely low relative to total plant demand [Vitousek and Sanford, 1986].

We present the results for transect cell 5 to illustrate how the increases in ecosystem C storage predicted with an open N cycle might be reduced if N supplies are derived solely from internal sources. With the closed N cycle, the increase in ecosystem C storage after 200 years was reduced from 80 to 63 Mg/ha, or about 21%. This was due to both a smaller increase in plant biomass and a net decrease in soil C (Table 4). Soil C stocks decreased because inputs of plant litter decreased relative to soil respiration.

We used (1) - (4) to examine how changes in C-N interactions constrained the increase in C storage when the N cycle was closed. Table 5 shows that C gains associated with two of these factors declined dramatically. First, because no new N could be sequestered from outside the ecosystem, C storage by this mechanism was zero, or 43 Mg/ha less than predicted for the open N cycle. Second, the amount of N redistributed from soil organic matter to vegetation decreased sharply, reducing the increase in C stored by this mechanism from 67 to 33 Mg/ha. Less N was redistributed from soil to vegetation because the demand for inorganic N by immobilization into decomposing litter was stronger when N availability was low. The reduced C gains associated with these two factors were partially counteracted by gains associated with an increase in the C:N ratio of vegetation. With the open N cycle the C:N ratio of vegetation decreased from 86 to 80, decreasing C storage by 21 Mg/ha. In contrast, with the closed N cycle the C:N ratio of vegetation increased from 86 to 94, increasing C storage by 26 Mg/ha. Thus there was a net gain of 47 Mg C/ha ($21 + 26 \text{ Mg C/ha}$) due to increased N use efficiency by vegetation. Finally, a net gain of 13 Mg C/ha associated with the interaction of all three factors also tended to counteract the overall reduction in C storage.

Table 4. Predicted Changes in Transect Cell 5 Carbon Stocks After 200 Years Under Elevated CO_2 and Associated Changes in Climate

	Change from Initial C Stocks, Mg/ha	
	Open N Cycle	Closed N Cycle
Plant C	+79	+71
Soil C	+ 1	- 8
Ecosystem C	+80	+63

Associated changes in climate when external N inputs are either $4 \text{ gm}^{-2} \text{ yr}^{-1}$ ("open N cycle") or $0 \text{ gm}^{-2} \text{ yr}^{-1}$ ("closed N cycle"). All changes are the difference between initial and year 200 C stocks. Initial plant and soil C stocks were 253 and 150 Mg/ha, respectively.

Table 5. Predicted Changes in Transect Cell 5 Total Ecosystem Carbon ("Total Change") Partitioned Among Various Components of the Interaction Between Carbon and Nitrogen

	Change in Total Ecosystem C, Mg/ha ^a	
	Open N Cycle	Closed N Cycle
ΔN	+43	0
N Redistribution	+67	+33
C:N	-21	+26
Interaction	- 9	+ 4
Total Change	+80	+63

Results are the cumulative changes after 200 years under elevated CO_2 and associated changes in climate when external N inputs are either $4 \text{ gm}^{-2} \text{ yr}^{-1}$ ("open N cycle") or $0 \text{ gm}^{-2} \text{ yr}^{-1}$ ("closed N cycle"). " ΔN " is the change in ecosystem carbon that can be attributed to changes in the total amount of nitrogen in the ecosystem. "N redistribution" is the change in ecosystem carbon that can be attributed to a redistribution of nitrogen between vegetation (with high C:N ratios) and soils (with low C:N ratios). "C:N" is the change in ecosystem carbon that can be attributed to changes in the ecosystem C:N ratio. "Interaction" represents the change in ecosystem carbon associated with the interaction of all the factors. Initial total ecosystem carbon was 403 Mg/ha.

^aDue to partitioning factor

The preceding analyses suggest that open and closed nutrient cycles may differ substantially with respect to C-nutrient interactions and that these differences may have an important impact on the response of ecosystems to changes in CO_2 and climate. For relatively closed nutrient cycles like P, increases in C storage will be limited by low inputs and low sequestration of nutrients from outside the ecosystem and by strong limitations on nutrient uptake by vegetation as a result of greater immobilization into soil organic matter. However, these constraints on C storage may be partially counteracted by greater nutrient use efficiency by vegetation.

Step 3: How Might C-P Interactions Constrain Changes in C Storage?

To address the assumption that P most strongly limits the productivity of tropical forests in the Amazon Basin, the third step of our analysis examined how C-P interactions might constrain the MBL-GEM predicted increases in C storage. We first calculate the P requirements needed to support the predicted increases in plant C stocks and NPP, then assess whether those P requirements can be met based on what is known about P cycling in Amazonian forests. We use the predictions from step 2 for this analysis because the closed N cycle is more analogous to the situation with P.

How much P do the predicted increases in NPP and plant biomass require? On the basis of reported ratios of C, N, and P in Amazonian forests [Jordan, 1985; Vitousek and Sanford, 1986], plant P stocks must increase by 2.2 g/m^2 (from 7.9 to 10.1 g/m^2) to support the 7090 g/m^2 increase in plant C stocks predicted after 200 years under the GISS climate scenario with increased CO_2 . If we assume that the N:P ratio of NPP remains constant, P uptake from Amazonian soils must increase by 0.11

$\text{g m}^{-2} \text{ yr}^{-1}$ (from 0.59 to 0.70 $\text{g m}^{-2} \text{ yr}^{-1}$) to support the predicted 285 $\text{g C m}^{-2} \text{ yr}^{-1}$ increase in NPP (Figure 9).

Two questions must be addressed to determine how C-P interactions might constrain the MBL-GEM predicted increase in C storage. First, is it possible to increase plant P stocks by 2.2 g/m^2 over 200 years? With respect to the hypothetical soil P pools in Figure 9, this amount of P represents about 2% of total soil P and about 4% of organic soil P. Thus it appears that the required increase in plant P could be satisfied by redistributing a relatively small fraction of soil P stocks to plants. From this standpoint, the MBL-GEM predicted increase in C storage does not appear to be unreasonable.

Second, is it possible to increase P uptake by 0.11 $\text{g m}^{-2} \text{ yr}^{-1}$ to support the predicted increase in NPP? This question is more difficult, but can be approached by comparing the projected increases in N and P uptake in the context of what is known about the N and P cycles. On the basis of total soil N and P pools of 925 and 132 g/m^2 , respectively, the projected increases in annual N and P uptake require that the turnover time (pool

size / uptake rate) of these pools must decrease by about 15% over 200 years (Figure 9). This decrease in turnover time applies to whichever soil nutrient pool(s) is assumed to be the source of uptake. For the hypothetical soil P fractions in Figure 9, if most P uptake is derived from labile inorganic P, the turnover time of this pool must decrease by 15%, that is, from about 1.4 to 1.2 years. If the substantially larger pool of organic P is also important, the turnover time of the labile inorganic and organic P pools combined must decrease from 103 to 87 years. Although there are no data to indicate how the turnover times of soil nutrient pools in tropical forests will change in response to global change, fundamental differences in the N and P cycles suggest that increases in P cycling might be more difficult to achieve. Whereas the N cycle is mostly biologically mediated, the P cycle has competing geochemical and biological components. Fixation of soluble phosphate as relatively insoluble Fe and Al phosphates is an especially important geochemical process in tropical soils (*Uehara and Gillman, 1981*) that is presumed to have long time constants (*Parton et*

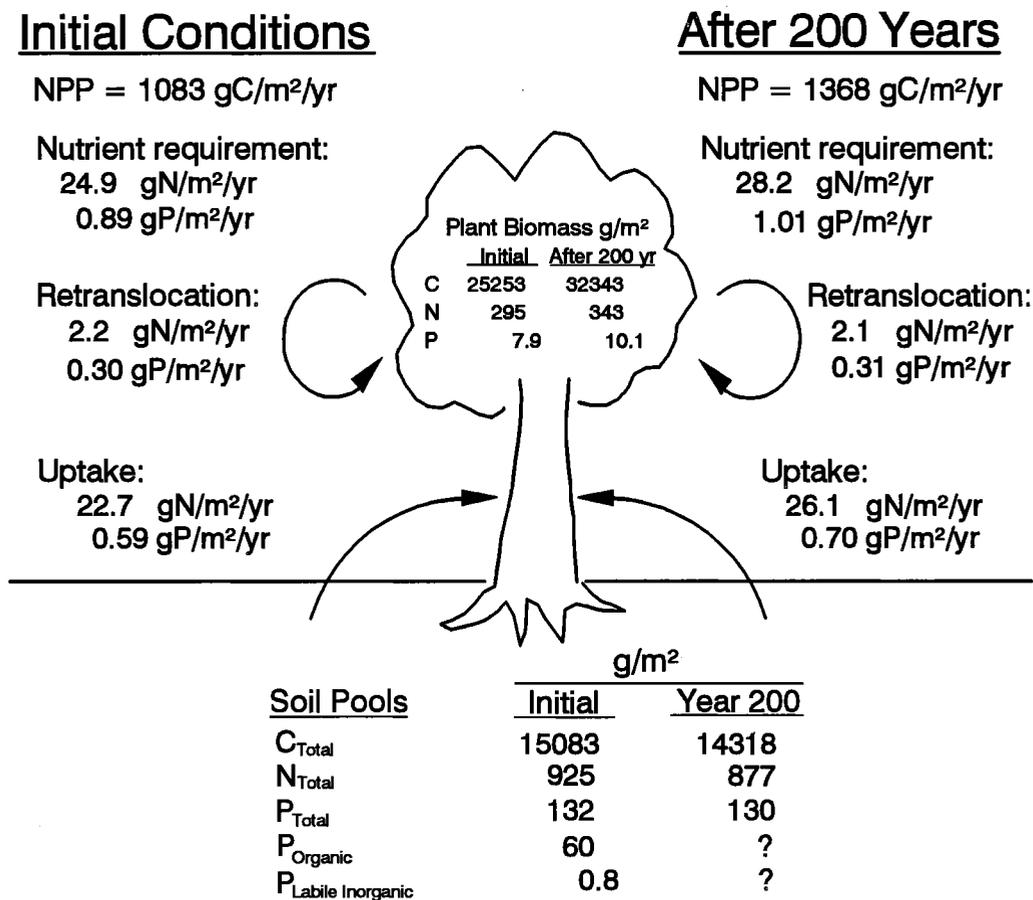


Figure 9. Carbon, N and P budgets for transect cell 5 (Figure 2) for initial conditions and after 200 years under doubled atmospheric CO_2 and associated changes in climate (Table 3). The C and N budgets are based on MBL-GEM predictions when there are no external N inputs to the ecosystem. The P budget for vegetation is based on stoichiometric relationships between C, N, and P in moist tropical forests [*Vitousek and Sanford, 1986*]. The total soil P pool is based on a soil N:P ratio of 7 reported for moist tropical forest on an oxisol soil at San Carlos, Venezuela [*Jordan, 1985*]. The organic and labile inorganic soil P pools are based on fractions (as a percentage of total soil P) determined for moist tropical forest on an alluvial soil (Andic Dystropept) at La Selva, Costa Rica [*Fernandes and Sanford, 1995*].

al., 1988). Consequently, for any predicted increase in the turnover of soil organic matter, increases in P availability may be less sustainable than increases in N availability. From this standpoint, it appears that the predicted rates of P uptake, NPP, and ecosystem C storage shown in Figure 9 are too high.

Thus our analysis of C-N-P interactions suggests that the MBL-GEM prediction of 63 Mg C/ha represents an upper limit to the change in C storage over the next 200 years. This upper limit does not seem unreasonable because present-day differences in ecosystem C stocks across the Amazon Basin (Figure 4), which are also constrained by P availability and climate, are almost as large.

We emphasize that although the size of the change in C storage is uncertain, this change will almost certainly be positive. It must be positive because a primary mechanism for storing C in Amazonian forests will be to redistribute P from soil organic matter (with a C:P ratio < 20) to plants (with a C:P ratio > 3000). This stoichiometric difference between soil and plants favors an increase in C storage even if only a small fraction of the P released during decomposition is taken up by plants.

Conclusions and Recommendations for Further Research

We have presented the preceding analyses as a heuristic exercise to highlight those areas where further research is needed to better understand and predict the response of moist tropical forests to global change. The central hypothesis of this exercise is that changes in ecosystem C storage in response to climate and CO₂ will interact strongly with changes in other element cycles, particularly the N and P cycles. Our analyses of C-N and C-N-P interactions suggests that C storage in tropical forests may be very sensitive to a number of assumptions about the N and P cycles. In summary, if we assume that Amazonian forests are N-limited and that external N inputs are constant near the high end of the reported range (~4 g m⁻² yr⁻¹), our C-N based model predicts that ecosystem C stocks will increase by 80 Mg/ha during the next 200 years, a 20% increase above present-day stocks. If external N inputs are assumed to be negligible (~0 g m⁻² yr⁻¹), the predicted increase in C storage is reduced to 63 Mg/ha, a 16% increase above present-day stocks. In the more likely case that most Amazonian forests are P-limited, we argue that constraints imposed by the P cycle will result in smaller increases in C storage than our model predicts, but it is impossible to know how much smaller until more is known about the controls on soil P availability.

The uncertainties in our model predictions have important implications for the global C budget and need to be resolved. For example, the predicted 63 Mg/ha increase in C storage over the next 200 years translates to a 25 Pg (10¹⁵ g) C increase over the forested 400 × 10⁶ ha in the Amazon Basin, or a 139 Pg C increase if this number is extrapolated globally assuming a total area for tropical forests of 2200 × 10⁶ [Melillo *et al.*, 1993]. In comparison, a doubling of CO₂ during the next 100 to 200 years would increase the pool of atmospheric C by about 750 Pg [Houghton *et al.*, 1990]. Thus if our model prediction is viewed as an upper limit, tropical forests globally might reduce the

increase in atmospheric CO₂ by anywhere between 0 and 19%. This estimate will of course be reduced or even reversed if tropical deforestation continues at its current rate.

From our analyses we have identified the following as high priority topics for further research in the moist tropics:

1. There are currently few biome-specific studies describing climatic controls on whole canopy photosynthesis, plant and soil respiration, stabilization of soil organic matter, and N and P cycling. To better constrain models such as the one used here, more whole ecosystem studies are needed along climatic gradients within the tropics. A number of such studies have been proposed for the Amazon Basin as part of the International Geosphere-Biosphere Programme [IGBP, 1990] and the Global Change and Terrestrial Ecosystems research program [GCTE, 1994].

2. Our model predicts that increases in productivity and C storage will depend upon the synergistic effect of increases in CO₂ and nutrient availability. This could be tested by using growth-chamber experiments or free-air CO₂ enrichment (FACE) techniques to grow tropical forest species at different levels of CO₂ and nutrient fertilization. To effectively focus this and other research on C-nutrient interactions, fertilizer studies need to be established in intact moist tropical forests on the major soil types to determine which nutrients are most limiting. For example, does productivity on oxisol sites respond to added P and/or Ca, or spodosol/psamment sites to added N and/or P [Cuevas and Medina, 1986, 1988]?

3. We have hypothesized that several components of C-nutrient interactions will constrain changes in C storage in response to projected increases in CO₂ and associated changes in climate. Our model predicts that C should accumulate in tropical forest ecosystems mostly as a result of the redistribution of nutrients from soils (with low C:nutrient ratios) to vegetation (with high C:nutrient ratios). Experiments are needed to determine if such a redistribution actually occurs when soils are warmed. Our model also predicts that C will be stored within tropical forests if the C:nutrient ratio of the ecosystem increases. Vegetation generally has a more flexible C:nutrient ratio than soil and will therefore be more important in this regard. Increases in the C:nutrient ratio of vegetation can occur through an increase in nutrient use efficiency [Vitousek, 1982] or through an increase in the proportion of high C:nutrient tissues, especially wood. Studies are needed to determine whether such changes occur in response to CO₂, temperature, and/or nutrient availability. Finally, our model predicts that C storage will increase if nutrients can be sequestered from external sources. To place limits on this sequestration, more extensive studies are needed to define the geographic patterns of atmospheric deposition of limiting nutrients. Where N is limiting, rates of N fixation will also need to be quantified.

4. Several major questions specific to the P cycle need to be resolved. First, the turnover of organic P is not well understood. Studies are needed to quantify organic P fractions and their turnover rates and how these will respond to global change. A key question is, given accelerated decomposition and mineralization, will organic P be partitioned to relatively insoluble mineral phases or to biomass? This will require a better predictive understanding of P sorption and desorption. Second, the development and function of fine roots and mycorrhizae in various soil and climatic conditions need to be

better understood. For example, how will fine root/mycorrhizae production respond to changes in nutrient availability and climate? Will changes in the surface area of fine roots/mycorrhizae affect rates of P uptake? Will organic acid production by mycorrhizae change, and will this affect P desorption in rhizosphere soil? An overall goal of this research should be to generate sufficient information to move from conceptual to predictive models of P cycling.

5. Although this study represents our current understanding of how changes in CO₂ and climate will affect C storage in mature tropical forests, it does not consider the effects of changes in land use. Future studies with MBL-GEM will evaluate how changes in land use within the tropics (e.g., logging, slash and burn, and secondary succession) affect ecosystem C storage and how these disturbed ecosystems respond to changes in CO₂ and climate.

Appendix

We calibrated MBL-GEM using detailed data on carbon stocks and fluxes for tropical evergreen forests near Manaus, Brazil, San Carlos, Venezuela, and in the state of Mato Grosso, Brazil, that form a 2400-km transect through the Amazon Basin. The purpose of our calibration procedure was to derive a single parameter set that encompassed the response of tropical forests throughout the Amazon Basin to changes in temperature, soil moisture, light, nutrients, and atmospheric CO₂ (see Model Calibration and Testing sections). This single parameter set is presented in its entirety in Table A1 (initial state variables, specified initial fluxes, and parameters) and Figure A1 (temperature and moisture response curves).

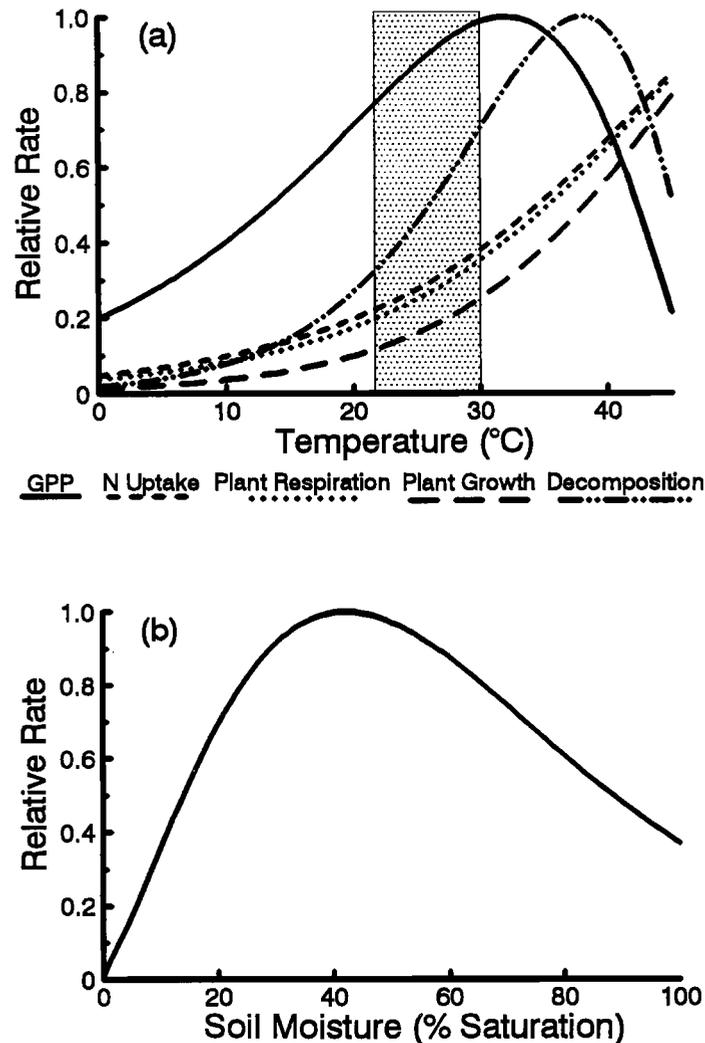


Figure A1. Metabolic response functions for (a) the effect of temperature on gross photosynthesis [Larcher, 1980], plant respiration [Larcher, 1980], plant growth (calibrated), N uptake (calibrated), and decomposition [Peterjohn *et al.*, 1994], and for (b) the effect of soil moisture on soil decomposition [Waring and Schlesinger, 1985]. These response functions were used in MBL-GEM for Amazonian tropical forest. The shaded area from 22° to 30 °C indicates the range of temperatures pertinent to this study.

Table A1. Initial State Variables, Specified Initial Fluxes, and Parameters Used in MBL-GEM.

Acronym	Definition	Value	Units	Reference
<i>State Variables</i>				
F_{LC}	Foliage labile C	2.00	g/m ²	Calibrated
F_{SC}	Foliage structural C	437	g/m ²	<i>Klinge and Rodrigues</i> [1973]
S_{LC}	Stem labile C	6.08	g/m ²	Calibrated
S_{SC}	Stem structural C	2527	g/m ²	<i>Klinge and Rodrigues</i> [1973]
Hwc	Heartwood C	22738	g/m ²	<i>Klinge and Rodrigues</i> [1973]
R_{LC}	Fine root (<3mm) labile C	0.80	g/m ²	Calibrated
R_{SC}	Fine root (<3mm) structural C	451	g/m ²	Assumed ~ 2/3 root mass < 6 mm in diameter reported by <i>Stark and Spratt</i> [1977]
H_C	Total soil + litter C ^a	15030	g/m ²	<i>Klinge</i> [1976]
Cc	Humus C	14776	g/m ²	Back calculated
Ec	Litter cellulose C	152	g/m ²	Back calculated
Lc	Litter extractives C	38	g/m ²	Back calculated
Ll	Litter lignin C	64	g/m ²	Back calculated
F_{LN}	Foliage labile N	0.03	g/m ²	Calibrated
F_{SN}	Foliage structural N	16.0	g/m ²	<i>Jordan et al.</i> [1982]
S_{LN}	Stem labile N	0.24	g/m ²	Calibrated
S_{SN}	Stem structural N	27.3	g/m ²	<i>Jordan et al.</i> [1982]
HwN	Heartwood N	246.0	g/m ²	<i>Jordan et al.</i> [1982]
R_{LN}	Root labile N	0.05	g/m ²	Calibrated
R_{SN}	Root structural N	9.0	g/m ²	<i>Jordan et al.</i> [1982]
T_{LN}	Total soil + litter N ^a	922	g/m ²	<i>Klinge</i> [1976]
Hn	Humus N	916	g/m ²	Back calculated
Cn	Litter cellulose N	1.9	g/m ²	Back calculated
En	Litter extractives N	2.6	g/m ²	Back calculated
Ln	Litter lignin N	1.6	g/m ²	Back calculated
N	Soil inorganic N	1.0	g/m ²	<i>Raich et al.</i> [1991]
<i>Specified Initial Fluxes</i>				
P	Photosynthesis (GPP)	276	g C m ⁻² mo ⁻¹	Based on M. Ryan, unpublished data for tropical evergreen forest at La Selva, Costa Rica
$L_{FLC} + L_{FSC}$	From foliage labile + structural C (= foliage NPP)	28.6	g C m ⁻² mo ⁻¹	<i>Klinge and Rodrigues</i> [1968]
$L_{SLC} + L_{SSC}$	From stem labile + structural C (= stem NPP)	25.4	g C m ⁻² mo ⁻¹	<i>Jordan</i> [1985]
$L_{RLC} + L_{RSC}$	From root labile + structural C (= root NPP)	38.0	g C m ⁻² mo ⁻¹	Calculated based on <i>Raich and Nadelhoffer</i> [1989]
U	Uptake of N by plants	1.9	g N m ⁻² mo ⁻¹	Calculated based on tissue NPP and C/N
N_{in}	Input of inorganic N	0.33	g N m ⁻² mo ⁻¹	<i>Vitousek and Sanford</i> [1986] (N fixation to 2.0 g N m ⁻² yr ⁻¹ on ultisols; atmospheric deposition to 2 g N m ⁻² yr ⁻¹).
<i>Plant Processes</i>				
P_m	Photosynthetic capacity	87.97	g C-fixed g ⁻¹ foliar N mo ⁻¹	Back calculated
Df	Foliar carbon density	48	g C m ⁻² leaf area	<i>Klinge and Rodrigues</i> [1973], <i>Jordan</i> [1985]
C_{max}	Maximum stomatal conductance	2.5	g C-fixed m ⁻² leaf area ppm CO ₂	Calibrated
k_{CO2}	CO ₂ half-saturation constant for photosynthesis	500	ppm	Calibrated based on R.B. McKane et al. [1995]
k_t	Canopy light extinction coefficient	0.5	ground area/leaf area, m ² m ⁻²	Calibrated

Table A1. (continued)

Acronym	Definition	Value	Units	Reference
S_{tr}	Stem transport conductivity parameter	1.0	$g\ C\ m^{-2}$	Calibrated (always set to 1.0 to preserve units)
D_{fsc}	Foliage to stem C transport coefficient	6461.7	$g\ C\ m^{-2}\ mo^{-1}$	Back calculated
D_{src}	Stem to root C transport coefficient	8730.7	$g\ C\ m^{-2}\ mo^{-1}$	Back calculated
D_{fSN}	Root to stem N transport coefficient	12475.5	$g\ N\ m^{-2}\ mo^{-1}$	Back calculated
D_{fFN}	Stem to foliage N transport coefficient	7175.04	$g\ N\ m^{-2}\ mo^{-1}$	Back calculated
g_f	Maximum growth rate for foliage	31.92	$g\ C\ m^{-2}\ mo^{-1}$	Back calculated
g_s	Maximum growth rate for stems	33.77	$g\ C\ m^{-2}\ mo^{-1}$	Back calculated
g_r	Maximum growth rate for roots	39.69	$g\ C\ m^{-2}\ mo^{-1}$	Back calculated
a_f	Growth efficiency parameter for foliage	5.1e-06	$g\ labile\ N\ g^{-1}\ structural\ C$	Calibrated
a_s	Growth efficiency parameter for stems	2.1e-06	$g\ labile\ N\ g^{-1}\ structural\ C$	Calibrated
a_r	Growth efficiency parameter for roots	8.0e-07	$g\ labile\ N\ g^{-1}\ structural\ C$	Calibrated
k_{fN}	Growth parameter for foliage ^a	1.2e-09	$g\ lab.\ C\ g\ lab.\ N\ g^{-2}\ str.\ C$	Calibrated
k_{sN}	Growth parameter for stems ^b	1.0e-08	$g\ lab.\ C\ g\ lab.\ N\ g^{-2}\ str.\ C$	Calibrated
k_{rN}	Growth parameter for roots ^b	0	$g\ lab.\ C\ g\ lab.\ N\ g^{-2}\ str.\ C$	Calibrated
b_f	C to N range for foliage	1.41	unitless	Calibrated
b_s	C to N range for stems	2.93	unitless	Calibrated
b_r	C to N range for roots	1.49	unitless	Calibrated
A_f	Non-restricted C/N ratio for foliage ^c	26.87	$g\ C\ g^{-1}\ N$	Back calculated
A_s	Non-restricted C/N ratio for stems ^c	102.47	$g\ C\ g^{-1}\ N$	Back calculated
A_r	Non-restricted C/N ratio for roots ^c	50.50	$g\ C\ g^{-1}\ N$	Back calculated
$[S_{Om}]$	Stem minimum labile C concentration	0.01	$g\ labile\ C\ g^{-1}\ structural\ C$	Calibrated
F_m	Metabolic respiration coefficient	3.08	$g\ C\ g^{-1}\ N\ mo^{-1}$	Back calculated
f_c	Construction respiration coefficient	0.25	unitless	Ryan [1991]
U_m	Maximum N uptake rate by plants	0.42	$g\ N\ g^{-1}\ root-N\ mo^{-1}$	Back calculated
k_{sp}	Plant N uptake half saturation constant	1.0	$g\ N\ m^{-2}$	Calibrated
t_r	Retranslocation parameter	0.17	unitless	Klinge and Rodrigues [1968], Jordan et al. [1982]
<i>Litterfall</i>				
l_f	Foliage litterfall rate parameter	0.065	mo^{-1}	Back calculated
l_h	Heartwood litterfall rate parameter	0.001	mo^{-1}	Back calculated
l_k	Root litterfall rate parameter	0.084	mo^{-1}	Back calculated
l_s	Stem litterfall rate parameter	0.001	mo^{-1}	Back calculated
<i>Litterfall Fractionations</i>				
a	Cellulose to lignin ratio in litterfall	2.07	$g\ cellulose\ C\ g^{-1}\ lignin\ C$	Aber et al. [1984]
z	Litterfall partitioning parameter	1.00	unitless	Back calculated
w	Litterfall quality partitioning parameter	0.66	unitless	Aber et al. [1984]
<i>Soil Transformations</i>				
b_{CE}	Cellulose to extractives transformation efficiency	0.41	$g\ extractives\ C\ g^{-1}\ cellulose\ C$	M. Ryan, unpublished
b_{EL}	Extractives to lignin transformation efficiency	0.27	$g\ lignin\ C\ g^{-1}\ extractives\ C$	M. Ryan, unpublished
b_{LE}	Lignin to extractives transformation efficiency	0.21	$g\ extractives\ C\ g^{-1}\ lignin\ C$	M. Ryan, unpublished
b_{LH}	Lignin to humus transformation efficiency	0.90	$g\ humus\ C\ g^{-1}\ lignin\ C$	M. Ryan, unpublished
b_{HE}	Humus to extractives transformation efficiency	0.21	$g\ extractives\ C\ g^{-1}\ humus\ C$	M. Ryan, unpublished

Table A1. (continued)

Acronym	Definition	Value	Units	Reference
d_{CE}	Cellulose to extractives transformation rate parameter	0.0792	mo^{-1}	M. Ryan, unpublished
d_{EL}	Extractives to lignin transformation rate parameter	0.27	mo^{-1}	M. Ryan, unpublished
d_{LE}	Lignin to extractives transformation rate parameter	0.06	mo^{-1}	M. Ryan, unpublished
d_{HE}	Humus to extractives transformation rate parameter	3.88e-5	mo^{-1}	M. Ryan, unpublished
d_{LH}	Lignin to humus transformation rate parameter	0.01	mo^{-1}	M. Ryan, unpublished
Ac	C to N ratio of cellulose	71	$g C g^{-1} N$	Calibrated
Ae	C to N ratio of extractives	10	$g C g^{-1} N$	M. Ryan, unpublished
Al	C to N ratio of lignin	40	$g C g^{-1} N$	M. Ryan, unpublished
Ah	C to N ratio of humus	16.1	$g C g^{-1} N$	Back calculated
se	LCl shielding parameter for extractives	2.5	unitless	M. Ryan, unpublished
sc	LCl shielding parameter for cellulose	1.7	unitless	M. Ryan, unpublished
an	N loss parameter	0.67	mo^{-1}	Back calculated
k_{ND}	Decomposition N half saturation constant	0.001	$g N m^{-2}$	Calibrated
$Q_x(T)$	Temperature response curves for P, R (plant basal respiration), U, G (plant tissue growth), or D (decomposition); see Figure A1.			
m(M)	Moisture response curve for decomposition; see Figure A1.			

Variables, fluxes, parameters for tropical evergreen forests of the Amazon Basin (see "Model Calibration and Testing"). A complete description of the model is given by *Rastetter et al.* [1991]. Variables and parameters for which references are provided were constrained by measured data. "Back calculated" variables and parameters were calculated to be consistent with the assumption of year-to-year equilibrium in C and N stocks. "Calibrated" parameters were adjusted to provide a best fit to the measured data for tropical evergreen forests near Manaus, Brazil, San Carlos, Venezuela, and in the state of Mato Grosso, Brazil (see "Model Calibration and Testing: Calibration Procedure").

^a Although not represented as state variables by *Rastetter et al.* [1991], total soil + litter C and N must be specified during model calibration to enable calculation of C and N in humus and the three litter fractions of cellulose, extractives and lignin.

^b The growth parameter, k_{SX} , does not appear in work by *Rastetter et al.* [1991]. For X = foliage, stems, or roots, k_{SX} is added to the denominator of the equation for tissue growth with respect to C and N, that is, G_{XC} and G_{XN} .

^c Unlike other rate parameters in our model, the rate parameters for N use do not have inverse time units because the rate of N use in tissue growth is calculated as being proportional to C use.

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