

Interactions Between Carbon and Nitrogen Dynamics in Estimating Net Primary Productivity for Potential Vegetation in North America

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INTERACTIONS BETWEEN CARBON AND
NITROGEN DYNAMICS IN ESTIMATING NET
PRIMARY PRODUCTIVITY FOR POTENTIAL
VEGETATION IN NORTH AMERICA

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Abstract. We use the terrestrial ecosystem model (TEM), a process-based model, to investigate how interactions between carbon (C) and nitrogen (N) dynamics affect predictions of net primary productivity (NPP) for potential vegetation in North America. Data on pool sizes and fluxes of C and N from intensively studied field sites are used to calibrate the model for each of 17 non-wetland vegetation types. We use information on climate, soils, and vegetation to make estimates for each of 11,299 non-wetland, 0.5° latitude x 0.5° longitude, grid cells in North America. The potential annual NPP and net N mineralization (NETNMIN) of North America are estimated to be 7.032×10^{15} g C yr⁻¹ and 104.6×10^{12} g N yr⁻¹, respectively. Both NPP and NETNMIN increase along gradients of increasing temperature and moisture in northern and temperate regions of the continent, respectively. Nitrogen limitation of productivity is weak in tropical forests, increasingly stronger in temperate and boreal forests, and very strong in tundra ecosystems. The degree to which productivity is limited by the

availability of N also varies within ecosystems. Thus spatial resolution in estimating exchanges of C between the atmosphere and the terrestrial biosphere is improved by modeling the linkage between C and N dynamics. We also perform a factorial experiment with TEM on temperate mixed forest in North America to evaluate the importance of considering interactions between C and N dynamics in the response of NPP to an elevated temperature of 2° C. With the C cycle uncoupled from the N cycle, NPP decreases primarily because of higher plant respiration. However, with the C and N cycles coupled, NPP increases because productivity that is due to increased N availability more than offsets the higher costs of plant respiration. Thus, to investigate how global change will affect biosphere-atmosphere interactions, process-based models need to consider linkages between the C and N cycles.

INTRODUCTION

Terrestrial ecosystems play a major role in the global carbon budget. Through the process of photosynthesis, land plants annually remove between 90 and 120×10^{15} g carbon from the atmosphere [Houghton et al., 1985]. This is about 20 times more carbon than is emitted to the atmosphere during fossil fuel combustion. Approximately half of the carbon taken up by plants is returned to the atmosphere during plant respiration, and the remainder, known as net primary productivity (NPP), is incorporated into plant matter. Humans are dependent on a fraction of this NPP for food, fuel, and fiber.

Global change has the potential to alter the magnitude and temporal and spatial patterns of NPP for the terrestrial biosphere. Changes in a variety of factors including temperature, moisture, cloudiness,

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atmospheric CO₂ concentration, nutrient inputs in precipitation, and land-use patterns will affect NPP. These changes may alter productivity by affecting plant physiology and/or nutrient cycling rates. An important challenge is to develop the ability to predict how global change will affect NPP. Working toward this goal, we have developed the terrestrial ecosystem model (TEM) [Raich et al., 1991].

The TEM is a process-based model that was designed to estimate the spatial and temporal distribution of major carbon (C) and nitrogen (N) fluxes and pool sizes at continental to global scales. It was first applied to estimate the net primary productivity of potential vegetation in South America [Raich et al., 1991]. Although the spatial and temporal predictions of NPP in South America were evaluated by Raich et al. [1991], interactions between the C and N cycles in estimating productivity were not explicitly explored. Because much of the Amazon Basin is covered with phosphorous-deficient soils [Sanchez et al., 1982], this evaluation was not appropriate for South America.

In many northern and temperate ecosystems, NPP is known to be limited by the availability of inorganic N [Mitchell and Chandler, 1939; Safford and Filip, 1974; Van Cleve and Zasada, 1976; Auchmoody and Smith, 1977; Dodd and Lauenroth, 1979; Ellis, 1979; Shaver and Chapin, 1980; Risser et al., 1981; Aber et al., 1982; Peterson, 1982; Pastor et al., 1984; Chapin et al., 1986; Shaver and Chapin, 1986; Chapin, 1991a; Vitousek and Howarth, 1991]. In North America these ecosystems have been well studied relative to other continents. Patterns of NPP are understood, at least qualitatively, along north-south temperature gradients in northern North America and east-west moisture gradients in temperate North America. These gradients provide an opportunity to qualitatively check predictions of NPP and to examine how the strength of the linkages between C and N dynamics varies spatially. In this study we apply TEM to North America and evaluate how interactions between the C and N cycles affect predictions of NPP.

Interactions between the C and N cycles are predicted to be important in the response of some ecosystems to elevated temperature [Pastor and Post, 1986, 1988; Bonan et al., 1990; Schimel et al., 1990; Nadelhoffer et al., 1991; Rastetter et al., 1991]. We were interested in evaluating the importance of considering the linkage between C and N dynamics in predicting the response of NPP. We do this by performing a factorial experiment on temperate mixed forest in North America in which we run TEM under different temperature scenarios with the C and N cycles either coupled or uncoupled.

MODEL DESCRIPTION AND MODIFICATIONS

Model Description

The TEM uses spatially referenced information (resolution: 0.5° latitude x 0.5° longitude) on climate, soils, and vegetation to make monthly estimates of important C and N fluxes and pool sizes. TEM is a

highly aggregated model (Figure 1) that consists of five pools (C in vegetation, N in vegetation, C in soil, organic N in soil, inorganic N in soil) and nine fluxes (gross primary productivity, plant respiration, C in litter production, soil respiration, N input to the ecosystem, N uptake by vegetation, N in litter production, net N mineralization, N lost from the ecosystem).

The basic strategy in extrapolating TEM for a region is to run the model to equilibrium for each grid cell (0.5° latitude x 0.5° longitude). Running the model for a particular grid cell requires the use of monthly climatic data and the soil- and vegetation-specific parameters appropriate to the grid cell. The water balance model (WBM) of Vorosmarty et al. [1989] is used to produce hydrologic inputs for TEM. Although some of the vegetation-specific parameters in the model can be defined from published information, others must be determined by calibrating the model to the steady state fluxes and pool sizes of an intensively studied field site, the calibration site (see Table 1).

The version of the model applied to South America is fully described by Raich et al. [1991]. We have made several modifications to the original model. Foremost among these is the design of a new feedback algorithm between C and N uptake. Other changes involve calculation of N in litter production, temperature effects on gross primary productivity and plant maintenance respiration, and leaf conductivity to carbon dioxide in arid regions.

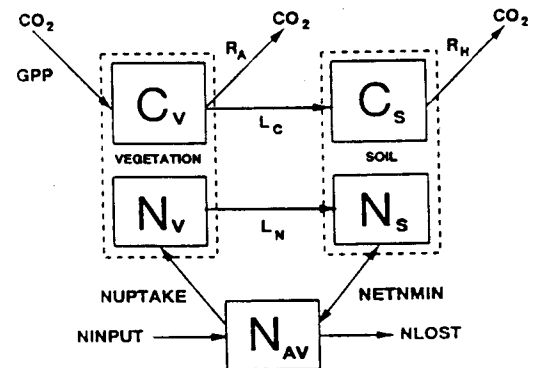


Fig. 1. The terrestrial ecosystem model (TEM). The state variables are: carbon in vegetation (C_v); nitrogen in vegetation (N_v); organic carbon in soils and detritus (C_s); organic nitrogen in soils and detritus (N_s); and available soil inorganic N (N_{AV}). Arrows show carbon and nitrogen fluxes: GPP , gross primary productivity; R_A , autotrophic respiration; R_H , heterotrophic respiration; L_C , litterfall C; L_N , litterfall N; $NUPTAKE$, N uptake by vegetation; $NETNMIN$, net N mineralization of soil organic N; $NINPUT$, N inputs from outside the ecosystem; and $NLOST$, N losses from the ecosystem.

TABLE 1. Study Sites From Which Data Was Gathered and Used to Calibrate Some of the Vegetation-Specific Parameters in the Terrestrial Ecosystem Model

Site Name	Vegetation Type	Location	
Toolik Lake (USA)	polar desert/alpine tundra	65° 26'N,	145° 30'W
Toolik Lake (USA)	wet/moist tundra	65° 26'N,	145° 30'W
Schefferville (Canada)	boreal woodland	54° 43'N,	66° 42'W
Bonanza Creek (USA)	boreal forest	64° 45'N,	148° 15'W
H. J. Andrews (USA)	temperate coniferous forest	44° 15'N,	122° 20'W
Curlew Valley (USA)	arid shrubland	41° 05'N,	113° 05'W
Pawnee (USA)	short grassland	40° 49'N,	104° 46'W
Osage (USA)	tall grassland	36° 57'N,	96° 33'W
Cedar Creek (USA)	temperate savanna	45° 35'N,	93° 10'W
Harvard Forest (USA)	temperate deciduous forest	42° 32'N,	72° 10'W
Harvard Forest (USA)	temperate mixed forest	42° 32'N,	72° 10'W
Taita (New Zealand)	temperate broadleaved evergreen forest	41° 11'S,	174° 58'E
Nylsvley (South Africa)	tropical savanna	24° 39'S,	28° 42'E
Guanica (Puerto Rico)	xeromorphic woodland	17° 55'N,	66° 55'W
Chakia (India)	tropical deciduous forest	25° 20'N,	83° 00'E
Ducke (Brazil)	tropical evergreen forest	2° 50'S,	59° 57'W

Feedback Between C and N Uptake by the Vegetation

In the initial version of TEM, feedback between C and N uptake by the vegetation was designed to maintain the vegetation C to N ratio at a target ratio that was specific to the vegetation type. This was accomplished by allowing the vegetation to acclimate to the environment of the grid cell by adjusting allocation of effort between C and N uptake. This is analogous to adjusting the shoot to root ratio of the vegetation.

This feedback algorithm, although interesting from the perspective of allocation theory, has several drawbacks. First, because the rate of acclimation in the model is chosen arbitrarily, the algorithm can only be used to find the equilibrium solution of a grid cell; the transient response may be inappropriate. Second, the algorithm is not designed to respond to changes in carbon-nitrogen balance that occur on a monthly time scale; use of the model to look at seasonal exchanges of gases with the atmosphere requires subannual feedback. Finally, C to N ratios of many vegetation types are known to change during succession. This is especially the case for forests in which C-rich heartwood increases through succession resulting in an increasing C to N ratio. To assist in future development of a successional version of TEM, we needed to modify the model so that the aggregated C:N of vegetation was not maintained as a constant. We therefore designed a new feedback algorithm between C and N uptake.

Photosynthesis is known to decrease when the availability of inorganic N is restricted [Chapin, 1980; Evans, 1983; Clarkson, 1985; Chapin et al., 1988; Chapin, 1991b]. This response is the result of the feedback of N availability on C uptake. The C to N ratio of new production (P_{cn}) is commonly measured in ecosystem studies, and this information can be used by TEM to determine when the vegetation is stressed by the availability of N: if the calculated C to N ratio of

production ($PPROD_{cn}$, the potential C to N ratio of production) is greater than P_{cn} , then the vegetation is stressed by the availability of N. We expect photosynthesis to monotonically decrease as N stress increases. This relationship, as we have described it, is a feedback curve of the effect of N availability on C uptake.

If the relationship is scaled to decrease from 1 to 0 as N stress increases, then the feedback curve $f(NA)$ can be used in the GPP equation to quantify the effect of N availability on C uptake (similar to the effects of other factors):

$$GPP = C_{max} f(PAR) f(CO_2, H_2O) f(LEAF) f(T) f(NA)$$

where C_{max} is the maximum rate of C assimilation, PAR is photosynthetically active radiation, LEAF (i.e., leaf phenology) is leaf area relative to the maximum leaf area, T is temperature, and NA is nitrogen availability. We assume that the shape of $f(NA)$ is parabolic (Figure 2). The amount of C potentially available for production is the calculated NPP based on GPP with $f(NA)$ set to 1. The point at which $f(NA)$ becomes 0, the parameter CN_{max} , is important in quantifying the severity of the feedback.

If, after applying $f(NA)$ on the calculation of GPP, the resulting NPP to N uptake ratio falls below P_{cn} , then feedback is curtailed during model operation so that the ratio equals P_{cn} . Thus the photosynthetic machinery is only slowed to the point at which the vegetation takes up enough C to match N uptake. For the case when the final NPP to N uptake ratio is greater than P_{cn} , the additional N required to build tissue is implicitly assumed to come from the recycling of N within the vegetation. On an annual basis this means that N in production must equal the sum of N in uptake and recycled N. This aspect of the feedback algorithm is

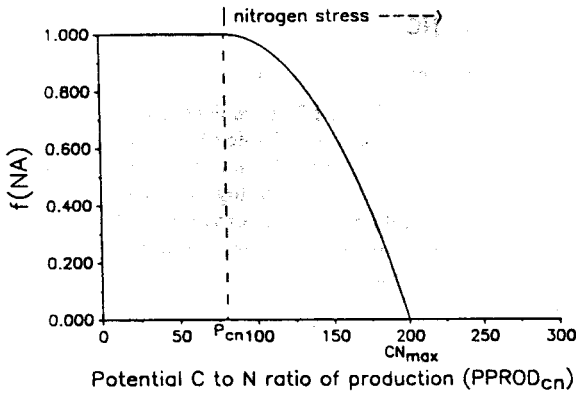


Fig. 2. Effect of nitrogen availability (NA) on the relative uptake of C by the vegetation [$f(\text{NA})$], i.e., relative GPP. Nitrogen stress increases as the potential C to N ratio of production (PPROD_{cn}) rises above P_{cn} , the annual C to N of production at the calibration site. When PPROD_{cn} is less than P_{cn} , $f(\text{NA})$ is unaffected. As PPROD_{cn} increases above P_{cn} , $f(\text{NA})$ decreases according to a parabolic function. The calibrated parameter CN_{max} , which describes the severity of the feedback, is the point at which $f(\text{NA})$ goes to 0.

particularly important in the N cycle of arctic and subarctic ecosystems, where recycling of N by the vegetation is substantial [Chapin et al., 1980; Chapin and Kedrowski, 1983; Jonasson and Chapin, 1985; Shaver et al., 1990; Chapin and Moilanen, 1991; Shaver and Chapin, 1991].

Similar to the effect of N availability on C uptake, the uptake of N should monotonically decrease as the potential C to N ratio of production decreases below P_{cn} , i.e., the uptake of N should decrease as C stress increases. We have incorporated this relationship into the equation for N uptake as the parabolic function $f(\text{CA})$:

$$\text{NUPTAKE} = N_{\text{max}} f(\text{inorganic N, H}_2\text{O}) f(\text{T}) f(\text{CA})$$

where N_{max} is the maximum rate of N uptake by the vegetation, T is temperature, and CA is carbon availability. The amount of N potentially available for production is determined with $f(\text{CA})$ set to 1. In the implementation of this feedback, $f(\text{CA})$ goes to 0 as NPP goes to 0.

N in Litter Production

In the previous version of TEM, N in litter production was controlled to maintain the C to N ratio of the vegetation at a target ratio. Because we are not directly controlling the C to N ratio of vegetation in this version of TEM, we changed the calculation of this flux. We calculate the amount of N in litter production similar to the calculation of the amount of C in litter production:

$$\text{NFALL} = \frac{(\text{annual N uptake})}{12 (\text{mean annual } N_V)}$$

$$L_{N_t} = N_{V_t} (\text{NFALL})$$

where annual N uptake and mean annual N_V are defined from literature sources for the specific sites used to calibrate TEM, and L_{N_t} and N_{V_t} are the amount of N in litter production and vegetation, respectively, at the time step t. The parameter NFALL is assumed to be constant within each vegetation type. This algorithm causes L_N to track seasonal changes in N_V .

Temperature Effects on Gross Primary Productivity

In the initial version of TEM the temperature effects on gross primary production (GPP) were assumed to be the same as the measured effects on net photosynthesis. This was modeled with a parabolic function that rose from 0 to 1 between the minimum and optimum temperatures for photosynthesis and decreased from 1 to 0 between the optimum and maximum temperatures for photosynthesis. Although the shape of this relationship is reasonable for net photosynthesis, which is the difference between gross photosynthesis and leaf respiration, it is not appropriate for gross photosynthesis. Because of photorespiration, gross photosynthesis generally approaches an asymptote as temperature increases [Larcher, 1980; Fitter and Hay, 1981] and does not decrease until temperatures are high enough to cause denaturing of photosynthetic enzymes. In the current version of TEM we allowed the temperature effects on GPP to increase from 0 to 1 between the minimum and optimum temperature of photosynthesis as in the original version of TEM but maintained the temperature multiplier of GPP to be 1 above the optimum temperature. We did not simulate the denaturing effects of temperature because the temperatures in our climatic data sets never rise into the region of denaturation. Even if the temperatures were to rise into the denaturing region, other factors in the model would invariably cause GPP to drop to very small values.

Temperature Effects on Plant Maintenance Respiration

As in the initial version of TEM, we model plant maintenance respiration (R_m) as follows:

$$R_m = K_r (C_V) e^{(r_T) T}$$

where K_r is the per-gram-biomass respiration rate of the vegetation at 0°C , C_V is the mass of carbon in the vegetation, T is the mean monthly air temperature, and r_T is the instantaneous rate of change in respiration. In the initial version of TEM, r_T was determined by assuming that Q_{10} , the rate of change in respiration due to a 10° increase in temperature, is 2. Because $r_T = \text{Ln}(Q_{10})/10$, this resulted in r_T of 0.0693. The measured

values of Q_{10} are commonly around 2 in the region of 5°-20° C but below 5° C become greater and above 20° C fall off to 1.5 or less [Larcher, 1980]. We assumed a linear increase of Q_{10} from 2.0 to 2.5 between 5° and 0° C, a constant Q_{10} of 2.0 between 5° and 20° C, and a linear decrease of Q_{10} from 2.0 to 1.5 between 20° and 40°. We modeled this temperature dependence with a third-order polynomial regression using integer values of temperature between 0° and 40° C to obtain the smooth relationship:

$$Q_{10} = 2.35665 - 0.05308T + 0.00238T^2 - 0.00004T^3$$

where T is the mean monthly temperature.

Leaf Conductivity to Carbon Dioxide in Arid Regions

G_V , the unitless multiplier in the model that causes leaf conductivity to CO_2 to change in response to moisture availability, was modified for $EET/PET \leq 0.1$, as follows:

$$G_V = -10 (EET/PET)^2 + 2.9 (EET/PET)$$

where EET is estimated evapotranspiration and PET is potential evapotranspiration. This function allows the minimum possible G_V to be 0 instead of 0.1, a plant response that seems possible in extremely arid regions. For $EET/PET > 0.1$, calculation of G_V is the same as in the work by Raich et al. [1991]. The shape of the new function allows the slopes to match at $EET/PET = 0.1$.

METHODS

Parameterization of TEM

Parameters in TEM are vegetation-specific (Tables 2 and 3), soil-specific (Table 4), or constant [see Raich et al., 1991]. We defined the vegetation-specific parameters of the leaf phenology submodel (see Table 2) based on data from numerous phenology studies. To define the parameters that determine the response of gross primary production to temperature for each vegetation type (T_{min} and T_{opt} ; see Table 3), we used information compiled by Larcher [1980].

We used data from intensively studied field sites to estimate the remaining vegetation-specific parameters (see Table 3) for 16 non-wetland ecosystems (see appendix for compilation of data). Mediterranean shrubland, another ecosystem considered by TEM, uses the same calibrated parameters as xeromorphic woodland. However, the two ecosystems have different parameters for the leaf phenology submodel. The WBM does not adequately represent the water balance for ecosystems with permafrost (i.e., boreal forest, boreal woodland, wet/moist tundra, polar desert/alpine tundra). For these ecosystems we calibrated and ran the model with soil moisture equal to field capacity and estimated evapotranspiration equal to potential evapotranspiration.

Fertilization studies in natural ecosystems have often been conducted to determine the degree to which NPP is limited by N availability. We used data on the

TABLE 2. Values of Parameters Used to Estimate the Relative Photosynthetic Capacity of the Vegetation, $f(LEAF)$

Vegetation Type	Parameter			
	a	b	c	min
Polar desert/alpine tundra	0.7964	0.4664	-0.0287	0.00
Wet/moist tundra	0.7964	0.4664	-0.0287	0.00
Boreal woodland	0.7149	0.2944	0.1329	0.20
Boreal forest	0.4289	0.3330	0.3223	0.50
Temperate coniferous forest	0.0000	0.0000	0.0000	1.00
Arid shrubland	0.4640	0.6708	-0.0068	0.25
Short grassland	0.4437	0.6520	0.0098	0.10
Tall grassland	0.4746	0.5807	-0.0564	0.05
Temperate savanna	0.7808	0.4427	-0.0828	0.05
Temperate deciduous forest	0.8330	0.3520	-0.0754	0.02
Temperate mixed forest	0.4162	0.3516	0.2874	0.50
Temperate broadleaved evergreen forest	0.0000	0.0000	0.0000	1.00
Mediterranean shrubland	0.2669	0.9592	-0.0773	0.25
Tropical savanna	0.3366	0.6451	0.0422	0.15
Xeromorphic woodland	0.4423	0.5426	0.0713	0.25
Tropical deciduous forest	0.4423	0.5426	0.0713	0.25
Tropical evergreen forest	0.4423	0.5426	0.0713	0.25

Parameters are defined by Raich et al. [1991].

TABLE 3. Values of the Vegetation-Specific Parameters Used in the Terrestrial Ecosystem Model Except for the Parameters of the Leaf Phenology Model

Vegetation Type	P_{cn}	CN_{max}	C_{max}	K_r	K_d	KFALL	N_{max}	N_{up}	NFALL	T_{min}	T_{opt}
Polar desert/alpine tundra	36.54	1041.00	591.80	0.038900	0.001048	0.01204	0.21400	0.12000	0.00603	-1.0	15.0
Wet/moist tundra	30.00	1022.20	955.50	0.038900	0.000645	0.01333	0.39800	0.19800	0.00444	-1.0	15.0
Boreal woodland	41.50	465.20	761.80	0.009528	0.001082	0.00644	0.68500	0.15000	0.00521	-1.0	15.0
Boreal forest	53.00	344.60	676.20	0.002185	0.001396	0.00204	0.57150	0.06110	0.00938	-1.0	15.0
Temperate coniferous forest	89.17	462.75	1013.90	0.001316	0.001219	0.00103	0.48400	0.02900	0.00467	-1.0	18.0
Arid shrubland	30.56	214.00	492.00	0.006180	0.000973	0.01698	0.37680	0.13000	0.01154	1.0	31.0
Short grassland	54.42	170.88	779.20	0.017150	0.004323	0.05291	0.44290	0.17020	0.03314	0.0	27.0
Tall grassland	70.25	223.75	987.40	0.017150	0.001008	0.05449	0.27985	0.11552	0.07639	0.0	27.0
Temperate savanna	71.15	262.43	1092.75	0.006720	0.004620	0.01786	0.38860	0.06978	0.02865	-1.0	24.0
Temperate deciduous forest	67.71	235.52	1207.90	0.001465	0.002303	0.00348	0.68265	0.04846	0.01802	-1.0	20.0
Temperate mixed forest	76.92	283.73	1125.90	0.002255	0.002422	0.00366	0.47080	0.04960	0.01505	-1.0	19.0
Temperate broadleaved evergreen forest	92.95	313.30	780.75	0.001833	0.002110	0.00403	0.46610	0.04968	0.01191	0.0	25.0
Tropical savanna	70.00	250.00	717.50	0.008772	0.003439	0.02417	2.58800	0.08960	0.03333	1.0	30.0
Xeromorphic woodland	60.00	250.00	1312.60	0.009685	0.001841	0.01066	0.94270	0.08555	0.01296	-1.0	25.0
Tropical deciduous forest	70.00	250.00	2947.00	0.006678	0.002242	0.00514	2.13700	0.10141	0.01324	0.0	27.0
Tropical evergreen forest	65.00	250.00	2748.80	0.005104	0.001250	0.00389	2.80800	0.07110	0.00667	2.0	28.0

See Table 2 for parameters of the leaf phenology model. Sites used to calibrate the vegetation types are listed in Table 1. Parameters not defined in this paper are defined by Raich et al. [1991].

maximum response of NPP to N fertilization (NPPSAT in the tables of the appendix) to determine, and therefore constrain, the maximum rate of C assimilation by the vegetation, i.e., the parameter C_{max} in the GPP equation. With this information in TEM we are able to run the C cycle uncoupled from the N cycle to determine productivity as if N were not limiting.

For the calibration sites that were determined to be N limited, i.e., the first 12 ecosystems in Table 1, we calculated P_{cn} as the ratio of NPP to N in production; N in production is assumed to equal the sum of NUPTAKE and NMOBIL in the tables of the appendix. The parameter CN_{max} was then determined for these ecosystems by calibrating the model to the equilibrium pools and fluxes of the calibration site. This procedure assumes that N in production equals N required for production, i.e., "N requirement." However, for systems that are not N limited, N in production may not reflect N requirement because of the possibility of luxury N uptake. We calibrated the tropical and subtropical ecosystems, i.e., the last four ecosystems in Table 1, as if they were not N limited. For these calibrations we set CN_{max} to 250, a value approximately equal to that for temperate deciduous forest, and adjusted P_{cn} upward from the ratio of NPP to N in production until there was no N limitation.

An estimate of gross primary production (GPP) is required to calibrate a parameter in the plant respiration equation. In cases where the GPP budget of the calibration site was lacking, we used the method of Ryan [1991a] to estimate GPP. This method determines a gross production budget by estimating the following quantities: net primary production and associated construction respiration of aboveground wood and foliage, aboveground maintenance respiration, and belowground carbon allocation. Aboveground wood and foliage production are determined from field studies and construction respiration is estimated to be 25% of production. Empirical relationships between respiration and structural nitrogen [Ryan, 1991b] are used to estimate aboveground maintenance respiration. Belowground carbon allocation is estimated from fine litterfall using an empirical relationship [Raich and Nadelhoffer, 1989].

In this version of TEM, field capacities for different soil textures (FC in Table 4) were defined from Ratliff et al. [1983] rather than from Saxton et al. [1986]; the estimates of the former are based on field studies, whereas those of the latter are based on laboratory studies. The soil-specific parameters that define the influence of soil moisture on decomposition were defined for the new field capacities as described by Raich et al. [1991].

In the initial version of TEM the half-saturation constant for the effect of atmospheric CO_2 concentration on GPP was chosen to yield a 23% increase with a doubling of CO_2 . This value is at the low end of those obtained in empirical studies that provided adequate nutrients and water to plants (range 24 to 50% [see Raich et al., 1991]). In this version of TEM we chose an intermediate yield of 37% to define this parameter.

TABLE 4. Values of Soil-Specific Parameters Used in the Terrestrial Ecosystem Model

Parameter	Texture				
	Sand	Sandy Loam	Loam	Clay Loam	Clay
FC (% saturation)	54.0	58.0	62.0	63.0	64.0
M _{opt} (% saturation)	62.0	65.0	68.0	71.0	73.0
m1	0.350	0.044	-0.289	-0.425	-0.732
M _{sat}	0.5000	0.5625	0.6250	0.6875	0.7500

Parameters are defined by Raich et al. [1991].

Application of TEM to North America

The sources for the air temperature, cloudiness, elevation, precipitation, and soil texture data that we used for North America are described by Raich et al. [1991]. We used the water balance model (WBM) of Vorosmarty et al. [1989] with refinements by E. B. Rastetter (personal communication, 1991) to produce estimates of potential evapotranspiration, actual evapotranspiration, and soil moisture. Monthly data sets of photosynthetically active radiation and relative leaf phenology were generated as described by Raich et al. [1991]. As in the application of the model to South America, we set the monthly atmospheric concentration of CO₂ to 340 ppmv for all grid cells. We also assumed N inputs and losses to be negligible in each grid cell.

Each of the 12,260 grid cells in North America was assigned to an ecosystem type (Plate 1). For Alaska, Canada, and the continental United States we digitized maps of potential, i.e., undisturbed natural, vegetation to a resolution of 0.5° latitude x 0.5° longitude [Joint Federal-State Land Use Planning Commission for Alaska, 1973; Rowe, 1972; Kuchler, 1964]. For Mexico

and Central America we modified an extant 1° x 1° data set [Matthews, 1983] to more accurately represent transitions between vegetation types at the 0.5° x 0.5° resolution. The 11,299 grid cells for which we ran the model account for 93.8% of the 22.14 x 10⁶ km² in North America. We did not make predictions for ice, wetland ecosystems, and open water.

For extrapolating TEM the run for each grid cell starts with the January values of the driving variables. Therefore the initial values of the pools for a grid cell were set equal to those of December from the appropriate vegetation-specific calibration (Table 5). A grid cell was determined to have reached equilibrium when the annual fluxes of NPP, C in litter production, and soil respiration differed by less than 1 gC m⁻² yr⁻¹, and those of NETNMIN, N uptake by vegetation, and N in litter production differed by less than 0.01 gN m⁻² yr⁻¹.

Experiment Examining the Interactions of C and N in the Response of NPP to Elevated Temperature

We used TEM in a factorial experiment on temperate mixed forest in North America to examine interactions

TABLE 5. Initial Values of the State Variables for Extrapolating the Terrestrial Ecosystem Model to Grid Cells Within Each Vegetation Type

Vegetation Type	C _v	N _v	C _s	N _s	N _{AV}
Polar desert/alpine tundra	454.20	6.53	5997.40	259.92	0.42
Wet/moist tundra	757.69	15.05	17997.88	1099.70	0.41
Boreal woodland	2208.73	24.10	13340.88	735.16	0.51
Boreal forest	9006.52	20.06	10991.50	370.11	0.68
Temperate coniferous forest	43496.64	75.02	21011.28	420.03	0.96
Arid shrubland	533.51	19.50	10994.65	799.59	1.68
Short grassland	324.38	8.89	3805.65	389.61	2.24
Tall grassland	675.25	6.15	16016.03	1549.38	4.38
Temperate savanna	2120.73	16.28	4337.19	399.51	4.37
Temperate deciduous forest	15596.35	37.42	11227.59	558.93	2.13
Temperate mixed forest	14845.94	36.37	10675.52	529.92	2.01
Temperate broadleaved evergreen forest	14986.23	41.92	13002.84	460.12	0.97
Tropical savanna	1422.26	24.03	8006.78	401.07	1.89
Xeromorphic woodland	4516.18	93.14	11121.72	949.23	2.53
Tropical deciduous forest	12053.10	175.32	7844.72	943.53	1.82
Tropical evergreen forest	22512.07	300.34	15059.09	900.06	0.59

The values are defined from the December pools of the corresponding vegetation-specific calibration. The state variables are defined in Figure 1. All values are in g m⁻².

