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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 CO_2 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.

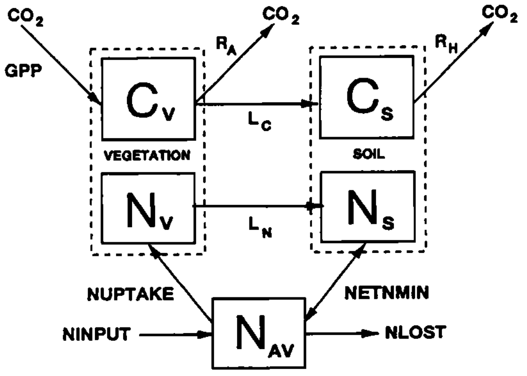

Fig. 1. The terrestrial ecosystem model (TEM). The state variables are: carbon in vegetation (C_V); nitrogen in vegetation (N_V); organic carbon in soils and detritus (C_S); organic nitrogen in soils and detritus (N_S); and available soil inorganic N (N_{AV}). Arrows show carbon and nitrogen fluxes: 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 analagous 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

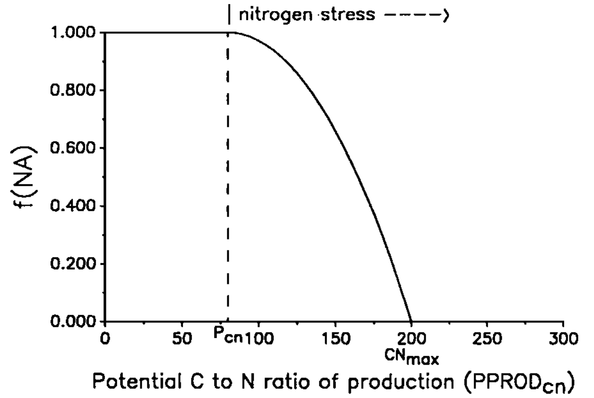

Fig. 2. Effect of nitrogen availability (NA) on the relative uptake of C by the vegetation [f(NA)], i.e., relative GPP. Nitrogen stress increases as the potential C to N ratio of production ($PPROD_{cn}$) rises above P_{cn}, the annual C to N of production at the calibration site. When $PPROD_{cn}$ is less than P_{cn}, f(NA) is unaffected. As $PPROD_{cn}$ increases above P_{cn}, f(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(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(CA):

$$\mathrm{NUPTAKE} = N_{max}\, f(\text{inorganic N}, H_2O)\, f(T)\, f(CA)$$

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(CA) set to 1. In the implementation of this feedback, f(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:

$$\mathrm{NFALL} = \frac{(\text{annual N uptake})}{12\,(\text{mean annual } N_v)}$$

$$L_{Nt} = N_{Vt}\,(\mathrm{NFALL})$$

where annual N uptake and mean annual N_V are defined from literature sources for the specific sites used to calibrate TEM, and L_{Nt} and N_{Vt} 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 $r_T = \mathrm{Ln}(Q_{10})/10$, 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 ≤ 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 CO_2 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 10^6 km^2 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}.

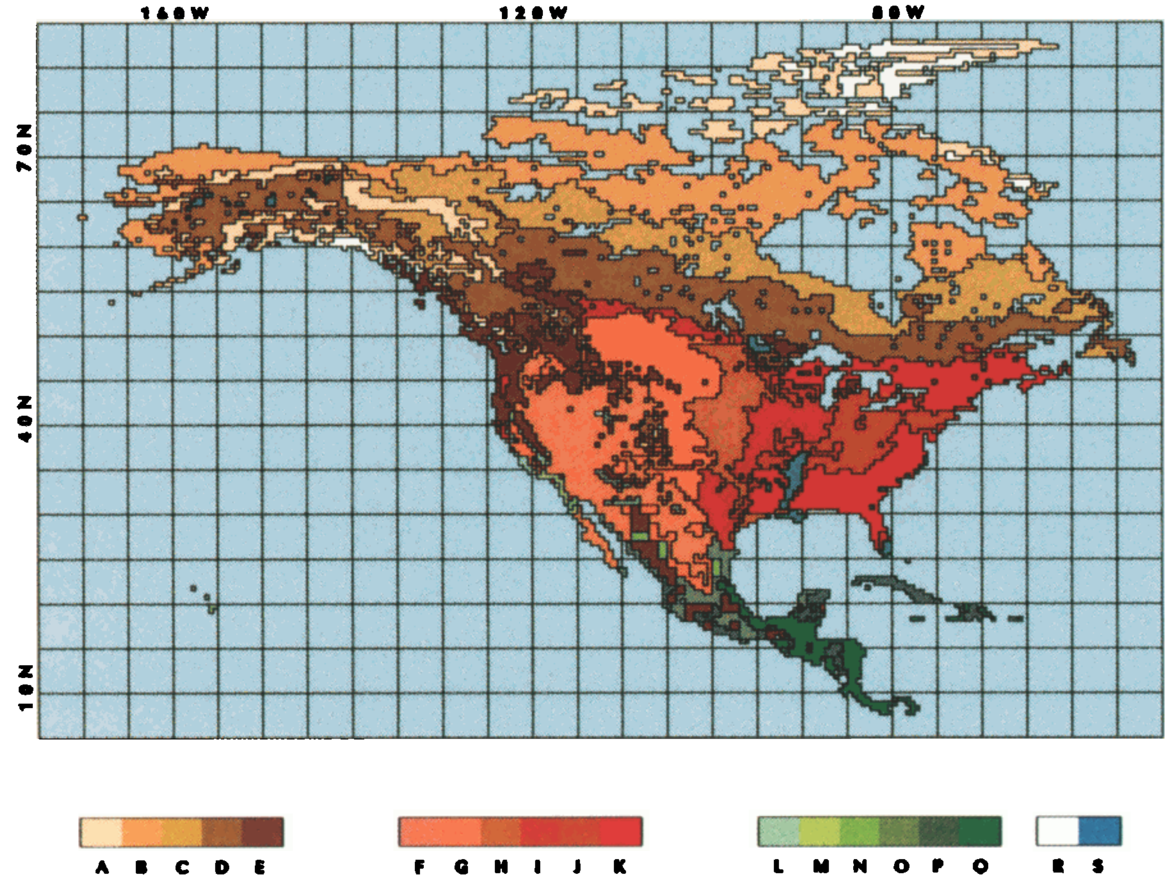

Plate 1. Potential natural vegetation of North America as defined for the terrestrial ecosystem model. The vegetation types are: A, polar desert/alpine tundra; B, wet/moist tundra; C, boreal woodland; D, boreal forest; E, temperate coniferous forest; F, arid shrubland; G, short grassland; H, tall grassland; I, temperate savanna; J, temperate deciduous forest; K, temperate mixed forest; L, temperate broadleaved evergreen forest; M, mediterranean shrubland; N, tropical savanna; O, xeromorphic woodland; P, tropical deciduous forest; Q, tropical evergreen forest; R, ice; and S, wetland ecosystems.

of the C and N cycles in the response of NPP to an elevated temperature of 2° C. The C cycle in TEM can be uncoupled from the N cycle by not allowing any feedback of N availability on C uptake. This is implemented in the model by setting f(NA) to 1. The basic design of the experiment is a 2 x 2 factorial of nitrogen coupling (uncoupled, coupled) x temperature change (TEM[+0° C], TEM[+2° C]). For the response in the uncoupled treatments to be comparable with that of the coupled treatments, we adjusted the parameter C_{max} in the uncoupled calibration so that the baseline NPP calculated for the calibration site was identical for both the uncoupled and coupled versions of the model. In the elevated-temperature treatments we increased each monthly temperature for all grid cells by 2° C.

Increased temperature may affect the response of NPP due to effects of temperature on the metabolism of plant/soil processes. However, soil moisture may also change as a result of increased evapotranspiration. Therefore the response of NPP may also be due, in part, to the effects of changes in soil moisture on the metabolism of plant/soil processes. We attempted to separate these effects by using the WBM-generated hydrologic inputs for TEM as a third factor (WBM [+0° C], WBM[+2° C]) in the experiment (Table 6). In the elevated-temperature scenarios for WBM we increased each monthly temperature for all grid cells by 2° C.

Plate 2. Annual net primary productivity of potential vegetation in North America as determined by the terrestrial ecosystem model.

Plate 3. Annual net nitrogen mineralization of potential vegetation in North America as determined by the terrestrial ecosystem model.

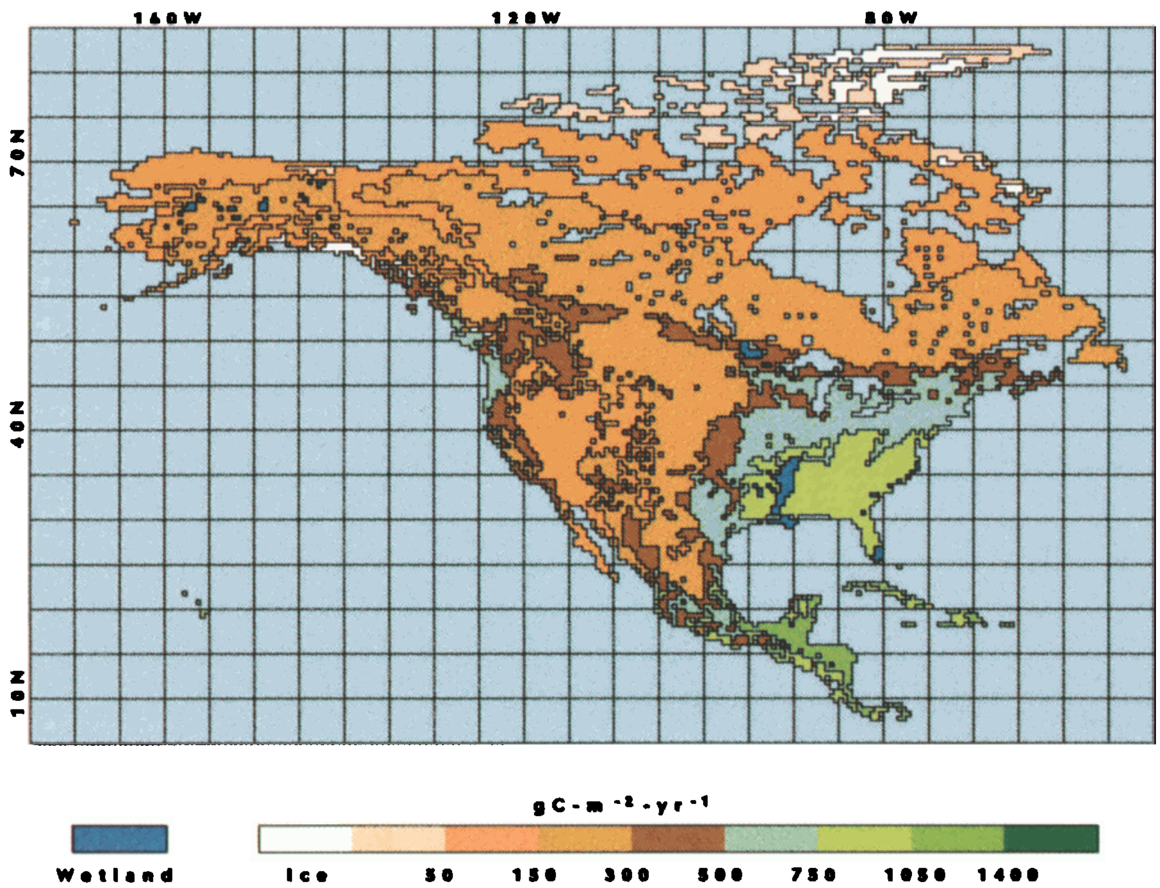

Plate 2.

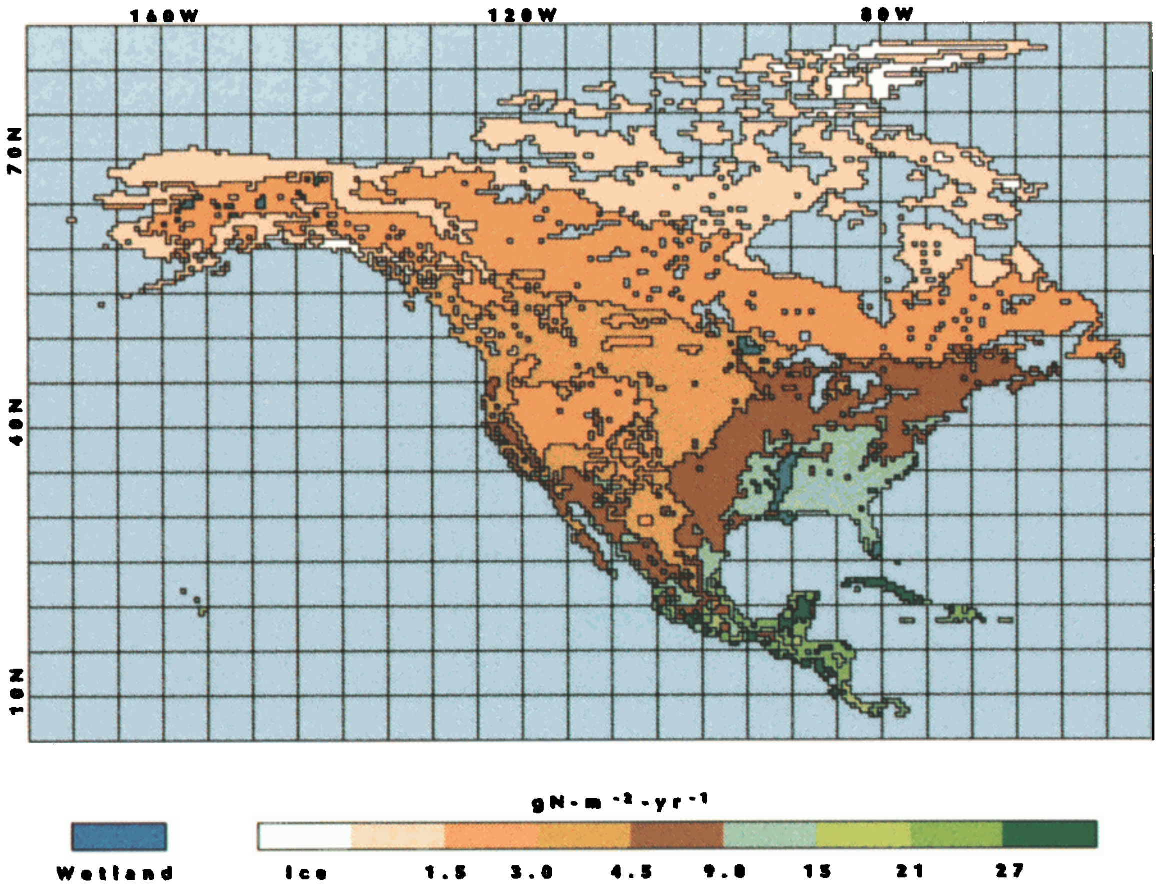

Plate 3.

TABLE 6. Design of Experiment on Temperate Mixed Forest in North America to Examine Interactions of the C and N Cycles in the Response of NPP to an Elevated Temperature of 2° C

	C Cycle Uncoupled From the N Cycle		C Cycle Coupled to the N Cycle	
	TEM[+0° C]	TEM[+2° C]	TEM[+0° C]	TEM[+2° C]
WBM [+0° C]	baseline for uncoupled response	effects of temperature on plant processes	baseline for coupled response	effects of temperature on plant and soil processes
WBM [+2° C]	effects of soil moisture on plant processes	effects of temperature and soil moisture on plant processes	effects of soil moisture on plant and soil processes	effects of temperature and soil moisture on plant and soil processes

The C cycle is uncoupled from the N cycle by not allowing the availability of N to affect the uptake of C. Mean monthly temperature was increased by 2° C for each grid cell when running the terrestrial ecosystem model (TEM) or the water balance model (WBM) for an elevated temperature scenario.

RESULTS

Annual Net Primary Productivity

For undisturbed non-wetland vegetation, TEM estimates the annual NPP for North America to be 7.032 x 10^{15} gC yr^{-1}, or 338.7 gC m^{-2} yr^{-1} (Table 7). Among all ecosystems, temperate mixed forest accounts for the greatest exchange of CO_2 with the atmosphere in North America (18.8%, Table 7). Mean NPP estimates for ecosystems range from 69.5 gC m^{-2} yr^{-1} for polar desert of northern Canada to 1113.0 gC m^{-2} yr^{-1} for tropical evergreen forest of Central America. Estimates for individual grid cells range from 31.3 gC m^{-2} yr^{-1} in polar desert to 1489.4 gC m^{-2} yr^{-1} in tropical deciduous forest (Table 7, Plate 2).

Polar desert, moist tundra, boreal woodland, boreal

TABLE 7. Estimates by the Terrestrial Ecosystem Model of Annual Net Primary Productivity (NPP) for Potential Vegetation in North America

Vegetation Type	Area, 10^6 km^2	Cells	Total NPP, 10^{15} gC yr^{-1}	Max NPP, gC m^{-2} yr^{-1}	Min NPP, gC m^{-2} yr^{-1}
Polar desert/alpine tundra	1.11	1060	0.077	124.9	31.3
Wet/moist tundra	2.54	2093	0.246	169.3	56.6
Boreal woodland	2.18	1387	0.415	257.5	94.7
Boreal forest	3.43	1991	0.789	358.5	116.8
Temperate coniferous forest	1.51	693	0.596	684.0	185.7
Arid shrubland	2.01	810	0.267	265.2	53.4
Short grassland	1.60	706	0.334	398.2	131.6
Tall grassland	0.77	329	0.252	723.3	201.8
Temperate savanna	1.09	464	0.564	946.8	278.0
Temperate mixed forest	1.80	757	1.323	1020.1	380.7
Temperate deciduous forest	0.90	376	0.659	948.6	408.6
Temperate broadleaved evergreen forest	0.05	19	0.022	915.2	289.2
Mediterranean shrubland	0.06	24	0.021	429.1	212.0
Tropical savanna	0.11	40	0.046	827.3	212.0
Xeromorphic forest	0.48	169	0.212	722.8	150.4
Tropical deciduous forest	0.46	159	0.472	1489.4	639.0
Tropical evergreen forest	0.66	222	0.737	1413.5	716.5
Total	20.76	11,299	7.032	1489.4	31.3

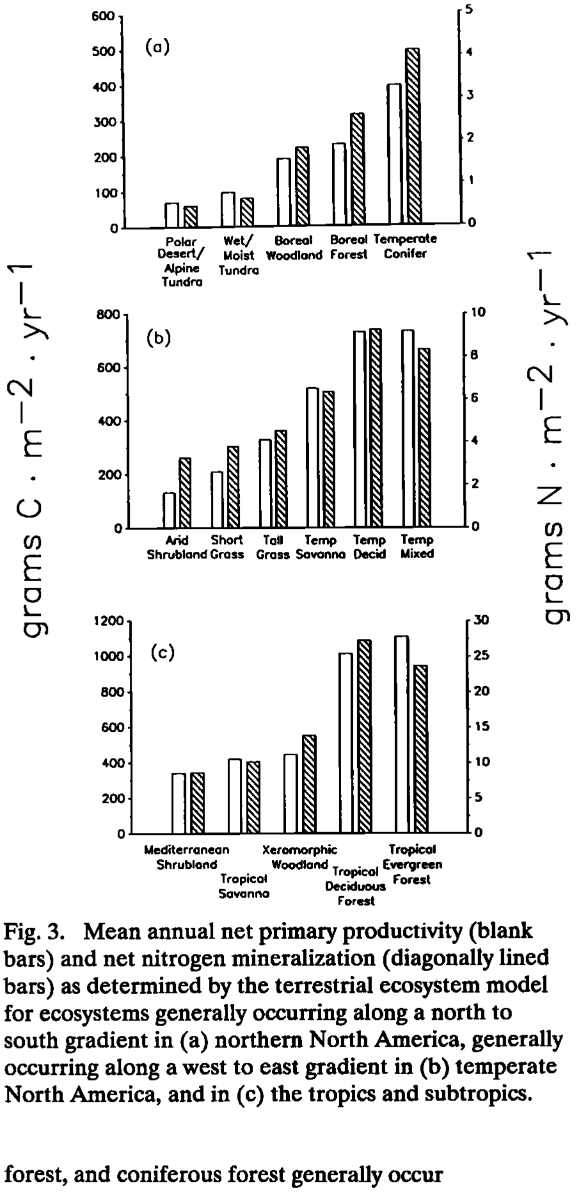

Fig. 3. Mean annual net primary productivity (blank bars) and net nitrogen mineralization (diagonally lined bars) as determined by the terrestrial ecosystem model for ecosystems generally occurring along a north to south gradient in (a) northern North America, generally occurring along a west to east gradient in (b) temperate North America, and in (c) the tropics and subtropics.

forest, and coniferous forest generally occur sequentially from north to south in northern North America (Plate 1). Estimates of mean annual NPP increase across this ecosystem gradient (Figure 3a). Mean annual temperature and NPP generally increase along a north-south transect in western Canada that spans this ecosystem gradient (Figure 4a). However, as the transect crosses the Canadian Rockies, NPP changes rapidly because the vegetation is very heterogeneous (temperate coniferous forest, boreal forest, and alpine tundra). Mean annual temperature is probably overestimated in this region because of the lack of meteorological stations at the higher elevations. The simulated NPP in this area is lower than would be expected on the basis of the temperature data because C and N dynamics in TEM are constrained by the parameters associated with boreal forest and alpine tundra.

Arid shrublands, short grassland, tall grassland, temperate savanna, and temperate deciduous and mixed forests generally occur sequentially from west to east in temperate North America (Plate 1). Estimates of mean annual NPP increase along this ecosystem gradient (Figure 3b). Both annual precipitation and mean annual NPP increase along a west-east transect that travels through this ecosystem gradient (Figure 4b). In the transition zone between tall grassland and temperate savanna, NPP changes rapidly because the vegetation is switching back and forth between the two ecosystem types. In the tropics and subtropics, TEM predicts that forested ecosystems are more productive than non-forested ecosystems (Figure 3c).

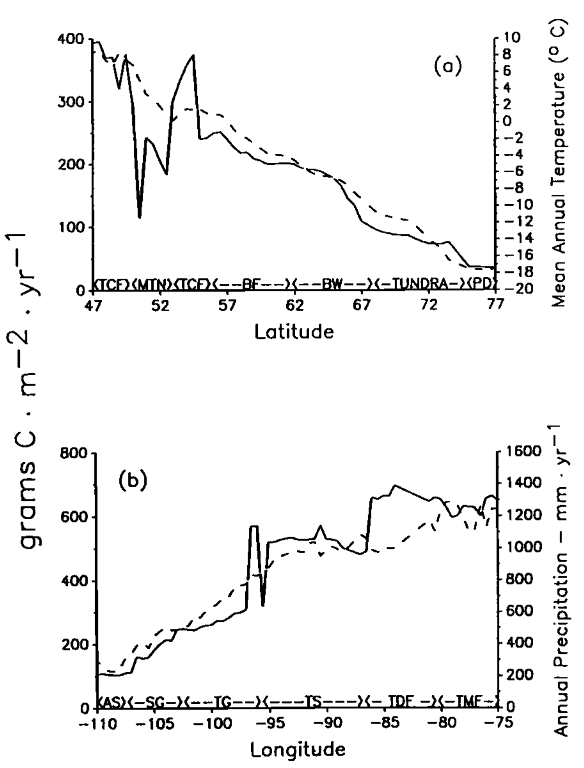

Fig. 4. Mean annual net primary productivity (solid lines) as determined by the terrestrial ecosystem model for a (a) temperature gradient along longitude 117° W between latitudes 47° N and 77° N and a (b) moisture gradient along latitude 41.5° N between longitudes 110° W and 75° W. Dashed lines indicate mean annual temperature in Figure 4a and annual precipitation in Figure 4b. Abbreviations: TCF, temperate coniferous forest; MTN, mountainous region; BF, boreal forest; BW, boreal woodland; TUNDRA, wet/moist tundra; PD, polar desert; AS, arid shrubland; SG, short grassland; TG, tall grassland; TS, temperate savanna; TDF, temperate deciduous forest; and TMF, temperate mixed forest.

TABLE 8. Estimates by the Terrestrial Ecosystem Model of Annual Net N mineralization (NETNMIN) for Potential Vegetation in North America

Vegetation Type	Area, 10^6 km^2	Cells	Total NETNMIN, 10^{12} gN yr^{-1}	Max NETNMIN, gN m^{-2} yr^{-1}	Min NETNMIN, gN m^{-2} yr^{-1}
Polar desert/alpine tundra	1.11	1060	0.5	1.96	0.15
Wet/moist tundra	2.54	2093	1.7	1.43	0.30
Boreal woodland	2.18	1387	4.0	2.68	0.92
Boreal forest	3.43	1991	9.0	4.76	1.61
Temperate coniferous forest	1.51	693	6.2	11.26	2.14
Arid shrubland	2.01	810	6.6	6.51	1.53
Short grassland	1.60	706	6.1	6.56	2.47
Tall grassland	0.77	329	3.5	9.30	2.85
Temperate savanna	1.09	464	6.9	10.60	3.33
Temperate mixed forest	1.80	757	15.0	15.71	4.58
Temperate deciduous forest	0.90	376	8.3	13.54	5.78
Temperate broadleaved evergreen forest	0.05	19	0.2	9.58	4.36
Mediterranean shrubland	0.06	24	0.5	10.46	7.53
Tropical savanna	0.11	40	1.1	18.14	6.93
Xeromorphic forest	0.48	169	6.6	24.38	5.39
Tropical deciduous forest	0.46	159	12.7	35.48	15.72
Tropical evergreen forest	0.66	222	15.7	31.56	15.93
Total	20.76	11,299	104.6	35.48	0.15

Annual Net Nitrogen Mineralization

For undisturbed non-wetland vegetation, TEM estimates the mean annual net nitrogen mineralization (NETNMIN) of North America to be 104.6 x 10^{12} gN yr^{-1}, or 5.04 gN m^{-2} yr^{-1} (Table 8). Mean NETNMIN estimates for ecosystems range from 0.50 gN m^{-2} yr^{-1} in polar desert to 27.29 gN m^{-2} yr^{-1} in tropical deciduous forest. Estimates for individual grid cells range from 0.150 gN m^{-2} yr^{-1} in polar desert to 35.48 gN m^{-2} yr^{-1} in tropical deciduous forest (Table 8, Plate 3). Ranges within ecosystems are comparable to those reported by Nadelhoffer et al. [1991] (Figure 5).

In northern ecosystems, mean annual NETNMIN increases along a gradient from polar desert to temperate coniferous forest (Figure 3a). Similarly, in temperate North America NETNMIN increases along a gradient from arid shrubland to temperate deciduous and mixed forests (Figure 3b). In the tropics and subtropics, estimates of NETNMIN are higher for forested than for non-forested ecosystems (Figure 3c).

Limitation of Productivity by Nitrogen Availability

When the availability of N does not restrict the uptake of C by the vegetation (i.e., the C cycle is uncoupled from the N cycle), the estimate of mean annual NPP for North America is 448.9 gC m^{-2} yr^{-1}. This suggests that productivity could be 32.5% higher if N is not limiting. The strength of N limitation differs regionally in North America (Figure 6). It is very weak in forests of the tropical region, increasingly stronger in forests of the temperate and boreal regions, and strongest in tundra ecosystems. In tundra ecosystems, NPP in the N-limited scenario is on average about 50% of that predicted when there is no N limitation. The degree to which productivity is limited by the availability of N also varies within ecosystems (Figure 6). Along a transect from south to north through arctic ecosystems in western Canada, productivity initially becomes more limited by N availability and then becomes less limited (Figure 7). In the northern portion of this transect the decrease in the strength of N limitation may be the

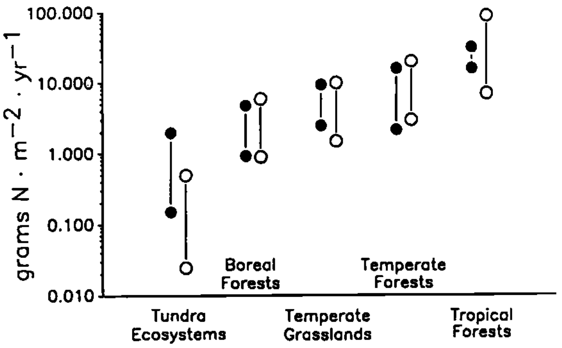

Fig. 5. Comparison between the ranges of annual net nitrogen mineralization predicted by the terrestrial ecosystem model (filled circles) and those reported by Nadelhoffer et al. [1991] (open circles) for tundra and grassland ecosystems, and forests of the boreal, temperate, and tropical regions.

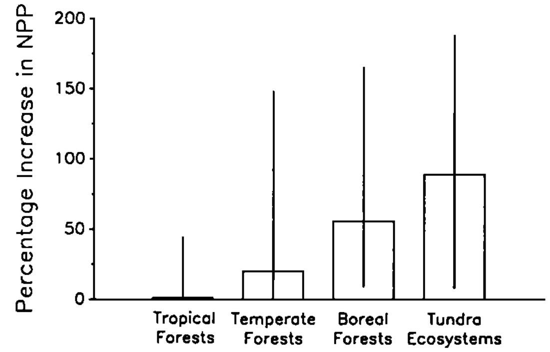

Fig. 6. Predicted effect on regional net primary productivity of eliminating limitation due to nitrogen availability. Percentage increase in NPP (mean and range) is shown for tundra ecosystems and for forests in the tropical, temperate, and boreal regions.

result of photosynthetic processes becoming increasingly more affected by lower temperatures than by N availability. Thus the tightness of the coupling between the C and N cycles may change within ecosystems due to interactions with other factors.

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

When TEM is run with the C cycle coupled to the N cycle, the estimate of mean annual NPP for temperate mixed forest in North America is 735.6 gC m^{-2} yr^{-1} (Table 7). The estimate for the C cycle calibrated and run uncoupled from the N cycle is within 10% of this value. We use these estimates as the baseline values for comparing the response of NPP of temperate mixed forest to an elevated temperature of 2° C (Table 6).

When the temperature is elevated by 2° for WBM, but not for TEM, NPP of temperate mixed forest does not respond if N cycling is uncoupled (Figure 8). In the case of coupled C and N cycling the negative response of NPP is similar to the decrease in NETNMIN. These results suggest that lower soil moisture affected NPP more strongly through N availability than through lower leaf conductivity to CO_2.

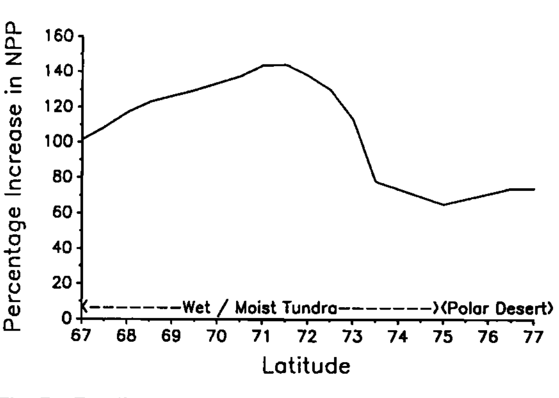

Fig. 7. Predicted effect on net primary productivity in the arctic of eliminating limitation due to nitrogen availability. Percentage increase in NPP is shown for a transect at 117° W.

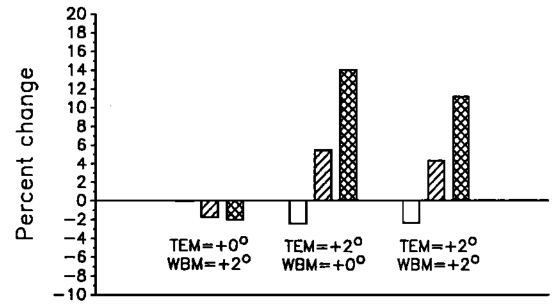

Fig. 8. Response of net primary productivity (NPP) and net nitrogen mineralization (NETNMIN) for temperate mixed forests of North America in an elevated-temperature experiment. Monthly temperature was increased 2° for the terrestrial ecosystem model (TEM) or the water balance model (WBM), which provides climatic inputs to TEM. Blank and diagonally-lined bars correspond to the NPP response when TEM was run with the carbon cycle uncoupled or coupled to the nitrogen cycle, respectively. The crosshatched bar is the NETNMIN response with the carbon cycle coupled to the nitrogen cycle.

When temperature is elevated by 2° for TEM, but not for WBM, NPP of temperate mixed forest responds negatively if N cycling is not considered (Figure 8) but positively in the case of coupled C and N cycling. Because the positive response is much greater than the negative response, these results suggest that NPP is more affected by elevated N availability than by increased plant respiration.

When temperature is elevated by 2° for both TEM and WBM, the NPP response is essentially the additive results of the two previous treatments (Figure 8). The net result is that NPP responds negatively for the C cycle uncoupled from the N cycle, but positively in the case of coupled C and N cycling. Again, the positive response is greater than the negative response. This suggests that NPP is more affected by increased N availability because of higher mineralization rates than by higher plant respiration or lower leaf conductivity to CO_2.

The parameter P_{cn}, which is the ratio of NPP to N requirement for the calibration site, is a measure of the efficiency of N use by the vegetation. To investigate the sensitivity of the net result of the experiment to this parameter, we used N requirement and associated organic matter increment from the woodlands data set of Cole and Rapp [1981] to define P_{cn} for 13 temperate coniferous and 14 temperate deciduous forest stands. The calculated values of P_{cn} range from 34.19 to 109.11, with temperate deciduous and temperate coniferous forest stands occupying the lower and upper ends of the distribution, respectively. We developed two additional calibrations for temperate mixed forest using the low and high values of P_{cn} in this distribution and ran the model with each of these calibrations for both the baseline treatment and the treatment with temperature elevated 2° C for both TEM and WBM. In our experiments with temperate mixed forest the ranges in response of NPP and NETNMIN to elevating temperature by 2° are 2.3 to 4.0% and 9.0 to 13.2%, respectively. Thus the net responses of NPP and NETNMIN in the experiment are robust to our original definition of P_{cn} for temperate mixed forest. The results of this experiment indicate that the coupling of the N cycle to the C cycle is important to consider in predicting the response of NPP to elevated temperature.

DISCUSSION

Importance of C and N Interactions in Estimating NPP

It has long been recognized that the spatial pattern of NPP at continental to global scales can be explained by spatial patterns in temperature and moisture [Lieth, 1973, 1975]. For the northern region of North America, NPP estimates of the Miami model of Lieth [1975] generally increase from north to south, a pattern primarily representing that generated by the temperature submodel of the Miami model. Similarly, in temperate North America, NPP estimates of the Miami model generally increase west to east; this pattern primarily represents that generated by the precipitation submodel. The Century model [Parton et al., 1987] also predicts NPP to increase west to east across the Great Plains in the United States, a pattern that correlates with increasing precipitation. The spatial patterns of NPP generated by TEM in northern and temperate North America agree qualitatively with the patterns generated by the Miami and Century models.

In northern and temperate regions of North America, estimated patterns of productivity by TEM mirror those of NETNMIN. This occurs because the availability of inorganic N limits productivity in the ecosystems of those regions. Thus the exchange of CO_2 between much of the terrestrial biosphere and the atmosphere is coupled to the N cycle. The models developed by Lieth [1975] and his coworkers implicitly rely on the correlation between mineralization rates and environmental factors to predict NPP. However, as we have shown, the degree to which the availability of N limits productivity can vary substantially within ecosystems. Thus models that explicitly incorporate the effect of the N cycle on plant productivity should be capable of better spatial resolution in estimating the exchanges of C between the atmosphere and the terrestrial biosphere.

Importance of C and N Interactions in Predicting the Response of NPP to Elevated Temperature

Because productivity of much of the terrestrial biosphere is limited by the availability of N, determining how global change will affect productivity requires understanding how it will affect the interaction between the C and N cycles. In our elevated-temperature experiment the response of NPP is very different depending on whether or not N cycling is considered. Thus, to investigate how global change will affect biosphere-atmosphere interactions, process-based models need to incorporate linkages between the C and N cycles.

We did not intend to use our elevated-temperature experiments to define the NPP response of temperate mixed forest to global change. Changes in CO_2, precipitation, nutrient deposition, and land use may be substantial in temperate regions, and these were not considered in our experiment. However, our results may have implications for arctic and boreal ecosystems where annual temperature increases of between 5° and 10° C are expected to occur sometime during the next century [Mitchell et al., 1990]. These ecosystems contain substantial amounts of organic C and N in their soils that could be released in inorganic forms in response to elevated temperature [Nadelhoffer et al., 1991]. A large release of CO_2 from these systems has the potential to increase the CO_2 concentration of the atmosphere. However, increased N availability associated with elevated temperature should result in increased NPP. This response has the potential to buffer the carbon loss from the soil.

In our experiments the increased NPP in response to elevated temperature indicates that such buffering could occur. Rastetter et al. [1991] report a similar result in elevated-temperature experiments with a general biogeochemical model (MBLGEM). The degree of buffering will depend on the fate of the "newly available" N that has resulted from warming. Increased decomposition of soil organic matter because of warming will result in the release of C as CO_2 to the atmosphere and an increase in the size of the soil inorganic N pool. If much of the N is taken up by the vegetation, the entire ecosystem will function as a net carbon sink because the vegetation has a much higher C to N ratio than soil. Alternatively, if "newly available" N is lost from the ecosystem, then the ecosystem will function as a net carbon source.

Future Application of TEM Results to Trace Gas Modeling

Our results on NETNMIN are the first reported estimates of N cycling at continental to global scales. Explicitly modeling the N cycle in a spatially defined manner will be important to investigating the interaction of the terrestrial biosphere with trace gases such as methane and nitrous oxide. Although other factors besides N are important in controlling the exchange of these gases [Conrad, 1989; Galbally, 1989], a link does exist between NETNMIN and both the uptake of methane [Steudler et al., 1989; Mosier et al., 1991; Steudler et al., 1992] and the production of nitrous oxide [Melillo et al., 1983; Matson and Vitousek, 1987; Bowden et al., 1991; Steudler et al., 1992]. The dynamics of these gases are spatially and seasonally variable

[Matson et al., 1989]. The ability of TEM to make estimates of NETNMIN that are spatially and temporally resolved is an important development in our efforts to investigate the net exchange of these gases with the terrestrial biosphere.

Recommendations for Ecosystem-Level Studies

Significant improvements in the calibration of TEM include the use of information on N recycling and N fertilization. These enhancements have advanced our ability to model the linkage between the C and N cycles. Information on N recycling, in part, is used to define carbon-nitrogen balance for an ecosystem. Data on the maximum response of NPP to N fertilization are used during calibration to define the maximum rate of carbon assimilation, a procedure that implicitly constrains leaf area. Better data on N recycling and the NPP response to N fertilization in ecosystem-level studies would certainly improve our calibration of TEM. They would also aid in developing new versions of the model to more explicitly model the allocation of resources to C versus N uptake.

An improvement in the calibration of the C cycle is the ability to estimate GPP for the calibration site in a spatially explicit fashion. This improvement, we believe, results in better spatial resolution in the estimates of plant respiration by TEM. However, our estimates of GPP could be greatly improved if ecosystem-level studies consistently measured several quantities [see Ryan, 1991a]: aboveground wood production, aboveground leaf production, belowground NPP, C in sapwood, C in heartwood, organic N in foliage, organic N in sapwood, and organic N in heartwood.

The availability of inorganic phosphorous is known to be low in soils of tropical [Jones and Wild, 1975; Sanchez et al., 1982] and arctic [Chapin et al., 1980; Shaver et al., 1990; Giblin et al., 1991; Nadelhoffer et al., 1991] ecosystems. As discussed by Raich et al. [1991], the omission of phosphorous is partially overcome by the calibration of the model to correctly predict NPP on phosphorous-deficient soils. However, this procedure assumes that phosphorous either does or does not limit NPP over the entire ecosystem. Therefore the inclusion of the effects of phosphorous into TEM would improve the spatial resolution of model predictions. Unfortunately, compared to the N cycle, the phosphorous cycle has been much less studied. Measurement in ecosystem-level studies of the saturation response of NPP to phosphorous fertilization, recycling rates of phosphorous in vegetation, and NPP response in factorial studies of phosphorous and nitrogen fertilization would greatly improve our ability to incorporate phosphorous into our modeling efforts.

Conclusion

Other models have been developed to examine exchanges of CO_2 between the atmosphere and the terrestrial biosphere [Houghton et al., 1983; Emanuel et al., 1984; Gillette and Box, 1986; Esser, 1987; Fung et al., 1987; King et al., 1989]. The TEM model is unique among these models because it incorporates feedbacks between the C and N cycles in estimating the exchange of CO_2. The most significant improvement in TEM is the design of a new feedback algorithm between C and N uptake. The algorithm was designed so that information from field studies on N recycling and the NPP response to N fertilization can be used to calibrate the linkage between C and N dynamics. Because nitrogen limitation of productivity can vary substantially within ecosystems, modeling the linkage between C and N dynamics improves spatial resolution in estimating exchanges of CO_2 between the atmosphere and the terrestrial biosphere. Also, the linkage between C and N dynamics is essential to consider in estimating the response of terrestrial ecosystems to elevated temperature. The evaluation in this study of the linkage between C and N dynamics in estimating NPP is a step forward in our goal of applying TEM to investigate the response of the terrestrial biosphere to global change, that is, changes in climate, environmental chemistry, and land use.

APPENDIX

Data used to calibrate the terrestrial ecosystem model for each vegetation type are described in the 16 tables of this appendix. Mean annual values of carbon in vegetation (C_V), nitrogen in vegetation (N_V), carbon in soil (C_S), nitrogen in soil (N_S), and inorganic nitrogen in soil (N_{AV}) are in g m^{-2} of either carbon or nitrogen. Values of gross primary productivity (GPP), net primary productivity (NPP), nitrogen uptake by vegetation (NUPTAKE), saturation response of NPP to nitrogen fertilization (NPPSAT), and the annual amount of nitrogen mobilized for production via recycling (NMOBIL) are in g m^{-2} yr^{-1}. We assume that NPP = carbon in litter production = carbon in heterotrophic respiration and that NUPTAKE = nitrogen in litter production = net nitrogen mineralization (NETNMIN) during calibration of the model.

TABLE A1. Polar Desert/Alpine Tundra: Toolik Lake, Alaska

Variable	Value	Source and Comments
C_V	450	based on Table 11 by Shaver and Chapin [1991].
N_V	6.5	based on Table 5 by Shaver and Chapin [1991].
C_S	6000	based on Tables 4 and 5 by Giblin et al. [1991].
N_S	260	based on Tables 4 and 5 by Giblin et al. [1991].
N_{AV}	0.4	estimated.
GPP	255	based on respiration budgets of Chapin et al. [1980].
NPP	65	based on Table 11 by Shaver and Chapin [1991].
NPPSAT	130	based on evergreens at Toolik in Table 2 of Shaver and Chapin [1986].
NUPTAKE	0.5	NETNMIN in Table 5.2 of Shaver et al. [1990].
NMOBIL	1.3	based on 75% recycling (values for evergreen leaves range from 60 to 80% in Table 9 of Shaver and Chapin [1991]).

Data are based on vegetation in the heath site.

TABLE A2. Wet/Moist Tundra: Toolik Lake, Alaska

Variable	Value	Source and Comments
C_V	750	based on Table 11 by Shaver and Chapin [1991].
N_V	15	based on Table 5 by Shaver and Chapin [1991].
C_S	18000	based on Tables 4 and 5 by Giblin et al. [1991].
N_S	1100	based on Tables 4 and 5 by Giblin et al. [1991].
N_{AV}	0.4	estimated.
GPP	440	based on respiration budgets of Chapin et al. [1980].
NPP	120	based on Table 11 by Shaver and Chapin [1991].
NPPSAT	225	based on Table 2 by Shaver and Chapin [1986].
NUPTAKE	0.8	based on Table 5 by Shaver and Chapin [1991] and 80% recycling (values for tundra leaves range from 50 to 80% in Table 9 of Shaver and Chapin [1991]).
NMOBIL	3.2	based on Table 5 by Shaver and Chapin [1991] and 80% recycling.

Assumes that vegetation typical of the tussock site, wet site, heath site, and shrub site covers 40%, 40%, 15%, and 5% of the landscape, respectively.

TABLE A3. Boreal Woodland: Schefferville, Quebec, Canada

Variable	Value	Source and Comments
C_V	2200	based on Tables 5 and 7 by Auclair and Rencz [1982].
N_V	24	based on Table 5 by Auclair and Rencz [1982].
C_S	13350	based on tundra and boreal forest calibrations.
N_S	735	based on tundra and boreal forest calibrations.
N_{AV}	0.5	based on tundra and boreal forest calibrations.
GPP	456	based on tundra and boreal forest calibrations.
NPP	170	based on tundra and boreal forest calibrations.
NPPSAT	265	based on tundra and boreal forest calibrations.
NUPTAKE	1.5	based on tundra and boreal forest calibrations.
NMOBIL	2.6	based on tundra and boreal forest calibrations.

Assumes that vegetation typical of tundra and forest covers 50% of the landscape, respectively. Results from running the calibrations for wet/moist tundra and boreal forest on the Schefferville grid cell were used to estimate some of the values for this site.

TABLE A4. Boreal Forest: Bonanza Creek Experimental Forest, Alaska

Variable	Value	Source and Comments
C_V	9000	based on Table 2 by Van Cleve et al. [1983].
N_V	24	based on Table 2 by Van Cleve et al. [1983].
C_S	11000	based on Tables 9 and 13 by Van Cleve et al. [1983].
N_S	735	based on Tables 10 and 13 by Van Cleve et al. [1983].
N_{AV}	0.6	based on Weber and Van Cleve [1984].
GPP	550	see procedure described in methods.
NPP	220	based on Table 3 by Van Cleve et al. [1983] and Oechel and Van Cleve [1986].
NPPSAT	330	based on Van Cleve and Zasada [1976].
NUPTAKE	2.3	based on Table 9.5 by Oechel and Van Cleve [1986] and application of recycling estimates from Tables 3 and 7 by Van Cleve et al. [1983].
NMOBIL	1.9	based on Tables 3 and 7 by Van Cleve et al. [1983].

Assumes that vegetation typical of black spruce, white spruce, and upland hardwoods covers 80%, 10%, and 10% of the landscape, respectively.

TABLE A5. Temperate Coniferous Forest: Andrews Experimental Forest, Watershed 10, Oregon

Variable	Value	Source and Comments
C_V	43500	based on Table 7 by Grier and Logan [1977].
N_V	75	based on Table 2 by Sollins et al. [1980].
C_S	21000	based on Table 7 by Grier and Logan [1977].
N_S	420	based on Table 2 and Figure 4 by Sollins et al. [1980].
N_{AV}	0.9	based on Sollins et al. [1980] and Vitousek et al. [1982].
GPP	2200	see procedure described in methods.
NPP	535	based on Table 10 by Grier and Logan [1977].
NPPSAT	670	based on Peterson [1982].
NUPTAKE	4.2	based on Figure 3 by Sollins et al. [1980].
NMOBIL	1.8	based on Figure 3 by Sollins et al. [1980].

TABLE A6. Arid Shrubland: Curlew Valley, Utah

Variable	Value	Source and Comments
C_V	540	based on Table 1 by Caldwell et al. [1977].
N_V	19.5	based on Table 1 by Bjerregaard [1971].
C_S	11000	based on Table 1 by Bjerregaard [1971].
N_S	800	based on Table 1 by Bjerregaard [1971].
N_{AV}	1.6	estimated.
GPP	235	based on Figure 7 by Caldwell et al. [1977].
NPP	110	modified from Figure 7 by Caldwell et al. [1977] based on below ground carbon allocation analysis method of Raich and Nadelhoffer [1989].
NPPSAT	120	based on 10% response [Lajtha and Whitford, 1989].
NUPTAKE	2.7	based on Figure 7 by Caldwell et al. [1977], Table 1 by Bjerregaard [1971], and 25% recycling [Lajtha, 1987].
NMOBIL	0.9	based on Figure 7 by Caldwell et al. [1977], Table 1 by Bjerregaard [1971], and 25% recycling [Lajtha, 1987].

Assumes that vegetation typical of the *Atriplex confertifolia* site and the *Ceratoides lanata* site covers 50% of the landscape, respectively.

TABLE A7. Short Grassland: Central Plains Experimental Range, Colorado

Variable	Value	Source and Comments
C_V	315	based on Table 1 by Clark [1977].
N_V	8.8	based on Table 1 by Clark [1977].
C_S	3800	based on Table 1 by Clark [1977].
N_S	390	based on Table 1 by Clark [1977].
N_{AV}	2.0	based on Table 1 by Woodmansee et al. [1978].
GPP	388	based on respiration budget at Osage Grassland in the work by Risser et al. [1981].
NPP	200	based on data by Sims and Singh [1978], Webb et al. [1983], and Burke et al. [1990].
NPPSAT	400	based on Dodd and Lauenroth [1979].
NUPTAKE	3.5	based on Woodmansee et al. [1978] and Schimel et al. [1985].
NMOBIL	0.2	based on 5% recycling (estimated).

TABLE A8. Tall Grassland: Osage prairie, Oklahoma

Variable	Value	Source and Comments
C_V	650	based on Table 6.7 by Risser et al. [1981] and Table 2 of Connant and Risser [1974].
N_V	6	based on Table 9.4 by Risser et al. [1981] and Table 3 by Bokhari and Singh [1975].
C_S	16000	see Raich et al. [1991].
N_S	1550	see Raich et al. [1991].
N_{AV}	4.0	see Raich et al. [1991].
GPP	965	based on respiration budget by Risser et al. [1981].
NPP	425	based on Figure 6.4 and Table 9.7 by Risser et al. [1981].
NPPSAT	635	based on Table 10.30 by Risser et al. [1981].
NUPTAKE	5.5	see Raich et al. [1991].
NMOBIL	0.6	based on 10% recycling [Risser et al. 1981, Figure 10.10].

TABLE A9. Temperate Savanna: Cedar Creek Natural History Area, Minnesota

Variable	Value	Source and Comments
C_V	2100	based on Table 6 by Ovington et al. [1963].
N_V	16	based on assuming 88% of biomass in forest with C:N of 150 and 12% of biomass in grassland with C:N of 75.
C_S	4350	based on Table 7 by Grigal et al. [1974].
N_S	400	based on Table 7 by Grigal et al. [1974].
N_{AV}	4.3	based on grassland and forest calibrations.
GPP	890	based on grassland and forest calibrations.
NPP	450	based on grassland and forest calibrations.
NPPSAT	720	based on grassland and forest calibrations.
NUPTAKE	5.5	based on grassland and forest calibrations.
NMOBIL	0.8	based on 13% recycling (estimated).

Assumes that vegetation typical of tall grassland and deciduous forest each covers 50% of the landscape. Results from running the calibrations for tall grassland and temperate deciduous forest on the Cedar Creek grid cell were used to estimate some of the values for this site.

TABLE A10. Temperate Deciduous Forest: Harvard Forest Hardwood Site, Massachusetts

Variable	Value	Source and Comments
C_V	15500	based on McClaugherty et al. [1982] and K. J. Nadelhoffer (unpublished data, 1991).
N_V	37	based on McClaugherty et al. [1982], Pastor et al. [1984], and J. D. Aber (unpublished data, 1991).
C_S	11250	assume soil C:N of 20.
N_S	560	based on Figure 2 by Aber et al. [1983].
N_{AV}	2.0	based on Vitousek et al. [1982].
GPP	1410	see procedure described in methods.
NPP	650	based on McClaugherty et al. [1982], Aber et al. [1983], and K. J. Nadelhoffer (unpublished data, 1991).
NPPSAT	810	based on 25% response (J. M. Melillo, personal communication, 1991).
NUPTAKE	8.0	based on Figure 2 by Aber et al. [1983].
NMOBIL	1.6	based on 17% recycling (estimated).

Some of the values have been adjusted to account for the sandy soil texture of the grid cell.

Table A11. Temperate Mixed Forest: Harvard Forest, Massachusetts

Variable	Value	Source and Comments
C_V	14800	based on McClaugherty et al. [1982] and K. J. Nadelhoffer (unpublished data, 1991).
N_V	36	based on McClaugherty et al. [1982], Pastor et al. [1984], and J. D. Aber (unpublished data, 1991).
C_S	10700	assumes soil C:N of 20.
N_S	530	based on Figure 2 by Aber et al. [1983].
N_{AV}	2.0	based on Vitousek et al. [1982].
GPP	1670	see procedure described in methods.
NPP	650	based on calibrations for deciduous and coniferous forests.
NPPSAT	810	based on 25% response (J.M. Melillo, personal communication, 1991).
NUPTAKE	6.5	based on Figure 2 by Aber et al. [1983] and coniferous forest calibration.
NMOBIL	2.0	based on recycling in calibrations for deciduous and coniferous forests.

Assumes that vegetation typical of deciduous forest and coniferous forest covers 50% of the landscape, respectively. Data from the red pine plantation were used where appropriate. The calibration for temperate coniferous forest was run on the Harvard Forest grid cell to help estimate some of the values for this calibration.

TABLE A12. Temperate Broadleaved Evergreen Forest: Taita Experimental Station, North Island, New Zealand

Variable	Value	Source and Comments
C_V	15000	see Raich et al. [1991].
N_V	42	see Raich et al. [1991].
C_S	13000	see Raich et al. [1991].
N_S	460	see Raich et al. [1991].
N_{AV}	1.0	see Raich et al. [1991].
GPP	1700	see procedure described in methods.
NPP	725	see Raich et al. [1991].
NPPSAT	810	based on 25% response (estimated).
NUPTAKE	6	see Raich et al. [1991].
NMOBIL	1.8	based on 23% recycling (same as for temperate mixed forest calibration).

TABLE A13. Tropical Savanna: Nylsvley Nature Reserve, South Africa

Variable	Value	Source and Comments
C_V	1500	see Raich et al. [1991].
N_V	25	see Raich et al. [1991].
C_S	8000	see Raich et al. [1991].
N_S	400	see Raich et al. [1991].
N_{AV}	2.0	based on Frost [1985].
GPP	1100	used assumption of 80% biomass in tropical deciduous forest and 20% in tall grassland to define plant respiration parameter for this site.
NPP	435	see Raich et al. [1991].
NPPSAT	435	based on assumption that productivity is not N limited.
NUPTAKE	10	see Raich et al. [1991].
NMOBIL	0.0	estimated.

TABLE A14. Xeromorphic Forest: Guanica State Forest, Puerto Rico

Variable	Value	Source and Comments
C_V	4300	see Raich et al. [1991].
N_V	90	see Raich et al. [1991].
C_S	11150	see Raich et al. [1991].
N_S	950	see Raich et al. [1991].
N_{AV}	5.0	see Raich et al. [1991].
GPP	3150	see procedure described in methods.
NPP	550	see Raich et al. [1991].
NPPSAT	550	based on assumption that productivity is not N limited.
NUPTAKE	14	see Raich et al. [1991].
NMOBIL	0.0	estimated.

TABLE A15. Tropical Deciduous Forest: Chakia, India

Variable	Value	Source and Comments
C_V	11350	see Raich et al. [1991].
N_V	170	see Raich et al. [1991].
C_S	7900	see Raich et al. [1991].
N_S	950	see Raich et al. [1991].
N_{AV}	5.0	estimated.
GPP	5600	see procedure described in methods.
NPP	700	see Raich et al. [1991].
NPPSAT	700	based on assumption that productivity is not N limited.
NUPTAKE	27	see Raich et al. [1991].
NMOBIL	0.0	estimated.

TABLE A16. Tropical Evergreen Forest: Ducke Forest, Manaus, Brazil

Variable	Value	Source and Comments
C_V	22500	see Raich et al. [1991].
N_V	300	see Raich et al. [1991].
C_S	15000	see Raich et al. [1991].
N_S	900	see Raich et al. [1991].
N_{AV}	1.0	see Raich et al. [1991].
GPP	8500	see procedure described in methods.
NPP	1050	see Raich et al. [1991].
NPPSAT	1050	based on assumption that productivity is not N limited.
NUPTAKE	24	see Raich et al. [1991].
NMOBIL	0.0	estimated.

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