

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
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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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Paper number 92GB00219.
0886-6236/92/92GB-00219\$10.00

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.

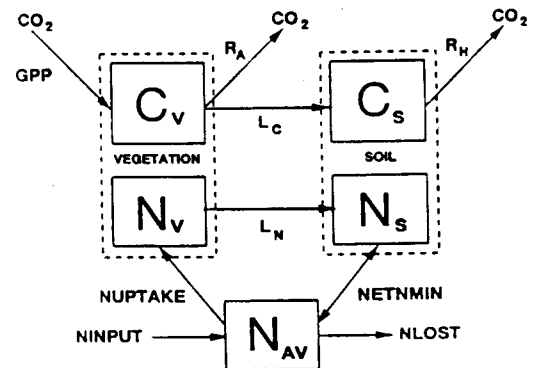


Fig. 1. The terrestrial ecosystem model (TEM). The state variables are: carbon in vegetation (C_v); nitrogen in vegetation (N_v); organic carbon in soils and detritus (C_s); organic nitrogen in soils and detritus (N_s); and available soil inorganic N (N_{AV}). Arrows show carbon and nitrogen fluxes: 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

