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Modeling nitrogen saturation in forest ecosystems in response to land use and atmospheric deposition

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Abstract

A generalized, lumped-parameter model of carbon (C), water, and nitrogen (N) interactions in forest ecosystems (PnET-CN) is presented. The model operates at a monthly time step and at the stand-to-watershed scale, and is validated against data on annual net primary productivity, monthly carbon and water balances, annual net N mineralization, nitrification, foliar N concentration and annual and monthly N leaching losses for two sites, Hubbard Brook (West Thornton, NH) and Harvard Forest (Petersham, MA). It is then used to predict transient responses in function resulting from changes in land use and N deposition, as well as the maximum rate of N cycling which can be sustained for any given combination of site, climate and species. Model predictions suggest a very long legacy effect of land use history on N cycling. Even with only one 'active' soil organic matter pool, complete recovery from three modest harvests at Hubbard Brook is predicted to require more than two centuries at current N deposition rates. Complete recovery is predicted to take even longer at the Harvard Forest where biomass removals have been more intense. PnET-CN is used to predict maximum sustainable rates of N cycling for 14 sites throughout the northeastern USA. Predicted maximum values were higher, as expected, than measured N mineralization rates for all but one site. The measured fraction of N mineralization nitrified at these 14 sites showed a general relationship with the ratio of measured to maximum net N mineralization. This latter ratio is discussed as a potentially useful indicator of the degree of nitrogen saturation in forest ecosystems. A regional map of predicted maximum N cycling rates is presented based on regressions between model predictions and summary climatic variables. © 1997 Elsevier Science B.V.

Keywords: N mineralization; Nitrification; GIS; Regional predictions; Hubbard brook; Harvard forest; NPP; Water yield; Nitrate leaching; Ecosystem model

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1. Introduction

Human activity has altered the N cycle in temperate forest ecosystems of the northeastern USA by increasing deposition via atmospheric pollution, and by extractive land use practices. Both nitrogen depletion through intensive forest management (Weetman and Webber, 1972; Kimmins and Krumlik, 1976; Hornbeck et al., 1986), and, more recently, nitrogen saturation through increased atmospheric deposition (Agren and Bosatta, 1988; Schulze, 1989; Stoddard, 1994; Aber et al., 1989; Aber, 1992), have been put forward as threats to the integrity of these systems. In addition, most of the forested landscapes of this region have experienced at least one cycle of land use change, including forest clearing for agriculture and abandonment of agricultural land to regrowing forests (e.g. Raup, 1966; Foster, 1994), as well as occasional major fires, which may also result in long-lasting changes in N cycling rates.

While patterns of atmospheric deposition are fairly continuous over the landscape, responding to regional patterns of emission and transport (e.g. Ollinger et al., 1993, 1995; Dise and Wright, 1995), land use occurs at the scale of individual ownership, and can vary widely over small distances, creating a fine-scale mosaic in N cycling rates. N amendment research has confirmed that significant increases in leaching of nitrate and associated cations from forest soils can be induced by N saturation (Emmett et al., 1995; Boxman et al., 1995; Kahl et al., 1993; Magill et al., 1996a). However, certain forest ecosystems exhibit considerable lag-times before nitrate leaching begins (e.g. Wright and Tietema, 1995; Gundersen and Rasmussen, 1995; Magill et al., 1996a). Comparative studies in different sites have shown that the degree of response to N additions are not easily predicted from total historical N deposition (e.g. Kahl et al., 1993; Magill et al., 1996a). We propose that the previous land use history of a site plays a critical role in determining responses to N additions.

Predicting future productivity and N cycling in northern temperate forests then poses two problems. The first is the inherent difficulty in mod-

elling N cycling in forest ecosystems, including interactions with other important cycles such as C and water, during periods of rapid changes in N deposition. The second is the reconstruction of land use histories for individual sites, and the impacts of these histories on current rates of N cycling.

The purpose of this paper is to present a generalized, lumped-parameter model of carbon, water and nitrogen interactions in forest ecosystems (PnET-CN), and to attempt validation of this model against existing data from two sites with very different land use histories: the Hubbard Brook Experimental Forest in the White Mountain National Forest, NH, and the Harvard Forest, Petersham, MA. The validated model is then used to predict rates of change in N cycling and N leaching in forests experiencing increased N deposition, and to predict the maximum sustainable rate of N cycling which can be supported for any combination of site, climate and species. We propose that the maximum N cycling rate, in comparison with measured rates of N mineralization on a given site, can be a valuable indicator of the current degree of N saturation, and test this idea by examining nitrification:mineralization ratios as a function of measured:maximum mineralization rates for 14 sites in the northeastern USA. Finally, we put these results in a regional GIS context and propose a method for predicting the timing of N saturation at the regional-scale.

2. Methods

2.1. Model structure

2.1.1. Process interactions

The original PnET model (Aber and Federer, 1992) was a simple, lumped parameter model of monthly carbon and water balances for temperate and boreal forest ecosystems. The second version of the model (PnET-II, Aber et al., 1995) included an improved canopy photosynthesis routine summarized in a separate daily time-step model (PnET-Day, Aber et al., 1996), an empirical soil respiration algorithm, and improved plant allocation and respiration terms which allowed predic-

tion of total system carbon balance. The empirical soil respiration term side-stepped the need for litterfall and decomposition routines to complete the carbon cycle. The version presented here (PnET-CN) adds live biomass, litter and soil organic matter compartments, adds N to all compartments and fluxes, N mineralization and nitrification, plant N uptake and leaching losses (Fig. 1) to produce complete cycles for both carbon and nitrogen. The single soil organic matter pool represented in PnET-CN is functionally equivalent to the 'active pool' in the Century model (Parton et al., 1993).

Carbon and nitrogen cycles interact at several points in the model. Unlike PnET-II, foliar N concentrations are not fixed in PnET-CN, but change year-to-year depending on the relative availability of C and N to plants. When internal plant pools of N (PlantN) are high, the efficiency of N uptake from the available soil pool is re-

duced. Increases in N concentrations in foliage, wood and root also occur, increasing demands on the PlantN pool. The increase in foliar N increases net photosynthesis (in the absence of water stress) and so increases internal plant pools of C (PlantC). As PlantC increases, NPP will increase and the demand for incorporating N in tissues will increase, again reducing PlantN. C:N ratios in biomass are reflected in litter, and high C:N ratios decrease net N mineralization. In addition, the same variable which determines N concentrations in tissues (NRatio) is also applied to net nitrification. Thus the degree to which nitrification occurs is dependent on the strength of plant demand for N in competition with nitrifiers. Finally, nitrate leaching occurs in proportion to the amount of NO₃ remaining in the soil solution after plant uptake, and to water drainage rates. A complete description of the variables and equations used in these algorithms is contained in Appendix A.

Changing N concentration in foliage and other tissues from an input variable to one calculated by the model means that sites within a forest type which were parameterized differently in PnET-II (such as hardwood stands at both the Harvard Forest and Hubbard Brook) now carry the same parameter set (for a generalized broad-leaved deciduous forest) with differences in N concentrations resulting now from differences in past site history and climate alone. This increases the rigor of the validation process as N concentration in foliage is the most sensitive variable in determining whole canopy carbon gain (Aber et al., 1996) and thus the production of biomass and litter. The quantity and C:N ratio of litter produced control future N mineralization rates, completing a positive feedback loop (Mooney and Gulmon, 1982). Tissue N concentrations are only specified to fall within a wide range of values, representing the range of values measured in the field.

2.1.2. Site history

With long-term storage pools for C and N (soils and wood) present in the model, validating model predictions against current measurements requires some information about the history of

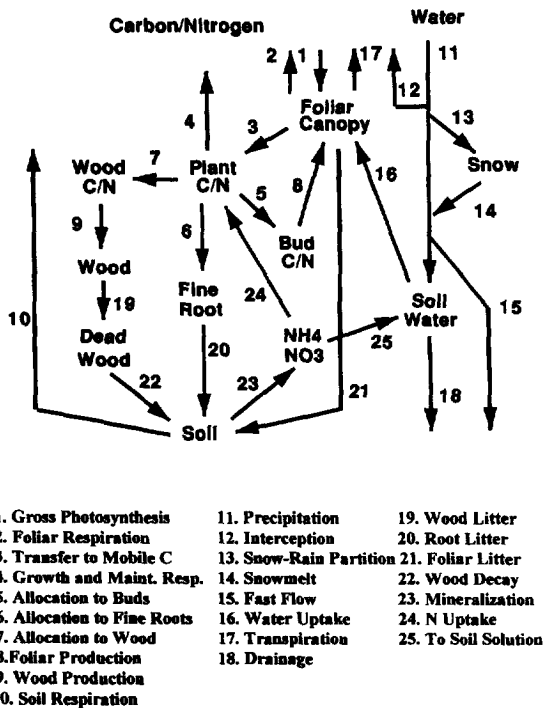


Fig. 1. Structure of the PnET-CN model. Compartments with 'C/N' contain mobile or storage pools of these elements. All biomass pools and the soil pool, as well as all fluxes between these contain both carbon and nitrogen.

Table 1

Values for parameters required to run PnET-CN in addition to those described for PnET-II (Aber et al., 1995)

| Name | Source | Description | Value | | |
|---------------|--------|--|-----------|------|------------|
| WoodTurnover | 1 | Fractional mortality of live wood per year | 0.025 | | |
| WoodLitTrans | 2 | Fractional transfer from dead wood to SOM per year | 0.1 | | |
| WoodLitCLoss | 2 | Fractional loss of mass as CO ₂ in wood decomposition | 4 | | |
| RootTurnoverA | 3 | / Coefficients for fine root turnover (fraction · year ⁻¹) | 0.789 | | |
| RootTurnoverB | 3 | as a function of annual net N | 0.191 | | |
| RootTurnoverC | 3 | \ mineralization | 0.0211 | | |
| MaxNStore | — | Max. N content in PlantN pool (g · m ⁻²) | 20 | | |
| Kho (Ksom) | 3 | Decomposition constant for SOM pool (year ⁻¹) | 0.075 | | |
| NImmoba | see | / Coefficients for fraction of mineralized N | 151 | | |
| NImmobb | text | \ reimmobilized as a function of SOM C:N | – 35 | | |
| | | | Deciduous | Pine | Spruce-Fir |
| RLPctN | 4 | Min. N concentration in root litter (%) | 1.2 | 1.2 | 1.1 |
| FLPctN | 4 | Min. N Concentration in foliar litter (%) | 0.8 | 0.4 | 0.35 |
| WLPctN | 4 | Min. N concentration in wood litter (%) | 0.2 | 0.2 | 0.2 |
| FolNConRange | 4 | Max. fractional increase in N concentrations | 0.6 | 0.7 | 0.6 |

Values which are the same for all forest types are listed first, followed by those which vary for the three forest types described. See Appendix for a complete description of equations and algorithms. Sources of data: 1, calculated from Whittaker et al., 1974; 2, Aber et al., 1991; 3, Aber et al., 1985; 4, Magill et al., 1996b; Likens and Bormann, 1970; McNulty et al., 1991.

carbon and nitrogen removal from each site simulated. A general lack of accurate removal data for most sites is perhaps the biggest obstacle to understanding the existing pattern of N mineralization and cycling rates over any human-dominated landscape.

Information on site history, as well as data on rates of N deposition to the modeled site, are contained in an executable subroutine (Scenario) which is called at the beginning of each month, and specifies any changes in climate, N deposition or disturbance history. For example, ramped increases in N deposition over time can be expressed as a linear function of the year or month of execution. Harvesting or other disturbance events are entered as conditional blocks to be executed at the specified time. Other changes in driving variables, such as climate change, or simulated experiments, such as increases in water or N inputs, can also be described in this routine.

2.2. Model parameterization

2.2.1. Process parameters

In PnET-CN a total of 14 new input parameters (Table 1) have been added to those required

in PnET-II (Aber et al., 1995). For the validation and regional application runs described here, it was necessary to obtain these parameters for hardwood, pine and spruce-fir forest types. These three types are the same as used in PnET-II (Aber et al., 1995), so only the values for the parameters added in this version are described. Of the parameters added here, only those relating to foliar concentration range vary between forest types. As with PnET-Day and PnET-II, the majority of input parameter are considered as constants across all forest types.

2.2.2. Site history

PnET-CN is validated against data from two sites, The Harvard Forest, Petersham, MA and The Hubbard Brook Experimental Forest, near West Thornton, NH, both part of The National Science Foundation's Long-Term Ecological Research (LTER) program. Site histories differ markedly between the two sites. The part of the Harvard Forest from which validation data are drawn was part of a working farm from the mid-1700s to about 1850, at which time about 90% of the Prospect Hill tract was cleared (Raup, 1966). While annual rates of C and N removal

Table 2

Time line of C and N removals from, and N deposition to, the Hubbard Brook and Harvard Forest Sites as realized in the PnET-CN model

| | Site | | | |
|--|--|--------------------|---|--------------------|
| | Harvard Forest | | Hubbard Brook | |
| History of biomass removal | 2.5% of standing biomass per year, 1750–1850 | | 20% harvest, 1905 50% harvest, 1920 50% harvest, 1939 | |
| N Deposition (current) | NO ₃ -N | NH ₄ -N | NO ₃ -N | NH ₄ -N |
| Wet (mg N·l ⁻¹) | 0.29 | 0.13 | 0.32 | 0.17 |
| Dry (g N·m ⁻² ·year ⁻¹) | 0.204 | 0.050 | 0.120 | 0.012 |

Wet deposition is calculated as concentration values times monthly precipitation inputs, dry deposition as a total annual value divided into 12 equal monthly amounts. Values represent long-term means extracted from regional data (Ollinger et al., 1993). Actual deposition ramps linearly from 0 in year 1600 to current values in year 2000 and stays constant after that year.

from these sites cannot be known precisely, it is clear that areas which were farmed or used as woodlots would be expected to have a significant fraction of NPP removed on an annual basis. We have used an average annual biomass removal rate (Table 2) to represent this land use pattern. In addition, the particular site used for validation of the productivity predictions (control stand, chronic N experiment, Magill et al., 1996a) was harvested again around 1930.

In contrast, the Hubbard Brook valley has seen little farming activity, and was relatively free of human disturbance until about 1900 (Likens, 1985). Most of the valley was cutover lightly for removal of spruce around 1905, and more heavily for hardwoods around 1920. An additional significant salvage harvest occurred after the 1938 hurricane. This is summarized in the Scenario routine for Hubbard Brook as shown in Table 2.

In addition to harvest removals, significant changes in N deposition have occurred over time to both sites. This change is approximated roughly as a simple linear increase in N deposition from near zero in 1600 to current rates in 1990. Beyond 1990, N deposition is held constant (Table 2).

2.3. Model validation

Model predictions are compared with measured values for NPP, monthly carbon balance, foliar N concentration, N mineralization and nitrate con-

centration in leachate at the Harvard Forest (Wofsy et al., 1993; Aber et al., 1996; Magill et al., 1996a). At Hubbard Brook, data are available for NPP, annual net N mineralization, nitrification, foliar N concentration, N leaching losses in streamwater and total water yield (Gosz et al., 1972; Whittaker et al., 1974; Melillo, 1977; Covington and Aber, 1980; Federer et al., 1990).

2.4. Model predictions

2.4.1. Long-term recovery and maximum nitrogen cycling rates

To the extent that PnET-CN can be validated, it can then be used to predict the future time course of N cycling rates, including N mineralization, nitrification and N leaching losses, including the time required for full recovery from disturbance. This is done to give some perspective on the time course over which past disturbance can affect N cycling rates (the 'legacy' effect). It can also be used to predict the maximum sustainable rate of N cycling for any site given constraints of climate and species. By comparing this with current measured rates, a quantitative estimate of the current N status of a site can be determined, which may relate to important processes such as nitrification and nitrate leaching. By combining this estimate of the current degree of N saturation with the predictions of rates of change in N cycling, an estimate of temporal changes in N leaching and associated changes in stream water chemistry can be attempted.

Table 3

Foliar and wood production, and N concentration and cycling data, as estimated by PnET-CN for the hardwood and pine control stands at the Harvard Forest, compared with measured values from the Chronic N experiment at the Harvard Forest

| | Hardwoods | | Pines | |
|-------------------------------|-----------|----------|-------|----------|
| | PnET | Measured | PnET | Measured |
| NPP | | | | |
| Foliage | 295 | 287 | 303 | 316 |
| Wood | 591 | 505 | 379 | 377 |
| N Cycling | | | | |
| Net N mineralization | 7.6 | 7.4 | 7.0 | 7.9 |
| Net nitrification | 0.86 | 0.05 | 2.4 | 1.9 |
| N leaching | 0.15 | 0 | 0.33 | 0 |
| Foliar N concentration | 1.9 | 2.0 | 1.1 | 1.1 |

Both predicted and measured values are means for five years (1988–1993, data from Magill et al., 1996a). All values are in $\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ except foliar concentrations which are %.

2.4.2. Regional predictions

The PnET models are designed to require relatively few input variables so that they can be run over large regional areas within a GIS (Aber et al., 1993). Even so, it may be possible to summarize the results of process-level models by developing simple statistical models which contain the variability in model results over a given range of inputs. We attempted regressions between model-predicted maximum N cycling rate and simple climatic indices (total annual precipitation and total annual growing degree days, 0°C base), as well as with latitude, longitude and elevation. One hundred random combinations of latitude, longitude and elevation which occur within the region were selected, and climate variables were derived using the models of Ollinger et al. (1995). PnET-CN was then run for each of the three vegetation types at each of these sites, and predicted maximum N cycling rate regressed against both climatic and locational variables.

To the extent that the above regressions are significant and precise, predicted maximum N cycling rate can be mapped regionally given summary climatic maps, and a digital elevation model (DEM) and a forest type map for the region. The Ollinger et al. (1995) models were used in conjunction with a 1 km-scale digital elevation model (DEM) for the northeastern USA (USGS, 1987) to generate the precipitation and growing degree

day maps. An existing land use/land class map (Lathrop and Bognar, 1994) developed for use with the PnET models determined the forest type for each forested pixel in the region.

3. Results and discussion

3.1. Validation

NPP at both Hubbard Brook and the Harvard Forest are accurately predicted by PnET-CN (Tables 3 and 5). Data from Hubbard Brook are separated into a wet period (1956–1960) and a dry period (1961–1965), with significant differences in wood production expressed in both the field data and PnET-CN predictions. Foliar production values for these two periods were estimated by allometry with wood production rather than direct measurement. There are no direct measurements which suggest leaf production values as high as $374 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ at Hubbard Brook.

Predictions and measurements of current N cycling rates are also in general agreement for both sites (Tables 3 and 5). Both nitrification rates and N leaching losses are predicted to be somewhat higher than measured values, suggesting that the algorithm for predicting the fraction of N mineralization which is nitrified can be improved, and

Table 4
Predicted (PnET-CN) and measured (eddy correlation, Wofsy et al., 1993, personal communication) total annual net carbon exchange for the tower site at the Harvard Forest

| Source | Year | | | Mean |
|--------------------------------|------|------|------|------|
| | 1991 | 1992 | 1993 | |
| Tower | 260 | 220 | 170 | 217 |
| PnET-CN (with water stress) | 103 | 178 | -49 | 77 |
| PnET-CN (without water stress) | 228 | 209 | 109 | 182 |

Two PnET-CN runs are shown, with and without water stress.

that other N retention mechanisms, beyond only biological reimmobilization included in the model, may operate in soils to remove nitrate produced in active upper soil horizons.

In two earlier papers (Aber et al., 1995, 1996), we described the effects of water stress on the total net carbon balance at the Harvard Forest. Data on net ecosystem carbon exchange collected by eddy correlation at a tower location at the Harvard Forest (Wofsy et al., 1993; Aber et al., 1996) give no indication of reductions in carbon gain due to soil-based water stress. PnET-CN simula-

tions using an average soil water holding capacity (12 cm, plant available) predict significant water stress and under-predicted monthly carbon gain over the course of a growing season (Table 4). It is unclear whether the models contain inaccurate transpiration algorithms, or if the forest around the tower has access to inflows of water or a perched water table. The accuracy of the Hubbard Brook water balance suggests the latter. Artificially removing the effects of water stress from the PnET-CN predictions brings total annual net carbon exchange to within $35 \text{ g C} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$, or near 3% of the total gross annual carbon flux. This result again confirms the importance of determining the spatial extent to which water stress is an important factor in northeastern forests.

For purposes of regional extrapolation, we needed to derive a data set for spruce-fir forests, as was done for PnET-II. Values used were selected to be within the range of those reported in the literature and which gave predicted NPP values similar to those reported for Whiteface Mountain, NY, by Johnson and Lindberg (1992), (Table 6). As vegetation data were selected to give the best fit to measured NPP values, this represents a calibration rather than a validation exercise.

Table 5
Predicted and measured foliar and woody biomass production for the Hubbard Brook forest ecosystem

| Years | Net primary production | | | | Total | |
|----------------------|------------------------|----------|------|----------|-------------------|----------|
| | Foliage | | Wood | | PnET | Measured |
| | PnET | Measured | PnET | Measured | | |
| 1956–1960 | 314 | 374 | 932 | 921 | 1246 | 1295 |
| 1961–1965 | 314 | 294 | 770 | 761 | 1084 | 1055 |
| 1968 | 313 | 316 | — | — | — | — |
| 1969 | 294 | 273 | — | — | — | — |
| 1974 | 329 | 296 | — | — | — | — |
| Nitrogen cycling | | | | | | |
| Net N mineralization | | | | | Net nitrification | |
| | PnET | Measured | | | PnET | Measured |
| 1974–1975 | 9.4 | 10.0 | | | 2.2 | 1.3 |

All data are for the lowest elevation zones at Hubbard Brook which is dominated by deciduous species. The PnET-CN run specified all deciduous species. All values in $\text{g biomass} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$. Data from Whittaker et al. (1974); Gosz et al. (1972); Covington and Aber (1980); Melillo (1977). All data in $\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$.

Table 6

Predicted and measured biomass production at Whiteface Mountain spruce-fir site (data from Johnson and Lindberg, 1992).

| Foliage | | Wood | | Root | | Total | |
|---------|----------|------|----------|------|----------|-------|----------|
| PnET | Measured | PnET | Measured | PnET | Measured | PnET | Measured |
| 195 | 221 | 363 | 364 | 170 | 153 | 728 | 738 |

Predicted water yield compares well with measured mean monthly water yield from watershed 6 at Hubbard Brook (Fig. 2). Values represent the means for the period 1956–1990 (± 1 S.E.). None of the predicted values are significantly different from measured values. PnET-CN also captures the general trend of dissolved inorganic N concentration through the year (Fig. 3). The only statistically significant difference occurs in November, although there is a clear trend of predicted concentrations being higher than measured values during the dormant season. The mechanisms behind this difference are not clear, but may be related to the continuation of chemical and biological process in cold but non-frozen soils below the deep winter snow-pack which generally develops at Hubbard Brook. It may also relate to the overprediction of nitrification rates as discussed above.

PnET-CN also captures at least the general trend in interannual variations in weighted mean concentrations of inorganic N in streamwater from watershed 6 at Hubbard Brook (Fig. 4). While factors such as soil frost and partial defoliation have been cited as possible contributors to the increase in N losses in the early 1970s, the PnET-CN simulation predicts that at least part of this increase can be explained on the basis of long-term responses to climate (e.g. the drought years in the early 1960s) as amplified by internal interactions between plant and soil C and N pools.

Both dissolved inorganic N losses (Fig. 3 and 4) and net carbon exchange (Table 4) represent the net balances of much larger fluxes. Internal N cycling at Hubbard Brook is on the order of 9–10 $\text{g N} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ (Likens et al., 1977; Melillo, 1977). Total gross carbon flux at the Harvard Forest is close to 1200 $\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$. The net

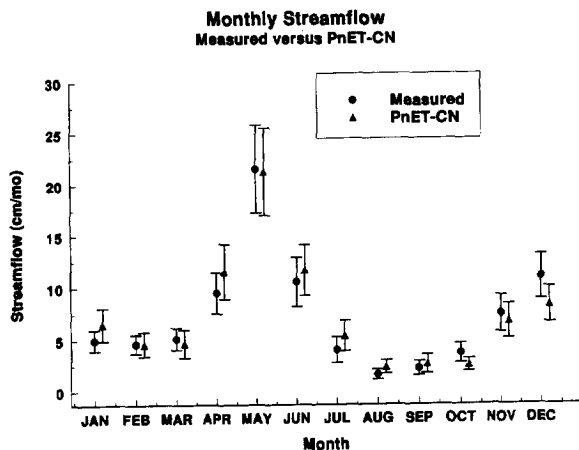


Fig. 2. Comparison of measured and predicted (PnET-CN) mean monthly streamflow (water yield) from watershed 6 at the Hubbard Brook Experimental Forest. Values are means of all values for the years 1957–1990 (data from Federer et al., 1990).

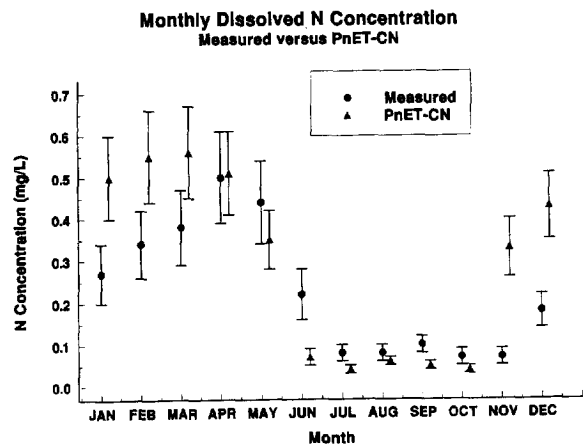


Fig. 3. Comparison of measured and predicted (PnET-CN) mean monthly dissolved inorganic N concentrations for watershed 6 at Hubbard Brook (± 1 S.E.). Values are means for the years 1964–1990 (Hubbard Brook Archive).

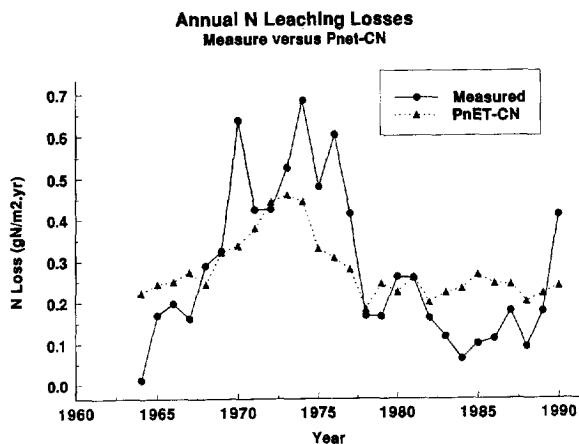


Fig. 4. Comparison of measured and predicted total dissolved inorganic N leaching losses for watershed 6 at Hubbard Brook (data from Hubbard Brook Data Archive).

fluxes predicted here represent only about 5 and 16% of gross fluxes, respectively. PnET-CN generally predicts the mean annual and monthly values of these fluxes to within $\pm 10\%$. It also predicts general temporal trends in these values from actual temporal trends in climate drivers. Differences between measured and predicted values for specific months and years (e.g. Fig. 4) are very subtle features of ecosystem dynamics which may be difficult or impossible to capture with lumped-parameter models such as PnET-CN.

3.2. Predictions

3.2.1. Long-term patterns of N cycling in response to disturbance

If we assume that the forests at Hubbard Brook experienced no major extractive N losses prior to 1905 (Fig. 5a), predicted total annual N cycling rate was about $11 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ with just less than half of that cycling as nitrate. The decline in plant uptake caused by the cutting results, in the model predictions, in an increase in nitrification and nitrate leaching, and a slight increase in N mineralization resulting from the temporary reduction of inputs of high C:N litter material. These same responses are accentuated by the second cutting about 1920, and the simulated salvage operation which followed the 1938 hurricane.

Longer-term trends are also visible, however. The initial stimulation of mineralization following cutting is followed by a longer-term decrease as the result of reduced N inputs to soils as litter. By the beginning of the actual climate record in 1956, annual net N mineralization has fallen, as a result of biomass and N removals, from about $11 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$. Net nitrification has declined by a larger fraction, from about $4.5 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$, as a result of the increased ratio of plant demand to N availability.

Results from the period 1956–1990 demonstrate the extent to which interannual climatic variability can alter predicted N cycling rates. Variation results first from variation in the climate record itself, and also from the internal

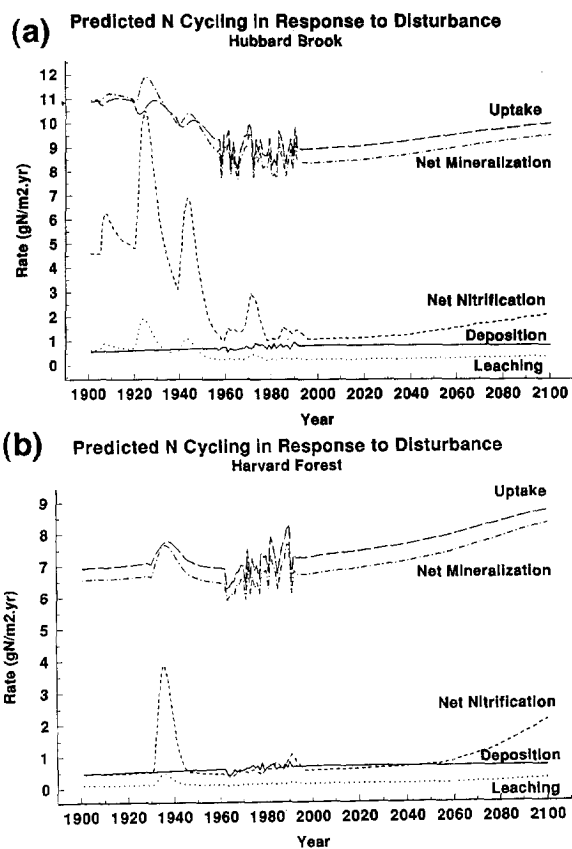


Fig. 5. Predicted time course of components of the N cycle of forest ecosystems in response to disturbance: a, Hubbard Brook; b, Harvard Forest.

responses of C:N ratios in plant and soil compartments, as well as rates of NPP and litter production. If this variability is correct, then it is apparent that the predicted trends in N mineralization would be impossible to detect by field measurement even over a 34 year period.

Even in the absence of additional disturbances, the N cycle is not predicted to return to pre-cutting levels until well after 2100. This very long recovery time holds even though PnET-CN has only a single active soil N pool with an assumed average residence time of about 15 years.

At the Harvard Forest site simulated (deciduous control plot, chronic N experiment, Fig. 5b), the period of intensive removals through agriculture ended about 1850. PnET-CN predicts that N mineralization was reduced, nitrification was very low and N leaching near zero at this time (Table 3). The long period of recovery was interrupted by the harvest in 1930, but it is clear that 300 years or more will be required to achieve pre-settlement rates of N cycling, even in the absence of further disturbance. The N additions made to plots within this stand (over 85 g N m^{-2} in 6 years, all of which has been retained, Magill et al., 1996a) have accelerated this recovery, and have also demonstrated the very large N retention capacity present in a stand which has been so severely disturbed in terms of N availability and cycling.

3.2.2. Predicting maximum N cycling rates: an application to N saturation

We predicted maximum N cycling rates by allowing PnET-CN to run to equilibrium. At this point in the model, deposition inputs equal N leaching losses, and N mineralization equals plant uptake and return in litter over the course of a year. While such a condition is unlikely ever to occur in the field, we propose that this predicted maximum rate is useful, in comparison with current measured rates of N cycling, as an indicator of the degree of N limitation on plant growth, and as a predictor of nitrification and nitrate leaching.

Predictions of maximum N cycling rates were obtained for hardwood and pine stands at the Harvard Forest, for watershed 6 at Hubbard

Brook, and for 9 additional sites in the northeastern USA for which measured net annual N mineralization rates were available (Table 7). Actual mean climate data were available for the Hubbard Brook and Harvard Forest sites. Climate data for the remaining sites were derived from latitude, longitude and elevation using the model of Ollinger et al. (1995).

If model predictions of maximum N cycling rates are accurate, then measured rates should be lower than predicted rates for all sites. Only one has a measured value above the predicted value (Table 7, Fig. 6). This is the Boone hardwood stand, a maple stand located adjacent to a stream and with access to groundwater. PnET-CN predicts that water stress is an important determinant of maximum N cycling rates for low elevation deciduous stands in this region (see Section 3.2.3). If water stress is removed for the Boone hardwood stand, predicted maximum N cycling rate is above $12 \text{ g m}^{-2} \cdot \text{year}^{-1}$. This again reinforces the need for an improved understanding of the extent and spatial distribution of soil water availability and water stress in northeastern forests.

It has been predicted that continued N deposition to northeastern forests will result in increased nitrification in soils and N leaching to streams (Aber et al., 1989; Stoddard, 1994; Murdoch and Stoddard, 1991). To date, no method has been proposed for predicting the timing of approach to N saturation, or to map the current degree of N saturation in the region using forest- or soil-based measurements. We propose that the ratio of current to predicted maximum N cycling rate is a potentially valuable indicator of the degree of N saturation on a site. This value should be correlated with nitrification rates and N leaching rates, and can be mapped regionally.

The data on maximum versus measured N mineralization rates (Table 7) can be used as a preliminary test of this working hypothesis. We hypothesized that the ratio of measured nitrification to measured N mineralization should increase as the ratio of measured N mineralization to predicted maximum N mineralization rate increases. While a trend in this direction is apparent (Fig. 7), the data set available is too small for a

Table 7
 Predicted maximum N mineralization rate for stands with published measured rates

| Location/stand type | Predicted maximum net annual mineralization | Measured | | Reference |
|---------------------|---|---------------------------|--------------------------|---|
| | | Net annual mineralization | Net annual nitrification | |
| Harvard Forest | | | | |
| Pine | 8.8 | 7.9 | 1.9 | Magill et al., 1996a |
| Pine | 8.8 | 8.4 | — | Aber et al., 1982 |
| Deciduous | 10.2 | 7.4 | 0.05 | Magill et al., 1996a |
| Deciduous | 10.2 | 9.5 | — | Aber et al., 1982 |
| Hubbard Brook | | | | |
| Deciduous | 11.7 | 10.0 | 1.3 | Melillo, 1977 |
| Spruce-fir transect | | | | |
| Acadia | 6.7 | 2.3 | 0.0 | McNulty et al., 1991 and |
| Mount | 6.2 | 4.6 | 0.0 | |
| Washington | | | | R.A. Hallett, personal communication (Johnson and Lindberg, 1992) |
| Mount | 6.2 | 5.6 | 0.4 | |
| Mansfield | | | | |
| Whiteface | 6.0 | 2.1 | 0.2 | |
| Mountaint | | (4.2) | | |
| Mount Ascutney, VT | | | | |
| Spruce-fir | 6.6 | 1.5 | 0.0 | McNulty and Aber, 1993 |
| Woods Hole, MA | | | | |
| Deciduous | 9.6 | 5.3 | 0.0 | J.M. Melillo (personal communication) |
| Bear Brook, ME | | | | |
| Hardwoods | 9.9 | 10.0 | 1.0 | Magill et al., 1996b |
| Central MA | | | | |
| Deciduous | 10.0 | 10.8 | 5.0 | Boone, 1992 |
| Pine | 9.0 | 9.0 | 0.0 | Boone, 1992 |

Maximum values obtained by running PnET-CN to equilibrium using either mean climate data for a site or predicted data using models of Ollinger et al. (1995) and vegetation parameters for the dominant species on the site.

rigorous test. The Whiteface stand does not fit this trend unless an estimate of N cycling derived from biomass production and N concentration (Johnson and Lindberg, 1992) is used in place of the direct measurement (open points, Figs. 6 and 7). Otherwise, all stands with measurable nitrification have ratios of measured to maximum N

mineralization rates above 0.75, and all stands below 0.7 show no nitrification. A much larger data set is required to accurately assess the value of the measured:maximum N cycling ratio.

3.2.3. Regional extrapolations

While the moderate complexity of the PnET-

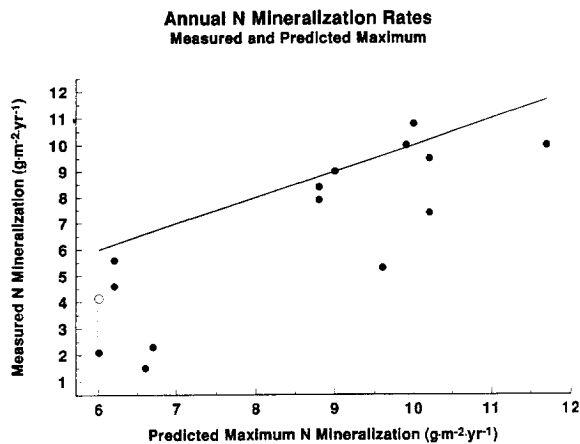


Fig. 6. Measured annual net N mineralization rates compared with predicted maximum values for several forested sites within the northeastern USA. (See Table 7 for data sources, dotted line and open circle represent second estimate of current N cycling rate at the Whiteface Mountain site.)

CN model is required to capture transient responses in N cycling to disturbance, and to predict maximum N cycling rates for different sites, the resulting patterns in predicted maximum rates within the northeastern USA can be summarized in a series of single-equation models.

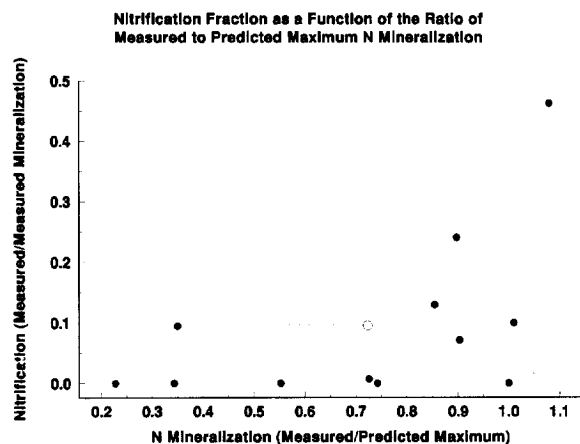


Fig. 7. Measured ratio of net annual nitrification to net annual N mineralization as a function of the ratio of measured net N mineralization to predicted maximum N mineralization. Data sources same as for Fig. 8.

For deciduous forests (Fig. 8a) the best statistical relationship is with total annual precipitation. For both pine and spruce-fir forests, the best relationship is with growing degree days, and is asymptotic rather than linear. These relationships were better than multiple correlations with latitude, longitude and elevation, and were not improved significantly by the addition of other summary climate variables.

The differences between the deciduous and evergreen responses (Fig. 8b and c) relates to the higher photosynthetic capacity and therefore higher transpirational demand in the deciduous forests (Aber et al., 1996), resulting in increased water stress and the importance of precipitation in alleviating this stress. Maximum photosynthetic rate is lower in pine and spruce groups, and so is transpirational demand, reducing the influence of precipitation. Length of growing season, as indicated by total growing degree days, is more important. The asymptotic relationship is due to increasing respiration at higher total growing degree days and some water stress in certain areas, which begin to offset the effects of a longer growing season.

Autocorrelations between precipitation and temperature are strong in this data set. Regressions against one variable, such as precipitation, include the effects of other variables as well. This means that these regressions are specific to this region alone and cannot be extrapolated to any other region.

These regressions can be used to generate regional maps of maximum N cycling for the northeastern USA (Fig. 9) given data planes for total annual precipitation, total annual growing degree days (Ollinger et al., 1993, 1995) and a forest type map (Lathrop and Bognar, 1994) for the region. These rates are lowest (below 6.5) in spruce-fir forests in the northern sections of the region, and at the highest elevations. Values between 6.5 and 8 occur in pine and mixed deciduous-evergreen forests throughout the region. The highest values are in deciduous stands at moderate elevations, where precipitation is greater, and water stress lower, than at lower elevations.

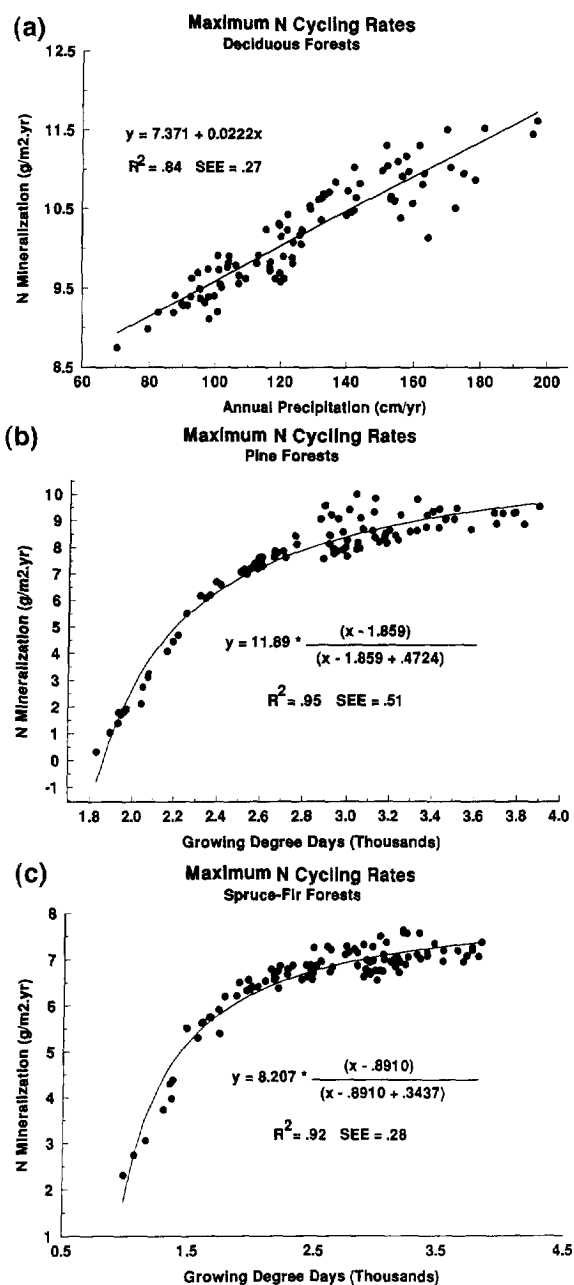


Fig. 8. Relationships between predicted maximum annual N cycling rates and annual climatic variables: a, deciduous forests; b, pine forests; c, spruce-fir forests. Values derived by running PnET-CN to equilibrium with mean climate values for 100 randomly selected combinations of longitude, latitude and elevation within the northeastern USA. Climate values for each site derived from Ollinger et al. (1995).

4. Conclusions

We conclude that the ratio of measured to maximum annual net N mineralization rates offers promise as an integrated measure of site N status and the approach to nitrogen saturation. With the availability of additional data sets on this ratio for the northeastern USA, it would be possible to both map the current degree of N saturation across the region, and, by application of the PnET-CN model and available scenarios for future N deposition, to predict future N mineralization and N leaching rates, including nitrate concentrations in streamwater.

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Appendix A. Detailed description of coded algorithms

The algorithms for the added processes are contained in five subroutines. CNTrans calculates litterfall and transfers to soil organic matter (SOM). Decomp calculates C and N mineralization and nitrification and also matches N availability with plant N demand to determine N uptake. NUptake combines N availability with the strength of plant demand to determine uptake of N into the PlantN pool. Leach calculates leaching losses of nitrate. AllocateYr determines the degree of N limitation on plant growth and also the allocation of C and N to buds and wood storage which determine next year's total foliage and wood production. The first four routines are executed monthly as part of the regular cycling of C and N. AllocateYr is called at the end of the growing season.

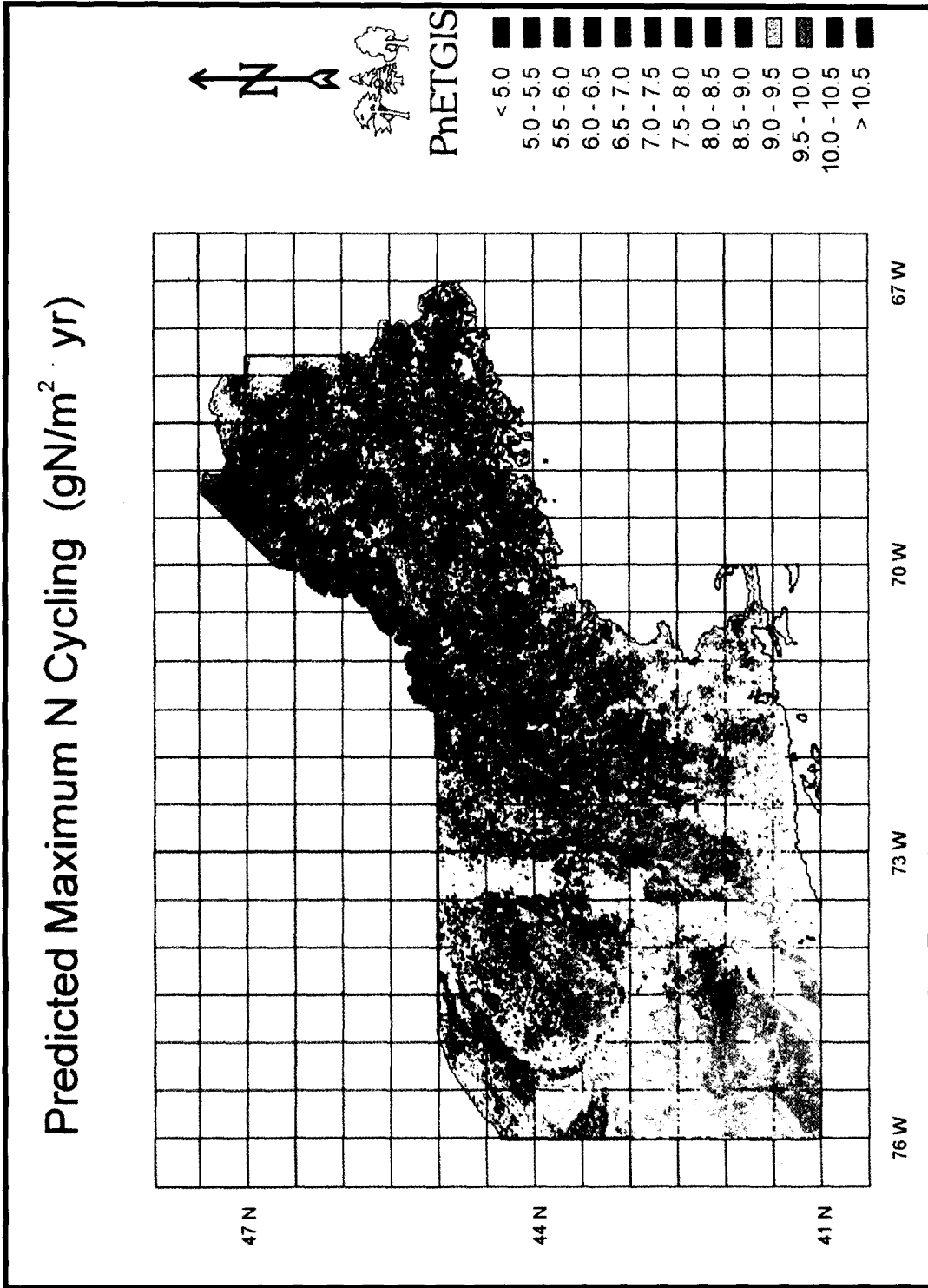


Fig. 9. Spatial variation in predicted maximum N cycling rates for the northeastern USA, given current land use and forest type distributions.

In CNTrans, woody litter production is calculated as:

$$\text{WoodLitM} = \text{WoodMass} * \text{WoodTurnover} \quad (1)$$

This turnover carries with it the same fraction of N from WoodMassN. Woody litter is held in a separate pool (DeadWoodM, DeadWoodN) and transferred to soil organic matter at a rate determined by WoodLitTrans. The variable WoodLitCLoss specifies a ratio of CO₂ production from decaying wood to residue transfer to SOM. This results in an increasing concentration of N in woody material as it decays in this pool.

Fine root turnover rate is determined by the equation:

$$\begin{aligned} \text{RootTurnover} = & \text{RootTurnoverA} \\ & + \text{RootTurnoverB} * \text{NMin} \\ & + \text{RootTurnoverC} * \text{NMin}^2 \quad (2) \end{aligned}$$

derived from Aber et al. (1985). Total fine root litter is then

$$\text{RootLitM} = \text{RootMass} * \text{RootTurnover} \quad (3)$$

with a similar calculation for RootLitN. Unlike woody litter, Root litter is transferred directly to the SOM pool for decomposition.

The Decomp routine determines the mineralization of C and N, net nitrification and, along with plant uptake demand, total plant N uptake. In earlier models (Aber et al., 1982; Aber, 1992), we have described the process of litter decay and humus formation in some detail. Sensitivity analyses with these models determined that highly resolved submodels of litter dynamics exerted little control over N dynamics relative to the much larger pool of soil organic matter. Because of this, PnET-CN contains only a single soil pool with a turnover rate roughly equivalent to the SLOW pool in the CENTURY model (Parton et al., 1993). The variable Ksom determines the annual average turnover rate for this pool which is modified by a temperature scalar TMult where:

$$\text{TMult} = 0.68 * e^{(0.1 * (\text{tave} - 7.1))} \quad (4)$$

and tave is monthly average temperature. This function results from an empirical fit to seasonal

decomposition data from several temperate forest sites (McClougherty et al., 1985; Aber et al., 1990). Carbon release from SOM is then:

$$\text{DSOM} = \text{SOM} * (1 - e^{-\text{Ksom} * \text{TMult}}) \quad (5)$$

Gross N mineralization (GrossNMin) is assumed to be equal to DSOM times the concentration of N in SOM.

As litter inputs have much lower N concentrations than SOM, it is necessary to describe a process of N reimmobilization. We defined a simple function:

$$\begin{aligned} \text{NReten} = & (\text{NImmobA} + \text{NImmobB} * \text{SoilPctN}) \\ & / 100 \quad (6) \end{aligned}$$

where NReten is the fraction of mineralized N which is reimmobilized, NImmobA and B are parameters, SoilPctN is the percentage of N in soil organic matter. Gross N immobilization is calculated as GrossNMin * NReten and net N mineralization is gross N mineralization minus gross N immobilization. The values for NImmobA and NImmobB were selected to allow complete reimmobilization of all mineralized N at 1.5%N in SOM, and decreases to zero reimmobilization at 4.3%N. This curve is, in effect, a calculation of the degree of N limitation on microbial production, and the effectiveness of microbial demand for N in competing with plants for mineral N. This formulation is similar to that used in FORNUTS (Binkley, 1986) and embodies the concept that net N mineralization increases with decreasing C:N ratios. The endpoints of the relationship are determined by empirical data on N concentrations in litter when net N mineralization begins and on maximum observed N concentrations in soil organic matter (i.e. the C:N concentration where reimmobilization approaches zero).

Nitrification is controlled in PnET-CN by competition between nitrifiers and plants for NH₄. The effect of high soil pH on nitrification is ignored in this version. The fraction of NH₄ nitrified in any one month is

$$\text{NRatioNit} = ((\text{NRatio} - 1) / \text{FolNConRange})^2 \quad (7)$$

This varies between zero (when NRatio is 1 and N concentrations in tissues are at minimum values), and 1 (when NRatio = FolNConRange and N concentrations are at maximum values, see discussion of AllocateYr routine below).

NUptake calculates a root sink strength for N as:

$$\text{RootNSinkEff} = \text{SQRT}(1 - (\text{PlantN}/\text{MaxNStore})) \quad (8)$$

This varies between 1 (when PlantN = 0) and 0 (when PlantN = MaxNStore). Actual total plant N uptake each month is:

$$\text{PlantNUptake} = (\text{NH}_4 + \text{NO}_3) * \text{RootNSinkEff} \quad (9)$$

Thus as the internal plant N pool increases, plant demand for N, and actual N uptake, decreases. By Eq. (6), net nitrification will also increase as PlantN increases.

In the Leach routine, all available nitrate is assumed to be in the soil solution. The fraction of soil water which drains in any month is multiplied by the total NO₃ pool to determine total nitrate leaching in that month.

AllocateYr contains the algorithms by which the relative degree of N limitation on plants is calculated and the effect of this on N content of foliage and other tissues is determined. Carbon and nitrogen for next year's foliar and wood production are also transferred to Bud and Wood compartments.

A calculated variable (NRatio) is central to the interactions between carbon and nitrogen cycles and expresses the degree of N limitation on plant function. This in turn affects both the nitrogen concentration in foliage, and so maximum rates of photosynthesis, and also the fraction of mineralized N which is nitrified. NRatio is determined by the amount of mobile N in the plant (PlantN) relative to a specified maximum value (MaxNStore). An additional variable (FolNConRange) limits the range of NRatio, which is calculated as:

$$\text{NRatio} = 1 + (\text{PlantN}/\text{MaxNStore}) * \text{FolNConRange} \quad (10)$$

NRatio varies between 1 and 1 + FolNConRange. FolNConRange establishes the maximum fractional increase in N concentration in foliage relative to the minimum or critical concentration. This in turn is twice the minimum concentration in litter, as the model assumes a constant 50% retranslocation from senescing foliage. No retranslocation is assumed to occur from wood and fine roots.

The amount of Plant N transferred to BudN for next year's foliar growth is:

$$\text{BudN} = (\text{BudC}/\text{CFracFol}) * \text{FLPctN} * 2 * \text{NRatio} \quad (11)$$

where BudC is the amount of carbon allocated to next year's foliar production (calculation same as in PnET-II, Aber et al., 1995), CFracFol is the fraction of carbon in foliar biomass, FLPctN is the minimal percent N in foliar litter, 2 results from the assumption of 50% retranslocation and NRatio is calculated as above. This calculation assures that the N concentration in next year's foliage will be NRatio times the minimum specified as (2*FLPctN).

NRatio affects the concentration in other tissues as well. For wood and fine roots, live and litter concentrations are the same and are calculated as litter concentration times NRatio. Thus elevated N availability to plants is reflected in increased N concentration in biomass, which will, in turn, decrease the C:N ratio in litter, decrease reimmobilization into SOM and increase net N mineralization.

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