GLOBAL BIOGEOCHEMICAL CYCLES, VOL. 11, NO. 4, PAGES 639-648, DECEMBER 1997

Effects of land use, climate variation, and N deposition on N cycling and C storage in northern hardwood forests

John D. Aber
Complex Systems Research Center, University of New Hampshire, Durham

Charles T. Driscoll
Department of Civil and Environmental Engineering, Syracuse University, Syracuse, New York

Abstract. We hypothesized that much of the variability in dissolved inorganic nitrogen (DIN) loss from forested catchments can be explained by land use history and interannual climatic variation, and that these factors determine the degree to which N deposition results in increased storage of C in forests. We used an existing model of C, N, and water balances in forest ecosystems in conjunction with long-term climate and N leaching loss data from several northern hardwood forest ecosystems to predict the effects of land use, climate variability and N deposition on C storage and N cycling and loss. Six sites from the White Mountains of New Hampshire with very different land use histories and annual stream DIN losses were used. The only model parameter that varied between sites was land use or disturbance history. Each site was simulated using both mean climate data for each year and actual time series climate data. Vegetation removal resulted in a period of increased DIN leaching, followed by losses below those in control stands for both measured and simulated data. One site with an extreme fire event over 170 years ago still showed reduced N losses in both modeled and measured data. Significant interannual variation in DIN loss is evident in the field data. Model predictions using actual climate time series data captured much of this variation. This high interannual variability along with the slow rate of change in DIN loss predicted by PnET-CN using mean climate throughout the simulations suggests that statistically significant increases in DIN leaching losses due to long-term increases in N deposition will not be detectable for several decades, given current rates of N deposition. N deposition increased C storage in all simulations, but the quantity stored was about 50% that predicted by another published model. This difference results from differences in the efficiency with which added N is retained in the ecosystem. The previous model used an 80% retention value, while retention was closer to 50% over most of the time period examined here.

Introduction

Several papers presented as part of the AGU Chapman Conference on "Nitrogen Cycling in Forest Catchments" summarized in this volume suggest that forest ecosystems are a critical part of the biosphere's response to human alterations of the global cycles of nitrogen (N) and carbon (C). This is due both to the presence of large areas of forest land in regions experiencing anthropogenically-increased N deposition and human-altered land use, and to the fact that forest ecosystems have the potential to store more of the CO_2 generated by human activity than other ecosystem types.

Some general patterns emerged from the data presented at this meeting and from previous work. These included: (1) the role of soil C:N ratio as a useful predictor, along with N deposition, of nitrate leaching from forests [*Tietema and Beier*, 1995; *McNulty et al.*, 1991; N. B. Dise personal communication, 1996], (2) the large differences in N retention efficiency between forests of nearly identical age and composition [*Dise and Wright*, 1995; *Driscoll et al.*, 1989; N. B. Dise personal communication, 1996], (3) the long-term nature of increasing nitrate leaching from forests in response to N additions and the difficulty in detecting these changes in measured nitrate losses due to large interannual variability [e.g., *Mitchell et al.*, 1996], and (4) the potential importance of N deposition to forest ecosystems in increasing C storage, accounting for some of the "missing" C in the global carbon cycle [*Peterson and Melillo*, 1985; *Schindler and Bayley* 1993; *Townsend et al.*, 1996].

We hypothesized that patterns 1-3 above relate to the long-term legacy effects of historical land use practices and that long-term mean dissolved inorganic N (DIN) loss rates can be explained in large part by site history. We also hypothesized that the large interannual variation in DIN loss is related to, and can be explained by, interannual changes in climate as it affects water stress, carbon gain, and soil metabolism. Finally, we hypothesized that the degree to which N deposition leads to increased C storage in forest ecosystems will depend on the N status of the forest, which will in turn depend on the past history of N-extractive disturbances such as fire and harvesting.

Paper number 97GB01366.
0886-6236/97/97GB-01366$12.00

The purpose of this paper is to use a recently developed model of C, N, and water balances in forest ecosystems in conjunction with long-term data bases on N leaching losses from several northern hardwood forest ecosystems as part of the Hubbard Brook Ecosystem Study to address the question of long-term effects of land use, climate variability, and N deposition on C storage and N cycling and loss in these systems. The model represents an interactive set of working hypotheses which are tested using the measured patterns of DIN loss. After determining the possible value of the model by this validation exercise, we use it to predict the extent to which increased N deposition has resulted in increased C storage for each system.

Methods

Overview

Field measurements of DIN losses in stream flow are compared with model predictions for sites with very different land use histories. Watershed losses of DIN were used because: (1) This measurement is recognized as a key indicator of forest N status [e.g., *Wright and van Breeman*, 1995; *Stoddard*, 1994; *Aber et al.*, 1989], (2) nitrate mobility and loss are linked to other important processes such as surface water acidification [e.g., *Emmett et al.*, 1995; *Boxman et al.*, 1995; *Kahl et al.*, 1993] and (3) stream DIN data, collected using consistent and reliable methods, are available for considerable periods of time from several sites. Long-term time series measurements of internal N cycling processes are very rare.

Nitrogen Fluxes From Six Northern Hardwood Watersheds

Site descriptions. Six sites from the White Mountains of New Hampshire having very different land use histories, and annual stream DIN losses were used (Table 1). These include four experimental watersheds in the Hubbard Brook Experimental Forest (HBEF), as well as Cone Pond Watershed (CPW) and the Bowl Natural Area (BNA). These sites represent the range of stand age and disturbance history that occurs in the northern forest of the northeastern United States.

The HBEF (43°56'N, 71°45'W) is a 3037-ha experimental forest, with several gauged watersheds, some of which have been experimentally manipulated. Hubbard Brook has hilly terrain, ranging from 222 to 1015 m elevation. Except for some of the experimental watersheds, the HBEF is an unbroken forest of northern hardwoods, with coniferous vegetation at higher elevations. Mean total DIN (NO_3^- + NH_4^+) deposition has been estimated at 0.87 g N$\cdot$m^{-2}yr^{-1}, representing bulk wet deposition of 0.69 g N$\cdot$m^{-2}yr^{-1} (for the period 1964-1991[*Butler and Likens*, 1991; *Likens*, 1992; *Likens and Bormann*, 1995]) and dry deposition of 0.18 g N$\cdot$m^{-2}yr^{-1} (for the year 1989; G. Lovett, unpublished data, 1997]. The site is described in detail elsewhere [*Likens et al.*, 1977; *Bormann and Likens*, 1979; *Likens et al.*, 1994] and has been studied extensively since 1963.

Watershed 6 (W6), the reference watershed, was logged intensively from 1910-1917 and experienced some salvage removals following the hurricane of 1938. Watershed 2 (W2) was manipulated as a devegetation experiment beginning in 1965-1966 when all vegetation was cut and left on site. Herbicide was applied during the summers of 1966, 1967, and 1968 to prevent regrowth of vegetation, which began in 1969.

Table 1. Forest Disturbance History for the Watersheds Used in this Analysis

Site	Hubbard Brook W2	Hubbard Brook W4	Hubbard Brook W5	Hubbard Brook W6	Cone Pond	The Bowl
Treatment or Disturbance*	DV	SC	WT	logged	burned	none
Dates of Disturbance	1965-1968	1970-1974	1983-1984	1910-1917	~1820	none
Regrowth Initiated	1969	1971-1975	1984	1918	~1821	-
Stand age, years	28	22-28	13	79	~175	200+

* DV means devegetated (cut and herbcided for 3 years), SC means strip cut and WT means whole tree harvesting. All sites were also affected by the hurricane of 1938. Some salvage harvesting occurred in the Hubbard Brook watershed following this event.

Watershed 4 (W4) was commercially clear-cut in 25-m-wide strips along the elevational contour. Every third strip was harvested in 1970. The remaining strips were harvested in 1972 and 1974. Regrowth began in 1971, 1973, and 1975. Watershed 5 (W5) was whole-tree harvested in 1983-1984.

Cone Pond Watershed (43°54' N, 71°36'W) is a 53-ha catchment, ranging from 480 to 640 m in elevation. The forest is dominated by mixed coniferous vegetation (80%), with lesser amounts of northern hardwoods (15%). Historical records suggest that there has been very little cutting at CPW. Less than 10% of the conifers were cut during two periods: (1) 1890-1910 and (2) 1933. The watershed was disturbed by a major fire around 1820. This may have followed a major hurricane that struck New England in 1815. Charcoal is evident in over 90% of the catchment. A description of CPW is provided by *Bailey et al.*, [1995, 1996]. Bulk wet deposition of DIN to the watershed for 1990-1991 was 0.67 g N$\cdot$m^{-2}yr^{-1}, very similar to the mean value for HBEF. No measurements of dry deposition of N have been made for CPW.

The BNA (43° 56' N, 71° 23' W) is a 607-ha watershed ranging in elevation from 580 to 1240 m. The major tree species of the BNA are characteristic of the northern hardwood forest. The 206 ha west branch of the watershed is one of the last remaining mixed deciduous and coniferous forests in the northeastern United States with no history of logging, human settlement or forest fire. A description of the BNA is provided by *Martin* [1979]. Measurements of atmospheric deposition of N to the BNA were made in 1973-1974 (0.88 g N$\cdot$m^{-2}yr^{-1}). Values were found to be similar to the nearby (27 km) HBEF [*Martin* 1979].

DIN losses in stream flow. Data on annual DIN losses in stream flow are available from 1963 for the HBEF [*Likens et al.*, 1994; *Likens and Bormann*, 1995], from 1990 at CPW [*Bailey et al.*, 1995] and from 1973-74 and 1995-96 at BNA [*Martin*, 1979, C. T. Driscoll unpublished data, 1977]. The sampling and analytical methods are described in detail elsewhere (see *Likens et al.*, 1994; *Bailey et al.*, 1995; *Martin*, 1979]. For the experimental watersheds at the HBEF and at CPW, annual outputs of DIN were calculated based on stream samples collected weekly and analyzed for NO_3^- and NH_4^+ and continuous measurements of stream discharge. For the BNA, stream samples were collected at intervals ranging from 2 to 4 weeks, and samples were analyzed for NO_3^- and NH_4^+ concentrations. Because of restrictions on research activities that can be conducted at Research Natural Areas, a stream gauging station has not been established for the BNA. As a result, stream flow for W6 at the HBEF was used to estimate stream discharge for the Bowl during the periods of stream sampling. Due to similarities in climate, soils, aspect and topography stream discharge for W6 is thought to be similar to the BNA [*Martin*, 1979].

Model Structure and Parameterization

PnET-CN (Figure 1) [*Aber et al.*, 1997] is a lumped-parameter model which uses generalized representations of physiological processes including photosynthesis, transpiration, respiration, allocation, phenology, litter production, decomposition, and nitrification along with monthly time step climate data to predict monthly dynamics of C, N, and water in forest ecosystems. The model incorporates a multilayered canopy model of phenology and photosynthesis (PnET-Day) [*Aber et al.*, 1996] which has been validated against daily gross carbon flux measurements at the Harvard Forest, and allocation, respiration, and transpiration algorithms from a second model (PnET-II) [*Aber et al.*, 1995b] which has been validated against both carbon and water balance data from the Harvard Forest and Hubbard Brook. Added to this structure in the PnET-CN model [*Aber et al.*, 1997] are accumulated live biomass, litter, and soil organic matter compartments. N is also added to all compartments and fluxes, and the additional processes of net N mineralization and nitrification, plant N uptake, and leaching losses (Figure 1) are also included to produce complete cycles for both C and N. N deposition is calculated using an average concentration in precipitation for that year times measured monthly precipitation. Dry deposition is as annual total divided into 12 equal monthly values. The single soil organic matter pool represented in PnET-CN is functionally equivalent to the sum of all pools in the Century model [*Parton et al.*, 1993], except the slowest "passive" pool. Without this pool, total ecosystem C content as modeled is not equivalent to total published inventories which include total soil C. Therefore only changes in C storage between treatments predicted by PnET-CN are relevant here, and the validity of this comparison assumes that the treatments applied do not affect this large but very inactive (residence time equal to 1000 years) mass of C in the "passive" soil pool.

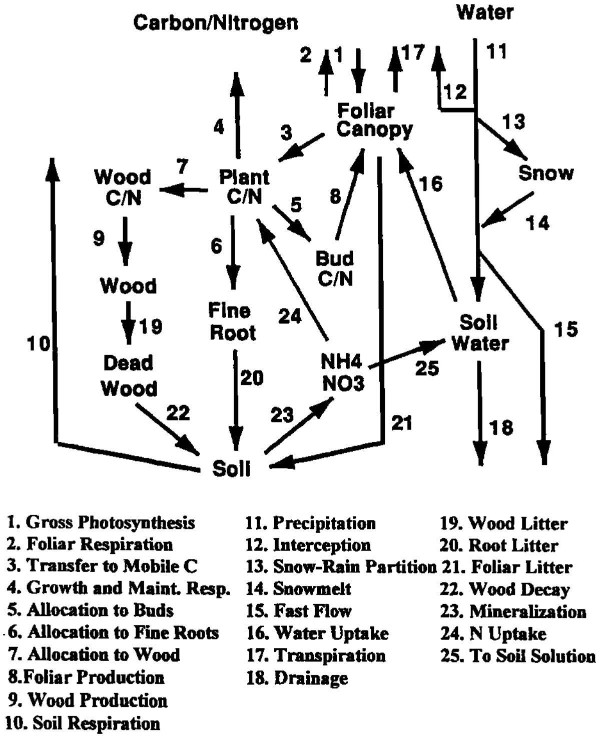

Figure 1. Diagram of the interactions in PnET-CN model. See text, Table 2, and references [*Aber et al.*, 1997] for complete discussion.

C and N cycles interact at several points in the model. 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 diminished. Increases in N concentrations in foliage, wood, and roots also occur, increasing demands on the PlantN pool. The increase in foliar N increases net photosynthesis (unless limited by water stress) and so increases internal plant pools of C (PlantC). As PlantC increases, NPP increases and so does the demand for incorporating N in tissues, 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 also determines the fraction of available NH_4 which is nitrified. 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 NO_3 remaining in the soil solution after plant uptake, and to water drainage rates.

One new algorithm was added to the model as originally described by *Aber et al.* [1997] which represents the effects of soil water content on microbial activity. This factor was not included in earlier versions because we had assumed that, in humid regions, occasional soil water stress affected plant photosynthesis far more than microbial decomposition and mineralization. A review of the literature [*Skoop et al.*, 1990; *Linn and Doran*, 1984; *Myers et al.*, 1982] suggests rather a linear decrease in CO_2 production as soil water content decreases from field capacity. The version used here includes this linear decrease in decomposition and mineralization from full activity at field capacity to zero activity when no plant available soil water remains. The current version has also been recoded from QuickBasic to VisualBasic, includes a windows-based interface which allows alteration of all variables at run time, and is available free of charge from the first author.

Every effort has been made to limit the number of vegetation and site variables required to run PnET-CN so that as many as possible can be derived directly from field measurements. PnET-CN is not a tuned or calibrated model. Rather, data from the literature are used to determine the best value for each parameter, and the model is then run for sites for which data on predicted or output parameters are available. Comparing measured and predicted values (model validation) is a critical test of the accuracy with which the model represents field conditions and is central to determining the possible accuracy of model predictions. For this exercise, all site and vegetation parameters were held constant across sites, with the exception of one application for Cone Pond in which the effects of spruce/fir versus northern hardwood vegetation are compared (see Table 2 for a complete listing of variables and values used; see *Aber et al.* [1995b, 1996, 1997] for complete model descriptions).

Only two factors differ between model runs reported here: site history and the use of mean climate data versus real time series data. PnET-CN contains a Scenario routine in which changes in climate drivers, N deposition, harvesting, fire, agricultural use, and fertilization can be specified. Harvest and fire effects are described in terms of the fraction of plant and soil organic matter and N lost for each event. N deposition is described as a constant background rate and a ramp to current levels. For all runs reported here, background N deposition is assumed to be

Table 2. Input Parameters Required to Run the PnET-CN Model and the Values Used for Each Variable for Northern Hardwoods (NH) and Spruce-Fir (SF) Simulations

Name	Definition (units)	Value	
		NH	SF
Site and soil variables			
Lat	latitude, degrees	45	45
WHC	water holding capacity, plant available water, cm	12	12
Canopy Variables			
k	canopy light attenuation constant (no units)	0.58	0.5
FolReten	foliage retention time, years	1	4
SLWMax	specific leaf weight at top of canopy, g·m^{-2}	100	170
SLWdel	change in SLW with increasing foliar mass above, g·m^{-2}g^{-1}	0.2	0
FolRelGrowMax	maximum relative growth rate for foliage, %·yr^{-1}	0.95	0.3
GDDFolStart	growing degree days at which foliar production begins	100	300
GDDFolEnd	growing degree days at which foliar production ends	900	1400
GDDWoodStart	growing degree days at which wood production begins	100	300
GDDWoodEnd	growing degree days at which wood production ends	900	1400
Photosynthesis Variables			
AmaxA	intercept /relationship-foliar N-max photosyn. rate,	-46.	5.3
AmaxB	slope \ umoles CO$_2$·m^{-2} leaf.sec^{-1}	71.5	21.5
BaseFolRespFrac	respiration as a fraction of maximum photosynthesis	0.1	0.1
HalfSat	half saturation light level, umoles·m^{-2}sec	200	200
AmaxFrac	daily A_{max} as a fraction of early morning instantaneous rate	0.75	0.75
PsnTOpt	optimum temp. for photosynthesis, °C	24	20
PsnTMin	minimum temp. for photosynthesis, °C)	4	0
RespQ10	Q_{10} value for foliar respiration	2	2
Water Balance Variables			
DVPD1	/ coefficients for power function converting VPD to	0.05	0.05
DVPD2	\ fraction loss of photosynthesis	2.0	2.0
PrecIntFrac	fraction of precipitation intercepted and evaporated	0.11	0.15
WUEConst	constant in equation for WUE as a function of VPD	10.9	10.9
FastFlowFrac	fraction of water inputs lost directly to drainage	0.1	0.1
f	soil water release parameter	0.04	0.04
Carbon Allocation Variables			
CFracBiomass	carbon as fraction of foliage mass	0.45	0.45
RootAllocA	intercept / of relationship between	0	0
RootAllocB	slope \ foliar and root allocation	2	2
GRespFrac	growth respiration, fraction of allocation	0.25	0.25
RootMRespFrac	ratio of fine root maintenance resp.to biomass production	1	1
WoodMRespA	wood maint. resp. as a fraction of gross photosynthesis	0.07	0.07
PlantCReserveFrac	fraction of PlantC held in reserve after allocation to BudC	0.75	0.75
MinWoodFolRatio	minimum ratio of carbon allocation to wood and foliage	1.5	1.25
Biomass Turnover and N Concentration Variables			
WoodTurnover	fractional mortality of live wood per year	0.025	0.025
WoodLitTrans	fractional transfer from dead wood to SOM per year	0.1	0.1
WoodLitCLoss	fractional loss of mass as CO$_2$ in wood decomposition	0.8	0.8
RootTurnoverA	/ coeficients for fine root turnover, fraction·yr^{-1}	0.789	0.789
RootTurnoverB	| as a function of annual net N	0.191	0.191
RootTurnoverC	\ mineralization - quadratic equation	0.0211	0.0211
MaxNStore	max. N content in PlantN pool, g·m^{-2}	20	20
Kho (Ksom)	decomposition constant for SOM pool, yr^{-1}	0.075	0.075
NImmobA	/ coeficients for fraction of mineralized N	151	151
NImmobB	\ reimmobilized as a function of SOM C:N	-35	-35
RLPctN	min. N concentration in root litter, %	1.2	1.1
FLPctN	min. N Concentration in foliar litter, %	0.9	0.35
WLPctN	min. N concentration in wood litter, %	0.2	0.2
FolNConRange	max. fractional increase in N concentrations	0.6	0.6

See *Aber et al.*, [1995], [1996], and [1997] for more complete explanations

Table 3. Disturbance Scenarios as Coded for PnET-CN.

Watershed	Year	Mortality	Biomass Removed	Soil C and N
Cone Pond	1820	.99	.99	.8
	1938	.2	.01	0
The Bowl	1938	.2	.01	0
Watershed 6	1904	.2	.8	0
	1919	.6	.8	0
	1938	.2	.4	0
Watershed 2[a]	1965	.995	.01	0
	1966	.98	.01	0
	1967	.98	.01	0
Watershed 4[a]	1970	.25	.8	0
	1972	.375	.8	0
	1974	.75	.8	0
Watershed 5[a]	1983	.8	.8	0

All biomass removals occur in December of the year specified and will affect N cycling in the following year. The fire at Cone Pond was assumed to consume essentially all above ground biomass and all of the forest floor, containing 80% of the total" active" soil N pool. The 1938 hurricane was assumed to affect all watersheds equally, but with a salvage removing 40% of downed trees in the Hubbard Brook sites. Devegetation on Watershed 2 killed nearly all plants, but left all biomass on site. The strip cutting on Watershed 4 is assumed to have removed 80% of the remaining biomass in each strip, each year, producing an increasing total of all biomass removed, expressed on a whole watershed basis, each time.

[a] All other Hubbard Brook watersheds include the disturbance history for Watershed 6 with the following additions.

25% of current rates with a ramp which increases N inputs linearly from 1930 to the present. Removal events (Table 3) attempt to capture the disturbance history of each site as described above. The values used for removal rates cannot be known with certainty in most cases. A lack of accurate site disturbance history data may be the greatest impediment to the application of the PnET-CN model and to the understanding of differences in N cycling and N losses from different stands of apparently similar vegetation, soils, and climate.

Runs with real time series climate data use measurements from Hubbard Brook weather stations summarized to monthly values for average maximum and minimum temperature, total monthly precipitation and average monthly radiation. These data are derived from *Federer et al.* [1990] as updated from the Hubbard Brook website data gopher (data from 1990-1994). Runs using mean climate data use the monthly mean values for each climate parameter as derived from the time series data set for all years in the run.

Results and Discussion

Effects of Historical Land Use and Species Composition: Mean Climate Data

Different rates of N cycling and N loss are predicted by PnET-CN for the six different watersheds. The effects of disturbance history can be seen most clearly using the mean climate data series, which removes the interannual variability due to climate variation.

The three watersheds which have not been experimentally disturbed in recent times (Watershed 6, The Bowl, and Cone Pond) still have very different patterns of disturbance which yield different temporal patterns of N cycling and different current rates of DIN loss. Using mean climate data for each simulated year, predictions for The Bowl (Figure 2a) showed constant N cycling rates, consistent with equilibrium, steady state or mature status. The small perturbation in the late 1930s was the predicted effect of the 1938 hurricane, assuming no salvage harvesting occurred. Recent analyses have suggested that the actual effects of hurricanes on biogeochemical cycling are relatively small unless followed with a salvage harvest, and that the regional-scale changes in species composition and, in particular, water balances following the 1938 hurricane resulted more from salvage operations than from direct wind damage [*Foster et al.*, 1997]. Inputs and outputs of DIN are predicted to be nearly equal in the 1990s.

In contrast, watershed 6 (Figure 2b) experienced two harvesting episodes in the early 1900s, as well as a salvage event following the 1938 hurricane. Each event resulted in predicted declines in plant uptake leading to increased net nitrification and DIN loss. Net N mineralization declined slightly after each harvest due to the addition of woody biomass with a high C:N ratio to soils as slash. The long-term (1990s) result of these N extractions was a predicted 15% decline in net N mineralization and a 50% reduction in net nitrification and DIN losses from 1900 levels.

The Cone Pond watershed experienced a severe fire around 1820 and is currently dominated by spruce/fir rather than northern hardwood vegetation. With the values of C and N loss and initial revegetation assigned to this event in the model (Table 3), very long term reductions in N cycling and DIN loss were predicted (Figure 2c). This results largely from the actual losses associated with the fire and also with additional DIN losses during the period in which spruce/fir vegetation is predicted to have slowly recreated a full canopy (1820-1840). One hundred and seventy years later, with the 1938 hurricane (with no salvage harvest) as the only additional disturbance, both net nitrification rates and DIN loss rates were still near zero. Net N mineralization rates were substantially below the levels in The Bowl and Watershed 6 even in the 1990s because of the low N demand and cycling rates of spruce/fir vegetation, reflecting both the evergreen habit and low N concentration in foliage which limit the uptake capacity of this vegetation type. Had the watershed recovered with northern hardwoods vegetation (Figure 2d), net N mineralization would have increased more rapidly but would still be well below the potential N cycling rate for this vegetation type. Both net nitrification and DIN loss rate would still be greatly reduced in comparison with an undisturbed site (cf. Figure 2a).

Each of the experimentally treated watersheds at Hubbard Brook (Figure 3) showed similar patterns, with the timing and degree of response reflecting the timing and degree of disturbance. Watershed 2 was devegetated for 3 years which resulted in very large increases in net nitrification and losses in DIN. Recovery was delayed by the low initial foliar biomass in the first year after devegetation ceased. Watershed 4 also showed extended, but much reduced responses to the strip cutting which occurred over a five year period. Watershed 5 showed a very rapid response and recovery to the commercial whole-tree harvest in 1983. This was in contrast to watersheds 2

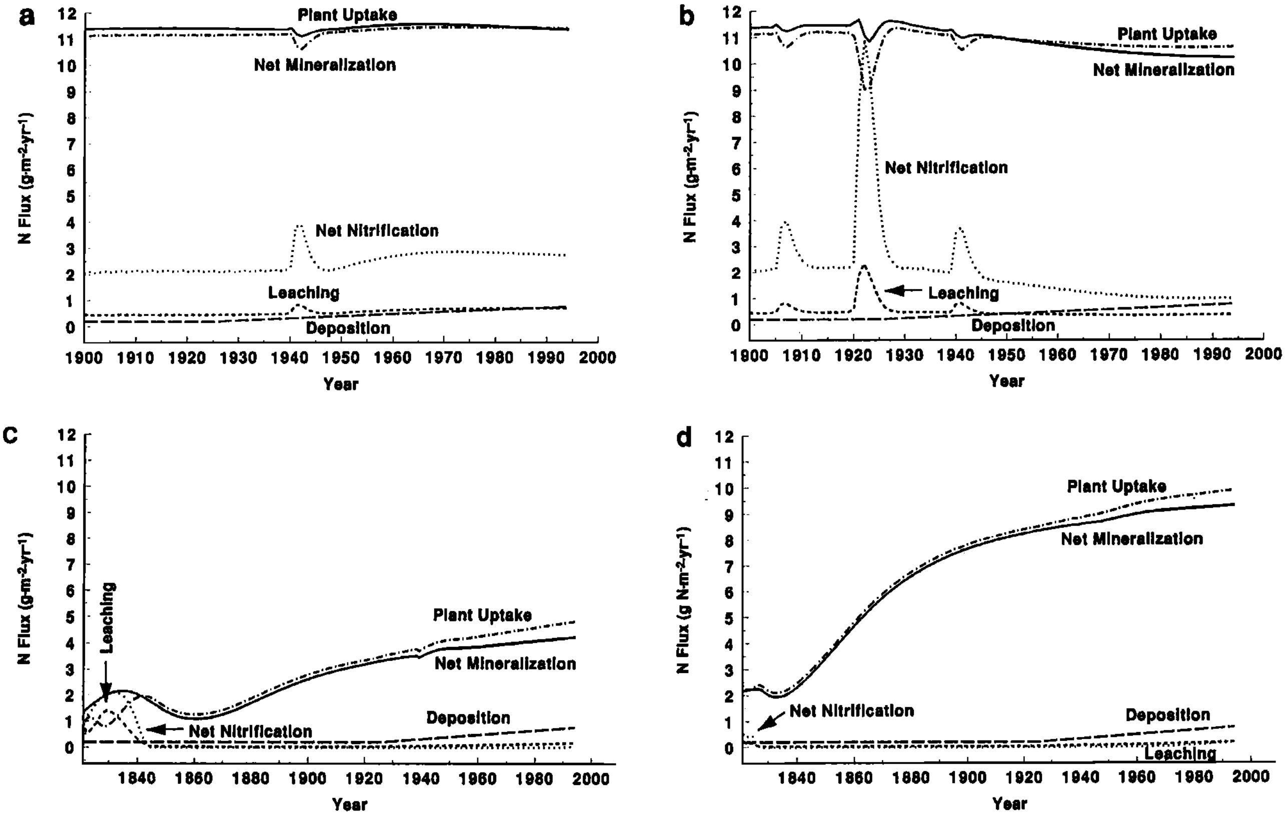

Figure 2. Predicted long-term changes in N cycling in the nonmanipulated watersheds: (a) The Bowl Natural Area, (b) Watershed 6 at Hubbard Brook Experimental Forest, (c) Cone Pond with spruce/fir vegetation, and (d) Cone Pond with northern hardwood vegetation..

and 4 where the disturbance was extended over 3 and 4 years, respectively.

Interactive Effects of Land Use and Climatic Fluctuations: Model Validation

Measured rates of DIN loss do not follow the smooth, consistent patterns shown in Figures 2 and 3. Rather, significant interannual variation is evident when DIN losses are expressed in absolute terms or as a fraction of annual N deposition [*Mitchell et al.,* 1996; *Likens and Bormann,* 1995]. Synchrony in periods of increasing and decreasing N loss between watersheds throughout the northeastern United States [*Mitchell et al.,* 1996] has been used to argue for regional-scale climatic control of these patterns. If this control is exerted through climatic effects on processes included in PnET-CN, then the model should be able to predict this interannual variability.

Interannual patterns in untreated watersheds. PnET-CN predictions using real climate data tracked observed annual DIN losses well for Watershed 6, at least up to 1990 (Figure 4a). The measured increases in DIN losses in the 1970s have been attributed to soil frost and defoliating caterpillar outbreak around 1970. Neither of these processes were captured in PnET-CN, although they could be added. These results suggest that much of the increase may be due to decadal timescale responses to climatic variability, including perhaps the severe drought of 1962-1964. Measured increases in DIN loss began at the end of this drought period (Figure 4a).

Episodes of elevated N loss reduce N availability in the ensuing years. Thus the losses of the 1970s would contribute in part to the below average DIN losses in the 1980s. Both drought and soil frost occurred together in 1989, and measured and predicted DIN losses increased. However, the model completely failed to predict the dramatic decrease in DIN losses noted for several watersheds in the northeast, including Watershed 6, in the early 1990s. However, simulations of both interannual variability and response to disturbance show that the model responds more slowly than the real systems. The model may then predict lower DIN losses in the mid-1990s once real climate data for those years are added.

The addition of the relationship between soil moisture content and microbial decomposition activity had a major impact on these results (Figure 4b). Without this equation, DIN losses were higher during the 1960s drought event as plant growth was reduced by water stress, while decomposition and mineralization were affected only by temperature. This loss moderated the predicted losses during the 1970s. Without the moisture stress effect on decomposition, the model failed to capture declines in DIN loss throughout the 1980s and 1990s.

The very large interannual variation evident in the DIN data from Watershed 6 and the PnET-CN results suggesting that this is driven by climatic variability demonstrated that it will be

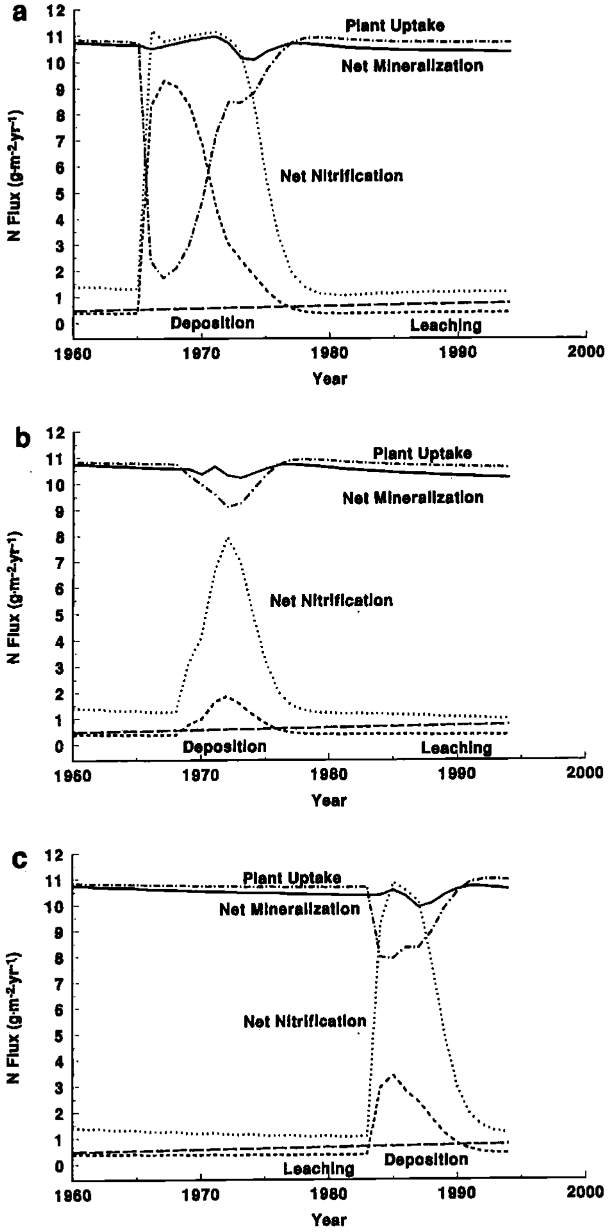

Figure 3. Predicted long-term changes in N cycling in the manipulated watersheds at Hubbard Brook: (a) Watershed 2, (b) Watershed 4, and (c) Watershed 5.

impossible to use DIN loss data to follow long-term changes in ecosystem N status due to N deposition unless the effects of climate variability can be removed. The slow rate of change in annual average DIN loss predicted under mean climate conditions (Figure 4a) may be indicative of the actual rate at which DIN losses increase in maturing stands under current rates of N deposition. This very slow rate of change will not be statistically visible for many decades given the high variability in measured DIN losses associated with climatic variation.

Measured data from the two other nonmanipulated watersheds covered a much shorter time period (Figure 4c). The model predicted the high DIN losses measured at The Bowl in 1973 and 1974 fairly well, but, as with Watershed 6, failed to predict the much lower losses in 1994. For Cone Pond, the model did predict losses lower than those for Watershed 6 and The Bowl but failed to predict the near-zero values actually measured. Since the model accurately predicted a complete lack of net nitrification at Cone Pond, the nonzero DIN losses resulted from incomplete retention of N deposited in precipitation outside the growing season. This suggests that the model inaccurately predicts inactivity in N uptake or immobilization processes during the winter or the activity of other N retention processes such as chemical reactions.

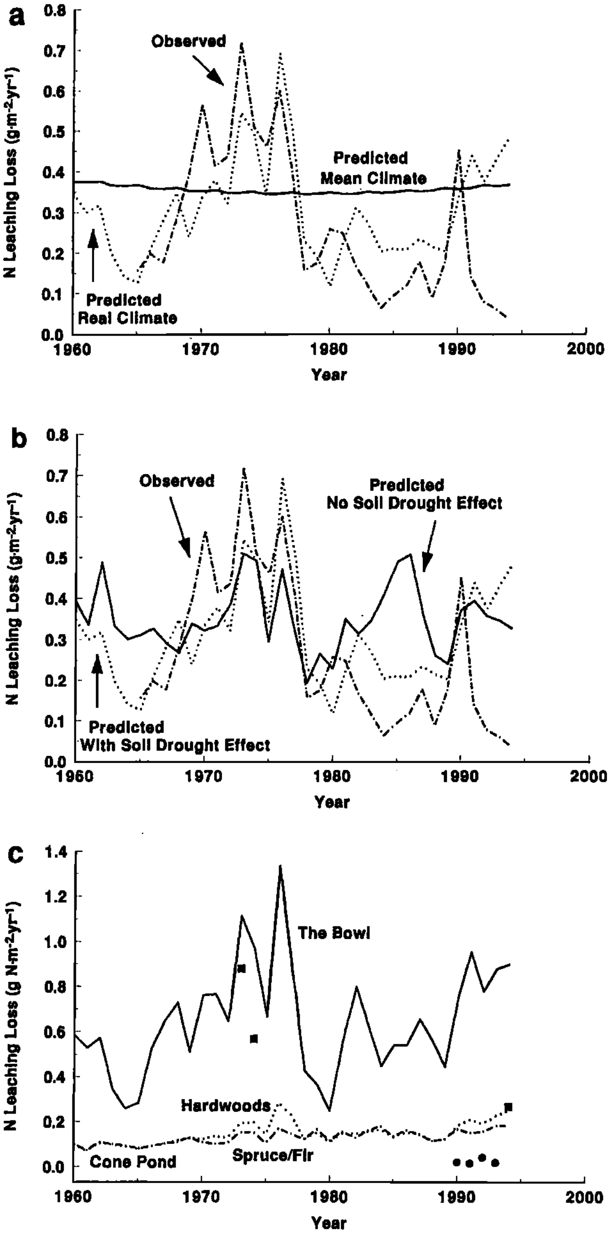

Figure 4. Predicted and observed annual variation in total DIN losses for nonmanipulated watersheds: (a) Watershed 6 using both mean and actual climate data to drive PnET-CN predictions, (b) Watershed 6 using actual climate data with and without an algorithm for soil moisture effects on decomposition, and (c) Cone Pond and The Bowl.

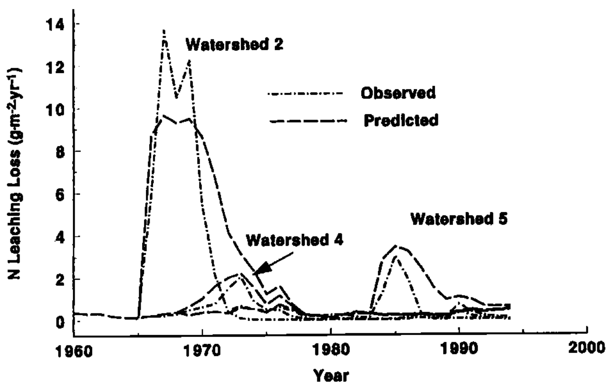

Figure 5. Predicted and observed annual variation in total DIN losses for manipulated watersheds at Hubbard Brook.

N loss responses to recent pulse disturbances. In contrast to the untreated watersheds, measured data from Watersheds 2, 4, and 5 showed relatively large pulse losses of DIN which tend to mask the more subtle effects of climate (Figure 5). In each case, the model captured the general pattern of response but differed from measured data in certain ways.

On Watershed 2, the predicted magnitude of the response was lower than observed in the first 3 years, but modeled N losses were above measured values for a longer period following the treatment. This may be due to the absence from the model of a micrometeorological algorithm increasing soil temperature under totally devegetated conditions, which, along with higher soil water content due to a lack of transpiration, would increase net N mineralization in the first 3 years. Higher losses of DIN in years 1-3 following the treatment would lead to lower losses in the ensuing years.

On Watershed 4, the timing of N losses was similar for predicted and observed data sets, while the predicted magnitude of losses was slightly higher than the observed. In Watershed 5, the difference was more substantial. These differences result mainly from the described severity of the harvest removals and could be calibrated to achieve closer agreement between predicted and observed. No such attempt was made.

Interactive Effects of Disturbance and N Deposition on Carbon Storage

The previous comparisons were validation exercises which suggest that the predictions obtained from the PnET-CN model for a wide range of disturbance regimes are generally consistent with measured patterns. Significant and specific model failures (e.g., overprediction of DIN losses from Cone Pond) suggest areas in which additional detail could be added to the model to improve validation success even further (e.g., use of soil temperature rather than air temperature to drive root activity). While no generally agreed upon standards exist for quantifying the "success" of a validation exercise, the relative degree of agreement between predicted and observed values should be used to suggest the possible accuracy of the type of predictions presented in this section.

As discussed above, PnET-CN contains only a single soil organic matter (SOM) pool with an annual turnover rate of about 7.5% yr^{-1}, such that total C stocks predicted here may be significantly smaller than total C inventories published elsewhere. However, assuming that the large passive soil pool content is not affected by the disturbances and timescales discussed here, predicted changes in total C storage should reflect those expected in the field.

As expected, the main factor which determined simulated differences in total C storage between treatments was the degree and timing of major C removal disturbances (Figure 6a). Thus Watershed 5, harvested in 1983, had the lowest predicted total C content. Watershed 2 contained less total C than Watershed 4 because of the greater severity of the disturbance. Total C storage was reduced in the Cone Pond simulation with spruce/fir vegetation because of the lower potential for total biomass production by this vegetation type relative to the deciduous type. Watershed 6 and The Bowl had the two highest totals for C storage.

Predicted changes in total C storage in response to N deposition were determined by running the model with and without the N deposition ramp which increased inputs above background levels. Removing anthropogenic N deposition reduced total C storage in all stands at the end of the simulation period (1994, Figure 6a, Table 4). The smallest changes were in the most recently or more severely disturbed ecosystems in which some of the long-term additions of C through N deposition would be offset by C and N losses.

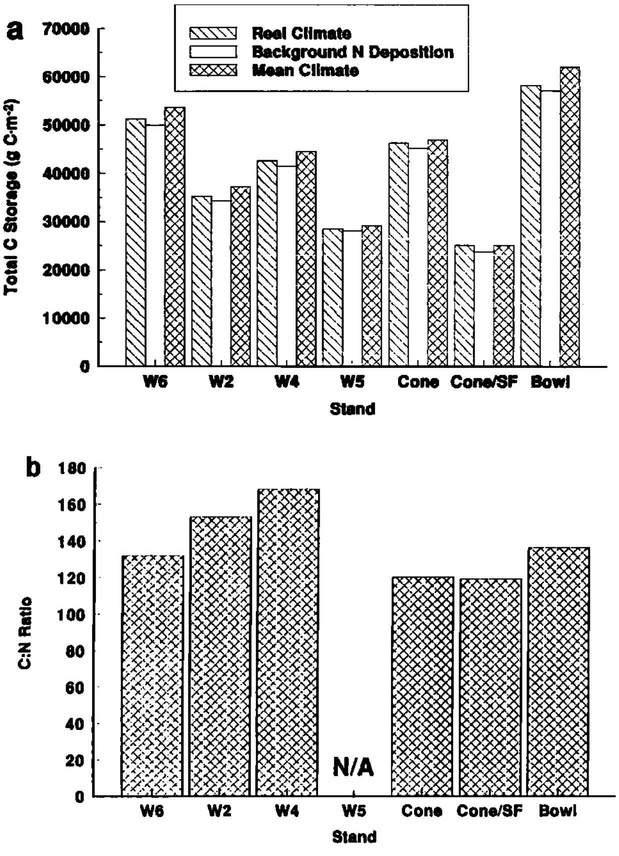

Figure 6. Predicted effects of increased N deposition and climate variability on C storage in six watersheds: (a) Total C storage by stand, and (b) Ratio of increases in C storage to increase in N storage.

Table 4. Differences in Total Carbon Storage and Net Ecosystem Production for the Different Watersheds Between Runs With and Without Increased N Deposition and Between Runs With Real or Mean Climatic Data

Watershed	W6	W2	W4	W5	Cone Pond (NH)	Cone Pond (SF)	Bowl
Change in Total Storage							
With Added N	1282	978	1200	469	1059	1469	1114
Difference in Net Ecosystem Production							
With Added N	44	46	47	[a]	24	37	30
With Mean Climate	38	51	45	[a]	44	25	36

The two runs for Cone Pond are with northern hardwood (NH) or spruce/fir (SF) vegetation. Data represent the total change in stored carbon over the entire course of the simulation (differences in total C content in 1994 g $C m^{-2}$), and differences in mean net ecosystem production in from 1980 to 1994 (g $C m^{-2} yr^{-1}$).

[a] Mean values in for net ecosystem production are not reported for W5 as this watershed was harvested during this period.

When expressed on an annual basis (Table 4), differences in net C accumulation in these simulations was significantly lower (24-47 g $C m^{-2} yr^{-1}$) than were predicted for temperate forests using a perturbation model [*Towsend et al.*, 1996]. Those authors estimated an annual increase of about 190 g $C m^{-2} yr^{-1}$ for a forest receiving 1.8 g $N m^{-2} yr^{-1}$ in N deposition. Assuming this result scales linearly, the average N deposition at Hubbard Brook (0.87 g $N m^{-2} yr^{-1}$) would yield 92 g $C m^{-2} yr^{-1}$. Two factors could have caused this difference: (1) the retention efficiency of added N differed between the two models, or, (2) the C:N ratio at which retained N was stored differed. The latter is not the case. The C:N ratio of 133 predicted in the Townsend et al. simulations is in the same range predicted by PnET-CN (Figure 6b). These values resulted from a roughly equal distribution of increased biomass between wood (C:N ~ 200) and soil (C:N ~ 25). The difference, then, is in N retention efficiency, which *Townsend et al.* [1996] fixed at 80% of annual deposition. PnET predicted retention values were closer to 50% over the 1980-1994 period. As discussed above, PnET-CN overestimated N losses in the 1990-1994 period and so would underestimate increased C storage. However, over the entire period in which real climate values were used and for which N loss data were available for W6 (Figure 4a) the 50% retention value is closer to the mean. This analysis emphasized once again the importance of accurately predicting N retention efficiency and its change over time.

Increases in C storage due to N deposition were roughly equal to decreases which occurred due to climate variability (Table 4). Climate drivers tended to vary inversely in real climate time series data such that wet months tended to be cool or have low radiation, leading to reduced photosynthesis, while sunny and warm months were dry, leading to water stress and reduced photosynthesis. This suggests that alterations in the interactions between climate drivers resulting from global climate change may also have important effects on ecosystem C storage, even if mean climate conditions remain the same. It also demonstrates that climate data with the characteristics of real time series interactions should always be used in simulations such as those presented here.

Conclusions

The PnET-CN model captured much of the variation in DIN losses from northern hardwood forest ecosystems in and around Hubbard Brook. This variation had two major components: (1) differences between watersheds in long-term trends in mean DIN loss due to land use legacies, and (2) interannual variability within watersheds due to interactions between climatic variability and short- to mid-term biological responses. Rates of change in mean annual DIN losses were predicted to be very low relative to interannual variability, given the current moderate rates of N deposition in the White Mountain, New Hampshire region. This means that assessing changes in watershed N status due to N deposition through measurements of mean DIN losses will be very difficult, even over decadal time frames, unless the effects of climate variability on DIN losses can be determined and factored out of the measured data.

Models are often more interesting when they fail than when they succeed. While capturing the larger patterns of variation in DIN losses due to disturbance and climate, the model did not simulate retention of N deposited outside the growing season or the dramatic decline in DIN losses in several watersheds in the 1990s. The first of these limitations might be reconciled by driving root uptake mechanisms with soil temperature rather than air temperature or by incorporating chemical reactions which are less sensitive to temperature. The second may be resolved with the inclusion of real climate data into the mid-1990s. If not, then a structural problem may exist in the model.

PnET-CN predicted changes in storage of C in response to added N were smaller than have been published elsewhere. This resulted from differences in the retention efficiency of N in atmospheric deposition, rather than in differences in the C:N ratio of the organic materials created, reemphasizing the importance of increasing our ability to predict the timing and quantity of N leaching losses from ecosystems affected by N deposition.

Acknowledgments. We would like to thank many individuals who helped with this study or provided data including Don Buso, Gene Likens, Wayne Martin, Jim Hornbeck, Scott Bailey, Tony Federer, and Kim Postek. Support for this study was provided by the National Science Foundation - Long-Term Ecological Studies Program, the U.S. Environmental Protection Agency, the USDA Forest Service - Northern Global Change Program, and the IBM Environmental Research Program. This is a contribution of the Hubbard Brook Ecosystem Study.

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J. D. Aber, Complex Systems Research Center, University of New Hampshire, Durham, NH 03824. (e-mail john.aber@unh.edu).

C. T. Driscoll, Department of Civil and Environmental Engineering, Syracuse University, Syracuse, NY 13244. (e-mail ctdrisco@mailbox.syr.edu)

(Received November 6, 1996; revised April 23, 1997; accepted May 5, 1997.)