Biogeochemistry **57/58:** 239–266, 2002.

Forest nitrogen sinks in large eastern U.S. watersheds: estimates from forest inventory and an ecosystem model

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Key words: forest growth, forest inventories, nitrogen budget, nitrogen sinks, nitrogen uptake, wood production

Abstract. The eastern U.S. receives elevated rates of N deposition compared to preindustrial times, yet relatively little of this N is exported in drainage waters. Net uptake of N into forest biomass and soils could account for a substantial portion of the difference between N deposition and solution exports. We quantified forest N sinks in biomass accumulation and harvest export for 16 large river basins in the eastern U.S. with two separate approaches: (1) using growth data from the USDA Forest Service's Forest Inventory and Analysis (FIA) program, and (2) using a model of forest nitrogen cycling (PnET-CN) linked to FIA information on forest age-class structure. The model was also used to quantify N sinks in soil and dead wood, and nitrate losses below the rooting zone. Both methods agreed that net growth rates were highest in the relatively young forests on the Schuylkill watershed, and lowest in the cool forests of northern Maine. Across the 16 watersheds, wood export removed an average of 2.7 kg N ha^{-1} yr^{-1} (range: 1–5 kg N ha^{-1} yr^{-1}), and standing stocks increased by 4.0 kg N ha^{-1} yr^{-1} (–3 to 8 kg N ha^{-1} yr^{-1}). Together, these sinks for N in woody biomass amounted to a mean of 6.7 kg N ha^{-1} yr^{-1} (2–9 kg N ha^{-1} yr^{-1}), or 73% (15–115%) of atmospheric N deposition. Modeled rates of net N sinks in dead wood and soil were small; soils were only a significant net sink for N during simulations of reforestation of degraded agricultural sites. Predicted losses of nitrate depended on the combined effects of N deposition, and both short- and long-term effects of disturbance. Linking the model with forest inventory information on age-class structure provided a useful step toward incorporating realistic patterns of forest disturbance status across the landscape.

Introduction

Human activity has dramatically increased the emission of fixed nitrogen compounds to the atmosphere and the deposition of fixed N across large regions in the temperate zone, particularly in western Europe, eastern Asia, and the eastern U.S. (Galloway et al. 1995; Holland et al. 1999; Vitousek 1994). Watershed-scale mass balance studies repeatedly show that riverine N export can account for only about 20–30% of the total N input to terrestrial systems; the fate of the remaining 70–80% is not well quantified, but likely consists of a combination of storage in biomass, soils, and groundwater, and loss to the atmosphere through denitrification (Galloway et al. 1995; Howarth et al. 1996). One potentially large N sink in terrestrial systems is incorporation of N into forest biomass and soils. Aggrading forests in the eastern U.S. currently act as a considerable sink for atmospheric carbon (Birdsey & Heath 1995; Turner et al. 1995). In this paper, we used forest inventory data and an ecosystem process model (PnET-CN; Aber et al. 1997) to quantify the N sinks in forest biomass, harvested material, dead wood, and soil in the eastern U.S. We focused on forested lands in 16 large watersheds ranging from Maine to Virginia for which other components of N budgets have been quantified (see Boyer et al. and van Breemen et al. 2002). Together, these watersheds occupy 248,000 km^2, and forests cover 72% of this area (Figure 1).

Nutrient uptake into forest biomass is not measured directly in the field, but rather is inferred from measurements of the production of wood and litter, and the nutrient concentrations of those components (e.g. Whittaker et al. 1979; Woodwell et al. 1975). Most of the N that trees take up annually is allocated to foliage and fine roots, but these components provide only a transient sink for N, as fine litter annually returns much of this N to the forest floor. In contrast, N accumulation in wood of aggrading forests represents a long-term N sink. Woody tissue has a low N concentration, but it makes up about 95% of total forest biomass (Whittaker et al. 1974, 1979). Here, we focused on N accumulation in woody tissues and export in harvested material.

Forest standing stocks and growth are measured regularly across the U.S. as a part of the USDA Forest Service's Forest Inventory and Analysis (FIA) program (Hansen et al. 1992; Woudenberg & Farrenkopf 1995). We used these data as the basis for estimating sinks of N into wood and harvested material, but the other N fluxes needed to calculate net forest N retention – such as nitrate losses or changes in woody debris or soil N stocks – are not presently measured throughout the inventory program. Ecosystem process models were designed to be able to estimate the importance and temporal variation of several of these unmeasured fluxes. However, biogeochemical models are just beginning to consider the effects of forest harvests and other

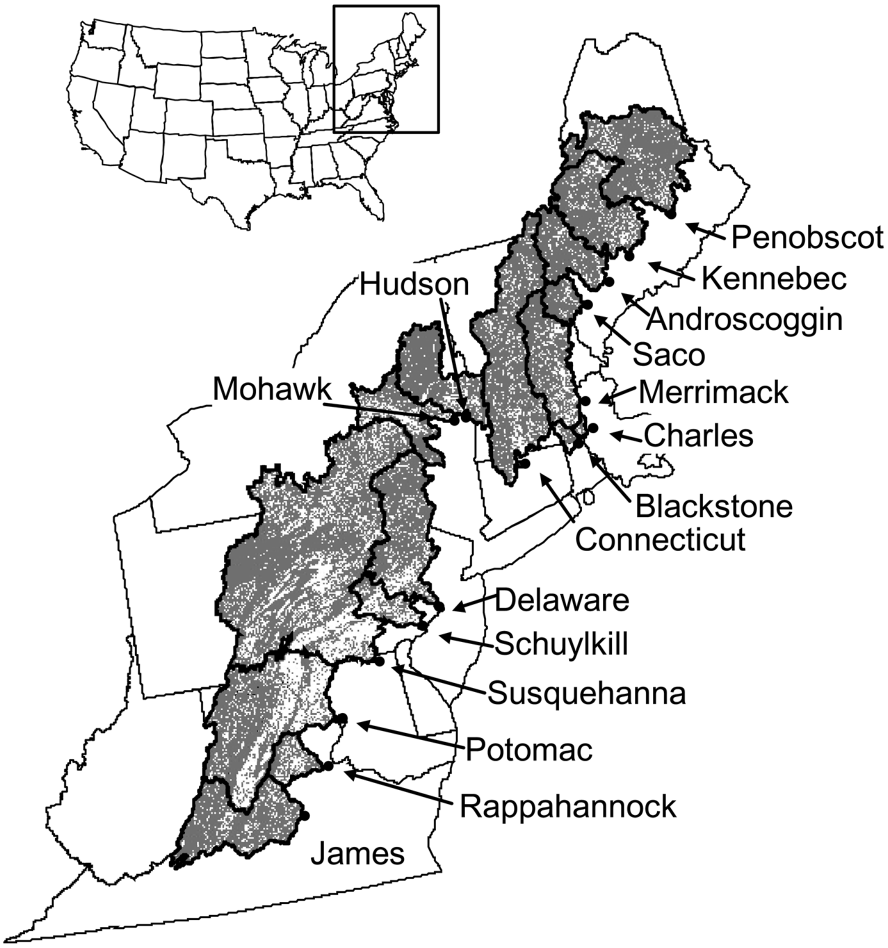

Figure 1. Boundaries of the focus watersheds and MRLC (1995) forest cover.

disturbances in complex landscapes (e.g. McGuire et al. 2001; Schimel et al. 1997, 2000). Disturbances have major impacts on forest N cycles that cannot be ignored when simulating N retention at large scales. Although aggrading forests retain N in biomass and soil, disturbed systems often experience large pulses of nitrate loss, due to reduced plant uptake and continued or enhanced N mineralization (e.g. Likens et al. 1970; Vitousek et al. 1979; Vitousek & Matson 1984). For this modeling effort, we used FIA data on forest age structure to simulate forests in a variety of stages of growth, disturbance, and recovery within the 16 watersheds. This linkage represents a first step toward consideration of both natural and human-induced disturbances in the ecosystem process model at the landscape scale.

The FIA age class information was combined with two contrasting scenarios of land-use history (long-term forestry and agricultural abandonment) to bracket the range of known short-term and potential long-term effects of disturbance on forest N retention. These disturbances, combined with input data on monthly climate and N deposition, allowed model predictions of forest N retention that incorporated the net effects of watershed differences in age-class structure, N deposition, and spatial and temporal variations in climate. On all 16 watersheds, both FIA data and PnET-CN were used to estimate forest growth, mortality, harvest export, and standing stocks. The model was also used to estimate N sinks in dead wood and soil, and losses of nitrate below the rooting zone.

Methods

Forest N sinks were quantified for 16 river basins: the Penobscot, Kennebec, Androscoggin, Saco, Merrimack, and Connecticut Rivers in northern New England; the Charles and Blackstone Rivers in southern New England; the Hudson, Mohawk, Delaware, Schuylkill, and Susquehanna Rivers in the Mid-Atlantic states; and the Potomac, Rappahannock, and James Rivers largely in Virginia. (Figure 1, Table 1). Boyer et al. (2002) describe characteristics of the 16 river basins in detail. This paper focused on only the forested portion of the basins, and all stocks and fluxes were expressed per unit forest area.

Our modeling efforts focused on predictions for the years of 1988–1992 in order to be consistent with river flux and N deposition records from this period (Boyer et al. 2002). The forest inventory data reflect the varied dates of surveys in different states, completed 1983–1995 and covering 6–20 years.

Forest inventory

County-level estimates of forest volume, area, age-class structure, and annual net growth, mortality, and harvests were obtained for Maine through Virginia from the FIA program, available on-line at: http://www.srsfia.usfs.msstate.edu/scripts/ew. htm (Hansen et al. 1992). Growth, mortality and harvest data were not available from this source for Vermont and New Hampshire; limited net growth data for these states were obtained from FIA's Forest Inventory Tablemaker, version 1.0 (Jan. 1, 1997, USDA Forest Service). County-level data were converted to watershed-level estimates by weighting forest biomass or N in each county by the percent of that county within each watershed boundary, as obtained by GIS overlays of county and watershed boundaries using Arc/Info (Redlands, CA).

Table 1. Watershed, forest, and timberland area (km^2), and percent of timberland area by type and by age class. Forest type in bold indicates the types used in PnET-CN simulations

Watershed	Area (km^2)			[2]Forest Type (%)				[2]Forest Age Class (%)						
	Total	[1]Forest land	[2]Timber-land	Pine	Spruce-Fir	Mixed Oak	North. Hardwd.	1–10	11–20	21–40	41–60	61–80	>80	Mixed
Penobscot	20,109	16,854	16,488	5	**41**	1	**53**	9	9	3	9	18	29	23
Kennebec	13,994	11,155	12,884	4	**33**	1	**61**	9	10	5	7	14	16	38
Androscoggin	8,451	7,142	7,092	10	**23**	5	**61**	2	7	4	14	15	12	47
Saco	3,349	2,932	2,764	**22**	10	13	**55**	1	2	3	8	11	6	69
Merrimack	12,005	8,853	8,854	**31**	4	29	**35**	<1	0	3	13	14	2	69
Charles	475	275	218	**23**	0	**56**	22	0	0	2	28	34	8	27
Blackstone	1,115	691	686	**20**	0	**65**	15	0	0	2	28	44	3	24
Connecticut	25,019	20,802	20,193	**17**	14	13	**56**	1	0	3	11	10	3	72
Hudson	11,942	9,662	6,336	**20**	5	15	**60**	1	0	8	19	26	27	19
Mohawk	8,935	5,751	4,491	**21**	2	11	**65**	4	0	20	22	24	23	8
Delaware	17,560	13,098	10,166	9	1	43	**46**	1	2	32	30	18	14	3
Schuylkill	4,903	2,370	1,565	4	1	**70**	23	3	15	53	24	1	3	0
Susquehanna	70,189	46,782	39,801	8	1	45	**45**	3	7	39	32	8	9	1
Potomac	29,940	18,200	15,296	7	0	**80**	12	3	7	17	21	19	20	14
Rappahannock	4,134	2,546	1,943	**15**	0	**82**	2	6	5	23	30	24	11	0
James	16,206	12,876	11,497	**16**	0	**81**	2	10	9	14	21	26	20	<1
Total/Wtd. Ave.	248,326	179,989	160,275	12	11	34	43	4	6	17	20	15	14	24

[1] From GIS overlays of watershed boundaries and the National Land Cover Database (NLCD) of the Multi-Resolution Land Characteristics Interagency Consortium (MRLC).

[2] From weighted averages of county-level FIA timberland data.

The FIA data were reported in terms of growing-stock volume by forest type and size- or age-class. Growing stock consists of the merchantable portion of commercial tree species ≥ 5 inches diameter at breast height (12.7 cm dbh) growing on land classified as timberland. Timberland is land capable of producing at least 20 ft^3 $acre^{-1}$ yr^{-1} (1.4 m^3 ha^{-1} yr^{-1}) of commercial wood, on which harvesting is not prohibited by law or regulation. Nonmerchantable tree parts (e.g. branches, coarse roots) and small, poor-quality, and noncommercial trees are excluded in these estimates, as are lands such as the state-owned ‘forever wild’ forests in New York’s Adirondack Park.

The FIA growth data are reported as net growth of growing stock. Net growth represents the total production of growing stock (gross growth) after losses due to natural mortality.

(1) Net growth = gross growth – natural mortality

When converted to units of forest biomass, gross growth is essentially net primary production of wood (woody NPP), excluding woody litter production other than whole-tree mortality (e.g. branch drop). Subtracting harvest losses from net growth yields the forest’s net change in standing stock.

(2) Net change = net growth – harvest mortality

Net growth represents the forest’s rate of accumulation of wood into live trees; net change in standing stock represents the net balance of wood production and consumption across the landscape. After harvest, a portion of the harvested biomass is removed from the forest. The rest (woody roots, tops, etc.) remains as harvest debris that decomposes and eventually releases its N. In the northeastern U.S., 55–67% of harvested biomass (including roots) is removed (Birdsey 1996); we used a default of 60% for all watersheds.

(3) Harvest export = harvest mortality – logging debris

For estimating watershed-level sinks for N in wood, we focused on two terms representing long-term net N sinks: net change in standing stock, and harvest export. Using FIA data to estimate woody N sinks required three steps: (1) converting FIA estimates of growing-stock volume (m^3/ha) to estimates of total forest biomass (Mg/ha); (2) calculating the N in this biomass; and (3) extending these estimates to forest land not classified as timberland.

Two approaches have been developed to convert U.S. growing-stock volume data to estimates of dry biomass of the whole forest, methods developed largely in order to quantify forest carbon balance. In the first approach (Method 1), Birdsey (1992) and Turner et al. (1995) multiplied growing-stock volume by forest-type specific wood density values and two additional factors: the ratio of all tree species to commercial species; and the ratio of all woody tree parts (above- and belowground) to bolewood (Appendix 1, Table 1). Alternatively, (Method 2) Schroeder et al. (1997), Brown and Schroeder (1999), and Brown et al. (1999) developed a method for predicting biomass expansion factors (BEF) or empirical conversion factors that vary with both forest type and growing-stock volume. Low-volume forests are predicted to have high BEF values, roughly compensating for the FIA practice of including only trees $\leq$12.7 cm dbh in growing stock statistics. Although the conversion factors for Method 1 were developed to quantify both above- and belowground woody biomass, the Method 2 equations predict aboveground biomass, only. Coarse root biomass generally amounts to 15–25% of aboveground biomass (Birdsey 1992; Cairns et al. 1997; Johnson & Lindberg 1992; Whittaker et al. 1974). We added 20% to values derived from Method 2 to account for belowground woody biomass. We applied both conversion approaches to the same set of growing-stock volume data to obtain two sets of FIA-based estimates for each watershed. To obtain a single set of final values, we used the mean of these two biomass conversion methods and present their range as an additional component of uncertainty.

For both sets of biomass estimates, mass of N was calculated by multiplying woody biomass by its mean percent N as derived from the literature (Table 2). Nitrogen concentrations are quite low in all woody tissues, but concentrations in branches and woody roots are two to three times those of the bole (Table 2). We used the mean ($\pm$1 SD) weighted average N concentration of all woody tissues for softwoods (0.19% ± 0.08%) and for hardwoods (0.26% ± 0.06%). Concentrations varied considerably, and we assessed the potential variability of our FIA-based estimates of woody N sinks by varying %N by the standard deviation of the estimates from the literature (Table 2).

For lack of additional information, we assumed that forests growing on land designated as timberland were representative of those growing on other forested land. Total N stocks of all forests observed on the watersheds were estimated by multiplying mean values for timberland by the total area of forest land, as determined by GIS overlays of land cover data and watershed boundaries. The land cover data were obtained from the Multi-Resolution Land Characteristics (MRLC) consortium's National Land Cover Data Base (http://www.epa.gov/mrlc) (MRLC 1995). Our approach of weighting county-level FIA data by fractional watershed coverage assumed a fairly even distribution of forest coverage within each county. Comparison of the area of land classified as timberland by the Forest Service with the MRLC estimates of forest area (Table 1) indicated that this approach did

Table 2. Weighted average nitrogen concentrations of wood in branches, boles, and roots in eastern North American forests (% of dry weight)

Location	Forest type	Woody tissue N concentration (%)			
		Branch	Bole	Root	Wtd. Ave.
Hardwoods					
[1]Brookhaven, NY	Mixed oak	0.32	0.18	0.23	0.22
[2]Hubbard Brook, NH	N. hardwood	0.46	0.16	0.70	0.33
[3]Oak Ridge, TN	Yellow poplar	0.29	0.18	0.34	0.24
[3]Walker Branch, TN	Poplar/hardwoods	0.26	0.16	0.39	0.23
[3]Walker Branch, TN	Oak-hickory	0.50	0.19	0.39	0.29
[3]Walker Branch, TN	Chestnut oak	0.46	0.18	0.37	0.27
[3]Coweeta, NC	Oak-hickory	0.45	0.18	0.83	0.40
[4]Berlin, NH	N. hardwood				*0.20
[5]Oak Ridge, TN	Mixed oak	0.24	0.17	0.20	0.19
[6]Cockaponset, CT	Ctrl. hardwood	0.30	0.13	0.35	0.20
[7]Coweeta, NC	S. hardwood	0.23	0.20	0.83	0.33
[7]Smoky Mtns., TN	American beech	0.14	0.14	0.80	0.22
[7]Huntington Forest, NY	N. hardwood	0.10		0.25	0.21
[7]Turkey Lakes, ON	N. hardwood	0.35	0.16	0.15	0.20
[8]Hubbard Brook W5, NH	N. hardwood; 6 yr.		0.33		0.33
[9]Nantahala NF, NC	Mixed oak				*0.22
[10]Harvard Forest, MA	Mixed oak		0.16		
Average		0.32	0.19	0.46	0.26
Standard Deviation		0.13	0.05	0.25	0.06
Softwoods					
[1]Brookhaven, NY	Pitch pine	0.22	0.11	0.17	0.15
[3]Oak Ridge, TN	Shortleaf pine	0.24	0.11	0.34	0.19
[7]Coweeta, NC	White pine	0.39	0.13	0.70	0.31
[7]Duke Forest, NC	Loblolly pine	0.23	0.11	0.11	0.13
[7]Gainesville, FL	Slash pine	0.24	0.13	0.41	0.20
[7]Oak Ridge, TN	Loblolly pine	0.14	0.09		0.10
[7]Howland Forest, ME	Red spruce	0.31	0.15	0.22	0.19
[7]Smoky Mtns., NC	Red spruce	0.13	0.07	0.27	0.13
[7]Smoky Mtns., NC	Red spruce	0.16	0.06	0.47	0.14
[7]Whiteface, NY	Spruce-fir	0.75	0.12	0.53	0.36
[9]Nantahala NF, NC	Mixed pine				*0.18
[10]Harvard Forest, MA	Red pine		0.06		
Average		0.28	0.10	0.36	0.19
Standard Deviation		0.18	0.03	0.19	0.08

*mixed bole and branch.
From: [1]Woodwell et al. 1975; [2]Whittaker et al. 1979; [3]Cole & Rapp 1981; [4]Hornbeck & Kropelin 1982; [5]Johnson et al. 1982; [6]Tritton et al. 1987; [7]Johnson & Lindberg 1992; [8]Mou et al. 1993; [9]Vose & Swank 1993; [10]Nadelhoffer et al. 1999a.
N. hardwood = northern hardwood.

not introduce large biases. However, county-based estimates of timberland area occasionally exceeded estimates from MRLC overlays (the Kennebec and Merrimack), presumably due to slightly less forest cover observed within watershed boundaries than occurred within the county as a whole. The reverse case (MRLC estimates of forest area exceeded county-weighted estimates of timberland) more likely indicated watersheds that contained non-timberland forest, reaching 22–34% of the forest area on the Hudson, Mohawk, Delaware, Schuylkill, and Rappahannock. Some of this land is not classified as timberland because of low productivity, and our approach likely overestimated growth rates on these areas. However, most of the non-timberland forest was within watersheds where the timberland designation was prevented by administrative rule rather than growth potential (e.g. portions of the Adirondack Park, NY or Shenandoah Park, VA).

Forest ecosystem modeling

Although nitrogen sinks in wood production and harvest are likely most reliably quantified with forest inventory data, an alternative approach is needed to estimate N sinks in dead wood and soil and nitrate losses below the rooting zone. We used an ecosystem process model, PnET-CN, to estimate these fluxes, and we used forest inventory information on age-class structure to better represent patterns of disturbance within the model.

Model description

The PnET-CN model simulates the cycles of carbon, water, and N through forest ecosystems. The model uses inputs of monthly climate and N deposition to predict photosynthesis (Pn), evapotranspiration (ET), and N cycling on a monthly time-step for several forest types. The model's photosynthetic routine (PnET-Day) has been tested against C flux data from the eddy covariance tower at the Harvard Forest, MA (Aber et al. 1996); its water balance (PnET-II), against measured stream flow at Hubbard Brook, NH (Aber & Federer 1992) and elsewhere in the northeastern U.S. (Ollinger et al. 1998). The N cycling routine was added in Aber et al. (1997), and tested against measurements of production, N cycling, and nitrate loss at Harvard Forest and Hubbard Brook (Aber et al. 1997; Aber & Driscoll 1997). Currie and Aber (1997) and Currie et al. (1999) developed more detailed soil models to describe fluxes of dissolved organic matter (DOCMOD) and gross N cycling in litter and humus (TRACE). For our simulations, we used the simpler version described in Aber et al. (1997). Both PnET-CN and TRACE use the same formulation for net N mineralization from humus, although TRACE distinguishes humus in the forest floor and the mineral soil and includes a separate routine to describe litter decomposition. PnET-CN mineralizes N along with C from a single soil pool that contains both non-woody litter and soil humus. This pool represents the top, active layers of litter and soil organic matter, and does not include ‘passive’ carbon. The pool’s turnover (0.075 yr^{-1}) is modified by empirical temperature and moisture relationships (Aber et al. 1997; Aber & Driscoll 1997). A fraction of the mineralized N is re-immobilized in the soil pool, as determined by soil C:N ratio; no other direct or indirect mechanisms of soil N retention are considered. After net mineralization, N is available for plant uptake, and excess N can nitrify and leach below the rooting zone. Predicted rates of N cycling and nitrate losses can vary greatly from year to year due to climatic variation and its relative effects on plant growth and decomposition (Aber & Driscoll 1997).

Modeled plant N uptake, N concentrations in foliage and wood, and net nitrification are all controlled by an index of plant N limitation, which is the ratio of mobile, unallocated plant N to a specified maximum. Increasing the foliar N concentration drives an increase in photosynthesis and production as long as light, water, N and temperature limitations permit. Net primary production and available N are allocated first to foliage, then fine roots, and finally to wood. Modeled dead wood pools result from logging residue and from annual production of woody litter, determined as a constant fraction of woody biomass (1.7% yr^{-1}). This term includes both whole-tree mortality and branch turnover. FIA measurements indicate that whole-tree mortality in these forests averages ~0.8–1.0% yr^{-1} of biomass (Brown & Schroeder 1999). Data from Whittaker et al. (1974, 1979) suggest that dropped branches and other woody litter production not associated with whole-tree mortality amounts to an additional 0.7% yr^{-1}. Dead wood turns over at 10% yr^{-1} (Arthur et al. 1993); 80% of the mass lost is respired and the residual 20% enters the soil pool along with 100% of the turned-over N, effectively decreasing the C:N ratio of the decayed woody material transferred to the soil pool (Aber et al. 1991).

Input data

PnET-CN requires monthly climate data, N deposition values, and scenarios describing past disturbances and historical removals of C and N. As described below, the model was run for each watershed using its 1–2 most dominant vegetation types (Table 1), a single climate time-series, a range of age classes, and two historical disturbance scenarios.

We developed spatially averaged climate time-series for each watershed from the climate data set developed for the VEMAP II modeling comparison. For VEMAP II, Kittel et al. (1997) reconstructed historical (1895–1993) monthly precipitation, solar radiation, and monthly averaged maximum and minimum daily temperature on a half-degree grid. We weighted climate values in each grid cell by the fraction of watershed area covered by that grid cell, as determined by GIS overlays of grid cells and watershed boundaries. Simulations of years prior to 1895 used average monthly climate values.

Wet and dry deposition of inorganic N was estimated for each watershed using spatial regression equations developed by Ollinger et al. (1993), which we modified by using dry deposition coefficients from the review in Lovett and Rueth (1999). The Potomac, Rappahannock, and James watersheds were outside of the range in which the regression equations applied, and total inorganic N deposition on these watersheds was estimated by doubling wet N deposition, as measured by the National Atmospheric Deposition Program/National Trends Network (NADP/NTN). See Boyer et al. (2002) for additional details. Preindustrial N deposition was set at 1 kg ha^{-1} yr^{-1} (Galloway et al. 1995, Holland et al. 1999), increased linearly from 1880 to 1980, and was held constant through 1993.

Forest inventory data were used to partition forests on each watershed into six age classes and a seventh mixed-age class (Table 1). Forests in each age class likely resulted either from even-aged forest harvest or from agricultural abandonment. We performed sets of simulations for each of these scenarios, with model predictions weighted by the fraction of forest area in each age class (Figure 2). In the first, continuous-forest (forest-only) scenario, forests were assumed to be on 80-year cycles of harvest since the mid- to late-1700s. Growth and N losses vary greatly within the first decade after disturbance, and so the 1-10 year age class was split into smaller increments. On each watershed, harvests were simulated 0, 2, 5, and 8 years before 1990 for the 1–10 year age class, and 15, 30, 50, 70, and 90 years before 1990 for the 11–20, 21–40, 41–60, 61–80, and >80 year old forests, respectively. Harvest intensity was assumed to increase over time from affecting 40% of stand biomass in the late 1700s to 90% for harvests after 1950, and the fraction of harvested material removed increased from 40% in the late 1700s to 60% after 1970. Mixed-aged forests potentially reflect a wide range of management histories. A subset of FIA data suggested that these forests had approximately the same net growth rate as 41–60 year-old forests, and so, for lack of additional disturbance information, they were assumed to also have similar N cycling rates. FIA harvest data suggested that in addition to stand-replacing harvests, logging in older or mixed-aged forests occurred at a rate of approximately 1.0% yr^{-1}; we used this value in the model for all watersheds, for both the forest-only and old-field scenarios.

In the second, post-agricultural (old-field) scenario, forests were assumed to have regenerated on old fields abandoned 5, 15, 30, 50, 70, and 90 years before 1990, after a century of farming with minimal N inputs. Farming in the eastern U.S. peaked around 1880 (Figure 2), and has declined steadily

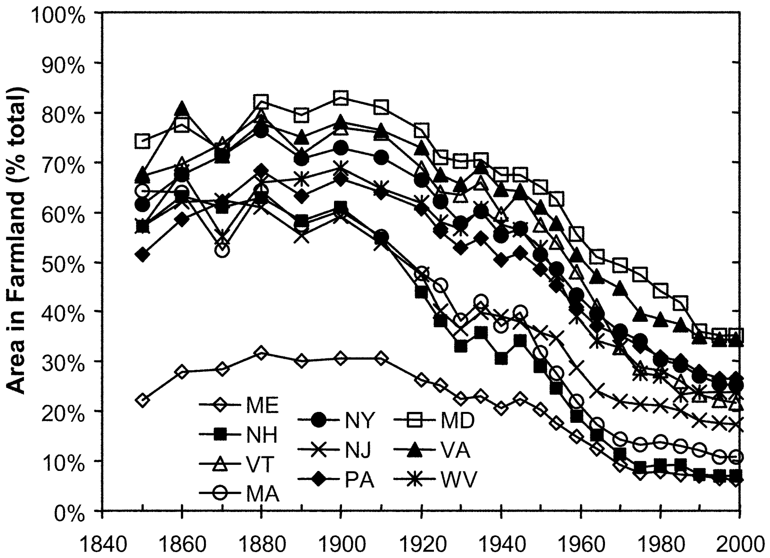

Figure 2. Percent of eastern U.S. land area in farmland, 1850 to 1999, by state. Data for 1850–1969 from U.S. Bureau of Census (1977); 1970–1999 from the National Agricultural Statistics Service (http://www.nass.usda.gov:81/ipedb/).

since then (Ramankutty & Foley 2001; U.S. Bureau of the Census 1977). We roughly estimated the relative importance of agricultural abandonment as a land-use history on each watershed using state-level agricultural statistics for 1850–1969 (U.S. Bureau of the Census 1977) and 1970–1995 (http://www.nass.usda.gov:81/ipedb/) (Figure 2). These data suggested that 25% of Maine consisted of former farm land, with higher fractions for the Mid-Atlantic states (37–49%), Vermont and New Hampshire (both 56%) and southern New England (52–72%). This approach ignores all spatial variation of land-use history within states, and assumes no bias of whether former farmland reverted to forest or to other land uses. The true disturbance histories of these watersheds likely consisted of forest harvest, agriculture, and other land-uses of varied intensity; this set of simulations offers a preliminary consideration of disturbance on these watersheds.

Results

We first present results of forest biomass, N uptake and harvest export as derived from forest inventory data, and then compare these with PnET-CN estimates of these terms. We then present PnET-CN estimates of N sinks in pools that cannot be estimated from forest inventory data.

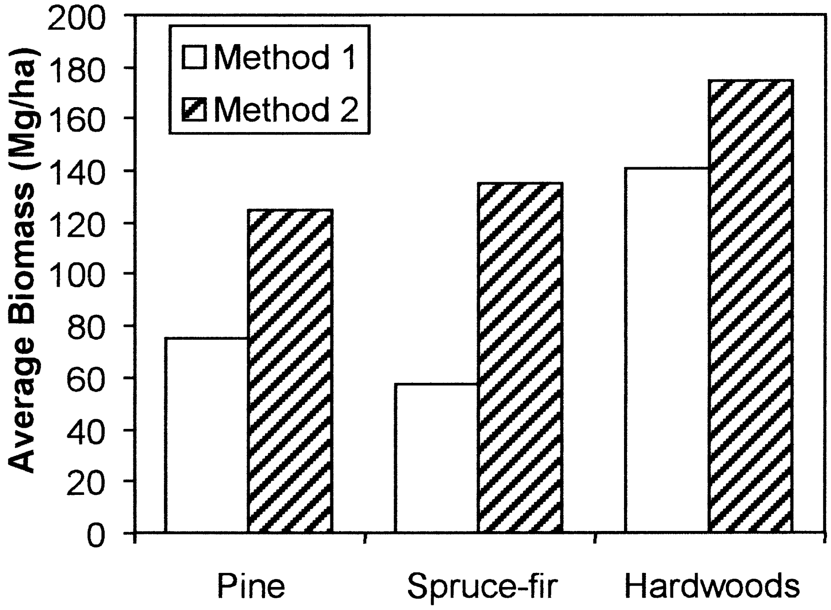

Figure 3. Comparison of two methods of converting growing stock volume data to estimates of total (above- and belowground) biomass for pine, spruce-fir, and hardwood forests. Method 1 used conversion factors from Birdsey (1992) and Turner et al. (1995); Method 2 used an approach described in Brown et al. (1999).

Forest inventory data

The two methods used to convert growing stock volume to biomass produced different estimates of forest biomass, growth and harvest. Above- and belowground forest biomass averaged 126 Mg ha^{-1} using Method 1 (Birdsey 1992; Turner et al. 1995), and 164 Mg ha^{-1} using the Method 2 (Brown & Schroeder 1999 + 20% for belowground biomass). Corresponding N stocks in woody biomass were calculated using mean ± 1 SD of %N values in Table 2, and averaged 310 ± 84 and 400 ± 110 kg ha^{-1}, respectively. Overall, Method 2 produced biomass estimates 30% greater than Method 1, with larger differences in the Penobscot (57%) and Kennebec (46%) watersheds. These two watersheds had large areas of spruce-fir forests (Table 1), and conversion differences were far greater for estimates of spruce-fir biomass than for pine or hardwoods (Figure 3). Both conversion approaches agreed that forests on the Rappahannock watershed had the greatest biomass, and those on the Penobscot and Kennebec had the least.

Uptake of N in net growth varied across the region (Figure 4). Our county-level calculations of aboveground biomass production using Method 2 closely matched those reported by Brown and Schroeder (2000). Slower growth occurred in the cool forests of northern Maine and along the Appalachian Mountain range in Pennsylvania and Virginia. The fastest net growth occurred on the Schuylkill, Rappahannock, and James, and the slowest, on the Penobscot and Kennebec watersheds in northern Maine. Across all watersheds, net growth averaged 2.9 Mg ha^{-1} yr^{-1} using Method 1, and 3.8 Mg ha^{-1} yr^{-1} using Method 2. These net growth rates corresponded to rates of N uptake into live wood of 7.1 ± 1.9 kg ha^{-1} yr^{-1} and 9.2 ± 2.5 kg ha^{-1} yr^{-1}. Nitrogen uptake into net wood growth approximately balanced N deposition (Figure 5). Net wood growth correlated with N deposition (Figure 5; $R = 0.70$ for Method 1; $R = 0.65$ for Method 2), but this does not necessarily indicate that N deposition stimulated forest production, as N deposition co-varied with mean annual temperature ($R = 0.73$) and correlations of wood growth and temperature ($R = 0.65$ for Method 1 and 0.62 for Method 2) are nearly as strong as correlations between wood growth an N deposition.

Not all N taken up in net growth remains in long-term storage, as harvests allow some of this N to be recycled through production and decomposition of logging debris. The main forms of N sinks that we considered here were N in harvest exports and N in accumulated wood. Harvest rates could not be estimated for the Saco, Merrimack, or Connecticut River basins because FIA harvest data were not available for New Hampshire or Vermont. On the remaining 13 watersheds, harvest mortality was highest in Maine, on the Kennebec and Penobscot, followed by the Rappahannock and James in Virginia. Harvest rates were lowest on the Mohawk and Delaware. Harvest mortality on the Penobscot and Kennebec between 1979 and 1995 exceeded net growth during this period, causing declines in forest biomass (negative rates of forest increment) (Figure 6). On the other watersheds, net growth exceeded harvest mortality and allowed forest biomass to accumulate, particularly on the Mohawk and the Delaware. Across the 13 watersheds with harvest data, harvest mortality rates averaged 1.3 and 1.8 Mg ha^{-1} yr^{-1}, containing 3.8 ± 1.0 and 5.1 ± 1.4 kg N ha^{-1} yr^{-1}, using the Method 1 and Method 2 conversion approaches, respectively. However, not all harvested material was removed from the watershed; woody roots, stumps, and other slash were presumably left behind to decompose. Assuming that 60% of harvested biomass was removed from the forest, we estimated that export of N in harvested wood averaged 2.3 ± 0.6 (Method 1) and 3.0 ± 0.8 kg N ha^{-1} yr^{-1} (Method 2). Harvest export was the dominant N sink for the northern Maine watersheds, while N accumulation in living tree biomass was the dominant N sink on the other watersheds (Figure 6).

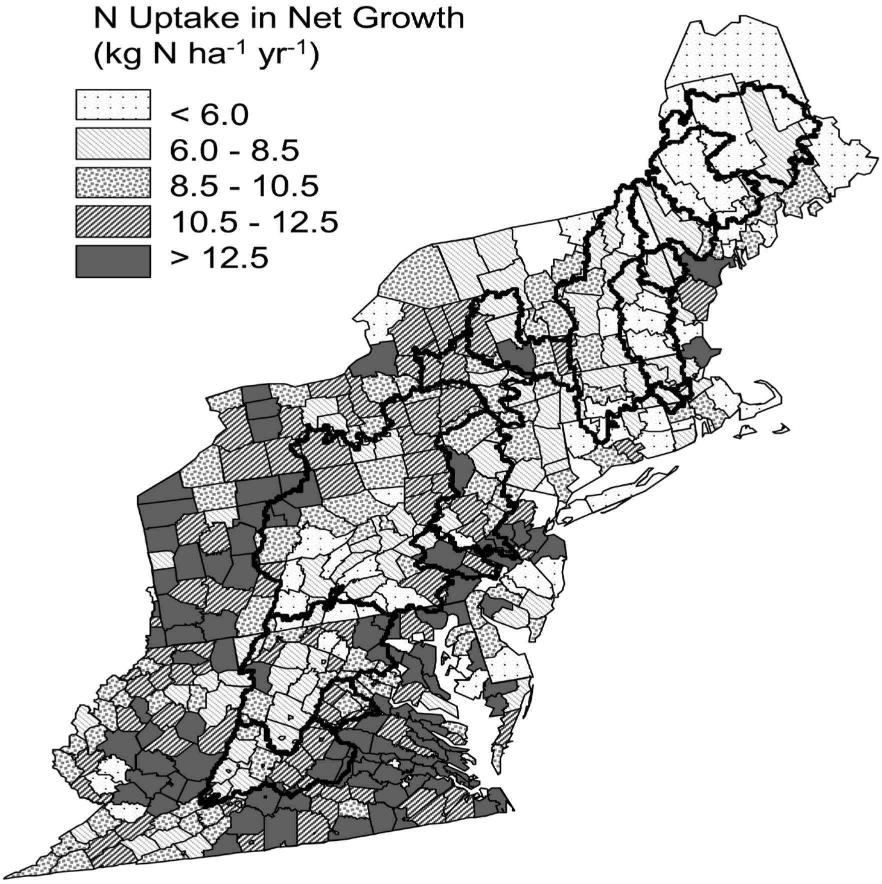

Figure 4. Uptake of N in net growth of wood (kg N ha^{-1} yr^{-1}) across the eastern U.S., estimated from FIA data using the mean of two methods of biomass conversion and%N values derived from a literature review (Table 2).

Model-inventory comparison

Comparing inventory and model-based estimates of forest growth, harvest, and standing stocks allows for evaluation of model performance. This testing is important for determining whether the use of forest age classes and assumptions about past land-use history fit with observed patterns of biomass and growth, and it helps identify potential strengths and weaknesses in model predictions of unmeasured fluxes.

Standing biomass is particularly challenging to predict, as it depends on accurately representing both growth and mortality (natural and harvested) correctly over time. Modeled estimates of stand biomass compared rather

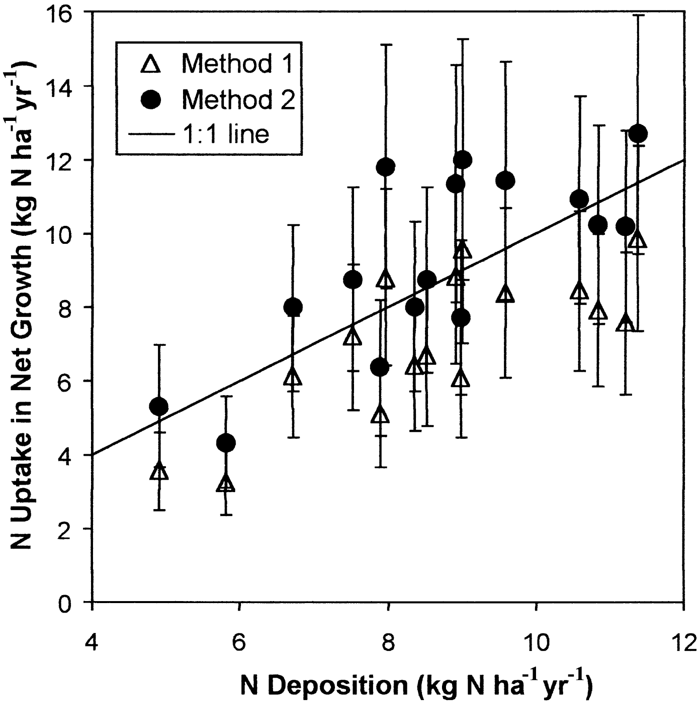

Figure 5. Comparison between N deposition and estimated N uptake in net wood growth for 16 watersheds, using two methods of biomass conversion. Error bars represent ± 1 SD of %N values from a literature review.

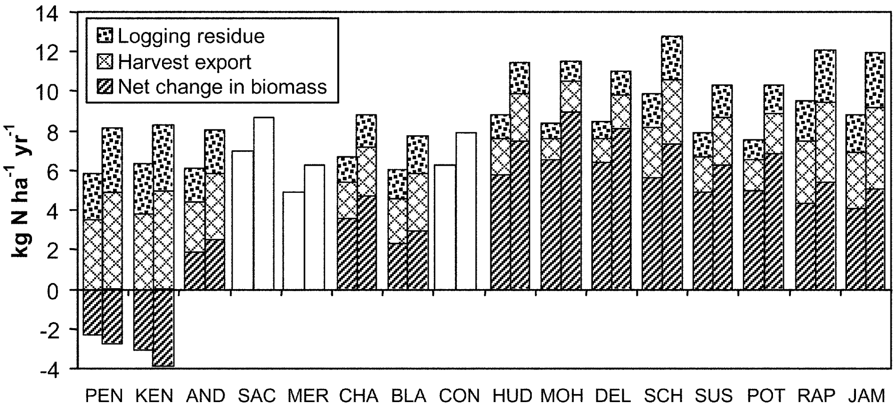

Figure 6. Nitrogen sinks in aggrading biomass and harvest export (kg N ha^{-1} yr^{-1}). Nitrogen in harvest residue is retained in the forest and eventually recycled. Together, these three terms amount to N uptake in net growth. Harvest data were not available for the Saco, Merrimack, and Connecticut, and only net growth is shown. Paired bars represent different methods of biomass conversion, with Method 1 on the left and Method 2 on the right.

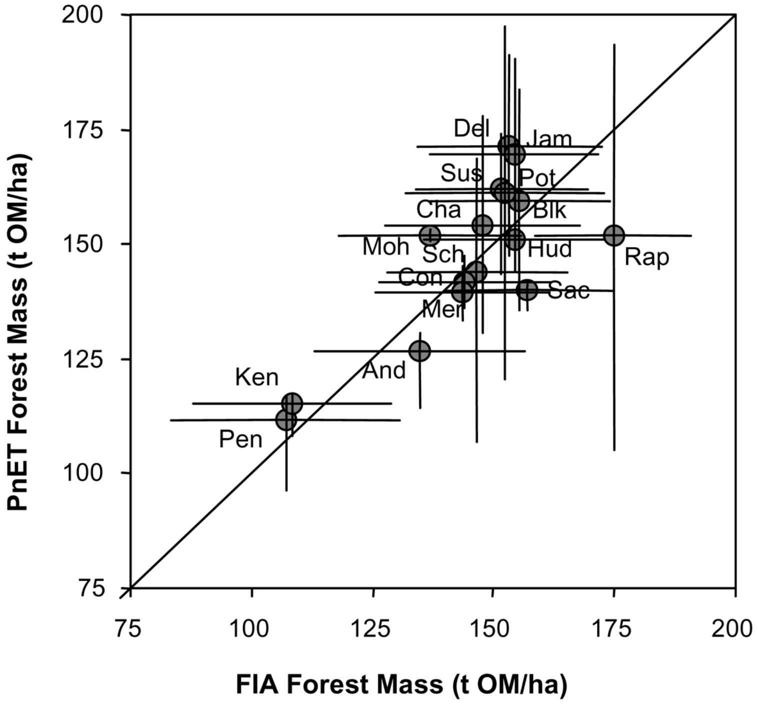

Figure 7. Comparison of modeled and FIA-based estimates of stand biomass by watershed. FIA values indicate the mean and range of two methods of biomass conversion, with Method 1 on the low end of the range and Method 2 on the high. Modeled values represent the weighted mean and range of contrasting scenarios of past land-use history, with forestry scenarios on the high end of the range and old-field scenarios on the low end.

well with estimates based on FIA data, although there were large uncertainties for both approaches (Figure 7). FIA-based estimates are presented as the mean and range of the two biomass conversion methods, while PnET-based estimates are presented as the weighted mean and range from simulations using the two land-use histories. Averaged across all watersheds, PnET-CN estimates of standing biomass were lower under old-field simulations (136 Mg/ha) than simulations assuming only harvest disturbances (158 Mg/ha). Differences due to land-use history were pronounced in the mixed-oak dominated stands of the southern watersheds. Comparisons of stand N stocks were similar to comparisons of stand biomass, although there is additional uncertainty in the FIA-based estimates due to potential variability of wood %N (Table 2).

Climate, age-class structure, and land-use history all affected PnET-CN's predictions of net growth and N uptake. Predicted net growth rates were highest during the first two decades after harvest, when woody NPP was

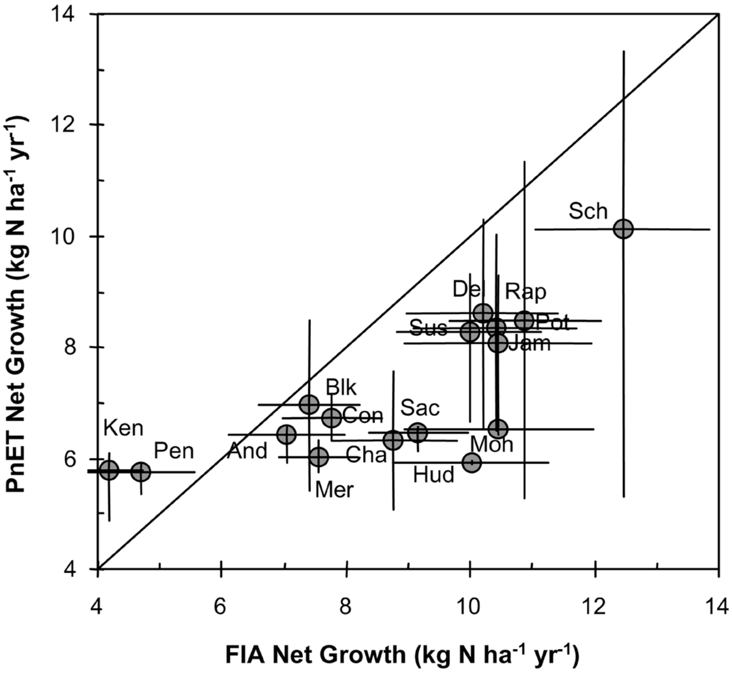

Figure 8. Comparison of modeled and FIA-based estimates of uptake of N in net growth of wood. Error bars represent ranges as described for Figure 7. Additional variation in FIA-based values due to variability of wood %N is not included in this figure.

greatest and mortality was low. The model does not have any prescribed effects of age on growth rate; these changes resulted from predicted changes in C and N pool sizes and fluxes. Net growth rates declined in later years due to increases in natural mortality and woody litter production. High net growth rates were predicted for watersheds with mild climates and large fractions of forest area made up of young forests. Consistent with the FIA data, the model predicted the lowest net growth rates for forests on the cool northern Maine watersheds and the highest uptake rate for forests on the Schuylkill (Figure 8), the watershed with the greatest fraction of forest area in the 11–20 and 21–40 year age classes (Table 1). The greatest discrepancy between modeled and FIA-based net growth occurred on the Mohawk and Hudson watersheds, where the model underestimated net growth by about 4 kg N ha^{-1} yr^{-1}. Forest-harvest simulations for the other watersheds matched the mean FIA-based estimates of N accumulation in net growth rather well (Figure 8). Across the watersheds, N uptake in net growth averaged 8.1 kg N ha^{-1} yr^{-1} using the forest-harvest scenario. Slower net growth rates were predicted for forests on former agricultural sites, averaging 6.2 kg N ha^{-1} yr^{-1} in wood production. As for biomass, differences due to land-use history were particularly large on the mixed oak-dominated southern watersheds. Weighting these land-use history scenarios by their approximate historical importance as suggested by state-level farmland data (Figure 2), we underestimated mean FIA-based estimates of net growth by 1.6 kg N ha^{-1} yr^{-1} (Figure 8).

PnET-CN simulated harvests through both stand-replacing clearcuts and chronic, low-intensity logging of older stands. Stand-replacing clearcuts were assigned based on the land area in 1–10 year age class (Table 1) and selective cutting of older stands was set at 1.0% yr^{-1} of stand biomass, as indicated by a subset of FIA data. Hence, modeled and FIA estimates of harvest mortality were not wholly independent. Simulated N fluxes in harvest-induced mortality were naturally much higher under the scenario that the forest age structure was determined by stand-replacing harvests (6.0 kg N ha^{-1} yr^{-1}) rather than through patterns of agricultural abandonment (3.1 kg N ha^{-1} yr^{-1}). Weighting PnET-CN simulations by roughly estimated land-use histories, predicted harvest mortality was within 2 kg N ha^{-1} yr^{-1} of the FIA-derived values for all watersheds but the Kennebec and Androscoggin, where the model underestimated harvest mortality by 2.8 and 3.0 kg N ha^{-1} yr^{-1}, respectively. Harvest mortality was underestimated on these two watersheds even under the forest-only scenario alone. Harvest mortality was partitioned into harvest export and logging debris using the same method for both model- and FIA-based estimates, and so model-FIA comparisons for harvest export and residue had patterns similar to the comparison for harvest mortality. Mean estimates of harvest export were about 0.8 kg N ha^{-1} yr^{-1} lower using land-use history-weighted PnET simulations (2.3 kg N ha^{-1} yr^{-1}) than using mean FIA-based estimates (3.1 kg N ha^{-1} yr^{-1}), with larger underestimates (about 2.0 kg N ha^{-1} yr^{-1}) for the Maine watersheds.

Model-based estimates of net changes in standing stock depended on accurately predicting both net growth and harvest rates, and, like the results for net growth, model-based estimates of the net change in standing stock were on average 1.5 kg N ha^{-1} yr^{-1} lower than FIA-based estimates. The model-based approach overestimated net increment on the Maine watersheds where harvest rates were underestimated, and the model underestimated net increment on the Mohawk due to an underestimate of net growth and a slight overestimate in harvest rates.

Simulated N sinks

Both FIA data and PnET-CN can provide estimates of forest N sinks in accumulating biomass or exported wood, but the ecosystem process model is needed to estimate net N sinks in dead wood, green plant tissues (foliage, fine roots, internal N stores), and soil, and nitrate losses below the rooting zone. The model's ability to generally reproduce patterns of wood growth supports its ability to estimate N sinks in the unmeasured pools.

Dead wood

Dead wood is produced by both natural mortality and harvest debris. Dead wood pools might be expected to be increasing due to increasing woody litter production by aggrading eastern forests. Harvest slash contributed variable amounts of dead wood on the different watersheds, depending on the amount and biomass of recently cut forest. In forest harvest scenarios, dead wood pools were largest immediately following harvests, and they decreased in size as decomposition of harvest slash exceeded woody litter production by the recovering forests. PnET-CN suggested that on average, dead wood was an extremely small net sink for N in the harvest scenario (0.1 kg N ha^{-1} yr^{-1}), and only a slightly larger sink in the old-field scenario (0.6 kg N ha^{-1} yr^{-1}). In the forest harvest scenario, inputs of N in woody litter and harvest debris were largely balanced by decomposition and release from older dead wood. On the Penobscot, Schuylkill, and Susquehanna, decomposition of dead wood produced by large harvests 10–30 years ago exceeded new production of dead wood, so that the dead wood pool was a small source of N (Figure 9a). In the old-field scenario, dead wood pools were small at agricultural abandonment, and formed a consistent but small sink across all watersheds as forests aggraded.

Soil

PnET-CN predicted variations in N pools in litter and soil organic matter due to differences in land-use history, forest age-class structure, and spatial and interannual variability in climate. Losses were predicted to occur on watersheds with relatively large areas of recent harvest, due to reduced inputs of litter and continued decomposition and net N mineralization. Older, never-farmed forests were predicted to have small changes in soil organic matter and N that varied from year-to-year due to variability in temperature and moisture conditions. In the continuous-forest scenario, changes in soil N stocks varied by watershed due to local climate conditions experienced during 1988–1992 – or even during one year with particularly large effects. For example, the three Virginia watersheds had climate conditions in 1989 that were unusually favorable toward net N mineralization, and the predicted soil N losses from this year dominated the 1988–1992 period (Figure 9a). On the Mohawk and Hudson, 1989 and 1991 had climate conditions particularly conducive to litter production and N immobilization relative to decomposition, driving net increases in soil N for the 1988–1992 period (Figure 9a). Averaged over all watersheds, PnET-CN estimated that litter and soils were a small net source

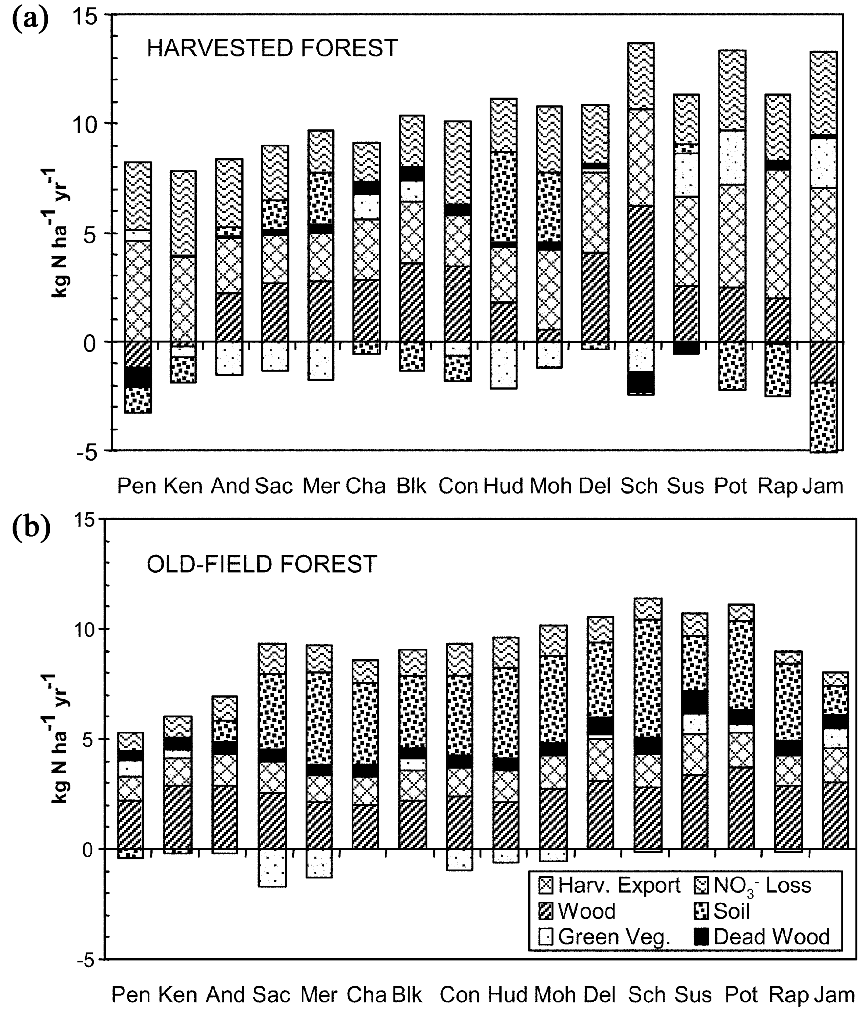

Figure 9. Modeled N balance for all watersheds using FIA forest age class information and scenarios assuming that forests of different ages derived wholly form forest harvest (top) or abandoned fields (bottom). Harvest export and NO_3^- loss represent net losses from the system; all other terms are the net sink (or source) of N into wood, green tissues (foliage, roots or internal stores), soil and litter, and dead wood.

of N (0.1 kg N ha^{-1} yr^{-1}) under the forest harvest scenario, and a substantial sink for N (2.5 kg N ha^{-1} yr^{-1}) under the old-field scenario (Figure 9). In these simulations, harvests induced relatively small losses of C and N from soil pools, thereby allowing rapid recovery. In the agricultural scenarios, 100 years of farming with minimal inputs severely depleted the soil C and N pools, which became net sinks for N as forests regrew.

Green vegetation

Foliage, fine roots, and internal N stores do not form significant N sinks over the long term, because they turn over so quickly. However, N in these pools can fluctuate from year to year in response to interannual variability in climate conditions, and transient changes in these pools predicted for 1988–1992 can cause short-term sources or sinks of N. Short-term changes in these pools generally counteracted changes in the soil pool, such that N stores in green vegetation pools increased in years that climate conditions favored net N mineralization over N accumulation in forest litter and soils (Figure 9).

Nitrate loss

Predicted nitrate losses did not correlate with N deposition across the watersheds, but instead varied with short- and long-term disturbance patterns. In PnET-CN, net mineralization from the soil is available for uptake by plants; the excess can nitrify and leach below the rooting zone with drainage water. Large nitrate losses were predicted to occur during the first decade after harvest, when soil N pools are large and forest uptake is low. This pattern was damped in the old-field scenario, where more N was immobilized in the N-poor soil than was leached below the rooting zone. In the forest harvest scenario, watersheds with relatively large amounts of forest area in the 1–10 year age class (the Penobscot, Kennebec, and James) were predicted to have relatively high rates of nitrate loss, despite low N deposition rates (Figure 9a). These differences in harvesting regimes obscured any direct correlations between N deposition and predicted nitrate leaching ($R < 0.02$). Land-use history had a large effect on predicted nitrate losses. Forests growing on degraded agricultural sites, where soils were large N sinks, had much lower mean predicted rates of nitrate loss (1.1 kg N ha^{-1} yr^{-1}) than forests growing on never-farmed land (2.9 kg N ha^{-1} yr^{-1}) (Figure 9).

Discussion

Forests of the eastern U.S. are aggrading, forming sinks for atmospheric carbon (Birdsey & Heath 1995; Turner et al. 1995), and as suggested here, for nitrogen. Much of the observed C sink is due to regrowth of previously cleared lands, with harvest rates lagging rates of regrowth (Birdsey & Heath 1995). On these watersheds and elsewhere in the eastern U.S., the potential for continued and future accumulation of C and N in living biomass is largely constrained by the extent to which historically disturbed forests have recovered. Current forests contain about half the biomass observed in some old-aged northern hardwood forests, suggesting that, if left unharvested, these forests could continue to sequester large amounts of C (and N) (Brown et al. 1997). Harvesting is likely to continue, however, and forest harvest can remove significant quantities of N through export of harvested wood (e.g. Hornbeck & Kropelin 1982; Johnson et al. 1982; Tritton et al. 1987). For the basins studied here, export of N in harvested wood amounted to 18–88% of the N received in atmospheric deposition. Increasing forest harvest rates is not an advised means of managing excess N deposition, however, as harvests in regions of elevated N deposition cause local episodic pulses of nitrate in streams (e.g. Hornbeck & Kropelin 1982; Likens et al. 1970; Martin & Pierce 1980), and export of other nutrients in wood, particularly calcium, may lead to future nutrient limitations (Federer et al. 1989). Observed harvest rates on the Penobscot and Kennebec already exceeded growth rates, and hence were not sustainable.

Local patterns of disturbance and recovery across the landscape cause substantial variation in forest C and N accumulation. This variation can lead to highly variable nitrate export within regions of relatively homogeneous N deposition (e.g. Lovett et al. 2000; Goodale et al. 2000; Williard et al. 1997), and can obscure direct correlations between nitrate export and deposition across large gradients (e.g. Dise et al. 1998). Linking the model with forest inventory information on age-class structure provided a useful step toward incorporating realistic patterns of forest disturbance status across the landscape.

Both predicted (PnET-CN) and observed (FIA-based) rates of N uptake into wood are large enough to nearly balance the N input from deposition, allowing for little net accumulation of N in soil. Similarly, Johnson (1992) observed that across a range of intensively studied forested sites, N taken up in aggrading vegetation was of the same magnitude as N received in atmospheric deposition. However, these observations do not necessarily indicate that vegetation takes up N deposition directly, nor that increased deposition will directly increase vegetation growth and N uptake. Studies using ^{15}N tracers indicate that when ^{15}N is added to forested sites, little of it enters the vegetation; most is rapidly incorporated into forest floor and mineral soil organic mater, for at least the first 1–3 years after application (Nadelhoffer et al. 1999a, b). These field studies of ^{15}N tracers and related simulations (Currie et al. 1999; Currie & Nadelhoffer 1999) suggest that the N taken up and accumulated in forest vegetation does not derive directly from deposition, but from N redistributed from litter and soils. Although the ^{15}N studies indicate that soils are the immediate direct sink for added N, it is less clear whether this N is later mineralized from soil organic matter, and if so, how quickly. Soils of the eastern U.S. have been exposed to elevated N deposition for many decades, and these long-term additions may have altered current soil N availability. The mass balance of net sequestration of N in plant biomass requires a significant source of N. If new additions of N from atmospheric deposition are largely retained in the soil, then there must be a source of older or otherwise available soil N for plant uptake. Understanding controls on soil N retention remains a vitally important question for determining the rate at which N becomes available for plant uptake. Aggrading forests can accumulate N in woody biomass, but the extent to which this process can truly offset N from deposition requires a better understanding of processes controlling soil N retention and turnover.

Acknowledgments

We are grateful to the Forest Service's FIA Program for making these data available on the Web, and to T. Kittel and N. Rosenblum for sharing the VEMAP II climate data sets. Thanks to Bill Currie, John Aber, and Rita Freuder for modeling advice and to Jennifer Jenkins, Sandra Brown, and Tom Frieswyk for assistance in interpreting the FIA data. This work was initiated as part of the International SCOPE N Project, which received support from the Mellon Foundation and the National Center for Ecological Analysis and Synthesis. CLG was supported by the Alexander Hollaender Postdoctoral Fellowship Program, which is sponsored by the Office of Biological and Environmental Research of the U.S. Department of Energy, and administered by the Oak Ridge Institute for Science and Education.

Appendix 1

Table 1: Multipliers used in converting growing-stock volume (m^3/ha) to total forest biomass (Mg/ha) for the northeastern U.S.; from Turner et al. (1995).

Forest type	Wood Density (Mg/m^3)	Noncommercial species	Biomass ratio (total wood: bole)
Pine	0.378	1.01	1.61
Spruce-fir	0.369	1.01	1.69
Oak-hickory	0.636	1.14	1.75
Northern hardwood	0.600	1.14	2.08
Bottomland hardwood	0.580	1.14	1.64

*Specific gravity of wood, ratio of all trees to commercial species, and the ratio of total wood (bolewood plus roots, stumps, branches, and cull trees) to merchantable bolewood.

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