



Redistributions of ^{15}N highlight turnover and replenishment of mineral soil organic N as a long-term control on forest C balance

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Abstract

A large-scale ^{15}N tracer study was initiated at the Harvard Forest in 1991 in two forest types (red pine and mixed hardwoods) as a means to test hypotheses concerning long-term dynamics in ecosystem-level N cycling and carbon–nitrogen interactions. Here we describe the application of a biogeochemical process model TRACE, with the ability to simulate ^{15}N tracer redistributions, to help interpret the field study and explore its ramifications. We had three main goals: (1) to compare field results of 8-year time series in $^{15}\text{NH}_4$ and $^{15}\text{NO}_3$ redistributions against previous model predictions; (2) to gain insight into ecosystem C/N interactions through an iterative set of model changes and direct model-data comparisons; and finally (3) to forecast temporal dynamics in the future effects of elevated N inputs on altered C storage in the regionally representative hardwood forest.

Model interpretations of field-observed ^{15}N redistributions indicated that mineral soil organic matter contains a fraction that retains illuviated ^{15}N rapidly (within 1 year), then releases some of this ^{15}N for plant uptake through the following 5–8-year period. Our simulations also suggested that the mineral soil supplied a long-term source of N for the aggrading pools of N in vegetation and the O horizon over the course of stand development. The model structure that best fits the decadal-scale field data for pools and fluxes of C, N, and ^{15}N forecasted an elevated C storage relative to elevated N inputs that is much lower than published estimates based on ecosystem stoichiometry. TRACE forecasted a maximum differential C storage in N-amended plots of 725 g C m^{-2} , occurring largely in living and dead wood, peaking 30 years after the start of N amendment treatments of $+5 \text{ g N m}^{-2}$ per year (a cumulative $+150 \text{ g N m}^{-2}$). This amounts to a ratio of elevated C storage to cumulative, elevated N inputs of less than 5:1 over the 30-year period. These results imply that mineral soil supplies much of the N needed for forest aggradation, partially regulating changes in ecosystem C storage, and that elevated N deposition may cause relatively small amounts of elevated C storage after a time lag of decades.

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1. Introduction

The degree to which elevated atmospheric N deposition will stimulate increased rates of C storage in forests has been a subject of research and debate for nearly 20

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years (Peterson and Melillo, 1985; Nadelhoffer et al., 1999). Global estimates of the effect of elevated N deposition on C storage range widely from 0.1 to 2.3 Pg C per year (Peterson and Melillo, 1985; Schindler and Bayley, 1993; Townsend et al., 1996; Vitousek et al., 1997). Typically, analyses of this topic emphasize the potential for C storage in forests because large forested areas exist in the regions receiving elevated N deposition and because forest production in temperate regions is often N-limited. Another factor is that forests produce large amounts of woody biomass at very high ratios of C:N; if wood production increased at an unaltered C:N ratio, correspondingly large increases in C storage could result from elevated N deposition. The primary reasons for the wide range in estimates of this effect on C storage are the varying assumptions made in three areas: (i) the degree of system retention versus loss of elevated N inputs; (ii) the entry of elevated N inputs into soil pools, at lower C:N ratios, versus vegetation at higher C:N ratios; and (iii) the allocation of N to new wood production at very high C:N ratios.

Progress on this topic requires analyses that go beyond simple stoichiometric calculations to those that can consider realistically integrated ecosystem responses to elevated N deposition. Forest ecosystems have the ability to shift C:N stoichiometries, change patterns of N allocation in tissues, and alter the fluxes of N among vegetation and soil pools (Townsend and Rastetter, 1996; Rastetter et al., 1997). The retention of elevated N inputs in a particular forest ecosystem results from both short-term partitioning and longer-term redistributions that are likely to include complex interactions with C, light, water, and ecology of the existing vegetation.

Dynamic biogeochemical models provide a means of organizing this understanding. Models allow us to quantitatively link fine-scale processes in an effort to understand the manner in which their interactions may control system-level dynamics. This is a key step in gaining a predictive understanding of ecosystem responses to global change (Canadell et al., 2000); it requires not only synthesis but also testing of the manners in which models integrate processes across scales.

Prediction of the movement of the stable isotope ^{15}N into ecosystem pools can be tested because changes in $^{15}\text{N}/^{14}\text{N}$ ratios in vegetation and soil pools can be easily detected (Nadelhoffer et al., 2004). Using a biogeochemical process model to interpret

the redistributions of field-applied ^{15}N tracers provides an opportunity to test model formulations of C/N interactions with more sensitivity than can be achieved with non-isotope models. Sensitivity is greater because the background variability in field-measured $^{15}\text{N}/^{14}\text{N}$ ratios is small compared to the $^{15}\text{N}/^{14}\text{N}$ ratios of tracers applied experimentally.

A challenge inherent in modeling this new dimension in forest N cycling lies in the fact that patterns of ^{15}N are sensitive to multiple competing processes that can be difficult to resolve. To meet that challenge we took a two-step approach in the present study. We first used new field observations of ^{15}N redistributions among vegetation and soil pools to test previous predictions of the tracer redistributions among compartments in ecosystems (TRACE) model (Currie and Nadelhoffer, 1999) made in an integrated study of forest responses to elevated N inputs at the Harvard Forest (Magill et al., 2004). After interpreting the model successes and failures, we used an iterative set of model-data comparisons to gain insight into ecosystem C/N interactions at this site. We tested whether certain model alterations, suggested both by model-data discrepancies and by independent research, could better account for 8-year patterns of ^{15}N redistributions in our 8-factorial field study at the Harvard Forest. This iterative analysis amounted to a form of “inverse modeling”, a heuristic technique used to explore or test the plausibility of competing conceptual models after the field data are known (Luo et al., 2001).

An additional objective was to use our final representation of C/N interactions to calculate and forecast the effects of elevated N inputs on ecosystem C storage in our regionally representative hardwood stand. In doing so, we were able to go beyond a simple stoichiometric analysis, incorporating vegetation physiology and detailed N dynamics in litter and soil, together with complex plant-soil feedbacks tested through the simulation of decadal-scale ^{15}N redistributions.

2. Methods

2.1. Site description, N amendments and ^{15}N tracer applications

The field study of large-scale ^{15}N tracer redistributions (Nadelhoffer et al., 1999, 2004) took place at the

Harvard Forest in central Massachusetts, USA. Elevations are ca. 370–390 m; monthly mean temperatures are -7°C in January and 19°C in July. Precipitation averages 110 cm per year, distributed fairly evenly throughout the year (Van Cleve and Martin, 1991). The field study took place in two contrasting stands of temperate forest vegetation: a red pine stand (*Pinus resinosa* Ait.) and a mixed hardwoods stand dominated by oaks (*Quercus velutina* Lam., *Q. rubra* L., *Betula lenta* L., *Acer rubrum* L.). Soils in both stands are coarse-loamy (in the oak stand, coarse-loamy over sandy-skeletal), mixed, frigid Typic Dystrochrepts. Soils are well drained and contain well-defined O horizons (mor type).

The field study took place in some of the plots from the Chronic N Amendment Study described by Magill et al. (1997, 2004), in which large-scale forest plots (30 m \times 30 m) have been fertilized with NH_4NO_3 in 6 monthly additions during each growing season from 1988 through the present. In each stand there are four experimental treatments: control, low-N, low-N + S, high-N. Control plots receive ambient N deposition (estimated to be 0.8 g N m^{-2} per year), while low-N and high-N plots receive ambient deposition plus 5 and 15 g N m^{-2} per year (respectively) as NH_4NO_3 . Here we consider only the control and low-N plots of each forest stand because in these, enriched ^{15}N tracers were added in 1991 and 1992 (fertilization years 4 and 5). Separate $^{15}\text{NO}_3$ and $^{15}\text{NH}_4$ labels were applied on each half of experimental plots (15 m \times 30 m); samples were subsequently collected for ^{15}N analyses separately on each half plot allowing for separate analysis of $^{15}\text{NO}_3$ and $^{15}\text{NH}_4$ fates and redistributions. Greater detail concerning the ^{15}N tracer applications and field recoveries are provided by Nadelhoffer et al. (1999, 2004).

2.2. Model overview

TRACE is a biogeochemical process model of C, N, and water fluxes in forest ecosystems (Currie et al., 1999; Fig. 1). TRACE also predicts redistributions of ^{15}N and ^{14}N isotopes through time by simulating $^{15}\text{N}:^{14}\text{N}$ ratios of individual N pools and of N transferred between pools, incorporating principles of pool dilution and mass balance (Wessel and Tietema, 1992; Nadelhoffer and Fry, 1994). TRACE was explicitly designed for use with large-scale ^{15}N -labeled field studies, as it simulates the timing, at.%, and forms of

^{15}N added to large plots. TRACE combines a complex soil process model (DocMod; Currie and Aber, 1997) with the vegetation component of the PnET-CN ecosystem model (Aber et al., 1997). PnET-CN emphasizes links between vegetation physiology, biogeochemistry, and hydrology. PnET models photosynthesis, stomatal conductance and transpiration as a function of foliar N content, radiation, temperature, and soil water availability (Aber and Federer, 1992). TRACE runs on a monthly time step and models decades or centuries of forest change, including past instances of forest harvest and other disturbances. An accurate disturbance history is required to accurately predict nitrate leaching and net nitrogen balances (Aber et al., 2002). Previous publications have described the fundamental vegetation and soil processes in TRACE and PnET-CN (Currie et al., 1999; Aber et al., 1997; Currie and Nadelhoffer, 1999; Currie and Aber, 1997).

A strength of TRACE lies in its detailed treatment of soil C and N interactions and in its separation of O horizon C and N pools from those in mineral soil. This separation of soil into organic and mineral horizons was key in the present analysis, because distinct and unexpected patterns of ^{15}N time series in the two horizons were observed. The model includes separate pools of available NH_4 , NO_3 , and dissolved organic N (DON) within each soil layer. In the O horizon, fine litter enters detrital pools representing distinct 'C classes' (acid-insoluble material, acid-soluble, and extractives; Ryan et al., 1990). Each carbon class loses dissolved organic C (DOC) via leaching and CO_2 via respiration, while undergoing N dynamics. Briefly, each C class has an attractor C:N value; ratios above or below this value result in net mineralization or immobilization of N, respectively, within each C class separately, at rates based on field studies (Aber et al., 1984). As litter decays, TRACE models the stabilization and humification of C and N in fine litter and woody debris in the forest floor and mineral soil. Leaching of NH_4 , NO_3 , and DON are modeled as transfers from O horizon to mineral soil pools. The model explicitly includes gross N transformations including mineralization, nitrification, and gross detrital-microbial assimilation of NH_4 and NO_3 in litter and humified matter, necessary for simulating ^{15}N redistributions and at.% ^{15}N values of plant-available NH_4 and NO_3 pools. These, in turn, determine the $^{15}\text{N}:^{14}\text{N}$ ratios of N taken up by plants. Soil processes

link directly to plant production through water and N availability. Plant uptake of NH_4 and NO_3 occurs in both horizons based on fine root distributions, plant N demand, and competition for N with soil processes.

As in previous uses of TRACE for model-data comparisons, we express model results for ^{15}N tracer recoveries in ecosystem pools as the mass of tracer ^{15}N recovered above background in each ecosystem compartment. We refer to this quantity as PR ^{15}N , calculated in TRACE as follows:

$$\text{PR } ^{15}\text{N}(C_i, t) = \frac{N_{C_i}(t)(\text{at.}\% \text{ } ^{15}\text{N}_{C_i}(t) - \text{at.}\% \text{ } ^{15}\text{N}_b)}{A(t - t_0)(\text{at.}\% \text{ } ^{15}\text{N}_a - \text{at.}\% \text{ } ^{15}\text{N}_b)} \quad (1)$$

where $N_{C_i}(t)$ is the amount of N (g m^{-2}) in C_i at time t , $A(t - t_0)$ is the sum of N amendments (g m^{-2}) to time t , C_i is an ecosystem compartment, and the ‘a’ subscript denotes amendment, ‘b’ denotes background (Currie et al., 1999).

2.3. Model changes from previous applications

Prior to the present analysis, some changes were made to TRACE to improve model consistency and allow improvements in some direct comparisons against field measures of C, N, and ^{15}N . Given the importance of C:N ratios in wood for the present analysis, we improved TRACE to treat concentrations

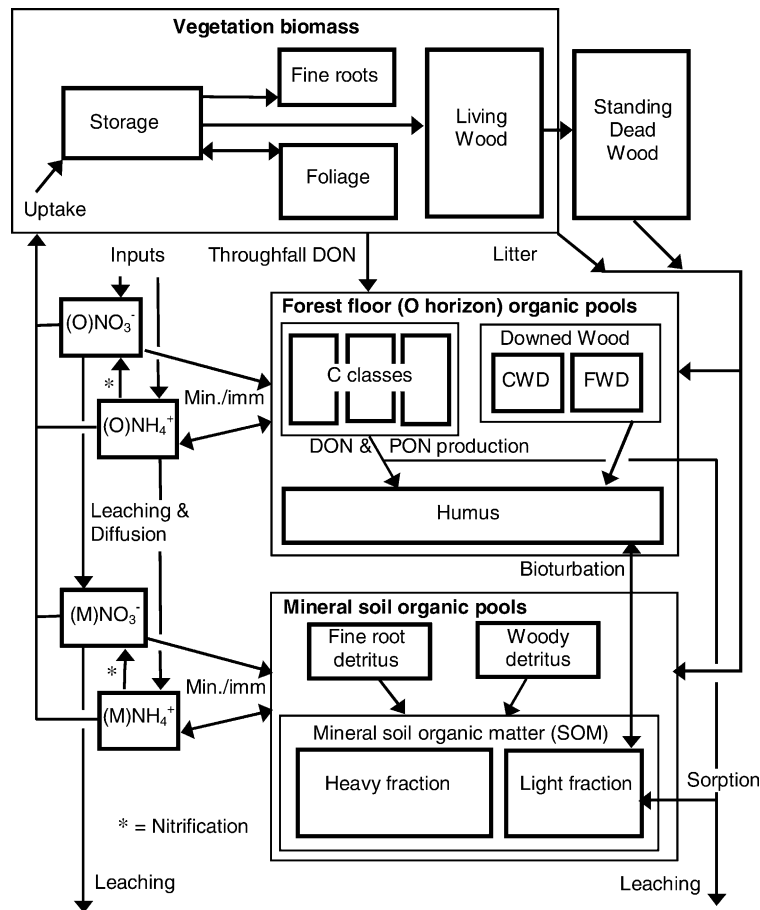


Fig. 1. Schematic of pools and fluxes of N in TRACE 4.20. Plant uptake of N, detrital N dynamics, and N transformations are calculated separately in each soil layer. Pools of available N are separated by soil layer: O, O horizon; M, mineral soil; DON, PON, dissolved and particulate organic nitrogen; CWD, FWD, coarse and fine woody detritus; Min./imm., mineralization and assimilation. Inputs: NO_3 and NH_4 in atmospheric deposition, fertilizer, and isotopic tracer additions. For clarity, not all fluxes are shown in detail. Shown is the final version developed in the present analysis.

of N in living wood tissues more realistically and mechanistically. Consistency in modeled N in roots was improved in the process. TRACE includes a plant-internal pool of mobile N, *VascN*, that mixes isotopically with N taken up from the soil and with N resorbed from senescing foliage. This pool previously had no physical location in the model. It is now physically distributed between living wood and fine roots. Tissue N concentrations in living wood and fine roots, now reflecting the size of this internal storage pool, fluctuate over time as mechanistic predictions rather than model parameters; in addition, these can now be compared more realistically against field data.

Another significant change to TRACE was in the parameterization of realistic pool sizes of downed woody debris. Because wood mass, both living and dead, exhibits a high C:N ratio, dynamics in pool sizes of wood are critical to an accurate accounting of ecosystem C balances and C/N interactions. Sizes of woody debris pools at a particular site are also sensitive to the particulars of land use, management, and disturbance history (Harmon et al., 1986; Kranina and Harmon, 1995; Brown and Schroeder, 1999). After ensuring that TRACE modeled realistic rates of wood production (Magill et al., 2004), and taking into account the particular land use and disturbance histories, we calibrated the rates of wood mortality to produce present-day pool sizes of C and N in downed woody debris. We recently quantified the present-day pool sizes in a field study in these two forest stands (Currie and Nadelhoffer, 2002).

Prior to the present analysis, we tested TRACE for N mass balance, C mass balance, and isotopic mass balance. Values of PR ^{15}N were checked to ensure that they summed to 100% immediately following tracer application in all cases.

2.4. Model parameterization for present simulations

Model runs began in the year 1940 for the pine forest and 1900 for the hardwood forest. Although C and N pool sizes in these initialization years are not known with precision, it is important to explain our choices of values because they impact the results of our analysis. For the pine stand, a 14-year-old plantation in 1940, developing on previously agricultural

(plowed) land, we estimated stocks of organic matter (OM) as 1670 g OM m^{-2} in the O horizon and $14,230 \text{ g OM m}^{-2}$ in mineral soil (Hooker and Compton, 2003, their Fig. 4). We used a C:OM mass ratio of 0.52 (the value used in TRACE and determined from litter and humus collected at the site; Currie, 2003) and assumed a C:N ratio of 30:1 for the O horizon and 20:1 for mineral soil, yielding initial pool sizes of 29 and 370 g N m^{-2} , respectively. For the hardwood stand, similarly drawing on the results of Hooker and Compton (2003) and assuming a forest age of 30 year in 1900 (Foster, 1992) we estimated initial pool sizes of 2170 g OM m^{-2} for the O horizon and $14,615 \text{ g OM m}^{-2}$ in mineral soil. We estimated a C:N ratio of 30:1 for the O horizon in 1900, thus an initial N pool size of 37.6 g N m^{-2} . We estimated a slightly higher value for the mineral soil C:N ratio in the hardwood stand (23:1) because it was probably in less intensive agriculture than the land in the pine stand and was abandoned 40–60 years earlier (Foster, 1992). This produced an initial N pool size of 330 g N m^{-2} in mineral soil. For each forest stand, we estimated an initial pool size of root litter in mineral soil as 260 g OM m^{-2} (Gaudinski et al., 2000).

The values we used for exogenous inputs of N over time also played a key role in our analysis and our findings, so we describe them in detail here. We included wet and dry deposition of inorganic N, deposition of atmospheric organic N (AON), and N fixation in woody debris, together with additional N inputs from an unknown source that were needed to produce present-day patterns of N capital in ecosystem pools. Our modeled deposition of inorganic and organic N inputs increased linearly from 25% of present-day values in 1930 to present-day values in 1980 and stable from 1980 onward (Howarth et al., 2002). Our present-day flux of wet + dry inorganic N deposition was 0.84 g N m^{-2} per year. This derived from N concentrations in wet deposition of $0.13 \text{ mg NH}_4\text{-N l}^{-1}$ and $0.293 \text{ mg NO}_3\text{-N l}^{-1}$ (Ollinger et al., 1993) and precipitation of 112 cm per year, together with dry deposition rates of $0.073 \text{ g NH}_4\text{-N m}^{-2}$ per year and $0.294 \text{ g NO}_3\text{-N m}^{-2}$ per year (Ollinger et al., 1993). To this we added AON deposition equal to 0.5 times the value of inorganic N (wet + dry) deposition (Neff et al., 2000).

Non-symbiotic nitrogen fixation, such as that occurring in free-living microbes growing in decaying

woody debris, probably amounts to a small exogenous input of N to forests in this region. Its importance is debated. We included a small flux which we introduced in a mechanistic manner. We simulated non-symbiotic N fixation as proportional to masses of downed woody debris as measured by Roskoski (1980) in hardwood forests of New Hampshire. Average annual rates from 1980 to 2000 in our simulations were ca. 0.1 and 0.29 g N m⁻² per year in the hardwood and pine stands, respectively. The latter value falls at the high end of the range of 0.0002–0.20 g N m⁻² per year reported in a literature summary by Boyer et al. (2002). However, the biomass of downed woody debris present in this pine stand at the Harvard Forest is greater than that measured in other undisturbed forests of this type or in this region (Currie and Nadelhoffer, 2002).

In tests of TRACE with these initial conditions and input fluxes of exogenous N, the modeled N supply for plant uptake was insufficient to produce both the biomass production observed today and the accumulation of N capital observed in the present-day forest O horizons (Magill et al., 2004; Nadelhoffer et al., 2004). To produce the needed growth and accumulation of N capital in each stand we added a flux of ‘extra N inputs’ as an explicit flux of exogenous N into the forest ecosystems from an unknown source or mechanism. In the hardwood stand our value for this flux equaled 1 g N m⁻² per year from 1900 to 1937, 0.4 g N m⁻² per year from 1938 to 1960, and zero from 1960 on. (The significance of the year 1938 is that a hurricane damaged 76–90% of the canopy in the hardwood stand, which we included in TRACE simulations; Motzkin et al., 1999.) For the pine forest simulations, our values of extra exogenous N inputs stepped downward from 1.2 g N m⁻² per year in 1940 to 0.4 g N m⁻² per year in 1999, and zero from the year 2000 on.

We used a few key variables to calibrate whole-system C and N cycling independent of ¹⁵N before making model-data comparisons of ¹⁵N recoveries. We adjusted parameters controlling the decay rates of O horizon humus and mineral SOM and the rate of DOC (dissolved organic carbon) leaching from the O horizon. We tested for realism in key present-day characteristics of system biogeochemistry including NPP (net primary production), present-day O horizon mass and C:N ratio, leaching fluxes, tissue N concen-

trations, and pool sizes of living and downed wood (Table 1). We emphasize two key points regarding this calibration of broad-scale aspects of system-level C and N cycling: first, we did not conduct multivariate statistical analyses, but adjusted of a small set of key parameters that are difficult to measure in field studies and that the model is highly sensitive to; second, no ¹⁵N data were used. This system-level calibration step made the inverse modeling analysis of ¹⁵N redistributions more focused and relevant because broad-scale N cycling patterns (independent of isotopic ratios) were realistic.

2.5. Inverse modeling analysis

We made iterative sets of model-data comparisons in the 8-year time series in PR ¹⁵N across all vegetation and soil pools from the 8-factorial field study. We refer to steps in this analysis as simulation sets (A), (B), and (C); we also refer to set (A) as the baseline and set (C) as the final version (Table 2). Our goal was to identify reasons for disagreements between predicted and observed patterns of PR ¹⁵N and to test the plausibility and explanatory power of certain limited sets of model changes. Our goal in this iterative analysis was not to fit the time series patterns of ¹⁵N, which could have been easily achieved through a multivariate optimization of parameter sets. Existing parameters that controlled fine-scale ¹⁵N movements and transformations were left unchanged, including gross:net ratios of N mineralization and nitrification, the degree of microbial preference for NH₄ over NO₃, and other such parameters. (One exception was the leaching of inorganic N from O horizon to mineral soil, which we increased because this worked together conceptually with our other changes.) Instead, our goal was to use the discrepancies in model-data comparisons to suggest plausible changes to the model structure and in testing those changes, to see whether agreement was improved across the 8-factorial time series patterns.

As steps in this analysis, we made three major changes to the model structure and fine-scale processes. In the first step we divided mineral soil organic matter (and associated organic C and N) into two pools with different turnover rates, and altered the plant “preference” for N uptake from the O horizon to the mineral soil. We conceived of the new mineral soil

Table 1
Pools and fluxes of C and N used to assess model realism prior to analysis of ^{15}N redistributions

	Model		Field data		Year(s)	Reference for field data
	Control	Low-N	Control	Low-N		
Pine forest						
Foliar production (g OM m ⁻² per year)	327	352	320	370	1989–1993	Magill et al. (1997)
Fine root production (g OM m ⁻² per year)	291	294	254 ± 120	–	1989–1993	Nadelhoffer and Raich (1992) ^a
Wood production (g OM m ⁻² per year)	278	298	306	275	1989–1996	Magill et al. (2000)
N concentration in green foliage (%)	1.06	1.20	1.05	1.35	1988–1993 ^b	Magill et al. (1997)
N concentration in fine roots (%)	1.64	1.62	1.43	1.89	1992	Nadelhoffer et al. (1999)
N concentration in living wood (%)	0.18	0.18	0.19	–	–	Goodale et al. (2002) ^c
Living wood biomass (g OM m ⁻²)	13680	13680	14660	–	1988	Aber et al. (1993)
Downed woody debris (g OM m ⁻²)	3830	3820	3960	–	1999	Currie and Nadelhoffer (2002) (after ash correction)
Soil O horizon OM mass (g OM m ⁻²)	5120	5170	4900	5780	1996	Magill et al. (2000) ^d
Soil O horizon C:N ratio (g g ⁻¹)	28.5	26.4	23.7	27.1	1996	Magill et al. (2000)
Net N mineralization (g N m ⁻² per year)	3.2	2.7–3.5	7.0–12.5	7.0–12.0	1990–1996	Magill et al. (2000) ^e
Net nitrification (g N m ⁻² per year)	0.8	0.5	1.1–2.3	2.0–4.1	1990–1996	Magill et al. (2000) ^e
Oa DOC leaching flux (g C m ⁻² per year)	40.0	42.3	39.8	36.8	1994	Currie et al. (1996)
Oa DON leaching flux (g N m ⁻² per year)	0.51	0.82	0.95	1.14	1994	Currie et al. (1996)
Oa NH ₄ -N leaching flux (g N m ⁻² per year)	0.57	3.00	0.14	1.30	1994	Currie et al. (1996)
Oa NO ₃ -N leaching flux (g N m ⁻² per year)	0.50	2.33	0.60	3.25	1994	Currie et al. (1996)
NO ₃ losses from solum (g N m ⁻² per year)	0.15	2.42	<0.001	0.506	1994	Currie et al. (1996)
Hardwood forest						
Foliar production (g OM m ⁻² per year)	297	297	290	290	1989–1993	Magill et al. (1997)
Fine root production (g OM m ⁻² per year)	264	264	231 ± 120	–	1989–1993	Nadelhoffer and Raich (1992) ^a
Wood production (g OM m ⁻² per year)	446	446	460	460	1989–1996	Magill et al. (2000)
N concentration in green foliage (%)	2.19	2.19	2.2	2.2	1988–1993 ^b	Magill et al. (1997)
N concentration in fine roots (%)	0.88	2.2	1.2	1.3	1992	Nadelhoffer et al. (1999)
N concentration in living wood (%)	0.25	0.27	0.26	–	–	Goodale et al. (2002) ^c
Living wood biomass (g OM m ⁻²)	11570	11570	11130	–	1988	Aber et al. (1993)
Downed woody debris (g OM m ⁻²)	2710	2710	2660	–	1999	Currie and Nadelhoffer (2002) (after ash correction)
Soil O horizon OM mass (g OM m ⁻²)	4650	4650	3885–5530	6020	1996	Gaudinski et al. (2000) and Magill et al. (2000) ^d
Soil O horizon C:N ratio (g g ⁻¹)	24.7	22.9	25.6	25.1	1996	Magill et al. (2000)
Net N mineralization (g N m ⁻² per year)	4.1	6.7–7.0	6.0–10.0	6.0–13.5	1990–1996	Magill et al. (2000) ^e
Net nitrification (g N m ⁻² per year)	–0.5	–0.7	0–0.15	0–0.25	1990–1996	Magill et al. (2000) ^e
Oa DOC leaching flux (g C m ⁻² per year)	24.1	24.1	22.5	26.6	1994	Currie et al. (1996)
Oa DON leaching flux (g N m ⁻² per year)	0.54	0.71	0.61	0.70	1994	Currie et al. (1996)
Oa NH ₄ -N leaching flux (g N m ⁻² per year)	0.58	5.32	0.10	1.23	1994	Currie et al. (1996)
Oa NO ₃ -N leaching flux (g N m ⁻² per year)	0.10	1.88	0.20	2.08	1994	Currie et al. (1996)
NO ₃ losses from solum (g N m ⁻² per year)	0	1.22	0.002	0.002	1994	Currie et al. (1996)

'Control' plots receive ambient N inputs; 'low-N' plots have received ambient N inputs plus 5 g N m⁻² per year as NH₄NO₃ since 1988. Year(s) indicate time periods of field data and model results for comparison; where multiple years are listed, annual averages are given. OM, organic matter (ash-free, oven-dry weight); Oa: lowest sub-horizon of the soil O horizon; DOC, dissolved organic carbon; DON, dissolved organic nitrogen.

^a Mean values with 95% confidence intervals from a regression meta-analysis against foliar litter production in forests based on a N-budget technique (Nadelhoffer and Raich, 1992, their Fig. 1D).

^b Averages 1988–1993 for control; 1991–1993 for low-N.

^c Weighted averages for (A) softwoods and (B) hardwoods in eastern North America.

^d Using a ratio of C mass:OM mass = 0.52, the value used in TRACE simulations (Currie, 2003).

^e Field results are for O horizon plus upper mineral soil (0–10 cm) summed. (Ranges rather than means are shown because of high inter-annual variabilities.) Model results are for the entire solum, O horizon plus mineral soil.

Table 2
Description of model changes made in simulations sets in the present inverse modeling analysis

Simulation set	Changes to model
(A) Baseline	Starting point for present analysis
(B) Intermediate	Preferential uptake of N from mineral soil pools of NH ₄ and NO ₃ , as opposed to NH ₄ and NO ₃ pools in the O horizon Mineral soil organic matter (SOM) pool split into two, representing light-fraction and heavy-fraction, with faster turnover of C and N in light-fraction
(C) Final	Leaching of particulate organic matter from O horizon to mineral soil added; leaching of NH ₄ and NO ₃ from O horizon increased Diffusion of N isotopes between horizons added Pine forest: no change in size or turnover of light-fraction SOM; oak forest: light-fraction SOM pool decreased in size, increased in turnover rate

pools as light-fraction and heavy-fraction SOM (Compton and Boone, 2002), parameterized initially as 39% light-fraction based on a recent field study of Harvard Forest soils (Gaudinski et al., 2000). The remainder of mineral SOM (and associated SON) we put in the heavy-fraction pool. The light- and heavy-fraction pools were initialized with identical C:N ratios. We made all inputs to mineral soil organic C and N (including leaching of dissolved organics, and humification of root litter in mineral soil) enter the light-fraction pool. The change in plant preference for N uptake from the mineral horizon in simulation sets (B) and (C) (Table 2) from the O horizon (Table 2) had no effect on overall rates of N uptake.

We introduced the leaching of particulate organic matter (POM) from the O horizon as an additional fine-scale process in TRACE. This carried C and N from the O horizon to the mineral soil, replenishing the light-fraction pools of mineral soil organic C and N that turned over relatively rapidly. We parameterized POM formation and leaching from litter C classes in a manner analogous to that of DOM formation and leaching already present in TRACE (Currie and Aber, 1997). We set the flux of POM leaching equal to the flux of DOM leaching in the hardwood stand, but had to limit it to 15% of the rate of DOM leaching in the pine stand. DOM leaching was much higher in the pine

stand (Table 1) and high rates of POM leaching there made the O horizon mass fail to aggrade in our simulations.

Finally, we introduced diffusion of N isotopes between pools of available N in the O horizon and mineral soil. This resulted in no mass movement of NH₄ or NO₃, but an equilibration of ¹⁵N/¹⁴N ratios between horizons within each species of available inorganic N. This had the effect of moving ¹⁵N tracers to mineral soil horizons somewhat more rapidly following tracer applications. Model testing revealed this difference to be slight, indicating that the suite of processes in place already closely constrained any differences in ¹⁵N/¹⁴N ratios in pools of soil available N between horizons.

Following the inverse modeling analysis, we used the final version of TRACE to calculate the effects of elevated N deposition on C storage in the regionally representative hardwood forest.

3. Results

3.1. Comparison of baseline model predictions against field data

Direct tests of predicted system-level redistributions in ¹⁵N enabled us to identify some key strengths and weaknesses in the integration of ecological and biogeochemical processes in the model. Predictions of the baseline model correctly showed soil pools to be the dominant sink for ¹⁵N tracers in both the 1-year (1992) and 8-year (1999) time frames (Figs. 2 and 3). This indicates that the modeled dominance of soil pools over vegetation pools as N sinks for both ¹⁵NH₄ and ¹⁵NO₃ tracers in the pine and hardwood forests at this location, in both control and low-N plots, was correct. However, weaknesses were evident in the quantitative rates of modeled soil sinks relative to other ecosystem processes. Patterns of percent recoveries of ¹⁵N tracers (PR ¹⁵N) in vegetation pools were incorrectly predicted in control versus low-N plots in both forest stands (Fig. 3).

Recoveries of ¹⁵N tracers in vegetation in control plots were over-predicted in the first few years following tracer applications. This discrepancy was evident in foliage, wood, and roots; the discrepancies were more dramatic in the pine stand but also present in the

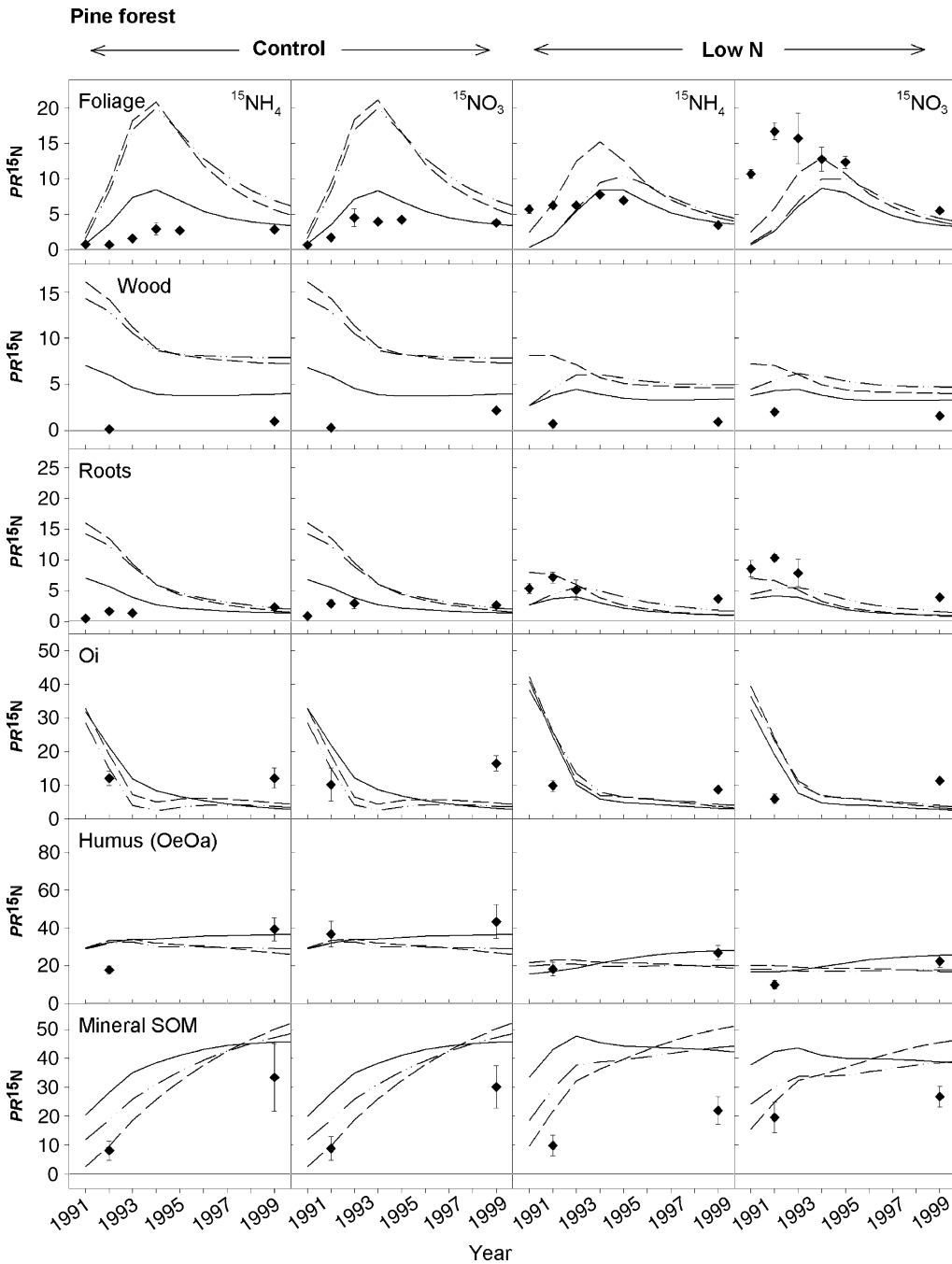


Fig. 2. Pine stand: model results compared against field data for percent recoveries of ^{15}N tracers (PR ^{15}N) in ecosystem N pools over sets of 9-year time series. ‘Control’ and ‘low-N’ are as in Table 1. $^{15}\text{NH}_4$ and $^{15}\text{NO}_3$ indicate results from half-plots in which these alternate forms of ^{15}N labels were applied. ‘Foliage’ results shown are sums across current year and previous year cohorts in living foliage. ‘Wood’ refers to living wood. Field study results (from Nadelhoffer et al. (2004)) are shown here as symbols with error bars (SE). Model results are shown as three sets of lines from the inverse modeling analysis: the dashed line (---) represents the baseline version (set (A); Table 2), the dashed-dotted line (-.-.-) represents the intermediate version (set (B); Table 2), and the solid line (—) represents the final version (set (C); Table 2).

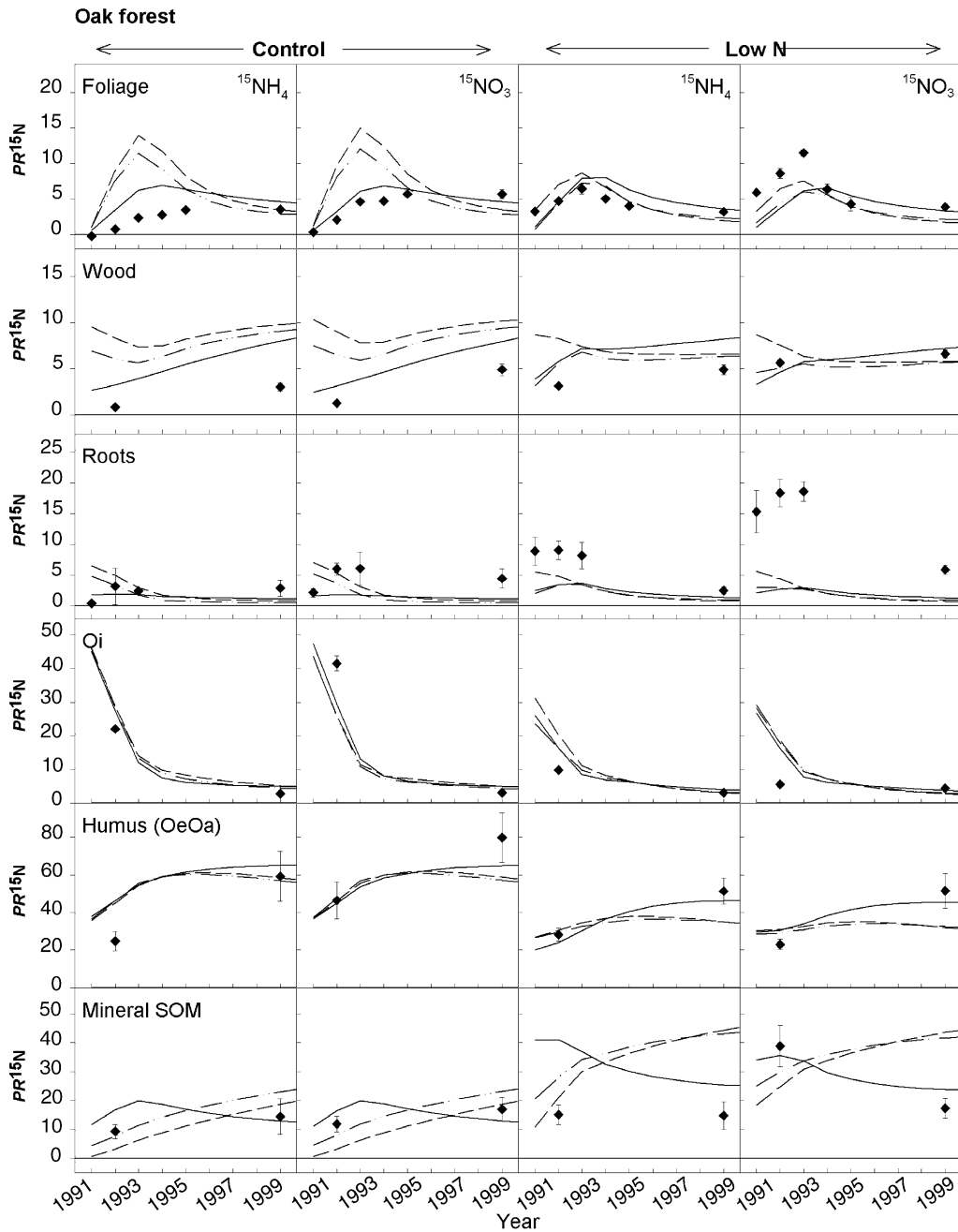


Fig. 3. Hardwood stand: model results compared against field data for percent recoveries of ^{15}N tracers (PR ^{15}N) in ecosystem N pools over sets of 9-year time series. 'Control' and 'low-N' are as in Table 1. $^{15}\text{NH}_4$ and $^{15}\text{NO}_3$ indicate results from half-plots in which these alternate forms of ^{15}N labels were applied (Nadelhoffer et al., 2004). Pool definitions, field data, and model results are shown as in Fig. 2.

hardwood stand. TRACE predicted the high values of PR ^{15}N in vegetation of control plots because pool sizes of available inorganic N in soil were small, and the ^{15}N tracers used in control plots were highly enriched (Nadelhoffer et al., 2004), thus creating very highly enriched pools of NH_4 and NO_3 in the model. Modeled soil N sinks were strong and out-competed plant uptake demand in the control plots, but at the same time the N that was taken up by vegetation was very highly enriched in the model. In the low-N plots, modeled rates of N uptake were higher, as soil sinks were overcome, but ^{15}N tracers were more dilute for two reasons: field applications were accompanied by N amendments and available pools of soil inorganic N were larger. Thus, although modeled values of PR ^{15}N were greater in control plots, modeled fluxes of N uptake were greater in the low-N plots. This highlights an important subtlety in the interpretation of model results.

Since the PR ^{15}N values in TRACE sum to 100% initially, if ^{15}N recoveries in control-plot were over-predicted in vegetation pools then ^{15}N recoveries must have been under-predicted in soil pools. Comparing the model results against the field study results for the year 1992, it is not evident in which soil pool or pools the model under-predicted ^{15}N sinks. We thought that the ^{15}N sink in mineral soil was the most likely under-predicted for the following reasons. The total system recovery in the field study in 1992 averaged 85% in the oak stand and 55% in the pine stand, whereas in 1999 the total recoveries averaged 93% in the oak stand and 82% in the pine stand (Nadelhoffer et al., 2004). We thought that ^{15}N tracer recoveries overall were probably underestimated in the 1992 field study and that the most likely location for underestimates was mineral soil. Measuring ^{15}N recoveries and scaling up to plots for the vegetation pools is more straightforward and less subject to underestimation. Another factor was that mineral soil pools were sampled only to a depth of 20 cm. If leaching were an important mechanism of rapid transfer of ^{15}N tracers downward, we would have missed any illuviation occurring below 20 cm. The overall lower summed PR ^{15}N recoveries in the pine stand relative to the hardwood are consistent with this view, because leaching fluxes of inorganic and dissolved organic N are greater in the pine stand (Currie et al., 1996; McDowell et al., 1998).

Another key disagreement we noted between model results and field data were in the temporal patterns of PR ^{15}N in foliage. The steady rise of foliar PR ^{15}N in control plots of both stands exhibited a pattern quite unlike the rise and fall predicted by TRACE. Similarly, ^{15}N recoveries in fine roots in 1999 were under-predicted by the model.

In summary, we identified three main disagreements between model and data to address with our inverse modeling analysis: (i) the model needed stronger soil sinks for the ^{15}N tracers in early years under ambient (control) conditions; (ii) the model needed movement of ^{15}N tracers downward into mineral soil pools on the 1–2 years time scale since it was likely to be underestimating the presence of ^{15}N tracers for 1992 in the mineral soil horizon; (iii) the model needed more rapid release of ^{15}N from soil pools for continuing plant uptake over the 8-year period.

3.2. Inverse modeling analysis of 8-year time series

Preferential N uptake from mineral soil pools, together with a division of mineral soil organic N into two pools with widely different turnover rates (simulation set B, Tables 2 and 3), improved the patterns of PR ^{15}N to some degree. Mineral soil PR ^{15}N was higher in the early 1990s as a result, in better agreement with field data (Figs. 1 and 2). However, the model continued to severely over-predict recovery of ^{15}N tracers in the foliage and living wood in control plots, as well as roots in the control plot of the pine stand. Not until additional changes were made to increase the movement of N from the O horizon to mineral soils (set (C), Table 2) did most of these

Table 3
Rates of turnover of soil organic matter pools in our final model

	k , O horizon humus (HOM)	$\Delta\text{LSOM}/$ ΔHOM	$\Delta\text{HSOM}/$ ΔLSOM
Pine forest	0.0008	1.8	0.005
Hardwood forest	0.0014	10	0.005

Turnover of O horizon humus is expressed as a single-order decay constant k in the equation $M(t) = M_0 e^{-kt}$, where M is mass and k has the unit month^{-1} . Turnover of light-fraction mineral SOM (LSOM) and heavy-fraction mineral SOM (HSOM) are expressed as ratios of changes (Δ) in mass among pools per model time step (1 month).

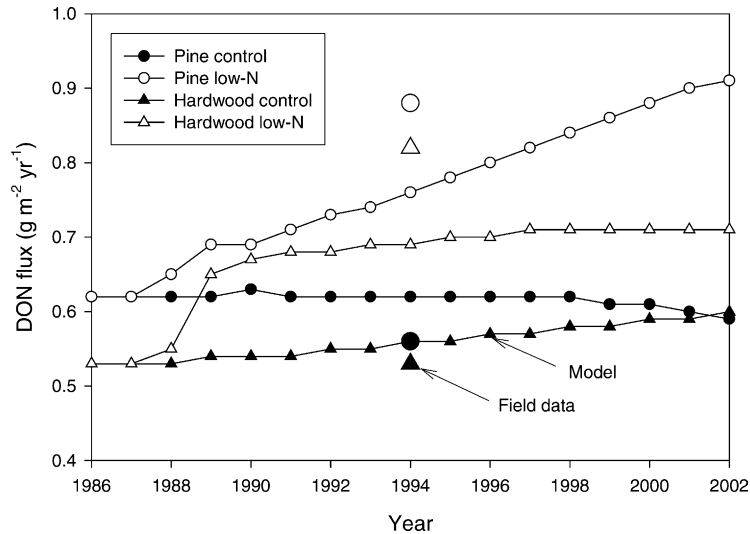


Fig. 4. Model and field-data comparisons of leaching fluxes of DON (dissolved organic N) from the O horizon. Symbols connected with lines indicate TRACE model results in the final version developed here; larger symbols without lines indicate field data (Currie et al., 1996).

simulated patterns in PR ¹⁵N in control plots provide improved agreement with field observations. In the pine stand the vegetation PR ¹⁵N values in the early 1990s continued to be over-predicted.

Increased movement of N from the O horizons to mineral soils, together with increases in N uptake from mineral soil pools, produced improved patterns of PR ¹⁵N time series in several key respects. These changes produced modeled increases in the PR ¹⁵N in O horizon humus from 1992 to 1999 that more closely matched field observations (Figs. 1 and 2). The model changes also produced temporal patterns in ¹⁵N recoveries in mineral soils that appeared more realistic: a substantial rise in PR ¹⁵N in the pine control plot, but a small rise or even a decline in other cases (Figs. 1 and 2). Most significantly, this suite of model changes produced PR ¹⁵N in foliage of both stands that much more closely resembled the 8-year time series in field data: the 1999 recoveries in foliage were high without the early 1990s recoveries being dramatically over-predicted. Increased movement of N to mineral soil into a pool that comprised only a fraction of the mineral soil organic N and that turned over much more rapidly than did bulk soil N reproduced the observed sustained recovery of ¹⁵N in foliage at the decadal time scale.

In making these model changes, we maintained model realism in pools and fluxes of C and N. An

example and a form of validation is provided by the modeled fluxes of DON leaching from the O horizon (Fig. 4). Although TRACE DOC fluxes were calibrated, DON fluxes were not. The latter result from the modeled net N dynamics in litter C classes. The leaching of dissolved organics is a central fine-scale process in TRACE and sensitive in its links to several other important fine-scale processes, including litter production, litter decay, O horizon mass, and the replenishment of mineral soil organic matter.

3.3. Modeled effects of N amendments on N cycling and C balances

For several reasons, we limited our analysis of elevated N inputs on NPP and forest C balance to the hardwood forest. Through the inverse modeling analysis we were able to simulate the time series in PR ¹⁵N in vegetation and soil pools better for the hardwood stand. The TRACE model also captured the change in wood production with N amendment realistically in the hardwood stand (Table 1) but not the pine stand (Table 1). In the field study, the pine stand went into decline, falling off of the foliar N-photosynthesis relationship in a way that is not captured in PnET-CN. Furthermore, the hardwood stand is more regionally representative both in the

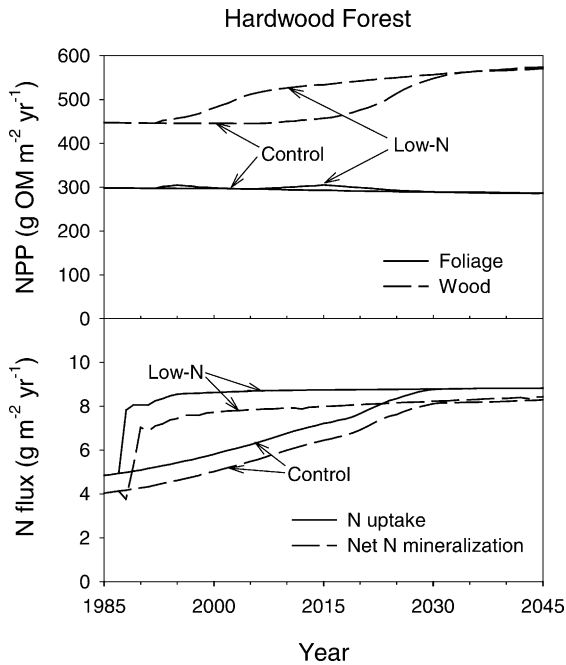


Fig. 5. Modeled foliar and wood NPP (net primary productivity), net N mineralization, and vegetation N uptake from soil pools over the period 1985–2045 in the hardwood stand. 'Control' and 'low-N' treatments are as in Table 1; model simulations assume treatments continue. OM, organic matter mass (ash-free, oven-dry weight).

vegetation present and in its land use and disturbance history (Foster, 1992, 1993; Foster et al., 1992).

In model results, net N mineralization and N uptake by vegetation increased rapidly following the start of N amendments, while NPP (net primary productivity) experienced a lag time of 5–10 year and rose more slowly (Fig. 5). Modeled N uptake rose about 3 g N m^{-2} per year over the control almost immediately. Modeled foliar NPP was little changed by the increased N uptake, while modeled NPP of woody tissues rose by 76 g OM m^{-2} per year (where OM is organic matter mass) after 20 years of elevated N inputs.

Model results suggested that the control plots should ultimately experience similar increases in N uptake and NPP to those in the low-N plots, albeit over a longer time frame. Modeled N mineralization underwent a slow, sustained rise over a period of 40 year, followed by an increase in wood NPP after a lag time of about 30 year (Fig. 5). Nitrogen mineralization, N uptake, and woody NPP ultimately converged to the

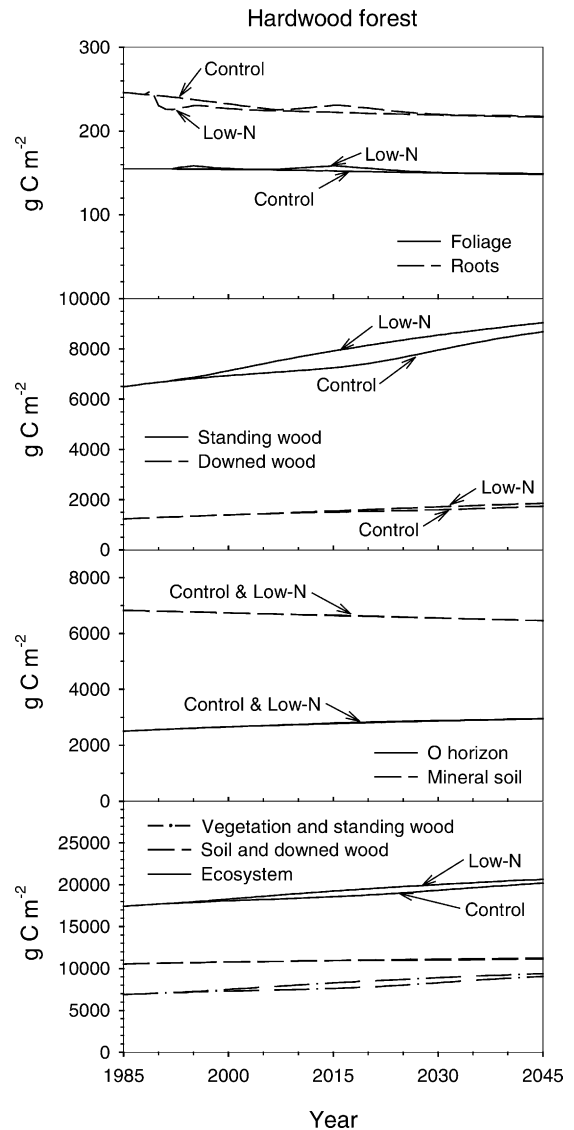


Fig. 6. Modeled pool sizes of organic carbon in vegetation and soil over the period 1985–2045 in the hardwood stand. 'Control' and 'low-N' treatments are as in Table 1; model simulations assume treatments continue. 'Standing wood' refers to living wood plus dead, standing woody debris. 'Downed wood' refers to fine and coarse woody debris in the O horizon and buried in the surface mineral soil horizon. 'Ecosystem' (lower panel) refers to the sum total of organic C pools in vegetation, woody debris, and soil (to 1 m depth).

same levels in control and low-N plots in the model. This modeled rise in control-plot N availability occurred through an accumulation of N capital in the soil O horizon due to the retention of ambient

N inputs. Given a constant decay rate of O horizon humus in the model, as O horizon N capital rose so did N mineralization and uptake, foliar and root tissue N concentrations, and litter N concentrations in a slow but accumulating positive feedback. Model results indicated that this positive feedback would ultimately cease to raise N availability as other factors worked to limit tissue (and thus litter) N concentrations.

Modeled dynamics in ecosystem C pools exhibit some changes over time and differences between control and low-N plots, attributable primarily to dynamics in living and dead wood. TRACE simulations forecast increasing storage of C in this ecosystem over time in both control and low-N treatments (Fig. 6). Increases in modeled C storage in the control plot derive primarily from increases in standing wood (living wood plus standing woody debris), followed by increases in downed woody debris and in the soil O horizon. Decreases in soil organic C in mineral soil essentially offset those in the O horizon, however. Most ecosystem pools exhibited negligible differences in modeled C storage between control and low-N plots. The exceptions were standing and downed wood. Standing wood (living plus standing dead) exhibited a modeled elevation in C storage of up to 725 g C m^{-2} in the low-N plot over control. The greatest N treatment-induced elevation in standing wood occurred in year 2020 (Fig. 6), a few years after the peak elevation in wood NPP over control (Fig. 5). In the model results after 2020, NPP converged between control and low-N plots but a difference in the pool sizes of C in standing wood persisted. This difference narrowed over time as living trees died in the model; after ca. year 2020, the low-N plot began to exhibit significantly increased (over control) C storage in downed woody debris.

4. Discussion

4.1. Mineral soil organic N as a decadal-scale source of N for vegetation

One of the most unexpected results in the comparisons of field data against model predictions was in the sustained recovery of ^{15}N in foliage over the 8-year period rather than the declines in foliar ^{15}N predicted by the model. One of the primary results of our inverse

modeling analysis was that not only could this pattern of ^{15}N in foliage be better simulated, but the O horizon and mineral soil ^{15}N patterns better simulated as well, by positing a light-fraction component of mineral soil organic matter that provided a source of ^{15}N for the trees over the decadal time scale.

In our inverse modeling analysis, numerous other changes to our conceptual model could have been tested but were eschewed because they would not have led to better model-data agreement in patterns of ^{15}N redistributions. For example, we might have tested a view in which plants access soil organic N directly (Chapin et al., 1993; Wallander et al., 1997; Näsholm et al., 1998). However, an additional means of plant N uptake was not needed; in control plots, modeled plant uptake of ^{15}N tracers was already over-predicted.

We tested the proposition that mineral soil organic matter provided the sustained plant uptake of ^{15}N (over the 5–8-year period) for a number of reasons. First, in our simulations, if trees took up too much N from the O horizon as the stand aggraded, it was impossible to realistically model the field-observed accumulation of N in both vegetation and the soil O horizon (Table 1) over the time scale of stand development. In other words, nitrogen had to enter the combined vegetation–O horizon subsystem either through exogenous inputs or from the mineral soil. Second, the pattern of mismatches between modeled and field-measured ^{15}N recoveries in mineral soil suggested that ^{15}N tracers were moving from mineral soil to vegetation over this time scale. Third, the ‘mining’ of mineral soil N to supply nitrogen for long-term accumulation in both vegetation and the O horizon, through stand aggradation, is a process that appears consistent with findings in other recent research. Richter et al. (2000) found that in an aggrading pine forest over a 40-year period, N pool sizes increased in vegetation and the soil O horizon, while decreasing in mineral soil. Finzi and Schlesinger (2003), in finding a greater accumulation of N in the soil O horizon in CO_2 -fertilized plots relative to controls, concluded that the additional N probably came from the mineral soil. Similar results have been reported by Ross et al. (2002) for a *Pinus radiata* forest in New Zealand and by Ritter et al. (2003) for two pasture-to-forest chronosequences in Denmark; in all three cases, N was evidently transferred over

decadal time scales to vegetation and O horizons from mineral soil.

Ours seemed to be a reasonable interpretation and to involve some of the most easily justified new assumptions. Soil organic matter is often considered in terms of light-fraction versus heavy-fraction material (Paul and Clark, 1996; Gaudinski et al., 2000), with the light-fraction material exhibiting more rapid N turnover (Compton and Boone, 2002). Additionally, as we showed, the altered conceptual model (Table 2) substantially improved the temporal patterns in ^{15}N tracer recovery in foliage, O horizon humus, and mineral soil organic matter in both forests.

The mining of N from mineral soils is related to the need we found to include extra, exogenous inputs of N from an unknown mechanism. If the mining of mineral soil N were even greater than we assumed through the 20th century in these stands, we would not have needed to posit additional, unknown inputs of N to the vegetation–O horizon subsystem. It is possible that the hardwood forest had a greater N capital in the O horizon in 1900 than we estimated, but in the pine stand our need to include additional N inputs poses a greater difficulty. Our simulations could not produce the low O horizon C:N ratios observed in the field under ambient (control) conditions (Table 1). We have no information on whether this area may have been heavily manured during the agricultural period prior to 1926; we did assume it began with a narrower initial C:N ratio in the SOM here than in the hardwood stand. An intriguing possibility was recently raised by Seagle (2003) who showed that in a landscape containing a mixture of agricultural and forest land cover, deer populations foraging outside of the forest patches could, through their waste, transfer substantial fluxes of N into forest patches. The mixed landscape that was present in central Massachusetts through much of the 20th century raises the possibility of whether such a process could have supplied additional N to these forests.

4.2. Rapid movement of ^{15}N tracers to mineral soil pools

If a portion of mineral soil organic N turns over more rapidly than the bulk mineral soil N, the N in this soil fraction needs to be replenished. If such a portion of mineral soil N was the source of the continuing ^{15}N

uptake by vegetation, then this pool needed to receive the ^{15}N tracers through a rapid movement downward in the first few years following ^{15}N applications. The eluviation of ^{15}N tracers out of the O horizon must have occurred prior to the 5–8-year period in this study. TRACE already contains bioturbation of O horizon and mineral soil organic matter, and it is difficult to believe that bioturbation could be underestimated here because there is an abrupt transition from O horizon to mineral soil in both stands. One possibility is that DO ^{15}N leached from the O horizon early in the study and was mineralized in the mineral horizon. TRACE already included DON leaching at a rate matching fluxes measured with zero-tension lysimeters at this site and with ^{14}N : ^{15}N ratios mechanistically modeled. We increased the downward transport of ^{15}N tracers in the model through a combination of inorganic N leaching, diffusion of isotopes, and by adding a new flux of PON (particulate organic N) transport. The resulting rates of inorganic N leaching are much higher than those measured using zero-tension lysimeters (Table 1). This raises the question of whether zero-tension lysimeters beneath the Oa horizon quantitatively capture the eluviation of N out of forest O horizons. Because the method of multiplying nutrient concentrations in lysimeter samples by hydrologic flow (Currie et al., 1996) estimates vertical transport of nutrients by mass flow, it may underestimate nutrient transport where significant rates of diffusion occur (as in fertilized soils), where plant uptake is significant, and where soils experience unsaturated periods (Smethurst, 2000).

Relatively rapid entry of inorganic forms of ^{15}N into the mineral SOM was also an important process in the model. In previously applying TRACE in these forest stands, we were able to account for the initial 1–2-year partitioning of ^{15}N between plants and soils by constructing rapid and strong sinks for ^{15}N in humified matter in both the O horizon and mineral soil (Currie et al., 1999). These rapid ^{15}N sinks required gross movements of NH_4 and NO_3 into soil-organic pools to be decoupled from the supply of labile C to soil microorganisms; these nontraditional soil N sinks continue to be included and important in the present formulation of TRACE. The model previously assumed that the pools of humified matter exhibiting such rapid N sinks were homogeneous, well-mixed pools with one rate of turnover in each soil horizon.

The assumption of homogeneity now appears incorrect, and has been altered for the mineral soil by dividing the pool of SOM into two fractions with widely diverging rates of N turnover (Table 3). The combined set of model changes made for the present analysis both (i) moved ^{15}N tracers down into mineral horizons more rapidly during the years of ^{15}N application and (ii) released the ^{15}N tracers more rapidly, from the new light-fraction pool, for plant uptake. This result highlights the importance of mineral soil for supplying N to an aggrading vegetation–O horizon subsystem and the importance of rapid vertical transport of labeled fertilizer N to allow initial retention of ^{15}N tracers in mineral soil.

4.3. Elevated ecosystem C storage

TRACE simulations allowed us to go beyond a simple stoichiometric approach to the question of the effects of elevated N inputs on changes in ecosystem C storage. Beyond calculating what proportion of the elevated N inputs entered foliage and what the change in foliar N concentration was, the PnET-CN component of TRACE allowed us to simulate the controls and constraints that physiology, phenology, and water balance would have on changes in NPP. These constraints resulted in an increase in C storage that is quite small from a stoichiometric perspective. Our forecasted increase in ecosystem C storage peaked at 725 g C m^{-2} about 30 years after the start of N amendment treatments. This amounted to a differential C storage, relative to the control, of 4.0% of ecosystem C capital over a 30-year period. In the model simulations, the low-N treatment of $+5 \text{ g N m}^{-2}$ per year continued, amounting to a cumulative differential N input of $+150 \text{ g N m}^{-2}$ over the 30-year period until the peak in differential C storage between treatments. This was a cumulative ratio of $\Delta\text{C}:\Delta\text{N}$ amounting to $725 \text{ g C}/150 \text{ g N}$, or a stoichiometric mass ratio, at the peak of differential C storage, equaling 4.8:1.

One of the most intriguing results of this analysis is the 30-year lag time that TRACE predicts will occur before the maximum differential C storage is obtained from the experimentally elevated inputs of N. Following the start of the +N treatment, net N mineralization rose rapidly in the model (Fig. 5), in agreement with field results (Magill et al., 1997, 2004). The ecosys-

tem-level time delay in differential C storage arises in the model from a number of sequential delays that occur in individual processes following the rise in N availability. The main process responsible for the differential C storage in TRACE is a difference in wood production, in agreement with previous analyses (e.g. Townsend et al., 1996). A key point to understand in the present result is that wood production does not exhibit a 30-year delay; the rise in wood production in the low-N plot relative to control begins to occur at the 5–10-year time scale. It is the ecosystem-level accumulation of differential C storage, driven by differential wood production, that peaks after 30 years. The 5–10-year delay in the rise of wood production is consistent with the plant physiology submodel in TRACE and also appears consistent with field data for this stand. In the modeled physiology (deriving from PnET-CN), the plant-internal source–sink model for C includes a large buffer of stored C derived from photosynthate. Once foliar N increases after a short delay following the start of N amendments, and photosynthesis begins to increase in the model, the large pool of plant-internal C storage in the model serves to dampen the rise in C allocation to wood, introducing the time delay. The small initial effect of N amendments on any change in wood production is in agreement with field data (Table 1). Evidence that wood production may rise after a lag period is provided by the substantial rise in wood production that has been observed in this hardwood stand in the high-N plots, which receive 15 g N m^{-2} per year (Magill et al., 2004).

The reason that TRACE simulations showed the differential C storage narrowing after 30 years was because, in our simulations, N capital continued to accumulate in the control plot in the model, eventually causing N mineralization to rise as high there as in the low-N plot. TRACE simulations suggested this forest O horizon is nearing its long-term steady-state in mass and the continuing accumulation of N in the control plot is likely to make it a more N-rich stand over time. If the control-plot ecosystem continues to accumulate N in soils and the C:N ratio in the O horizon lowers over time, the idea that this would lead to increased net N mineralization in the control plot is consistent with some current views on the relationship between soil C:N stoichiometry (particularly the O horizon) and net N mineralization

in some forest types (Gundersen et al., 1998; Dise et al., 1998; Lovett and Rueth, 1999).

Other investigators have suggested that in forests, vegetation pools are more likely to provide increased C sinks than are soil pools (Schlesinger, 1995). Our simulations suggested that C storage in wood would provide the main change in ecosystem C storage. Our modeling analysis showed that the change in N availability necessary for increased wood production may be regulated by the turnover of light-fraction mineral soil organic N. Over decadal time scales and longer, the release of N from mineral soil for aggradation of N in vegetation and the O horizon pools appears to be a key process. This raises the question of how, over longer time scales, mineral soil N is replenished and the interaction this might have with land history.

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