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Dynamic Redistribution of Isotopically Labeled Cohorts of Nitrogen Inputs in Two Temperate Forests

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ABSTRACT

We compared simulated time series of nitrogen-15 (^{15}N) redistribution following a large-scale labeling experiment against field recoveries of $^{15}NH_4^+$ and $^{15}NO_3^-$ in vegetation tissues. We sought to gain insight into the altered modes of N cycling under long-term, experimentally elevated N inputs. The study took place in two contrasting forests: a red pine stand and a mixed deciduous stand (predominantly oak) at the Harvard Forest, Massachusetts, USA. We used TRACE, a dynamic simulation model of ecosystem biogeochemistry that includes $^{15}N/^{14}N$ ratios in N pools and fluxes. We simulated input–output and internal fluxes of N, tracing the labeled cohorts of N inputs through ecosystem pools for one decade. TRACE simulated the peaks and timing of ^{15}N recovery in foliage well, providing a key link between modeling and field studies. Recovery of tracers in fine roots was captured less well. The model was structured to provide rapid, initial sinks for $^{15}NO_3^-$ and $^{15}NH_4^+$ in both forests, as indicated by field data. In simulations, N in litter turned over rapidly, even as humus provided a long-term sink for rapidly cycling N. This sink was greater in the oak forest. Plant uptake fluxes of N in these fertilized plots were on the same order of magnitude as net assimilation fluxes in forest-floor humus. A striking result was the small rate of incorporation of N in humus resulting from the transfer of litter material to humus, compared with large fluxes of N into humus and its associated microorganisms through direct transfers from pools of inorganic N in soils.

Key words: tracer; simulation model; biogeochemistry; decomposition; humification; immobilization; nutrient cycling; nitrogen saturation; turnover; forest floor; synthesis.

INTRODUCTION

Implicit in the *system* concept is the view that components interact dynamically with some degree of linkage and connectedness, shaping and determining phenomena that are observable at the whole-system level of organization. The validity of a whole-system level of organization was a key concept in the historical development of ecosystem science (Tansley 1935) and continues to be key in theoretical work (O'Neill and others 1987). Nitrogen (N) cycling in forests is an example of a systemic phenomenon (Flanagan and Van Cleve 1983). The onset of N saturation in a forest, or N availability increased beyond the capacity of the ecosystem to store or cycle N internally (Aber and others 1989; Gundersen 1991), is an example of a significantly

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altered systemic phenomenon. In the past, temperate forests were largely N limited (Vitousek and Howarth 1991), but recent decades have seen major increases in global cycling and near continental-scale N deposition (Galloway 1995). Alterations in biogeochemistry that can arise after a period of chronic N inputs to forests include increased nitrification and soil acidification, increased production of N_2O (a greenhouse gas), leaching losses of nutrient cations from soil, and increased concentrations of NO_3^- in surface waters.

Ågren and Bosatta (1988) emphasized that mechanisms of N saturation should be primarily "not associated with the statics of the system but with the dynamics of the system." In a synthesis of results from five manipulated forest ecosystems across Europe that composed the NITREX (*nit*rogen *ex*periment) project, Gundersen and colleagues (1998) concurred. They concluded that although mineral soil may have a large capacity to retain N, changes in the vegetation and forest floor were sufficient to change the functioning of the N cycle and result in NO_3^- leaching. Thus, the ability to predict N saturation will require a quantitative understanding of the rates of internal cycling within vegetation, within forest-floor detritus, and within the plant–soil cycle.

The application and recovery of nitrogen-15 (^{15}N)-enriched tracers in forests has proven to be a powerful tool for gaining insight into N fluxes and transformations in soils (Davidson and others 1990; Tietema and Wessel 1992) and vegetation (Preston and others 1990). The ratio of $^{15}N/^{14}N$, when observed in combination with N-pool sizes and fluxes, provides an additional dimension of observational data that facilitates closer investigation of controlling mechanisms (Hart and others 1994b; Stark and Hart 1997). In a few manipulations of N inputs to forests, ^{15}N has been added as a tracer to study altered fates and redistributions of NH_4^+ and NO_3^- at the ecosystem level (Nadelhoffer and Fry 1994; Nadelhoffer and others 1995; Tietema and others 1998; Nadelhoffer and others 1999). The essential need for appropriate mathematical models for the interpretation of observed isotope ratios in terms of N movements and transformations (Schimel 1993) presents a challenge in ecosystem-level experiments. Algebraic or differential equations can be used when conceptual models are relatively simple (Kirkham and Bartholomew 1954; Nadelhoffer and Fry 1994), but are intractable when conceptual models are more complex, for example, when tracers are able to recycle.

Here we compare simulated patterns of ^{15}N redistribution against those observed in field data following a large-scale labeling experiment [described by Nadelhoffer and colleagues (1999)]. We use TRACE (Tracer Redistributions Among Compartments in Ecosystems), a dynamic simulation model of ecosystem biogeochemistry that includes $^{15}N/^{14}N$ ratios. Our primary objective was to use the model to gain further insight into the altered ecosystem-level modes of N cycling under chronically elevated N inputs in forest plots at the Harvard Forest (MA, USA).

The Chronic Nitrogen Addition Study at the Harvard Forest

The Harvard Forest is a site in the US Long-Term Ecological Research network. In the Chronic N Study, N additions have been made continuously since 1988 in an effort to observe the effects of elevated N inputs en route to N saturation. The study takes place in two contrasting, temperate forests: an even-aged red pine stand planted in 1926, and a 45-year-old mixed deciduous stand of predominantly oak that naturally regenerated after cutting (Table 1). Four permanent plots (30×30 m each) are studied in each forest: ambient (no N addition), low N (receiving 5 g N m^{-2} $year^{-1}$ as NH_4NO_3), high N (15 g N m^{-2} $year^{-1}$), and N + S (5 g N m^{-2} $year^{-1}$ + 7.4 g SO_4-S m^{-2} $year^{-1}$) (Aber and others 1993). Amendments are sprayed onto the forest floor in six equal applications per year, approximately once monthly, in May through October.

Isotopic characterizations of plant and soil pools were made beginning in 1990. Isotopic labeling took place in 1991 and 1992, in six equal applications per year at the time of NH_4NO_3 additions; fertilizer N was enriched with ^{15}N in the low-N treatments (but not in the high-N or N + S treatments). Labels were applied as $^{15}NH_4^+$ on half of each plot and $^{15}NO_3^-$ on the other half. The ^{15}N labels on the treated plots increased the atom% ^{15}N of NH_4^+ amendments from 0.3663 to 0.7173 and those of NO_3^- amendments from 0.3663 to 0.6433 ($\delta^{15}N$ from 0 to 965‰ and 0 to 761‰, respectively). On the same schedule, ambient plots also received ^{15}N labels, which were highly enriched in order to keep N inputs minimal. These tracers increased atom% ^{15}N levels from 0.3663 to 99.1 and 98.6 atom% ^{15}N for NH_4^+ and NO_3^- amendments, respectively (Nadelhoffer and others 1999). Note that, in the analyses that follow, the differences in strengths of labels are accounted for in both the model and field results when we compare ^{15}N levels in terms of the percent recovery of ^{15}N-tracer masses added.

In the 10 years since fertilization began, numerous process studies have been conducted on these plots to observe changes in foliar and fine-root

Table 1. Characteristics of the Two Forests Studied

	Oak Forest	Pine Forest
Vegetation (% biomass)[a]	*Quercus velutina* Lam. and *Q. borealis* Michx. f. (78%)	*Pinus resinosa* Ait. (98%)
Tree biomass (sum of all species)[a]	11,100 g m^{-2}	14,700 g m^{-2}
Age[b]	45 years	65 years
Soil type	Coarse–loamy (oak forest) or coarse–loamy over sandy–skeletal (pine forest), mixed, frigid Typic Dystrochrepts	
O horizon (forest floor) organic-matter mass[a]	9500 g m^{-2}	8400 g m^{-2}
O horizon thickness[c]	8.5 ± 2.0 cm	8.7 ± 2.0 cm
O horizon C/N mass ratio[a]	24:1	24:1
pH in A horizon (0.01 M $CaCl_2$)	3.99	3.80
Plant N uptake[d]	14 g N m^{-2} $year^{-1}$	14 g N m^{-2} $year^{-1}$
Net N mineralization[d]	7.9 g N m^{-2} $year^{-1}$	10 g N m^{-2} $year^{-1}$
Foliar production (NPP)[d]	290 g m^{-2} $year^{-1}$	370 g m^{-2} $year^{-1}$

[a]*Initial characteristics in 1988 (Aber and others 1993).*
[b]*Age in 1991, when nitrogen-15 tracers were added (Magill and others 1997).*
[c]*Averaged among all nitrogen-addition treatments and controls in August 1992 (Currie and others 1996).*
[d]*Annual averages over the period 1988–93 or 1989–93 (Magill and others 1997) for low-nitrogen fertilized plots (5 g N m^{-2} $year^{-1}$) considered in the present study.*

nutrient concentrations, plant production and litterfall, litter N dynamics, net N mineralization and net nitrification, soil solution inorganic and organic chemistry, soil gas fluxes, and more. Over the course of the study, net N mineralization increased more rapidly in the pine forest than in the oak, concomitant with much greater increases in net nitrification and in NO_3^- concentrations in soil solution in the pine forest. By 1990, the high-N treatment in the pine forest had shown "breakthrough" of NO_3^- into mineral soil solution, whereas the low-N treatment had not and all of the oak treatments had not (Aber and others 1993). By 1993 in the low-N pine plot, NO_3^- concentrations in mineral soil solution had just begun to rise (Magill and others 1997). In 1994 in the low-N pine plot, the flux of NO_3^- leaching from below the rooting zone was 500-fold greater than in the ambient plot, while the fluxes of NO_3^-, NH_4^+, and DON (dissolved organic N) leaching from the O horizon were all elevated over ambient (Currie and others 1996). These details illustrate that the timing of the ^{15}N enrichments in 1991 and 1992 took place just prior to the apparent onset of N saturation in the pine forest low-N treatment.

Average precipitation at the Harvard Forest is approximately 110 cm $year^{-1}$, distributed fairly evenly throughout the year; monthly mean temperatures are −7°C in January and 19°C in July (Van Cleve and Martin 1991). Plot elevations in the Chronic N Study are approximately 400 m; soils in both forests are well drained and contain well-defined O horizons (mor type). Atmospheric N deposition has been estimated from a regional survey as 0.78 g N m^{-2} $year^{-1}$ (wet + dry) (Ollinger and others 1993) and measured at the site in 1993 (wet only) as 0.35 g NH_4^+-N m^{-2} $year^{-1}$, plus 0.51 g NO_3^--N m^{-2} $year^{-1}$ (Currie and others 1996).

METHODS

TRACE Model Summary

A full description of TRACE has been provided by Currie and colleagues (1999); here we present a summary, including a brief history of previous applications and testing of the model, followed by a description of changes made for the present analysis. TRACE simulates major pools and fluxes of organic N, NO_3^-, and NH_4^+, together with the ratio of $^{15}N/^{14}N$ in each pool and flux. Plant and soil pools of C and N in TRACE are physically meaningful, in most cases designed to allow straightforward comparison with field or laboratory sampling methods. TRACE operates on a monthly time step, linking the vegetation processes of the PnET-CN model (Pn = net photosynthesis, ET = evapotranspiration; Aber and others 1997) with more-detailed soil submodels for the forest floor and mineral soil (Figure 1) (Currie and others 1999). TRACE uses PnET-CN to model plant physiological processes, biomass production, and hydrology, producing dynamics of C and N in vegetation tissues and litter together with evapotranspiration and soil water fluxes on a monthly time step.

Land-use history and N-deposition history affect present pools and cycling of C and N in TRACE as in the PnET-CN model. Our model runs began in the year 1700, with deposition of NO_3^--N and NH_4^+-N

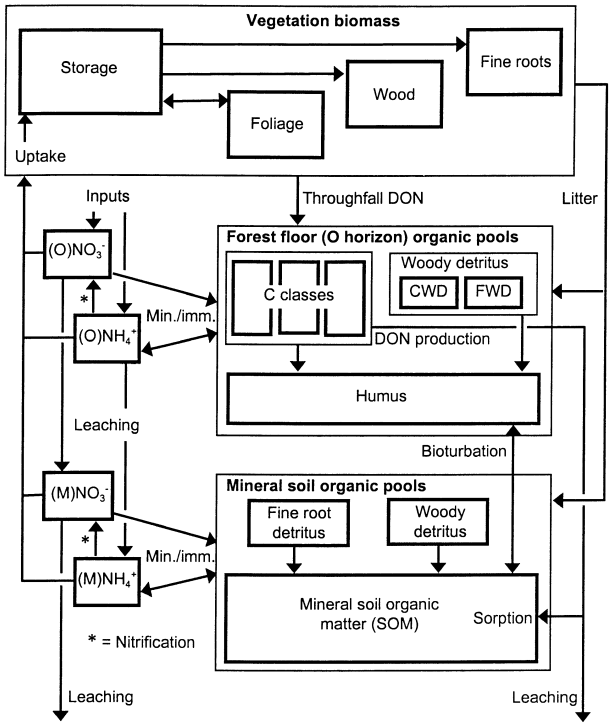

Figure 1. Schematic of the hierarchical structure of pools and fluxes of nitrogen in TRACE 2.2. Plant uptake of N, detrital N dynamics, and N transformations are calculated separately in each soil layer. Pools of available N are separated by soil layer: O, O horizon; M, mineral soil; DON, dissolved organic nitrogen; CWD and 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. Modified from Currie and others (1999).

at 25% of present levels, increasing linearly to present levels beginning in 1930. We used long-term average monthly temperature and precipitation data (Harvard Forest Weather Station). In our simulations, both forests were lightly harvested from 1750 to 1850 (2.5% of biomass cut per year, with 10% of that left on site as slash) and heavily harvested once in the 20th century (60% of biomass cut, and 20% of that left as slash), the red pine forest in 1926, and the oak forest in 1938.

Pools of soil-organic C and N in TRACE are microbial–detrital pools containing microbial biomass implicitly. The forest-floor module derives from DOCMOD, a model of litter decomposition, humification, and production of dissolved organic C and N in the forest floor (Currie and Aber 1997). Fine litter enters detrital pools representing *C classes* (acid-insoluble material, acid-soluble, and extractives) (Ryan and others 1990). Each C class loses mass to leaching and to CO_2 mineralization, while undergoing N immobilization or mineralization at rates based on field studies conducted in Wisconsin and at Harvard Forest (Aber and others 1984, 1990). TRACE also includes mass and N dynamics, including humification, of fine and coarse woody debris. The model includes direct, gross transfers of NH_4^+ and NO_3^- between plant-available pools in soil and microbial-detrital pools, together with leaching fluxes of NO_3^-, NH_4^+, and DON between soil horizons.

Previous Model Development and Testing

For interpreting ^{15}N redistributions, it is important that N-pool sizes and fluxes are modeled well for the site. PnET-CN was previously tested against field data for N cycling at the Harvard Forest (Aber and others 1997); it has been tested against C and water balance data from the Harvard Forest and Hubbard Brook (New Hampshire, USA). A related model, PnET-Day (Aber and others 1996), has also been tested against daily gross carbon-flux measurements at the Harvard Forest. DOCMOD was previously tested in blind predictions of foliar-litter decay at four sites with widely varying climates and soils: the Harvard Forest; Luquillo Experimental Forest, Puerto Rico; Arctic Tundra, Alaska; and Jornada Field Station, Arizona (Moorhead and others forthcoming). Although the vegetation and soil submodels in TRACE had thus been fully tested, we also tested the completed TRACE model against Harvard Forest data for aspects of production and C and N cycling (Currie and others 1999). We calibrated a small number of model parameters to reproduce reasonably the C and N cycles (independent of ^{15}N observations) in the two forest types (humus decay rate and leaching fluxes of DOC, DON, NO_3^-, and NH_4^+). We then incorporated $^{15}N/^{14}N$ ratios in TRACE with the principles of pool dilution and mass balance.

Our first use of TRACE (Currie and others 1999) was to compare model predictions against field data for the recovery of ^{15}N at a single point in time in 1992, at the end of the 2-year period of ^{15}N additions. Currie and colleagues (1999) made a limited number of iterative model changes and comparisons with the ^{15}N field data at this single point in time. They examined the implications, for plant versus soil partitioning of ^{15}N tracers, of alternative hypotheses concerning N turnover and strengths of microbial-detrital sinks. The model structure that produced best agreement with ^{15}N field data included direct assimilation of NO_3^--N from plant-available to soil-detrital pools in both the oak and pine forests, and no plant preference for NO_3^- or NH_4^+, but a microbial preference for NH_4^+ over NO_3^-. In addition, high gross rates of exchange between plant-available and soil-detrital pools were

required in order to produce general agreement in patterns of plant versus soil recovery of $^{15}NO_3^-$ and $^{15}NH_4^+$ at the single point in time, the end of the 2-year period of tracer additions (Currie and others 1999).

Model Changes Made for the Present Analysis

Here we use TRACE to simulate temporal patterns in ^{15}N redistributions over a 4-year period, comparing results against time series of field recoveries of ^{15}N in vegetation tissues. We then extend the analysis by running the model beyond the period of observations, simulating and tracing the 2-year labeled cohorts of N inputs as they are expected to redistribute among ecosystem pools over 1 decade. We limit our analysis here to the low-N treatments. The summed percent recoveries of ^{15}N in the field study were closer to 100% in the low-N treatments versus ambient. Moreover, TRACE predicted recoveries of ^{15}N with greater accuracy in the low-N treatments versus ambient (Currie and others 1999).

Four changes were made in the present application of TRACE to interpret ^{15}N time-series data. First, for the pine forest, foliage was separated into two age-class cohorts to allow greater resolution in comparisons with field data. *Cohort 1* contains foliage produced in the current year; *cohort 2* contains that produced in all previous years and still retained on trees. Litterfall takes place from cohort 2. Needles are retained an average of 2.25–2.5 years at this site (K. Nadelhoffer personal observation). Second, we allowed woody detritus in the forest floor to sustain gross transfers of N with soil inorganic pools, clearly indicated in field data from a ^{15}N enrichment study at Bear Brooks, Maine (Nadelhoffer and others 1995). Third, N storage in buds in each vegetation type was combined with the plant–internal storage pool *VascN*. This allowed N taken up in spring to mix with N already stored in plants and thus to be allocated to foliage in the year it was taken up. Finally, to compare model predictions against field data, it was necessary to predict how the *VascN* pool, which is one conceptual pool in the model, might be distributed among tissue samples taken in the field. The ^{15}N that TRACE predicted to be present in the storage pool *VascN*, we partitioned between fine roots (33%) and wood/bark/buds (67%). Although bark and wood are considered to be the primary sites of N storage, Marmann and others (1997) observed remobilization of ^{15}N from roots to produce foliage in spring in *Fraxinus excelsior*; similarly, H. Majdi (personal communication) observed a midsummer dip in fine-root N concentration in *Picea abies*.

Nitrogen Isotope Movements and Notation

TRACE reproduced the masses, atom%, and timing (May to September) of ^{15}N applications as $^{15}NO_3^-$ or $^{15}NH_4^+$ in ambient and fertilized plots in 1991 and 1992. For fertilized plots, the model also included the six, equal NH_4NO_3 additions per year beginning in 1988. Because N fertilizer and ^{15}N tracers were sprayed onto the forest floor in the field study, TRACE added deposition, fertilizer, and ^{15}N-tracer fluxes to pools of available NO_3^- and NH_4^+ in the forest floor.

As just described, the tracer applications at the Harvard Forest carried a strong ^{15}N signal compared with the atmospheric standard. In the years following tracer applications, isotopic ratios in plant and soil samples were also well elevated over natural-abundance levels. For example, at this site, the mean natural-abundance values of $\delta^{15}N$ in foliage ranged from $-1.8‰$ to $-2.9‰$, with standard errors of means $\pm$ 0.21‰ in each pool, whereas labeled samples we consider here ranged from $+11 \pm 0.5‰$ to $+50 \pm 5‰$ (Nadelhoffer and others 1999; Nadelhoffer unpublished data). Initial differences in natural abundances of ^{15}N were neglected in the present application of TRACE, as was fractionation of N isotopes during N transformations. All pools in the model were initialized with atom% ^{15}N equal to the atmospheric standard. We express distribution of ^{15}N above background in each ecosystem compartment at each point in time as the percent recovery of the total mass of tracer ^{15}N added above background:

$$PR^{15}N(C_i, t) = \frac{N_{Ci}(t)(\text{atom\%}\,^{15}N_{Ci}(t) - \text{atom\%}\,^{15}N_b)}{A(t - t_0)(\text{atom\%}\,^{15}N_a - \text{atom\%}\,^{15}N_b)} \quad (1)$$

where $N_{Ci}(t)$ 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 subscripts "a" and "b" refer to amendment and to background, respectively.

Field observations of N content and $^{15}N/^{14}N$ ratio were made annually in vegetation tissue samples, translated to an areal basis by using observations of biomass pool sizes made at the site, and were expressed as $PR^{15}N$ as in Eq. (1) by Nadelhoffer and others (1999).

Nitrogen-Flux Simulations

We used the concept of *percent recovery* to refer to annual fluxes (F_i) of N, where the mass of ^{15}N above background in an annual flux is related to the total amount of tracer added to time *t*, simply by replacing C_i with F_i in Eq. (1). We denote the resulting term $PR_f{}^{15}N$, with the units of (% year^{-1}). Note that $PR^{15}N$ in ecosystem pools sum to 100%, minus the tracer ^{15}N lost from the system, but to the extent that recycling occurs within an annual period, $PR_f{}^{15}N$-flux values may sum to more than 100% year^{-1}. The $PR_f{}^{15}N$-flux values are used simply as a metric for quantifying the relative importances among N flowpaths.

TRACE predictions of ^{15}N recovery can be viewed as simulating a labeled, 2-year cohort of NH_4^+ or NO_3^- inputs as it redistributes, over time, within each ecosystem. We thus used simulated dynamics in ^{15}N recovery in forest pools expressed as $PR^{15}N$, together with dynamics in N fluxes expressed on the basis of $PR_f{}^{15}N$, to conduct an analysis of N flows. Enriched tracer additions took place from May 1991 to September 1992; we consider the end of 1991 to be the midpoint when calculating the average age of the labeled 2-year cohort in each forest.

Uncertainty Analysis

To estimate uncertainty in model predictions, we performed a multivariate Monte Carlo analysis, in which 63 parameters in TRACE varied stochastically. This list included all parameters in the model that were not internally calculated, were not well-known constants or empirical coefficients, and were not initial conditions or climatic data. (Exceptions were the historical years of harvest, and litter chemistry, which did vary stochastically.) Other examples of parameters that did vary stochastically included the rates of light extinction in the canopies, the rates of litter humification, the decay rates of humus, and the ratios of gross to net N dynamics in detrital pools. Parameters in the set varied independently, in normal distributions with expectation equal to 100% and standard deviation equal to $\pm$10% of the nominal value. One set of model runs with nominal parameter values, plus 50 stochastic sets of model runs, were made in groups of eight cases each (pine vs oak forest, ambient vs N-fertilized, $^{15}NH_4^+$ vs $^{15}NO_3^-$) with equal parameters to enable direct comparisons. Results from the 408 model runs were analyzed in a data base (Stata). We calculated means and standard deviations within the set of 51 runs for each modeled pool and flux, for each year, in each case.

RESULTS

Recovery of Nitrogen-15 in Plant Tissues

For both $^{15}NO_3^-$ and $^{15}NH_4^+$ applications and in both forests, percent recovery of ^{15}N in current-year foliage in the field peaked in 1992 or 1993, followed by a decline in 1994. TRACE simulated the timing of these peaks well and simulated the values of $PR^{15}NO_3^-$ well in both forests (Figure 2). The much greater 1991 values of both $PR^{15}NO_3^-$ and $PR^{15}NH_4^+$ in pine foliage relative to oak arose in the model because tracer additions (simulated and actual) began in May, closer to the timing of foliar expansion in the pine forest. Foliar expansion occurred earlier in spring in the oak forest. These predicted differences in 1991 foliar ^{15}N recoveries were in agreement with field data, though somewhat overpredicted by the model.

Allocation and turnover of N in fine roots were captured less well (Figure 3). TRACE predicted peaks in fine-root $PR^{15}N$ in the first year of ^{15}N additions in all cases, in contrast to field data which showed greater percent recovery in the second year of ^{15}N additions in most cases. The approximate value of $PR^{15}NO_3^-$ was captured during the years of tracer addition in the oak forest, but overestimated by a factor of 2 in the pine forest.

Differences in recovery of $^{15}NH_4^+$ vs $^{15}NO_3^-$ in foliage and fine roots were apparent in the field data but not captured by the model (Figures 2 and 3). TRACE predicted slightly lower $PR^{15}NH_4^+$ relative to $PR^{15}NO_3^-$ in pine foliage and fine roots, but field observations showed much greater differences in these plant tissues in both forests.

Relative uncertainties in model results varied among results and among years (Figures 2 and 3). In random sample sets from our Monte Carlo analysis for 1991 and 2001, covering C cycling, N cycling, and N isotopes in pools and fluxes, the average standard deviation (SD) ranged from 17% to 28% of the mean for each result. Input parameters varied randomly with SD = 10%. The increased uncertainty in model results compared with input parameters indicates that interactions among model parameters tended to increase uncertainty. Our uncertainty analysis provides a caveat on the limits of precision that should be recognized in results of complex ecosystem models like TRACE.

Comparisons against field data for time series in soil pools are not possible because field observations

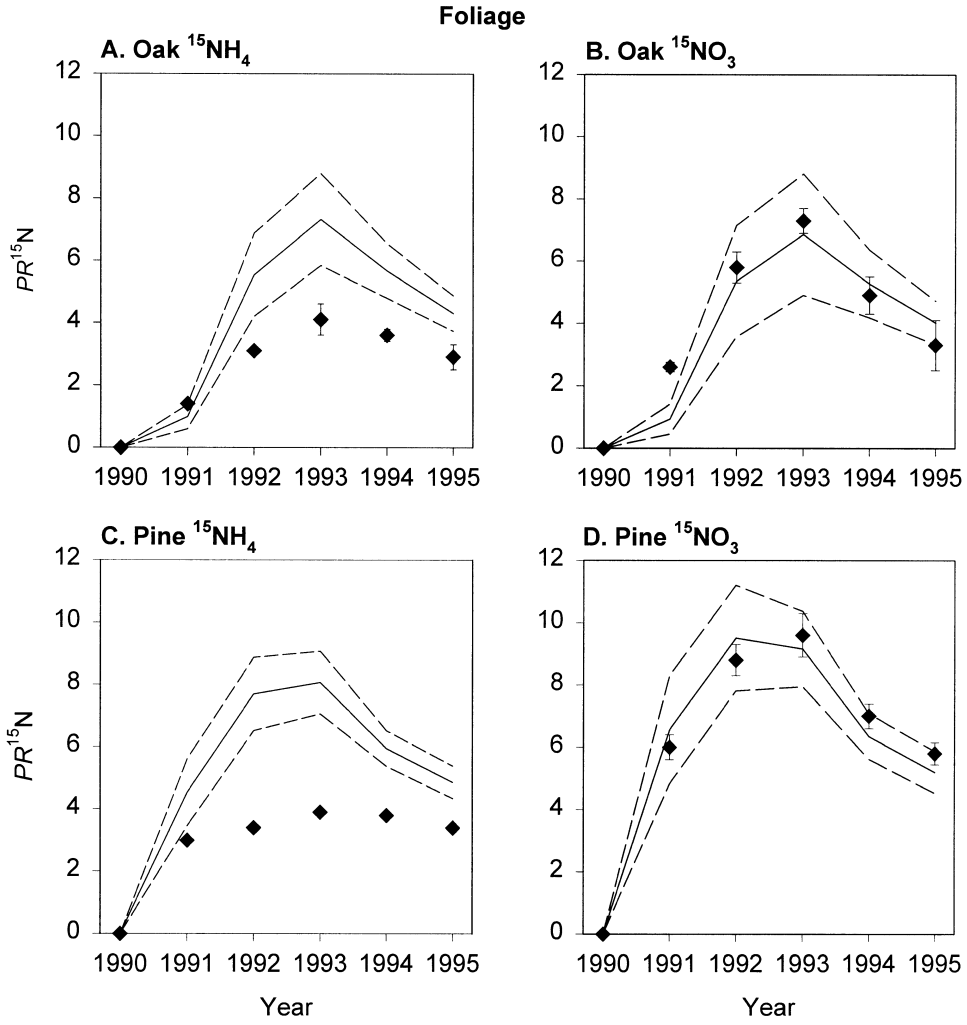

Figure 2. Predicted and field-measured percent recovery of ^{15}N tracers in foliage. Symbols and error bars represent field-measured means ± SE (Nadelhoffer and others forthcoming). Some SE values are too low to be visible. TRACE model results are shown as means (solid line) ± SD (dashed lines) of stochastic model runs (n = 51).

were made only at two points: prior to and immediately following tracer additions. In comparisons against soil pools in the single observation set in 1992 (Nadelhoffer and others 1999), TRACE exhibited overall agreement with plant vs soil partitioning of $^{15}NO_3^-$ and $^{15}NH_4^+$ in both forests (Currie and others 1999).

Nitrogen Flows in the Ecosystems

For N flows, we focus on redistributions of $^{15}NO_3^-$ because TRACE predicted recovery of $^{15}NO_3^-$ in plant tissues more closely than $^{15}NH_4^+$, and because NO_3^- is the primary form of N in deposition at this site. (Many of the results we present were also true for $^{15}NH_4^+$ simulations.) The following results refer to model simulations unless stated otherwise.

Forest-floor litter and humus provided rapid, initial sinks for $^{15}NO_3^-$ (Figure 4) and $^{15}NH_4^+$ (data not shown) in both forests. For humus, the initial sink was greater in the oak forest. Humus showed sustained increases in $PR^{15}N$, peaking about 4 years after ^{15}N additions. The ^{15}N for these increases came from the rapid loss of ^{15}N from Oi + Oe pools in the forest floor (fresh and partly decayed fine litter) after 1992. Pools of N in Oi + Oe litter were small and turned over rapidly, composing a rapid sink followed by rapid release of ^{15}N. Negative values for Oi + Oe assimilation fluxes beginning in 1993 indicate that forest-floor litter became a net source for N from the labeled N cohort immediately following the end of label additions (Figure 5). Pools of N in humus were large and turned over more slowly, comprising a more sustained sink for ^{15}N. Humified matter in the mineral soil (referred to in Figure 4 as SOM, soil organic matter) grew slowly in $PR^{15}N$ through DON illuviation, inputs of fine-root litter, and bioturbation (Figure 1).

Simulated fluxes of plant uptake of N in these fertilized plots were on the same order of magnitude as net assimilation fluxes in forest-floor humus

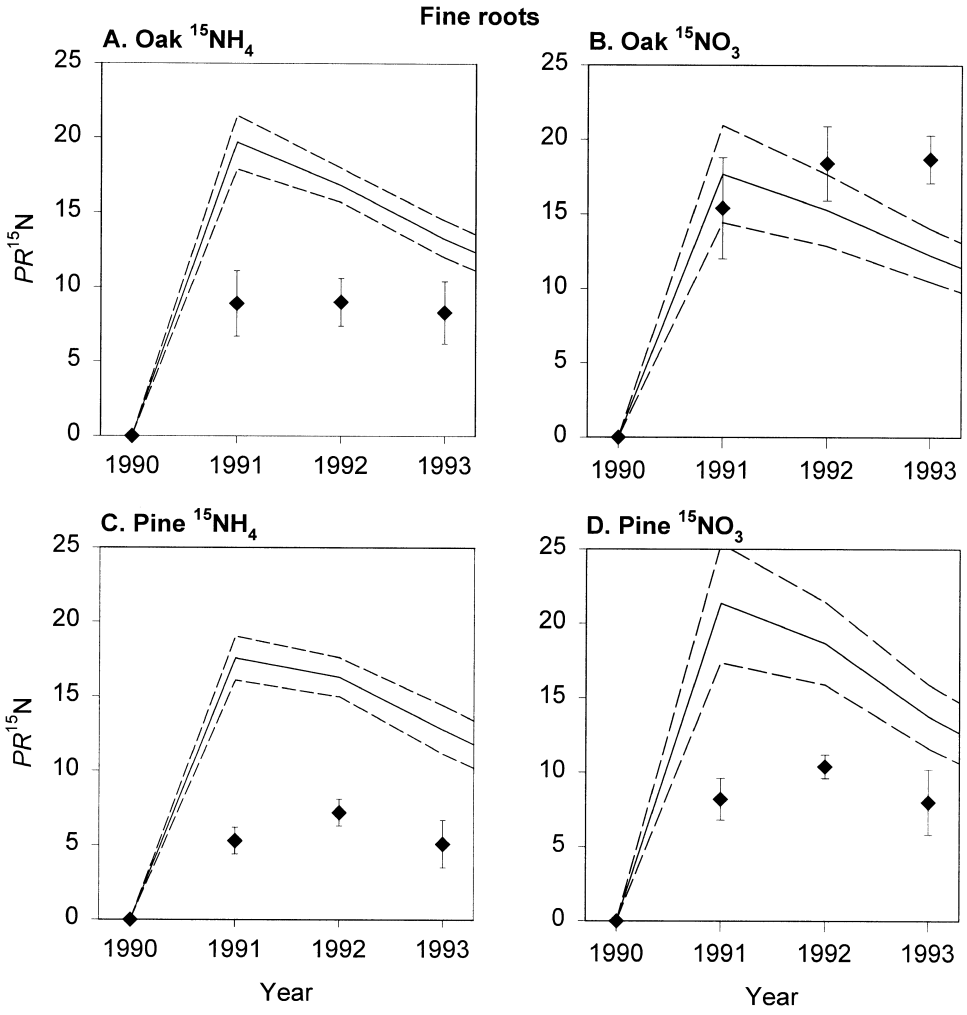

Figure 3. Predicted and field-measured percent recovery of ^{15}N tracers in fine roots. Symbols and lines are as in Figure 2. (For fine roots, field measurements were made only through 1993.)

(Figure 5). Plant uptake exceeded humus assimilation in the pine forest but not in the oak forest. This arose partly because of the timing of ^{15}N applications relative to the timing of foliar expansion in the two forests, and partly because of a more rapid sink for ^{15}N in humus of the oak forest. Plant uptake of ^{15}N was projected to continue through the decade beyond the end of tracer additions, the greatest net source of which, in each forest, was a gross flux of N mineralization from Oi + Oe litter (Table 2). A much smaller source for plant uptake was the slow, long-term net mineralization of ^{15}N from humus in the forest floor that began when the N cohort was about 5 years old. Release of this labeled cohort of N from forest-floor litter and humus together approximately equaled plant uptake in years 5 and beyond (Table 2).

The most striking feature of these model results was the very small flux of N from plant litter to humus via *litter humification* in each forest (Figure 5). By this process, we mean the transfer (amounting to 20% of initial litter mass) of well-decayed litter, well after the end of its N-immobilization phase, to humus (Berg 1986; Aber and others 1990). In the first few years, humification fluxes of plant detritus were far exceeded by direct assimilation of $^{15}NO_3^-$ (Figure 5) and $^{15}NH_4^+$ (not shown) in the combined pools of humified matter plus associated microorganisms. This was true in both organic and mineral horizons in both the deciduous and coniferous forest types. Even as the average age of the labeled N cohort reached 10 years, humification of plant litter composed smaller annual N fluxes than release of N from humified matter in the forest floor.

In model projections, there were no second peaks in $PR^{15}N$ in plant pools appearing after the initial peaks. Nitrogen assimilated and released from Oi + Oe material did not cycle to plants as a recognizable pulse in the simulations; likewise, N taken up by plants, allocated to tissues, lost as litter, and mineralized, did not cycle back to plants as a recognizable pulse. In other words, TRACE predictions result in the hypothesis that the labeled N cohorts should rapidly

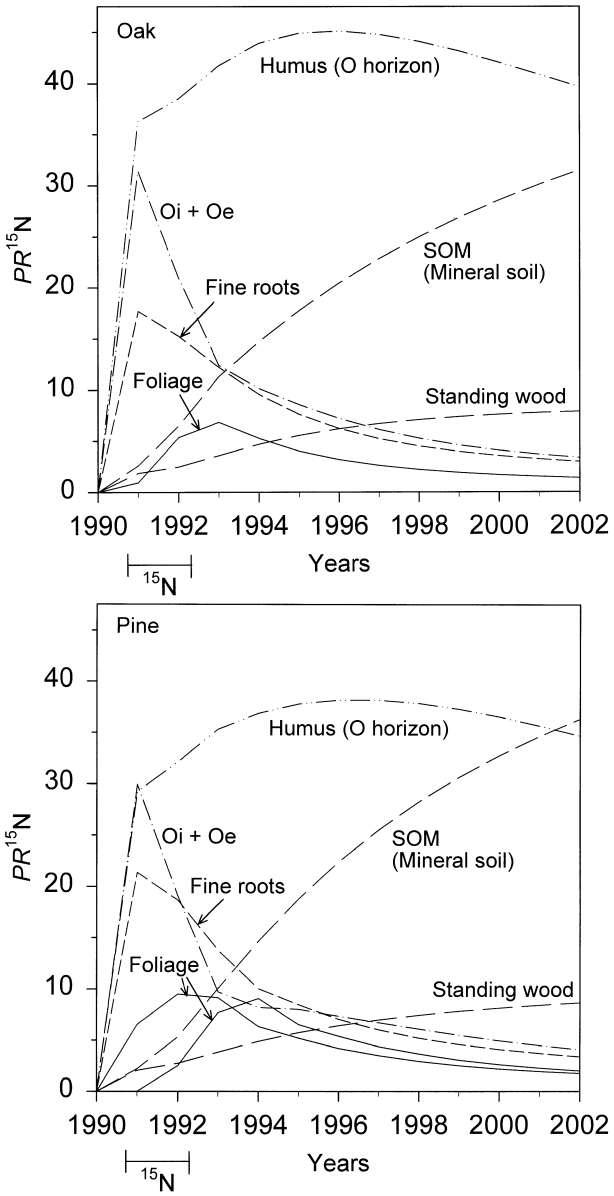

Figure 4. Simulated percent recovery of ^{15}N in ecosystem pools at the Harvard Forest. Results simulate $^{15}NO_3$ additions in fertilized plots of the (top) oak forest and (bottom) pine forest. Data represent means of 51 stochastic model runs in each case, indicating simulated $PR^{15}N$ in August of each year. In the pine forest (B), foliage produced in the current year is shown separately from foliage produced in previous years. Oi + Oe refers to nonhumified foliar and fine-root detritus in the forest floor; SOM, mineral soil organic matter. The period of tracer ^{15}N addition (1991–92) is indicated on the *x* axis.

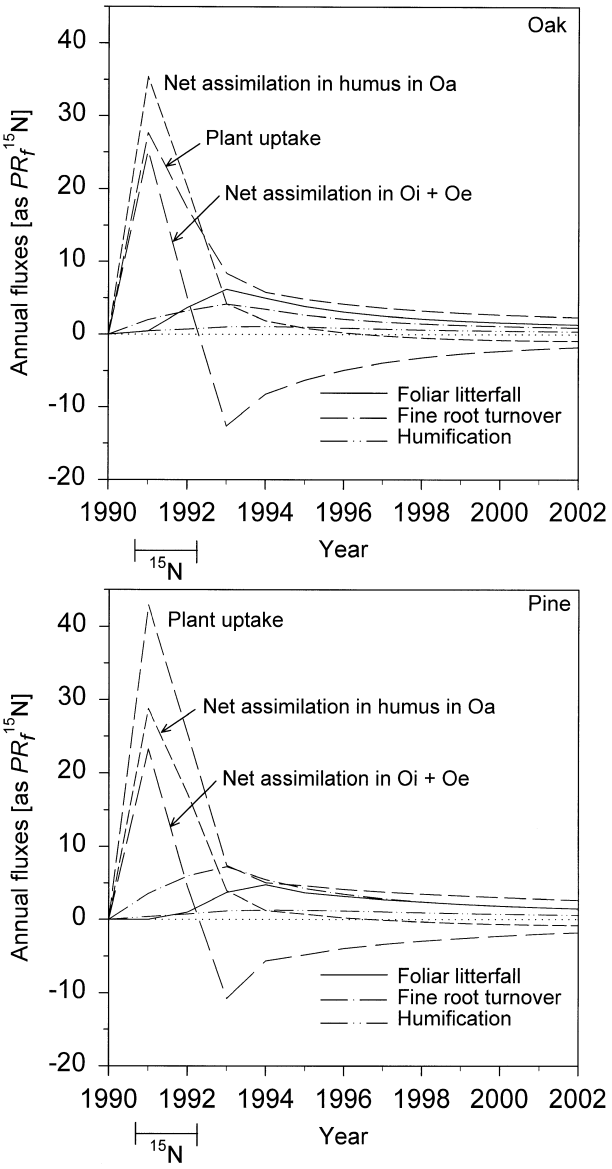

Figure 5. Simulated annual fluxes of ^{15}N in intra-ecosystem transfers, expressed as $PR_f{}^{15}N$ for comparative flux analysis of N from a labeled, 2-year cohort. Results simulate $^{15}NO_3$ additions in the (top) oak forest and the (bottom) pine forest. Data represent means of 51 stochastic model runs in each case. The period of tracer ^{15}N addition (1991–92) is indicated on the *x* axis. Plant uptake, humification, and fine-root turnover fluxes refer to the entire solum. Oi + Oe refers to nonhumified foliar and fine-root detritus in the O horizon (woody debris excluded). Net assimilation in humus in Oa (and associated microorganisms) refers to assimilation directly from pools of inorganic N (humification flux from litter is not included) minus mineralization. Negative values for net assimilation indicate net release.

lose coherence due to assimilation into large pools of soil detrital N. Field data would need to be collected over a longer period to test this aspect of model projections.

Table 2. Simulated Annual Redistribution Fluxes of Labeled $^{15}NO_3^-$ Cohorts (Expressed as $PR_f{}^{15}N$)[a]

Flux	Soil Horizon	Oak Forest		Pine Forest	
		5 years[b]	10 years	5 years	10 years
Plant N uptake flux	Whole solum	4.1 ± 0.6	2.5 ± 0.3	4.1 ± 0.4	2.8 ± 0.2
Foliar litterfall N flux	To O horizon	3.1 ± 0.5	1.5 ± 0.2	3.2 ± 0.6	1.6 ± 0.3
Fine root litter N flux	Whole solum	2.1 ± 0.4	1.0 ± 0.2	3.5 ± 0.4	1.6 ± 0.2
N flux in humification of litter	O horizon	0.65 ± 0.1	0.32 ± 0.05	0.76 ± 0.1	0.43 ± 0.05
	Mineral soil	0.23 ± 0.05	0.12 ± 0.03	0.41 ± 0.09	0.21 ± 0.04
	Whole solum	0.88 ± 0.2	0.44 ± 0.07	1.2 ± 0.1	0.64 ± 0.07
Net N assimilation dynamics in humified pools[c]	O horizon	0.23 ± 0.3	−0.86 ± 0.1	0.22 ± 0.3	−0.74 ± 0.2
	Mineral soil	1.4 ± 0.1	0.62 ± 0.06	2.0 ± 0.2	0.80 ± 0.07
	Whole solum	1.6 ± 0.3	−0.23 ± 0.1	2.2 ± 0.3	0.06 ± 0.18
Net N assimilation dynamics in Oi + Oe[c]	O horizon	−4.9 ± 0.7	−2.0 ± 0.3	−3.9 ± 0.5	−2.0 ± 0.3

[a]Plots were amended with NH_4NO_3 at the rate of 5 g N m^{-2} $year^{-1}$ beginning in 1988; these results refer to half-plots in which the NO_3^- amendment was labeled with enriched ^{15}N in 1991 and 1992. $PR^{15}N$ = percent recovery of ^{15}N tracer added [Eq. (1)]; fluxes resulting from a flow analysis are expressed here as $PR_f{}^{15}N$. Values represent means ± SD for 51 model runs with stochastically varied parameters.

[b]5 years and 10 years refer to elapsed time since the approximate midpoint of ^{15}N tracer additions; 5 years = 1996, 10 years = 2001.

[c]Terms are as in Figure 5. Net N assimilation dynamics exclude humification of litter.

DISCUSSION

Comparisons with Field Data

There are several reasons why we did not employ optimization algorithms to set model parameters by fitting TRACE results to time-series observations. One purpose for using the model was to test our understanding. When a multivariate optimization technique is used, a model is used as a complex framework for a statistical curve-fitting analysis, but the results are precluded from disagreement with observations. The choice of a measurement of agreement is arbitrary, and there is no guarantee that the parameter set obtained is unique or ecologically reasonable. In the present work and previously (Currie and others 1999), we instead made limited, informed changes to the model that appeared justified by independent research results, and then performed tests for agreement between field data and model results. Some degree of parameter calibration is desirable, because model results that differ radically from field data are of limited use. Our calibrations were carefully chosen and well understood. We should stress that the total recovery of ^{15}N in plants at the end of 1992 (in Figures 2 and 3) was a calibrated result, but the interannual temporal dynamics were uncalibrated model predictions. The further that TRACE makes projections beyond the 2-year mass-balance period, the less valid we expect the results of our plant–soil calibration exercise to be (Rastetter 1996).

We made one model change for the present analysis after we viewed the ^{15}N time-series data. We allowed N stored by vegetation to mix with N taken up in the current year prior to allocation to new tissues. TRACE had originally modeled N allocation to foliage as deriving from overwintered buds. It was clear from the field data that ^{15}N was recovered in foliage in the first year of ^{15}N applications, 1991. This was also consistent with the findings of Marmann and colleagues (1997), in which N was mobilized from bark and roots (not exclusively buds) to produce foliage in *Fraxinus excelsior*. We simply melded the pools *BudN* and *PlantN* from PnET-CN into the single pool *VascN* in TRACE. NH_4^+ and NO_3^- were then taken up into *VascN*, isotopically mixed with all of the N stored previously in this pool, and subsequently allocated to new growth in foliage, wood, and fine roots, where it mixed isotopically with N already present in each tissue.

Capturing the temporal patterns of $PR^{15}N$ in foliage was a significant success. Levels of ^{15}N in foliage depended on simulations of several processes: soil N mineralization and nitrification, uptake of NO_3^- and NH_4^+ from both the organic and mineral horizons, physiological mixing of new N with plant-stored N, foliar allocation, foliar phenology, and leaching of DON in throughfall. After the first year, foliar ^{15}N levels also depended on simulations of N resorption, mixing again with stored N, and reallocation. Capturing the net effect by including these processes in an ecosystem model provides a key link between modeling and field studies. Foliar N and foliar litter N concentrations are easily measured and are typically quantified as indicators of N cycling in the field [for example, see Sollins and others (1980), Vitousek (1982), and Fahey and others (1985)].

We were not surprised that our predictions of ^{15}N recovery in fine roots showed disagreement with field data. We know significantly less about production of, allocation to, resorption from, and turnover of fine roots than foliage (Hendricks and others 1993). The N-storage function of fine roots also makes interpretation of TRACE results difficult; our predictions assumed that one-third of the plant internal storage pool *VascN* was recovered in fine roots (Marmann and others 1997). It is certainly an oversimplification to use a constant value of one-third throughout the year and for different plant communities. Modeled patterns of ^{15}N recovery in fine roots were also quite sensitive to assumptions about plant physiology: whether N storage in buds, wood, or bark could mix with N storage in roots affects ^{15}N mixing and pool dilution within vegetation pools. Capturing *PR*^{15}N values in fine roots correctly could require a more complex treatment of plant physiology, requiring independent research to construct and parameterize.

The differences between $^{15}NH_4^+$ versus $^{15}NO_3^-$ recovery in foliage and fine roots in the field, which TRACE underpredicted, could have arisen several ways. Possibilities are plant preferences for NO_3^-, a microbial preference for NH_4^+, or an abiotic soil sink (including but not limited to simple cation exchange) with a preference for NH_4^+. TRACE included a preference for assimilation of NH_4^+ over NO_3^- into microbial–detrital pools at a ratio of 3.3:1, based on field studies summarized in Davidson and colleagues (1992). Though this facet of TRACE was apparently structured in the right direction, it did not reproduce observed differences in $^{15}NH_4^+$ versus $^{15}NO_3^-$ recovery in plant tissues. TRACE included no plant preference between NO_3^- and NH_4^+.

N Cycling and Storage in the Forest Floor

Forest-floor litter and humus both acted as rapid sinks for ^{15}N in TRACE. The equally rapid release of ^{15}N from forest-floor litter arose as a consequence of the small size of this pool of N relative to gross turnover rates of N in our simulations. In contrast to litter, forest-floor humus did not release ^{15}N as rapidly as it assimilated ^{15}N. This arose as a consequence of the large size of this pool of N relative to gross turnover rates of N in our simulations, even though our ratio of gross–net fluxes of N assimilation in humus was 12:1 (Currie and others 1999). In the model, because of the large size of the humus pool, the tracer ^{15}N that was assimilated in humus mixed with the large amount of N present at the background ratio of $^{15}N/^{14}N$, diluting the tracer prior to mineralization from humus. Thus, in our simulations, the humus pool served as an important net sink for rapidly cycling ^{15}N from the labeled cohort. Obviously, the modeling assumption that humus N in the forest floor is one large, homogeneous, well-mixed pool is highly simplified. However, this assumption did reasonably reproduce plant-soil partitioning of $^{15}NH_4^+$ and $^{15}NO_3^-$ tracers in our previous 2-year mass balance study of tracer recoveries (Currie and others 1999).

Humus in the oak forest floor was a stronger simulated ^{15}N sink than in the pine forest floor, in agreement with field observations made in 1992 (Nadelhoffer and others 1999). In the model, this occurred because the humus pool was simply larger in the oak forest. (Field data unfortunately lack the precision to test this assumption rigorously.). The field observation of a greater ^{15}N sink in the deciduous forest humus could also have arisen from a faster N-turnover rate, perhaps linked to a faster humus decay rate relative to the coniferous forest. From ongoing work at the Harvard Forest, field data may become available to test this possibility.

Litter Humification versus Direct Assimilation

Absent in our simulations was a large flux of N arising from the transfer of well-decayed litter to humus, which we have called a *litter humification* flux. A large value of this flux should be expected from conceptual models that emphasize the production of humus from litter at a certain point along the decay continuum (Berg 1986; Melillo and others 1989; Aber and others 1990). Our results suggest a revised view of N fluxes to and from humus pools in the forest N cycle (Figure 6). In this revised view, humification of N in plant residues and of N immobilized in decaying litter, while providing one pathway for N to enter humus, appears small compared with direct assimilation. *Direct assimilation* refers to any means of N transfer from available, inorganic soil pools to humus and its associated microorganisms. This revised view arose not from the ^{15}N field study or modeling study alone, but through a direct comparison of field and model results. Model simulations indicated that litter production and transfer to humus could not account for the rapid assimilation of ^{15}N into humus observed in the Oa horizons of both forests.

Several lines of research support the potential importance of direct assimilation as depicted in Figure 6: N budgets, fine-scale and large-scale ^{15}N recoveries, and ^{15}N-pool dilution experiments. From budgets of N retention for this site, Magill and colleagues (1997) concluded that 50%–83% of the retained N was to be found in long-term, recalci-

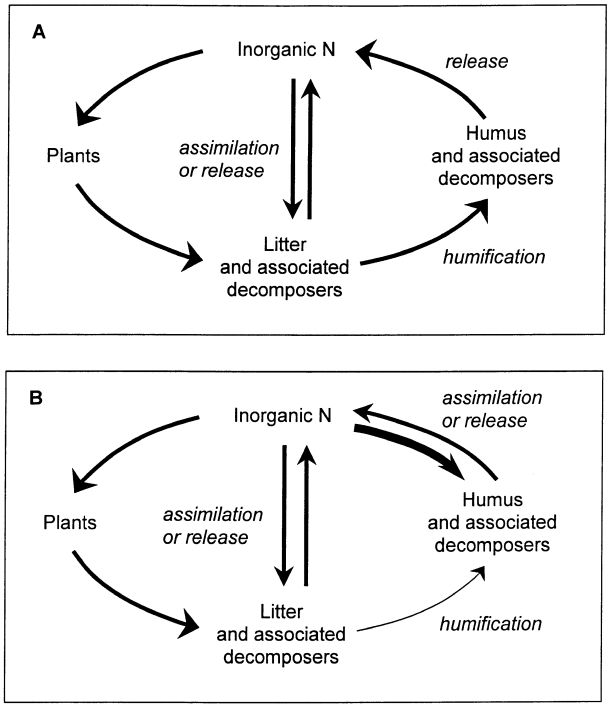

Figure 6. Traditional and revised views of the relative fluxes of N to and from pools of humified organic material in temperate forest soil. In the more traditional view A, humification of litter N provides a stabilized pool of N in soil. In a revised view B, direct assimilation significantly exceeds humification of plant litter as a pathway for the entry of N into humus.

trant pools in soils. Our simulations show this is unlikely to have occurred through plant litter humification. In short-term, fine-scale studies utilizing ^{15}N tracers to study plant-microbial competition, greater recovery of ^{15}N has been observed in microbial biomass than in plant biomass in grasses and forest herbs (Schimel and others 1989; Zak and others 1990). Likewise, in a longer-term study in a clear-cut forest, more ^{15}N was recovered in microbial biomass and forest-floor detritus than in regrowing vegetation (Vitousek and Matson 1984). Pool dilution studies in forest soils typically indicate that gross fluxes of inorganic N assimilation, mineralization, or nitrification are much higher than net rates (Davidson and others 1992; Hart and others 1994b; Stark and Hart 1997). Our simulation results illustrate how humus and its associated microorganisms (as a combined pool) may provide a source of N for plant uptake, yet still be a strong sink for an ^{15}N label: the high gross assimilation flux, together with the large pool size, results in a net movement of ^{15}N into the pool.

Direct assimilation refers in our model (Figure 6) to biotic or abiotic means of N incorporation in microbial-detrital pools. Mechanisms through which inorganic N is assimilated into microbial-detrital material are a subject of current debate. All assimilation of inorganic N may be through microbial uptake (He and others 1988; Hadas and others 1992; Tietema and Wessel 1992). Johnson (1992), however, in a review of literature on N retention, suggested that abiotic incorporation of inorganic N may be significant. Current conceptions of humus formation allow N to enter from primary organic material (plant litter), secondary organic material (microbial biomass), and potentially through chemical reactions with decomposition intermediates (Zech and Kögel-Knabner 1994). Questions of carbon (C) bioavailability complicate the question further (Hart and others 1994a). If N does enter completely through microbial uptake, traditional concepts and values of microbial C-use efficiency can not account for the rates of assimilation observed in TRACE (Currie and others 1999). Microbes should theoretically be C limited when substrates have a C/N ratio of less than 30:1 (Kaye and Hart 1997). Aber and others (1998) have suggested that plant-supplied C to mycorrhizae could fuel N assimilation in forest soils.

Use of Combined Microbial–Detrital Pools

There were both positive and negative ramifications of our construction of the soil detrital pools in TRACE to contain microbial biomass implicitly. On the positive side, it provided a simplification of the model. On the negative side, we know that each detrital-microbial pool in reality does have an internal structure with heterogeneous kinetics. For a short-term mass balance, it is valid to conclude that a sink for N in an aggregated pool is strong, even if the pool has internal structure (Currie and others 1999). To extrapolate the turnover rate of the aggregated pool to model ^{15}N release over a period of years may be invalid, however, because N is probably not released from a pool homogeneous in $^{15}N/^{14}N$ ratio. We must consider the utility of having made such a simplifying assumption and consider the impact of this assumption on interpretations of model results.

We found the simplifying assumption of combined microbial-detrital pools to be useful not only because it facilitated direct comparisons with field data for soil pools. Just as importantly, it enabled us to analyze the interplay of fluxes at the ecosystem level without making the results sensitive to dozens of fine-scale parameters that are difficult to quantify. For example, we circumvented the need to estimate the fractions of microbial biomass that

enter various litter classes and humified matter (Van Veen and others 1984; Currie and Aber 1997).

To examine the validity of this simplifying assumption, suppose its alternative were true: that ^{15}N-labeled N cohorts preferentially entered one fraction (the microbes) of our aggregated pool of humus and associated microorganisms. Then, to the degree that such a fraction released N more rapidly than the remainder of the pool, there would be a more rapid release of ^{15}N. This suggests two main possibilities. First, the ^{15}N thus released could be immediately reassimilated into the same pool. In that case, TRACE would simply have underestimated gross mineralization and assimilation fluxes (further exacerbating the problem of C bioavailability), but *PR*^{15}N in model pools would be little changed. Alternatively, if the ^{15}N thus released were taken up by plants, we would expect greater ^{15}N recovery in plant biomass. As pointed out in the Methods section, however, part of our iterative approach to TRACE development effectively calibrated gross rates of ^{15}N dynamics of humus to produce observed plant versus soil recovery of $^{15}NO_3^-$ and $^{15}NH_4^+$ (Currie and others 1999; Nadelhoffer and others 1999). This view that a stronger microbial sink for ^{15}N or increased plant uptake of ^{15}N are mutually exclusive may apply only when heterotrophic soil flora outcompete plants for inorganic N, as is the case in our conceptual model. It is plausible that microbial assimilation, while rapid, results in later N release over a period of years that is highly plant available. For example, low-molecular-weight organic N compounds may be highly available to plants or mycorrhizal symbionts (Näsholm and others 1998). In our present analysis, we have not assessed the effects of such alternate conceptual models on our results. We suggest that both empirical and modeling research is needed in this area.

TRACE results for partitioning of ^{15}N between vegetation and soils agreed well with findings across a range of other forests. Our simulated partitioning of N to vegetation pools from the labeled 2-year cohort of N inputs peaked in the range of about 15%–35% in these fertilized plots. The rest was partitioned to soils, primarily to the forest floor. The partitioning was similar in four NITREX forests to which ^{15}N tracers were added: Independent of the amount of N in throughfall (which ranged from 2.0 to 9.1 g m^{-2} $year^{-1}$), recovery in vegetation of ^{15}N added to soils ranged from 10% to 30% of the throughfall flux (Tietema and others 1998). In the NITREX forests, as in our simulations, the bulk of ^{15}N in the first few years was recovered in the soil organic horizon, with a smaller fraction recovered in mineral soil.

Implications and Conclusions

The forest floor appeared to be a critical ecosystem component for N retention. A key difference between the oak and pine forests at Harvard Forest, directly related to differences in N saturation response, lies in the rates of N retention in the forest floors (Currie and others 1996). TRACE simulations showed that relatively small fluxes of N to long-term organic pools were derived from the transfer to humus of well-decayed litter with its indigenous and immobilized N. In a 2-year mass balance, the Oa horizon was a large and rapid sink for added ^{15}N (Nadelhoffer and others 1999). We interpreted the main N fluxes to humus and its associated microorganisms as a form of direct assimilation of both NH_4^+ and NO_3^- in both forests.

When continued N retention drives the mass ratio of C/N to lower levels, the forest floor should reach a limit in its ability to store additional N. In a multivariate analysis of dozens of observations taken in the five NITREX forests along a deposition gradient in Europe, Gundersen and colleagues (1998) found the C/N ratio in the forest floor to exhibit a close, inverse correlation to the overall degree of N saturation at the whole-system level. Because litter in the forest floor has the capacity to assimilate and release large fluxes of N, we should expect current and critical values of the C/N ratios in litter [sensu McClaugherty and others (1985)] to be good predictors of the limit of N cycling and storage in these pools. Following this reasoning, N saturation in the northeastern United States should occur more quickly in higher-elevation forests, where forest-floor C/N ratios are lower and N capitals are higher (Currie and Aber 1997). This pattern has been reported by Vitousek and colleagues (1997) and is consistent with findings of greater nitrification rates with greater N deposition in high-elevation forests (McNulty and others 1990).

The combined field and modeling study of ^{15}N redistributions proved to be a powerful combination of tools for the study of dynamics in pools and fluxes in the context of whole-system behavior. At the same time, modeling the isotopic redistributions illuminated areas where detailed understanding of the forest N cycle is lacking. Our work indicated two obvious areas where greater understanding is needed in order to describe the processes giving rise to ecosystem-level N retention. The first is in physiological storage and cycling of N within vegetation tissues, including fine roots. The second concerns mechanisms through which N is cycled by microbial biomass and incorporated into humus, including

the problem of the availability of C or energy to drive these processes.

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