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SOIL DETRITAL PROCESSES CONTROLLING THE MOVEMENT OF ^{15}N TRACERS TO FOREST VEGETATION

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Abstract. Controlled field experiments to study the effects of heightened atmospheric inputs of nitrogen (N) to forests typically demonstrate that most N enters nonextractable pools in soil, while some N is taken up by vegetation, and varying amounts are exported. In a few experimental manipulations of N inputs to forests, ^{15}N has been added as a tracer to more closely study the fates and redistributions of NH_4^+ and NO_3^- at the ecosystem level. We developed TRACE, a biogeochemical process model based on previous models, to interpret ecosystem-level ^{15}N field data following applications of ^{15}N-enriched NO_3^- or NH_4^+ at the Harvard Forest, Massachusetts, USA. We simulated the forms, masses, atom%, and timing of ^{15}N applications in ambient and chronically fertilized plots over two growing seasons in coniferous and deciduous forest stands. Incorporating principles of stable-isotope redistributions, such as mass balance and pool dilution, into the process model provided a strong means of comparing alternative model formulations against field data.

TRACE explicitly illustrated the manner in which rates of gross N turnover in soils could be high enough to provide strong sinks for ^{15}N in ambient plots, while limited enough to allow much greater uptake of ^{15}N by vegetation in fertilized plots. Ectorganic horizons, including litter and humified matter, were key in retaining ^{15}N inputs. We found that fine root uptake and turnover could not account for the rapid movement of ^{15}N into soil pools; direct assimilation into soil pools was required for both NH_4^+ and NO_3^- in both deciduous and coniferous forests. Such high rates of N assimilation could not be accounted for by microbial biomass production using detrital C as the substrate. These findings have far-ranging implications for understanding the reciprocal effects of N deposition on forest C budgets, and forest C cycling on ecosystem N retention.

Key words: acid deposition; biogeochemistry; decomposition; forest floor; humus; isotope tracers; leaching; litterfall; mineralization; N retention and saturation; nitrification; nutrient uptake, model.

INTRODUCTION

Forests worldwide are projected to continue receiving inputs of NO_x and NH_3 that are elevated over background levels (Galloway 1995). The mechanisms through which forest ecosystems can retain atmospherically deposited nitrogen (N) are receiving attention for several reasons. N retention can alter forest nutrient cycling and soil biogeochemistry (Gundersen 1991, Aber et al. 1995*a*), together with production and decomposition, thus impacting the global carbon budget (Schindler and Bayley 1993, Townsend et al. 1996). In addition, when the ability of a forest to store or cycle N is surpassed, N saturation can result in nitrate movement to groundwater and aquatic ecosystems (Aber et al. 1989, Stoddard 1994, Peterjohn et al. 1996). Controlled field experiments designed to study the effects of heightened N inputs have demonstrated varying degrees of N retention and increased NO_3^- mobility. Of the N retained, results typically show that most enters nonextractable (and presumably plant-unavailable) pools in soil, while some is taken up by vegetation (Aber et al. 1993, Nadelhoffer et al. 1993, Wright and Tietema 1995). Current research addresses many open questions: among them, the importance of mineral vs. ectorganic horizons in N retention, microbial assimilation of NH_4^+ vs. NO_3^-, plant–microbial competition for N, the differential fates of NH_4^+ and NO_3^- inputs at the ecosystem level, stabilization of N in detrital pools, and links to carbon cycling.

Adding the stable isotope ^{15}N as a tracer has proven to be a powerful tool for studying gross fluxes and transformations of N in soils (Schimel et al. 1989, Davidson et al. 1990, Emmett and Quarmby 1991, Tietema and Wessel 1992, Hart et al. 1994, Stark and Hart 1997). In a few experimental manipulations of N inputs in the U.S. and Europe, ^{15}N has been added as a tracer to study the fates and redistributions of NH_4^+ and NO_3^- at the ecosystem level (Nadelhoffer and Fry 1994, Nadelhoffer et al. 1995, Tietema et al. 1998). One such study was recently conducted at the Harvard Forest in Massachusetts, USA (Nadelhoffer et al. 1999).

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Mathematical models are essential for interpreting measured isotope ratios in terms of N movements among conceptual-model pools (Schimel 1993). When the conceptual model contains a small number of pools and fluxes, algebraic or differential equations can be formulated and solved for fluxes of interest (Kirkham and Bartholemew 1954, Davidson et al. 1991, Schimel 1993, Nadelhoffer and Fry 1994). Analytical approaches are intractable, however, when the conceptual model is more complex, for example when it allows tracer recycling. For this reason, dynamic simulation modeling has been used. The focus typically has been to interpret redistributions of ^{15}N among only soil and detrital pools (e.g., Molina et al. 1983), though investigators have begun to use dynamic simulation models to study ^{15}N patterns in both plants and soils at the ecosystem level (Hobbie 1997, Koopmans and van Dam, 1998). For simulated isotope redistributions to be realistic, conceptual pools in the model must correspond, in sizes and rates of turnover, with homogeneous, well-mixed pools of N in nature. Because of the high degree of uncertainty in setting constants and coefficients, mathematical techniques are sometimes employed for optimization and simultaneous calibration of numerous model parameters (Molina et al. 1983, Hadas et al. 1992, Tietema and Wessel 1992, Koopmans and van Dam, 1998; Tietema and van Dam, 1996).

Here we report a different approach: we used an iterative procedure to develop a biogeochemical model of ^{15}N tracer redistributions and simultaneously interpreted ecosystem-level ^{15}N tracer data. We developed and applied TRACE (Tracer Redistribution Among Compartments in Ecosystems), a process model that calculates mixing and redistribution of ^{14}N and ^{15}N as NH_4^+, NO_3^-, and organic N in soluble and solid phases, while linking the fluxes of C, N, and water in forest vegetation and soil. Our primary objective was to use the model to provide a synthesis enabling us to examine hypotheses about mechanisms of N retention and redistribution at the ecosystem level. Incorporating principles of stable-isotope redistributions into the process model provided a strong means of comparing alternative model formulations against field data. We found that fine root uptake and turnover could not account for the rapid movement of ^{15}N into soil pools; direct assimilation into soil pools was required for both NH_4^+ and NO_3^- in both deciduous and coniferous forests. We found that high ratios of gross: net turnover of N in soil detrital pools were indicated, and that such high rates of N assimilation could not be accounted for by microbial biomass production using detrital C as the substrate. These findings have far-ranging implications for understanding the reciprocal effects of N deposition on forest C budgets, and forest C cycling on ecosystem N retention.

Methods

We simulated $^{15}NH_4^-$ and $^{15}NO_3^-$ additions over two growing seasons to both ambient and chronically fertilized plots in coniferous and deciduous stands. We incorporated transfers of ^{14}N and ^{15}N among model pools by applying principles of mass balance and pool dilution (Nadelhoffer and Fry 1994). By designing the model to represent field-measured pools where possible, we made testable predictions in distributions of ^{15}N. After parameterizing the model for each stand at the Harvard Forest, we varied the strength and structure of detrital–microbial N sinks in the model through an iterative approach. We compared three successive sets of model predictions with field data (Nadelhoffer et al. 1999) for patterns of $^{15}NH_4^+$ and $^{15}NO_3^-$ recovery in vegetation and soils.

Model structure

TRACE is a synthetic model based largely on field data from process studies and on previous, well-tested models (Table 1). Pools of C and N in TRACE are physically meaningful. TRACE combines the vegetation processes of the PnET-CN model (Aber et al. 1997) with the soil processes of the DOCMOD model (Currie and Aber 1997). TRACE runs on a monthly time step. The description here emphasizes soil processes because the vegetation model in TRACE is unchanged from PnET-CN.

PnET-CN is a lumped-parameter model that uses generalized representations of physiological processes including photosynthesis, transpiration, respiration, allocation, phenology, litter production, and decomposition along with monthly time-step climate data to predict monthly dynamics of C, N, and water in forest ecosystems. The model incorporates a multilayered canopy model of phenology and photosynthesis, tested against gross carbon flux measurements at the Harvard Forest (Aber et al. 1996), together with allocation, respiration, and transpiration algorithms tested against both C and water balance data from the Harvard Forest and Hubbard Brook, New Hampshire.

A more complex soil model was required to study gross transfers of NH_4^+ and NO_3^-, to include leaching fluxes of NO_3^-, NH_4^+, and DON (dissolved organic N) between soil horizons, to investigate N retention in the ectorganic horizon and mineral soil, and to follow the experimental design of the field recovery of ^{15}N. DOCMOD is a model of litter decomposition, humification, and production of dissolved organic C and N in the forest floor. The model separates fine litter into detrital pools based on proximate carbon fractions (acid-insoluble material, acid-soluble, and extractives; Ryan et al. 1990), hereafter referred to as "C classes." DOCMOD has been tested in blind predictions of litter decomposition at four sites with widely varying climates and soils: the Harvard Forest; Luquillo Experimental Forest, Puerto Rico; Arctic Tundra, Alaska, USA; and Jornada Field Station, Arizona, USA (D. Moorhead et al., *unpublished manuscript*).

Notation.—In equations that follow, F refers to gross and f refers to net monthly fluxes of N in grams of nitrogen per square meter per month. Subscripts are

TABLE 1. Sources of submodel processes in TRACE.

Modeled processes	Source
N deposition (wet and dry) and land use history	PnET-CN†
Hydrology, including actual evapotranspiration (AET), snowmelt, and drainage	PnET-CN†
Controls on plant uptake of NO_3^- and NH_4^+	PnET-CN†, modified by separating into two soil horizons
Plant internal storage of N and allocation of C and N to foliage, fine roots, and wood; resorption of N from senescing foliage	PnET-CN†
Photosynthesis and plant respiration	PnET-CN†
Canopy phenology, litter production, fine root turnover, controls on N content of litter	PnET-CN†
Separation of fine root litter inputs by soil horizon	New‖
Decomposition of litter in C classes in O horizon; production of humus and soluble organics from C classes in O horizon	DOCMOD‡, modified
Climatic effect on decay rates	DOCMOD‡
N dynamics of foliar and fine root detritus	New
Decomposition, N dynamics, and humification of litter in mineral soil	New
Humification of woody detritus	New
Decay rate of humus in O horizon	DOCMOD‡
Decay rate of mineral soil organic matter	New
Net mineralization and immobilization in humus and mineral soil organic matter	PnET-CN†
Gross mineralization and immobilization in humus and mineral soil organic matter	New
Controls on gross nitrification rates	New
Leaching of inorganic N from O horizon to mineral soil	New§
Leaching of dissolved organic N (DON) from O horizon to mineral soil	DOCMOD‡
Retention of DON in mineral soil and loss of DON from solum	New§

† Aber et al. (1997).
‡ Currie and Aber (1997).
§ Based on field measurements made at the Harvard Forest (Currie et al. 1996).
‖ Based on fine-root distribution measured at Hubbard Brook, New Hampshire, USA (Fahey et al. 1988).

used as follows: F_M for mineralization, F_U for plant uptake, F_T for nitrification, and F_A for assimilation by a detrital–microbial pool, meaning transfer of N from a plant-available pool to a plant-unavailable pool in detritus. All soil organic pools in TRACE are detrital–microbial pools, containing microbial biomass implicitly; detrital mass always refers to organic-matter (OM) mass (ash free). State quantities of mass in model pools (grams per square meter) are represented by capital letters: $H(l, t)$ for humified material, $W(l, t)$ for woody detritus, and $L_i(l, t)$ for nonhumified, nonwoody litter, where (l) refers to soil layer and (t) to monthly time step. State quantities of organic N in detrital pools (grams of nitrogen per square meter) are represented by N followed by a subscript denoting the pool, e.g., $N_H(l, t)$ for the quantity of N in the humified pool in layer l at time t. The change in a state quantity of mass or N in one time step is indicated by Δ. First-order decay constants are designated k, e.g., k_H for humified material. Modifiers to decay rates are indicated by γ terms (see *Detrital mass loss and humification*). Microbial efficiency, defined as the ratio of the mass of microbial biomass produced to the mass of substrate utilized, is designated by e with a subscript referring to the substrate, e.g., e_H. The base of natural logarithms is denoted "exp." Additional symbols are defined in the following *Methods* sections.

Uptake and allocation of N by vegetation.—Photosynthesis in the model is controlled by water availability, solar radiation, temperature, and foliar N content. C allocation to new tissues depends on photosynthesis, maintenance respiration, and growth respiration of foliage, fine roots, and wood. Plant demand for N depends on ambient temperature and the quantity of N in VascN, a pool in vegetation that stores N until it is allocated to new tissue production in foliage, fine roots, wood, and buds. VascN is conceived as the total of N in plants in transportable form (inorganic N and transport amino acid N). This pool is necessary in order to model nutrient resorption from senescing foliage (50% of foliar N), an important control on ^{15}N levels in foliar litter.

TRACE contains pools of plant-available N (presumed equivalent to KCl-extractable pools) separately as NO_3^- and NH_4^+ in each soil layer (Fig. 1). N is taken up first from the forest floor, then from mineral soil, based on N availability and plant demand. Available NO_3^--N and NH_4^+-N are drawn down in equal proportions during uptake. The model includes no plant preference for NO_3^- or NH_4^+, and organic N is not taken

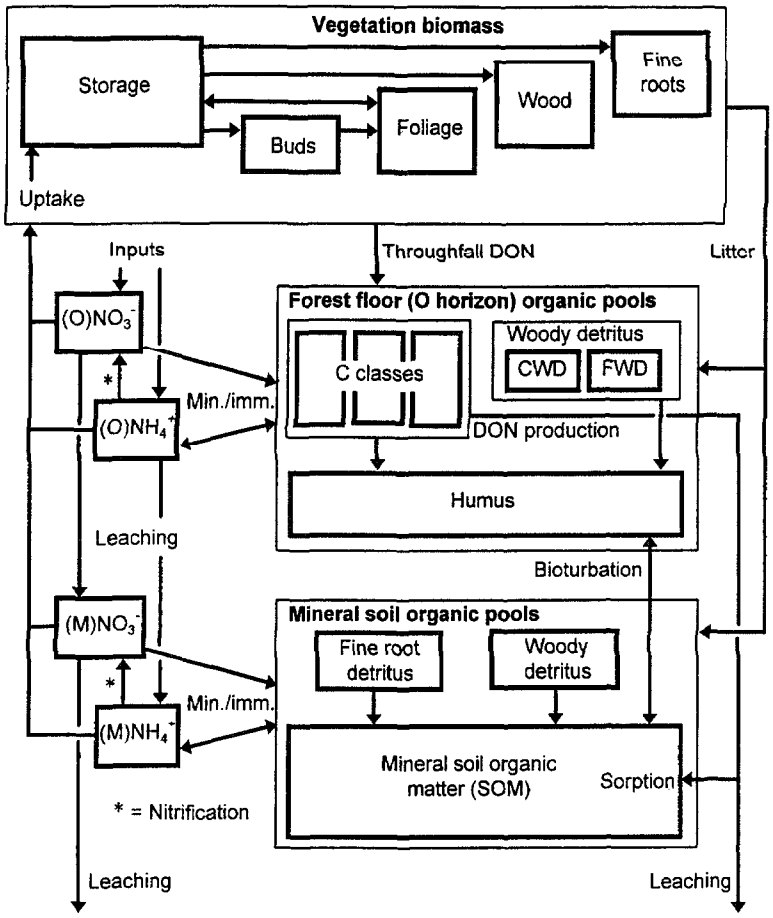

FIG. 1. Schematic of the hierarchical structure of pools and fluxes of nitrogen in TRACE 2.1. Plant uptake of N, detrital N dynamics, and N transformations are calculated separately in each soil layer. Pools of KCl-extractable N are separated by soil layer: (O) = O horizon, (M) = mineral soil. DON = dissolved 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.

up in TRACE. N concentrations in allocations to new tissues increase in the model as N storage in VascN increases. In effect, plant N uptake correlates positively with net N mineralization (Reich et al. 1997) until increased plant storage of N and cycling of N in litter become saturated (Aber et al. 1991). Greater detail on plant-internal C and N processes have been provided by Aber et al. (1997).

Detrital mass loss and humification.—Mass loss from litter pools follows

$$\Delta L_i(t) = \gamma_c \gamma_l L_i(1 - \exp[-k_{Li}(t)]) \quad (1)$$

where the decay constants $k_{Li}(t)$ are time-varying functions of overall-litter LCI (lignocellulose index) for fine root and foliar litter (slowing decay rates as lignin concentration increases), derived from field studies by Aber et al. (1990). This provides an interaction between C classes in the model, representing physical protection of more labile fractions by recalcitrant material (Swift et al. 1979). As in many decomposition models (e.g., Pastor and Post 1986) and field studies (Meentemeyer 1978, Berg et al. 1993), actual evapotranspiration (AET) is used as an index to model the effects of temperature and moisture on decay rates. AET affects decay through γ_c, a factor accounting for both seasonal and annually averaged effects:

$$\gamma_c(t) = \frac{\mathrm{AET}(t)}{\mathrm{AET}_{\mathrm{ann}}} \exp[0.00189(\mathrm{AET}_{\mathrm{ann}} - \mathrm{AET}'_{\mathrm{ann}})]. \quad (2)$$

Previous testing has shown the monthly distribution of AET to work well in fitting intra-annual time series in mass loss and litter N dynamics in humid forest (Currie 1995). Eq. 2 also accounts for differences in climate between the site of application and sites where k constants were derived (represented by $\mathrm{AET}'_{\mathrm{ann}}$): Blackhawk Island, Wisconsin, for foliar and fine root litter, and Hubbard Brook, New Hampshire, for humified matter. Because no clear pattern exists in the literature, we included no climatic effect for woody litter. AET is calculated through a daily time-step model of soil water storage and the relationship between vapor-pressure deficit and saturated vapor pressure, based on

mean and minimum daily temperatures (Aber et al. 1995*b*).

Foliar, fine root, and woody litter are humified in TRACE at rates producing average transfers (summed over all years for a given litter cohort) of 20% of initial OM mass within each litter type (Aber et al. 1990). From the C-class pools, acid-soluble and acid-insoluble components are transferred to humus in a 1:1 mass ratio, representing lignocellulose. Based on field-study results (Aber et al. 1984), roots decay slightly faster in mineral soil than in the forest floor (in Eq. 1, γ_l = 1 in the O horizon, γ_l = 1.16 in mineral soil).

The humified pools in each soil layer undergo first-order mass loss in the model:

$$\Delta H(l, t) = \gamma_c \gamma_H H(1 - \exp[-k_H]). \quad (3)$$

Based on results of 270-d laboratory incubations performed on soil layers from the Harvard Forest (K. J. Nadelhoffer et al., *unpublished data*), mineral SOM in TRACE decays at a rate 0.22 times the rate of humus decay in the O horizon (γ_H = 1 in the O horizon, γ_H = 0.22 in mineral soil). TRACE includes faunal bioturbation as a means of mixing humus and mineral SOM. Each month an equal amount of mass (amounting to 2% of humus mass annually), together with associated organic N, is exchanged between the two layers.

N dynamics of detrital C classes.—Inputs and transfers of N into model C-class pools in the forest floor occur via throughfall, foliar and fine-root litter, and gross assimilation; outputs of N occur via DON leaching, NH_4^+ mineralization, and transfers to humified matter. Litter inputs enter the forest floor in either the acid-insoluble pool (C:N ratio of material entering has the same C:N ratio of initial litter) or the extractives pool (all remaining N). N in fresh litter does not enter the acid-soluble pool, based on analyses of N in the C classes of fresh litter conducted by Aber et al. (1984). In mineral soil, N inputs to the litter pool occur via fine root litter and gross assimilation of inorganic N. Outputs are NH_4^+ mineralization and N transfers to humified matter. For each C-class pool (and for whole litter in the mineral horizon) TRACE calculates gross N assimilation mechanistically, net N dynamics based on empirical data, and gross N mineralization by difference. Gross N assimilation is modeled as microbial biomass production with varying efficiencies on each substrate:

$$F_{A,Li}(l, t) = \left(\frac{n_m e_{Li}}{1 - e_{Li}}\right)(1 - \lambda_{Li})\Delta L_i \quad (4)$$

where n_m is N concentration in microbial biomass (0.03 g/g). The λ_{Li} indicates the fraction of mass loss due to leaching of DOM from each litter pool (λ = 0 in mineral soil layer). The term $e_{Li}/(1 - e_{Li})$ in Eq. 4 arises from the fact that detrital pools contain microbial biomass implicitly; values of e_{Li} approaching 1.0 are not physically realistic, and produce a singularity in the equation.

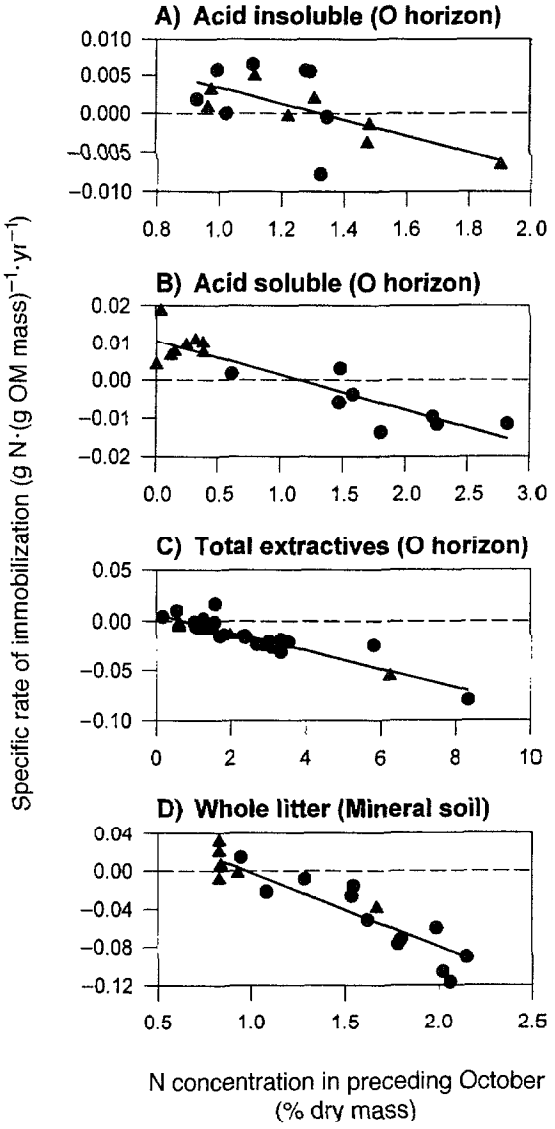

FIG. 2. Net annual nitrogen dynamics in foliar and fine root litter (regression lines). Data derive from litterbag studies in Wisconsin, USA (Aber et al. 1984): ▲ = first year of decay; ● = second year of decay. The *x* axis represents N concentration in the litter pool in October; the *y* axis represents the subsequent annual change in N concentration in the pool. (A–C) Carbon classes in the O horizon; (D) whole litter in mineral soil. (A) $y = -1.052x + 0.0139$; $r^2 = 0.37$; (B) $y = -0.920x + 0.0105$; $r^2 = 0.80$; (C) $y = -0.934x + 0.0068$; $r^2 = 0.83$; (D) $y = -0.776x + 0.0076$; $r^2 = 0.85$.

The net change in N concentration in each litter pool is predicted for each annual period, based on the N concentration of the pool in October of the preceding year (Fig. 2); the net change is distributed seasonally as in Eq. 2. Gross mineralization in each month is then calculated by difference:

$$F_{M,Li}(t) = F_{A,Li}(t) - f_{A,Li}(t). \quad (5)$$

Woody detritus.—Woody litter is divided into CWD (coarse woody debris) and FWD (fine woody debris);

TABLE 2. Differences among the three stages in the iterative generation of model predictions.

Modeled process	TRACE prediction set		
	A	B	C
Gross : net ratio of N mineralization from humified matter	2.5:1 (ω = 1 in Eq. 8)	12:1 (ω = 5 in Eq. 8)	12:1 (ω = 5 in Eq. 8)
Microbial-detrital preference for gross assimilation of NH_4^+ over NO_3	Unlimited	Unlimited	3.3:1
Nitrification	Net monthly, after plant uptake (Eq. 10)	Net monthly, after plant uptake (Eq. 10)	Gross, prior to plant uptake (Eq. 11)

FWD is defined as 5 cm in diameter or finer when fresh. CWD is mineralized to CO_2 and fragmented to FWD at equal rates in TRACE. Woody root litter entering the forest floor and mineral soil is modeled as entirely FWD (larger roots and stumps are included conceptually with CWD in the forest floor).

N concentrations in woody detritus increase over long time periods (Lang et al. 1981, Alban and Pastor 1993). Recent research has shown, however, that N can be exported via fungal spores and sporocarps from woody detritus in early stages (Harmon et al. 1994). More research is needed to quantify transfers of N between throughfall, woody detritus, flora, soil solution, and other soil components. Pastor and Post (1986) modeled the N dynamics of woody detritus in three stages: no N exchanges initially, followed by N immobilization when in a well-decayed state, followed by humification at a critical C:N ratio, after which mineralization occurred. We used a similar model consisting of two stages and allowing earlier mineralization. N is conserved in decaying wood above a C:N ratio of 30:1; excess N is mineralized. Simultaneously, OM mass and N are passed from woody pools to humified matter in each horizon, which then undergoes gross N exchanges with pools of available N.

Leaching fluxes.—Dissolved organic C and N (DOC and DON) leaching from the canopy to the forest floor in throughfall are included as transfers of C and N from plants to soil (Currie et al. 1996), entering the extractives pool in the forest floor. Dissolved organic matter (DOM) is also produced during decomposition in the forest floor; humus is not solubilized, nor does woody detritus contribute to eluviated DOM. Fractions of detrital mass loss in forest-floor C classes that are attributed to leaching are $\lambda_{ACI} = 0.31$, $\lambda_{ACS} = 0.56$, $\lambda_{TEX} = 0.077$ in the coniferous stand; $\lambda_{ACI} = 0.28$, $\lambda_{ACS} = 0.20$, $\lambda_{TEX} = 0.054$ in the deciduous stand. We calibrated these parameters to produce correct qualities and quantities of DOM in forest-floor leachate as in DOCMOD (Currie and Aber 1997), but with changed definitions of C classes, to match laboratory methods and thus facilitate future comparisons with field measurements of ^{15}N in C classes. TRACE calculates DON leaching fluxes mechanistically by assuming all DOM leached from C classes carries the associated concentration of organic N from each source pool. A fraction of the eluviated DOC and DON is sorbed in the mineral soil in TRACE. The model does not include soil inorganic chemistry or the soil exchange complex. Leaching fluxes of NH_4^+ and NO_3^- are modeled as fractions of KCl-extractable pools, with the balance remaining in water stored in each horizon (plus the cation exchange complex for NH_4^+) in a given month. For the purposes of studying ^{15}N redistributions, these parameters were simply set to produce realistic leaching fluxes at the site.

N dynamics of humified material.—Transfers of organic N from litter to humified matter in TRACE (humus in the O horizon, SOM in mineral soil) are proportional to transfers of OM mass and concentrations of N in each source pool. Monthly net N mineralization from humified matter is somewhat less than C mineralization multiplied by the C:N ratio in TRACE, governed by the variable ρ (unitless), which causes humus C:N ratios to decrease relative to those in litter (McClaugherty et al. 1984, Berg 1986, Melillo et al. 1989):

$$f_{M,H}(l, t) = (1 - \rho)\frac{N_H}{H}\Delta H \tag{6}$$

$$\rho(l, t) = a - b\frac{N_H}{H} \tag{7}$$

where the constants $a = 1.5$ (unitless) and $b = 35$ g OM mass/g N derive from fitting the end points of Eq. 7 to humus C:N mass ratios of 12:1 and 35:1 ($\rho = 0$ and $\rho = 1$, respectively). TRACE calculates gross N mineralization from humified matter based on mass loss, N concentration, and an additional factor (ω) (unitless):

$$F_{M,H}(l, t) = \omega\frac{N_H}{H}\Delta H. \tag{8}$$

Combining Eqs. 6 and 8 illustrates that ω is related to the ratio of gross to net N mineralization from humified matter as follows:

$$F_{M,H}/f_{M,H} = \frac{\omega}{(1 - \rho)}. \tag{9}$$

Nitrification.—We modeled nitrification in two alternative ways (Table 2). First, we modeled it as a net

monthly flux, equal to the difference between net mineralization and plant uptake of NH_4^+ in each soil layer:

$$f_T(l, t) = f_M - F_{U:NH_4}. \quad (10)$$

Alternatively, we modeled gross nitrification as a fraction of gross N mineralization, and net nitrification as the difference between gross nitrification and gross assimilation of NO_3^- in detrital–microbial pools:

$$F_T(l, t) = \eta(l)F_M \quad (11)$$

$$f_T(l, t) = F_T - F_{A:NO_3}. \quad (12)$$

Parameters specific to each forest type and soil horizon, $\eta(l)$, were introduced because nitrification fluxes can vary by soil horizon (Vitousek et al. 1982, Tietema et al. 1992, Persson and Wirén 1995) and among forested sites (Vitousek et al. 1982, Tietema et al. 1992), even under similar vegetation with similar values of soil pH (Barford and Lajtha 1992).

Parameterization and application of TRACE at the Harvard Forest

Plot elevations at the Harvard Forest are ~400 m; monthly mean temperatures are −7°C in January and 19°C in July. Precipitation averages 110 cm/yr, distributed fairly evenly throughout the year (Van Cleve and Martin 1991). We consider the two forest stands that are part of the ongoing Chronic N study (Aber et al. 1993, Magill et al. 1997): an even-aged red pine (*Pinus resinosa* Ait.) stand planted in 1926; and a predominantly oak (*Quercus velutina* Lam., *Q rubra* L., *Betula lenta* L., *Acer rubrum* L.) stand that naturally regenerated after clear-cutting in the 1930's. 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).

We used long-term average data (1964–1993) for monthly mean temperature and precipitation (Harvard Forest Weather Station). Model runs began in the year 1700, allowing feedbacks to operate between plant and soil processes as N deposition fluxes rose and as land use history was simulated. Modeled dry and wet deposition of NO_3^--N and NH_4^+-N began at 25% of present levels in the year 1700, and increased linearly to present levels beginning in 1930. In our simulations, both forests were lightly harvested from 1800 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, 20% of that left as slash), the red pine forest in 1926 and the oak forest in 1938.

Nitrification parameters $\eta(l)$ were set higher in the pine than in the oak forest, and higher in the mineral soil than in the O horizon (Appendix), based on laboratory and field incubations at the site (Vitousek et al. 1982, Magill et al. 1997). Fluxes of inorganic N leached downward from the O horizon each month (following mineralization, detrital–microbial assimilation, plant uptake, and nitrification) were 100% of available NO_3^- and 25% of available NH_4^+. Fractions of available N leached from below the mineral soil were 5% of NO_3^- and 0% of NH_4^+. Loss of N through denitrification was neglected, because denitrification fluxes were small compared to leaching fluxes at Harvard Forest (Bowden et al. 1991, Magill et al. 1997).

Incorporation of N isotopes into the model

TRACE simulated the masses, atom%, and timing of ^{15}N applications as $^{15}NO_3$ or $^{15}NH_4^+$ in ambient and fertilized plots in 1991 and 1992 (Nadelhoffer et al. 1999). In the field, ^{15}N tracers were applied in low-N-addition (5 g $N \cdot m^{-2} \cdot yr^{-1}$ as NH_4NO_3) plots (30 × 30 m each) in each forest stand, as $^{15}NH_4^+$ on half of each plot and $^{15}NO_3^-$ on the other half. ^{15}N tracers were also added in concentrated forms to the ambient (nonfertilized) plots. For fertilized plots, TRACE included the six equal NH_4NO_3 additions per year beginning in 1988. In TRACE, the deposition, fertilizer, and ^{15}N-tracer fluxes enter pools of available NO_3^- and NH_4^+ in the forest floor.

The tracer applications at the Harvard Forest carried a strong ^{15}N signal compared to natural-abundance values of ^{15}N at Harvard Forest ($\delta^{15}N$ ranged from about −4 to +6‰; Nadelhoffer et al. 1999). 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. As a result, predicted values of $\delta^{15}N$ cannot be compared directly to field data where $\delta^{15}N$ values are small. We can make direct comparisons in the percent recovery, in each ecosystem compartment, of the total mass of tracer ^{15}N added above background. We refer to this quantity as PR^{15}N, calculated in TRACE as follows:

$$PR^{15}N(C_i, t) = \frac{N_{Ci}(t)(\text{atom\%}^{15}N_{Ci}(t) - \text{atom\%}^{15}N_b)}{A(t - t_0)(\text{atom\%}^{15}N_a - \text{atom\%}^{15}N_b)} \quad (13)$$

where $N_{Ci}(t)$ is the amount of N in C_i at time t, $A(t - t_0)$ is the sum of N amendments (both in grams per square meter) to time t, C_i is an ecosystem compartment, and the "a" subscript denotes amendment, "b" denotes background. We report model predictions of PR^{15}N in all ecosystem pools at the end of October 1992, with the exception of foliage, in which we report PR^{15}N for August 1992, in order to compare directly with field data. To avoid double-counting any label, ^{15}N above background in August 1992 foliage was excluded from 1992 litter pools in simulations here.

TRACE recreates "pool dilution" in mathematical models of isotope movements (e.g., Davidson et al. 1991, Wessel and Tietema 1992). The source pool for each N transfer was assumed to be homogeneous in its ratio of $^{15}N/^{14}N$, leaving the ratio of isotopes in the

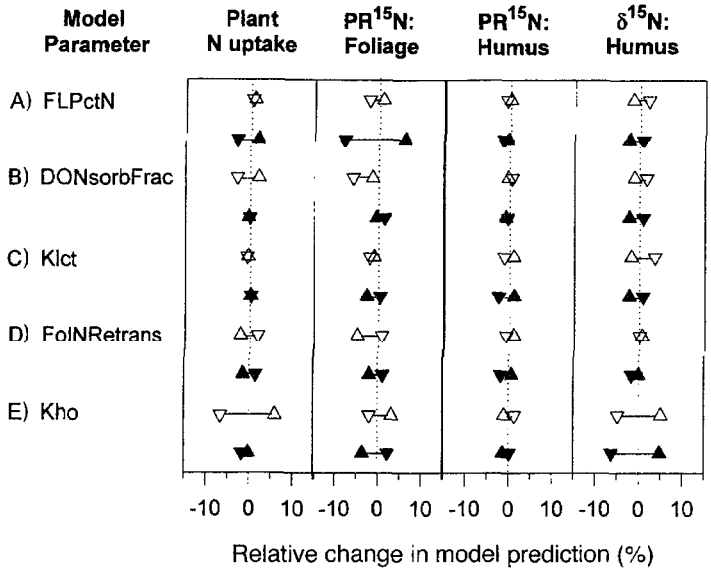

FIG. 3. Sensitivity analysis of parameters in the TRACE model. Relative changes in model predictions are shown for a +10% (△) and a −10% (▽) change in each parameter. Model results are for August 1993 in the oak stand at the Harvard Forest; open symbols indicate ambient plots, solid symbols, fertilized plots. (A) FolPctN = N concentration in foliar litter. (B) DONsorbFrac = fraction of DON eluviated from O horizon that is sorbed in mineral soil. (C) Klct = parameter controlling transfer of litter lignocellulose to humus. (D) FolNRetrans = maximal fraction of foliar N that may be resorbed from senescing foliage. (E) Kho = decay constant for humus.

source pool unchanged, but affecting isotope ratios in the target pool. In an important step that is too often omitted in modeling analyses, we tested the model for mathematical self-consistency. We verified the following: that the total mass of N in the ecosystem remained constant (after accounting for inputs and losses) through time; that values of $PR^{15}N_{Ci}$ summed over C_i to 100%; and that with tracer additions set to zero enrichment, atom%^{15}N remained at background in all pools over the temporal domain of our simulations.

Comparisons of model predictions with field data

We varied three facets of soil N dynamics in TRACE to make successive comparisons of model predictions with field data (Table 2). Prediction sets A and B embodied the hypothesis that no direct entry of NO_3^- into microbial-detrital pools occurred. Prediction set A also embodied the hypothesis that gross fluxes of N release from humified pools were proportional to OM mass turnover multiplied by N concentration (i.e., $\omega = 1$ in Eq. 8). For prediction set B, we investigated the changes in model predictions when gross NH_4^+ transfers to and from humified matter were increased substantially ($\omega = 5$ in Eq. 8). Net N dynamics were not affected in any pools, nor were gross N dynamics of foliar, fine-root, and woody pools.

We further investigated the changes in model predictions (set C) by allowing transfers of N to occur between detrital pools and plant-available NO_3^- pools, while leaving total N dynamics of all detrital pools unchanged from set B. Gross nitrification fluxes were modeled as a significant fraction of gross mineralization, and direct assimilation of NO_3^- into microbial–detrital pools was allowed. TRACE included a preference for gross assimilation of NH_4^+ over NO_3^- (intended to represent a microbial preference and parameterized at 3.3:1; Davidson et al. 1992) when both NH_4^+ and NO_3^- were available in excess. Otherwise, gross transfers of N to detrital pools were met by either form of N when available in each soil layer.

RESULTS

Model sensitivity and testing

Sensitivity to selected parameters showed the model to be functioning realistically (Fig. 3). In the ambient plot, increased turnover of humus (10% higher from the year 1700 on) allowed increased N uptake (7% greater in 1992) by the N-limited vegetation. In the fertilized case the greatest sensitivity was the positive correlation between foliar litter N concentration and predicted $PR^{15}N$ in foliage. General characteristics of N cycling and NPP in TRACE reasonably matched field study results (Table 3). In TRACE, net N mineralization showed the following characteristics: it was slightly greater than N uptake in ambient plots, it increased under fertilization, and in fertilized plots it was lower than plant uptake. Enough of these patterns agreed with our expectations and with calculations based on field data that we had confidence in the N cycle and its responses to fertilization in TRACE. Predicted increases in fluxes of DON under fertilization (Table 3) also indicated that the mechanistic model of DON production from C classes worked reasonably well. Close agreement with all fluxes calculated from field data was not possible, because N fluxes in TRACE compose a balanced budget, while data-based calculations derive from independent datasets and were not so constrained (Magill et al. 1997).

Redistributions of ^{15}N under varying soil sinks for NH_4^+ and NO_3^-

In prediction set A, TRACE over-predicted the recovery of both $^{15}NH_4^+$ and $^{15}NO_3^-$ in vegetation relative

TABLE 3. TRACE results vs. field data for selected nitrogen (N) fluxes and components of NPP (net primary production of biomass).

Flux	Pine forest				Oak forest			
	Ambient		Fertilized		Ambient		Fertilized	
	TRACE	Field data	TRACE	Field data	TRACE	Field data	TRACE	Field data
Plant N uptake† (g N·m^{-2}·yr^{-1})	5.5	6.0	11	14	6.9	8.1	13	14
Net N mineralization† (g N·m^{-2}·yr^{-1})	4.8	7.9	6.0	10	6.3	7.3	7.4	7.9
NO_3^- in Oa leachate‡ (g N·m^{-2}·yr^{-1})	0.14	0.60	1.1	3.2	0.04	0.20	1.0	2.1
NH_4^+ in Oa leachate‡ (g N·m^{-2}·yr^{-1})	0.20	0.14	1.3	1.3	0.28	0.10	2.7	1.2
DON in Oa leachate‡ (g N·m^{-2}·yr^{-1})	0.79	0.95	1.1	1.1	0.53	0.61	0.82	0.70
Net nitrification in O horizon§ (g N·m^{-2}·yr^{-1})	−0.1	0.1	0.1	0.8	−0.4	0	−1.2	0
Net nitrification in M horizon§ (g N·m^{-2}·yr^{-1})	1.4	1.8	1.6	3.2	0.1	0.1	0.2	0.1
Foliar production (NPP)‖ (g·m^{-2}·yr^{-1})	230	320	300	370	230	290	270	290
Fine root production (NPP)‖ (g·m^{-2}·yr^{-1})	200	...	250	...	200	...	240	...
Wood production (NPP)‖ (g·m^{-2}·yr^{-1})	520	330	540	330	880	450	870	480

† Field data (Magill et al. 1997) and TRACE results are annual averages for the period 1988–1993.
‡ Field data (Currie et al. 1996) and TRACE results are for 1994.
§ Field data (Magill et al. 1997) and TRACE results are averages for 1991 and 1993. M horizon refers to mineral soil.
‖ Field data (Magill et al. 1997) and TRACE results are annual averages for the period 1989–1993. For wood production, TRACE calculations include belowground production, whereas data-based calculations refer only to aboveground.

to field data (Fig. 4). This indicated that soil sinks for ^{15}N during the period of tracer application were not strong enough in the model. In set B, the higher gross transfers of N between plant-available and unavailable pools produced predictions for $PR^{15}NH_4^+$ in plant biomass that were reduced by up to 50% from set A, in closer agreement with field data.

Simulated recoveries of $^{15}NO_3^-$ showed large discrepancies between field data and prediction sets A and B (Fig. 4). This indicates that in the field there were direct soil sinks for $^{15}NO_3^-$ in both ambient and fertilized plots of both forest types, because the TRACE set B predictions of soil recovery of $PR^{15}NO_3^-$ provide a high estimate of the entry of $^{15}NO_3^-$ into soil pools through plant uptake and litter production. Simulation of direct entry of NO_3^- into plant-unavailable pools in set C dramatically improved the prediction of patterns of $PR^{15}NO_3^-$ between vegetation and soils (Fig. 4).

Closest overall agreement with field data was in TRACE set C, though not all of the broad patterns in field data were captured correctly. Increases in $PR^{15}N$ in vegetation biomass from ambient to fertilized plots in both forests and for both forms of ^{15}N were captured (Fig. 4). Absolute increases in $PR^{15}N$ in vegetation between ambient and fertilized plots were predicted more closely than relative increases; TRACE under-predicted relative increases. The greater percent recovery of $^{15}NO_3^-$ vs. $^{15}NH_4^+$ in plant biomass was captured correctly in the pine forest but not the oak forest.

Discrepancies occurred between model predictions and field data for $PR^{15}N$ in plant tissues. In ambient plots, TRACE predicted a fairly uniform distribution of $PR^{15}N$ among foliage, fine roots, wood, and VascN (Fig. 5a), whereas field data showed the highest $PR^{15}N$ to be in fine roots (Nadelhoffer et al. 1999). In fertilized plots, field data showed greater increases in $PR^{15}N$ than predicted by TRACE for foliage, fine roots, and wood. TRACE predicted the predominant recovery of ^{15}N to occur in the VascN pool in fertilized plots. Direct model–data comparisons for tracer recovery among plant tissue samples are limited because in the field, the storage of transportable N represented by VascN would be distributed among plant tissues.

Among soil pools, predictions and field data agreed more closely in fertilized plots than in ambient plots. Field data showed the highest values of $PR^{15}N$ in recent litter in ambient plots, changing to the Oa pool in fertilized plots (Nadelhoffer et al. 1999). The range of TRACE predictions for $PR^{15}N$ in O horizon litter (15–30%) agreed approximately with the appropriate pools in field data, Oi + Oe. However, TRACE predicted higher values of $PR^{15}N$ in O horizon humus in all cases (Fig. 5b).

TRACE predictions of ^{15}N recovery in mineral soil were similar to field measurements for ambient plots ($PR^{15}N$ of 3–5%), but underestimated for fertilized plots, particularly for $^{15}NO_3^-$ in the oak forest. TRACE predicted cumulative eluviation from the forest floor as inorganic ^{15}N (expressed as $PR^{15}N$) to comprise up to 1% of tracer additions in ambient plots and 9–10% in fertilized plots over this time period. Eluviation of DON from the forest floor in TRACE comprised up to 1.4% of tracer additions in ambient plots, with slightly lower values in fertilized plots (even though DON fluxes were higher). Bioturbation of ^{15}N to mineral soil in the model accounted for <1% of tracer additions. Over longer time periods, the model predicted increasingly important contributions from both leaching and bioturbation (data not shown).

DISCUSSION

Nitrate assimilation

Evidence has been mounting that assimilation of NO_3^- by decomposers can be significant in forest soils

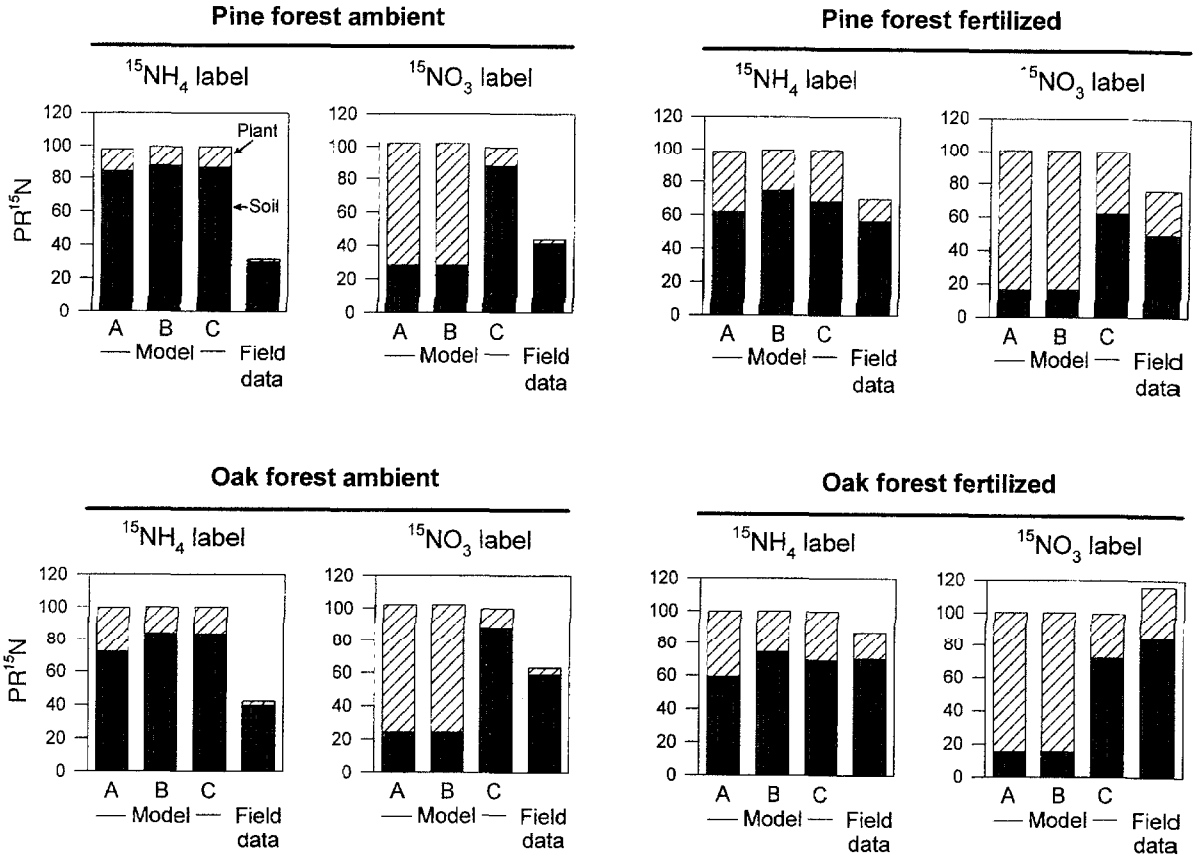

FIG. 4. Percent recovery (PR^{15}N) for total mass of ^{15}N tracers at the end of tracer applications, which spanned two growing seasons. Hatched bars = sum of plant pools; solid bars = sum of soil pools. Three iterations of model predictions are shown (indicated by A, B, C; described in Table 2). Field data are from Nadelhoffer et al. (1999).

(Davidson et al. 1992, Tietema and Wessel 1992, Stark and Hart 1997), although results to the contrary are still observed across multiple sites (Tietema 1998). We initially structured TRACE to embody the hypothesis that gross nitrification fluxes were small and that direct assimilation of NO_3^- into microbial–detrital pools did not occur at the Harvard Forest. But our subsequent incorporation of gross nitrification and NO_3^- assimilation, structured to be competitive against plant uptake based on findings of fine-scale studies in both grassland and forest ecosystems (Jackson et al. 1989, Zak et al. 1990, Stark and Hart 1997), produced much better agreement with field data in both forests. Movement of $^{15}NO_3^-$ into native foliar litter was observed in litterbag studies conducted in both of these stands (P. Micks and K. Nadelhoffer, *unpublished data*) and in a mixed deciduous forest in Maine (Downs et al. 1996). In the latter case, $^{15}NO_3^-$ continued to be incorporated into litter after net N immobilization had ceased. These litter studies together with our TRACE results make a compelling case that significant nitrate assimilation into detrital pools does occur in forests of this region.

Gross nitrification fluxes have traditionally been considered small in undisturbed forests. However, recent analyses are causing a reassessment of their importance (Johnson 1992, Stark and Hart 1997). We have no information at present on fluxes of gross nitrification in situ in these forests. TRACE results for gross nitrification minus NO_3^- assimilation produced patterns observed in field incubations for net nitrification (Table 3). Model results show that gross nitrification of 15–30% of gross NH_4^+ mineralization are not inconsistent with observed redistributions of ^{15}N.

Controls on gross rates of N assimilation

Our final set of simulations exhibited high rates of gross assimilation of NH_4^+ (about 2–4 times plant N uptake) and NO_3^- (0.7–1.3 times plant N uptake; Tables 3 and 4). At the same time, an important source of agreement between simulated and observed patterns of PR^{15}N arose from the ultimate limitation on detrital–microbial pools in competing against plant demand. The increase in PR^{15}N in plants in fertilized vs. ambient plots arose in TRACE simulations because under fertilization, pools of plant-available NH_4^+ and NO_3^- rose faster than did gross transfers of N to plant-unavailable (i.e., detrital organic) pools in soils.

Bioavailability of carbon substrates may be a factor ultimately limiting microbial activity (Lynch 1982) and gross rates of N turnover in soils (Hart et al. 1994).

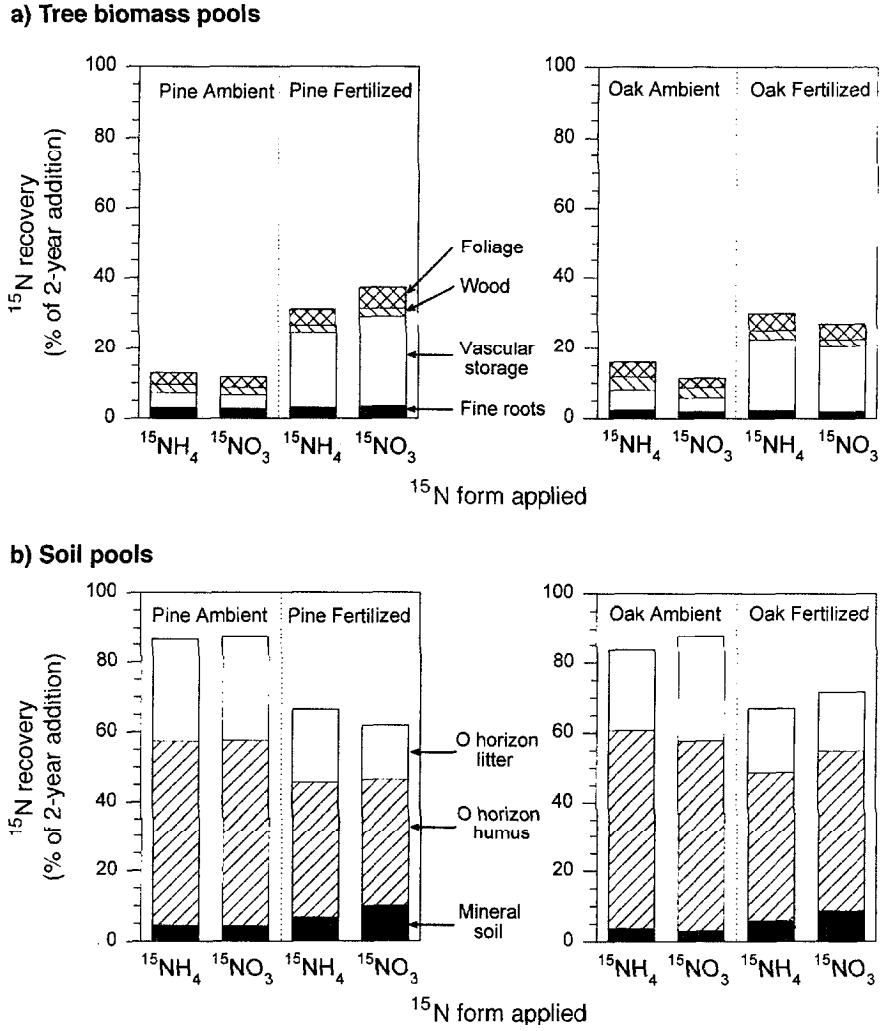

FIG. 5. Predicted percent recovery ($PR^{15}N$) for total mass of ^{15}N tracers added over two growing seasons in TRACE prediction set C: (a) vegetation; (b) soils. O horizon litter refers to a sum of the O-horizon carbon classes. Mineral soil includes fine root litter and SOM in mineral soil. Field data for comparison are provided by Nadelhoffer et al. (1999).

Applying mathematical models to interpret ^{15}N data from fine-scale mineral-soil incubations, Hadas et al. (1992) calculated a microbial C-use efficiency of 0.40, while Stark and Hart (1997) calculated values ranging from 0.25 to 0.53. Koopmans and van Dam (1998), optimizing the NICCCE (Nitrogen Isotopes and Carbon Cycling in Coniferous Ecosystems) model (van Dam and van Breemen 1995) for ecosystem-level ^{15}N tracer recoveries, calculated a microbial efficiency of 0.57, also finding this to be one of the most sensitive parameters in their model. In TRACE, gross N assimilation in nonhumified litter was fixed by microbial C-use efficiencies in each C class, while we varied the gross N turnover in humified matter (Table 2). We can back-calculate the microbial efficiency implied by a given view of C and N use by humus decomposers. If humus itself supplied the C for respiration and microbial growth, and production of complete fungal or bacterial

TABLE 4. Microbial nitrogen fluxes (g $N \cdot m^{-2} \cdot yr^{-1}$) in whole soil as simulated by TRACE (prediction set C for 1992).

N flux	Pine forest		Oak forest	
	Ambient	Fertilized	Ambient	Fertilized
Gross mineralization	35.1	39.9	38.6	42.4
Gross nitrification	8.3	9.4	6.4	7.0
Gross assimilation of NH_4^+	23.2	25.4	25.6	26.2
Gross assimilation of NO_3^-	7.0	7.7	6.7	8.0

biomass resulted, then if P_H is biomass production, ΔH is OM mass loss, and biomass is included implicitly in the detrital pool H:

$$e_H = \frac{P_H}{P_H + \Delta H} \tag{14}$$

$$P_H n_m = F_{A,H}. \tag{15}$$

We can substitute H for L_i in Eq. 5 and solve for $F_{A,H}$, substitute into Eq. 15, and further substitute from Eqs. 6 and 9 to write P_H in terms of the gross : net ratio of N mineralization from humified matter:

$$P_H = \frac{(1 - \rho)}{n_m} \frac{N_H}{H} \Delta H \left(\frac{F_{M,H}}{f_{M,H}} - 1 \right). \tag{16}$$

In our simulations for Harvard Forest, humus C:N $\approx$ 19, and $\rho \approx 0.58$. For the high gross assimilation rates in sets B and C of TRACE predictions (Table 4), this yields a microbial efficiency of 0.81 on humus. This result is sensitive to the C:N ratio of microbial biomass; we used 17:1 (the average among fungal biomass on leaves and wood and bacterial biomass on leaves, as reviewed in Swift et al. 1979). Had we used half that value, e.g., as observed by Hart et al. (1994), Eqs. 14 and 16 would yield a microbial efficiency on humus of 0.68. These values are unrealistically high (particularly for NO_3^- assimilation).

We conclude therefore that the high rates of gross transfer of N to unavailable pools must arise partly from mechanisms other than production of complete microbial biomass from detrital C. Other sources of C or energy, or other mechanisms of N incorporation into detrital–microbial pools, must be considered as possibilities. Throughfall or litter-derived DOC would not represent additional substrates, because TRACE already includes these within a balanced C budget. Aber (1992) suggested a potential importance of plant-derived C in driving soil N turnover through root exudation or mycorrhizal supply. TRACE included no such C source in the present study. Chemical incorporation of inorganic N directly into detrital pools has been suggested (Johnson 1992). Still another possibility may be fungal production of N-rich exoenzymes, at C:N ratios much narrower than that of microbial biomass, which then enter unavailable pools. Fungi break down large molecules through production of exoenzymes that bind to substrates (Ljungdahl and Eriksson 1985) and can be difficult to remove from soil (Stevenson 1986). Exoenzymes could be complexed by tannins or other polyphenolics, including polyfunctional intermediates of decomposition.

N retention in the forest floor vs. mineral soil

TRACE captured the high rate of ^{15}N retention in forest floors, but underpredicted the movement of ^{15}N to mineral soils. Could TRACE have underestimated the downward leaching fluxes of ^{15}N over this time interval? Patterns in the field data are inconclusive. Mineral-soil $PR^{15}N$ was greater under higher N inputs, and under $^{15}NO_3^-$ vs. $^{15}NH_4^+$ labels, indicating that leaching may have been significant. TRACE did predict both of these patterns for inorganic N eluviation. Leaching has been indicated as an important means of $^{15}NO_3^-$ movement in coniferous forests in British Columbia (Preston et al. 1990) and The Netherlands (Koopmans et al., 1996), and a mixed deciduous–coniferous forest in Maine (Nadelhoffer et al. 1992). The pattern of differences in mineral-soil $PR^{15}N$ between the two stands at the Harvard Forest, however, appears incongruous with leaching as the reason for the high $PR^{15}N$ in mineral soil of the oak stand. In these plots, leaching fluxes of NO_3^-, NH_4^+, and DON from the forest floor were all greater in the pine stand (Currie et al. 1996). We ran TRACE using long-term average climate in order to facilitate smoother predictions of isotope redistributions with clear interpretations. In 1992, actual precipitation in spring was 15% below, in summer was 30% above, and in fall was 25% below the long-term averages. Greater-than-average leaching in summer may have moved ^{15}N to deeper horizons; the answer may be that leaching carried more ^{15}N to deeper, unsampled soil horizons in the pine stand. An alternative explanation of the patterns of ^{15}N recovery might be greater root uptake in the forest floor of the oak stand, followed by translocation of N to roots downward into the upper mineral soil. In these plots, however, neither biomass nor N concentration of fine roots had increased after 3 yr at this level of fertilization (5 $g \cdot m^{-2} \cdot yr^{-1}$) in the upper mineral soil of the oak forest (Hendricks 1994). Thus, the means of movement of ^{15}N into the mineral soil of the oak forest remains unresolved.

Model structure

We have equated plant-available N with KCl-extractable, inorganic N throughout this analysis. If plants or their mycorrhizal symbionts take up organic N at this site, it is difficult to assess the impact on our results. Various hypotheses may be that mycorrhizae take up compounds forming from condensation with polyphenols in foliar litter (Northup et al. 1995), or from all pools of organic N in soil. If uptake of organic N is significant, research is required to identify the sources before such a mechanism can be synthesized into models like TRACE.

We viewed as a success the fact that we modeled soil pools based on what could be resolved in the observation dataset. This led us to model soil–detrital pools as implicitly containing microbial biomass. Separating microbial biomass explicitly would have meant introducing additional parameters concerning both microbial transformations and the relative significance or insignificance of abiotic reactions transferring inorganic N into organic pools (Nommik 1965, Davidson et al. 1991, Johnson 1992). Constructing empirical pools in TRACE allowed us to avoid making conten-

tious hypotheses about detailed mechanisms. The value of this approach can be debated. A criticism is that pool dilution calculations in TRACE assume that pools are homogeneous and well-mixed whenever N is exported from a pool, whereas we know that microbes and detritus are distinct, presumably with different N turnover kinetics. To answer this criticism, we point out that our conclusions regarding the strength of soil–detrital sinks for $^{15}NH_4^+$ and $^{15}NO_3^-$ remain valid even though each soil–detrital pool has internal structure with heterogeneous internal kinetics. Our conclusions about sink strength are based on the observed entry of ^{15}N into soil detrital pools as opposed to vegetation, not on the release of ^{15}N from soil detrital pools. The empirically "lumped" pools exhibited strong sinks for ^{15}N. Likewise, our calculation of implied microbial C-use efficiency is still valid within the assumptions stated, because it relies not on turnover of detrital pools but simply on the exhibited sink strength for ^{15}N.

The criticism regarding pool kinetics does mean that our values for gross mineralization are more speculative, because they rely on extrapolation from rates of assimilation to kinetics of turnover. Still, TRACE results for ratios of gross to net mineralization are within the range of values reported elsewhere. In fine-scale studies of ectorganic horizons in forest soils, this ratio calculated through the use of mathematical models and ^{15}N tracer data has ranged from 2:1 and higher (Tietema 1998) to greater than 7:1 (Davidson et al. 1992). Best agreement with field data in plant vs. soil recovery of ^{15}N was produced with TRACE when this ratio ranged from about 4:1 to 6:1 over entire solums (compare Tables 3 and 4), driven largely by a ratio of 12:1 in humus. (The over-prediction of $PR^{15}N$ in humus suggests that high gross N sinks may be more evenly distributed among other detrital pools).

Implications and conclusions

TRACE explicitly illustrated the manner in which rates of gross N assimilation in soils could be structured to provide very strong sinks for $^{15}NH_4^-$ and $^{15}NO_3^-$ in ambient plots, while limited enough to allow much greater uptake of ^{15}N by vegetation in fertilized plots. The ectorganic horizon was a particularly important sink for ^{15}N. In other studies as well, retention of N in the forest floor has been found to be an important facet of ecosystem N retention through ^{15}N tracer recovery (Tietema et al. 1998), budgeting (Currie et al. 1996), and regional gradient analysis (Gundersen et al. 1998).

When soil sinks are overcome, or higher rates of N mineralization lead to increased primary production (Aber et al. 1993, Reich et al. 1997), C inputs to soil detritus should increase, with complex influences on both soil N retention and ecosystem C storage. Clearly, to understand the implications of these interactions, C controls on gross rates of N turnover in soils need to be better understood, evidenced by the unreasonably high microbial C-use efficiency required for putative production of microbial biomass in TRACE. In another combined large-scale manipulation and ^{15}N modeling study in The Netherlands, using an alternative modeling approach, Koopmans and van Dam (1998) similarly concluded that processes in the soil organic layer were understood insufficiently.

For managing the landscape-scale losses of N from forests to surface waters, Gardner et al. (1996) emphasized the need to scale results of process-level studies up to landscapes. A simulation model like TRACE can be ideal, when linked to a Geographic Information System, for translating results to larger scales if the causes of landscape-scale heterogeneity in patterns and processes are correctly captured by the model (King 1991, Levin 1992, Currie and Aber 1997). Soil detrital processes are key in determining C/N interactions in forests and the availability of N to vegetation. Yet current understanding of these processes is inadequate, limiting our insight into large-scale patterns of N retention and controls on C budgets in forests.

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Literature Cited

Aber, J. D. 1992. Nitrogen cycling and nitrogen saturation in temperate forest ecosystems. Trends in Ecology and Evolution **7**:220–223.

Aber, J. D., and C. T. Driscoll. 1997. Effects of land use, climate variation and N deposition on N cycling and C storage in northern hardwood forests. Global Biogeochemical Cycles **11**(4):639–648.

Aber, J. D., A. Magill, R. Boone, J. M. Melillo, P. Steudler, and R. Bowden. 1993. Plant and soil responses to three years of chronic nitrogen additions at the Harvard Forest, Massachusetts. Ecological Applications **3**:156–166.

Aber, J. D., A. M. Magill, S. G. McNulty, R. D. Boone, K. J. Nadelhoffer, M. Downs, and R. Hallett. 1995*a*. Forest biogeochemistry and primary production altered by nitrogen saturation. Water, Air and Soil Pollution **85**:1665–1670.

Aber, J. D., C. A. McClaugherty, and J. M. Melillo. 1984. Litter decomposition in Wisconsin forests—mass loss, organic-chemical constituents and nitrogen. School of Natural Resources, University of Wisconsin-Madison, Madison, Wisconsin, USA.

Aber, J. D., J. M. Melillo, and C. A. McClaugherty. 1990. Predicting long-term patterns of mass loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. Canadian Journal of Botany **68**:2201–2208.

Aber, J. D., J. M. Melillo, K. J. Nadelhoffer, J. Pastor, and R. D. Boone. 1991. Factors controlling nitrogen cycling

and nitrogen saturation in northern temperate forest ecosystems. Ecological Applications **1**:303–315.

Aber, J. D., K. J. Nadelhoffer, P. Steudler, and J. M. Melillo. 1989. Nitrogen saturation in northern forest ecosystems. BioScience **39**:378–386.

Aber, J. D., S. V. Ollinger, and C. T. Driscoll. 1997. Modeling nitrogen saturation in forest ecosystems in response to land use and nitrogen deposition. Ecological Modelling **101**:61–78.

Aber, J. D., S. V. Ollinger, C. A. Federer, P. B. Reich, M. L. Goulden, D. W. Kicklighter, J. M. Melillo, and R. G. J. Lathrop. 1995*b*. Predicting the effects of climate change on water yield and forest production in the northeastern US. Climate Research **5**:207–222.

Aber, J. D., P. B. Reich, and M. L. Goulden. 1996. Extrapolating leaf CO_2 exchange to the canopy: a generalized model of forest photosynthesis validated by eddy correlation. Oecologia **92**:463–474.

Alban, D. H., and J. Pastor. 1993. Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. Canadian Journal of Forest Research **23**:1744–1749.

Barford, C., and K. Lajtha. 1992. Nitrification and nitrate reductase-activity along a secondary successional gradient. Plant and Soil **145**:1–10.

Berg, B. 1986. Nutrient release from litter and humus in coniferous forest soils—a mini review. Scandinavian Journal of Forest Research **1**:359–369.

Berg, B., et al. 1993. Litter mass loss rates in pine forests of Europe and Eastern United States: some relationships with climate and litter quality. Biogeochemistry **20**:127–159.

Bowden, R. D., J. M. Melillo, P. A. Steudler, and J. D. Aber. 1991. Effects of nitrogen additions on annual nitrous oxide fluxes from temperate forest soils in the Northeastern United States. Journal of Geophysical Research—Atmospheres **96**:9321–9328.

Currie, W. S. 1995. Forest floor leachate biogeochemistry and decomposition dynamics. Dissertation. Institute for the Study of Earth, Oceans and Space, University of New Hampshire, Durham, New Hampshire, USA.

Currie, W. S., and J. D. Aber. 1997. Modeling leaching as a decomposition process in humid, montane forests. Ecology **78**:1844–1860.

Currie, W. S., J. D. Aber, W. H. McDowell, R. D. Boone, and A. H. Magill. 1996. Vertical transport of dissolved organic C and N under long-term N amendments in pine and hardwood forests. Biogeochemistry **35**:471–505.

Davidson, E. A., S. C. Hart, and M. K. Firestone. 1992. Internal cycling of nitrate in soils of a mature coniferous forest. Ecology **73**:1148–1156.

Davidson, E. A., S. C. Hart, C. A. Shanks, and M. K. Firestone. 1991. Measuring gross nitrogen mineralization, immobilization, and nitrification by 15-N isotope dilution in intact soil cores. Journal of Soil Science **42**:335–349.

Davidson, E. A., J. M. Stark, and M. K. Firestone. 1990. Microbial production and consumption of nitrate in an annual grassland. Ecology **71**:1968–1975.

Downs, M. R., K. J. Nadelhoffer, J. M. Melillo, and J. D. Aber. 1996. Immobilization of a 15N-labelled nitrate addition by decomposing forest litter. Oecologia **105**:141–150.

Emmett, B. A., and C. Quarmby. 1991. The effect of harvesting intensity on the fate of applied N-15-ammonium to the organic horizons of a coniferous forest in N. Wales. Biogeochemistry **15**:47–63.

Fahey, T. J., J. W. Hughes, M. Pu, and M. A. Arthur. 1988. Root decomposition and nutrient flux following whole-tree harvest of northern hardwood forest. Forest Science **34**(3): 744–768.

Galloway, J. N. 1995. Acid deposition: perspectives in time and space. Water, Air and Soil Pollution **85**:15–24.

Gardner, R. H., M. S. Castro, R. P. Morgan, and S. W. Seagle. 1996. Perspectives on Chesapeake Bay: nitrogen dynamics in forested lands of the Chesapeake Basin. Chesapeake Research Consortium Publication Number 151, Edgewater, Maryland, USA.

Gundersen, P. 1991. Nitrogen deposition and the forest nitrogen cycle role of denitrification. Forest Ecology and Management **44**:15–28.

Gundersen, P., B. A. Emmett, O. J. Kjønaas, C. J. Koopmans, and A. Tietema. 1998. Impacts of nitrogen deposition on nitrogen cycling: a synthesis. Forest Ecology and Management **101**:37–55.

Hadas, A., J. A. E. Molina, S. Feigenbaum, and C. E. Clapp. 1992. Factors affecting nitrogen immobilization in soil as estimated by simulation-models. Soil Science Society of America Journal **56**(5):1481–1486.

Harmon, M. E., J. Sexton, B. A. Caldwell, and S. E. Carpenter. 1994. Fungal sporocarp mediated losses of Ca, Fe, K, Mg, Mn, N, P, and Zn from conifer logs in the early stages of decomposition. Canadian Journal of Forest Research **24**: 1883–1893.

Hart, S. C., G. E. Nason, D. D. Myrold, and D. A. Perry. 1994. Dynamics of gross nitrogen transformations in an old-growth forest: the carbon connection. Ecology **75**:880–891.

Hendricks, J. J. 1994. Assessing the effects of nitrogen availability on fine root turnover and tissue chemistry in forest ecosystems. Dissertation. Institute for the Study of Earth, Oceans, and Space, University of New Hampshire, Durham, New Hampshire, USA.

Hobbie, E. A. 1997. Insights into N dynamics during succession: linking isotopic evidence and modeling. Dissertation. Department of Environmental Sciences, University of Virginia, Charlottesville, Virginia, USA.

Jackson, L. E., J. P. Schimel, and M. K. Firestone. 1989. Short-term partitioning of nitrate and ammonium between plants and microbes in an annual grassland. Soil Biology and Biochemistry **21**:409–415.

Johnson, D. W. 1992. Nitrogen retention in forest soils. Journal of Environmental Quality **21**(1):1–12.

King, A. W. 1991. Translating models across scales in the landscape. *In* M. G. Turner and R. H. Gardner, editors. Quantitative methods in landscape ecology. Ecological Studies **82**:479–517.

Kirkham, D., and W. V. Bartholomew. 1954. Equations for following nutrient transformations in soil, utilizing tracer data. Soil Science Society of America Proceedings **18**:33–34.

Koopmans, C., and D. van Dam. 1998. Modelling the impact of lowered atmospheric nitrogen deposition on a nitrogen saturated forest ecosystem. Water Air and Soil Pollution. **104**:181–203.

Koopmans, C., A. Tietema, and A. W. Boxman. 1996. The fate of ^{15}N enriched throughfall in two coniferous forest stands at different nitrogen deposition levels. Biogeochemistry **34**:19–44.

Lang, G. E., C. S. Cronan, and W. A. Reiners. 1981. Organic matter and major elements of the forest floors and soils in subalpine balsam fir forests. Canadian Journal of Forest Research **11**:388–399.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology **73**:1943–1967.

Ljungdahl, L. G., and K.-E. Eriksson. 1985. Ecology of microbial cellulose degradation. Advances in Microbial Ecology **8**:237–299.

Lynch, J. M. 1982. Limits to microbial growth in soil. Journal of General Microbiology **128**:405–410.

Magill, A. H., J. D. Aber, J. J. Hendricks, R. D. Bowden, J. M. Melillo, and P. A. Steudler. 1997. Biogeochemical response of forest ecosystems to simulated chronic nitrogen deposition. Ecological Applications **7**:402–415.

McClaugherty, C. A., J. D. Aber, and J. M. Melillo. 1984.

Decomposition dynamics of fine roots in forested ecosystems. Oikos **42**:378–386.

Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. Ecology **59**:465–472.

Melillo, J. M., J. D. Aber, A. E. Linkins, A. Ricca, B. Fry, and K. J. Nadelhoffer. 1989. Carbon and nitrogen dynamics along the decay continuum: plant litter to soil organic matter. Plant and Soil **115**:189–198.

Molina, J. A., C. E. Clapp, M. J. Shaffer, F. W. Chichester, and W. E. Larson. 1983. NCSOIL, a model of nitrogen and carbon transformations in soil: description, calibration, and behavior. Soil Science Society of America Journal **47**: 85–91.

Nadelhoffer, K. J., J. D. Aber, M. R. Downs, B. Fry, and J. M. Melillo. 1993. Biological sinks for nitrogen additions to a forested catchment. Pages 64–70 *in* L. Rasmussen, T. Brydges, and P. Mathy, editors. Experimental manipulations of biota and biogeochemical cycling in ecosystems. Proceedings of a symposium held 18–20 May 1992 in Copenhagen, Denmark. Commission of the European Communities, Directorate-General for Science, Research and Development, Brussels, Belgium.

Nadelhoffer, K. J., M. Downs, and B. Fry. 1999. Sinks for N additions to an oak forest and a red pine plantation at the Harvard Forest, Massachusetts, USA. Ecological Applications **9**:72–86.

Nadelhoffer, K. J., M. R. Downs, B. Fry, J. D. Aber, A. H. Magill, and J. M. Melillo. 1995. The fate of ^{15}N-labelled nitrate additions to a northern hardwood forest in eastern Maine, USA. Oecologia **103**:292–301.

Nadelhoffer, K. J., and B. Fry. 1994. Nitrogen isotope studies in forest ecosystems. Pages 22–44 *in* K. Lajtha and R. Michener, editors. Stable isotopes in ecology. Blackwell Scientific, Oxford, UK.

Nommik, H. 1965. Ammonium fixation and other reactions involving a nonenzymatic immobilization of mineral nitrogen in soil. Pages 198–257 *in* W. V. Battholomew and F. E. Clark, editors. Soil nitrogen. 10th edition. American Society of Agronomy, Madison, Wisconsin, USA.

Northup, R. R., Z. Yu, R. A. Dahlgren, and D. A. Vogt. 1995. Polyphenol control of nitrogen release from pine litter. Nature **377**:227–229.

Pastor, J., and W. M. Post. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. Biogeochemistry **2**:3–27.

Persson, T., and A. Wiren. 1995. Nitrogen mineralization and potential nitrification at different depths in acid forest soils. Plant and Soil **168–169**:55–65.

Peterjohn, W. T., M. B. Adams, and F. S. Gilliam. 1996. Symptoms of nitrogen saturation in two central Appalachian hardwood forest ecosystems. Biogeochemistry **35**: 507–522.

Preston, C. M., V. G. Marshall, K. McCullough, and D. J. Mead. 1990. Fate of 15N-labelled fertilizer applied on snow at two forest sites in British Columbia. Canadian Journal of Forest Research **20**:1583–1592.

Reich, P. B., D. F. Grigal, J. D. Aber, and S. T. Gower. 1997. Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. Ecology **78**:335–347.

Ryan, M. G., J. M. Melillo, and A. Ricca. 1990. A comparison of methods for determining proximate carbon fractions of forest litter. Canadian Journal of Forest Research **20**:166–171.

Schimel, D. S. 1993. Theory and application of tracers. Academic Press, San Diego, California, USA.

Schimel, J. P., and M. K. Firestone. 1989. Nitrogen incorporation and flow through a coniferous forest soil profile. Soil Science Society of America Journal **53**:779–784.

Schimel, J. P., L. E. Jackson, and M. K. Firestone. 1989. Spatial and temporal effects on plant–microbial competition for inorganic nitrogen in a California annual grassland. Soil Biology and Biochemistry **21**:1059–1066.

Schindler, D. W., and S. E. Bayley. 1993. The biosphere as an increasing sink for atmospheric carbon: estimates from increasing nitrogen deposition. Global Biogeochemical Cycles **7**:717–734.

Stark, J. M., and S. C. Hart. 1997. High rates of nitrification and nitrate turnover in undisturbed coniferous forests. Nature **385**:61–64.

Stevenson, F. J. 1986. Cycles of soil. Carbon, nitrogen, phosphorus, sulfur, micronutrients. John Wiley and Sons, New York, New York, USA.

Stoddard, J. L. 1994. Long-term changes in watershed retention of nitrogen: its causes and aquatic consequences. Pages 223–284 *in* L. A. Baker, editor. Environmental chemistry of lakes and reservoirs. Advances in Chemistry Series Number 237. American Chemical Society, Washington, D.C., USA.

Swift, M. J., O. W. Heal, and J. M. Anderson. 1979. Decomposition in terrestrial ecosystems. University of California Press, Berkeley, California, USA.

Tietema, A. 1998. Microbial carbon and nitrogen transformations in litter from coniferous forest ecosystems along an atmospheric nitrogen input gradient. Forest Ecology and Management **101**:29–36.

Tietema, A., W. Deboer, L. Riemer, and J. M. Verstraten. 1992. Nitrate production in nitrogen-saturated acid forest soils—vertical-distribution and characteristics. Soil Biology and Biochemistry **24**:235–240.

Tietema, A., B. A. Emmett, P. Gundersen, O. J. Kjönaas, and C. J. Koopmans. 1998. The fate of ^{15}N-labelled nitrogen deposition in coniferous forests. Forest Ecology and Management **101**:19–27.

Tietema, A., and D. van Dam. 1996. Calculating microbial carbon and nitrogen transformations in acid forest litter with 15-N enrichment and dynamic simulation modeling. Soil Biology and Biochemistry **28**(7):953–965.

Tietema, A., and W. W. Wessel. 1992. Gross nitrogen transformations in the organic layer of acid forest ecosystems subjected to increased atmospheric nitrogen input. Soil Biology and Biochemistry **24**:943–950.

Townsend, A. R., B. H. Braswell, E. A. Holland, and J. E. Penner. 1996. Spatial and temporal patterns in terrestrial carbon storage due to deposition of fossil fuel nitrogen. Ecological Applications **6**:806–814.

Van Cleve, K., and S. Martin, editors. 1991. Long-term ecological research in the United States. Sixth revised edition. Long-Term Ecological Research Network Office, University of Washington, Seattle, Washington, USA.

van Dam, D., and N. van Breemen. 1995. NICCCE: a model for turnover of nitrogen and carbon isotopes in coniferous forest ecosystems. Ecological Modelling **79**:255–275.

Vitousek, P. M., J. R. Gosz, C. C. Grier, J. M. Melillo, and W. A. Reiners. 1982. A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. Ecological Monographs **52**:155–177.

Wessel, W. W., and A. Tietema. 1992. Calculating gross N transformation rates of ^{15}N pool dilution experiments with acid forest litter: analytical and numerical approaches. Soil Biology and Biochemistry **24**(10):931–942.

Wright, R. F., and A. Tietema. 1995. Ecosystem response to 9 years of nitrogen addition at Sogndal, Norway. Forest Ecology and Management **71**:133–142.

Zak, D. E., P. M. Groffman, K. S. Pregitzer, S. Christensen, and J. M. Tiedje. 1990. The vernal dam: plant–microbe competition for nitrogen in northern hardwood forests. Ecology **71**:651–656.

APPENDIX

Summary of TRACE input parameters needed for site-specific applications. Values used for application at the Harvard Forest are listed. The final version of the model presented here is TRACE 2.1.

Parameter	Description	Value	
		Pine forest	Oak forest
Photosynthesis and water budget†			
FolReten	Foliar retention time (yr)	2.25	1
WHC	Water-holding capacity in rooting zone (cm)	12	12
k	Canopy light attenuation constant (m^2/m^2)	0.50	0.58
SLWMax	Specific leaf mass at canopy top (g/m^2)	200	100
GDDFolStart	Growing degree-days for foliar expansion to begin	900	100
GDDFolEnd	Growing degree-days for foliar expansion to end	1600	900
Litter parameters			
FoLPctN	Ambient N content in foliar litter (g/g dry mass)	0.006	0.009
RLPctN	Ambient N content in fine root litter (g/g dry mass)	0.012	0.012
WLPctN	Ambient N content in woody litter (g/g dry mass)	0.0015	0.0015
FpctACI	Acid-insoluble fraction of foliar litter (% ash-free dry mass)	29.6	31.5
FpctACS	Acid-soluble fraction of foliar litter (% ash-free dry mass)	40.4	39.4
FpctTEX	Total extractives fraction of foliar litter (% ash-free dry mass)	30.1	29.1
RpctACI	Acid-insoluble fraction of fine root litter (% ash-free dry mass)	24.5	27.5
RpctACS	Acid-soluble fraction of fine root litter (% ash-free dry mass)	29	38.2
RpctTEX	Total extractives fraction of fine root litter (% ash-free dry mass)	46.5	34.3
FWDFrac	Fraction of woody litter that is FWD; remainder being CWD	0.36	0.36
Soil processes			
k_H	Decay rate of humus ($month^{-1}$)	0.00116	0.00116
γH	Ratio of turnover rates: mineral SOM to O-horizon humus	0.22	0.22
DOMsorbFrac	Fraction of DOC and DON fluxes from Oa, sorbed in mineral soil	0.5	0.5
η(O)	Ratio of gross nitrification to gross N mineralization, O horizon	0.2	0.15
η(M)	Ratio of gross nitrification to gross N mineralization, mineral soil	0.3	0.2

† A complete list of photosynthesis and hydrology parameters from PnET-CN appears in Aber and Driscoll (1997).