

Anthropogenic N Deposition Increases Soil C Storage by Decreasing the Extent of Litter Decay: Analysis of Field Observations with an Ecosystem Model

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ABSTRACT

Recent meta-analyses of experimental studies simulating increased anthropogenic nitrogen (N) deposition in forests reveal greater soil carbon (C) storage under elevated levels of atmospheric N deposition. However, these effects have not yet been included in ecosystem-scale models of soil C and N cycling and it is unclear whether increased soil C storage results from slower decomposition rates or a reduced extent of decomposition (for example, an increase in the amount of litter entering slowly decaying humus pools). To test these alternatives, we conducted a meta-analysis of litter decomposition data. We then used the results from our meta-analysis to model C and N cycling in four sugar maple forests in Michigan using an ecosystem process model (TRACE). We compared

model results testing our alternative hypotheses to field data on soil C storage from a 17-year N deposition experiment. Using data from published litter decomposition studies in forests, we determined that, on average, exogenous N inputs decreased lignin decomposition rates by 30% and increased cellulose decomposition by 9%. In the same set of litter decomposition studies increased exogenous N availability increased the amount of litter entering slowly decaying humus pools in a manner significantly related to the lignocellulose index of decaying litter. Incorporating changes to decomposition rates in TRACE did not accurately reproduce greater soil C storage observed in our field study with experimentally elevated N deposition. However, when changes in the extent of decomposition were incorporated in TRACE, the model produced increased soil C storage by increasing the amount of litter entering the humus pool and accurately represented C storage in plant and soil pools under experimental N deposition. Our modeling results and meta-analysis indicate that the extent of litter decay as humus is formed, rather than slower rates of litter decay, is likely responsible for the accumulation of organic matter, and hence soil C storage, under experimental N

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deposition. This effect should be incorporated in regional to global-scale models simulating the C balance of forest ecosystems in regions receiving elevated N deposition.

Key words: ecosystem model; nitrogen deposition; soil carbon storage; hardwood forests; limit value; litter decomposition.

INTRODUCTION

Atmospheric nitrogen (N) deposition has been increasing since pre-industrial times (Galloway and others 2004; IPCC 2007), wherein the anthropogenic production of reactive N presently exceeds natural N fixation by a factor of two. Increasing atmospheric N deposition affects terrestrial ecosystems through changes in plant community composition, net primary productivity (NPP), and soil carbon (C) storage. In N-limited northern temperate forests, anthropogenic N can increase biomass and NPP, and therefore ecosystem C storage (Townsend and others 1996; Magnani and others 2007; LeBauer and Treseder 2008; Sutton and others 2008; Xia and Wan 2008; Liu and Greaver 2010). Recent syntheses of experimental N deposition also demonstrate increased C storage in forest soils resulting from the slowing of microbial decay (Knorr and others 2005; Janssens and others 2010; Liu and Greaver 2010). However, the potential for atmospheric N deposition to increase soil C storage through decreased decomposition has gone unexplored in models of ecosystem biogeochemistry (Zak and others 2008).

The process of litter decay from fresh litter to soil organic matter can be conceived in three stages. After initial leaching of soluble compounds, the first phase of decomposition is dominated by cellulose metabolism, which is influenced by nutrient availability and environmental conditions (Berg and Staaf 1980; Melillo and others 1989; Berg 2000a, b). During this phase of decay, exogenous inorganic N stimulates the activities of cellulose degrading organisms, thereby accelerating decomposition (Fog 1988; Carreiro and others 2000; Knorr and others 2005). In the second phase of decomposition, decay is dominated by the microbial metabolism of lignin and lignified carbohydrates and is therefore regulated by the rate of lignin decay (Berg and Staaf 1980; Melillo and others 1989; Berg 2000a, b). At this point, decomposition rates can decrease with greater amounts of exogenous inorganic N, due to a reduction in the activity of lignolytic enzymes such as phenol oxidase (Fog 1988; Carreiro and others 2000; Sinsabaugh and others 2005; Knorr and others 2005). As a result, effects of exogenous N on

soil C storage in experimental studies depend both on the litter biochemistry (Carreiro and others 2000; Waldrop and others 2004; Keeler and others 2009) and the stage of decomposition examined (Fog 1988; Berg and Matzner 1997; Neff and others 2002; Knorr and others 2005; Hobbie 2008).

In addition to changes in decomposition rates during the first two phases of decay, exogenous N also influences the amount of organic material that fails to decompose during the first two phases, thus entering a final, more recalcitrant phase. During this stage of decay, the lignocellulose index, or ratio of lignin to lignin plus cellulose, reaches a constant level (approximately 0.7), and decomposition continues at a very slow pace (Berg and Staaf 1980; Melillo and others 1989; Berg 2000a, b). During this phase, the mixture of secondary compounds and organic residues that remain become increasingly dominated by humic substances and can essentially be considered humified matter, whether in the O horizon or in mineral soil. Depending on temperature and moisture regimes, oxygen availability, and the activities of soil fauna, humus can continue to decompose; however, in temperate forests it does so at a much slower rate, typically an order of magnitude less than the rate of fresh litter decay. Investigators have described the cumulative percentage of mass loss from fresh litter, before it reaches the stage of humus or stabilized organic matter, as the "limit value" of decomposition for a particular litter in a particular ecosystem. The limit value can be quantified using the asymptote of an exponential decay function fit to observations in field incubations (Berg and others 1996, 2000; Berg 2000a, b; Harmon and others 2009). Limit values of litter decomposition, which range from 35 to 100% of accumulated mass loss, are often negatively correlated with litter N concentration, meaning N-rich litter has a lower limit value of decomposition (Berg and others 1996, 2000; Berg 2000a, b; Berg and Meentemeyer 2002). If exogenous N decreases the limit value, then the extent of decay in the first two stages of decomposition will decline, that is, there will be an increased amount of material entering the phase of humus or stabilized organic matter, and soil C storage should increase over time.

We constructed hypotheses for changes in decomposition that could be responsible for in-

creases in the accumulation of organic matter in forest floor and surface mineral soil observed under elevated N deposition in our field studies. We hypothesized that increases in organic matter - under elevated N were due either to: (1) decreases in the rate of decomposition resulting from decreased lignin decomposition, despite an increased rate of cellulose decomposition; or due to (2) decreases in the extent of decomposition resulting in greater production of stabilized organic matter. To test these alternatives and examine the relevant importance of changes in decomposition rate and extent on soil C storage, we used field results from a 17-year N deposition experiment, a meta-analysis of data from published litter decomposition studies, and a biogeochemical process model of coupled forest C and N cycling, Tracer Redistributions Among Compartments in Ecosystems (TRACE); Currie and others 1999). The strength of using such a model is that it not only simulates decomposition but also includes C and N interactions such as immobilization and mineralization in soils, plant physiology such as tissue allocation and resorption of C and N, and ecosystem-level feedbacks through litter production and plant N uptake. We simulated C and N cycling in four sugar maple stands receiving ambient and experimental N deposition using TRACE and compared model results to field observations. Our goal was to gain an increased understanding of the interaction of fine-scale processes, by which atmospheric N deposition slows decay, with the ecosystem-level outcome of greater organic matter and C accumulation in the forest floor and surface soil.

METHODS

Our study sites are four ecologically and edaphically matched sugar maple-dominated northern hardwood forests in northern Michigan, all of which have received ambient and experimental N deposition treatments since 1994. We calibrated TRACE at one of the forest stands under ambient N deposition. We then ran TRACE under both ambient and experimental N deposition scenarios at all four forest stands without further changing model parameters or model structure. Our model runs started in 1930 when all four forest stands were approximately 20 years of age (Burton and others 2004) and ran for 170 years. We used a meta-analysis of published litter decomposition data to test our hypotheses that increased exogenous N (1) alters the rate of litter decomposition or (2) alters the proportion of litter entering slowly decaying soil organic matter pools. To examine

how changes in the rate and extent of decomposition altered soil biogeochemistry and C storage, we developed three alternative model versions. These three model versions incorporated results from our meta-analysis; one with altered decomposition rates of litter (Rate Model), one with lower limit values of litter decomposition (Extent Model), and one with both altered rates and lower limit values (Rate and Extent Model). We then compared model results from the original version and the three modified versions of TRACE to field data from the 17-year N deposition experiment to determine whether altered decomposition rates or extent had a great influence on observed changes in soil C storage.

Study Sites

The four forests we studied have similar soil properties, overstory composition, and age of re-establishment after logging (Pregitzer and others 2004; Zak and others 2006). In each location, three 30-m by 30-m plots receive ambient N deposition and three plots of the same dimensions receive ambient N deposition plus $3 \text{ g NO}_3^- \text{ N m}^{-2} \text{ y}^{-1}$. The additional N is delivered to the forest floor in six equal applications of NaNO_3 pellets during the growing season (May–September). Detailed descriptions of site characteristics and experimental methods have previously been provided (Burton and others 2004; Pregitzer and others 2004; Zak and others 2006).

Model Structure and Parameterization

To explore ecosystem feedbacks and interactions mediating biogeochemical responses to increased N deposition, we used the TRACE model of ecosystem processes (Figure 1). TRACE was developed to examine fluxes of C and N (including N stable isotopes) within ecosystems and was initially parameterized for use with N fertilization experiments at Harvard Forest, Massachusetts (Currie and Nadelhoffer 1999; Currie and others 1999, 2004). TRACE runs on a monthly time-step in Visual Basic 6 (Microsoft, Inc.). Within TRACE, plant physiology (including photosynthesis) is based on the PnET-CN model (Aber and others 1997) and soil C and N cycling are adapted from the DOCMOD model (Currie and Aber 1997). Pools within TRACE were chosen to represent measurable pools whenever possible, making model-data comparisons for soil C pools possible. To that end, the microbial community is represented within TRACE as part of the soil and litter C and N pools. C and N pools within litter and the organic horizon are divided into three operationally defined fractions:

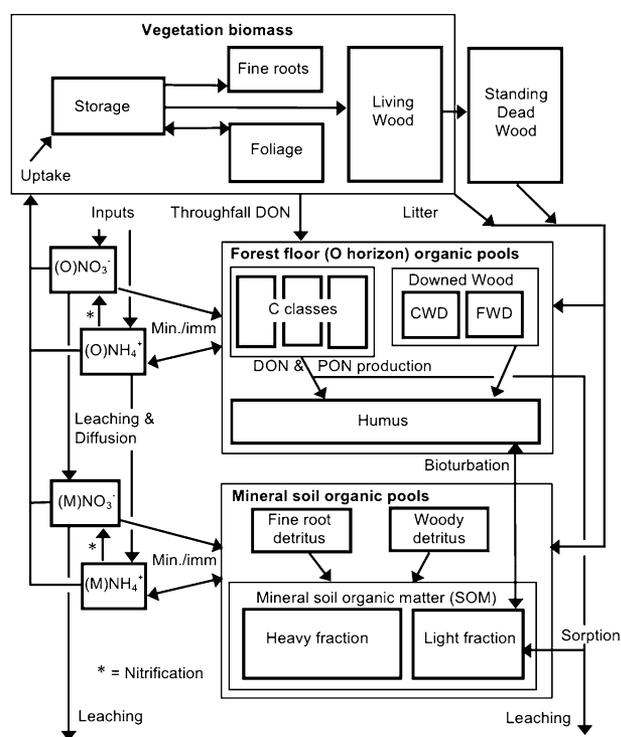


Figure 1. Diagram of TRACE model structure (Currie and others 1999). *DON* dissolved organic nitrogen; *PON* particulate organic nitrogen; *CWD* coarse woody debris; *FWD* fine woody debris; *min./imm.* mineralization and immobilization; $(O)NH_4^+$ organic soil layer ammonium; $(O)NO_3^-$ organic soil layer nitrate; $(M)NH_4^+$ mineral soil layer ammonium; $(M)NO_3^-$ mineral soil layer nitrate.

total extractives (polar and non-polar extractable compounds), acid soluble C (including cellulose and hemicellulose), and acid insoluble C (including lignin; Ryan and others 1990). In addition, the organic and mineral soil horizons contain pools of C and N in a separate humus pool. Prior versions of TRACE allowed for interactions between climate and litter lignin content to control decomposition rates, but did not include effects of increased N availability on litter decomposition rates or extent.

For each of the four sugar maple stands described above, we developed a set of input variables including climate, ambient N deposition, and initial pool sizes of C and N in vegetation and soils. Where possible, we obtained site-specific parameter values; however, when parameter values were not available for our study sites, we used either published results for North American sugar maple forests or mixed northern hardwoods containing sugar maple (Supplementary materials, Table S.1). For non-site-specific parameters, we used values previously tested for hardwood forests at Harvard Forest (Currie and Nadelhoffer 1999; Currie and

others 1999, 2004). To initialize soil pools of C and N, we assumed the forest stands were winter logged and had similar species composition prior to logging (Zak, *personal observations*); therefore, we set initial soil organic matter pools to present day values for each stand due to the lack of soil disturbance following harvesting (Supplementary materials, Table S.1). Climate data (monthly mean maximum temperature, monthly mean minimum temperature, and total monthly precipitation) were downloaded from NOAA (www.ncdc.noaa.gov/daily-form/) using the closest weather monitoring site to each forest stand (Hancock Houghton County Airport, Houghton County, MI for Site A; Pellston Regional Airport, Emmet County, MI for Site B; Mantisee 3e, Mantisee County, MI for Site C; and Muskegon County Airport, Muskegon County, MI for Site D). We used ArcGIS (ESRI, Inc.) to obtain spatially explicit photosynthetically active radiation and wet and dry N deposition data for all four study sites from previously created raster data layers; wet and dry N deposition raster datasets were adapted from Holland and others (2004). Monthly averages of daily mean irradiance, used to create our raster dataset, were estimated by Kittel and others (2004).

Anthropogenic N-Induced Changes in Litter Decomposition

To examine N-induced changes in the rate and limit value of litter decomposition, we compiled a database of litter decomposition studies from several N addition experiments in boreal, temperate, and tropical forests (Magill and Aber 1998; Prescott 1995; Prescott and others 1999; Hobbie 2000; Hobbie and Vitousek 2000; Thirukkumaran and Parkinson 2000; Table S.2; Figures 2, 3). We included only studies which had ambient N deposition and elevated N deposition treatments, with no other nutrients added (for example, N addition, but not N and phosphorous or N and sulfur additions). All the experiments included in our database have published decay curves of litter mass remaining throughout a litter decomposition experiment. We used DigitizeIt (Bormissoft, Inc.) to extract data from figures in those papers that did not report exact values for litter mass remaining over time.

For each individual litter study, we used linear regression to determine the slope of initial decay (during the first 12 months of decomposition) and slope of late stage decay (defined as after the first 12 months of decomposition) in both control and N addition treatments. To determine whether changes in decomposition rates were related to the amount of N added or the litter lignocellulose index (LCI, defined

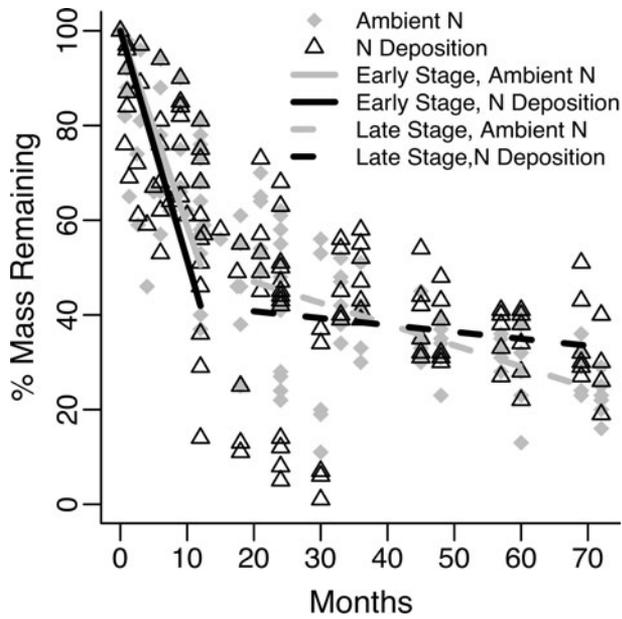


Figure 2. Mass remaining data from leaf litter decomposition experiments under ambient N deposition (*gray diamonds*) and N addition (*open triangles*) used to calculate changes in decomposition rates with N addition (Magill and Aber 1998; Prescott 1995; Prescott and others 1999; Hobbie 2000; Hobbie and Vitousek 2000; Thirukkumaran and Parkinson 2000). Tree species include *Pinus resinosa*, *Acer rubrum*, *Betula lenta*, *Quercus velutina*, *Pinus contorta*, *Meterosideros polymorpha*, and *Populus tremuloides*. Average rates of decomposition used to calculate in model modifications for the “Rate Model” and “Rate and Extent Model” in the present analysis: early phase decomposition (*solid lines*) and second phase decomposition (*dashed lines*) under ambient N deposition (*gray lines*) and elevated N deposition (*black lines*).

as acid-insoluble mass/(acid-soluble + acid-insoluble mass); Aber and others 1990), we used linear regression across all studies. All linear regression analyses were completed using R (www.r-project.org, 2010). We determined that N addition decreased lignin decomposition rates by 30% and increased cellulose decomposition by 9%, on average (Figure 2). There were no significant relationships between the rate of early stage decomposition and either lignocellulose index or the amount of N added to decomposing litter (Regression: N: $F_{1,20} = 4.25$, $P = 0.052$, $R^2 = 0.18$; LCI: $F_{1,19} = 2.65$, $P = 0.12$, $R^2 = 0.076$), or significant relationships between the rate of late stage decomposition and either N addition to litter or litter lignocellulose index (Regression: N: $F_{1,15} = 0.2018$, $P = 0.66$, $R^2 = 0.013$; LCI: $F_{1,15} = 0.094$, $P = 0.76$, $R^2 = 0.007$). Therefore, we increased decomposition in the acid-soluble C pool (which includes celluloses, primarily decomposed during early stages of decay) within TRACE by

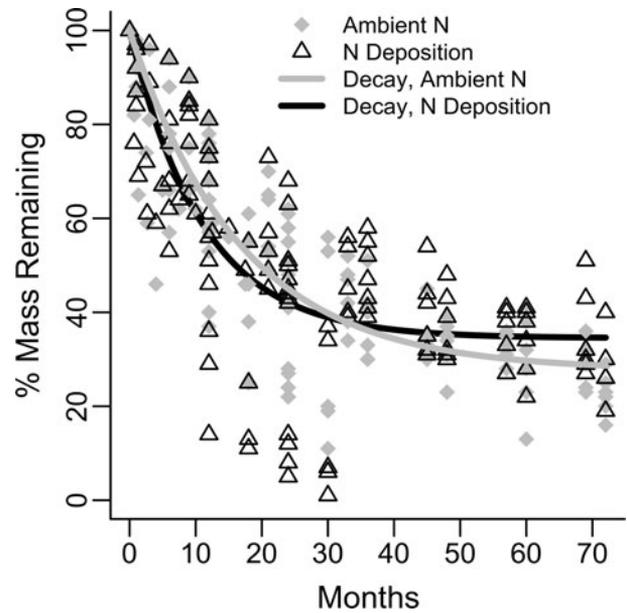


Figure 3. Mass remaining data from leaf litter decomposition experiments under ambient N deposition (*gray diamonds*) and N addition (*open triangles*) used to calculate changes in decomposition extent with N addition (Magill and Aber 1998; Prescott 1995; Prescott and others 1999; Hobbie 2000; Hobbie and Vitousek 2000; Thirukkumaran and Parkinson 2000). Lines represent average decomposition under ambient N deposition (*gray line*) and elevated N deposition (*black line*) used to calculate in model modifications for the “Extent Model” and the “Rate and Extent Model” in the present analysis.

multiplying the decay by a factor of 1.09 and decreased the decomposition of the acid insoluble C pool (which includes lignin, primarily decomposed during the late stages of decay) by multiplying the decay by a factor of 0.7 (Table 1). We will henceforth refer to this model version as the Rate Model, because it represents changes in the decomposition rate with elevated N deposition.

To analyze changes in decomposition limit values we fit an exponential decay model with an asymptote to each set of litter decomposition data for both control and N addition treatments (Figure 3). To fit exponential decay curves, we used the drc package (<http://cran.r-project.org/web/packages/drc/index.html>) for analyzing dose response curves in R using the following equation (Harmon and others 2009):

$$M(t) = (100 - A) * e^{-kt} + A \quad (1)$$

where $M(t)$ is the percent of initial litter mass remaining at time t (year), A (%) is the material that remains after the early phases of decomposition (the asymptote of the decay curve), and k is

Table 1. Decomposition Rate and Humification Rate Parameters Differing among TRACE Model Versions in the Current Analysis

Parameter description	Original Model	Rate Model	Extent Model	Rate and Extent Model
N effect on acid soluble carbon decay	1.00	1.09	1.00	1.09
N effect on acid insoluble carbon decay	1.00	0.70	1.00	0.70
N effect on transfer of litter to humus	1.00	1.00	4.00	4.00

the decomposition rate constant (γ^{-1}). We calculated the decomposition limit value as

$$LV = 100 - A \tag{2}$$

where LV (%) is the decomposition limit value and A is as in equation (1). Limit values calculated as part of our meta-analysis ranged from 47 to 91% (data not shown), within the range of limit values from the published literature of 35 to 100% (Berg and others 1996).

We calculated the percent change in extent of decomposition in response to exogenous N as:

$$\Delta E = (E_C - E_N)/E_C \tag{3}$$

where ΔE is the percent change in the maximum extent of decomposition, E_C is the maximum extent in the control treatment, and E_N is the maximum extent with exogenous N. We then used linear regression to determine if the change in decomposition extent was correlated with either the amount of N added to decomposing litter or the initial litter lignocellulose index (LCI). In our literature database, the asymptote of litter decomposition (A in equation 1) was approximately 60% higher with exogenous N addition, relative to ambient N; therefore, N addition increased the amount of litter entering the humus pool (Figure 3), lessening the extent of decay. This relationship was dependent on the initial LCI of litter (Regression: $F_{1,13} = 10.55$, $P = 0.006$, $R^2 = 0.41$), but not the amount of exogenous N (Regression: $F_{1,14} = 0.011$, $P = 0.92$, $R^2 = -0.071$). Therefore, the effect of N addition on the maximum extent of decomposition was as follows:

$$\Delta E_{LCI} = -4.54 + 16.131 * LCI \tag{4}$$

where ΔE_{LCI} is the change in the maximum extent of decomposition in relation to the litter LCI. Because the limit value represents the point at

which decomposition slows to a very low rate, it can be represented in TRACE as the amount of litter entering the slowly decomposing humus pool. Therefore, we added the change in limit value to TRACE as an increase in the litter transfer to humus by multiplying humus transfer by a factor of $1 + \Delta E_{LCI}$ (Table 1). We will henceforth refer to this model version as the Extent Model, because it represents a change in the extent of decomposition with elevated N deposition.

Model Runs and Data Analysis

We simulated C and N cycling in all four study sites using four different model versions and two levels of N deposition consisting of (1) the “Original Model” (for the present analysis this is TRACE 4.5 as described by Currie and others (2004)) under ambient N and experimental N deposition, (2) the “Rate Model” (with altered cellulose and lignin decomposition rates) under experimental N deposition, (3) the “Extent Model” (with altered decomposition limit values) under experimental N deposition, and (4) the “Rate and Extent Model” (with altered decomposition rates and limit values) under experimental N deposition. This approach allowed us to test the relative importance of altered decomposition rates and limit values for increased soil C storage under elevated N deposition. For each of the 20 combinations of model version, N deposition treatment, and field site, we performed a multivariate Monte Carlo analysis to examine uncertainty in model predictions. We created a set of 50 parameter input files in which we varied a subset of model parameters (63/155 parameters) stochastically and independently, using the identical parameter variations for all 20 sets of model runs to allow direct comparison among model versions. Within the set of parameter input files, each parameter varied independently within a normal distribution with a mean equal to the nominal value and a standard deviation of 10% of the nominal value (Currie and Nadelhoffer 1999). The first of the 50 input files included all parameters at their nominal values. Parameters perturbed in the Monte Carlo analysis included those that were not known constants or empirical coefficients, were not site-specific climate or input parameters, and were not internally calculated. Examples of parameters which varied stochastically include the rates of plant photosynthesis and respiration, the growing season length, the foliar and fine root litter chemistry, the ratio of gross to net N mineralization, and the rate of humus decay. We used the program R (www.r-project.org) to analyze the

results from the 800 model runs beginning by calculating means and standard deviations of all pools and fluxes within TRACE in each year for each model by treatment by site combination. We then used analysis of variance in R to examine differences among sites, differences between ambient and experimental N deposition for the “Original Model,” and differences among the three model versions under experimental N deposition.

RESULTS

TRACE accurately modeled pools and fluxes of C and N under ambient N deposition within Site B; how-

ever, TRACE dampened differences among sites (Table 2). Although modeled foliar and fine-root N concentrations were within 10% of field data for Site B and within 20% of field data across all sites, modeled N concentrations were uniformly higher than field results for the ambient N deposition treatment (Table 2). Modeled foliar and woody NPP were within 20% of field data at Site B, but increases in foliar NPP across the gradient observed in field data did not occur to the same extent in the model (Table 2). With the exception of Site C, TRACE reproduced (within 15%) the organic horizon C:N ratio measured in the field for the ambient N treatment (Table 2). Organic horizon mass was lower in

Table 2. Field Data and Model Results for Major Ecosystem C and N Pools and Fluxes under Ambient and Experimental N Deposition

Sites	Ambient N deposition				Experimental elevated N deposition									
	Field data*		Original Model		Field data*		Original Model		Rate Model		Extent Model		Rate and Extent Model	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Organic horizon C:N														
A	27.8	2.10	31.4	0.61	25.1	2.10	27.1	0.22	27.7	0.23	24.4	0.20	24.7	0.20
B	29.3	1.70	27.5	0.29	37.2	5.40	26.4	0.19	26.9	0.19	23.1	0.16	23.4	0.16
C	39.8	2.60	28.0	0.69	44.6	4.30	23.1	0.25	23.7	0.24	22.7	0.18	22.9	0.19
D	26.9	0.60	26.8	0.50	37.7	9.20	23.6	0.20	24.1	0.22	22.3	0.19	22.6	0.20
Foliar N (%)														
A	1.77	0.14	2.08	0.03	2.31	0.10	2.11	0.03	2.12	0.02	2.18	0.03	2.19	0.03
B	1.96	0.08	2.15	0.03	2.29	0.07	2.16	0.03	2.16	0.03	2.21	0.03	2.20	0.03
C	1.95	0.04	2.09	0.03	2.25	0.09	2.11	0.03	2.09	0.03	2.08	0.03	2.08	0.03
D	1.99	0.08	2.10	0.03	2.29	0.08	2.10	0.03	2.11	0.03	2.12	0.03	2.12	0.03
Fine root N (%)														
A	1.21	0.18	1.15	0.03	1.35	0.08	1.36	0.03	1.32	0.03	1.30	0.03	1.31	0.03
B	1.41	0.17	1.38	0.05	1.45	0.05	1.46	0.04	1.44	0.04	1.51	0.04	1.51	0.04
C	1.38	0.07	1.15	0.04	1.40	0.07	1.53	0.04	1.58	0.04	1.48	0.04	1.48	0.04
D	1.45	0.01	1.30	0.05	1.05	0.08	1.60	0.04	1.57	0.03	1.50	0.04	1.50	0.04
Foliar NPP (g m ⁻² y ⁻¹)														
A	302	41.0	262	6.2	316	10.0	280	7.1	280	7.0	286	7.0	283	6.8
B	333	13.6	277	6.5	363	14.8	280	6.5	279	6.5	286	6.1	286	6.2
C	377	17.5	291	6.1	371	38.2	318	6.1	323	6.8	329	5.2	322	5.7
D	440	48.6	311	6.5	477	13.6	322	5.5	316	5.6	315	5.4	316	5.8
Woody NPP (g m ⁻² y ⁻¹)														
A	425	13.1	441	12.9	503	9.6	439	11.7	440	11.5	461	14.3	467	16.1
B	547	17.7	443	13.0	658	80.8	445	12.9	444	12.9	458	12.5	456	12.6
C	651	23.1	759	20.7	748	81.2	1118	62.7	1044	60.2	1088	61.1	1036	53.7
D	638	92.5	680	20.8	721	32.5	800	40.7	816	44.2	902	48.6	880	47.6
Fine root NPP (g m ⁻² y ⁻¹)														
A			225	5.8			240	7.0	242	6.9	245	6.9	243	6.9
B			238	6.6			240	6.5	240	6.5	245	6.4	245	6.5
C			250	6.3			275	7.1	277	7.1	274	5.9	267	6.2
D			266	7.2			277	6.9	275	7.1	271	6.7	269	7.0

NPP = net primary productivity; OM = organic matter; C:N = carbon to nitrogen ratio; SE = standard error. * Burton and others (1991), Pregitzer and others (2008), and Zak and others (2008).

modeled results than under field conditions, with the exception of Site A; however, modeled values fell within one standard error of measured organic horizon mass for ambient N deposition (Figure 4).

Unlike field results in the experimental N deposition treatment, TRACE produced significant increases in foliar, woody, and fine root NPP (Table 2; ANOVA: foliar: $F_{3,310} = 6.36$, $P = 0.012$; woody: $F_{3,310} = 9.55$, $P = 0.002$; fine root: $F_{3,310} = 5.17$, $P = 0.024$). However, this simulated response in foliar NPP was minor and smaller than model-data discrepancies under either ambient or elevated N treatments (Table 2). TRACE did not reproduce increases in foliar N concentrations observed under experimental N deposition in the field (Table 2); however, TRACE did show increases in fine root NPP with experimental N deposition across all four sites, similar to field results for Sites A, B, and C (Table 2).

Although the “Original Model” produced a significant increase in organic horizon mass with experimental N deposition relative to ambient (Table 2; Figure 4; ANOVA: $F_{3,310} = 4.01$, $P = 0.046$), the increases were much smaller than those observed in the field. On average, increases in organic horizon mass under experimental N deposition in the “Original Model” were only 5% of observed increases in organic horizon mass in field experiments (Table 2). Different model versions produced differences in mass of the organic horizon under experimental N deposition with the highest organic horizon masses occurring with the “Extent Model” and the “Rate and Extent Model” (Figure 4; ANOVA: $F_{2,463} = 155.97$, $P < 0.001$; Tukey’s HSD: $\alpha = 0.05$). There were no significant differences in organic horizon mass between the “Original Model” and the “Rate Model” or between the “Extent Model” and the “Rate and Extent Model,” indicating no significant increases in soil C storage with altered decomposition rates alone (Figure 4; Tukey’s HSD: $\alpha = 0.05$). Only model versions with an altered extent of decomposition approached the magnitude of change in organic matter mass observed in field results (Figure 4). Changes in organic horizon mass in the “Extent Model” and the “Rate and Extent Model” were accompanied by increases in the organic horizon humus pool and decreases in the organic horizon litter pool (Figure 4). Altering decomposition rate and extent within TRACE did not lead to significant differences in NPP among model versions (Table 2; ANOVA: foliar: $F_{3,623} = 0.33$, $P = 0.81$; woody: $F_{3,623} = 0.73$, $P = 0.53$; fine root: $F_{3,623} = 0.079$, $P = 0.97$). This latter result indicated that direct effects of decomposition, not changes in production, were responsible for the modeled increases in mass of the organic soil horizon.

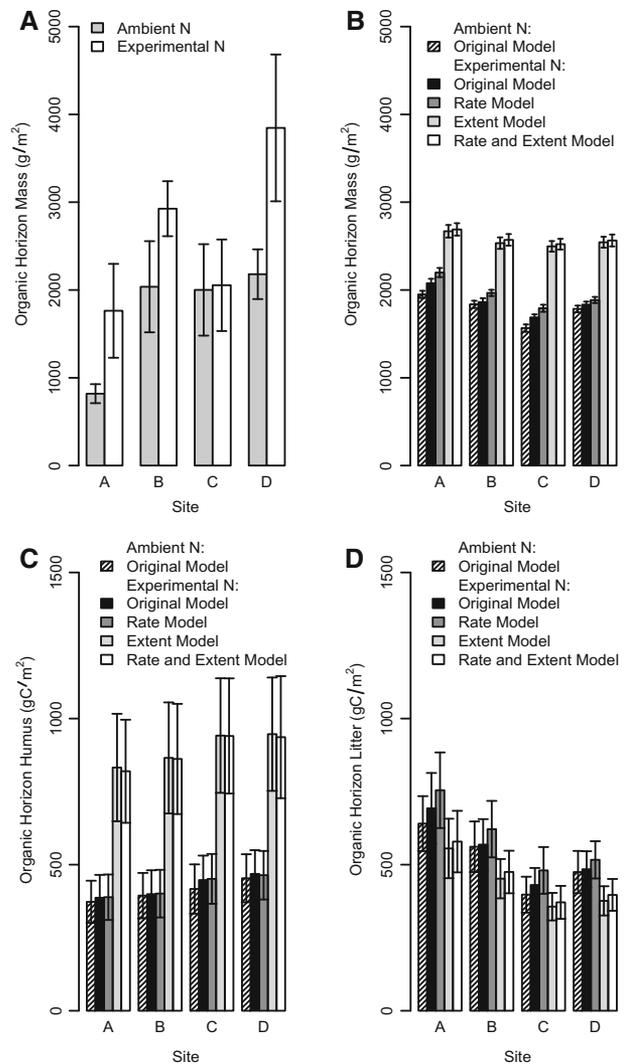


Figure 4. Organic horizon mass in **A** field plots and **B** model results under ambient and experimental (elevated) N deposition. Model results for organic horizon **C** humus C pools and **D** litter C pools under ambient and elevated N deposition. Here we present model results from the “Original Model” for both ambient and experimental N deposition, and results from the “Rate Model,” the “Extent Model,” and the “Rate and Extent Model” under experimental N deposition.

DISCUSSION

Our results indicate that increases in the extent of litter mass entering the humus pool before decomposition rather than simply changes in decomposition rate lead to increases in soil C storage under experimental N deposition. When both the rate and the extent of decomposition were altered in TRACE changes in the extent of decomposition had a much greater effect on soil C storage than changes in the rate of decomposition. The

mechanism for this change in model results was an increase in humus pools of C in the organic horizon, despite decreases in faster decomposing litter C pools. This result is supported by empirical evidence from field studies examining changes in long-term decomposition with experimental N addition which demonstrated declines in the extent of decomposition of 20–50% (Magill and Aber 1998; Sinsabaugh and others 2002). Increasing DOC export with elevated N deposition observed in field studies under elevated N deposition (Currie and others 1996; Pregitzer and others 2004; Liu and Greaver 2010) is also consistent with increasing production of humic substances in soils. Some of these humic substances would be soluble and leach to ground and surface waters, whereas others remain in soil, increasing soil C storage. Our results emphasize the importance of multi-year (to decade or longer) studies of how elevated N deposition affects soil C storage, because the effects of changes in the extent of decay may take years to decades to appear as stabilized material accumulates.

One hypothesis proposed for increasing soil C storage, due to transfer of a greater proportion of soil organic matter to humus, is alterations in the chemical composition of soil organic matter through reactions with exogenous N. As litter decomposes, inorganic N reacts with phenols and lignin enhancing the formation of recalcitrant compounds by increasing the randomization of chemical bonds which decreases the efficiency of extracellular enzymes mediating litter decay (Fog 1988; Berg and Matzner 1997; Carreiro and others 2000). Therefore, it is hypothesized that higher N availability might produce a greater proportion of recalcitrant compounds which enter humus rather than decomposing during the first two phases of decomposition (Fog 1988; Berg and Matzner 1997; Knorr and others 2005; Janssens and others 2010). Our results from the present modeling analysis and decomposition meta-analysis are consistent with this mechanism, indicating that decreases in the extent of decomposition are important for increasing C sequestration in forest soils under elevated N deposition.

Another hypothesis proposed for increased soil C storage with elevated N deposition is altered extent of decomposition due to changes in the microbial community. Altered microbial community composition may lead to shifts in microbial resource use and therefore reduced decomposition of soil organic matter. In field studies, N addition leads to reduced microbial biomass and often leads to decreased fungal to bacterial ratios (Compton and others 2004; Frey and others 2004; Wallenstein and others 2006; Treseder 2008; Liu and Greaver 2010; van Diepen and

others 2010). In addition, there is evidence for changes in microbial community composition under experimental N deposition (Hofmockel and others 2007; Zak and others 2008). Decreases in the amounts or activities of lignin degrading fungi would decrease both the rate of lignin decay and the amount of substrate accessible to other microbes as celluloses may remain chemically protected within lignin molecules. This could be an important mechanism for increasing the amount of litter mass eventually stabilized as humic substances, as indicated in our meta-analysis and simulated in our modeling analysis.

Within TRACE, changes in decomposition rates alone were not sufficient to produce observed increases in soil C storage produced by experimental N deposition under field conditions. Although there is evidence from field incubations that the rate of litter decomposition may decrease with elevated N deposition, these changes in rates do not appear to be sufficient to alter soil C storage over decadal time scales as observed at our field sites. Rates of heterotrophic respiration from the forest floor decrease by 15% on average with N addition, but there is large variability in the effect of elevated N deposition on respiration between studies and over time (Bowden and others 2004; Burton and others 2004; Frey and others 2004; Zak and others 2006; Janssens and others 2010; Liu and Greaver 2010). In addition, changes in extracellular oxidative enzyme activity with N addition are highly variable from study to study showing an increase or decrease depending on species composition, but even among forests with relatively similar composition (Carreiro and others 2000; Saiya-Cork and others 2002; Sinsabaugh and others 2002, 2005; DeForest and others 2004; Frey and others 2004; Gallo and others 2004; Waldrop and Zak 2006; Keeler and others 2009).

Despite large differences in ecosystem-level C and N cycling between model versions, leading to differences in organic horizon C storage, there were no differences in foliar NPP among model versions. This is consistent with the fact that experimental N deposition did not stimulate production of either aboveground or belowground litter in our field experiment (Burton and others 2004; Pregitzer and others 2008, 2010; Zak and others 2008), suggesting these sites are already N rich. This is supported by high N mineralization rates in sugar maple forests as compared to N mineralization rates in other Great Lakes forests (Zak and others 1993), as well as the substantial leaching loss (~75% of added N) of N under our experimental N deposition treatment (Pregitzer and others 2004). Furthermore, Liu and Greaver (2010) report that experimental N addition increases aboveground litter fall by 20%

on average across a variety of forest and grassland ecosystems, indicating NPP is more responsive to changes in N availability at other sites. However, both model predictions and field data show an increase in bolewood production with N addition (Pregitzer and others 2008), which may increase C storage in soils over longer timescales through increase woody litter inputs.

Areas receiving elevated N deposition, including forests, are expected to increase in geographic extent in coming decades (Galloway and others 2008). Changes in litter decomposition and soil organic matter production are an important factor determining ecosystem C balance, a set of dynamics that will be altered by future rates of anthropogenic N deposition in an uncertain manner. Our present modeling results, conducted as a direct analysis of our field studies across a long-term, large-scale field manipulation of atmospheric N deposition, indicate that changes in the extent, or end point, of litter decomposition should be incorporated into regional, biome, or global-scale models of C and N cycling to accurately simulate changes in ecosystem C storage. Further research is needed to determine the importance of litter biochemistry, levels of N deposition, edaphic factors, and variability among climates and forest types in controlling the changes in decomposition extent that may result from anthropogenic N deposition.

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