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Simulated chronic nitrogen deposition increases carbon storage in Northern Temperate forests

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Abstract

High levels of atmospheric nitrogen (N) deposition in Europe and North America were maintained throughout the 1990s, and global N deposition is expected to increase by a factor of 2.5 over the next century. Available soil N limits primary production in many terrestrial ecosystems, and some computer simulation models have predicted that increasing atmospheric N deposition may result in greater terrestrial carbon (C) storage in woody biomass. However, empirical evidence demonstrating widespread increases in woody biomass C storage due to atmospheric N deposition is uncommon. Increased C storage in soil organic matter due to chronic N inputs has rarely been reported and is often not considered in computer simulation models of N deposition effects. Since 1994, we have experimentally simulated chronic N deposition by adding 3 g N m^{-2} yr^{-1} to four different northern hardwood forests, which span a 500 km geographic gradient in Michigan. Each year we measured tree growth. In 2004, we also examined soil C content to a depth of 70 cm. When we compared the control treatment with the NO_3^- deposition treatment after a decade of experimentation, ecosystem C storage had significantly increased in both woody biomass (500 g C m^{-2}) and surface soil (0–10 cm) organic matter (690 g C m^{-2}). The increase in surface soil C storage was apparently driven by altered rates of organic matter decomposition, rather than an increase in detrital inputs to soil. Our results, for study locations stretching across hundreds of kilometers, support the hypothesis that chronic N deposition may increase C storage in northern forests, potentially contributing to a sink for anthropogenic CO_2 in the northern Hemisphere.

Keywords: carbon sink, global change, litter decomposition, microbial biomass, net primary productivity, soil

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Introduction

On a global scale, an unidentified terrestrial carbon (C) sink accounts for 15% to 30% or more of annual C emissions from anthropogenic activities (Field, 2001; Myneni *et al*., 2001). It is thought that this sink may exist in northern forests, above the 30th parallel, including the temperate forests of North America (Myneni *et al*., 2001). Greater tree growth due to 'CO_2 fertilization' appears to have the potential to account for no more than one half of the missing C sink, in part due to nutrient limitation (Field, 2001). A recent analysis of temperate and boreal forests in western Europe and the United States suggests that a portion net forest C sequestration is clearly driven by nitrogen (N) deposition (Högberg, 2007; Magnani *et al*., 2007), and certain simulation models suggest that atmospheric N deposition in temperate and boreal forests may be an important process contributing to the missing global C sink (White *et al*., 2000; Pepper *et al*., 2005). However, other modeling efforts, based in part on long-term N addition studies, suggest that elevated N deposition will result in relatively small increases in C storage after several decades, occurring primarily in living and dead wood (Currie *et al*., 2004). Furthermore, empirical evidence from the short-term study of ^{15}N cycling in North America and Europe suggests that tree growth, and hence C storage in woody biomass, would not respond to atmospheric N deposition (Nadelhoffer *et al*., 1999).

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Fig. 1 Locations of four northern hardwood research sites in Michigan, USA.

The potential for atmospheric N deposition to increase soil C storage via a reduction in decomposition (Berg & Meentemeyer, 2002; Waldrop *et al.*, 2004) is a mechanism that is not considered or predicted by most simulation models (White *et al.*, 2000; Pepper *et al.*, 2005).

In 1994, we began studying the effects of chronic atmospheric N deposition on northern hardwood forests by experimentally adding NO_3^- ($3\,g\,NO_3^-$-$N\,m^{-2}\,yr^{-1}$ as $NaNO_3$) to four northern hardwood sites in Michigan (Fig. 1). While each of the four study sites is representative of the typical soil and vegetation of this region, their locations span 500 km along a climatic and N deposition gradient. Nitrate contributes approximately 60% of wet N deposition in this region, and the experimental rates of N addition are approximately two to four times the ambient total N deposition rate over wide areas in the industrialized north central and northeastern US (MacDonald *et al.*, 1992; Harding ESE Inc., 2002). However, these rates are equal to or less than atmospheric N deposition in portions of Europe and at high deposition locations in the United States, where inputs already equal or exceed $3.0\,g\,N\,m^{-2}\,yr^{-1}$ (Fenn *et al.*, 1998; MacDonald *et al.*, 2002).

After a decade of experimental chronic N deposition, all four of our study sites have rapidly approached N saturation, a condition in which a large amount of N is exported to groundwater via leaching. Currently, 65–70% of experimentally added N annually leaches from the chronic NO_3^- deposition treatment in either organic or inorganic forms (Pregitzer *et al.*, 2004). Through the use of stable isotopes, we have learned that the portion of added NO_3^- assimilated by the microbial community rapidly turns over, with its subsequent mineralization creating elevated NH_4^+ in soil solution (Zak *et al.*, 2006). The trees assimilate the majority of NH_4^+ that is mineralized by the microbial community (Zak *et al.*, 2006). Soil organic matter is not a significant short-term sink for N additions in our experiment (Zak *et al.*, 2004), with added N incorporated in soil organic matter only after it is returned to the soil and forest floor during annual litter fall (Zak *et al.*, 2006). We have also observed reductions in soil respiration (Burton *et al.*, 2004), microbial biomass, and the activity of the extracellular enzymes which mediate lignin degradation (Deforest *et al.*, 2004). These responses have occurred with high fidelity across the four study sites, which span hundreds of kilometers, suggesting a common set of underlying mechanisms is at work. For more than a decade, we have carefully measured tree growth and studied C cycling and storage using standard protocols. The objective of this paper is to report, for the first time, long-term changes in ecosystem C storage.

Methods

Field research locations

The four study sites (Fig. 1, Table 1) are dominated by sugar maple (*Acer saccharum* Marsh.), are similar in stand composition ($82 \pm 4\%$, mean $\pm$ 1 SE, basal area in sugar maple), age (94 ± 3 years), stand structure, and soil properties, but differ in mean annual temperature, growing season length and ambient rates of N deposition (Table 1, Burton *et al.*, 1991a; MacDonald *et al.*, 1992). These second-growth forests grow on moderately fertile soil and support high tree densities. Stand basal areas ($34.7 \pm 0.8\,m^2\,ha^{-1}$) are near the maximum for second-growth forests of this region. The average leaf area index of our study sites ($6.8 \pm 0.2\,m^2\,m^{-2}$) is high compared with most temperate deciduous forests around the world (Burton *et al.*, 1991b). The dominant soil series, Kalkaska sand (Typic haplorthod), is found throughout the upper Great Lakes States of the United States; it covers more than 300 000 ha in Michigan alone. This soil is typically dominated by second-growth northern hardwood forests, forming a soil–vegetation combination common throughout this region. Three $30\,m \times 30\,m$ control plots at each study location were established in 1987, and three $30\,m \times 30\,m$ plots receiving chronic NO_3^- deposition were established in 1993, with NO_3^- amendments initiated in 1994 ($3\,g\,NO_3^-$–$N\,m^{-2}\,yr^{-1}$ applied as $NaNO_3$ in six $0.5\,g\,m^{-2}$ increments over the growing season to a $50\,m \times 50\,m$ area centered around each treated plot). Experimental

Table 1 Selected characteristics of four northern hardwood forests in Michigan, USA

Characteristic	Site A	Site B	Site C	Site D
Latitude (N)	46°52′	45°33′	44°23′	43°40′
Longitude (W)	88°53′	84°51′	85°50′	86°09′
Mean annual precipitation* (mm)	873	871	888	812
Mean annual temperature† (°C)	4.7	6.0	6.9	7.6
Growing season length‡ (days)	134	150	154	157
Overstory age (2004)	97	91	92	96
Soil texture, 0–10 cm depth (%sand–%silt–%clay)§	75–22–3	89–9–2	89–9–2	87–10–3
Soil texture, 10–70 cm depth (%sand–%silt–%clay)§	84–11–5	88–7–5	91–6–3	92–5–3
Coarse fragments, 0–10 cm depth (%)¶	4.6	1.8	0.6	1.7
Coarse fragments, 10–70 cm depth (%)¶	7.3	7.5	1.9	3.6
Wet + dry total N deposition ($g\,N\,m^{-2}\,yr^{-1}$)‖	0.68	0.91	1.17	1.18

*Mean annual precipitation, for the years 1994–2004, was recorded using weighing rain gages (Model 5-780, Belfort Instrument Co., Baltimore, MD) located in open areas within 5 km of each site.
†Mean annual temperature, for the years 1994–2004, was recorded on site at 2 m using thermistors which were read every 30 min throughout the year, with averages recorded every 3 h using data loggers (EasyLogger Models 824 and 925, Data Loggers Inc., Logan, UT).
‡Growing season length, for the years 1994–2004, was determined annually by project personnel, based on visual estimates of >50% leaf expansion in the spring and <75% of foliage remaining in the fall.
§Particle size data from three soil pits per site, sampled as described in MacDonald *et al*. (1991).
¶Data from this study, calculated as % of total dry sample mass.
‖Data from MacDonald *et al*. (1992).

NO_3^- deposition and routine long-term measurement protocols are described in detail elsewhere (Burton *et al*., 2004; Pregitzer *et al*., 2004; Zak *et al*., 2004).

Litter inputs and N concentration

Litterfall was collected using four 0.5 m^2 litter traps in each plot. Litter was collected monthly from April through September and biweekly during periods of heavy leaf fall in October and November. Litter from a subset of traps was sorted to determine relative contributions of foliage by species, as well as woody and reproductive components. Specific leaf area, $cm^2\,g^{-1}$, of the sorted foliage was determined and used with litter mass to estimate stand leaf area index (LAI, $m^2\,m^{-2}$), as described in Burton *et al*. (1991b). Sorted foliage was also analyzed for N and C concentrations using a CE Elantech NA1500 NC elemental analyzer. Treatment effects on litter C contents (mass × concentration), C and N concentrations, C : N ratio, and LAI were assessed using a repeated measures (year) two-factor (study site × treatment) analysis of variance, using plot-level data.

The contribution of below-ground litter inputs to soil C pools was determined by multiplying fine-root (<1 mm) turnover rates for the study sites (Burton *et al*., 2000) by fine-root biomass pools (Burton *et al*., 2004), and then converting this mass to C content using fine-root C concentration data for each site (512 ± 4 $g\,C\,kg^{-1}$, mean ± 1 SE for the four sites). We have previously documented no significant changes in fine-root biomass or turnover rate due to the NO_3^- deposition treatment (Burton *et al*., 2004).

Aboveground woody biomass increment and net primary productivity

Diameter at breast height (dbh, 1.37 m height) was measured annually during the dormant season for all trees with a dbh of 5 cm or greater. Total height of each tree was measured every 5–6 years, with heights for nonmeasured years linearly interpolated between measured values. Height and diameter for each year were used to calculate aboveground woody biomass for each tree using the biomass equations for forest species common to the Great Lakes States summarized by Host *et al*. (1989). Annual values of aboveground woody biomass increment for each 30 m × 30 m plot were calculated by summing the annual woody biomass increment for all living trees on the plot for that year. When smaller trees on the plots achieved a dbh of 5 cm (ingrowth), their annual woody biomass increments were calculated annually thereafter. For trees that died during the study, annual woody biomass increment was calculated through the tree's year of death. The C content of woody biomass increment was estimated by multiplying annual increments by C concentrations from samples of the outer 2.5 cm of wood taken from trees on all research plots during August 2004 (496 ± 2 $g\,C\,kg^{-1}$, mean ± 1 SE for the 24 plots). Above-

ground net primary productivity (ANPP) for each plot was calculated by summing the C contents of aboveground woody biomass increment and nonwoody litter. We also calculated live woody biomass accumulation for each plot over the 10-year period by subtracting live woody biomass in 1994 from live woody biomass in 2004, and we determined total mortality over the 10-year period by summing the biomass of all trees dying during the study. Treatment effects on woody biomass increment and ANPP were assessed using a repeated measures (year), two-factor (study site × treatment) analysis of variance. Treatment effects on live woody biomass in 1994 and 2004, 10-year live woody biomass accumulation, and 10-year mortality biomass were assessed using a two-factor (study site × treatment) analysis of variance using the mean values for each plot.

Soil C content

During August, 2004, soil cores (10 cm dia.) were taken at three locations per plot to a depth of 70 cm using the following depth increments: 0–10, 10–30, 30–50 and 50–70 cm. The loose litter layer (Oi horizon) was removed before sampling, and the 0–10 cm increment did contain all forest floor material (Oe + a) occurring beneath the loose litter layer. Roots were removed by hand sorting from each sample, which was then passed through a 2 mm soil sieve to remove coarse fragments. Organic coarse fragments were returned to the sample, and inorganic coarse fragments (stones) were weighed and discarded.

Additional samples of the soil organic horizons were made at three random locations per plot using 30 cm × 30 cm sampling frames. The Oi and Oe + a horizons within each frame were separately collected for analysis. All mineral and organic soil samples were dried (70 °C for 48 h) and weighed, then thoroughly mixed, with subsamples ground and analyzed for C and N concentrations using the elemental analyzer. The C content of each soil depth increment and organic horizon was calculated as mass × C concentration. Treatment effects on soil C contents for each soil depth increment and organic horizon were assessed using a two-factor (study site × treatment) analysis of variance using the mean values for each plot.

Results

In our NO_3^- deposition treatment, ANPP increased significantly at all four study sites due to a greater annual woody biomass increment (Table 2, Figs 2 and 3). The response was due primarily to increased growth of trees surviving the entire period, as the contributions to woody ANPP of ingrowth trees and trees dying during the study were 0.01% and 1.6% of total woody ANPP, respectively. For both treatments, the majority of trees dying were smaller suppressed trees. The dbh of trees dying during the study period was 12.7 ± 0.5 cm (mean ± 1 SE), compared with a dbh of 23.0 ± 0.5 cm for trees surviving the entire 10-year study. The NO_3 deposition treatment did not alter the numbers of trees dying per plot (14 ± 1 for the control; 17 ± 3 for NO_3^- depositon), but it did produce greater growth rates before death for the trees that died during the study (Table 3).

The magnitude of the NO_3^- deposition effect on ANPP increased over time (Fig. 2c), suggesting that the response is due to the continual, accumulating N

Table 2 Repeated measures analysis of variance for the effects of experimental NO_3^- deposition on C contents (g C m^{-2}) of woody biomass increment, foliar litterfall, and aboveground net primary productivity (ANPP) and foliar litter N concentration (g N kg^{-1}) from 1995 through 2004

		Woody increment C		Foliar litter C		ANPP C		Foliar litter N	
Source	df	MS	$P > F$	MS	$P > F$	MS	$P > F$	MS	$P > F$
Between subjects									
Study site	3	182 401	**0.002**	19 218	**< 0.001**	327 151	**< 0.001**	26.93	**0.001**
NO_3^- deposition	1	135 806	**0.031**	627	0.492	141 457	**0.037**	102.20	**< 0.001**
Study site × NO_3^- deposition	3	766	0.992	377	0.827	1720	0.981	4.49	0.215
Error	16	24 405		1268		29 228		2.70	
Within subjects									
Year	9	13 802	**< 0.001**	5601	**< 0.001**	24 063	**< 0.001**	15.12	**< 0.001**
Year × study site	27	9580	**< 0.001**	1226	**< 0.001**	14 291	**< 0.001**	3.67	**< 0.001**
Year × NO_3^- deposition	9	2565	**0.007**	376	**0.042**	4019	**< 0.001**	2.51	**< 0.001**
Year × NO_3^- × study site	27	1743	**0.015**	227	0.230	1836	**0.049**	0.70	**0.003**
Error	144	969		187		1170		0.33	

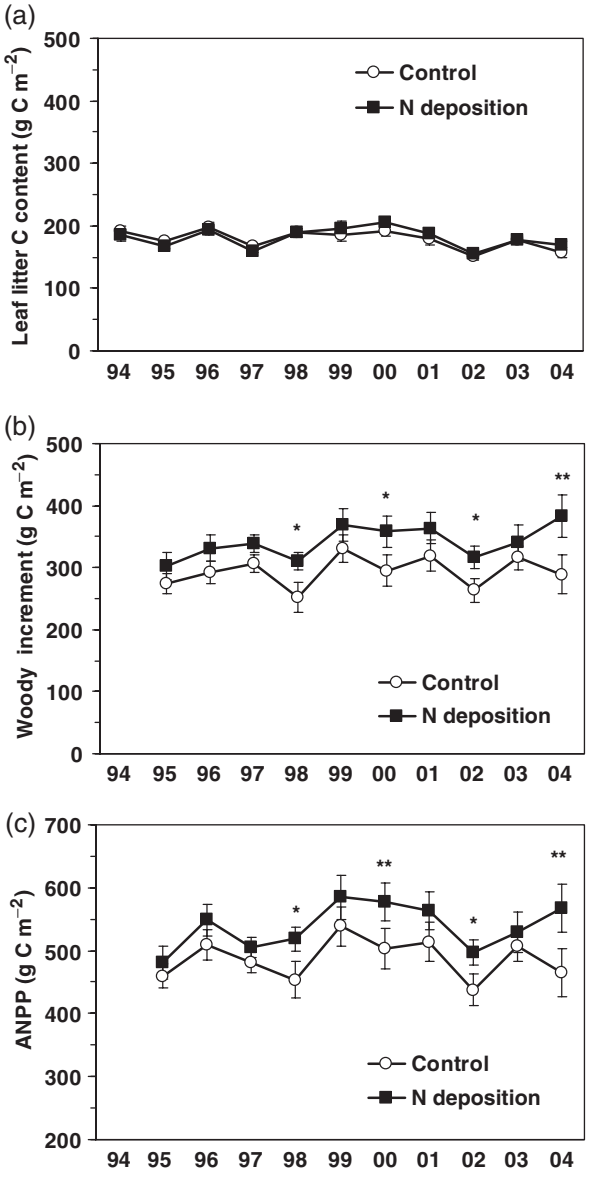

Fig. 2 Trends in the C contents of annual leaf litter biomass (a), aboveground woody biomass increment (b), and aboveground net primary productivity (ANPP) (c) from 1995 to 2004 for the control and NO_3^- deposition treatments. Values for each year are mean ± 1 SE across all sites for each treatment ($n = 12$ plots per treatment). Asterisks for individual years indicate significant treatment differences at the 0.05 (*) and 0.01 (**) level of probability. There is a significant increasing linear time trend ($P = 0.030$) for the difference between treatments in ANPP.

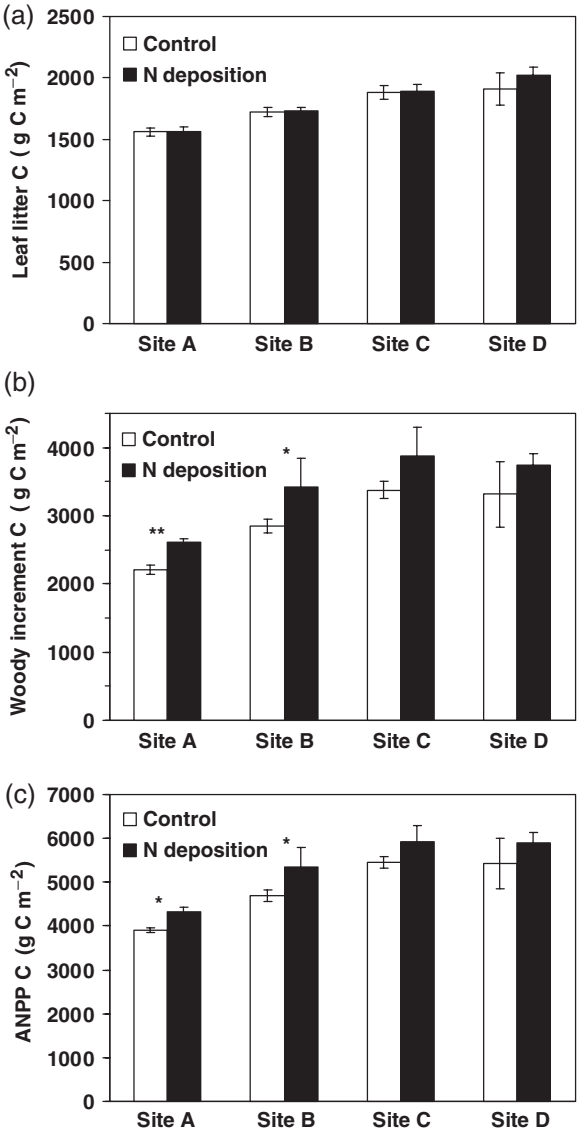

Fig. 3 Effects of the NO_3^- deposition treatment and study site on cumulative (1995–2004) C contents (g C m^{-2}) in leaf litter biomass (a), aboveground woody biomass increment (b), and aboveground net primary productivity (ANPP) (c). Values are mean ± 1 SE for three plots per treatment at each site. Asterisks for individual study sites indicate significant treatment differences at the 0.05 (*) and 0.01 (**) level of probability.

additions, and not pre-existing differences among the study plots assigned to each treatment. Furthermore, the significant year × NO_3^- deposition interaction for ANPP (Table 2) is indicative of this trend. Significant differences among study sites (main effect) in leaf litter production, aboveground woody increment and ANPP (Table 2) are the result of an increasing trend in productivity from north to south (Fig. 3). The increasing trend is presumably associated with longer growing seasons at the more southern sites (Table 1), but is also correlated with differences among sites in ambient N deposition (Table 1). A link between this trend and ambient N deposition cannot be made, due to the intercorrelation with climatic data and the lack of a similar trend in indices of soil N availability for the

Table 3 Contributions of ingrowth trees, trees dying during the study, and trees surviving the entire measurement period to woody ANPP, and the distribution of woody biomass accumulation to live and dead biomass pools

Source	Treatment	Site A	Site B	Site C	Site D	Significant effects
Ten-year cumulative woody ANPP ($g\,C\,m^{-2}$)						
ANPP of ingrowth trees	Control	0.2 (0.1)	0.0 (0.0)	0.0 (0.0)	0.2 (0.2)	
	NO_3^-	0.3 (0.3)	0.0 (0.0)	0.6 (0.6)	1.6 (0.8)	
ANPP of trees dying during period	Control	2 (1)	5 (5)	1 (1)	9 (5)	NO_3^-
	NO_3^-	22 (17)	52 (33)	173 (86)	134 (95)	
ANPP of trees surviving entire period	Control	2207 (68)	2840 (87)	3382 (118)	3308 (482)	Site, NO_3^-
	NO_3^-	2545 (33)	3371 (436)	3716 (361)	3613 (194)	
Total woody ANPP	Control	2209 (68)	2845 (92)	3383 (120)	3317 (481)	Site, NO_3^-
	NO_3^-	2614 (50)	3423 (420)	3889 (422)	3749 (169)	
Woody biomass accumulation ($kg\,m^{-2}$)						
Live biomass 1994	Control	29.4 (0.9)	28.3 (1.6)	31.6 (1.7)	28.9 (1.8)	
	NO_3^-	29.9 (0.9)	28.8 (4.4)	28.8 (0.7)	33.7 (1.5)	
Live biomass 2004	Control	32.5 (1.3)	32.5 (1.1)	36.2 (1.7)	33.9 (2.4)	
	NO_3^-	33.9 (0.5)	33.9 (5.6)	32.8 (0.8)	38.9 (0.2)	
Net live biomass accumulation (1994–2004)	Control	3.1 (0.4)	4.2 (0.6)	4.6 (0.1)	5.0 (1.1)	
	NO_3^-	4.0 (0.5)	5.2 (1.3)	4.0 (1.0)	5.2 (1.2)	
Mortality biomass (1994–2004)	Control	1.4 (0.4)	1.5 (0.7)	2.3 (0.3)	1.7 (0.2)	
	NO_3^-	1.3 (0.6)	1.7 (0.4)	3.9 (1.3)	2.4 (1.3)	
Total biomass production (1994–2004)	Control	4.5 (0.1)	5.7 (0.2)	6.8 (0.2)	6.7 (1.0)	Site, NO_3^-
	NO_3^-	5.3 (0.1)	6.9 (0.8)	7.8 (0.9)	7.6 (0.3)	

Values are the mean ($\pm$ 1 SE) for three plots per treatment per study site. Significant effects at the 0.05 level of probability. ANPP, aboveground net primary productivity.

study sites (Zogg *et al.*, 1996). Natural variability in productivity among years led to significant within subject effects for year and interactions with year for the productivity measures (Table 2).

Leaf litter C content (Figs 2a and 3a) and LAI (data not shown, results parallel those for leaf litter C) did not respond to the NO_3^- deposition treatment. On the other hand, an examination of foliar N concentrations in August 2001 revealed a consistent increase in response to N addition ($25.1 \pm 0.6\,g\,N\,kg^{-1}$, mean $\pm$ 1 SE, vs. $22.4 \pm 0.7\,g\,N\,kg^{-1}$ for the control). The increase in N concentration of green leaves during the growing season in the NO_3^- deposition treatment, which has been repeatedly observed periodically over the past decade (Zak *et al.*, 2004), is a treatment response consistent with leaf litter N concentrations (Fig. 4a). Higher leaf litter N concentrations in the N deposition treatment have decreased the C : N ratio of the leaf litter (Fig. 4b).

Sampling of soil C pools in 2004, a decade after the experiment began, revealed a significant increase in surface soil (0–10 cm) C content for the chronic NO_3^- deposition treatment (Table 4, Figs 5a and 6a). Much, but not all, of this change occurred in the mineral soil portion of the upper 10 cm, with a portion also occurring in the Oe + a organic horizon (Fig. 7). The trend for 0–10 cm soil was apparent at all sites, but was strongest at site B, leading to a significant site $\times$ treatment interaction (Table 4). Surface soil N content tended to increase in concert with C in the NO_3^- deposition treatment (Fig. 6c), but the change was not statistically significant ($P = 0.090$, Table 4). Surface soil C and N concentrations both increased in response to the NO_3^- deposition treatment (Table 5). As a result, surface soil C : N ratios also were not altered by experimental NO_3^- deposition (Table 5 and Fig. 5b). Greater N in the litter (Oi) layer for the NO_3^- deposition treatment led to significantly lower C : N ratios (Table 5).

Discussion

Experimental studies of simulated atmospheric N deposition at single geographic locations have also reported increases in ANPP (Elvir *et al.*, 2003; Magill *et al.*, 2004), similar to those we have consistently observed at all four study sites located across our regional study. Long-term measurements of leaf litter production (Figs 2 and 3) and LAI at our sites demonstrate no change in leaf mass or area in response to N deposition; thus, an increase in leaf area is not the factor driving the increase in ANPP for the NO_3^- deposition treatment.

A potential cause for the increase in ANPP we observed is greater net photosynthesis related to the

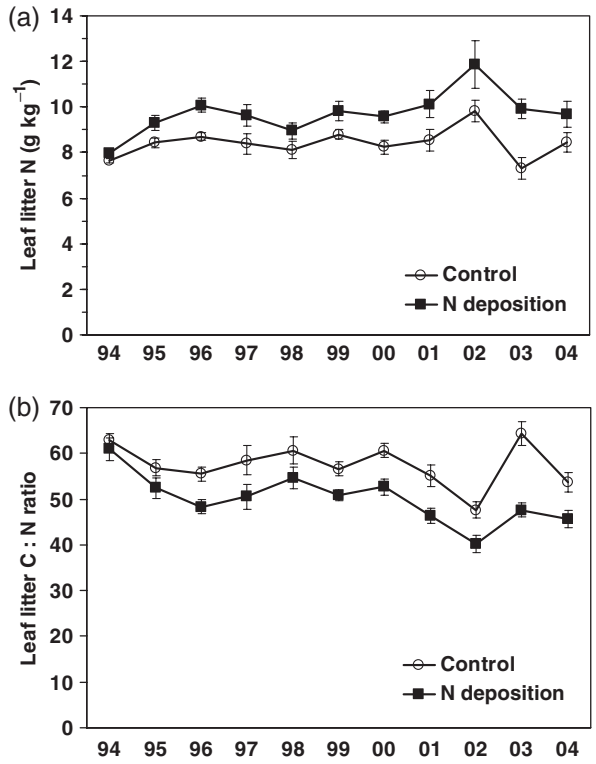

Fig. 4 Leaf litter N concentrations (a) and C : N ratios (b) for 1994 to 2004. Values for each year are mean ± 1 SE across all sites for each treatment ($n = 12$ plots per treatment). Leaf litter N concentrations and C : N ratios for the chronic NO_3^- deposition treatment (solid squares) have been significantly altered ($P < 0.001$) since 1995 compared with the control treatment (open circles).

increase in foliar N concentration (Fig. 4). Increases in foliar N are commonly observed in response to N deposition (Boggs *et al.*, 2005; Elvir *et al.*, 2005). Given the key role of N in photosynthesis (Evans, 1989), linking foliar N concentrations and enhanced aboveground productivity to increased photosynthesis seems obvious. Nonetheless, this relationship has rarely been tested in the context of chronic N deposition. We are aware of only two long-term N deposition studies that have measured net photosynthesis in fully developed forests receiving chronic N deposition treatments (Schaberg *et al.*, 1997; Bauer *et al.*, 2004); neither study observed increased photosynthesis despite elevated foliar N. However, these were studies in which the growth and vigor of conifer stands were declining. Our study sites are dominated by vigorous deciduous trees, which clearly exhibited significant increases in woody ANPP in response to simulated chronic N deposition (Figs 2b and 3b). The average increase in annual ANPP is 10%, and is driven by a 16% increase in aboveground woody biomass increment. We are now actively testing the hypothesis that an increase in photosynthesis in response to greater leaf N is the primary factor responsible for the highly significant increase in ANPP in the NO_3^- deposition treatment.

An alternative explanation for the increase in ANPP would be a reduction in allocation of C belowground. Measurements of root biomass, root respiration, and root turnover rates in our experiment all indicate no change in the amount of C being allocated to root respiration or annual root production for the NO_3^-

Table 4 Analysis of variance for the effects of experimental NO_3^- deposition and study site on soil C and N sampled during 2004

	Study site		NO_3^- deposition		Study site × NO_3^-		Error
Soil depth	MS	$P > F$	MS	$P > F$	MS	$P > F$	MS
C content (g C m^{-2})							
Oi	669	0.353	322	0.464	259	0.719	573
Oe + a	133 993	0.059	10 261	0.636	17 049	0.764	44 071
0–10 cm	5 079 730	**< 0.001**	2 824 420	**0.002**	1 043 140	**0.012**	209 932
10–30 cm	1 909 490	**0.001**	4036	0.889	48 404	0.866	199 830
30–50 cm	659 895	0.173	17 776	0.824	375 068	0.389	349 770
50–70 cm	549 957	**0.012**	230 755	0.164	248 952	0.117	108 529
0–70 cm	10 221 700	**< 0.001**	5 559 350	**0.030**	1 702 780	0.199	978 968
N Content (g N m^{-2})							
Oi	1.25	0.285	0.72	0.387	0.33	0.779	0.91
Oe + a	467	**0.026**	70	0.451	45	0.762	116
0–10 cm	9904	**0.008**	5723	0.090	2758	0.235	1755
10–30 cm	7118	**< 0.001**	28	0.829	112	0.897	569
30–50 cm	773	0.472	447	0.486	1072	0.335	879
50–70 cm	1152	0.055	343	0.348	581	0.233	368
0–70 cm	25 290	**0.004**	14 536	0.071	3007	0.526	3886

For all tests, degrees of freedom are 3 for study site, 1 for NO_3^- addition, 3 for study site × NO_3^- addition, and 16 for error.

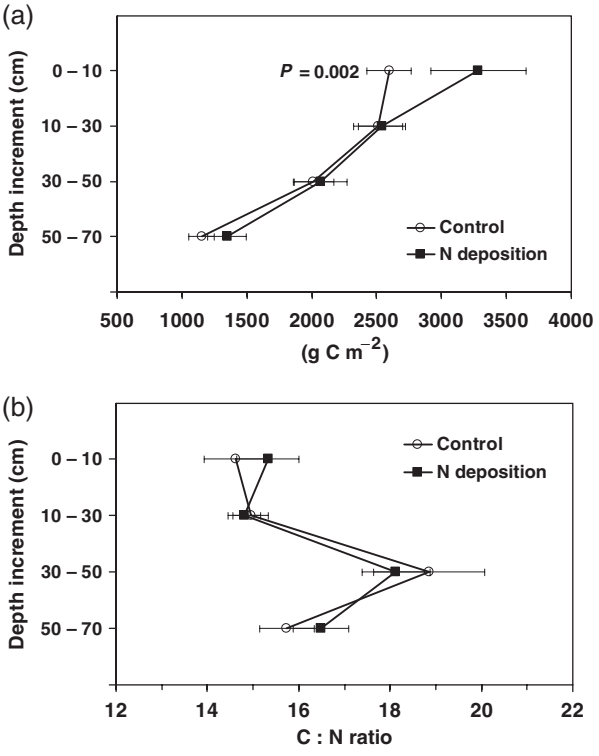

Fig. 5 Mean soil C contents (a) and soil C : N ratios (b) by depth measured in August 2004 for the control and NO_3^- deposition treatments. Values are mean ± 1 SE across all sites for each treatment ($n = 12$ plots per treatment).

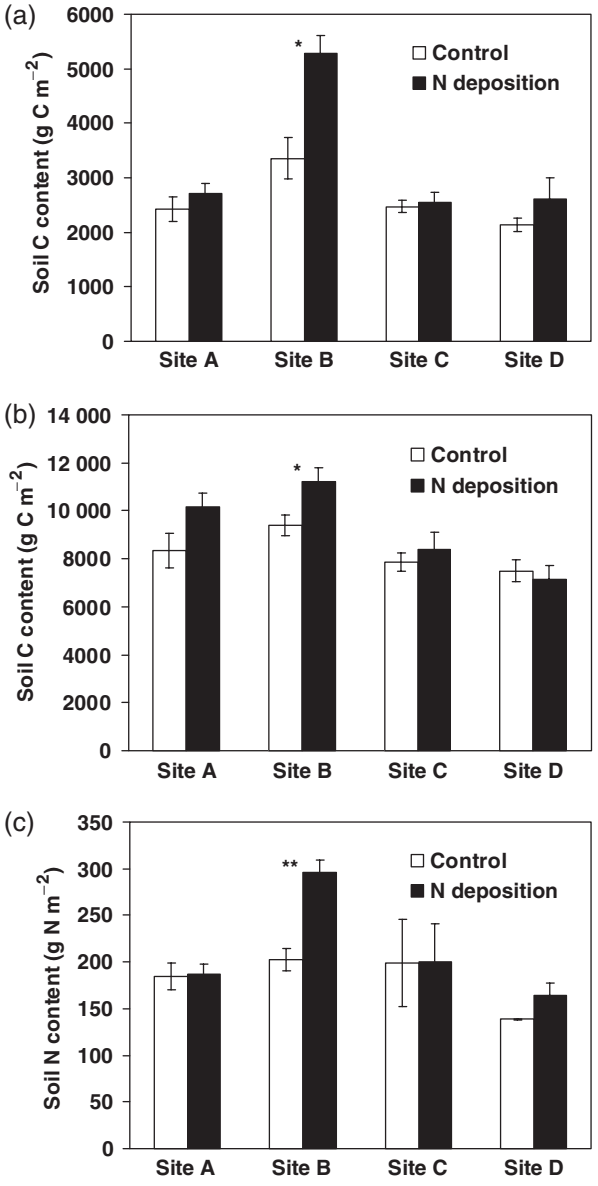

Fig. 6 Effects of experimental NO_3^- deposition and study site on soil C content from 0–10 cm (a), total soil C content to 70 cm (b) and soil N content from 0–10 cm (c) in August 2004. Values are mean ± 1 SE for three plots per treatment at each site. Asterisks for individual study sites indicate significant treatment differences at the 0.05 (*) and 0.01 (**) level of probability.

deposition treatment (Burton *et al*., 2004). In mature forests, others have found reductions in root biomass associated with N additions (Vogt *et al*., 1990; Haynes & Gower, 1995), in contrast to the results of our study. However, we have recently documented a decline in arbuscular mycorrhizal biomass and storage structures in roots of the NO_3^- deposition treatment (Van Diepen *et al*., 2007). This would result in a reduction in the amount of C allocated belowground and, thus could provide at least a portion of the C needed to create the observed increase in ANPP. Again, the alternative hypothesis that reduced C allocation to mycorrhizae is driving the observed increase in woody biomass increment needs to be rigorously tested. The idea that there is a direct C allocation tradeoff between mycorrhizae and woody biomass increment is certainly not a widely held physiological principle, nor is this notion embedded in simulation model architecture.

We estimate an additional 500 g C m^{-2} was stored in woody biomass during the 10-year measurement period (mean difference between control and NO_3^- deposition treatments in Fig. 3b; range 410–670 g C m^{-2}). Biomass accumulation was distributed to both living and dead biomass pools during the study period (Table 3). Living woody biomass increased 11% faster for the NO_3^- deposition treatment, and mortality biomass was 29% greater. Greater biomass accumulation for these individual pools under NO_3^- addition was not statistically significant (Table 3), but the combined biomass accumulation for the two pools, which is the same as woody increment ANPP, was significantly greater for the NO_3^- deposition treatment. It is interesting to note that if we had used measurements of living

biomass at the beginning and end of the study period, rather than careful annual measurements, we would not know that ANPP had increased. Our estimate of an additional 500 g C m^{-2} stored in woody biomass during the study is a maximum estimate of the increase in woody C still remaining on the study sites, as some of the increased C entering the dead biomass pool for the NO_3^- deposition treatment would have been respired during decay processes. However, about 70% of the increase in biomass occurred in net live biomass accumulation (Table 3), and the new woody debris produced during the study is still clearly visible and generally intact. A preliminary examination of coarse woody debris at the study sites in 2003 indicated that approximately 70% of the C contained in trees dying during the previous 10 years still remained in the dead woody material (A. J. Burton, unpublished data). Based on this value, we estimate that 91% of the increase in ANPP associated with greater annual woody increment (455 g C m^{-2}) still remains on the study sites in either living or dead biomass. Coarse woody debris from the study period would not be captured by our soil sampling methodology, thus it does not explain any of the observed treatment differences in surface soil organic C.

The accumulation of C in surface organic and mineral horizons for our NO_3^- deposition treatment is consistent with less complete decomposition of litter associated with a previously documented decline in lignolytic activity (DeForest *et al*., 2004). Both microbial biomass and soil respiration have declined significantly in the chronic NO_3^- deposition treatment (Burton *et al*., 2004; DeForest *et al*., 2004), despite unchanged detrital C inputs from leaf fall (Figs 2a and 3a) and fine root biomass turnover (Burton *et al*., 2004). The declines in microbial biomass and soil respiration instead result from a change in microbial community composition and function, particularly the decline in the activity of lignolytic fungi (DeForest *et al*., 2004). Berg & Meentemeyer (2002) report that increases in leaf litter N concentration in a wide variety of species result in a decline in the proportion of litter that is ultimately decomposed, whereas Franklin *et al*. (2003) demonstrate that N fertilization reduces litter decomposition and stimulates the rate of soil humus accumulation. Elevated foliar litter N (Fig. 4a) and the near-surface location of the observed increase in soil C content for our NO_3^- deposition treatment (Figs 5a, 6a and 7) suggest that such mechanisms are responsible for increased soil C stores in our experimental N deposition treatment. Organic matter resulting from the final stages of foliar litter decomposition should be located in the lower portions of the organic horizons and upper mineral soil, which is where our increase in soil C content occurred. The majority of fine root production and

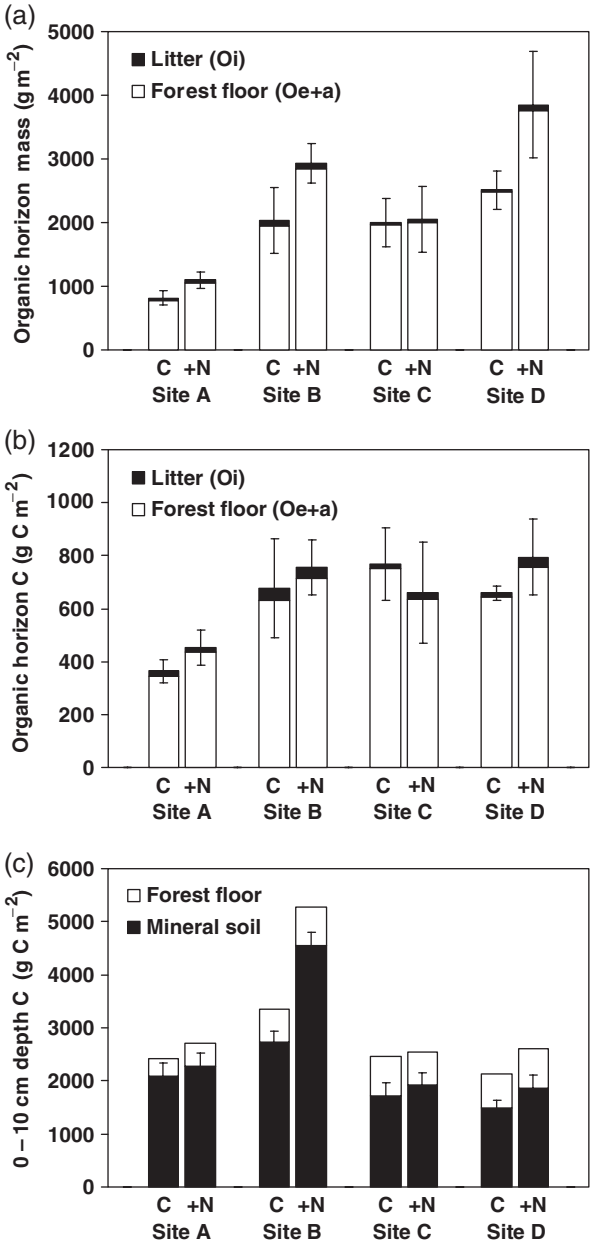

Fig. 7 Effects of experimental NO_3^- deposition and study site on organic horizon mass (a), organic horizon C content (b) and C content of the mineral soil portion of the 0–10 cm depth soil sample (c) collected in August 2004. In plates (a) and (b), error bars are ± 1 SE for the combined litter (Oi) plus forest floor (Oe + a) for three plots per treatment at each site. In plate (c), error bars are ± 1 SE for the mineral soil portion of the upper 10 cm sample. The NO_3^- deposition treatment effect for the Oe + a mass has $P = 0.060$. The NO_3^- deposition treatment effect for C content of the mineral soil portion of the upper 10 cm is highly significant ($P = 0.001$), with a significant site by NO_3^- deposition interaction ($P = 0.007$).

Table 5 Carbon concentrations, N concentrations, C : N ratios and soil bulk density by depth and study site for the control and NO_3^- deposition treatments

Depth	Treatment	Site A	Site B	Site C	Site D	Significant effects
C ($g\,kg^{-1}$)						
Oi	Control	437 (7)	458 (3)	445 (5)	468 (3)	Site
	NO_3^-	436 (18)	455 (6)	427 (18)	461 (14)	
0–10 cm	Control	24.2 (4.8)	37.3 (8.5)	21.3 (1.2)	21.0 (1.4)	Site, NO_3^-, Site × NO_3^-
	NO_3^-	25.0 (2.6)	74.6 (2.9)	22.0 (2.2)	29.3 (5.4)	
10–30 cm	Control	12.3 (2.5)	7.2 (0.4)	10.4 (0.6)	8.8 (1.0)	Site
	NO_3^-	12.6 (0.1)	6.3 (0.6)	10.2 (1.2)	8.5 (0.5)	
30–50 cm	Control	6.8 (3.9)	8.5 (4.9)	6.2 (3.6)	6.7 (3.9)	
	NO_3^-	8.4 (4.9)	8.5 (4.9)	6.2 (3.6)	4.5 (2.6)	
50–70 cm	Control	5.1 (3.0)	5.1 (2.9)	3.0 (1.8)	3.6 (2.1)	Site
	NO_3^-	5.9 (3.4)	4.8 (2.8)	3.8 (2.2)	2.7 (1.6)	
N ($g\,kg^{-1}$)						
Oi	Control	12.0 (0.9)	17.6 (0.6)	18.1 (0.6)	15.9 (0.5)	Site
	NO_3^-	15.1 (2.0)	17.7 (1.0)	18.2 (1.4)	17.0 (0.8)	
0–10 cm	Control	1.84 (0.36)	2.22 (0.37)	1.72 (0.44)	1.36 (0.01)	Site, NO_3^-, Site × NO_3^-
	NO_3^-	1.73 (0.16)	4.19 (0.10)	1.72 (0.35)	1.83 (0.18)	
10–30 cm	Control	0.84 (0.10)	0.51 (0.02)	0.64 (0.04)	0.59 (0.08)	Site
	NO_3^-	0.84 (0.02)	0.47 (0.02)	0.64 (0.06)	0.57 (0.02)	
30–50 cm	Control	0.35 (0.07)	0.43 (0.02)	0.33 (0.01)	0.37 (0.05)	
	NO_3^-	0.46 (0.12)	0.42 (0.07)	0.39 (0.03)	0.26 (0.05)	
50–70 cm	Control	0.33 (0.03)	0.30 (0.03)	0.20 (0.01)	0.24 (0.01)	Site
	NO_3^-	0.33 (0.05)	0.27 (0.04)	0.24 (0.05)	0.18 (0.01)	
C : N ratio						
Oi	Control	40.2 (3.4)	26.3 (0.8)	24.7 (0.6)	29.6 (1.0)	Site, NO_3^-
	NO_3^-	30.0 (3.1)	26.4 (1.5)	23.7 (1.0)	27.3 (0.5)	
0–10 cm	Control	13.1 (0.1)	16.4 (0.8)	14.6 (1.1)	15.3 (0.9)	Site
	NO_3^-	14.4 (0.3)	17.6 (0.2)	15.5 (0.8)	15.4 (0.9)	
10–30 cm	Control	14.2 (1.2)	13.8 (0.3)	16.2 (0.2)	15.1 (0.5)	Site
	NO_3^-	15.1 (0.3)	13.2 (0.8)	15.8 (0.6)	14.8 (0.5)	
30–50 cm	Control	19.0 (4.6)	19.1 (0.8)	18.8 (1.9)	19.0 (3.2)	
	NO_3^-	18.5 (0.6)	20.3 (0.9)	15.8 (0.5)	18.3 (2.1)	
50–70 cm	Control	15.9 (2.0)	16.9 (0.9)	15.4 (0.6)	14.9 (0.6)	
	NO_3^-	17.6 (0.3)	17.8 (2.0)	15.4 (0.5)	14.8 (0.2)	
Bulk density ($g\,cm^{-2}$)						
0–10 cm	Control	1.11 (0.16)	0.96 (0.10)	1.17 (0.04)	0.91 (0.12)	Site
	NO_3^-	1.14 (0.13)	0.72 (0.03)	1.17 (0.07)	0.84 (0.15)	
10–30 cm	Control	1.36 (0.07)	1.48 (0.04)	1.24 (0.11)	1.32 (0.08)	Site
	NO_3^-	1.28 (0.08)	1.54 (0.06)	1.39 (0.05)	1.38 (0.05)	
30–50 cm	Control	1.39 (0.04)	1.48 (0.06)	1.54 (0.03)	1.54 (0.06)	Site, NO_3^-
	NO_3^-	1.52 (0.05)	1.57 (0.07)	1.55 (0.03)	1.69 (0.03)	
50–70 cm	Control	1.38 (0.11)	1.66 (0.09)	1.53 (0.03)	1.53 (0.08)	
	NO_3^-	1.47 (0.11)	1.72 (0.16)	1.60 (0.08)	1.52 (0.15)	

Values are the mean (±1 SE) for three plots per treatment per study site.
Significant effects at the 0.05 level of probability.

turnover, and thus root litter input, also occurs in this depth increment for these forests (Burton *et al.*, 2000).

We estimate an additional 690 g C m^{-2} are stored in the 0–10 cm soil pool in the NO_3^- deposition treatment (mean difference between treatments in Fig. 6a, range 80–1910 g C m^{-2}; median 370 g C m^{-2}). If the nonsignificant increase in the 50–70 cm depth is included, the mean increase in total soil C content is 960 g C m^{-2} (Fig. 6b). The soil C pool in the upper 10 cm of soil in the NO_3^- deposition treatment averages 26% greater than that in the control treatment, with a median increase of 16%. The increase of 690 g C m^{-2} over a decade in the surface soil pool was unforeseen, and the possibility that high levels of atmospheric N deposition may result in increased C storage in the soil over decadal time steps must now be considered. We observed a consis-

tent trend for higher soil C for the NO_3^- deposition treatment at all study sites and an increase clearly large enough to biogeochemically meaningful at site B.

Summed over time, the magnitude of the previously observed decrease in soil respiration in the NO_3^- deposition treatment is in general agreement with measured soil C accrual. Soil CO_2 efflux ranged from 13% to 15% less for the NO_3^- deposition treatment from 1998 to 2001, with the average decrease in soil respiration for 2001 being equivalent to $177\,g\,C\,m^{-2}$ (Burton *et al.*, 2004). If similar reductions occurred from the time decreased soil respiration was first observed in 1998, through the 2004 soil sampling, from 1040 to $1200\,g\,m^{-2}$ less C may have left the sites through soil CO_2 efflux for the NO_3^- deposition treatment. This large decrease in soil respiration potentially suggests a significant decrease in decomposition of organic matter because neither aboveground litter flux (Fig. 2) nor belowground root biomass and turnover (Burton *et al.*, 2004) have responded to our N deposition treatment. Root litter inputs ($144 \pm 16\,g\,C\,m^{-2}$; mean $\pm$ 1 SE; see 'Methods') combined with the above-ground litter inputs (Figs 2a and 3a) average $352 \pm 17\,g\,C\,m^{-2}$ annually. From 1994 to 2004, decomposition of these litter inputs in the NO_3^- deposition treatment would have to be 18% less than rates of litter decomposition in the control treatment to account for 100% of the mean C accrual ($690\,g\,C\,m^{-2}$) we have documented in the top 10 cm of soil. This is a maximum change in decomposition rate, because it does not address the possibility of reduced decomposition of other, pre-existing soil C pools. Carbon accumulating due to inhibited long-term decomposition of high N litter should be relatively resistant to decay (Berg & Meentemeyer, 2002), but it should be noted that the primary locations of soil C accrual in our study are at or near the soil surface (Fig. 4), which may make this C susceptible to loss if the forest is disturbed.

Our results, spanning hundreds of kilometers, point to the importance of carefully designed and maintained long-term field experiments for understanding the effects of global change factors such as chronic N deposition. The increase in woody biomass in response to the NO_3^- deposition treatment (Fig. 2b) was not statistically significant in the early years of the experiment. Year-to-year climatic variation, periodic large mast years and occasional insect defoliation events all contribute to the interannual variation in aboveground productivity at these study sites (Pregitzer & Burton, 1991; Lane *et al.*, 1993; Reed *et al.*, 1994). However, with time, it has become very clear that ANPP has increased in response to the NO_3^- deposition treatment, a response driven largely by an increase in woody biomass increment (Fig. 2) The simulated N deposition rates used in our study are approximately three times greater than total N deposition commonly experienced by forests in the industrialized north central and northeastern US, but the total N load experienced by our sites during the first decade of the experiment was similar to the ambient N inputs that forests of the region have received during the past 35 years of chronic N deposition.

Our long-term field experiment suggests that chronic atmospheric N deposition has the potential to increase C storage in both woody biomass and soil in the Hemlock–White Pine–Northern Hardwood Forest Region, a region previously implicated as a potential sink for atmospheric C. The increase in ANPP is likely driven by higher rates of photosynthesis per unit leaf area and/or decreased C allocation to mycorrhizae, hypotheses which are not necessarily mutually exclusive. The accumulation of C in the surface 10 cm of soil in the NO_3^- deposition treatment appears to be driven by the direct suppression of the soil enzymes responsible for litter degradation when litter has a higher N concentration. We now have the real opportunity to address the mechanisms responsible for our long-term field observations; mechanisms that are not routinely contained in most conceptual or empirical simulation models of regional or global C cycling.

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