Sinks for nitrogen inputs in terrestrial ecosystems: a meta-analysis of ^{15}N tracer field studies

P. H. Templer,[1,27] M. C. Mack,[2] F. S. Chapin, III,[3] L. M. Christenson,[4] J. E. Compton,[5] H. D. Crook,[6] W. S. Currie,[7] C. J. Curtis,[8] D. B. Dail,[9] C. M. D'Antonio,[10] B. A. Emmett,[11] H. E. Epstein,[12] C. L. Goodale,[13] P. Gundersen,[14] S. E. Hobbie,[15] K. Holland,[16] D. U. Hooper,[17] B. A. Hungate,[18] S. Lamontagne,[19] K. J. Nadelhoffer,[20] C. W. Osenberg,[2] S. S. Perakis,[21] P. Schleppi,[22] J. Schimel,[10] I. K. Schmidt,[14] M. Sommerkorn,[23] J. Spoelstra,[24,25] A. Tietema,[26] W. W. Wessel,[26] and D. R. Zak[7,20]

[1]*Department of Biology, Boston University, 5 Cummington Street, Boston, Massachusetts 02215 USA*
[2]*Department of Biology, University of Florida, Gainesville, Florida 32611-8525 USA*
[3]*Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska 99775 USA*
[4]*Department of Biology, Vassar College, 124 Raymond Avenue, Poughkeepsie, New York 12604 USA*
[5]*U.S. Environmental Protection Agency, ORD-NHEERL-WED, 200 SW 35th Street, Corvallis, Oregon 97333 USA*
[6]*Natural Environment Research Council, Polaris House, Swindon SN2 1EU United Kingdom*
[7]*School of Natural Resources and Environment, University of Michigan, 440 Church Street, Ann Arbor, Michigan 48109 USA*
[8]*Environmental Change Research Centre, Geography Department, Pearson Building, University College London, Gower Street, London WC1E 6BT United Kingdom*
[9]*Department of Plant, Soil and Environmental Sciences, University of Maine, Orono, Maine 04469 USA*
[10]*Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, California 93106-9620 USA*
[11]*Centre for Ecology and Hydrology, Environment Centre Wales, Deiniol Road, Bangor, Gwynedd LL57 2UW United Kingdom*
[12]*Department of Environmental Sciences, University of Virginia, P.O. Box 400123, Charlottesville, Virginia 22904-4123 USA*
[13]*Department of Ecology and Evolutionary Biology, Cornell University, E215 Corson Hall, Ithaca, New York 14853 USA*
[14]*Forest and Landscape Denmark, University of Copenhagen, Rolighedsvej 23 DK-1958 Frederiksberg C, Denmark*
[15]*Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, Minnesota 55108 USA*
[16]*Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado 80309 USA*
[17]*Department of Biology, Western Washington University, Bellingham, Washington 98225-9160 USA*
[18]*Department of Biological Sciences and Merriam-Powell Center for Environmental Research, Northern Arizona University, Flagstaff, Arizona 86011 USA*
[19]*CSIRO Land and Water, Waite Campus, PMB 2 Glen Osmond, South Australia 5064 Australia*
[20]*Department of Ecology and Evolutionary Biology, University of Michigan, 830 North University Avenue, Ann Arbor, Michigan 48109-1048 USA*
[21]*U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Corvallis, Oregon 97331 USA*
[22]*Swiss Federal Institute for Forest, Snow and Landscape Research, Zürcherstr. 111, CH-8903 Birmensdorf, Switzerland*
[23]*James Hutton Institute, Craigiebuckler, Aberdeen AB15 8QH United Kingdom*
[24]*Groundwater Quality and Assessment Section, National Water Research Institute, Environment Canada, 867 Lakeshore Road, P.O. Box 5050, Burlington, Ontario L7R 4A6 Canada*
[25]*Department of Earth and Environmental Sciences, University of Waterloo, 200 University Avenue W., Waterloo, Ontario N2L 3G1 Canada*
[26]*Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94240, 1090 GE Amsterdam, The Netherlands*

Abstract. Effects of anthropogenic nitrogen (N) deposition and the ability of terrestrial ecosystems to store carbon (C) depend in part on the amount of N retained in the system and its partitioning among plant and soil pools. We conducted a meta-analysis of studies at 48 sites across four continents that used enriched ^{15}N isotope tracers in order to synthesize information about total ecosystem N retention (i.e., total ecosystem ^{15}N recovery in plant and soil pools) across natural systems and N partitioning among ecosystem pools. The greatest recoveries of ecosystem ^{15}N tracer occurred in shrublands (mean, 89.5%) and wetlands (84.8%) followed by forests (74.9%) and grasslands (51.8%). In the short term (<1 week after ^{15}N tracer application), total ecosystem ^{15}N recovery was negatively correlated with fine-root and soil ^{15}N natural abundance, and organic soil C and N concentration but was positively correlated with mean annual temperature and mineral soil C:N. In the longer term (3–18 months after ^{15}N tracer application), total ecosystem ^{15}N retention was negatively correlated with foliar natural-abundance ^{15}N but was positively correlated with mineral soil C and N concentration and C:N, showing that plant and soil natural-abundance ^{15}N and soil C:N are good indicators of total ecosystem N retention. Foliar N concentration was not significantly related to ecosystem ^{15}N tracer recovery, suggesting that plant N status is not a good predictor of total ecosystem N retention. Because the largest ecosystem sinks for [15]N

tracer were below ground in forests, shrublands, and grasslands, we conclude that growth enhancement and potential for increased C storage in aboveground biomass from atmospheric N deposition is likely to be modest in these ecosystems. Total ecosystem ^{15}N recovery decreased with N fertilization, with an apparent threshold fertilization rate of 46 kg N·ha^{-1}·yr^{-1} above which most ecosystems showed net losses of applied ^{15}N tracer in response to N fertilizer addition.

INTRODUCTION

Nitrogen (N) is an essential element that often limits net primary productivity in terrestrial ecosystems (LeBauer and Treseder 2008). Human activities such as fossil fuel combustion, synthetic-fertilizer application, and animal agriculture have greatly increased emissions of reactive N and its deposition to terrestrial ecosystems (Vitousek et al. 1997, Galloway et al. 2008). Initially, N inputs can increase productivity (LeBauer and Treseder 2008); however, once inputs exceed biotic demand and abiotic sinks for N, additional anthropogenic N inputs can induce plant nutrient imbalances, reduced productivity, increased N export from terrestrial ecosystems, and soil- and stream-water acidification (Ågren and Bosatta 1988, Aber et al. 1989, 1998). More recently, the potential effects of N inputs on terrestrial ecosystem carbon (C) retention and loss are receiving attention, due to concerns with the global C cycle. Terrestrial ecosystems represent major sources and sinks for atmospheric CO_2 (IPCC 2007), and because N is often the limiting nutrient in terrestrial ecosystems, N inputs from atmospheric deposition can increase C storage by increasing primary production and C storage within plants (Hungate et al. 2003, Thomas et al. 2010). In soils, N additions can increase C storage in some ecosystems by reducing decomposition and respiratory C loss (Fog 1988, Ågren et al. 2001, Zak et al. 2008, Janssens et al. 2010); however, N inputs can also stimulate C loss via decomposition, which in some ecosystems can more than offset positive impacts on productivity (Mack et al. 2004).

Applications of N enriched in the stable isotope ^{15}N (hereafter "^{15}N tracer") have produced considerable data on fates and retention of N inputs to terrestrial ecosystems (Schlesinger 2009), as they can be used to track cohorts of N inputs into ecosystem components and to determine the fate of N additions across time scales (Currie and Nadelhoffer 1999). To date, there has been one synthesis of ^{15}N tracer data from agricultural systems (Gardner and Drinkwater 2009), but no comparable synthesis across natural ecosystems that span broad geographical areas, except for a recent synthesis by Curtis et al. (2011) focusing on pathways for NO_3^- loss.

We used meta-analysis techniques to synthesize results from ecosystem-scale ^{15}N tracer experiments in natural ecosystems to compare N sinks across studies that varied in time scale of recovery, ecosystem types, and locations (Fig. 1). Our objectives were to identify: (1) variables controlling total ecosystem N retention, (2) impact of method and form of ^{15}N tracer application on measured N retention, (3) whether plant and soil ^{15}N natural abundances are useful indicators of total ecosystem N retention, (4) effects of N fertilization rates on partitioning of N among ecosystem pools and on total ecosystem N retention, and (5) implications for the N fertilization effect on C storage.

We predicted that most N would be retained in belowground ecosystem pools, but that grassland, tundra, and shrubland ecosystems would have a greater proportion of N retained below ground compared to forests due to greater C allocation to roots than shoots (De Deyn et al. 2008). Also, we expected that shrublands and evergreen forests, with typically low nutrient availability, would retain greater proportions of N additions than ecosystems such as deciduous forests and grasslands, which often have greater nutrient availability and are dominated by plant species with shorter leaf life spans (Aerts and Chapin 2000). We expected that sites with higher precipitation or temperature would exhibit less total ecosystem N retention because both of these factors can stimulate internal N-cycling rates and thereby enhance production and loss of mobile forms of N. However, as temperature and precipitation increase, so can rates of net ecosystem production, which can contribute to N retention. Furthermore, because others have shown strong positive correlations between natural-abundance ^{15}N of foliage and N losses (Meints et al. 1975, Gebauer and Schulze 1991, Garten 1993, Högberg 1997, Emmett et al. 1998, Pardo et al. 2006, Templer et al. 2007), we expected that foliar and soil ^{15}N natural abundances would correlate negatively with total ecosystem N retention. Foliar ^{15}N natural abundance is positively correlated with N losses due to fractionation during microbial processes, such as nitrification, which correlate with N losses, and enrichment of remaining soil N pools that plants take up. Foliar ^{15}N natural abundance has also been shown to negatively correlate with rates of N transfer from mycorrhizal fungi to plants (Hobbie and Ouimette 2009, Högberg et al. 2011), which can also indicate low N availability and relatively high ecosystem N retention. Finally, we predicted that ecosystems with higher N additions would retain smaller proportions of N inputs than ecosystems receiving low N inputs from ^{15}N tracer application alone, due to potential saturation of plant and microbial N demands.
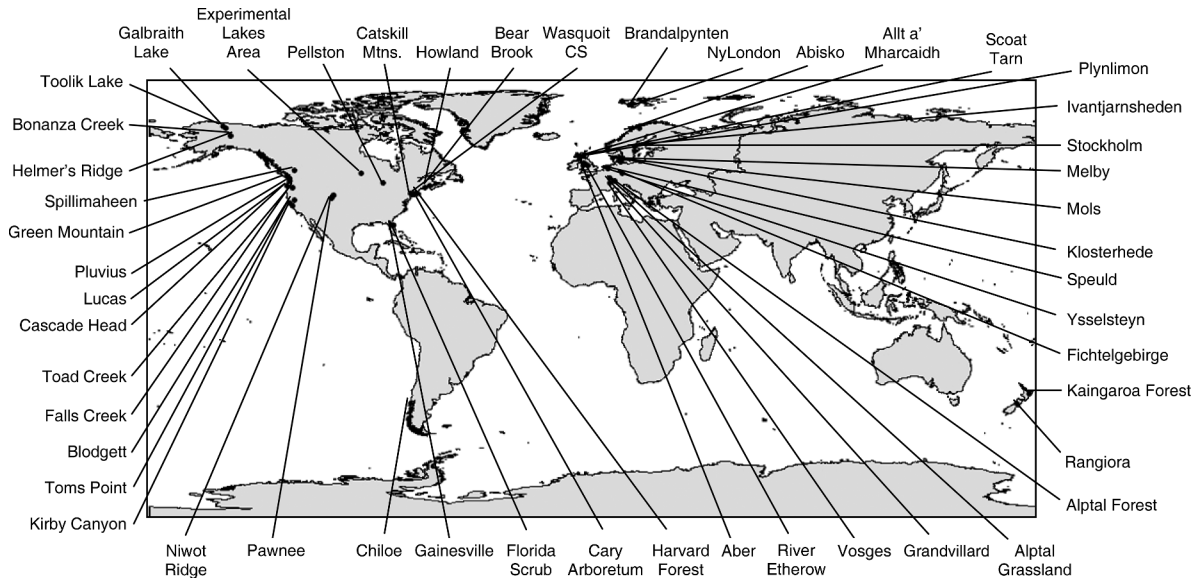
FIG. 1. Distribution of sites used in the meta-analysis.

METHODS

We assembled data from ecosystem-scale ^{15}N tracer studies (Appendix) reported in peer-reviewed sources using Biosis and Web of Science and from participants in workshops conducted at the National Center for Ecological Analysis and Synthesis (NCEAS) in Santa Barbara, California (USA). Criteria for inclusion in our analysis included (1) following the fate of ^{15}N tracers in nonagricultural ecosystems and (2) having been done in the field at a scale sufficiently large to examine plants and soils. We excluded studies using soil cores that did not include entire plants. We examined fates of ^{15}N inputs among ecosystem pools across ecosystem types including forests (32 sites), grasslands (7 sites), shrublands (4 sites), tundra (6 sites), and wetlands (2 sites) from locations in North America (26 sites), South America (1 site), Europe (19 sites), and Oceania (2 sites). Sites varied in elevation, mean annual temperature and precipitation, total N deposition, and rate of N addition (Fig. 2; Appendix). In some cases a site was represented more than once in an analysis if the ^{15}N-tracer recovery data were available from more than one treatment or ecosystem type. We averaged values for ^{15}N recovery in cases where a site was represented more than once with the same type of plot. "Plot" represented the experimental unit in the majority of studies included in this analysis.

Our analysis included studies that reported total ecosystem ^{15}N-tracer recovery, considered here as the sum of ^{15}N retained in soils, fine and coarse roots, leaf litter (Oi horizon), and aboveground biomass. Organic soil horizons included Oe, Oa, and sometimes partial A horizons. Mineral soil depths varied by study; we could not constrain these data to a particular depth due to the wide variability of depths measured by investigators. In some cases, researchers reported recoveries within only some of these pools without reporting total ecosystem recovery. Therefore, more studies were included in our analyses of recovery within individual pools than in analyses of total ecosystem ^{15}N recovery (Appendix). We compared total ecosystem ^{15}N tracer recovery between ambient (unfertilized) and fertilized plots. Fertilization was defined as studies that added >2.5 kg $N\cdot ha^{-1}\cdot yr^{-1}$ beyond atmospheric deposition. Although ^{15}N tracer applications alone involve N additions, this was not considered to be fertilization since ^{15}N tracer masses are very small (<2.5 kg $N\cdot ha^{-1}\cdot yr^{-1}$).

^{15}N recovery calculations

We used ^{15}N tracer recoveries based on N mass, amount of ^{15}N applied, and ^{15}N enrichments of ecosystem pools. Amounts of ^{15}N applied to plots ranged from 0.0069 to 18 kg $^{15}N/ha$ (0.5–99 atom% ^{15}N). We calculated the proportion of ^{15}N tracer recovered ($^{15}N_{rec}$) within each ecosystem pool as

$$^{15}N_{rec} = \frac{F_{sample} - F_{ref}}{F_{tracer} - F_{ref}} \times \frac{N_{pool}}{N_{tracer}}$$

where F = fractional abundance ($^{15}N/(^{14}N + ^{15}N)$) in the sample, in the non-labeled reference sample or the tracer; N_{pool} and N_{tracer} are the masses of N in the ecosystem pool at a point in time and in the tracer applied to that point in time, respectively (from Providoli et al. 2005). We used ^{15}N tracer recoveries as estimates of ecosystem net N retention of the cohort of N added at specific times. Total ecosystem retention of applied ^{15}N was calculated as the sum of ^{15}N tracer recoveries within soils (including microbial biomass), roots, and aboveground plant biomass.
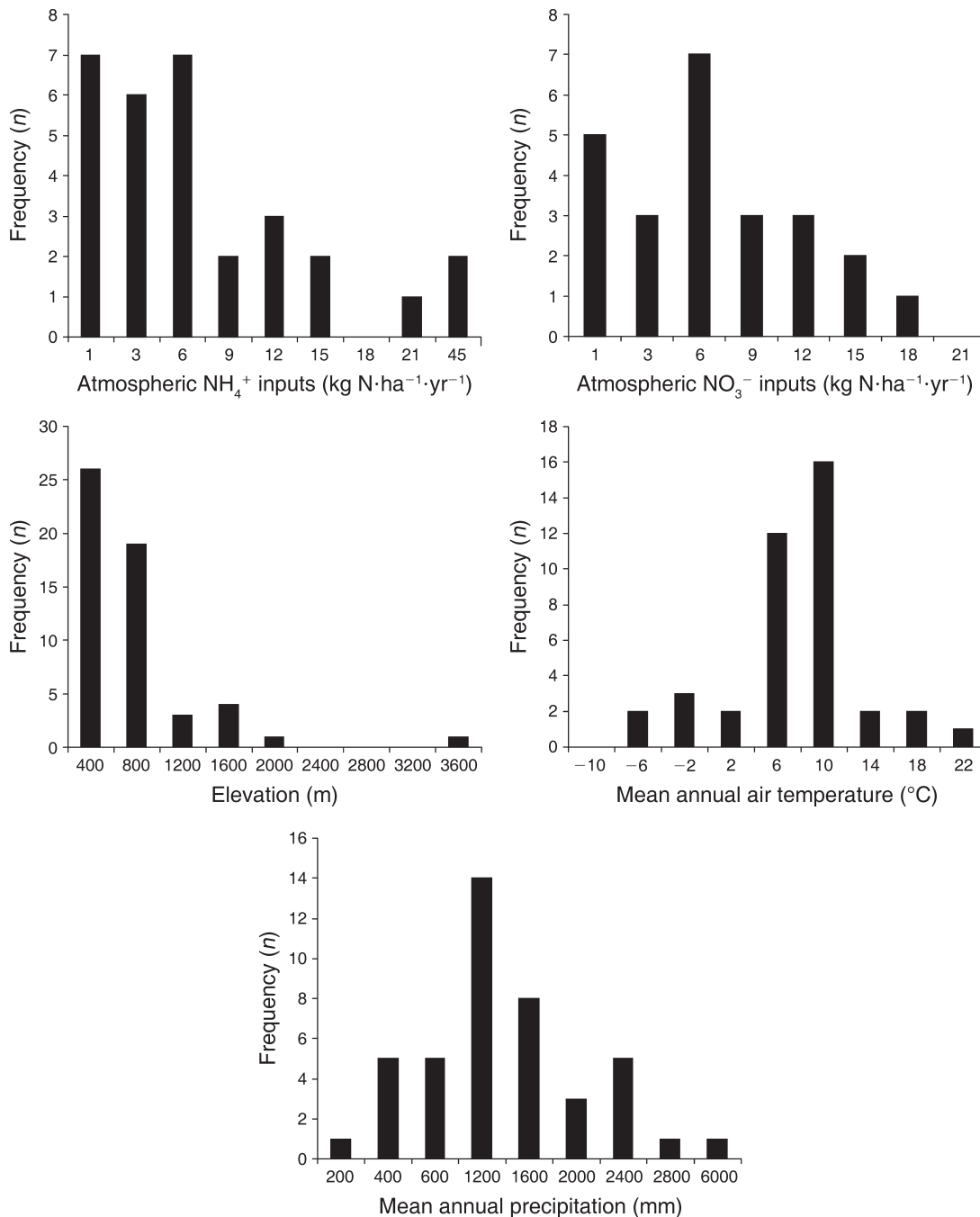
Fig. 2. Frequency (number of observations) diagrams showing atmospheric NH_4^+ and NO_3^- inputs, elevation, mean annual air temperature, and mean annual precipitation among sites used in analysis. Note different frequency bin sizes.

Total ecosystem ^{15}N tracer recovery was reported over a range of time scales from less than one day to 11 years after ^{15}N application. However, it was not possible to make meaningful comparisons among sampling periods due to the paucity of studies measuring ^{15}N tracer recovery over multiple time scales. We categorized the duration of a study into five time scales based on time from application of the tracer to data collection:

<1 week ($n = 30$ studies), 1 week to 1 month ($n = 11$ studies), >1 month to 3 months ($n = 32$ studies; hereafter 1–3 months), >3 to 18 months (hereafter 3–18 months; $n = 48$ studies) and >18 months ($n = 21$ studies). In a few studies data were reported from multiple times within one of these time scales as a series of ^{15}N applications across a growing season or across more than one year. In each case, we averaged values of ecosystem pools

within a study within a time scale. Values within a site were kept separate for distinct vegetation types, ^{15}N application forms, and experimental treatment. For studies in which ^{15}N was applied more than once, categories for time scale were based on the timing of the first ^{15}N application. Data from ambient and fertilized plots were kept separate.

Meta-analyses

We chose percentage of ^{15}N tracer recovery as the effect size of interest (Osenberg et al. 1999), and used an unweighted meta-analytic approach because not all studies were replicated and many (~25%) did not report variances. We examined fates of ^{15}N tracer applications among ecosystem pools for two time periods: short term, <1 week to examine short-term partitioning of N, and long term, 3–18 months to examine partitioning of ^{15}N tracers after one growing season.

We sought to identify factors leading to variation in ^{15}N recovery among studies using a mixed model for categorical classifications or correlation analyses for continuous descriptor variables. Categorical variables included ecosystem type (forest, grassland, shrubland, tundra, wetland), dominant plant species growth form (graminoid, evergreen tree plantation, evergreen tree, evergreen shrub, deciduous tree), mycorrhizal association (arbuscular mycorrhizae, ectomycorrhizae, and ericoid mycorrhizae), co-dominant growth form (graminoid, tree, shrub, forb, or other), previous disturbance to site (agriculture, grazing or pasture, hurricane, selective harvest [removal of particular plant species] and fire), form of ^{15}N application ($^{15}NH_4^{15}NO_3$, $^{15}NH_4^+$, $^{15}NO_3^-$), and method of ^{15}N application (application to canopy or to soil surface). A minimum of two studies per category was necessary to be included in the meta-analysis.

We used Spearman rank correlation analyses to examine correlations between total ecosystem ^{15}N tracer recovery and continuous independent variables. Continuous variables included elevation, mean annual temperature and precipitation, annual rates of atmospheric deposition of N ($NH_4^+ + NO_3^-$; most reported as total deposition, but some used throughfall as a proxy), foliar N concentration and ^{15}N natural abundance, fine-root ^{15}N natural abundance, and organic and mineral soil C and N concentration, C:N concentration ratio, and ^{15}N natural abundances. Natural-abundance samples were collected prior to or in separate plots from ^{15}N tracer applications.

We examined impacts of fertilizer addition and form on total ecosystem N retention by comparing ambient to fertilized studies. We also conducted a separate analysis of fertilization studies that was constrained to studies using "low N" and "high N" experimental treatments (12 sites; Appendix). We calculated change in total ecosystem ^{15}N tracer recovery in response to N fertilization and compared the effect size across studies. In most studies "low N" corresponds to ambient levels of atmospheric deposition, but in some cases N inputs were experimentally elevated (albeit at low levels). "High N" plots were always subject to additions well above ambient N inputs.

Studies using ^{15}N tracer have methodological limitations that constrain our ability to make precise quantitative measures of ecosystem N retention, and these limitations should be considered in our comparisons of sites and studies. Viewing the measures reported here of ecosystem recovery of ^{15}N as ecosystem N retention requires the assumption that ^{15}N recovery in vegetation and soil samples are scaled to ecosystem pools correctly with no systematic bias and low uncertainty. In reality, accurate scaling of ^{15}N tracer recoveries in soil and vegetation samples is difficult. Soil N pools, in particular, are large and heterogeneous, whereas sample numbers are typically small in comparison. Vegetation N pools are also difficult to scale because of difficulties in quantifying belowground biomass, uncertainties of relationships between aboveground and belowground allometry, and assumptions about tissue stoichiometry in large, variable tissues such as foliage, roots, and branches, which vary among vegetation types. Also, tracer experiments assume rapid mixing of the ^{15}N tracer into ecosystem inorganic-N pools, which is not always the case. For example, tracers sprayed on vegetation and soil might only enter relevant pools after the next rain event, and mixing effectiveness could depend on pool size. Total ecosystem recoveries are best viewed as relative ecosystem retention across studies, keeping in mind that many explanatory variables are not necessarily independent. Therefore, we cannot rank the importance of different factors with great confidence, nor can we characterize their interactions.

We used MetaWin 2.1 software (Rosenberg et al. 2000) for meta-analyses using categorical data and calculated unweighted means and 95% bias-corrected bootstrapped confidence intervals based on 999 iterations for nonnormally distributed data. Normality was tested with the Shapiro-Wilk test using SAS JMP software (version 8.0.2; SAS Institute 2009). We considered groups with non-overlapping confidence intervals to be significantly different. To analyze relationships between the responses and continuous variables, we calculated Spearman rank correlations using SAS JMP software (version 8.0.2).

RESULTS

Ambient conditions: controls on total ecosystem recovery of ^{15}N

Terrestrial ecosystems retained on average 62.7% of ^{15}N tracer applications. Mean (range) total ecosystem ^{15}N recovery was 59.6% (48.3–72.3%) for <1 week, 80.1% (62.9–99.4%) for 1 week to 1 month, 50.7% (40.5–61.2%) for 1 to 3 months, 69.4% (60.4–78.5%) for 3 to 18 months, and 61.6% (48.5–73.9%) for >18 months. Total ^{15}N recovery for the 1-week-to-1-month sampling
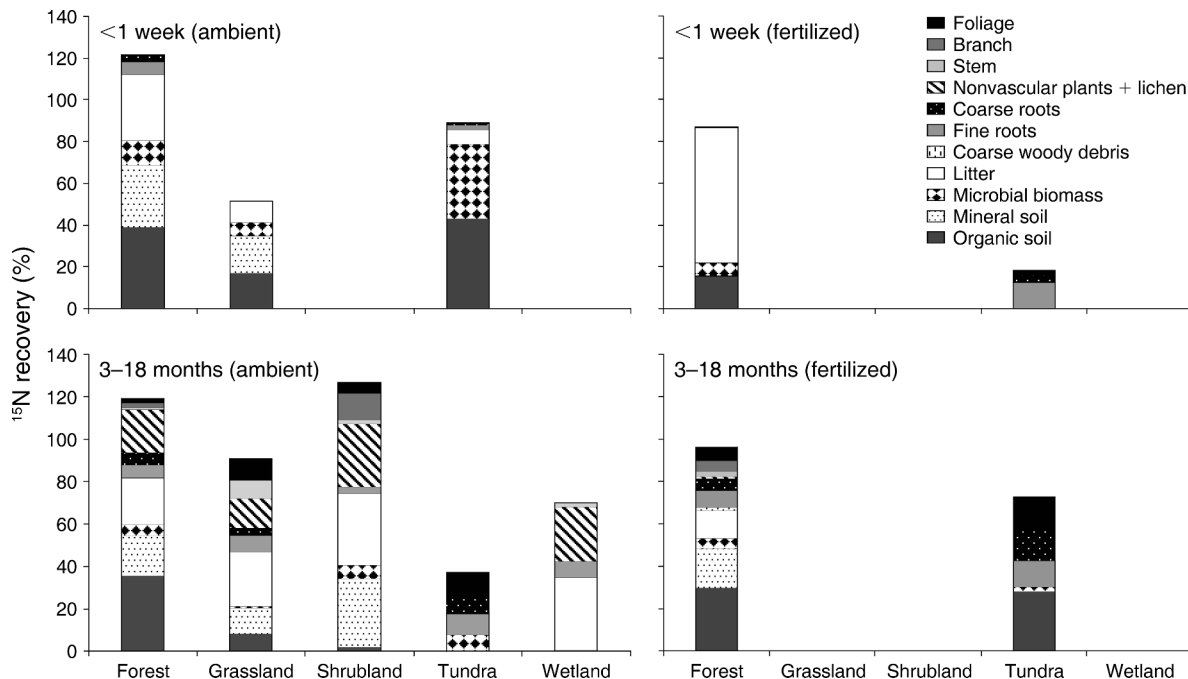
Fig. 3.   Mean ^{15}N tracer recovery among terrestrial ecosystem pools for short-term (<1 week) and long-term (3–18 months) time periods following ^{15}N addition. Not all studies are represented among each ecosystem pool, which may result in recovery >100%. Not all ecosystem pools or ecosystem types are available for each sampling time.

period was greater than the <1-week sampling period, but the range of values is large and overlaps between sampling periods. Also, we did not compare the different time periods because not all studies were included in each of the sampling periods.

The *sum* of ^{15}N recoveries among ecosystem pools can exceed 100% (Fig. 3) but is not equivalent to the reported *total* ecosystem ^{15}N recovery (Figs. 4 and 5). Some studies reported only a subset of ecosystem pools, while others reported all pools; therefore the two approaches are not directly comparable. Also, the sum of ^{15}N recoveries was sometimes >100% because of non-mutually exclusive categories shown in Fig. 3, such as microbial biomass and soil pools.

Many continuous variables were significantly correlated with total ecosystem ^{15}N tracer recovery in the short term (<1 week). Total ecosystem ^{15}N tracer recovery was negatively correlated with site elevation, fine root and soil ^{15}N natural abundance, and organic soil C and N concentration, but was positively correlated with mean annual air temperature and mineral soil C:N (Table 1). There were nearly significant negative relationships between total ecosystem ^{15}N recovery and both mean annual precipitation ($P = 0.08$) and atmospheric N deposition rate ($P = 0.06$).

Fewer significant correlations between total ecosystem ^{15}N tracer recovery and continuous variables emerged from the long-term (3 to 18 months) data set. However, most identified were fairly strong (Table 1). Total ecosystem ^{15}N tracer recovery was negatively correlated

only with foliar natural abundance ^{15}N, but was positively correlated with mineral soil C, N, and C:N. There was a positive relationship between total ecosystem ^{15}N recovery and precipitation, but it was not statistically significant ($P = 0.07$).

For the long-term data set, total ecosystem ^{15}N recovery differed significantly among categorical variables including ecosystem type, dominant plant species growth form, co-dominant growth form, mycorrhizal association, and site history (Fig. 4). The greatest total ecosystem recovery occurred in shrublands (mean, 89.5%; $n = 6$ sites), followed by wetlands (84.8%; $n = 2$), forests (74.9%; $n = 23$), and grasslands (51.8%; $n = 16$). Ecosystems dominated by evergreen shrubs had the greatest total ecosystem recovery (89.5%; $n = 6$), followed by deciduous trees (77.9%; $n = 11$), evergreen trees (74.0%; $n = 9$), graminoids (72.4%; $n = 12$), and evergreen plantations (66.9%; $n = 3$). Ecosystems with ericoid mycorrhizae (89.5%; $n = 6$) had significantly greater total ecosystem recovery than ecosystems associated with ecto- (72.5%; $n = 11$) or arbuscular mycorrhizae (53.0%; $n = 18$). Because all six shrubland sites were dominated by evergreen shrubs and had ericoid mycorrhizae, distinguishing effects of vegetation vs. mycorrhizal type on total ecosystem ^{15}N tracer recovery was not possible. The two sites (both at Harvard Forest) that had previously been disturbed by a hurricane had significantly greater total ecosystem ^{15}N tracer recovery (85.1%; $n = 2$) than ecosystems previously disturbed by burning (75.0%; $n = 2$), grazing

TABLE 1. Nonparametric correlations for total ecosystem percentage ^{15}N tracer recovery.

| | Sampling time after ^{15}N application | | | | | |
| | <1 week | | | 3–18 months | | |
Site characteristic	N	r_S	P	N	r_S	P
Mean elevation	30	**−0.52**	**0.0036**	48	0.15	0.32
Mean annual temperature	30	**0.52**	**0.0032**	47	−0.23	0.12
Mean annual precipitation	30	−0.33	0.076	48	0.27	0.067
Total nitrogen atmospheric deposition	28	−0.36	0.064	46	0.22	0.14
Foliar N concentration	22	−0.21	0.34	33	0.026	0.88
Foliar natural-abundance ^{15}N	20	−0.15	0.52	23	**−0.46**	**0.026**
Fine-root natural-abundance ^{15}N	26	**−0.57**	**0.0022**	29	0.11	0.59
Organic soil C concentration	26	**−0.79**	**<0.0001**	25	0.17	0.43
Organic soil N concentration	28	**−0.59**	**0.0011**	35	0.025	0.89
Organic soil C:N	26	0.30	0.14	25	0.18	0.38
Organic soil natural-abundance ^{15}N	26	**−0.79**	**<0.0001**	33	0.14	0.44
Mineral soil C concentration	28	−0.28	0.14	18	**0.72**	**0.0007**
Mineral soil N concentration	28	−0.29	0.14	24	**0.55**	**0.0057**
Mineral soil C:N	28	**0.67**	**<0.0001**	18	**0.72**	**0.0007**
Mineral soil natural-abundance ^{15}N	26	**−0.56**	**0.0028**	15	−0.13	0.63

Notes: The table includes ambient plots sampled at both a short-term (<1 week) and a long-term (3–18 months) time period. Significant relationships ($P < 0.05$) are in bold. N is the number of studies; r_S is the Spearman rank correlation coefficient. Nonparametric correlations are from JMP software, version 8.0.2 (SAS Institute 2009).

(68.3%; $n = 7$), selective harvest (67.7%; $n = 4$), or agriculture (57.2%; $n = 4$).

Form and method of ^{15}N tracer application also affected total ecosystem ^{15}N recovery (Fig. 5). Studies in which ^{15}N tracers were applied as ^{15}NH$_4^+$ had significantly lower total ecosystem ^{15}N tracer recovery (53.4 %,

$n = 23$) than those where ^{15}N was applied as ^{15}NH$_4$^{15}NO$_3$ (85.3%, $n = 15$) or ^{15}NO$_3^-$ (80.2 %, $n = 10$). Studies in which ^{15}N tracers were applied to the plant canopies had significantly greater total ecosystem ^{15}N tracer recovery (81.7 %, $n = 16$) than those studies where tracers were distributed onto the soil surface (63.1
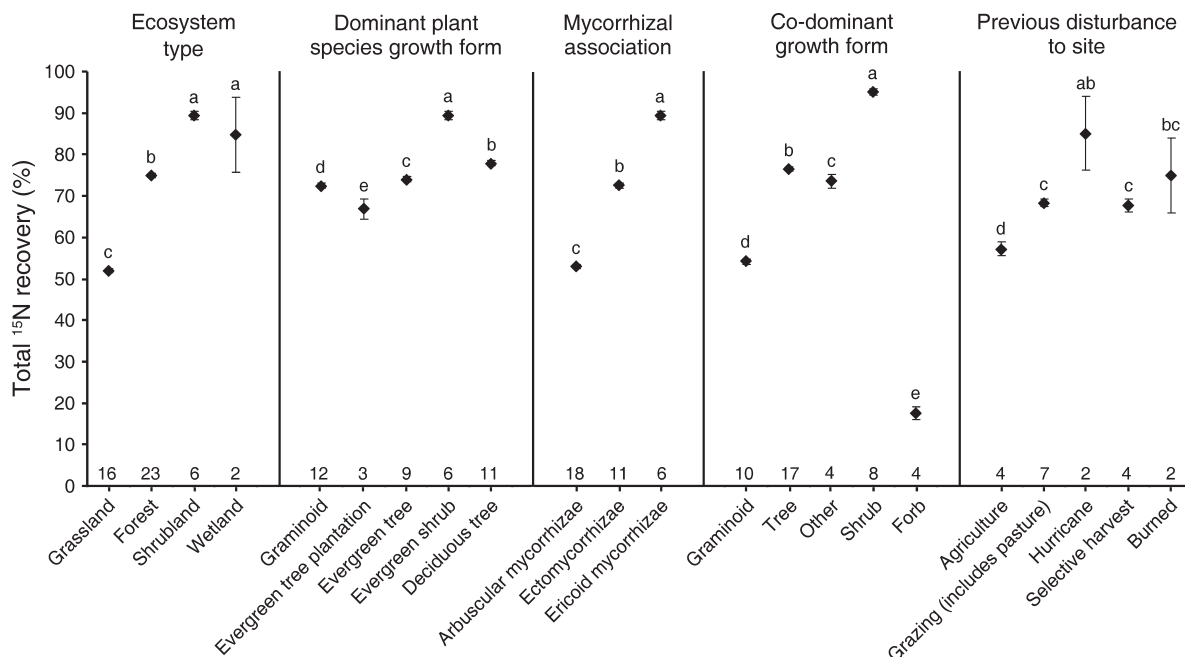

FIG. 4. Total ecosystem ^{15}N tracer recovery (mean and 95% confidence intervals) among ecosystem types, dominant plant species growth form, mycorrhizal association, co-dominant growth form, and major previous site disturbance. Data are from ambient plots sampled during the long-term time period. Nonoverlapping 95% confidence intervals and data points with different lowercase letters indicate significant differences at $P = 0.05$. Sample size (the number of studies within each ecosystem category) is given just above the *x*-axis.
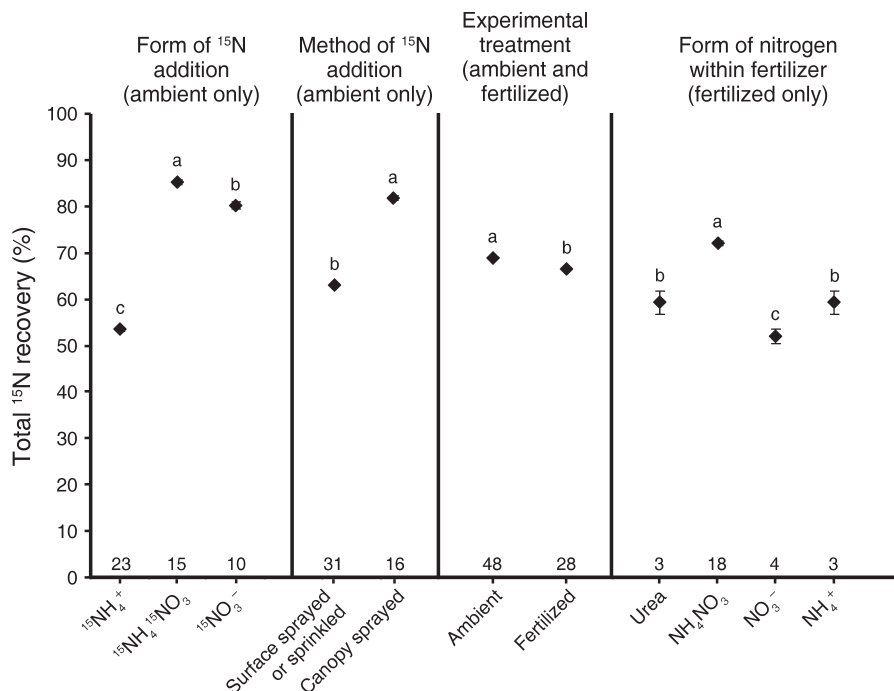
FIG. 5.   Total ecosystem ^{15}N tracer recovery (mean and 95% confidence intervals) among forms of ^{15}N addition, method of ^{15}N addition, experimental treatment, and form of N within fertilizer for the long-term time period. Nonoverlapping 95% confidence intervals and data points with different lowercase letters indicate significant differences at $P = 0.05$. Sample size (the number of studies within each category) is given just above the x-axis.

%, $n = 31$). The form of ^{15}N tracer applied varied with ecosystem type and therefore some of the effect of form of applied ^{15}N tracer may reflect ecosystem differences. ^{15}Nitrogen tracers were applied primarily as $^{15}NO_3^-$ or $^{15}NH_4^+$ to forest sites, but as $^{15}NH_4^{15}NO_3$ to a mixture of grassland, shrub, and tundra sites (only one forest site). Where ^{15}N was applied as $^{15}NO_3^-$, most researchers applied it to the soil surface. Application of ^{15}N tracers to the canopy occurred in low-statured ecosystems such as tundra, shrublands, wetlands, or grasslands.

Fertilization experiments: controls on total ecosystem recovery of ^{15}N

Fertilizer N additions reduced ecosystem ^{15}N recoveries compared to sites receiving only N inputs from ambient deposition and ^{15}N tracer applications (Fig. 5). This overall pattern, however, concealed significant differences in recoveries among fertilizer N forms where addition of NH_4NO_3 as fertilizer led to significantly greater total ecosystem ^{15}N tracer recovery compared to ambient plots where the other N forms (urea, NO_3^-, NH_4^+) all had lower recoveries (Fig. 5). In experiments containing both "low" and "high" N treatments, there was a negative relationship between rate of N added and the difference in total ecosystem ^{15}N tracer recovery between low and high N treatments (Fig. 6; $r = -0.46$; $P = 0.0013$).

Ambient conditions: fate of nitrogen among ecosystem pools

Overall, soil and litter retained more ^{15}N tracer than did plants in short- and long-term studies (Fig. 3). For the short term the largest sinks for ^{15}N tracers were below ground in (1) soil organic horizons, averaging 39.0% in forests ($n = 24$ studies), 16.9% in grasslands ($n = 8$), and 42.8% in tundra $n = 4$); (2) litter pools, averaging 31.6% in forests ($n = 20$), 10.6% in grasslands ($n = 8$), and 6.5% in tundra ($n = 2$); and (3) mineral soil horizons, averaging 29.9% in forests ($n = 22$) and 18.0% grasslands ($n = 10$). ^{15}N tracer recovery in soil microbial biomass was low in forests (11.5%, $n = 26$) and grasslands (6.2%, $n = 4$). In contrast, ^{15}N recovered in microbial biomass of tundra (36.1%, $n = 4$) was almost as high as in organic soil (42.8%, $n = 4$) and much greater than in litter (6.5%, $n = 2$) and roots (2.3% and 1.5% in fine and coarse roots, respectively, $n = 5$ and 5, respectively). Less than 10% of the recovered tracer was in plants for the short-term sampling period for all three ecosystem types, with most of that in roots. Fine-root biomass (6.3% and 2.3% in forests and tundra, respectively, $n = 14$ and 5, respectively) retained more ^{15}N tracer than did coarse-root biomass (3.5% and 1.5% in forests and tundra, respectively, $n = 4$ and 5, respectively) or foliage (0.6% in forests, $n = 2$). There were insufficient data to examine sinks for tracer ^{15}N in shrubland and wetland ecosystems for the short-term sampling period.
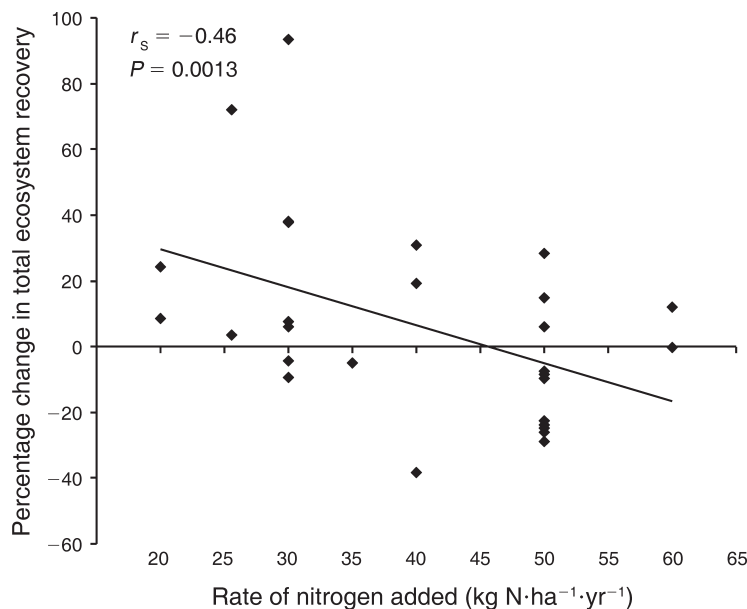
FIG. 6. Relationship between the percentage change in total ecosystem ^{15}N tracer recovery and the rate of N addition for all time periods. Positive values indicate greater total ecosystem ^{15}N tracer recovery following higher level of N addition. The Spearman rank correlation coefficient and P value are shown.

The largest sinks for ^{15}N tracers among ecosystem types for the long-term data set were organic soil in forests (35.5%, $n = 31$), litter in grasslands (25.5%, $n = 9$), shrublands (33.8%, $n = 6$), and wetlands (34.1%, $n = 2$), and foliage in tundra (12.1%, $n = 3$; Fig. 3). Total plant biomass (above- and belowground) retained less ^{15}N than soils and litter in forests (17.4% in vascular plant biomass), grasslands (30%), shrublands (23.2%), wetlands (9.6%), and tundra (29.9%). Proportions of ^{15}N tracer recovery in non-vascular plants (bryophytes and lichens; 20.1, 29.5 and 26% in forests, shrublands and wetlands, respectively, $n = 6$, 6 and 2, respectively) were significantly larger than other vegetation sinks, but were not different from belowground pools such as soil and litter. ^{15}Nitrogen tracer recovery in non-vascular plants of grasslands (14.2%, $n = 9$) was smaller than the total amount found in soils, litter, or live vascular plant biomass.

Fertilization experiments: fate of ^{15}N among ecosystem pools

Fertilizer N additions altered the partitioning of ^{15}N tracers in the short and long term for forest and tundra ecosystems (Fig. 3). In the short term the addition of fertilizer N in forests led to decreased ^{15}N recovery in organic soil, microbial biomass, and fine roots, but increased ^{15}N recovery in litter. Fertilization led to greater ^{15}N recovery in both fine and coarse roots in tundra for the short term. There were insufficient data to compare ambient to fertilized plots for soil and litter pools in tundra.

After one growing season, fertilizer N additions in forests also led to decreased ^{15}N in organic soil, but not

in mineral soil, microbial biomass, or fine roots. Total ^{15}N recoveries in live plants of forests increased with fertilizer N addition, with most tracer moving into aboveground plant biomass, while decreasing in soils and litter. Fertilization in tundra ecosystems decreased ^{15}N recovery in microbial biomass, but increased ^{15}N in fine roots and foliage. There were insufficient data to examine the impact of N addition on partitioning of N in grasslands, shrublands or wetlands.

DISCUSSION

Ecosystem nitrogen retention

Our results show that additions of N from either atmospheric deposition (<1-week data; Table 1) or from fertilization (Figs. 5 and 6) decreased total ecosystem N retention with an apparent threshold fertilization rate of 46 kg N·ha^{-1}·yr^{-1}. Above this rate, N addition decreased ^{15}N retention, while N fertilization at lower rates enhanced ^{15}N retention relative to unfertilized plots. The values for total ecosystem ^{15}N retention overlap with ecosystem N retention estimated for whole-watershed N mass balances (Aber et al. 2003, Dise et al. 2009). Nitrogen retention rates varied across 121 forested sites in Europe, with high N retention (87%) associated with low atmospheric N deposition rates (<8 kg N·ha^{-1}·yr^{-1}) and lower retention rates associated with higher N deposition (Dise et al. 2009). For the northeastern United States, N budgets from 83 forested watersheds show that N retention averages 76% of incoming atmospheric-N deposition, and decreases from >90% retention for sites receiving <7 kg N·ha^{-1}·yr^{-1} to <60% retention for sites receiving >11 kg N·ha^{-1}·yr^{-1}

(Aber et al. 2003). Our estimates of mean ecosystem N retention may be lower than these watershed studies, which included gaseous losses as part of their estimates of N retention, whereas our estimates of N retention rely on ^{15}N tracer recovered in plant biomass and soils only.

The convergence of results of ^{15}N tracer studies and watershed N input–output balances are suggestive of general patterns of the decreasing relative importance of biological sinks along gradients of increased N inputs. With greater N availability, it is possible that N sinks in plants or microbes, or on exchange sites on minerals or soil organic matter, became saturated when N fertilizer was added as urea, NH_4^+, or NO_3^-, such that more NO_3^- was lost due to leaching or lost as N gases (NO, N_2O, or N_2) from nitrification or denitrification. However, it is unclear why the same mechanisms did not occur following addition of fertilizer as NH_4NO_3. Ammonium nitrate fertilizer was added to a variety of ecosystems, including forests and tundra, suggesting that there was no bias between form of N fertilizer added and ecosystem type examined. Form of ^{15}N application also does not explain the relationship between N addition and total ecosystem ^{15}N retention as there was a mixture of forms of ^{15}N tracers applied in those sites that resulted in less ^{15}N retention following N fertilizer addition, as well as greater ^{15}N retention following N fertilizer addition (Fig. 6).

Tundra sites had increased total ecosystem ^{15}N retention following N fertilization compared to unfertilized controls. The three tundra sites included in this study (Niwot Ridge, Colorado, USA; Toolik Lake, Alaska, USA; Galbraith Lake, Alaska, USA) are N limited (Shaver and Chapin 1980, Chapin and Shaver 1985, Bowman et al. 1993), and may have been even after N fertilization. These sites may have retained greater amounts of applied ^{15}N through enhanced biological activity when N was in greater supply. In contrast to tundra sites, forest responses to N addition were mixed. Total ecosystem ^{15}N tracer recovery decreased with fertilization in the evergreen forests in Aber (Wales), the evergreen and deciduous forests in the Catskill Mountains (New York, USA), and deciduous stands that received $^{15}NO_3^-$ tracer application at Harvard Forest (Massachusetts, USA), but increased in the evergreen forests of Alptal (Switzerland) and some stands at Harvard Forest.

Studies that have quantified leachate ^{15}N found that <10% of ^{15}N tracer applied to non-fertilized plots (Tietema et al. 1998, Zak et al. 2004, Providoli et al. 2005) and 16% of ^{15}N tracer applied to fertilized plots (Lamontagne et al. 2000) is lost via leaching. These results suggest that the remaining N in ecosystems evaluated in this study could have been transported below the sampled soil depth or lost due to translocation within roots to outside of the experimental plots, movement with arthropods outside of the plots, wind (e.g., pollen or litter being blown out of plots), NH_3 volatilization, or by nitrification or denitrification

converting it to gaseous products (NO, N_2O and N_2). Losses via denitrification could account for only a small proportion of total ^{15}N applied. For example, Tietema et al. (1998) reported N_2O fluxes <4 kg·ha^{-1}·yr^{-1} from European forests, and Christenson et al. (2002) estimated that only 2.6% of applied ^{15}N tracer could have been lost as N_2O in a mixed-hardwood forest in the United States. We are not aware of any studies that have determined ^{15}N loss as NO or N_2. Alternatively, we may have underestimated ^{15}N incorporated into plant biomass.

Controls on ecosystem nitrogen retention

Results of our analyses demonstrate that a variety of factors influence ecosystem N retention. Total ecosystem N retention for the long-term sampling period varied significantly among ecosystem and mycorrhizal types, with shrublands and wetlands retaining significantly more tracer ^{15}N than forests or grasslands, though the sample sizes for shrublands ($n = 6$) and wetlands ($n = 2$) were small. Plant and microbial traits, and their interactions, could explain the high retention of ^{15}N tracers in shrublands. All shrubland sites included in this study were nutrient poor with high soil C:N (e.g., Johnson et al. 2003), likely contributing to relatively high N demand by plants and microbes. High mineral-soil C:N may promote microbial N immobilization and reduce net nitrification, which together could contribute to greater N retention. Such mechanisms may be operative in ecosystems in general, as mineral-soil C:N and total ecosystem retention of applied ^{15}N were positively correlated across our entire data set (Table 1). Similarly, total ecosystem ^{15}N recovery was negatively correlated with organic soil N concentration in the short-term (Table 1), suggesting that ecosystems are less likely to retain applied pulses of ^{15}N when soils are N rich. However, total ecosystem ^{15}N recovery was also negatively correlated with organic soil C concentration, suggesting a limited role of soil microbes in N retention given that microbial N immobilization is driven by soil C availability. This result is surprising given past work showing the importance of microbial uptake of N in ecosystem N retention (Vitousek and Matson 1984). Similar to soils, foliar N concentrations are considered indicators of N availability in terrestrial ecosystems (Aber et al. 1998). However, we found no relationship between foliar N concentration and ecosystem ^{15}N tracer recovery, nor did we find significant relationships between foliar N concentration and plant ^{15}N sink strength. Foliar N concentrations vary between species, masking potential changes due to N availability. Also, increases in foliar N content are often not accompanied by similar increases in N concentration due to a dilution effect caused by greater biomass. Overall, these findings suggest that compared to plant N concentrations, soil N concentrations or C:N are better predictors of ecosystem N retention. However, plants often control N retention through long-term C:N feedbacks such that lower

forest-floor C:N is associated with greater NO_3^- losses (Ågren and Bosatta 1988, Lovett et al. 2002). Although soils are the dominant sink for applied ^{15}N in this study, plants may still strongly influence the intensity of the soil sink through C:N feedbacks, which may not be evident in plant ^{15}N uptake or foliar N concentrations.

The relatively low N retention in grasslands was driven largely by results from a single site, Kirby Canyon, located in a Mediterranean climate in northern California, USA. Including Kirby Canyon, the mean ^{15}N tracer recovery in grasslands for the long-term sampling period was 51.8%. Excluding Kirby Canyon, mean ^{15}N recovery increased to 78.6%, or slightly greater than the mean tracer recovery of 74.9% in forests. Kirby Canyon could have had lower levels of ecosystem ^{15}N retention than other sites due to its extremely nutrient-poor serpentine soils and low potential for biotic assimilation by either plants or microbes. Application of ^{15}N tracer in Kirby Canyon occurred during a very wet El Niño year (1992) when soils were water saturated and annual plants were still germinating, which may have also contributed to lower total ecosystem N retention (Hooper and Vitousek 1997, Hooper 2011).

Disturbance history also influenced ecosystem ^{15}N tracer recovery for the long-term sampling period, with lower ^{15}N retention in former agricultural sites, possibly because prior fertilizer-N inputs decreased C:N of soils (Compton and Boone 2000) and reduced biotic demand or exchange sites in soils, reducing ecosystem N retention capacity. Nitrogen inputs from manure or fertilizer may have reduced ^{15}N retention in grazed and selectively harvested sites, respectively, through the same mechanisms. However, the net effect on N retention was smaller (Fig. 4), perhaps due to consumption and N removal during browsing and harvest.

The pattern of greater ecosystem N retention with higher mean annual air temperatures (Table 1) suggests that higher temperatures may have led to greater rates of N uptake by plants and microbes. Greater uptake could have more than offset possible increases in rates of soil N-cycling processes, such as mineralization and nitrification, and losses via gas emissions or leaching. These results agree with watershed mass balances showing that N export decreases with increasing temperatures (Schaefer and Alber 2007). The decrease in ^{15}N retention with increasing elevation is not surprising given that air temperature typically declines with increasing elevation and biological sinks may be attenuated. Also, as sites at higher elevations can be characterized by thinner soils, larger proportions of N additions could physically bypass biological sinks (Curtis et al. 2011).

Greater ecosystem recovery of ^{15}N tracers when applied by spraying the canopy (81.7%) compared to the ground (63.1%) is not surprising because N can be taken up by foliage or absorbed by the canopy surface. In contrast, N deposited on soil can be lost via leaching or gaseous loss. ^{15}Nitrogen tracers were applied as $^{15}NH_4^+$, $^{15}NO_3^-$, and $^{15}NH_4^{15}NO_3$, and to both the canopy and the ground in a variety of ecosystems, suggesting that there was not a bias between method of ^{15}N tracer application and ecosystem type examined.

The smaller recovery of ^{15}N tracer applied as $^{15}NH_4^+$ compared to $^{15}NO_3^-$ under ambient conditions (Fig. 5) is surprising because soon after NH_4^+ enters soil it is likely retained on cation exchange sites in soil organic matter and clays or preferentially taken up by soil microbes or plants. In contrast, NO_3^- is more prone to leaching losses or gaseous losses during denitrification or volatilization. It is possible that the lower tracer recoveries after $^{15}NH_4^+$ applications were due to losses by $^{15}NH_3$ volatilization (Nömmik and Vahtras 1982). However, few soils (i.e., Grandvillard) in our study likely had pH values high enough to drive NH_3 volatilization. Several reports have suggested that some NO_3^- may be incorporated into organic matter by abiotic reactions (Azhar et al. 1986, Berntson and Aber 2000, Dail et al. 2001, Davidson et al. 2003, Fitzhugh et al. 2003), but others suggest that this process is unlikely to occur in nature to an ecologically significant degree (Colman et al. 2008, Davidson et al. 2008, Morier et al. 2010). If NO_3^- incorporation was significant, this initial retention of ^{15}N could have contributed to the relatively high total ecosystem ^{15}N tracer recovery in those studies where ^{15}N was applied as $^{15}NO_3^-$ or $^{15}NH_4^{15}NO_3$. Volatilization of NO_3^- from plant canopies, as HNO_3 and other forms of N, has been estimated to be significant in several forest ecosystems, possibly accounting for losses up to 10% of experimentally added N (Dail et al. 2009). When added as fertilizer, NH_4NO_3 also had the highest total ecosystem ^{15}N retention. But unlike the ambient conditions, fertilizer with NH_4^+ had, as expected, a higher recovery than fertilizer with NO_3^- (Fig. 5). Thus, NO_3^- fertilizer may be more susceptible to leaching or gas loss than NH_4^+ and urea fertilizer, which may be retained by cation exchange.

^{15}N natural abundances of foliage, roots, and soils were negatively correlated with total ecosystem ^{15}N tracer recovery during the long-term sampling period. High plant ^{15}N natural abundance can be an indicator of an ecosystem with relatively fast N-cycling rates, high N losses, and low rates of N transfer from mycorrhizal fungi in terrestrial ecosystems (e.g., Högberg 1997). These ecosystems would be expected to retain smaller proportions of applied ^{15}N tracer compared to ecosystems with relatively slower N cycling, smaller losses, and greater N transfer from mycorrhizal fungi. The significant negative correlation we found suggests that plant and soil ^{15}N natural abundance are also good indicators of ecosystem N-retention capacities across different ecosystem types, including grasslands, forests, shrublands, and wetlands.

Atmospheric nitrogen inputs and carbon storage

This data set is the largest assembled to date of studies using ^{15}N-labeled N inputs to identify patterns and

drivers of N partitioning among ecosystem pools within non-agricultural systems. As such, this data set is also a valuable resource for assessing possible impacts of N deposition on C uptake and storage. Our observation that most ^{15}N tracer applications accumulated in belowground pools under ambient conditions and low levels of N-fertilizer input in forest, grassland, and shrubland ecosystems is consistent with results of a smaller study of plots in nine temperate forests in North America and Europe (Nadelhoffer et al. 1999), most of which are included within this meta-analysis. Carbon storage would be maximized if large proportions of N inputs were immobilized by aboveground plant tissues and contributed to increased rates of photosynthesis. However, this was not the case in our study; aboveground vegetation was a small sink for N additions relative to soils or to soils plus exports (whether measured by difference or directly). Similar to Nadelhoffer et al. (1999), we conclude that immediate growth enhancement from atmospheric N deposition should be modest in forests under ambient levels of N availability because little of the applied ^{15}N is recovered in aboveground biomass (6% recovery total) within one year of ^{15}N application. Compared to forests, a larger amount of ^{15}N tracer went into aboveground biomass in shrublands and grasslands (i.e., 19% and 20%, respectively) at the long-term timescale. However, ^{15}N tracer was applied to the canopies of the shrubland ecosystems in this study, enhancing the likelihood of N retention associated with aboveground biomass due to direct absorption immediately following ^{15}N tracer application. Data were not available to determine above vs. belowground partitioning of N for tundra or wetland ecosystems.

Data were available to examine the impact of elevated fertilizer N inputs on movement of N between soil and plant pools in forests only. In these ecosystems, elevated fertilizer N inputs led to movement of N from soil to plant pools, which could increase plant growth due to increased rates of photosynthesis and less allocation to short-lived roots and mycorrhizal fungi, which together could result in a larger C sink in forests. If N fertilizer additions can be used as a proxy for greater rates of atmospheric N deposition or accumulation of N over time, these results suggest that the size of the C sink in forests could increase as a result of elevated levels of atmospheric N deposition. However, the magnitude of this effect is not well known at present and is likely to vary with dominant species (Thomas et al. 2010).

Suggestions for future work on the fate of nitrogen

Ecosystems within North America and Europe are well represented by ^{15}N tracer studies, especially evergreen forests and arctic tundra. Additional ^{15}N tracer studies are needed at lower latitudes, particularly in warm and wet sites, to understand the fate of N inputs within savanna and tropical ecosystems. Future ^{15}N studies should explore N losses in the forms of NO_3^-,

dissolved organic N, NH_3, N_2O, NO, and N_2 or through lateral movement of N compounds across the landscape. We suggest that, at a minimum, researchers measure ^{15}N tracer recovery in roots, organic soil, mineral soil, litter, and aboveground plant pools to aid in mechanistic understanding of the fate of N inputs in terrestrial ecosystems and for future cross-site comparisons. Finally, additional studies that sample fates of tracers at multiple timescales would help separate mechanisms of N retention among microbial and plant pathways to better understand how N inputs are likely to affect ecosystem C balance. Studies on the decadal scale would be particularly valuable in assessing issues such as C sequestration.

Conclusions

Our meta-analysis of ^{15}N tracer studies demonstrates that local site characteristics such as ecosystem type, vegetation growth form, mycorrhizal type, soil C:N, and disturbance history, as well as the form of ^{15}N application, all influence ecosystem ^{15}N retention. Also, our results suggest that plant and soil natural-abundance ^{15}N values can be used as a qualitative indicator of total ecosystem N retention. Nitrogen inputs are largely incorporated into the soils of forests, shrublands, and grasslands, consistent with previous assertions that most atmospherically deposited N moves belowground. Total ecosystem N retention increased with mineral soil C:N, consistent with the idea that factors controlling microbial N uptake can shape the long-term sink for N in soils and thus total ecosystem N retention. At high rates of N input we found that N uptake by plants increased, but the magnitude of ^{15}N recovery in mineral soil decreased, with an apparent threshold fertilization rate of 46 kg·ha^{-1}·yr^{-1} above which whole ecosystems had a net loss of ^{15}N tracer relative to inputs. Given the importance of mineral soil as a nitrogen sink across the range of N inputs examined, we hypothesize that long-term increases in N input could lower mineral soil C:N (via direct N incorporation and/or lower litterfall C:N) and ultimately lead to decreased ecosystem N retention.

Literature Cited

Aber, J. D., C. L. Goodale, S. V. Ollinger, M.-L. Smith, A. H. Magill, M. E. Martin, R. A. Hallett, and J. L. Stoddard.

2003. Is nitrogen deposition altering the nitrogen status of northeastern forests? BioScience 53:375–389.

Aber, J. D., W. McDowell, K. Nadelhoffer, A. Magill, G. Berntson, M. Kamakea, S. McNulty, W. Currie, L. Rustad, and I. Fernandez. 1998. Nitrogen saturation in temperate forest ecosystems. Hypotheses revisited. BioScience 48:921–934.

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

Aerts, R., and F. S. Chapin, III. 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Advances in Ecological Research 30:2–69.

Ågren, G. I., and E. Bosatta. 1988. Nitrogen saturation of terrestrial ecosystems. Environmental Pollution 54:185–197.

Ågren, G. I., E. Bosatta, and A. H. Magill. 2001. Combining theory and experiment to understand effects of inorganic nitrogen on litter decomposition. Oecologia 128:94–98.

Azhar, E. S., O. Van Cleemput, and W. Verstraete. 1986. Nitrification mediated nitrogen immobilization in soils. Plant and Soil 94:401–409.

Berntson, G. M., and J. D. Aber. 2000. Fast nitrate immobilization in N-saturated temperate forest soils. Soil Biology and Biochemistry 32:151–156.

Bowman, W. D., T. A. Theodose, J. C. Schardt, and R. T. Conant. 1993. Constraints of nutrient availability on primary productivity in two alpine tundra communities. Ecology 74:2085–2097.

Chapin, F. S., III, and G. R. Shaver. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. Ecology 66:564–576.

Christenson, L. M., G. M. Lovett, M. J. Mitchell, and P. M. Groffman. 2002. The fate of nitrogen in gypsy moth frass deposited to an oak forest floor. Oecologia 131:444–452.

Colman, B. P., N. Fierer, and J. P. Schimel. 2008. Abiotic nitrate incorporation, anaerobic microsites, and the ferrous wheel. Biogeochemistry 91:223–227.

Compton, J. E., and R. D. Boone. 2000. Long-term impacts of agriculture on soil carbon and nitrogen in New England forests. Ecology 81:2314–2330.

Currie, W. S., and K. J. Nadelhoffer. 1999. Dynamic redistribution of isotopically labeled cohorts of nitrogen inputs in two temperate forests. Ecosystems 2:4–18.

Curtis, C. J., C. D. Evans, C. L. Goodale, and T. H. E. Heaton. 2011. What have stable isotope studies revealed about the nature and mechanisms of N saturation and nitrate leaching from semi-natural catchments? Ecosystems 14:1021–1037.

Dail, D. B., E. A. Davidson, and J. Chorover. 2001. Rapid abiotic transformation of nitrate in an acid forest soil. Biogeochemistry 54:131–146.

Dail, D. B., D. Y. Hollinger, E. A. Davidson, I. Fernandez, H. C. Sievering, N. A. Scott, and E. Gaige. 2009. Distribution of nitrogen-15 tracers applied to the canopy of a mature spruce–hemlock stand, Howland, Maine, USA. Oecologia 160:589–599.

Davidson, E. A., J. Chorover, and D. B. Dail. 2003. A mechanism of abiotic immobilization of nitrate in forest ecosystems: the ferrous wheel hypothesis. Global Change Biology 9:228–236.

Davidson, E. A., D. B. Dail, and J. Chorover. 2008. Iron interference in the quantification of nitrate in soil extracts and its effect on hypothesized abiotic immobilization of nitrate. Biogeochemistry 90:65–73.

De Deyn, G. B., J. H. C. Cornelissen, and R. D. Bardgett. 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. Ecology Letters 11:516–531.

Dise, N. B., J. J. Rothwell, V. Gauci, C. van der Salm, and W. de Vries. 2009. Predicting dissolved inorganic nitrogen leaching in European forests using two independent databases. Science of the Total Environment 4078:1798–1808.

Emmett, B. A., O. J. Kjønaas, P. Gundersen, C. J. Koopmans, A. Tietema, and D. Sleep. 1998. Natural abundance of ^{15}N in forests across a nitrogen deposition gradient. Forest Ecology and Management 101:9–18.

Fitzhugh, R. D., L. M. Christenson, and G. M. Lovett. 2003. Biotic and abiotic immobilization of ammonium, nitrite, and nitrate in soils developed under different tree species in the Catskill Mountains, New York, USA. Global Change Biology 9:1591–1601.

Fog, K. 1988. The effect of added nitrogen on the rate of decomposition of organic matter. Biological Reviews 63:433–462.

Galloway, J. N., A. R. Townsend, J. W. Erisman, M. Bekunda, Z. Cai, J. R. Freney, L. A. Martinelli, S. P. Seitzinger, and M. A. Sutton. 2008. Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. Science 320:889–892.

Gardner, J. B., and L. E. Drinkwater. 2009. The fate of nitrogen in grain cropping systems: a meta-analysis of ^{15}N field experiments. Ecological Applications 19:2167–2184.

Garten, C. T. 1993. Variation in foliar ^{15}N abundance and the availability of soil nitrogen on Walker Branch Watershed. Ecology 74:2098–2113.

Gebauer, G., and E. D. Schulze. 1991. Carbon and nitrogen isotope ratios in different compartments of a healthy and a declining Picea abies forest in the Fichtelgebirge, northeastern Bavaria [Germany]. Oecologia 87:198–207.

Hobbie, E. A., and A. P. Ouimette. 2009. Controls of nitrogen isotope patterns in soil profiles. Biogeochemistry 95:355–371.

Högberg, P. 1997. ^{15}N natural abundance in soil–plant systems. Tansley Review No. 95. New Phytologist 137:179–203.

Högberg, P., C. Johannisson, S. Yarwood, I. Callesen, T. Nasholm, D. D. Myrold, and M. N. Högberg. 2011. Recovery of ectomycorrhiza after 'nitrogen saturation' of a conifer forest. New Phytologist 189:515–525.

Hooper, D. U. 2011. Biodiversity, ecosystem functioning, and global change. Pages 329–357 in S. Harrison and N. Rajakaruna, editors. Serpentine: the evolution and ecology of a model system. University of California Press, Berkeley, California, USA.

Hooper, D. U., and P. M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. Science 277:1302–1305.

Hungate, B. A., J. S. Dukes, M. R. Shaw, Y. Luo, and C. B. Field. 2003. Nitrogen and climate change. Science 302:1512–1513.

IPCC [Intergovernmental Panel on Climate Change]. 2007. Climate change 2007: the physical science basis. Cambridge University Press, Cambridge, UK.

Janssens, I. A., et al. 2010. Reduction of forest soil respiration in response to nitrogen deposition. Nature Geoscience 3:315–322.

Johnson, D. W., B. A. Hungate, P. Dijkstra, G. Hymus, C. R. Hinkle, P. Stiling, and B. G. Drake. 2003. The effects of elevated CO_2 on nutrient distribution in a fire-adapted scrub oak forest. Ecological Applications 13:1388–1399.

Lamontagne, S., S. L. Schiff, and R. J. Elgood. 2000. Recovery of ^{15}N-labelled nitrate applied to a small upland boreal forest catchment. Canadian Journal of Forest Research 30:1165–1177.

LeBauer, D. S., and K. K. Treseder. 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. Ecology 89:371–379.

Lovett, G. M., K. C. Weathers, and M. A. Arthur. 2002. Control of nitrogen loss from forested watersheds by soil carbon:nitrogen ratio and tree species composition. Ecosystems 5:712–718.

Mack, M. C., E. A. G. Schuur, M. S. Bret-Harte, G. R. Shaver, and F. S. Chapin, III. 2004. Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. Nature 431:440–443.

Meints, V. W., L. V. Boone, and L. T. Kurtz. 1975. Natural ^{15}N abundance in soil, leaves, and grain as influenced by long term additions of fertilizer N at several rates. Journal of Environmental Quality 4:486–490.

Morier, I., P. Schleppi, M. Saurer, I. Providoli, and C. Guenat. 2010. Retention and hydrolysable fraction of atmospherically deposited nitrogen in two contrasting forest soils in Switzerland. European Journal of Soil Science 61:197–206.

Nadelhoffer, K. J., B. A. Emmett, P. Gundersen, O. J. Kjønaas, C. J. Koopmans, P. Schleppi, A. Tietema, and R. F. Wright. 1999. Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. Nature 398:145–148.

Nömmik, H., and K. Vahtras. 1982. Retention and fixation of ammonium and ammonia in soils. Agronomy 22:123–171.

Osenberg, C. W., O. Sarnelle, S. D. Cooper, and R. D. Holt. 1999. Resolving ecological questions through meta-analysis: goals, metrics, and models. Ecology 80:1105–1117.

Pardo, L., et al. 2006. Regional assessment of N saturation using foliar and root ^{15}N. Biogeochemistry 80:143–171.

Providoli, I., H. Bugmann, R. Siegwolf, N. Buchmann, and P. Schleppi. 2005. Flow of deposited inorganic N in two Gleysol-dominated mountain catchments traced with $^{15}NO_3^-$ and $^{15}NH_4^+$. Biogeochemistry 76:453–475.

Rosenberg, M. S., D. C. Adams, and J. Gurevitch. 2000. MetaWin: statistical software for meta-analysis. Version 2. Sinauer Associates, Sunderland, Massachusetts.

SAS Institute. 2009. JMP software, version 8.0.2. SAS Institute, Cary, North Carolina, USA.

Schaefer, S. C., and M. Alber. 2007. Temperature controls a latitudinal gradient in the proportion of watershed nitrogen exported to coastal ecosystems. Biogeochemistry 85:333–346.

Schlesinger, W. H. 2009. On the fate of anthropogenic nitrogen. Proceedings of the National Academy of Sciences USA 106:203–208.

Shaver, G. R., and F. S. Chapin, III. 1980. Response to fertilization by various plant growth forms in an Alaskan tundra: nutrient accumulation and growth. Ecology 61:662–675.

Templer, P. H., M. A. Arthur, G. M. Lovett, and K. Weathers. 2007. Plant and soil natural abundance δ^{15}N: indicators of relative rates of nitrogen cycling in temperate forest ecosystems. Oecologia 153:399–406.

Thomas, R. Q., C. D. Canham, K. C. Weathers, and C. L. Goodale. 2010. Increased tree carbon storage in response to nitrogen deposition in the US. Nature Geoscience 3:13–17.

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

Vitousek, P. M., J. D. Aber, R. H. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and D. G. Tilman. 1997. Human alteration of the global nitrogen cycle: Sources and consequences. Ecological Applications 7:737–750.

Vitousek, P. M., and P. A. Matson. 1984. Mechanisms of nitrogen retention in forest ecosystems: a field experiment. Science 225:51–52.

Zak, D. R., W. E. Holmes, A. J. Burton, K. S. Pregitzer, and A. F. Talhelm. 2008. Atmospheric NO_3^- deposition increases soil organic matter by slowing decomposition in a northern hardwood ecosystem. Ecological Applications 18:2016–2027.

Zak, D. R., K. S. Pregitzer, W. E. Holmes, A. J. Burton, and G. P. Zogg. 2004. Anthropogenic N deposition and the fate of $^{15}NO_3^-$ in a northern hardwood ecosystem. Biogeochemistry 69:143–157.

SUPPLEMENTAL MATERIAL

Appendix

Site characteristics and experimental design for ^{15}N tracer studies included in the meta-analysis (*Ecological Archives* E093-161-A1).