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Regional assessment of N saturation using foliar and root $\delta^{15}N$

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Abstract. N saturation induced by atmospheric N deposition can have serious consequences for forest health in many regions. In order to evaluate whether foliar $\delta^{15}N$ may be a robust, regional-scale measure of the onset of N saturation in forest ecosystems, we assembled a large dataset on atmospheric N deposition, foliar and root $\delta^{15}N$ and N concentration, soil C:N, mineralization and nitrification. The dataset included sites in northeastern North America, Colorado, Alaska, southern Chile and Europe. Local drivers of N cycling (net nitrification and mineralization, and forest floor and soil C:N) were more closely coupled with foliar $\delta^{15}N$ than the regional driver of N deposition. Foliar $\delta^{15}N$ increased non-linearly with nitrification:mineralization ratio and decreased with forest floor C:N. Foliar $\delta^{15}N$ was more strongly related to nitrification rates than was foliar N concentration, but concentration was more strongly correlated with N deposition. Root $\delta^{15}N$ was more tightly coupled to forest floor properties than was foliar $\delta^{15}N$. We observed a pattern of decreasing foliar $\delta^{15}N$ values across the following species: American beech > yellow birch > sugar maple. Other factors that affected foliar $\delta^{15}N$ included species composition and climate. Relationships between foliar $\delta^{15}N$ and soil variables were stronger when analyzed on a species by species basis than when many species were lumped. European sites showed distinct patterns of lower foliar $\delta^{15}N$, due to the importance of ammonium deposition in this region. Our results suggest that examining $\delta^{15}N$ values of foliage may improve understanding of how forests respond to the cascading effects of N deposition.

Introduction

Nitrogen saturation is the process by which chronically elevated N inputs alter forest ecosystems, ultimately resulting in increases in ecosystem N loss (Aber et al. 1989; 1998). N saturation can result in detrimental plant responses and have serious consequences for forest health (Nihlgard 1985; Aber et al. 1989; Schaberg et al. 2002) and may impact forests in many regions (Dise et al. 1998; Aber et al. 2003). Therefore, developing indicators useful for determining whether a forest is at N saturation and for predicting when a forest is nearing N saturation is valuable. Such indicators would facilitate both forest management and understanding of N cycling in forest ecosystems.

Aber et al. (1998) describe several stages of N saturation. Prior to N saturation (when N is limiting), net N mineralization rate approximately matches plant and microbial N uptake demands, and N leaching and gaseous losses are negligible. Stage 1 includes increasing N mineralization, slight increases in foliar N concentration, followed by increases in foliar biomass, increasing net nitrification and nitrate leaching. Stage 2 includes elevated nitrification and nitrate leaching, elevated foliar N concentration and foliar biomass. Stage 3 includes continued high nitrification, nitrate leaching and gaseous N losses, and declines in NPP and foliar biomass, and a plateau in foliar N concentration. Stoddard (1994) identified similar stages for surface waters draining forested catchments. Transitions from one stage to another may be gradual.

In order to better understand N saturation in forest ecosystems, it is critical to be able to identify when short-term disruptions or chronic shifts in N cycling occur within an ecosystem. Of particular interest are shifts that occur early in the process of N saturation–before nitrate or other N losses are detected–when the internal N cycle begins to shift from a closed N cycle with little N loss (when microbial and vegetation N cycling are closely coupled) toward an open, leaky N cycle with substantial N losses (stage 2 N saturation, when microbial and plant N cycling become decoupled; Aber et al. 1998; Corre et al. 2003).

A second challenge in evaluating N saturation is identifying symptoms of saturation over large areas. Atmospheric deposition is a regional-scale phenomenon, but most forest N cycle studies are done at the plot or watershed scale. Plot studies have documented changes in N cycling with deposition (e.g. Nitrogen Saturation Experiments project, NITREX, in coniferous forests in Europe; Tietema et al. 1998) and recent work in the northeastern U.S. demonstrated a pattern of increasing stream water nitrate concentration across a regional N deposition gradient (Aber et al. 2003). However, intensive assessments that include detailed measurements of N cycling processes are difficult to conduct at multiple sites on a broad scale.

In this paper, we investigate the idea that foliar $\delta^{15}N$ may be a robust, regional-scale measure of the onset of N saturation in forest ecosystems. Stable isotopes of nitrogen are a powerful tool for evaluating N cycling because of their ability to integrate over time and space (Nadelhoffer and Fry 1994). Recent studies have included the use of isotopic tracers; in this study, we evaluated the natural abundance of ^{15}N. We report all isotope data as $\delta^{15}N$ values, which represent the per mil (‰) difference between the isotopic composition of the sample and that of atmospheric dinitrogen:

$$\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000 \quad (1)$$

where R_{sample} represents the sample isotope ratio ($^{15}N/^{14}N$), and $R_{standard}$ is $^{15}N/^{14}N$ for atmospheric N_2, or 0.0036765. Isotopic fractionation occurs during enzymatic and other biological processes, discriminating against the heavier ^{15}N when chemical bonds are broken, such that the product generally has a lower ratio of $^{15}N/^{14}N$ than the remaining substrate (Mariotti et al. 1981; Robinson 2001). During nitrification, the nitrate produced is depleted in ^{15}N relative to the ammonium substrate, so that in ecosystems with high nitrification and nitrate loss, the remaining N pools become enriched in ^{15}N (Nadelhoffer and Fry 1994). These residual N pools include soil, vegetation and inorganic N pools (NH_4^+ and NO_3^-). Denitrification is also strongly fractionating (Hübner 1986) and, at sites where it is significant, causes similar enrichment in the remaining N pools (Piccolo et al. 1994).

We hypothesized that foliar $\delta^{15}N$ would respond to N saturation because previous studies have demonstrated that as forest floor C:N declines below about 23 due to N saturation, nitrification increases (Dise et al. 1998; Goodale and Aber 2001; Ollinger et al. 2002). Other studies have shown increases in foliar $\delta^{15}N$ (natural abundance) in response to changes in N cycling including increased nitrification (and loss of ^{15}N-depleted nitrate) following clear-cutting (Pardo et al. 2002), along an N deposition gradient (Emmett et al. 1998; Pardo et al. 2003), with N additions (Högberg and Johanisson 1993; Pardo et al. 1998), and with heavy industrial N pollution (Gebauer and Schulze 1991; Gebauer et al. 1994; Jung et al. 1997). When nitrification increases and ^{15}N-depleted nitrate is exported from the ecosystem, the N remaining in the

ecosystem (including N available for plant uptake) is enriched in ^{15}N. For example, at the Hubbard Brook Experimental Forest (HBEF), we observed an increase of $1-2‰$ in forest floor and $3.5‰$ in foliage immediately after clearcutting which significantly increased nitrification and nitrate loss. Small increases in $\delta^{15}N$ can indicate major changes in N cycling. It has also been observed that ecosystems with more open N cycles tend to show ^{15}N enrichment in plants and soils (Gebauer and Schulze 1991; Martinelli et al. 1999). Furthermore, foliar N concentration varies from year to year (Hughes and Fahey 1994), with position in the crown (van den Driessche 1974), and with leaf age (Jach and Ceulemans 2000). Therefore, we hypothesized that foliar $\delta^{15}N$, would be useful for regional-scale assessment of N saturation in forest ecosystems, and would be more useful than foliar N concentration alone. However, using measurements of both foliar $\delta^{15}N$ and N concentration may provide the clearest assessment of ecosystem N status, as is often the case with multiple ecosystem measures.

A major advantage of foliar $\delta^{15}N$ for regional-scale assessment of N saturation is that it is readily measured at large numbers of sites and is a fairly robust measure (i.e., differences in sampling protocol may not be important). For example, Pardo et al. (2002) observed no differences between litter and leaf $\delta^{15}N$ and negligible year-to-year variability (in the absence of disturbance) at the HBEF over 12 years. Some work has suggested that foliar $\delta^{15}N$ may vary through the growing season for hardwoods, particularly with significant changes in precipitation and soil moisture (Handley et al. 1999); others have reported for conifers that no seasonal patterns in foliar $\delta^{15}N$ were observed (Jung et al. 1997). However such variability was clearly not a factor in HBEF longitudinal study, since the samples were not collected at exactly the same point each year. Further work at seven sites across the northeastern U.S. found no difference between foliar $\delta^{15}N$ of current year needles and needles from all age classes combined (Pardo et al. 2003).

Plant species can affect N cycling patterns and, similarly, may influence foliar $\delta^{15}N$ values. Species differences in foliar $\delta^{15}N$ have been reported broadly (Högberg 1990; Michelson et al. 1998; Hobbie et al. 2000). Some studies have reported that conifers tend to have lower $\delta^{15}N$ than hardwoods, others have reported no difference (Gebauer and Dietrich 1993). Also, in several studies, strong and consistent patterns of the relative foliar $\delta^{15}N$ value by species have been reported (Nadelhoffer et al. 1996; Templer 2001; Miller and Bowman 2002; Pardo et al. 2002). One factor that may influence species patterns of foliar $\delta^{15}N$ is mycorrhizal association. Previous research has also shown that, in some ecosystems, plant association with mycorrhizal fungi regulates the plant $\delta^{15}N$ value, such that, within a site plant $\delta^{15}N$ varies with mycorrhizal association: ectomycorrhizal fungi < arbuscular mycorrhizae < non-mycorrhizal (Michelsen et al. 1998; Schmidt and Stewart 2003).

In addition to evaluating the use of foliar $\delta^{15}N$ as a measure of N saturation, we tested hypotheses about root $\delta^{15}N$ and N saturation. Templer (2001) found a significantly stronger relationship between root $\delta^{15}N$ and soil N cycling rates compared to foliar $\delta^{15}N$ and N cycling rates in forested stands of the Catskill Mountains, NY. Few other studies have examined root $\delta^{15}N$, but we expected that we might find an even stronger relationship between root $\delta^{15}N$ (compared to foliar $\delta^{15}N$) and soil N cycling rates since there is a more direct connection between roots and ^{15}N-enrichment processes driven by nitrification, i.e. fewer plant processes occur before the N is assimilated, and possibly discriminated against (Handley and Raven 1992) in tissue.

The objective of this study was to evaluate foliar $\delta^{15}N$ as a tool for assessing N saturation on the regional scale. To accomplish this objective, we assembled and analyzed foliar samples and data from a large number of studies as part of a project of the Northeastern Ecosystem Research Cooperative (NERC; http://www.ecostudies.org/nerc). NERC supports a range of activities devoted to analysis and synthesis of pressing questions in forest ecology (including N saturation) in the northeastern U.S./southeastern Canada region. We tested the following hypotheses:

1. Foliar $\delta^{15}N$ increases with net nitrification:mineralization.
2. Foliar $\delta^{15}N$ decreases with forest floor C:N.
3. Foliar $\delta^{15}N$ increases with N deposition.
4. Foliar $\delta^{15}N$ has a stronger relationship than foliar N concentration with nitrification rates.
5. Root $\delta^{15}N$ is more tightly coupled to forest floor or soil properties than is foliar $\delta^{15}N$.

Site description and methods

General site and data description

We assembled a large dataset of foliar $\delta^{15}N$ data coupled with information on soil C:N and N cycling. Most of the data were from northeastern North America; however, the dataset also included data from Colorado, Alaska, southern Chile and Europe (Figure 1, Table 1). In order to evaluate whether root $\delta^{15}N$ values could also be used to assess N cycling and N saturation, we assembled root $\delta^{15}N$ data from a subset of the same dataset (identified in Table 1). In most cases, collaborators provided us with foliar samples, which we prepared for $\delta^{15}N$ analysis at the Center for Stable Isotope Biogeochemistry at University of California, Berkeley (CSIB); these foliar samples are identified in Table 1. Root $\delta^{15}N$ data were provided by the collaborators. Roots were not separated by species, although in most cases they were collected from plots dominated by a single species. Roots included in the analysis were fine roots, less than 6 mm in diameter, collected from the forest floor. Sample collection and preparation methods varied among studies (see Table 1 for references).

Analytical methods

Foliar samples identified in Table 1 were pulverized in a shatterbox (SPEX Chemical and Sample Prep, model 8500), oven dried at 65 °C and loaded into tin capsules for isotope analysis. Isotopic analyses were

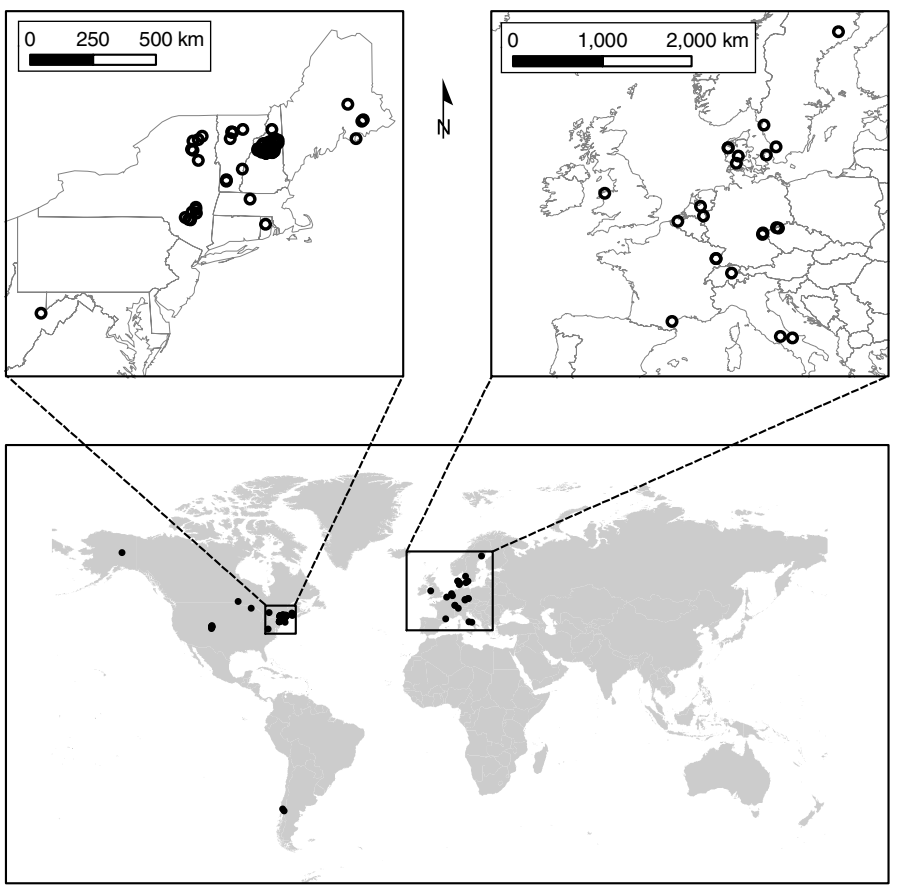

Figure 1. Site locations.

Table 1. Site description.

Site	N Deposition [a]kg ha^{-1} y^{-1}	N min. Nit.[b] Method	# Plots	# Foliar samples	Species analyzed[c]	References
Northeast						
Acadia, ME – NGS*	6	Lab	8	8	*PiRu*	McNulty et al. 1991
Ampersand Mt., Caitlin Lake, Hennessy Mt., Huntington Forest, Adirondacks, NY*	8–9	*In situ*	8	40	*AcRu, AcSa, BeAl, FaGr, FrAm, OsVi, PrSe, TiAm, ViAl*	Mitchell et al. 2001
Bear Brook, ME	5	*In situ*†	2	52‡	*AcSa, BeAl, FaGr, PiRu*	Nadelhoffer et al. 1995; Jefts et al. 2004
Bowl Research Natural Area, NH*	9	Lab	11	26	*AbBa, AcRu, AcSa, AcSp, BeAl, FaGr, PiRu, TsCa*	Martin 1979; Pardo 1999
Camels Hump, VT – NGS*	9	Lab	18	141	*AbBa, AcRu, BeAl, BeLe, BePa, PiRu, SoAm*	McNulty et al. 1991
Catskill sites (7), NY	11–12	Lab	41	41‡	*AcSa, FaGr, TsCa, QuRu*	Templer 2001
Cone Pond Watershed, NH*	8	Lab	12	81	*AbBa, AcRu, AcSa, AcSp, BeAl, FaGr, PiRu, TsCa*	Bailey et al. 1995; Pardo 1999
Fernow Experimental Forest, WV*	12	*In situ*	3	130	*AcRu, AcSa, BeLe, LiTu, PrSe, QuRu*	Gilliam et al. 1996; Adams et al. 1997
Gore Mt., NY – NGS*	11	Lab	24	130	*AbBa, BeAl, BePa, PiRu*	McNulty et al. 1991
Harvard Forest, MA	9	*In situ*†	2	11‡	*QuVe*	Magill et al. 1997; Nadelhoffer et al. 1999a
Howland, ME – NGS*	5	Lab	20	156	*AbBa, AcRu, BeAl, BePa, PiRu, PiSt, ThOc, TsCa*	McNulty et al. 1991
Hubbard Brook Experimental Forest, NH*	8	Lab	16	221	*AbBa, AcRu, AcSa, AcSp, BeAl, FaGr, PiRu, TsCa*	Pardo 1999; Bohlen et al. 2001
Lead Mt., ME – NGS*	5	Lab	7	7	*PiRu*	McNulty et al. 1991
Loon Mt., NH – NGS*	9	Lab	27	157	*AbBa, BeAl, BePa, PiRu, SoAm, TsCa*	McNulty et al. 1991
Lye Brook, VT*	10	Lab, *In situ*	5	49	*AbBa, AcRu, AcSa, BeAl, BePa, PiRu*	Campbell et al. 2000
Mt Ascutney, VT*	10	Lab, *In situ*†	11	109	*PiRu*	McNulty et al. 1996
Mt. Mansfield, VT – NGS*	9–10	Lab	10	97	*AbBa, AcSa, BeAl, PiRu*	McNulty et al. 1991
Mt. Moosilauke, NH – NGS*	10	Lab	22	133	*AbBa, BePa, PiRu*	McNulty et al. 1991
Mt. Washington, NH – NGS*	8	Lab	55	245	*AbBa, AcRu, AcSa, BeAl, BePa, BePo, FaGr, PiRu, SoAm*	McNulty et al. 1991

Table 1. Continued.

Site	N Deposition [a]kg ha^{-1} y^{-1}	N min. Nit.[b] Method	# Plots	# Foliar samples	Species analyzed[c]	References
Scituate, MA	9		12	20	*JuVi, PiRi, PiSt, QuVe*	Hooker and Compton 2003
Whiteface Mt., NY – NGS*	11	Lab	31	174	*AbBa, BeAl, BePa, PiRu, SoAm*	McNulty et al. 1991
Wildcat Mt., NH – NGS*	9	Lab	20	37	*PiRu*	McNulty et al. 1991
White Mtns., NH*	8	Lab†	30	206	*AbBa, AcPe, AcRu, AcSa, BeAl, BePa, FaGr, PiRu, PoTr, TsCa*	Goodale and Aber 2001
White Mtns., NH*	7–9	Lab†	27	229	*AbBa, AcPe, AcRu, AcSa, BeAl, BePa, FaGr, FrAm, PiRu, PiSt, SoAm, TsCa, ViAl*	Ollinger et al. 2002
Wolcott, VT*	7		1	60	*AbBa, PiGl, PiRu, PiRe, PiSt, TsCa*	DeHayes et al. 2001
Other North America						
Experimental Lakes Area, Ontario, CAN	4	*In situ*†	1	2	*PiMa, PiBa,*	Lamontagne 1998; Lamontagne et al. 2000
Harp Lake, Ontario, CAN	10	*In situ*†	1	3	*AbBa, AcSa, FaGr*	Schiff et al. 2002
Helmer's Ridge, AK	0.6	*In situ*†	4	8	*PiMa*	
Rockies east (3), CO	4	Lab	9	45	*PiEn*	Rueth and Baron 2002
Rockies west (5), CO	1.5	Lab	15	75	*PiEn*	Rueth and Baron 2002
Turkey Lake, Ontario, CAN	7	Lab†	3	9	*AcSa*	Sirois et al. 2001
South America						
Antillanca, CL	3	Lab†	1	3‡	*ChCo, NoBe, SaCo*	Oyarzún and Huber 2003
Paillaco, CL	3	Lab†	1	3‡	*ChQu, NoOb, PeLi*	Oyarzún and Huber 2003
Europe						
Aaheden, SE – CANIF	2	Lab†	1	18	*PiAb, PiSy*	**
Aber, UK – NITREX	15	*In situ*, Lab†	1	1	*PiSi*	Emmett et al. 1998
Alptal, CH – NITREX	16	*In situ* resin	1	5	*PiAb*	Schleppi et al.1999
Aubure, FR – CANIF	9; 18	Lab†	2	10	*FaSy, PiAb*	**Dambrine 2000; Bauer et al. 2000b
Collelongo, IT – CANIF	11	Lab†	1	1	*FaSy*	**Mosello 2000; Bauer et al. 2000b
Gardsjon, SE – NITREX	12	*In situ* resin†	3	32‡	*PiAb*	Emmett et al. 1998
Gribskov, DK – CANIF	13	Lab†	1	1	*FaSy*	**Anderson 2000; Bauer et al. 2000b
Gulkeputten, BE	37	Lab†	2	7	*AlIn, AmLa, BePe, CaBe, CoAv, QuRo, QuRu*	Vervaet et al. 2002

Hammer Moelle, DK	31		1	4	*PiAb*	Gundersen, unpublished data
Jels, DK	32		1	4	*AbAl*	Gundersen, unpublished data
Klosterhede, DK – NITREX	19	*In situ*†	3	15	*PiAb*	Emmett et al. 1998; Gundersen 1998
Schacht, DE – CANIF	20	Lab†	1	10	*FaSy, PiAb*	**Bauer et al. 2000b
Skogaby, SE – CANIF	16	Lab†	1	3	*PiAb*	**Bergholm 2000
Speuld, NL – NITREX	51	*In situ*†	1	17	*PsMe*	Emmett et al. 1998
Thezan, FR – CANIF		Lab†	1	4	*FaSy, PiPi*	**Bauer et al. 2000b
Waldstein, DE – CANIF	22	Lab†	1	3	*PiAb*	**Manderscheid 2000
Ysselsteyn, NL – NITREX	58	*In situ*†	1	6	*PiSy*	Emmett et al. 1998

[a]Inorganic N deposition rate (kg ha^{-1} y^{-1}) as throughfall in Europe and estimated wet + dry deposition at all other sites. Deposition for all Northeastern US sites was calculated using the ClimCalc model (Ollinger et al. 1993).

[b]Method used to measure net N mineralization and nitrification rate.

[c]Species code: *AbAl = Abies alba; AbBa = Abies balsamea; AcPe = Acer pensylvanicum; AcRu = Acer rubrum; AcSa = Acer saccharum; AcSp = Acer spicatum; AlIn = Alnus incana; AmLa = Amelanchier laevis; BeAl = Betula alleghaniensis; BeLe = Betula lenta; BePa = Betula papyrifera; BePo = Betula populifolia; BePe = Betula pendula; CaBe = Carpinus betula; ChCo = Chusquea coleu; ChQu = Chusquea quila; CoAv = Corylus avellana; FaGr = Fagus grandifolia; FaSy = Fagus sylvatica; FrAm = Fraxinus americana; JuVi = Juniperus virginiana; LiTu = Lirodendron tulipifera; NoBe = Nothofagus betuloides; NoOb = Nothofagus obliqua; OsVi = Ostrya virginiana; PeLi = Persea lingue; PiAb = Picea abies; PiEn = Picea engelmannii; PiGl = Picea glauca; PiMa = Picea mariana; PiRu = Picea rubens; PiSi = Picea sitchensis; PiBa = Pinus banksiana; PiPi = Pinus pinaster; PiRe = Pinus resinosa; PiRi = Pinus rigida; PiSt = Pinus strobus; PiSy = Pinus sylvestris; PoTr = Populus tremuloides; PrSe = Prunus serotina; PsMe = Pseudotsuga menziesii; QuRo = Quercus robur; QuRu = Quercus rubra; QuVe = Quercus velutina; SaCo = Saxegothaea conspicua; SoAm = Sorbus americana; ThOc = Thuja occidentalis; TiAm = Tilia americana; TsCa = Tsuga canadensis; ViAl = Viburnum alnifolium*

*Samples analyzed at the same analytical laboratory.

†Annual nitrification rates available.

‡ Root data available at this site.

**CANIF citations: Bauer et al. 2000a, Persson 2000, and Persson et al. 2000a, b.

performed using a Dumas combustion system in continuous flow mode (ANCA-SL Elemental Analyzer) followed by a PDZ Europa Scientific 20/20 mass spectrometer (CSIB). The standard deviation of the 10% of samples analyzed in triplicate was 0.13‰; the precision of the analysis for National Institute of Standards and Technology apple leaf standard, NIST 1515, (mean $\delta^{15}N = 0.71‰$) used as an internal standard was $\pm 0.14‰$ (SD).

Methods issues

In assembling a large dataset from diverse sites, concerns may arise about differences in sampling and analytical methodologies. The purpose of this synthesis was to evaluate whether it was possible to observe trends in foliar $\delta^{15}N$ data on the regional scale. For such an approach to be practical, it would need to be robust for different sampling and analytical methods. Nonetheless, for purposes of this analysis, we tried to minimize the differences in analytical method by analyzing most foliar samples (86% of samples) on the same instrument and using the same internal standard with each run.

Estimates of N deposition (wet + dry inorganic N) for sites in the northeastern U.S. were standardized by use of a statistical model of atmospheric deposition, ClimCalc, described by Ollinger et al. (1993), which estimates wet and dry deposition as a function of latitude, longitude, and elevation. This model was modified slightly by use of updated dry deposition coefficients indicated by Lovett and Rueth (1999), a modification also used in the assessment of N deposition effects compiled by Aber et al. (2003). Rates of N deposition for sites outside of the Northeast were provided by collaborators, as the best available estimate of wet + dry inorganic N deposition for sites in North and South America and throughfall N for European sites, where separate measures of dry and wet deposition were not available. Temperature (mean annual) and precipitation estimates for sites in the northeastern U.S. were calculated using ClimCalc; these estimates are based on data from the period 1951–1980. Temperature and precipitation data were provided by collaborators for some of the other sites.

Information on rates of soil N cycling and C:N ratio were provided by collaborators who used a range of methods (Table 1). The majority of sites had short-term lab-based estimates of net N mineralization and nitrification. Many others had annual (sequential) *in situ* measurements. Some sites used both approaches, and others (60 plots in the White Mountains, NH) extrapolated annual estimates from lab measurements based on field/lab relationships determined at a subset of sites (Goodale and Aber 2001; Ollinger et al. 2002). Differences in sample handling and analysis in the measurement of net nitrification and N mineralization can sometimes be normalized by using the ratio of nitrification to mineralization rather than rates of either process (e.g. Aber et al. 2003). The datasets from different studies were not always parallel with respect to: (1) the scale of the study (plot-scale and watershed scale); (2) which soil horizons were included (we grouped data as forest floor or mineral soil); (3) timing of the study (which year and which season); and (4) whether foliar and soil N cycling samples were collected in the same year. Eighty percent of foliar samples were collected between 1995–2000; the dataset ranged from 1987–2001.

Data handling

Data were separated for analysis when there were known differences between particular parameters. For example, conifers and hardwoods were analyzed separately, because conifers often have lower foliar $\delta^{15}N$ values than hardwoods (Pardo 1999). Fresh, green foliage was separated from litter in any analysis that included foliar N concentration, as retranslocation may alter N concentration in litter; they were not separated for analyses of foliar $\delta^{15}N$, because we observed no difference between litter and green leaf foliar $\delta^{15}N$ in a previous study (Pardo et al. 2002). The method used for measuring nitrification and mineralization can have a marked impact on the rate estimated. Because of this potential variation, we separated estimates of nitrification and mineralization into two categories: (1) year-long measurements (often *in situ*) or estimates expressed per area (kg N ha^{-1} y^{-1}), and (2) laboratory incubations that were either done for a

single time period or sequential incubations (expressed on a per mass basis; mg N kg^{-1} y^{-1}). Sites with recent disturbance or fertilization were excluded from this analysis.

Statistical methods

We calculated plot-wise means by species and used these values for all of our general statistical analysis in order to minimize pseudo-replication. This aggregation lumped the 2867 foliar samples into 1167 species-level means for 594 plots, with 1–8 species per plot. The 61 root samples were lumped into 19 means for 13 plots. We used non-parametric methods, because they are appropriate for non-linear relationships. In most cases, the data were not normally distributed, even after conventional transformations (e.g., log transformation). We examined the potential relationships between $\delta^{15}N$, %N and C:N in foliage, $\delta^{15}N$ in roots and N deposition, C:N, nitrification, mineralization and nitrification:mineralization for forest floor and mineral soil using Spearman's Rank Correlation Analysis ($\alpha = 0.05$). The same correlation analyses were conducted with the data aggregated in different ways: to evaluate species patterns (by species), by plot (overall mean with species lumped), by site, type of potential mycorrhizal association, scale of study (plot vs. watershed), and whether foliar and nitrification samples were collected in the same year.

For foliar $\delta^{15}N$, we also evaluated correlations with mean annual temperature, precipitation and elevation using Spearman's Rank Correlation Analysis ($\alpha = 0.05$). For root $\delta^{15}N$, we also evaluated the correlations with $\delta^{15}N$ and %N in foliage, and $\delta^{15}N$ and soil solution ammonium and nitrate in the forest floor using Spearman's Rank Correlation ($\alpha = 0.05$). All statistical analyses were performed using SAS software (Version 9.0) and SAS JMP software (Version 3.2.5, 1999).

Results

Foliar $\delta^{15}N$ patterns

Nitrification and mineralization

The strongest relationships we observed in this dataset were for foliar $\delta^{15}N$ increasing non-linearly with forest floor nitrification rates and nitrification:mineralization ratios (both conifer and hardwood $p < 0.0001$; Table 2; Figure 2a, b). For conifers, the Spearman rank correlation coefficient for foliar $\delta^{15}N$ with forest floor nitrification (annual area basis) was 0.77 for all regions and for the northeastern U.S. (Table 2); and for foliar $\delta^{15}N$ with forest floor nitrification:mineralization, the Spearman rank correlation coefficient was 0.61 for all regions and 0.83 for the northeastern U.S. (Table 2). For conifers, the correlations with nitrification (per mass basis) were similar ($\sim$0.46) for the northeastern U.S. and all regions combined (Table 2).

The correlation between hardwood foliar $\delta^{15}N$ and forest floor nitrification was stronger for the northeastern U.S. (0.33 for mg kg^{-1} d^{-1} and 0.42 for kg ha^{-1} y^{-1}) than for all regions combined (Table 2). Similarly, the relationship between foliar $\delta^{15}N$ and forest floor nitrification:mineralization was stronger for the northeastern U.S. (0.47) than it was for all regions combined (Table 2). Relationships between foliar $\delta^{15}N$ and forest floor N mineralization were weaker than for nitrification, and often not significant for year-long mineralization values for both conifers and hardwoods (Table 2).

Foliar $\delta^{15}N$ also increased with mineral soil nitrification and nitrification:mineralization. The Spearman rank correlation coefficients for conifers were higher than for hardwoods (Table 2), and, for conifers, were often lower than the coefficients for correlations between foliar $\delta^{15}N$ and forest floor N cycling measures. The strongest correlations were found between conifer foliar $\delta^{15}N$ and mineral soil nitrification (per mass basis) which was 0.75 for all regions and 0.67 for the northeastern U.S. alone (Table 2); and for conifer foliar $\delta^{15}N$ with forest floor nitrification:mineralization, the Spearman rank correlation coefficient was approximately 0.7 (Table 2).

Table 2. Statistical summary of correlation analysis for foliar $\delta^{15}N$ and %N with N deposition and forest floor and mineral soil N cycling measures.

	Forest Floor								Mineral Soil							
	NE U.S. Hardwood		All regions Hardwood		NE U.S. Conifer		All regions Conifer		NE U.S. Hardwood		All regions Hardwood		NE U.S. Conifer		All regions Conifer	
	$\delta^{15}N$	%N	$\delta^{15}N$	%N	$\delta^{15}N$	%N	$\delta^{15}N$	%N	$\delta^{15}N$	%N	$\delta^{15}N$	%N	$\delta^{15}N$	%N	$\delta^{15}N$	%N
C:N	**−0.44**	−0.055	**−0.37**	0.0056	**−0.51**	**−0.41**	**−0.51**	**−0.46**	**−0.37**	**−0.15**	**−0.30**	−0.075	**−0.41**	−0.16	**−0.37**	−0.18
	< 0.0001	0.3	< 0.0001	0.9	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.04	< 0.0001	0.3	0.002	0.2	0.0001	0.08
	298	298	322	315	254	254	308	307	192	192	216	209	55	55	103	102
Nitrification, mg kg^{-1} d^{-1}	**0.33**	**−0.15**	**0.30**	**−0.16**	**0.48**	**0.19**	**0.44**	**0.19**	**0.38**	0.10	**0.39**	0.080	**0.75**	−0.014	**0.67**	−0.033
	< 0.0001	0.005	< 0.0001	0.002	< 0.0001	0.0002	< 0.0001	0.0002	< 0.0001	0.1	< 0.0001	0.2	< 0.0001	0.9	< 0.0001	0.9
	357	356	371	363	360	360	386	386	245	244	260	252	35	35	35	35
Nitrification, kg ha^{-1} y^{-1}	**0.42**	**0.26**	**0.27**	**0.19**	**0.77**	**0.36**	**0.77**	**0.35**	**0.42**	**0.26**	**0.33**	0.13	**0.51**	0.26	**0.68**	0.16
	< 0.0001	0.0008	0.0003	0.01	< 0.0001	0.03	< 0.0001	0.007	< 0.0001	0.0009	< 0.0001	0.1	0.003	0.1	< 0.0001	0.3
	158	162	181	173	37	37	57	56	162	162	187	179	33	33	50	49
Mineralization, mg kg^{-1} d^{-1}	**0.28**	−0.014	**0.28**	−0.016	**0.25**	**0.20**	**0.33**	**0.26**	**0.35**	**0.17**	**0.37**	**0.14**	**0.67**	−0.018	**0.55**	−0.061
	< 0.0001	0.8	< 0.0001	0.84	< 0.0001	0.0001	< 0.0001	< 0.0001	< 0.0001	0.009	< 0.0001	0.03	< 0.0001	0.9	0.0005	0.7
	359	358	373	365	361	361	387	387	247	246	262	254	35	35	36	36
Mineralization, kg ha^{-1} y^{-1}	0.067	−0.011	0.064	−0.016	0.28	**0.47**	**0.63**	**0.23**	**0.26**	**0.23**	**0.21**	0.064	0.23	**0.34**	**0.55**	0.067
	0.4	0.9	0.4	0.8	0.09	0.004	< 0.0001	0.001	0.001	0.04	0.004	0.4	0.2	0.05	< 0.0001	0.6
	162	162	181	173	37	37	57	56	162	162	187	179	33	33	50	49
Nit:Min, mg $kg^{-1}d^{-1}$	**0.30**	**−0.16**	**0.25**	**−0.18**	**0.46**	**0.16**	**0.39**	**0.13**	0.35	0.25	**0.35**	0.026	**0.72**	0.011	**0.71**	0.016
	< 0.0001	0.002	< 0.0001	0.0004	< 0.0001	0.002	< 0.0001	0.008	0.1	0.7	< 0.0001	0.7	< 0.0001	0.9	< 0.0001	0.9
	359	358	373	365	361	361	387	387	247	246	262	254	35	35	36	36
Nit:Min, kg ha^{-1} y^{-1}	**0.47**	**0.26**	**0.27**	**0.2**	**0.83**	0.16	**0.61**	**0.4**	**0.45**	**0.22**	**0.34**	**0.24**	**0.70**	−0.12	**0.62**	0.18
	< 0.0001	0.0007	0.0002	0.01	< 0.0001	0.3	< 0.0001	0.0007	0.05	0.05	< 0.0001	0.001	< 0.0001	0.5	< 0.0001	0.2
	159	162	181	173	37	37	53	52	162	162	187	179	33	33	46	45
N deposition, kg ha^{-1} y^{-1}	**0.17**	**0.39**	**0.15**	**0.42**	**0.28**	**0.31**	**0.32**	**0.38**								
	0.0007	< 0.0001	0.0018	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001								
	403	402	427	419	400	400	454	453								

The table includes Spearman rank correlation coefficients, p, and number of observations; significant correlations are in bold type ($\alpha = 0.05$). Samples are fresh foliage (no litter) from sites.

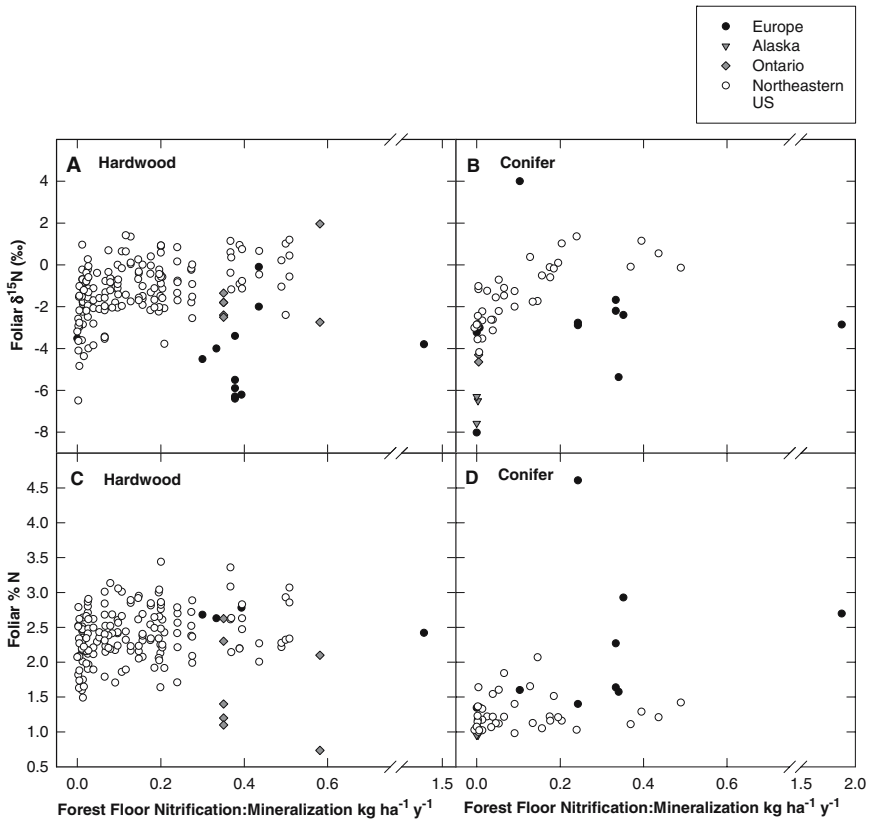

Figure 2. Foliar δ^{15}N and %N vs. forest floor nitrification:mineralization for hardwoods and conifers.

Forest floor and mineral soil C:N and $\delta^{15}N$

Foliar δ^{15}N decreased with increasing forest floor C:N (Figure 3b, d). For the combined dataset, the Spearman rank correlation coefficient was −0.51 for conifers and −0.37 for hardwood leaves; for the northeastern U.S., the Spearman rank correlation coefficient was −0.51 for conifer and −0.44 for hardwood leaves (for all correlations, $p < 0.0001$; Table 2).

Foliar δ^{15}N also decreased with mineral soil C:N although the correlations were weaker than with forest floor C:N (Table 2). In general, the relationship between foliar δ^{15}N and C:N was stronger within the northeastern U.S. region than for all regions combined.

Foliar δ^{15}N in hardwoods was generally lower than forest floor δ^{15}N (Figure 3a), except for the European sites. Foliar δ^{15}N in conifers was similar to or lower than forest floor δ^{15}N (Figure 3c; data are near or below the 1:1 line).

N deposition

Foliar δ^{15}N generally increased with increasing N deposition (Figures 4a and 4b). This trend was significant across all regions, with relatively weak Spearman rank correlation coefficients of 0.32 for conifer and 0.15 for hardwood leaves; $p < 0.0001$ and $p = 0.002$, respectively (Table 2). Considering just the northeastern U.S., the Spearman rank correlation coefficients were similar or slightly lower (0.28 for conifers and 0.17 for hardwood leaves) than for the global dataset (Table 2).

Foliar N concentration patterns

For all measures of local forest floor and mineral soil N cycling and C:N, except forest floor mineralization, foliar δ^{15}N showed considerably stronger relationships than did foliar N concentration (Table 2). In

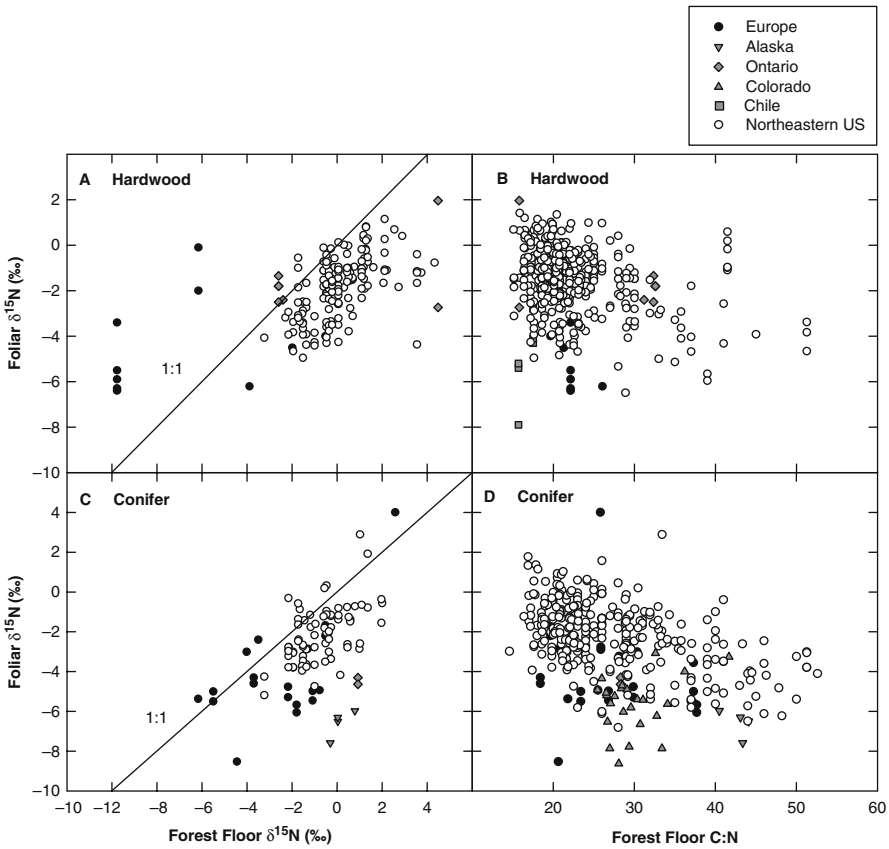

Figure 3. Foliar δ^{15}N vs. forest floor δ^{15}N and C:N for hardwoods and conifers.

general, however, patterns of foliar N concentration with N deposition were stronger than patterns of foliar δ^{15}N with N deposition (Figure 4; Table 2).

Species analysis

In general, the strongest correlations between foliar δ^{15}N and other measures were for red spruce (*Picea rubens*), and, amongst the hardwoods, for red maple (*Acer rubrum*) and yellow birch (*Betula alleghaniensis*; Table 3; Figures 5 and 6). The strength of these relationships may have been a function of the availability of data across the region, with some species (e.g. red spruce and red maple) occurring over a broader range of the measured variables than other species (Figure 6).

In order to assess differences in foliar δ^{15}N values among species for American beech (*Fagus grandifolia*), yellow birch and sugar maple (*Acer saccharum*), we evaluated plots where all three species were present (21 plots for leaves and 44 for litter). We observed a pattern in most plots where species δ^{15}N rankings for green leaves were sugar maple < yellow birch < beech. In 20 of the 21 plots where all three species were present, sugar maple had the lowest foliar δ^{15}N value. In 18 of the 21 plots, beech had the highest δ^{15}N values; in the other 2 plots yellow birch values were similar to those of beech. For 17 additional plots, we had data only for two of the three species, in each of these cases sugar maple had the lowest foliar δ^{15}N, although foliar δ^{15}N ranged from −5 to 0‰. For the 52 plots for which we had litter data, there were only 2 instances where the sugar maple δ^{15}N was higher than the beech δ^{15}N, and 6 instances where sugar maple δ^{15}N was higher than yellow birch δ^{15}N.

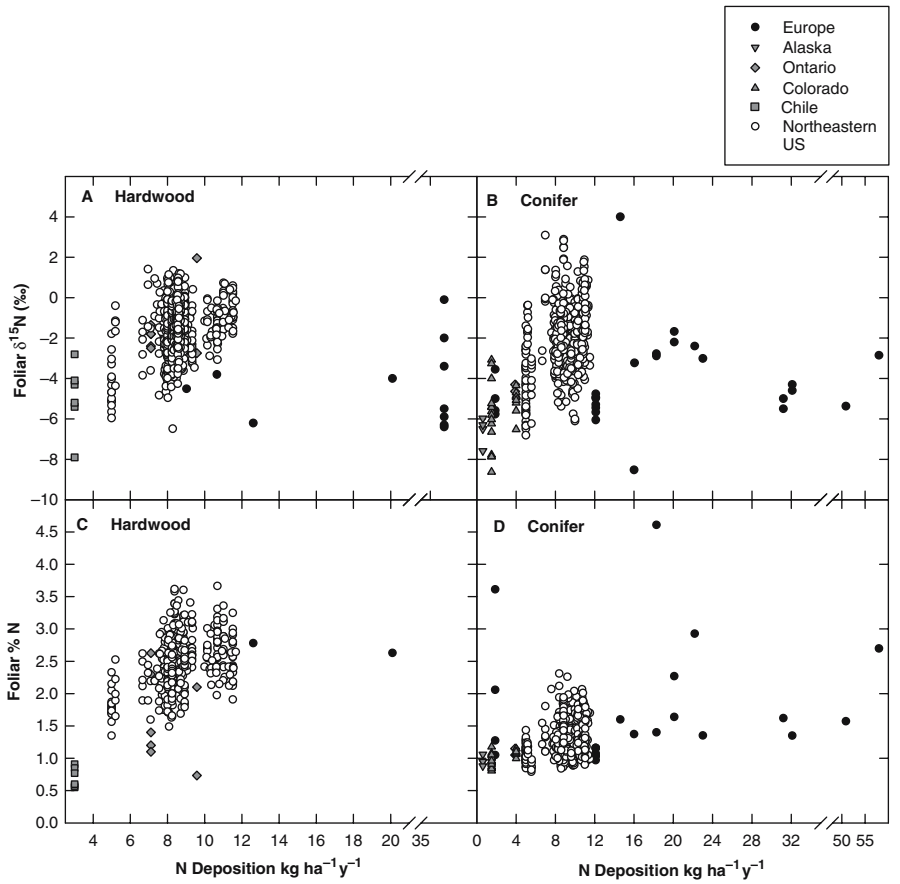

Figure 4. Foliar δ^{15}N and %N vs. N deposition for hardwoods and conifers.

Mycorrhizal associations

In order to evaluate the possible effects of mycorrhizal associations, we compared the correlations between foliar δ^{15}N and N deposition and between foliar δ^{15}N and N cycling measures for tree species that form ectomycorrhizal associations to those that form arbuscular mycorrhizal associations. Statistical analyses indicate that for trees with ectomycorrhizal association, foliar δ^{15}N is not correlated with N deposition, but for tree species with arbuscular mycorrhizal associations (sugar and red maple), the Spearman rank correlation coefficient was 0.42. Foliar δ^{15}N is more strongly correlated with forest floor C:N for ectomycorrhizal species (−0.52) than for arbuscular mycorrhizal species (−0.37). However, the species with arbuscular mycorrhizal associations are the maples, so it may be that the tighter correlation of a single species might be driving the stronger correlations. We observed that, contrary to previously reported patterns for arctic and tropical ecosystems (Michelsen et al. 1998; Schmidt and Stewart 2003), ectomycorrhizal species had higher foliar δ^{15}N than arbuscular mycorrhizal species.

Issues of scale in data analysis and sample collection

Aggregated at the plot scale

When the data are aggregated at the plot scale (for each plot, a single mean foliar δ^{15}N is calculated that combines all species measured), the strongest relationships with foliar δ^{15}N are observed for nitrification and for forest floor δ^{15}N and C:N (Table 4). Similarly, when the data are aggregated at the site scale (for

Table 3. Statistical summary of correlation analysis for foliar $\delta^{15}N$ with N deposition, mineral soil, and forest floor N cycling measures analyzed by species.

	American beech $\delta^{15}N$	Balsam fir $\delta^{15}N$	Eastern hemlock $\delta^{15}N$	Paper birch $\delta^{15}N$	Red maple $\delta^{15}N$	Red oak $\delta^{15}N$	Red spruce $\delta^{15}N$	Sugar maple $\delta^{15}N$	Yellow birch $\delta^{15}N$
N deposition,	0.09	**0.22**	**0.64**	0.11	**0.42**	**0.71**	**0.26**	**0.40**	0.13
kg ha^{-1} y^{-1}	0.3	0.01	< 0.0001	0.3	0.0002	0.05	< 0.0001	< 0.0001	0.09
	134	138	32	84	71	8	252	125	175
Forest Floor C:N	−0.21	**−0.24**	**−0.59**	**−0.41**	**−0.40**	**0.75**	**−0.56**	**−0.24**	**−0.33**
	0.08	0.02	0.0009	0.0002	0.001	0.05	< 0.0001	0.05	0.0004
	73	95	28	79	62	7	163	66	112
Forest Floor,	0.04	**0.33**	0.35	**0.41**	**0.57**	0.54	**0.47**	**0.21**	**0.23**
Nitrification,	0.7	0.0001	0.1	0.0001	< 0.0001	0.3	< 0.0001	0.04	0.01
mg kg^{-1} d^{-1}	97	130	22	81	46	6	226	100	131
Forest Floor,	**0.41**	0.64	**1.0**	0.14	**0.57**	.	**0.82**	0.59	**0.51**
Nitrification,	0.02	0.1	< 0.0001	0.5	0.005	.	< 0.0001	0.07	0.0005
kg ha^{-1} y^{-1}	30	7	3	23	22	0	25	29	43
Forest Floor,	0.11	−0.037	0.39	0.15	**0.55**	0.029	**0.33**	−0.018	0.17
Mineralization,	0.3	0.7	0.08	0.2	0.0001	1.0	< 0.0001	0.9	0.06
mg kg^{-1} d^{-1}	98	130	22	81	46	6	227	101	131
Forest Floor,	0.029	**0.79**	0.50	0.024	0.037	.	0.30	0.18	−0.025
Mineralization,	0.9	0.04	0.7	0.9	0.9	.	0.1	0.3	0.9
kg ha^{-1} y^{-1}	30	7	3	23	22	0	25	32	43
Forest Floor,	0.068	**0.27**	0.33	**0.36**	**0.53**	0.66	**0.46**	**0.33**	**0.22**
Nit:Min,	0.5	0.002	0.1	0.001	0.0002	0.2	< 0.0001	0.007	0.01
mg kg^{-1} d^{-1}	98	130	22	81	46	6	227	101	131
Forest Floor,	**0.51**	0.50	**1.0**	0.19	**0.60**	.	**0.89**	**0.65**	**0.62**
Nit:Min,	0.004	0.3	< 0.0001	0.4	0.003	.	< 0.0001	< 0.0001	< 0.0001
kg ha^{-1} y^{-1}	30	7	3	23	22	0	25	32	43

Mineral Soil,	**−0.45**	0.033	−0.32	**−0.56**	−0.20	0.57	**−0.54**	**−0.49**	**−0.67**
C:N	0.0002	0.9	0.3	0.006	0.2	0.2	0.0007	< 0.0001	< 0.0001
	63	9	13	23	43	7	36	61	74
Mineral Soil,	**0.24**	0.32	0.70	0.34	**0.68**	**0.88**	**0.72**	**0.41**	**0.31**
Nitrification,	0.03	0.5	0.2	0.1	< 0.0001	0.004	0.0002	0.001	< 0.004
mg kg^{-1} d^{-1}	76	7	5	23	28	8	21	84	85
Mineral Soil,	**0.41**	0.14	−0.50	0.23	**0.70**	.	**0.53**	**0.36**	**0.47**
Nitrification,	0.02	0.8	0.7	0.3	0.0002	.	0.01	0.05	0.002
kg ha^{-1} y^{-1}	30	7	3	23	22	0	21	32	43
Mineral Soil,	0.20	0.29	0.70	**0.51**	**0.77**	0.69	**0.64**	0.28	0.15
Mineralization,	0.09	0.5	0.2	0.01	< 0.0001	0.1	0.001	0.008	0.2
mg kg^{-1} d^{-1}	77	7	5	23	28	8	22	85	85
Mineral Soil,	0.29	0.071	−0.50	0.16	0.33	.	0.19	0.11	0.22
Mineralization,	0.1	0.9	0.7	0.5	0.1	.	0.4	0.6	0.2
kg ha^{-1} y^{-1}	30	7	3	23	22	0	21	32	43
Mineral Soil,	**0.24**	0.071	0.70	0.19	**0.60**	**0.93**	**0.76**	**0.35**	**0.38**
Nit:Min,	0.04	0.9	0.2	0.4	0.0008	0.0009	< 0.0001	0.001	0.0003
mg kg^{-1} d^{-1}	77	7	5	23	28	8	22	85	85
Mineral Soil,	**0.43**	−0.29	−0.50	0.26	**0.62**	.	**0.84**	**0.50**	**0.63**
Nit:Min,	0.02	0.5	0.7	0.2	0.002	.	< 0.0001	0.004	< 0.0001
kg ha^{-1} y^{-1}	30	7	3	23	22	0	21	32	43

The table includes Spearman rank correlation coefficients, *p*, and number of observations; significant correlations are in bold type ($\alpha = 0.05$). Samples are fresh foliage and litter from sites in the Northeastern U.S.

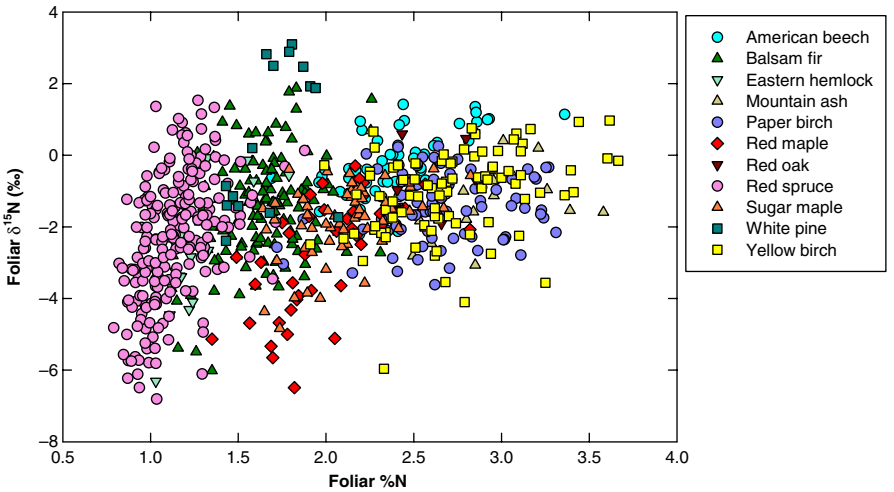

Figure 5. Foliar δ^{15}N vs. foliar %N for fresh leaves by species for sites in the Northeastern U.S.

each site, a single mean foliar δ^{15}N is calculated combining all species and all plots), the strongest relationships are foliar δ^{15}N with nitrification, mineralization, and forest floor δ^{15}N (0.70; Table 4).

Watershed vs. plot scale study

Another potentially significant methodological issue is the scale at which the data were collected. For most studies included in this analysis, the data were collected at the plot scale. However, a number of watershed scale studies were also included; the foliar and soil data in these studies integrate a much larger area. For hardwood leaves, the correlation of foliar δ^{15}N to N deposition was stronger for watershed-scale (0.36) than plot-scale studies (0.18); the correlation of foliar δ^{15}N to C:N was stronger for plot-scale studies (~0.43; Table 5).

Same year for soil and foliar sample collection

In addition to questions about spatial scale of sampling and analysis, timescale can have a significant effect on the strength of the correlations observed. Therefore, we tried to assess whether plots for which foliar and nitrification samples were collected within one year (same year) had tighter relationships than those plots where they were collected in different years (soil C:N was not included, because we assumed changes in soil C and N pools would be slow and not detectable).

For the correlation between foliar δ^{15}N and nitrification:mineralization (mg kg^{-1} d^{-1}), for hardwoods, the "different year" plots had a higher correlation coefficient (0.42) compared to the "same year" plots (0.23); for conifers, the correlation coefficients were similar (0.42). For plots where foliar and nitrification samples were collected in the same year, correlations between foliar δ^{15}N and N deposition or forest floor C:N were consistently higher. Because the year of sample collection should not affect the correlations between foliar δ^{15}N and N deposition or forest floor C:N, these results may suggest that the two datasets are not similar enough to attempt this comparison.

Mean annual temperature, precipitation and elevation

We evaluated several climate-related parameters (mean annual temperature, MAT; precipitation; and elevation) to determine whether differences amongst these parameters could explain any of the variability we observed (Table 6). For all regions combined, the only significant correlation for foliar δ^{15}N was a positive correlation with precipitation for conifers (0.43) and for hardwoods (0.13). For the northeastern U.S. sites, foliar δ^{15}N was more weakly correlated to precipitation; for hardwoods, the Spearman rank correlation coefficient was 0.11 and for conifers, it was 0.25. Correlations of foliar δ^{15}N with temperature and elevation

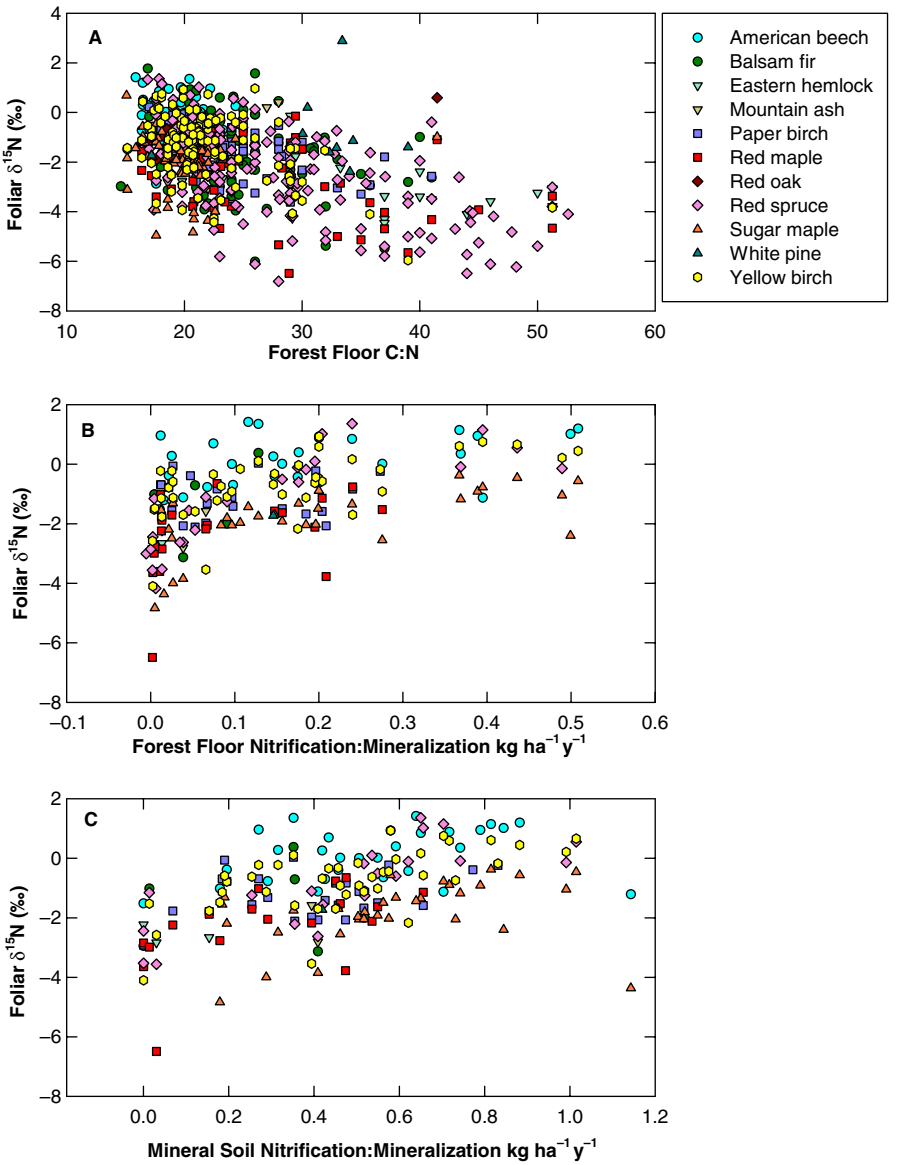

Figure 6. Foliar $\delta^{15}N$ vs. forest floor C:N and nitrification:mineralization and mineral soil nitrification:mineralization by species for sites in the Northeastern U.S.

were not significant, (except a correlation of −0.10 for conifers in the Northeast). Foliar N concentration for hardwoods in the northeastern U.S. was correlated with precipitation (0.45) and temperature (−0.47); for conifers, the correlations are considerably weaker, 0.19 and −0.13, respectively (Table 6). For hardwoods from all regions combined, the correlations between foliar N concentration and precipitation (0.39) and temperature (−0.41), were weaker than for the Northeast. For conifers, the correlation with precipitation was stronger (0.26) and there was no significant relationship with temperature.

Enrichment factor

The enrichment factor, defined as $\delta^{15}N_{foliar} - \delta^{15}N_{mineral\ soil}$, is a method of normalizing for the spatial heterogeneity in mineral soil $\delta^{15}N$ values. Most of these relationships are very weak/non-significant. The

Table 4. Statistical summary of correlation analysis for foliar $\delta^{15}N$ with N deposition and forest floor N cycling measures aggregated by plot and site.

	Aggregated by plot $\delta^{15}N$	Aggregated by site $\delta^{15}N$
N deposition, kg ha^{-1} y^{-1}	**0.27**	0.085
	< 0.0001	0.4
	497	98
Forest Floor, $\delta^{15}N$_1	**0.67**	**0.70**
	< 0.0001	< 0.0001
	108	31
Forest Floor, $\delta^{15}N$_2	**0.30**	0.63
	0.04	0.07
	50	9
Forest Floor, C:N	**−0.53**	**−0.49**
	< 0.0001	< 0.0001
	361	92
Forest Floor, Nitrification, mg kg^{-1} d^{-1}	**0.51**	**0.63**
	< 0.0001	< 0.0001
	417	72
Forest Floor, Nitrification, kg ha^{-1} y^{-1}	**0.51**	**0.53**
	< 0.0001	< 0.0001
	85	50
Forest Floor, Mineralization, mg kg^{-1} d^{-1}	**0.37**	**0.56**
	< 0.0001	< 0.0001
	413	72
Forest Floor, Mineralization, kg ha^{-1} y^{-1}	**0.45**	**0.59**
	< 0.0001	< 0.0001
	85	50
Forest Floor, Nit:Min, mg kg^{-1} d^{-1}	**0.45**	**0.52**
	< 0.0001	< 0.0001
	413	72
Forest Floor, Nit:Min, kg ha^{-1} y^{-1}	**0.42**	0.27
	< 0.0001	0.06
	84	49

The table includes Spearman rank correlation coefficients, *p*, and number of observations; significant correlations are in bold type ($\alpha = 0.05$). Samples are fresh foliage and litter.

Table 5. Statistical summary of correlation analysis for foliar $\delta^{15}N$ with N deposition and forest floor N cycling measures analyzed by plot and by watershed.

	NE U.S. Hardwood		NE U.S. Conifer	
	Plot $\delta^{15}N$	Watershed $\delta^{15}N$	Plot $\delta^{15}N$	Watershed $\delta^{15}N$
N deposition, kg ha^{-1} y^{-1}	**0.18**	**0.36**	**0.29**	−0.34
	< 0.0001	< 0.0008	< 0.0001	0.3
	573	85	438	12
Forest Floor, C:N	**−0.40**	**0.33**	**−0.45**	0.23
	< 0.0001	0.01	< 0.0001	0.5
	391	59	290	10
Forest Floor, Nit:Min, mg kg^{-1} d^{-1}	**0.30**	.	**0.41**	.
	< 0.0001	.	< 0.0001	.
	502	0	384	0
Forest Floor, Nit:Min, kg ha^{-1} y^{-1}	**0.47**	.	**0.83**	.
	< 0.0001	.	< 0.0001	.
	162	0	37	0

The table includes Spearman rank correlation coefficients, *p*, and number of observations; significant correlations are in bold type ($\alpha = 0.05$). Samples are fresh foliage and litter from sites in the Northeastern U.S.

Table 6. Correlation analysis for foliar $\delta^{15}N$, C:N, and % N with mean annual temperature and precipitation.

	NE U.S. Hardwood			NE U.S. Conifer			All regions Hardwood			All regions Conifer		
	$\delta^{15}N$	C:N	% N	$\delta^{15}N$	C:N	% N	$\delta^{15}N$	C:N	% N	$\delta^{15}N$	C:N	% N
Mean annual precipitation	**0.11**	**−0.46**	**0.45**	**0.25**	**−0.24**	**0.19**	**0.13**	**−0.40**	**0.39**	**0.43**	**−0.35**	**0.26**
	0.03	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.006	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
	403	306	402	400	394	400	428	319	419	453	426	452
Mean annual temperature	−0.031	**0.45**	**−0.47**	**−0.10**	**0.20**	**−0.13**	−0.084	**0.43**	**−0.41**	0.035	0.018	0.028
	0.5	< 0.0001	< 0.0001	0.05	< 0.0001	0.01	0.08	< 0.0001	< 0.0001	0.5	0.7	0.6
	403	306	402	400	394	400	428	319	419	453	426	452

The table includes Spearman rank correlation coefficients, p, and number of observations; significant correlations are in bold type ($\alpha = 0.05$). Samples are fresh foliage (no litter) from sites.

only strong patterns were the relationships of the enrichment factor with litterfall N for the NITREX sites in Europe which are discussed in Emmett et al. (1998).

Root $\delta^{15}N$ results

In general, fine root δ^{15}N correlated strongly with other measures of plant N, N deposition and many measures of N cycling. For example, fine root δ^{15}N was strongly correlated to foliar δ^{15}N ($r = 0.75$; $p = 0.0005$; Figure 7a) and with foliar N concentration ($r = 0.65$; $p = 0.005$; Figure 7c). Fine root δ^{15}N was also positively correlated with δ^{15}N of the forest floor ($r = 0.71$; $p = 0.004$; Figure 7b). The inverse relationship between fine root δ^{15}N and forest floor C:N ratio was significant ($r = -0.55$; $p = 0.04$; Figure 7g).

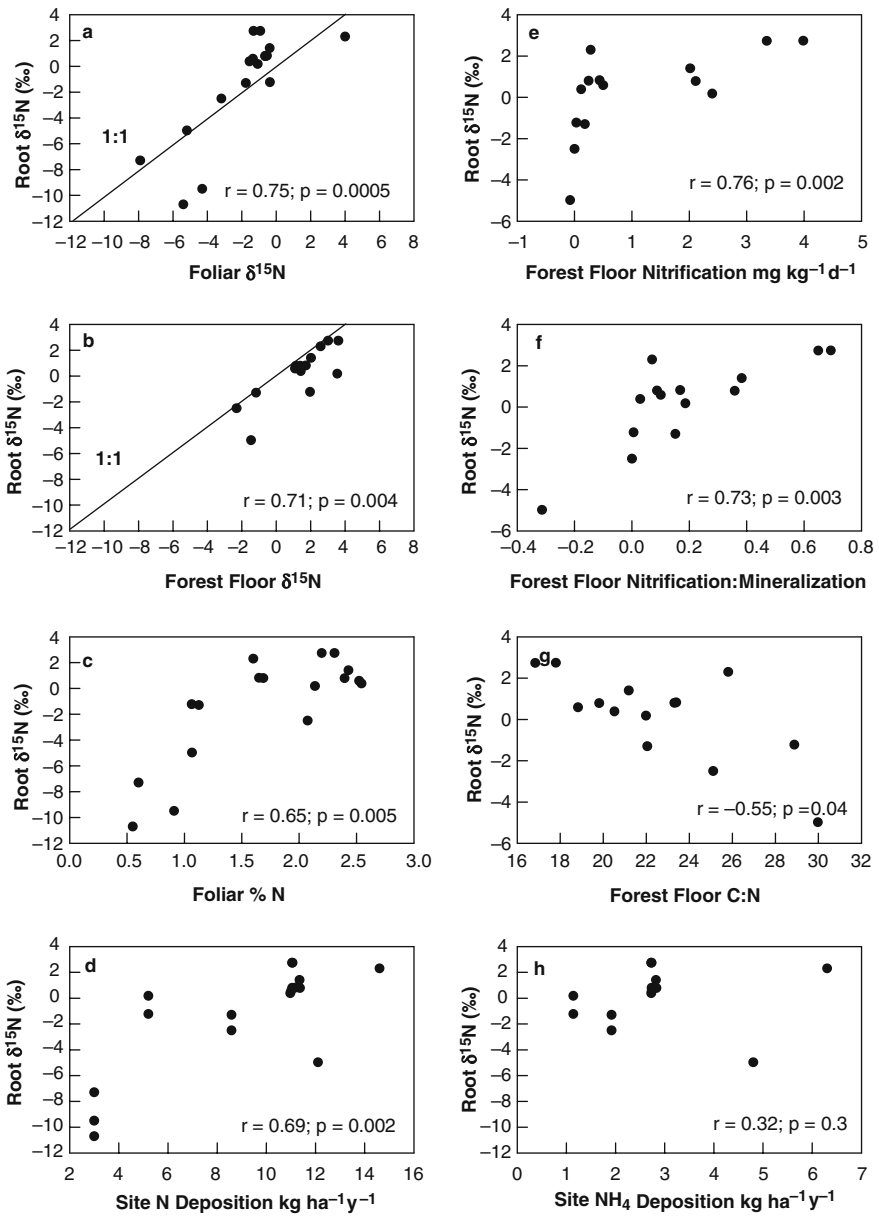

Figure 7. Fine root δ^{15}N vs. foliar δ^{15}N and %N, forest floor nitrification, nitrification:mineralization and C:N and N and ammonium deposition.

Table 7. Summary of results: relationship between fine root $\delta^{15}N$ and other variables.

	Root $\delta^{15}N$		Root $\delta^{15}N$	
			Forest Floor	Mineral Soil
Foliar $\delta^{15}N$	**0.75**	$\delta^{15}N$	**0.71**	−0.23
	0.0005		0.004	0.5
	17		14	13
Foliar % N	**0.65**	C:N	−0.55	−0.30
	0.005		0.04	0.2
	17		17	17
N Deposition, kg ha^{-1} y^{-1}	**0.69**	Nit:Min	**0.73**	0.16
	0.002		0.003	0.6
	17		14	14
NO_3 Deposition, kg ha^{-1} y^{-1}	**0.73**	Mineralization, mg kg^{-1} d^{-1}	**0.56**	0.35
	0.003		0.04	0.2
	14		14	14
NH_4 Deposition, kg ha^{-1} y^{-1}	0.32	Nitrification, mg kg^{-1} d^{-1}	**0.76**	0.25
	0.3		0.002	0.4
	14		14	14
N Pool Mean	−0.064			
	0.9			
	11			
Soil Solution NO_3, μmol l^{-1}	−0.12			
	0.7			
	15			
Soil Solution NH_4, μmol l^{-1}	0.32			
	0.2			
	15			
Soil Solution, NO_3:($NO_3 + NH_4$), μmol l^{-1}	**−0.53**			
	0.04			
	15			

The table includes Spearman rank correlation coefficients, p, and number of observations; significant correlations are in bold type ($\alpha = 0.05$).

Fine root $\delta^{15}N$ was positively correlated with N deposition (0.69; Figure 7d; Table 7). Fine root $\delta^{15}N$ values were positively correlated with the forest floor nitrification:mineralization ratio ($r = 0.73$; $p = 0.003$; Figure 7f), net nitrification ($r = 0.76$; $p = 0.04$; Figure 7e) and net mineralization ($r = 0.56$; $p = 0.04$; Table 7).

Discussion

General trends and significance

A multi-region, cross-site analysis can be a powerful tool for evaluating forest responses to atmospheric deposition which can be masked by variability on smaller scales. In this study, we were able to observe a pattern of increasing N deposition altering the function of forest ecosystems across several regions in the world. We observed increases in foliar N concentration and $\delta^{15}N$ with increasing deposition. The response of increased foliar N concentration is expected as N availability and N exports from ecosystems increase with N saturation (Aber et al. 1989), however, it can be difficult to observe on the regional-scale (Aber et al. 2003). The N cycle is complex, and many factors (land-use, species composition, stand age, site characteristics, hydrology) may influence N loss and retention at a given site (Aber et al. 2003). The N saturation hypothesis asserts that as N becomes more available, plant uptake of N initially increases, plant nutrient balances are altered, and, ultimately, the capacity for both plant and microbial uptake is exceeded and N is lost from the ecosystem (Aber et al. 1989). One reason it is difficult to assess N saturation status is

that it is difficult to quantify N availability in soil on a regional scale. A method that facilitates evaluation of regional patterns based on actual N plant availability and uptake might facilitate predictions of when forest ecosystems are nearing N saturation.

Foliar $\delta^{15}N$ is a useful tool because it integrates N cycling both spatially and over time. The foliar $\delta^{15}N$ value is a record of the inorganic N that the plant has taken up (although plant processes – e.g., translocation, assimilation, etc. – may fractionate and alter the $\delta^{15}N$ signature of plant tissues following plant uptake; Handley and Raven 1992). More significantly, the isotopic signature of the inorganic N is, itself, an integrated measure of the transformations that deliver and remove N from plant-available N pools. Our study shows that foliar $\delta^{15}N$ is a better measure of internal N cycling than is foliar N concentration alone (Figure 2b, d).

Influence of deposition $\delta^{15}N$ in Europe

In analyzing data from multiple regions, in some cases, smaller-scale local or regional factors must be taken into account. We address the influence of deposition $\delta^{15}N$ on foliar $\delta^{15}N$ in Europe in order to separate the deposition effects from other factors regulating foliar $\delta^{15}N$. Some of the sites in Europe appear to follow a different trajectory for increasing foliar $\delta^{15}N$ with N deposition (Figure 4a, b). This pattern is driven by the lower foliar $\delta^{15}N$ values at the highest deposition sites in the Netherlands and Belgium where about 65–80% of the deposition falls as ammonium. These sites are significantly impacted by intensive, local livestock farming (Koopmans et al. 1998; Vervaet et al. 2002), and the resulting liquid manure that can volatilize as NH_3 and be re-deposited as NH_4^+. Ammonia volatilization is a highly fractionating process (Hübner 1986) that produces very ^{15}N-depleted NH_3. If this NH_3, after being converted to NH_4^+, is re-deposited on the forest, it could significantly lower the foliar $\delta^{15}N$ value. Bauer et al. (2000) reported values of throughfall ammonium that were significantly depleted compared to wet deposition ($-20‰$) and with substantially higher NH_4^+ concentration, suggesting that dry deposition is the source of the ^{15}N-depleted N. These results underscore the need to use caution in analyzing and comparing results from different regions where different local conditions may complicate the relationships observed. Note, however, that this process of NH_3 volatilization (independent of N deposition level) would have no impact on foliar N concentrations. Therefore, evaluating both foliar $\delta^{15}N$ and %N may provide the most accurate assessment of N cycling status of forest ecosystems.

In the northeastern U.S., N mineralization is generally an order of magnitude greater than N deposition, in contrast to these European sites where N deposition is the same order of magnitude as N mineralization. Given that most nitrate passing through the soil is microbially produced (Kendall et al. 1996; Pardo et al. 2004) and, in the absence of canopy N uptake as a significant source of N in foliage, it is unlikely that ^{15}N in deposition would significantly affect foliar $\delta^{15}N$ in the northeastern U.S.

In spite of the relatively low foliar $\delta^{15}N$ values at the European hardwood sites, foliage is enriched in ^{15}N relative to the forest floor $\delta^{15}N$ (Figure 3), contrary to previously reported patterns (Nadelhoffer and Fry 1994). This pattern may suggest a strong accumulation of ammonium in the forest floor. One would not expect the relative enrichment of the foliage to be caused by elevated nitrification and nitrate loss, since that should enrich the forest floor as well as the foliage.

Similarly, the absence of significant relationships between the enrichment factor, EF ($\delta^{15}N_{foliar} - \delta^{15}N_{mineral\ soil}$), for sites other than the NITREX sites in Europe was surprising (Emmett et al. 1998). We expected that the EF would be a better measure of ecosystem N cycling because it normalizes for spatial heterogeneity. It is a less practical measure than foliar $\delta^{15}N$ because mineral soil $\delta^{15}N$ values currently are less widely available.

Specific mechanisms that regulate foliar $\delta^{15}N$

In addition to the general, regional patterns that we observed, specific mechanisms may regulate $\delta^{15}N$ on smaller scales. These factors include internal N cycling, species composition, land-use history and climate. We expected and observed that the local drivers of N cycling (nitrification and mineralization, and forest

floor and soil C:N) were more closely coupled with foliar $\delta^{15}N$ than was the regional driver of N deposition. Although increased N inputs to forests can stimulate net nitrification rates (McNulty et al. 1991; McNulty et al. 1996), there is variability in the extent to which nitrification rates increase, because of differences in site characteristics and history (Emmett et al. 1998; Dise et al. 1998). Therefore, the relationship between foliar $\delta^{15}N$ and nitrification itself would be expected to be stronger than with N deposition.

In fact, perhaps the best predictor of increased foliar $\delta^{15}N$ would be nitrification:mineralization, or percent nitrification, which should be a coarse measure of the ^{15}N-enrichment of the plant available inorganic NH_4^+ pool. Previous studies have demonstrated that increasing nitrification rate in an ecosystem leads to increased foliar $\delta^{15}N$ (Nadelhoffer and Fry 1994) suggesting that the increase in $\delta^{15}N$ of the NH_4^+ pool drives the increase in foliar $\delta^{15}N$ (Pardo et al. 2002). The $\delta^{15}N$ value of the NH_4^+ pool is a function of the relative rates of production and consumption of NH_4^+; the more that NH_4^+ is consumed by nitrification, the more enriched the remaining NH_4^+ pool becomes (Mariotti et al. 1981). While net nitrification:mineralization is not a direct measure of all of the transformations affecting the NH_4^+ pool, it may be a surrogate for the fraction of the NH_4^+ substrate pool consumed, which is a primary factor that regulates the $\delta^{15}N$ of that pool (Mariotti 1981). It is important to note that while the enrichment of the NH_4^+ pool may drive the foliar enrichment, it will also, ultimately, lead to enrichment of the NO_3^- produced from the enriched NH_4^+, so plants that take up either NH_4^+ or NO_3^- will be affected.

The non-linear relationship between foliar $\delta^{15}N$ and nitrification:mineralization, in particular, and nitrification as well, may be the result of increasing availability of nitrate as percent nitrification increases, which may shift the plant N uptake toward NO_3^-, which would tend to be lighter than NH_4^+. Although extensive data are not yet available for $\delta^{15}N$ of inorganic N, several studies have measured lower $\delta^{15}N$ in nitrate than in ammonium in soil solution or soil extracts (Miller and Bowman 2002; Koba et al. 2003).

Denitrification is another factor which can significantly alter $\delta^{15}N$ of different ecosystem compartments at sites where it is significant, because denitrification fractionates strongly. When rates of net nitrification are high, denitrification could contribute further to the ^{15}N-enrichment of soil and foliar N pools. We did not have data about denitrification rates at enough sites to include it in this analysis. We assumed that, at many of these well-drained sites, denitrification rates would not be high.

Scale of analysis

Local N cycling factors, more than regional N deposition, were more strongly correlated with foliar $\delta^{15}N$, as evidenced by the result that data collected at the plot-scale were better correlated with forest floor C:N and nitrification:mineralization ratio than with N deposition rate. For data collected at the watershed scale, C:N and nitrification were averaged for the whole watershed, so these data cannot capture the heterogeneity of local soil conditions. Perhaps because the variability in foliar $\delta^{15}N$ caused by local soil conditions was smoothed by averaging across the watershed, data collected at the watershed scale were better correlated with N deposition (Table 5).

The scale at which the analysis is conducted (in contrast to the scale at which the samples are collected) can also impact the trends observed. The fact that the significance of trends in this study was preserved regardless of the level of aggregation (plot or site scale) suggests that these patterns are robust (Table 4).

Species effects

Different species often respond differently to increases in N deposition (Lovett and Rueth 1999; McNeil et al. 2005) and variation in species composition leads to differences in N cycling rates among forest types (Lovett et al. 2002; Mitchell et al. 2003; Templer et al. 2003; Lovett et al. 2004; Templer et al. 2005). Species composition, therefore, could be an important factor controlling foliar $\delta^{15}N$ relationships. Soil N cycling in conifer stands has been reported to be more susceptible than hardwoods to increased N inputs (Waring 1987). Conifer foliar $\delta^{15}N$ tends to be lower than that of hardwoods in less disturbed sites, likely

because of tight N cycling (Pardo 1999). Foliar $\delta^{15}N$ in conifer stands may, therefore, be especially responsive to increased N inputs and N cycling rates. It may be for this reason that patterns for conifers in this dataset tended to be stronger than they were for hardwoods. Another possible explanation may simply be that there were fewer conifer species included in our analysis, therefore species-related variability was minimized.

Different species may have distinct isotopic signatures. For example, several studies in the northeastern U.S. have shown a pattern of decreasing foliar $\delta^{15}N$ values across the following species: American beech > yellow birch > sugar maple (Nadelhoffer et al. 1999b; Pardo 1999; Templer 2001; Pardo et al. 2002). We observed that for this dataset, in most cases, evaluating the data from a single species improved the relationship observed, suggesting that there are systematic differences among species. It is not clear what causes these species differences – possible explanations include variation in rooting depth, NH_4^+ vs. NO_3^- uptake preference, and mycorrhizal association (McKane et al. 2002; Pardo et al. 2002).

Despite variability in foliar $\delta^{15}N$ values within species (e.g. a range of 5‰ for sugar maple), $\delta^{15}N$ values of American beech, yellow birch and sugar maple have characteristic signatures relative to their neighbors in mixed stands. In strongly N-limited systems, this has been attributed to partitioning of N sources. Because of the consistency in the pattern across sites ranging from the Adirondacks, NY to Maine, and including sites in Ontario and numerous sites in the White Mountains, NH, this pattern suggests that the N that plants are taking up differs systematically among these species. One possible explanation for the enrichment of beech relative to sugar maple (i.e. beech consistently accessing a different, more enriched N pool (i.e., NH_4^+) than sugar maple) could be a difference in timing of initial uptake in the spring. If one species responds more quickly than another to early pulses of springtime nitrification, that species could consistently have a more depleted foliar $\delta^{15}N$. Since enrichment of ammonium is a function of how much of the ammonium pool has been consumed, it is possible that the more responsive or seasonally early species might have a lower foliar $\delta^{15}N$, if it takes up more N early in the season before nitrification has enriched the DIN (dissolved inorganic N) pools. Indeed, based on 12 years of phenology data at the HBEF (Richardson et al. In press) sugar maples consistently leaf out 2–4 days prior to beech at any given location. Leaf-out and nutrient uptake are necessarily linked via transpiration. Water uptake is necessary for leaves to develop, and emerging leaves have particularly high water demand by mass because of their lack of cuticle development; such conditions facilitate nutrient uptake by bulk flow (Taiz and Zeiger 2002). If the small difference in timing of initial water and nutrient uptake means that sugar maples have access to more depleted ammonium and nitrate, it could be responsible, at least in part, for the pattern that we observed.

Differences in ammonium vs. nitrate uptake preferences do not explain the pattern we observed, since that would suggest that sugar maples preferentially take up nitrate while beech preferentially take up ammonium, which does not appear to be the case (Rothstein et al. 1996; Templer and Dawson 2004). Rooting depth may explain some of the differences, since beech tends to be deeper-rooted than sugar maple. Because soil $\delta^{15}N$ generally increases with depth (Nadelhoffer and Fry 1994; Pardo et al. 2002), deeper rooted trees may have access to more enriched inorganic N. However, tree species with different rooting depth patterns do not necessarily have differences in foliar $\delta^{15}N$ (Gebauer and Dietrich 1993) as observed for spruce, larch, and beech in Germany.

Mycorrhizal associations with tree roots have the potential to alter not only N nutrition, but also the isotopic signature of the N assimilated by plants (Högberg et al. 1996; Högberg 1997; Hobbie 1999; Evans 2001). It was our expectation based on work in N-limited systems (which may or may not be applicable) that species with ectomycorrhizal associations would have lower foliar $\delta^{15}N$ than those with vesicular–arbuscular mycorrhizal (VAM) association. We observed the opposite pattern here, as sugar maple has VAM associations and birch and beech are ectomycorrhizal species, yet the former had more depleted foliar $\delta^{15}N$ values. There are several possible explanations for this pattern. The pattern of ectomycorrhizal species having lower foliar $\delta^{15}N$ than VAM species has been reported for arctic, boreal and seasonally dry N-limited systems. At an N-rich site in Alaska, Hobbie et al. (2000) observed that the ectomycorrhizal species present had a higher foliar $\delta^{15}N$. Such an increase in foliar $\delta^{15}N$ may be caused by the $\delta^{15}N$ of the source N the plant takes up, or it may be caused by plant uptake bypassing the mycorrhizae on uptake when N is more abundant, or it may have to do with shifts in mycorrhizal species as N availability increases. Lilleskov et al. (2002) observed that

as N availability increased, mycorrhizal species shifted from those able to utilize organic N and which fractionate strongly (passing depleted N to the plant) to those mycorrhizal fungi that are less able to take up dissolved organic N and do not fractionate much, passing N to the plant that has a higher $\delta^{15}N$ than their proteolytic neighbors. Schulze et al. (1994) also observed that as N availability increased, differences between plants with different mycorrhizal associations decreased.

Different species also showed different levels of correlation of foliar N concentration with N deposition. We compared our findings to those from a comprehensive foliar study in the Adirondack Mountains, NY (McNeil et al. 2005). They reported stronger correlations between foliar N concentration and N deposition for hardwoods (yellow birch, sugar maple, and red maple) than conifers (red spruce and balsam fir, *Abies balsamea*). They found no relationship between foliar N concentration and N deposition for American beech or Eastern hemlock (*Tsuga canadensis*). We observed correlations of similar magnitude as McNeil et al. (2005) for all of these species except sugar maple, for which the correlation was not significant, and hemlock, for which we found a strong correlation. For some species (e.g. beech, red spruce), correlations for foliar N concentration were stronger with forest floor C:N than with N deposition. One possible explanation for this difference is that species with stronger correlations of foliar N concentration with N deposition may be more influenced by direct canopy uptake of N than the other species.

Root patterns

For a subset of the sites included in the overall analysis, we were able to evaluate root $\delta^{15}N$ patterns in relation to foliar $\delta^{15}N$. Roots may provide better information about the $\delta^{15}N$ of plant-available N, because fewer processes occur before the N is assimilated in their tissue (and they do not have the potential for direct uptake of N deposition as in the canopy). Indeed, the correlation of fine root $\delta^{15}N$ with $\delta^{15}N$ of forest floor was strong and near the 1:1 line. If the forest floor is regarded as the primary source for plant-available inorganic N, the link between forest floor and root $\delta^{15}N$ (Figure 7b) suggests that root $\delta^{15}N$ must be closely coupled with $\delta^{15}N$ of available N. The strong positive correlation of root $\delta^{15}N$ with foliar $\delta^{15}N$ suggests that, at the regional scale, these two plant pools vary in similar ways with respect to plant-available N (Figure 7a). From Figure 7a, we observed that for these sites, fine root $\delta^{15}N$ is generally enriched with respect to foliar $\delta^{15}N$. The strong positive relationships we observed between fine root $\delta^{15}N$ values and forest floor nitrification and the nitrification:mineralization ratio are not surprising, and are likely driven by the same enrichment of NH_4^+ pools discussed with respect to leaves. Root $\delta^{15}N$ correlations with N deposition were similar in magnitude to those with nitrification:mineralization.

Additionally, the strong relationships we found between root $\delta^{15}N$ and measures of N saturation suggest that more studies need to measure the natural abundance isotopic ^{15}N values of these plant tissues. This will augment the amount of data available for determining which plant tissue (i.e. foliage vs. roots) is the most relevant for assessing whether a forest has reached N saturation.

Climate-related effects

Previous studies (Austin and Vitousek 1998; Austin and Sala 1999; Handley et al. 1999) have demonstrated a negative correlation between foliar $\delta^{15}N$ and precipitation. In contrast, we observed a positive relationship. However, most of our dataset fell into a precipitation range of 500–1800 mm y^{-1}, in contrast to the broader ranges (sites distributed between 0 and 5000 mm y^{-1}) previously reported (Handley et al. 1999; Amundson et al. 2003). The few points with precipitation greater than 2000 mm y^{-1} had foliar $\delta^{15}N$ levels that were very depleted ($< -5‰$), agreeing more with the previously reported pattern. The increasing foliar $\delta^{15}N$ at lower precipitation may be related to soil water availability enhancing nitrification at these sites. The negative relationship between foliar $\delta^{15}N$ and mean annual temperature may also be indirectly related to nitrification rates.

Summary

Our data suggest that although studying the relationship between N deposition and foliar N concentration may provide an understanding about the relationship between regional impact of changes in the N cycle, examining $\delta^{15}N$ values of foliage may also improve understanding of how forests respond to the cascading effects of N deposition, as evidenced by the strong relationships we found between foliar $\delta^{15}N$ and nitrification. These data also suggest that N deposition is altering soil N cycling enough to be detected at the regional, and perhaps even global, scale using foliar and root ^{15}N natural abundances. These results may, therefore, have implications for water quality, carbon sequestration and other ecosystem services associated with forest ecosystems.

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References

Aber J.D., Goodale C.L., Ollinger S.V., Smith M.-L., Magill A.H., Martin M.E., Hallett R.A. and Stoddard J.L. 2003. Is nitrogen deposition altering the nitrogen status of northeastern forests? Bioscience 53(4): 375–389.

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

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

Adams M.B., Angradi T.R. and Kochenderfer J.N. 1997. Stream water and soil solution responses to 5 years of nitrogen and sulfur additions at Fernow Experimental Forest, West Virginia. Forest Ecol. Manag. 95: 79–91.

Amundson R., Aystin A.T., Schuur E.A.G., Yoo K., Matzek V., Kendall C., Uebersax A., Brenner D. and Baisden W.T. 2003. Global patterns of the isotopic composition of soil and plant nitrogen. Global Biogeochem. Cycles 17(1), 1031, doi10.1029/2002GB001903, 2003.

Andersen B.R. 2000. Data – site Gribskov. CD-ROM-Database. In: Schulze E.-D. (ed.), Carbon and Nitrogen Cycling in European Forest Ecosystems. Ecological Studies, Vol. 142. Springer, Berlin.

Austin A.T. and Sala O.E. 1999. Foliar d^{15}N is negatively correlated with rainfall along with the IGBP transect in Australia. Aust. J. Plant. Physiol. 26: 293–295.

Austin A.T. and Vitousek P.M. 1998. Nutrient dynamics on a precipitation gradient in Hawai'i. Oecologia 113: 519–529.

Bailey S.W., Driscoll C.T. and Hornbeck J.W. 1995. Acid–base chemistry and aluminum transport in an acidic watershed and pond in New Hampshire. Biogeochemistry 28: 69–91.

Bauer G.A., Gebauer G., Harrison A.F., Högberg P., Högbom L., Schinkel H., Taylor A.F.S., Novak M., Buzek F., Harkness D., Persson T. and Schulze E.-D. 2000a. Biotic and abiotic controls over ecosystem cycling of stable natural nitrogen, carbon and sulphur isotopes. In: Schulze E.-D. (ed.), Carbon and Nitrogen Cycling in European Forest Ecosystems, Springer-Verlag, Berlin, pp. 189–214.

Bauer G.A., Persson H., Persson T., Mund M., Hein M., Kummetz E., Matteucci G., Van Oene H., Scarascia – Mugnozza G. and Schulze E.-D. 2000b. Linking plant nutrition and ecosytem processes. In: Schulze E.-D. (ed.), Carbon and Nitrogen Cycling in European Forest Ecosystems. Ecological Studies, Vol. 142. Springer, Berlin, pp. 63–98.

Bergholm J. 2000. Wet deposition and throughfall – site Skogaby. CD-ROM-Database. In: Schulze E.-D. (ed.), Carbon and Nitrogen Cycling in European Forest Ecosystems. Ecological Studies, Vol. 142. Springer, Berlin.

Bohlen P.J., Groffman P.M., Driscoll C.T., Fahey T.J. and Siccama T.G. 2001. Plant–soil–microbial interactions in a northern hardwood forest. Ecology 82: 965–978.

Campbell J.L., Eagar C., McDowell W.H. and Hornbeck J.W. 2000. Analysis of nitrogen dynamics in the Lye Brook Wilderness Area, Vermont, USA. Water Air Soil Pollut. 122: 63–75.

Corre M.D., Beese F. and Brumme R. 2003. Soil nitrogen cycle in high nitrogen deposition forest: changes under nitrogen saturation and liming. Ecol. Appl. 13(2): 287–298.

Dambrine E. 2000. Throughfall data. Site Aubure spruce. CD-ROM-Database. In: Schulze E.-D. (ed.), Carbon and Nitrogen Cycling in European Forest Ecosystems. Ecological Studies, Vol. 142. Springer, Berlin.

DeHayes D.H., Schaberg P.G. and Strimbeck G.R. 2001. Red spruce cold hardiness and freezing injury susceptibility. In: Bigras F. (ed.), Conifer Cold Hardiness, Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 495–529.

Dise N.B., Matzner E. and Gundersen P. 1998. Synthesis of nitrogen pools and fluxes from European forest ecosystems. Water Air Soil Poll. 105: 143–154.

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

Evans D. 2001. Physiological mechanisms influencing plant nitrogen isotope composition. Trends Plant Sci. 6: 121–127.

Gebauer G. and Dietrich P. 1993. Nitrogen isotope ratios in different compartments of a mixed stand of spruce, larch and beech trees and of understorey vegetation including fungi. Isotopenpraxis Environ. Health Stud. 29: 35–44.

Gebauer G., Giesemann A., Schulze E.-D. and Jäger H.-J. 1994. Isotope ratios and concentrations of sulfur and nitrogen in needles and soils of *Picea abies* stands as influenced by atmospheric deposition of sulfur and nitrogen compounds. Plant Soil 164: 267–281.

Gebauer G. and Schulze E.-D. 1991. Carbon and nitrogen isotope ratios in different compartments of a healthy and a declining *Picea abies* forest in the Fichtelbebirge, NE Bavaria. Oecologia 87: 198–207.

Gilliam F.S., Adams M.B. and Yurish B.M. 1996. Ecosystem nutrient responses to chronic nitrogen inputs at the Fernow Experimental Forest, West Virginia. Can. J. Forest Res. 26: 196–205.

Goodale C.L. and Aber J.D. 2001. The long-term effects of land-use history on nitrogen cycling in northern hardwood forests. Ecol. Appl. 11: 253–267.

Gundersen P. 1998. Effects of enhanced nitrogen deposition in a spruce forest at Klosterhede, Denmark, examined by NH_4NO_3 addition. Forest Ecol. Manag. 101: 251–268.

Handley L.L., Austin A.T., Robinson D., Scrimegour C.M., Raven J.A., Heaton T.H.E., Schmidt S. and Stewart G.R. 1999. The ^{15}N natural abundance (^{15}N) of ecosystem samples reflects measures of water availability. Aust. J. Plant Physiol. 26: 185–199.

Handley L.L. and Raven J.A. 1992. The use of natural abundance of nitrogen isotopes in plant physiology and ecology. Plant Cell Environ. 15: 965–985.

Hobbie E.A., Macko S.A. and Shugart H.H. 1999. Interpretation of nitrogen isotope signatures using the NIFTE model. Oecologia 120: 405–415.

Hobbie E.A., Macko S.A. and Williams M. 2000. Correlations between foliar $d^{15}N$ and nitrogen concentration may indicate plant-mycorrhizal interactions. Oecologia 122: 273–283.

Högberg P. 1990. ^{15}N natural abundance as a possible marker of the ectomycorrhizal habit of trees in mixed African woodlands. New Phytol. 115: 483–486.

Högberg P., Högbom L., Schinkel H., Högberg M., Johannisson C. and Wallmark H. 1996. Oecologia 108: 207–214.

Högberg P. and Johannisson C. 1993. ^{15}N abundance of forests is correlated with losses of nitrogen. Plant Soil 157: 147–150.

Högberg P. 1997. ^{15}N natural abundance in soil–plant systems. New Phytol. 137: 179–203.

Hooker T.D. and Compton J.E. 2003. Forest ecosystem carbon and nitrogen accumulation during the first century after agricultural abandonment. Ecol. Appl. 13: 299–313.

Hübner H. 1986. Isotope effects of nitrogen in soil and the biosphere. In: Fritz P. and Fontes J.C. (eds), Handbook of Environmental and Isotope Chemistry. Vol. 2b. The Terrestrial Environment, Elsevier, Amsterdam, pp. 361–425.

Hughes J.W. and Fahey T.J. 1994. Litterfall dynamics and ecosystem recovery during forest development. Forest Ecol. Manag. 63: 181–198.

Jach M.E. and Ceulemans R. 2000. Effects of season, needle age and elevated atmospheric CO_2 on photosynthesis in Scots pine (*Pinys sylvestris*). Tree Physiol. 20: 145–157.

Jefts S., Fernandez I.J., Rustad L.E. and Dail D.B. 2004. Decadal responses in soil N dynamics at the Bear Brook Watershed in Maine, USA. Forest Ecol. Manag. 189: 189–205.

Jung K., Gebauer G., Gehre M., Hofmann D., Weißflog L. and Schüürmann G. 1997. Anthropogenic impacts on natural nitrogen isotope variations in *Pinus sylvestris* stands in an industrially polluted area. Environ. Pollut. 97: 175–181.

Kendall C., Silva S.R., Chang C.C.Y., Burns D.A., Campbell D.H. and Shanley J.B. 1996. Use of the Delta ^{18}O and Delta ^{15}N of nitrate to determine sources of nitrate in early spring runoff in forested catchments. In: Isotopes in Water Resources Management. International Atomic Energy Agency Symposium, Vienna, Austria, 1995, pp. 167–176.

Koba K., Hirobe M., Koyama L., Kohzu A., Tokuchi N., Nadelhoffer K.J., Wada E. and Takeda H. 2003. Natural ^{15}N abundance of plants and soil N in a temperate coniferous forest. Ecosystems 6: 457–469.

Koopmans C.J., Tietema A. and Verstraten J.M. 1998. Effects of reduced N deposition on litter decomposition and N cycling in tow N saturated forests in the Netherlands. Soil Biol. Biochem. 30: 141–151.

Lamontagne S. 1998. Nitrogen mineralization in upland Precambrian Shield catchments: contrasting the role of lichen-covered bedrock and forested areas. Biogeochemistry 41: 53–69.

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

Lilleskov E.A., Hobbie E.A. and Fahey T.J. 2002. Ectomycorrhizal fungal taxa differing in response to nitrogen deposition also differ in pure culture organic nitrogen use and natural abundance of nitrogen isotopes. New Phytol. 154: 219–231.

Lovett G.M. and Rueth H. 1999. Soil nitrogen transformations in beech and maple stands along a nitrogen deposition gradient. Ecol. Appl. 9: 1330–1344.

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

Lovett G.M., Weathers K.W., Arthur M.A. and Schultz J.C. 2004. Nitrogen cycling in a northern hardwood forest: do species matter? Biogeochemistry 67: 289–308.

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

Manderscheid B. 2000. Wet deposition and throughfall data – site Waldstein. CD-ROM-Database. In: Schulze E.-D. (ed.), Carbon and Nitrogen Cycling in European Forest Ecosystems. Ecological Studies, Vol. 142. Springer, Berlin.

Mariotti A., Germon J.C., Hubert P., Kaiser P., Tardieux A. and Tardieux P. 1981. Experimental determination of kinetic isotope fractionations: some principles; illustration for denitrification and nitrification processes. Plant Soil 62: 413–430.

Martin C.W. 1979. Precipitation and streamwater chemistry in an undisturbed forested watershed in New Hampshire. Ecology 60: 36–42.

Martinelli L.A., Piccolo M.C., Townsend A.R., Vitousek P.M., Cuevas E., McDowell W., Robertson G.P., Santos O.C. and Treseder K. 1999. Nitrogen stable isotopic composition of leaves and soil: tropical vs. temperate forests. Biogeochemistry 46(1–3): 45–65.

McKane R.B., Johnson L.C., Shaver G.R., Nadelhoffer K.N., Rastetter E.B., Fry B., Giblin A.E., Kielland K., Kwiatkowski B.L., Laundre J.A. and Murray G. 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. Nature 415(6867): 68–71.

McNeil B.E., Read J.M. and Driscoll C.T. 2005. Identifying controls on the spatial variability of foliar nitrogen in a large, complex ecosystem: the role of atmospheric nitrogen deposition in the Adirondack Park, NY, USA. J. Agric. Meteorol.

McNulty S.G., Aber J.D. and Boone R.D. 1991. Spatial changes in forest floor and foliar chemistry of spruce-fir forests across New England. Biogeochemistry 14: 13–29.

McNulty S.G., Aber J.D. and Newman S.D. 1996. Nitrogen saturation in a high elevation New England spruce-fir stand. Forest Ecol. Manag. 84: 109–121.

Michelsen A., Quarmby C., Sleep D. and Jonasson S. 1998. Vascular plant ^{15}N natural abundance in health and forest tundra ecosystems is closely correlated with presence and type of mycorrhizal fungi in roots. Oecologia 115: 406–418.

Miller A.E. and Bowman W.D. 2002. Variation in Nitrogen-15 natural abundance and nitrogen uptake traits among co-occurring alpine species: do species partition nitrogen form? Oecologia 130: 609–616.

Mitchell M.J., Driscoll C.T., Inamdar S., McGee G., Mbila M. and Raynal D.J. 2003. Nitrogen biogeochemistry in the Adirondack mountains of New York: hardwood ecosystems associated with surface water. Environ. Pollut. 123: 355–364.

Mitchell M.J., Driscoll C.T., Owen J.S., Schaefer D., Michener R. and Raynal D.J. 2001. Nitrogen biogeochemistry of three hardwood ecosystems in the Adirondack Region of New York. Biogeochemistry 56: 93–133.

Mosello R. 2000. Wet deposition and throughfall data – site Collelongo. CD-ROM-Database. In: Schulze E.-D. (ed.), Carbon and Nitrogen Cycling in European Forest Ecosystems. Ecological Studies, Vol. 142. Springer, Berlin.

Nadelhoffer K.J., Downs M.R. and Fry B. 1999a. Sinks for ^{15}N-enriched additions to an oak forest and a red pine plantation. Ecol. Appl. 9: 72–86.

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

Nadelhoffer K., Downs M., Fry B., Magill A. and Aber J. 1999b. Controls on N retention and exports in a forested watershed. Environmental Monitoring and Assessment 55: 187–210.

Nadelhoffer K.J. and Fry B. 1994. Nitrogen isotope studies in forest ecosytems. In: Lajtha K. and Michener R.H. (eds), Stable Isotopes in Ecology and Environmental Science, Blackwell Scientific Publishers, Cambridge, UK.

Nadelhoffer K.J., Shaver G., Fry B., Giblin A., Johnson L. and McKane R. 1996. ^{15}N natural abundances and N use by tundra plants. Oecologia 107: 386–394.

Nihlgard B. 1985. The ammonium hypothesis – an additional explanation to the forest decline in Europe. Ambio 14: 2–8.

Ollinger S.V., Aber J.D., Lovett G.M., Milham S.E. and Lathrop R.G. 1993. A spatial model of atmospheric deposition for the northeastern US. Ecol. Appl. 3: 459–472.

Ollinger S.V., Smith M.L., Martin M.E., Hallet R.A., Goodale C.L. and Aber J.D. 2002. Regional variation in foliar chemistry and N cycling among forests of diverse history and composition. Ecology 83: 339–355.

Oyarzún C.E. and Huber A. 2003. Nitrogen export from forested and agricultural watersheds of southern Chile. Gayana Bot. 60: 63–68.

Pardo L.H. 1999. Natural Abundance of ^{15}N as a Tool for Assessing Patterns of Nitrogen Loss from Forested Ecosystems. Massachusetts Institute of Technology, Cambridge MA.

Pardo L.H., Hemond H.F., Montoya J.P., Fahey T.J. and Siccama T.G. 2002. Response of the natural abundance of ^{15}N in forest soils and foliage to high nitrate loss following clear-cutting. Can. J. For. Res. 32: 1126–1136.

Pardo L.H., Hemond H.F., Montoya J.P. and Siccama T.G. 2001. Long-term patterns in forest-floor nitrogen-15 natural abundance at Hubbard Brook, NH. Soil Sci. Soc. Am. J. 65(4): 1279–1283.

Pardo L.H., Kendall C., Pett-Ridge J. and Chang C.C.Y. 2004. Evaluating the source of streamwater nitrate using $\delta^{15}N$ and $\delta^{18}O$ in nitrate in two watersheds in New Hampshire, USA. Hydrol. Process. 18: 2699–2712.

Pardo L.H., McNulty S.G., Boggs J.L. 2003. Effects of N deposition on high elevation forests in the northeastern US: foliar $\delta^{15}N$ patterns. Proceedings of the 88th Annual Meeting of the Ecological Society of America, Savannah, GA.

Pardo L.H., Schaberg P.G. and McNulty S.G. 1998. Response of natural abundance of ^{15}N in spruce foliage to chronic N additions. Ecologcial Society of America Bulletin: Abstracts 83rd Annual Meeting, Baltimore, MD, 2–6 August 1998, p. 104.

Persson T. 2000. Soil carbon and nitrogen pools data. CD-ROM-Database. In: Schulze E.-D. (ed.), Carbon and Nitrogen Cycling in European Forest Ecosystems. Ecological Studies, Vol. 142. Springer, Berlin.

Persson T., Rudebeck A., Jussy J.H., Colin-Belgrand M., Priemé A., Dambrine E., Karlsson P.S. and Sjöberg R.M. 2000a. Soil nitrogen turnover – mineralization, nitrification and denitrification in European forest soils. In: Schulze E.-D. (ed.), Carbon and Nitrogen Cycling in European Forest Ecosystems. Ecological Studies, Vol. 142. Springer, Berlin, pp. 297–331.

Persson T., Van Oene H., Harrison A.F., Karlsson P.S., Bauer G.A., Cerny J., Coûteaux M.-M., Dambrine E., Högberg P., Kjøller A., Matteucci G., Rudebeck A., Schulze E.-D. and Paces T. 2000b. Experimental sites in the NIPHYS/CANIF Project. In: Schulze E.-D. (ed.), Carbon and Nitrogen Cycling in European Forest Ecosystems. Ecological Studies, Vol. 142. Springer, Berlin, pp. 14–46.

Piccolo M.C., Neill C. and Cerri C. 1994. Natural abundance of ^{15}N in soils along forest-to-pasture chronosequences in the western Brazilian Amazon Basin. Oecologia 99: 112–117.

Richardson, A.D., Bailey A.S., Denny E.G, Martin C.W. and O'Keefe J. In press. Phenology of a northern hardwood forest canopy. Global Change Biology.

Robinson D. 2001. delta^{15}N as an integrator of the nitrogen cycle. Trends Ecol Evol. 16(3): 153–162.

Rothstein D.E., Zak D.R. and Pregitzer K.S. 1996. Nitrate deposition in northern hardwood forests and the nitrogen metabolism of *Acer saccharum* marsh. Oecologia 108: 338–344.

Rueth H.M. and Baron J.S. 2002. Differences in Engelmann spruce forest biogeochemistry east and west of the Continental Divide in Colorado, USA. Ecosystems 5: 45–57.

Schaberg P.G., DeHayes D.H., Hawley G.J., Murakami P.F., Strimbeck G.R. and McNulty S.G. 2002. Effects of chronic N fertilization on foliar membranes, cold tolerance, and carbon storage in montane red spruce.

Schiff S.L., Devito K.J., Elgood R.J., McCrindle P.M., Spoelstra J. and Dillon P. 2002. Two adjacent forested catchments: dramatically different NO_3^- export. Water Resour. Res. 38: 1292, DOI 1029/2000WR000170.

Schleppi P., Bucher-Wallin I., Siegwolf R., Saurer M., Muller N. and Bucher J.B. 1999. Simulation of increased nitrogen deposition to a montane forest ecosystem: partitioning of the added ^{15}N. Water Air Soil Pollut. 116: 129–134.

Schmidt S. and Stewart G.R. 2003. d^{15}N values of tropical savanna and monsoon forest species reflect root specializations and soil nitrogen status. Oecologia 134: 569–577.

Schulze E.-D., Chapin F.S. III and Gebauer G. 1994. Nitrogen nutrition and isotope differences among life forms at the northern treeline of Alaska. Oecologia 100: 406–412.

Sirois A., Vet R. and MacTavish D. 2001. Atmospheric deposition to the Turkey Lakes Watershed: temporal variations and characteristics. Ecosystems 4: 503–513.

Stoddard J.L. 1994. Long-term changes in watershed retention of nitrogen: its causes and aquatic consequences. In: Baker L.A. (ed.), Environmental Chemistry of Lakes and Reservoirs, American Chemical Society, Washington, DC, pp. 223–284.

Taiz L. and Zeiger E. 2002. Plant Physiology, 3rd ed. Sinauer Associates Inc., Sunderland, MA.

Templer P.H. 2001. Direct and indirect effects of tree species on nitrogen retention in the Catskill Mountains, NY. Ph.D. Thesis, Cornell University, Ithaca, NY.

Templer P.H. and Dawson T.E. 2004. Nitrogen uptake by four tree species of the Catskill Mountains, New York: implications for nitrogen cycling. Plant Soil 262: 251–261.

Templer P.H., Lovett G.M., Weathers K.C., Findlay S.E. and Dawson T.W. 2005. Influence of tree species on ^{15}N sinks in forests of the Catskill Mountains, New York. Ecosystems 8: 1–16.

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

van den Driessche R. 1974. Prediction of mineral nutrient status of trees by foliar analysis. Bot. Rev. 40: 347–394.

Vervaet H., Massart B., Boeckx P., Van Cleemput O. and Hofman G. 2002. Use of principal component analysis to assess factors controlling net N mineralization in deciduous and coniferous forest soils. Biol. Fertil. Soils 36: 93–101.

Waring R.H. 1987. Nitrate pollution: a particular danger to boreal and subalpine coniferous forests. Proceedings of IUFRO Workshop, Human impacts and management of mountain forest, 4–13 Septmber 1987, Susono, Japan.