

7 NORTHERN FORESTS

L.H. Pardo, C.L. Goodale, E.A. Lilleskov, L.H. Geiser

7.1 Ecoregion Description

The Northern Forests ecological region spans much of Canada, from Saskatchewan to Newfoundland; its southern portion extends into the northern United States (CEC 1997). The U.S. component includes the northern hardwood and spruce-fir forest types and encompasses parts of the Northeast (mountainous regions in Pennsylvania, New York, New Jersey, Connecticut, Massachusetts, Maine, and most of Vermont and New Hampshire) and the northernmost parts of the upper Midwest (Minnesota, Wisconsin, Michigan; CEC 1997; see Chapter 2, Figure 2.2). The ecoregion description is adapted from CEC (1997). In Canada, the ecoregion is underlain by ancient Canadian Shield bedrock interspersed with glacial moraine deposits, creating a hilly terrain dotted with numerous lakes. Soils are generally coarse-textured and nutrient-poor, characterized typically by thick organic accumulations in the forest floor and leached layers in the mineral soil below. Shallow soils and exposed bedrock are covered with various plant communities dominated by shrubs, forbs, and lichens. Peatlands are extensive in northern Minnesota. The climate is characterized by long, cold winters (means of -20.5 °C in the west to -1 °C in the east) and short, warm summers (means of 11 to 18 °C). Annual precipitation varies from 400 to 1,000 mm. The ecoregion is more than 80 percent forested, and dominated by conifers, mostly white and black spruce (*Picea glauca* and *P. mariana*), jack pine (*Pinus banksiana*), balsam fir (*Abies balsamea*), and tamarack (*Larix laricina*) (CEC 1997). Toward its southern and eastern extremes in the upper midwest and northeastern United States, the ecoregion includes more paper birch (*Betula papyrifera*), yellow birch (*Betula alleghaniensis*), quaking aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), eastern white pine (*Pinus strobus*), red pine (*Pinus resinosa*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), beech (*Fagus* spp.), red spruce (*Picea rubens*), and various species of oak (*Quercus* spp.).

7.2 Ecosystem Responses to N Deposition

Most northern forests are naturally nitrogen (N) limited; cold temperatures limit rates of decomposition and slow rates of release of N from decomposing organic matter. These low rates of N mineralization limit the supply of N to plants and microbes. There is strong competition for N between plants and microbes and most of the N entering the ecosystem is tightly retained in soils and in vegetation, with little loss of inorganic N to drainage waters. When air pollution increases the supply of N to these ecosystems through N deposition, a range of ecosystem responses, described below, are anticipated. Some of these responses occur as gradual changes, others as cumulative threshold responses in progressive stages of N saturation (cf. Aber et al. 1998). See Chapter 1 for a more detailed explanation of the stages. Briefly, early stages (especially stage 1) are marked by increased supply of N to plants and to microbes, indicated by increasing plant foliar N concentration, growth rate, and soil N mineralization rate. Cumulative N inputs may decrease the carbon:nitrogen (C:N) ratio of soils and change rates of decomposition. Responding to increased N supply and low soil C:N ratios, net nitrification marks a next stage of ecosystem response (stage 2). Nitrification can acidify the soil and produce high levels of nitrate (NO_3^-), a form of N that readily leaches with runoff. This phase of response is marked by increased NO_3^- concentrations in surface water and leaching of N from catchments. When NO_3^- leaches, it removes base cations from the soil and leads to soil and drainage water acidification. Collectively, acidification and nutrient imbalances may cause growth declines or increased mortality rates (stage 3). These direct effects of N deposition may also lead to increased susceptibility to secondary stresses such as winter injury, drought damage, pest outbreak, and diseases, and may reduce cold tolerance (Schaberg et al. 2002). Declining vegetation is likely to take up less N than healthy vegetation, and so losses of NO_3^- are expected to accelerate as N saturation

proceeds. In addition to these ecosystem-level responses, N deposition can affect the competitive balance of different species, leading to changes in composition of mycorrhizal fungi, lichen, bryophyte, understory shrub and herb, and tree species composition. In this chapter, we review the evidence for impacts of N deposition on overstory trees, herbaceous vegetation, mycorrhizal fungi, and lichens in the Northern Forests ecoregion.

7.3 Range of Responses Observed

Three types of studies provide empirical information on the effects of N on ecosystem properties: (1) long-term observations at sites receiving increasing or chronically elevated N deposition; (2) long-term, low- to moderate-level N fertilization studies; and (3) observational studies along gradients of N deposition. All three study types are discussed below, and each approach has its strengths and limitations. Long-term observations can reveal trends through time, but also can be influenced by a great many factors in addition to N deposition, factors which are difficult to disentangle. Fertilization studies may provide some additional insight about the timing and nature of responses of forests to elevated N inputs. Often, fertilization studies utilize such high N inputs that they do not help define the actual threshold when a response is induced. Gradient studies examine ecosystem responses along gradients of N deposition, but can also suffer from difficulty in separating out effects of N from effects of other covariates.

7.3.1 Foliar N, Growth, and Mortality

Foliar N concentrations increased in most N fertilization experiments in the Northern Forests ecoregion (Table 7.1). This increase in foliar N might be expected to increase plant growth, since photosynthesis typically increases with foliar N concentration within and across most natural ecosystems. Increased foliar N was accompanied by increased tree growth in fertilized sugar maple stands in Michigan (Pregitzer et al. 2008) and Maine (Elvir et al. 2003). However, fertilized red spruce trees in Maine (Elvir et al. 2003) and black spruce and balsam fir stands in northern Quebec (Houle and Moore 2008) showed no change in growth rates. At a subalpine spruce-fir forest at Mt. Ascutney, Vermont, long-term fertilization with ammonium chloride (NH_4Cl) at 15.7

$\text{kg N ha}^{-1} \text{ yr}^{-1}$ (in addition to ambient wet plus dry N deposition of approximately $10 \text{ kg ha}^{-1} \text{ yr}^{-1}$) increased foliar N concentration and decreased growth and increased mortality, leading to an approximately 20 percent decline in live basal area after 14 years (McNulty et al. 2005). Other effects observed at this fertilization rate were reductions in foliar membrane-associated Ca, reduced cold tolerance, and increased winter freezing injury (Schaberg et al. 2002). The responses observed at the high treatment plot, where $31 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ above ambient deposition were added, are far more striking. In these plots, mortality is high (40 percent decline in live basal area) and species composition changes were induced after only 14 years of N addition (McNulty et al. 2005).

Overall, these fertilization experiments show modest growth enhancement by some, but not all, species. Sometimes the initial growth enhancement is followed by growth declines or increased mortality in the long-term studies, especially at the highest rates of N inputs or sites with soils containing few base cations. It is unclear precisely where this threshold for detrimental effects occurs, although the experimental work at Mt. Ascutney demonstrated substantial mortality by red spruce in response to just $15.7 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ above the ambient deposition of approximately $10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. While Mt. Ascutney clearly represents the sensitive end-member of forest ecosystems in the Northeast, it is instructive because the nonlinear path that the high treatment plots followed may also occur over time at the low treatment plot. It is possible, then, that inputs even lower than $26 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ would lead to N saturation over an extended period of time (e.g., 50 to 100 years).

Gradient studies have shown mixed evidence for foliar N response to atmospheric deposition to northern forest ecosystems. In a broad synthesis of data from 354 plots in upland forests across the Northeast, Aber et al. (2003) did not find patterns of increasing foliar N concentration with deposition, even when controlling for tree species; variation in foliar N was most strongly associated with elevation and climatic variables. In red spruce, foliar lignin:N ratio was related to N deposition, but deposition covaried with elevation

Table 7.1—Response of Northern Forest ecosystems to experimental N fertilization ($\leq 50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$)

Site Location	Michigan (4 sites)	Mt. Ascutney, Vermont	---- Bear Brook, ---- Maine		Adirondacks, NY (3 sites)	Northwest Ontario	---- Northern ---- Quebec		
Forest type	Sugar maple	Montane spruce-fir	Northern hardwoods	Red spruce	Northern hardwoods	Rock, Jack pine / spruce	Black spruce	Balsam fir	
Type of N deposition	Wet + dry	Wet + dry	Wet + dry		Throughfall	Bulk	Wet only		
N Deposition ($\text{kg ha}^{-1} \text{ yr}^{-1}$)	6.8-11.8	10	8.4		4.6-12.0	3.4-6.5	3	5.7	
N fertilization rate ($\text{kg ha}^{-1} \text{ yr}^{-1}$)	+30	+15.7, +31.4	+25		+14, +28	+36-40	+9, +30	+18, +60	
Form of N fertilizer	NaNO_3	NH_4Cl	$(\text{NH}_4)_2\text{SO}_4$		HNO_3 , $(\text{NH}_4)_2\text{SO}_4$	NaNO_3	NH_4NO_3		
Start year	1994	1988	1989		1991	1995	2001		
Duration (years)	10	14	13		3	2	3	3	
- Response relative to Control ^a -	Tree growth	+	-	+	0	ND	ND	0	0
	Mortality	+	+	ND	ND	ND	ND	ND	ND
	Foliar %N	+	+	+	+	ND	ND	+	0
	Foliar %Ca	ND	-	0, -	-	ND	ND	+	0
	NO_3^- leaching	+	ND	+		0, 0, +	+	+	+
	Cation loss	ND	ND	+		ND	ND	ND	ND
	Soil C/N	0	0	0	-	ND	ND	ND	ND
	N mineralization	0	0, -	+	+	ND	ND	ND	ND
	Nitrification	+	+	+	+	ND	ND	ND	ND
	Soil respiration	-	-	0	ND	ND	ND	ND	ND
Microbial biomass	0	-	0	ND	ND	ND	ND	ND	
References	1-5	6-7	7-11		12	13	14	14	

^aResponses are indicated as positive (+), negative (-) or no response (0) in fertilized relative to control plots, or no data (ND) in indicated references.

References: 1) Burton et al. 2004; 2) Pregitzer et al. 2004; 3) Pregitzer et al. 2008; 4) Zak et al. 2004; 5) Zak et al. 2006; 6) McNulty et al. 2005; 7) Wallenstein et al. 2006; 8) Elvir et al. 2003; 9) Elvir et al. 2006; 10) Fernandez et al. 2003; 11) Jefts et al. 2004; 12) Mitchell et al. 2001; 13) Lamontagne and Schiff 1999; 14) Houle and Moore 2008.

and climatic variables within this dataset (Aber et al. 2003). However, other studies have shown that foliar N concentration increases with increasing N deposition. McNeil et al. (2007) saw an increase in foliar N concentration for eight of nine canopy tree species across 73 plots spanning an N deposition gradient (3.5 to >7 $\text{kg ha}^{-1} \text{ yr}^{-1}$ of wet-only N deposition) in the Adirondack Park, New York. American beech (*Fagus grandifolia*) did not respond, but yellow birch (*Betula alleghaniensis*), paper birch, red maple (*Acer rubrum*), sugar maple, eastern white pine, eastern hemlock (*Tsuga canadensis*), balsam fir, and red spruce did. Another regional foliar analysis, which included 2702 foliar samples from 434

plots in the Northeast, found significant correlations between N deposition (5 to 12 $\text{kg ha}^{-1} \text{ yr}^{-1}$ of wet plus dry deposition) and foliar N concentration for both hardwoods and conifers (Pardo et al. 2006). This study also examined foliar $\delta^{15}\text{N}$, another measure used to assess the N status of ecosystems because it provides an integrated measure of past N cycling and often increases in response to disturbance (Emmett et al. 1998, Nadelhoffer and Fry 1994). Foliar $\delta^{15}\text{N}$ increased with deposition, although correlations were stronger for conifers than for hardwoods (Pardo et al. 2006); in all cases the correlation between N deposition and foliar N concentration was stronger than with foliar

$\delta^{15}\text{N}$. In another gradient study evaluating N cycling in red spruce stands from Maine to New York, sampling in 1987 and 1988 (McNulty et al. 1991) and again in 1999 (Boggs et al. 2007) showed an increase in foliar N concentration both over time and with deposition along the gradient from 5 to 11 kg N ha⁻¹ yr⁻¹ (Pardo et al. 2007). Hardwood foliar N concentration was measured only in 1999 and increased with deposition along the gradient. These relationships were weaker than for spruce, but were statistically significant (Pardo et al. 2007). These studies broadly demonstrate that foliar N concentration in Northern Forests tends to increase with increasing N inputs. Nonetheless, because of the variability in response and the lack of a threshold above which the rate of change is altered, it is difficult to use foliar N concentration alone as an indicator of N saturation.

Until recently, there has been little evidence outside of fertilization experiments for either enhanced growth or mortality in U.S. forests attributable to elevated N deposition. This lack of evidence is largely due to the difficulty of detecting such a signal against the large background variation due to factors that affect growth in natural ecosystems and the relative paucity of such studies. Caspersen et al. (2000) discerned a 2.0 percent enhancement of forest biomass in several states (Minnesota, Michigan, Virginia, North Carolina, and Florida) over the last century, but could not identify which mechanism (e.g., rising atmospheric CO₂ concentrations, climate changes, N deposition) might be responsible for this growth increase. Similarly, Hicke et al. (2002) reported changes in forest growth across North America over the last two decades derived from satellite observations of canopy properties, but saw no trends that were easily attributable to N deposition. In Europe, regional patterns of forest growth are largely driven by forest management decisions, but growth enhancement from N deposition has long been speculated (e.g., Kauppi et al. 1992, Nabuurs et al. 2003). Recently, Magnani et al. (2007) reported a strong correlation between wet N deposition and estimates of net ecosystem production derived from chronosequences and eddy flux towers at 20 temperate forest sites. This correlation implied a very large stimulation of C sequestration with increasing N

deposition of approximately 180 to 480 kg C ha⁻¹ yr⁻¹ per 1 kg ha⁻¹ yr⁻¹ received in N deposition (Magnani et al. 2007). Several researchers have questioned the plausibility of so large an effect (de Vries et al. 2008, Höglberg 2007, Sutton et al. 2008).

In a recent gradient analysis, Thomas et al. (2010) used forest inventory data from plots spanning the northern and eastern forests in the northeastern United States to discern a N deposition-induced tree-growth enhancement in plot-level biomass increment amounting to 5.5 percent per kg N ha⁻¹ yr⁻¹, or 61 kg C ha⁻¹ yr⁻¹ per 1 kg ha⁻¹ yr⁻¹ received in N deposition. Overall, this plot-level growth enhancement did not saturate or decline within the range of wet + dry deposition experienced in the region (3 to 11 kg N ha⁻¹ yr⁻¹). However, different tree species responded in different ways: some species had no response, some showed steady growth increases across the range of N deposition (e.g., yellow-poplar [*Liriodendron tulipifera*], black cherry [*Prunus serotina*], white ash [*Fraxinus americana*]), some showed growth rate peaks at mid-levels of N deposition (quaking aspen, scarlet oak [*Quercus coccinea*]), and one showed growth declines with increasing deposition (red pine). Tree survivorship increased with N deposition for some species (black cherry, red maple) and decreased for others (e.g., quaking and bigtooth aspen [*Populus grandidentata*], yellow birch, basswood [*Tilia* spp.], chestnut oak [*Quercus prinus*], and scarlet oak). Overall, this analysis indicates that current rates of N deposition enhance carbon sequestration in northeastern forests, but that N deposition can have negative impacts on growth and survivorship for some sensitive species.

7.3.2 Nitrate Leaching and Soil N

Conceptual models of N saturation indicate that NO₃⁻ leaching should increase in response to long-term increases in or chronic exposure to atmospheric N deposition (Aber et al. 1998, Stoddard 1994). In fact, long-term NO₃⁻ leaching trends in the northeastern United States have been inconsistent. Some sites have shown increases in NO₃⁻ loss over the last 20 to 30 years, particularly in regions with the highest deposition (10 to 15 kg N ha⁻¹ yr⁻¹) such as the Catskill Mountains, New York (Burns et al. 2006) or Fernow Experimental

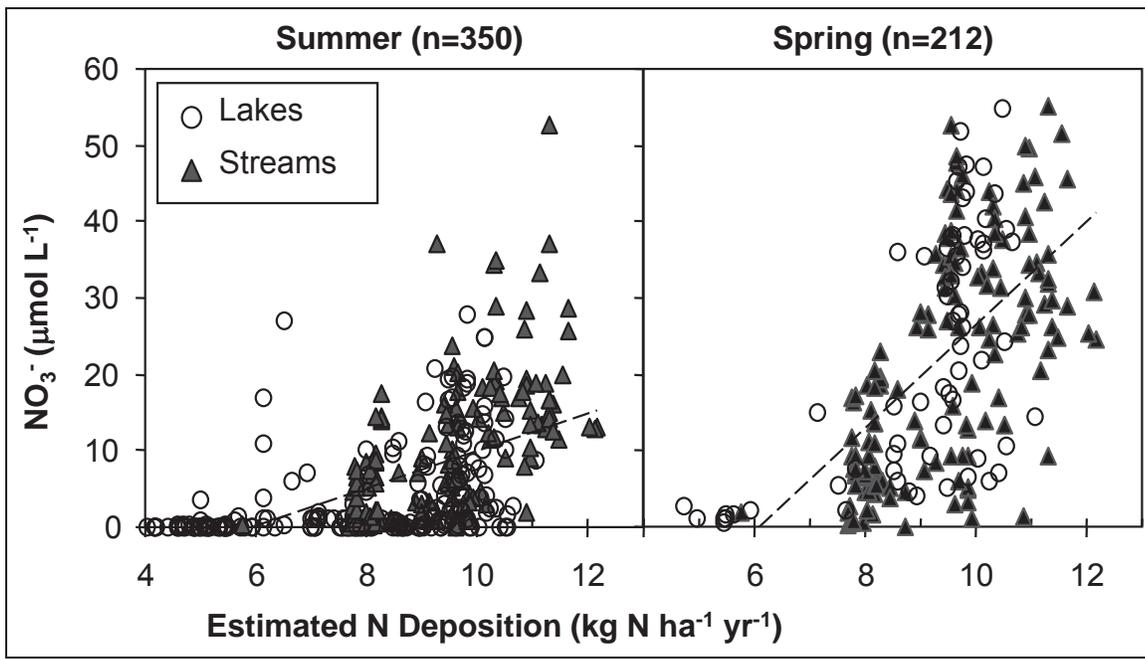


Figure 7.1—Surface water NO_3^- concentrations increase with estimates of N deposition at the base of study watersheds in both summer and spring. N deposition to the entire watershed may be approximately $1 \text{ kg ha}^{-1} \text{ yr}^{-1}$ greater than at the base (From Aber et al. 2003).

Forest, West Virginia (Peterjohn et al. 1996, Adams et al. 2006); however, there is considerable temporal variability within these records. At other sites in the Adirondacks (Driscoll et al. 2003, 2007) and at the Hubbard Brook Experimental Forest (Dittman et al. 2007) and other sites in the White Mountains, New Hampshire (Goodale et al. 2003), surface water NO_3^- concentrations have decreased over the last 20 to 30 years despite near-constant deposition.

The absence of a straightforward relationship between N deposition and surface water NO_3^- leaching over time highlights the value of other approaches for assessing N effects on leaching, such as gradient studies and fertilization experiments. In a synthesis of NO_3^- data across a northeastern N deposition gradient, Aber et al. (2003) report that surface water NO_3^- concentrations in catchments receiving less than $\sim 8 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ rarely exceed $1 \mu\text{mol L}^{-1}$ (Fig. 7.1). Nitrate concentrations increase on average above this threshold, though with substantial site-to-site variation. The wide range of NO_3^- concentrations observed likely reflect the many factors other than N deposition that impact NO_3^- leaching, such as tree species composition, soil and stand characteristics, land-use history, and hydrology. For example, a high abundance of sugar maple has

been associated with elevated nitrification and NO_3^- leaching (Lovett and Rueth 1999, Lovett et al. 2004). Shallow soils at Mt. Ascutney in southern Vermont may be implicated in the site's sensitivity to N inputs and rapid increases in nitrification rates (McNulty and Aber 1993, McNulty et al. 1996, 2005). Old-growth stands have been shown to have higher nitrification rates and NO_3^- leaching than second-growth historically logged or burned stands in the White Mountains of New Hampshire (Goodale and Aber 2001). However, elevated NO_3^- losses at some sites, including the old-growth Bowl Research Natural Area, New Hampshire, may reflect hydrologic flow paths more than biological controls on N saturation (Martin et al. 2000, Pardo et al. 2004). Because so many factors can affect stream NO_3^- losses, determining thresholds for NO_3^- leaching in response to N deposition requires information from a very large number of catchments to discern the leaching signal over variation driven by other factors.

The Aber et al. (2003) N gradient study included a synthesis of soil data from 250 plots in the northeastern United States, yet detected only weak relationships between N deposition and soil N cycling measures (e.g., forest floor C:N, nitrification), due to the great number of additional factors that affect N cycling

beyond just N deposition. Stronger relationships were found between forest floor C:N ratio and nitrification, which presumably should lead to increased N availability for NO_3^- leaching. The study evaluating N cycling in red spruce stands across an N deposition gradient from Maine to New York found significant increases in net nitrification potential with increasing deposition in 1987 (McNulty et al. 1991). When the same sites were evaluated in 1999, the relationship between N deposition and net nitrification potential was still observed, although the rate of nitrification had decreased significantly over time (Boggs et al. 2007). Decreasing patterns in stream water NO_3^- and nitrification rate contradict the expectation that an ecosystem exposed to elevated N deposition over an extended period would move toward N saturation. Instead, these data suggest that the other factors beyond N deposition, such as climate, contribute to the observed patterns of ecosystem N cycling and loss.

7.3.3 Herbaceous Layer

There are few studies of N deposition effects on the herb layer in northern forests. In a low-level fertilization study, Hurd et al. (1998) added N in two forms at varying rates at three sites in the Adirondack Mountains of New York: (1) biweekly as dissolved nitric acid (HNO_3) spray at the rate of $14 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (two times the ambient of $7 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ at the lowest deposition site); and (2) single applications of ammonium sulfate at 14 and $28 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (two and four times ambient). They found that cover of prominent herbaceous species declined significantly after only 3 years of treatment, particularly in response to ammonium sulfate ($(\text{NH}_4)_2\text{SO}_4$). This decline resulted from increased shading by ferns, which can substantially reduce light levels to the forest floor. The response to N additions was more pronounced at sites experiencing lower ambient inputs of atmospheric N.

7.3.4 Mycorrhizal Fungi

Ectomycorrhizal fungi. Lilleskov et al. (2008) found that community structure of ectomycorrhizal fungi changed over a regional N deposition gradient from northeastern New York to Maine. Frequency of the different morphotypes varied continuously with increasing root N, and root N was positively related to

N deposition. Wet deposition at the low N end of this gradient was estimated at approximately $3 \text{ kg N ha}^{-1} \text{ yr}^{-1}$; total N deposition would be approximately $4 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Ollinger et al. 1993). The estimated level of N deposition resulting in community change is 5 to $7 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. This is quite similar to patterns found in white spruce forests in Alaska (Lilleskov et al. 2001, 2002) and pitch pine forests in the Pine Barrens of New Jersey (Dighton et al. 2004).

If elevated soil NO_3^- availability is a good indicator of ectomycorrhizal fungal community change in oligotrophic N-limited conifer forests (Lilleskov et al. 2002, Lilleskov 2005), then N deposition thresholds that minimize excess NO_3^- availability should be sufficient to protect ectomycorrhizal fungal diversity in these forest types.

Arbuscular mycorrhizal fungi. We have less empirical data on arbuscular mycorrhizal community response to N in northern forests. One study in sugar-maple-dominated forests in Michigan has found declines of arbuscular mycorrhizal fungal biomass (van Diepen et al. 2007, 2010) and changes in community structure (van Diepen 2008) in response to N addition of $30 \text{ kg ha}^{-1} \text{ yr}^{-1}$ above background deposition of approximately 5 to $12 \text{ kg ha}^{-1} \text{ yr}^{-1}$ wet deposition, but the lower threshold of response to N is not yet known. There is some indication that arbuscular mycorrhizal biomass has declined and community composition has shifted over the N deposition gradient (van Diepen 2008), suggesting a threshold of $<12 \text{ kg ha}^{-1} \text{ yr}^{-1}$ of wet deposition, but it is likely that there are interactions with within-site factors, and definitive determination of a response threshold awaits further analysis.

7.3.5 Lichens and Bryophytes

Lichen and bryophyte responses documented in the Taiga and Eastern Temperate Forests ecoregions sections can also be expected in the U.S. portion of the Northern Forests ecoregion (see Chapters 6 and 10). Nearly all northern forest lichens belong either to the boreal or to the eastern flora (Brodo et al. 2001). However, air quality in this ecoregion is much more similar to the densely populated Eastern Forests ecoregion than it is to the relatively pristine Taiga ecoregion (see Chapter 3,

Table 7.2—Critical loads of nutrient N for the Northern Forests ecoregion. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Ecosystem component	Critical load for N deposition $kg\ ha^{-1}\ yr^{-1}$	Reliability	Response	Comments	Study
Trees	>3	#	Decreased growth of red pine, and decreased survivorship of yellow birch, scarlet and chestnut oak, quaking aspen, and basswood		Thomas et al. 2010
Lichens	4-6	(#)	Community composition shift	Application of model developed for Marine West Coast Forests to Northern Forests	Geiser et al. 2010
Ectomycorrhizal fungi	5-7	#	Change in fungal community structure		Lilleskov et al. 2008
Herbaceous species cover	>7 and <21	#	Loss of prominent species	Response observed in low-level fertilization experiment	Hurd et al. 1998
Northern Hardwood and Coniferous Forests	8	##	increased surface water nitrate leaching		Aber et al. 2003
Tree growth and mortality	>10 and <26	#	Decreased growth and/or induced mortality	Response observed in low-level fertilization experiment in old-growth montane red spruce	McNulty et al. 2005
Arbuscular mycorrhizal fungi	<12	(#)	biomass decline and community composition change	Observed along a Michigan N gradient	van Diepen 2008

air quality for the Taiga ecoregion). Responses to combined sulfur dioxide (SO_2), acidity, and enhanced N deposition in western Pennsylvania (Showman and Long 1992) and New York (Smiley and George 1974) have included dramatic declines in species diversity and a shifting of community composition favoring acid- and N-tolerant species. Information on lichen research methodology and terminology can be found in Chapter 4 of this report.

7.4 Critical Loads Estimates

Empirical critical loads for both hardwood and coniferous ecosystems within the Northern Forest ecoregion can be set at $8\ kg\ ha^{-1}\ yr^{-1}$ (Table 7.2), the observed threshold for surface water NO_3^- leaching from these forests (Aber et al. 2003). This estimate is very reliable because it is based on 354 data points from

sites around the northeastern United States (Aber et al. 2003). Rather than threshold responses, foliar N concentration and forest growth and survivorship all tend to show gradual responses with variation in N deposition received in the northern United States, with responses that often vary by species. Some sensitive tree species show declines in growth (red pine) or survivorship (yellow birch, scarlet and chestnut oak, quaking aspen, and basswood) as deposition increases across the Northeast from $3\ to\ 11\ kg\ N\ ha^{-1}\ yr^{-1}$ (Thomas et al. 2010); the critical load for negative tree growth response to N deposition is $>3\ kg\ ha^{-1}\ yr^{-1}$. This value is fairly reliable, based on measurements from thousands of trees of each species. Based on the N-addition study in montane spruce-fir systems at Mt. Ascutney, adverse growth and mortality responses are likely to occur at deposition > 10 but $<26\ kg\ N\ ha^{-1}\ yr^{-1}$

(McNulty et al. 2005). Although it only occurred at a single site, this striking and clear response of induced mortality is considered fairly reliable. Similarly, based on an N addition study in the Adirondacks, understory herbaceous composition is likely to be altered at deposition $>7 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ but $< 21 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Hurd et al. 1998). Because this response was observed at a single site, this value is considered fairly reliable. Ectomycorrhizal fungal-based critical loads appear to be about $5 \text{ to } 7 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Lilleskov et al. 2008); the upper end of this range converges with the critical load based on surface water NO_3^- leaching reported above. Arbuscular mycorrhizal fungal critical loads are tentatively set at $<12 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (van Diepen 2008). The value for ectomycorrhizal fungi can be considered fairly reliable, as it is based on the convergence of several studies in this and ecologically similar regions. The value for arbuscular mycorrhizal fungi is considered expert judgment as it is based on one gradient with only four sites.

Application of a model relating epiphytic lichen community composition of Oregon and Washington coniferous forests to N deposition, accounting for precipitation (Chapter 4; Geiser et al. 2010), to the Northern Forests ecoregion yields a critical load estimate of $4 \text{ to } 6 \text{ kg ha}^{-1} \text{ yr}^{-1}$. This value was calculated using a precipitation range of 100 to 240 cm modeled by PRISM for the U.S. portion of northern forests, and a lichen community-composition response threshold that allows as few as 30 percent oligotrophs and no more than 34 percent eutrophs. This is the same threshold that was used for western Oregon and Washington coniferous forests by Geiser et al. (2010). Because it relies on data from other ecoregions, the value for lichens is considered expert judgment.

7.5 Comparison to European Critical Loads

Critical loads for comparable forest ecosystems in Europe are reported to range from $10 \text{ to } 15 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ for boreal and temperate forest, based largely on changes in soil processes and NO_3^- leaching (Bobbink et al. 2003). Critical loads for expected changes in foliar N:P and N:Mg ratios were set at $15 \text{ to } 20 \text{ kg N}$

$\text{ha}^{-1} \text{ yr}^{-1}$; no critical load was set for growth (Bobbink et al. 2003). For herbaceous species in boreal forests, the critical load may be as low as $7 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. For ectomycorrhizal fungi, Bobbink et al. (2003) stated an expert judgment for critical loads of $10 \text{ to } 20 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. For lichens and epiphytic algae, the critical load is likely not higher than $10 \text{ to } 15 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Bobbink et al. 2003).

7.6 Future Research Directions and Gaps in Data

Fundamental gaps in understanding the regulation of N availability in forest ecosystems remain. Hence, simple relationships between inputs and ecosystem outputs and damage have been difficult to determine. Other factors that may be important include climate events (disturbance and variation), prior land use, species composition, site characteristics, and hydrology. Interactions between different stressors add complexity to the input/output relationship. Low-level fertilization induced substantial mortality in a montane spruce-fir ecosystem at Mt. Ascutney (McNulty et al. 2005), but it is not clear to what extent that research can be extrapolated to the rest of the region, especially to lowland forests. Determining whether this site is unique would be useful to understanding the potential consequences of elevated N deposition in the Northern Forest ecoregion.

Far less research exists for herbaceous vegetation than for trees. Future research might include additional low-level fertilizations with an emphasis on examining the responses of herbaceous species, mycorrhizal fungi, bryophytes (especially in bog ecosystems), and lichens. In addition, diversity and community structure could be included in the parameters measured. Better quantification of N deposition at high elevations would also help improve understanding of the susceptibility of the ecosystems and the thresholds when responses occur.

Finally, the results of this analysis may be useful in improving understanding of the value chosen for critical N concentrations or leaching values in the steady-state mass balance method for calculating critical loads.

LITERATURE CITED

- Aber, J.D.; Goodale, C.L.; Ollinger, S.V.; Smith, M.-L.; Magill, A.H.; Martin, M.E.; Hallet, R.A.; 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.; Fernandez, I. 1998. **Nitrogen saturation in temperate forest ecosystems.** *BioScience*. 48(11): 921-934.
- Adams, M.B.; DeWalle, D.R.; Hom, J.L., eds. 2006. **The Fernow watershed acidification study.** Dordrecht, Netherlands: Springer. 279 p.
- Bobbink, R.; Ashmore, M.R.; Braun, S.; Fluckiger, W.; van der Wyngaert, I.J.J. 2003. **Empirical nitrogen critical loads for natural and semi-natural ecosystems: 2002 update.** In: Achermann, B.; Bobbink, R., eds. *Empirical critical loads for nitrogen*. Environmental Documentation 164. Background document for expert workshop on empirical critical loads for nitrogen on semi-natural ecosystems; 2002 November 11-13; Berne, Switzerland: Swiss Agency for the Environment, Forests and Landscape: 143-170.
- Boggs, J.L.; McNulty, S.G.; Pardo, L.H. 2007. **Changes in conifer and deciduous forest foliar and forest floor chemistry and basal area tree growth across a nitrogen (N) deposition gradient in the northeastern US.** *Environmental Pollution*. 149: 303-314.
- Brodo, I.M.; Duran Sharnoff, S.; Sharnoff, S. 2001. **Lichens of North America.** New Haven, CT: Yale University Press. 795 p.
- Burns, D.A.; McHale, M.R.; Driscoll, C.T., Roy, K.M. 2006. **Response of surface water chemistry to reduced levels of acid precipitation: comparison of trends in two regions of New York, USA.** *Hydrological Processes*. 20: 1611-1627.
- Burton A.J.; Pregitzer K.S.; Crawford J.N.; Zogg G.P.; Zak D.R. 2004. **Chronic additions reduce soil respiration in northern hardwood forests.** *Global Change Biology*. 10: 1080-1091.
- Caspersen, J.P.; Pacala, S.W.; Jenkins, J.C.; Hurtt, G.C.; Moorcroft, P.R.; Birdsey, R.A. 2000. **Contributions of land-use history to carbon accumulation in U.S. forests.** *Science*. 290: 1148-1151.
- Commission for Environmental Cooperation (CEC). 1997. **Ecological regions of North America: Toward a common perspective.** Montreal, Canada: Commission for Environmental Cooperation. 71 p. Available at http://www.cec.org/files/pdf/BIODIVERSITY/eco-eng_EN.pdf. (Accessed May 24, 2010).
- de Vries, W.; Solberg, S.; Dobbertin, M.; Sterba, H.; Laubhahn, D.; Reinds, G.J.; Nabuurs, G.J.; Gundersen, P.; Sutton, M.A. 2008. **Ecologically implausible carbon response?** *Nature*. 451 (7180): 1-3.
- Dighton, J.; Tuininga, A.R.; Gray, D.M.; Huskins, R.E.; Belton, T. 2004. **Impacts of atmospheric deposition on New Jersey pine barrens forest soils and communities of ectomycorrhizae.** *Forest Ecology and Management*. 201: 131-144.
- Dittman, J.A.; Driscoll, C.T.; Groffman, P.M.; Fahey, T.M. 2007. **Dynamics of nitrogen and dissolved carbon at the Hubbard Brook Experimental Forest.** *Ecology*. 88: 1153-166.
- Driscoll, C.T.; Driscoll, K.M.; Roy, K.M.; Dukett, J. 2007. **Changes in the chemistry of lakes in the Adirondack region of New York following declines in acidic deposition.** *Applied Geochemistry*. 22: 1181-1188.
- Driscoll, C.T.; Driscoll, K.M.; Roy, K.M.; Mitchell, M.J. 2003. **Chemical response of lakes in the Adirondack region of New York to declines in acidic deposition.** *Environmental Science and Technology*. 37: 2036-2042.

- Elvir, J.A.; Wiersma, G.B.; Day, M.E.; Greenwood, M.S.; Fernandez, I.J. 2006. **Effects of enhanced nitrogen deposition on foliar chemistry and physiological processes of forest trees at the Bear Brook Watershed in Maine.** *Forest Ecology and Management*. 221: 207-214.
- Elvir, J.A.; Wiersma, G.B.; White, A.; Fernandez, I. 2003. **Effects of chronic ammonium sulfate treatment on basal area increment in red spruce and sugar maple at the Bear Brook Watershed in Maine.** *Canadian Journal of Forest Research*. 33: 862-869.
- Emmett, B.A.; Kjonaas, O.J.; Gundersen, P.; Koopmans, C.; Tietema, A.; Sleep, D. 1998. **Natural abundance of ^{15}N in forests across a nitrogen deposition gradient.** *Forest Ecology and Management*. 101: 9-18.
- Fernandez, I.J.; Rustad, L.E.; Norton, S.A.; Kahl, J.S.; Cosby, B.J. 2003. **Experimental acidification causes soil base-cation depletion at the Bear Brook Watershed in Maine.** *Soil Science Society of America Journal*. 67: 1909-1919.
- Geiser, L.H.; Glavich, D.A.; Jovan, S.; Porter, M. 2010. **Lichen-based critical loads for atmospheric nitrogen deposition in Western Oregon and Washington Forests, USA.** *Environmental Pollution*. 158: 2412-2421.
- Goodale, C.L.; Aber, J.D. 2001. **The long-term effects of land-use history on nitrogen cycling in northern hardwood forests.** *Ecological Applications*. 11: 253-267.
- Goodale, C.L.; Aber, J.D.; Vitousek, P.M. 2003. **An unexpected nitrate decline in New Hampshire streams.** *Ecosystems*. 6: 75-86.
- Hicke, J.A.; Asner, G.P.; Randerson, J.T.; Tucker, C.; Los, S.; Birdsey, R.; Jenkins, J.C.; Field, C.; Holland, E. 2002. **Satellite-derived increases in net primary productivity across North America, 1982-1998.** *Geophysical Research Letters*. 29 (10): 10.1029/2001GL013578.
- Högberg, P. 2007. **Nitrogen impact on forest carbon.** *Nature*. 447: 781-782.
- Houle, D.; Moore, J.D. 2008. **Soil solution, foliar concentrations and tree growth response to 3-year of ammonium-nitrate addition in two boreal forests of Québec, Canada.** *Forest Ecology and Management*. 255 (7): 2049-2060.
- Hurd, T.M.; Brach, A.R.; Raynal, D.J. 1998. **Response of understory vegetation of Adirondack forests to nitrogen additions.** *Canadian Journal of Forest Research*. 28: 799-807.
- Jefts, S.; Fernandez, I.J.; Rustad, L.E.; Dail, D.B. 2004. **Decadal responses in soil N dynamics at the Bear Brook Watershed in Maine, USA.** *Forest Ecology and Management*. 189: 189-205.
- Kauppi, P.; Mielikainen, K.; Kuusela, K. 1992. **Biomass and carbon budgets of European forests, 1971-1990.** *Science*. 256: 70-74.
- Lamontagne, S.; Schiff, S.L. 1999. **The response of a heterogeneous upland boreal shield catchment to a short term NO_3^- addition.** *Ecosystems*. 2: 460-473.
- Lilleskov, E.A. 2005. **How do composition, structure, and function of mycorrhizal fungal communities respond to nitrogen deposition and ozone exposure?** In: Dighton, J.; White, J.F.; Oudemans, P., eds. *The fungal community: its organization and role in the ecosystem*. Boca Raton, FL: Taylor and Francis: 769-801.
- Lilleskov, E.A.; Fahey, T.J.; Horton, T.R.; Lovett, G.M. 2002. **Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska.** *Ecology*. 83: 104-115.
- Lilleskov, E.A.; Fahey, T.J.; Lovett, G.M. 2001. **Ectomycorrhizal fungal aboveground community**

- change over an atmospheric nitrogen deposition gradient.** *Ecological Applications*. 11: 397-410.
- Lilleskov, E.A.; Wargo, P.M.; Vogt, K.A.; Vogt, D.J. 2008. **Mycorrhizal fungal community relationship to root nitrogen concentration over a regional atmospheric nitrogen deposition gradient in the northeastern US.** *Canadian Journal of Forest Research*. 38: 1260-1266.
- Lovett, G.M.; Rueth, H. 1999. **Soil nitrogen transformations in beech and maple stands along a nitrogen deposition gradient.** *Ecological Applications*. 9(4): 1330-1344.
- Lovett, G.M.; Weathers, K.C.; Arthur, M.A.; Schultz, J.C. 2004. **Nitrogen cycling in a northern hardwood forest: Do species matter?** *Biogeochemistry*. 67: 289-308.
- Magill, A.H.; Aber, J.D.; Currie, W.S.; Nadelhoffer, K.J.; Martin, M.E.; McDowell, W.H.; Melillo, J.M.; Steudler, P. 2004. **Ecosystem response to 15 years of chronic nitrogen additions at the Harvard Forest LTER, Massachusetts, USA.** *Forest Ecology and Management*. 196: 7-28.
- Magnani F.; Mencuccini, M.; Borghetti, M.; Berbigier, P.; Berninger, F.; Delzon, S.; Grelle, A.; Hari, P.; Jarvis, P.G.; Kolari, P.; Kowalski, A.S.; Lankreijer, H.; Law, B.E.; Lindroth, A.; Loustau, D.; Manca, G.; Moncrieff, J.B.; Rayment, M.; Tedeschi, V.; Valentini, R.; Grace, J. 2007. **The human footprint in the carbon cycle of temperate and boreal forests.** *Nature*. 447: 848-851.
- Martin, C.W.; Driscoll, C.T.; Fahey, T.J. 2000. **Changes in streamwater chemistry after 20 years from forested watersheds in New Hampshire, USA.** *Canadian Journal of Forest Research*. 30: 1206-1213.
- McNeil B.E.; Read, J.M.; Driscoll, C.T. 2007. **Foliar nitrogen responses to elevated nitrogen deposition in nine temperate forest canopy species.** *Environmental Science and Technology*. 41: 5191-5197.
- McNulty, S.G.; Aber, J.D. 1993. **Effects of chronic nitrogen additions on nitrogen cycling in a high-elevation red spruce-fir stand.** *Canadian Journal of Forest Research*. 23: 1252-1263.
- McNulty, S.G.; Aber, J.D.; 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.; Newman, S. D. 1996. **Nitrogen saturation in a high elevation New England red spruce-fir stand.** *Forest Ecology and Management*. 84: 109-121.
- McNulty, S.G.; Boggs, J.; Aber, J.D.; Rustad, L.; Magill, A. 2005. **Red spruce ecosystem level changes following 14 years of chronic N fertilization.** *Forest Ecology and Management*. 219: 279-291.
- Mitchell, M.J.; Driscoll, C.T.; Owen, J.S.; Schaefer, D.; Michener, R.; Raynal, D.J. 2001. **Nitrogen biogeochemistry of three hardwood ecosystems in the Adirondack Region of New York.** *Biogeochemistry*. 56 (2): 93-133.
- Nabuurs, G.-J.; Schelhaas, M.-J.; Mohren, G.M.J.; Field, C.B. 2003. **Temporal evolution of the European forest sector carbon sink from 1950-1999.** *Global Change Biology*. 9: 152-160.
- Nadelhoffer, K.J.; Fry, B. 1994. **Nitrogen isotope studies in forest ecosystems.** In: Lajtha, K.; Michener, R.H., eds. *Stable isotopes in ecology and environmental science*. Cambridge, U.K.: Blackwell Scientific Publishers: 22-44.
- Ollinger, S.V.; Aber, J.D.; Lovett, G.M.; Millham, S.E.; Lathrop, R.G.; Ellis, J.M. 1993. **A spatial model of atmospheric deposition for the northeastern U.S.** *Ecological Applications*. 3: 459-472.
- Pardo, L.H.; Kendall, C.; Pett-Ridge, J.; Chang, C.C.YR. 2004. **Evaluating the source of streamwater nitrate using $\delta^{15}\text{N}$ and $\delta^{18}\text{O}$ in nitrate**

- in two watersheds in New Hampshire, USA.** Hydrological Processes. 18: 2699-2712.
- Pardo, L.H.; McNulty, S.G.; Boggs, J.L.; Duke, S. 2007. **Regional pattern in foliar ^{15}N across a gradient of nitrogen deposition in the northeastern U.S.** Environmental Pollution. 149(3): 293-302.
- Pardo, L.; Templer, P.; Goodale, C.; Duke, S.; Groffman, P.; Adams, M.; Boeckx, P.; Boggs, J.; Campbell, J.; Colman, B.; Compton, J.; Emmett, B.; Gundersen, P.; Kjonaas, J.; Lovett, G.; Mack, M.; Magill, A.; Mbila, M.; Mitchell, M.; McGee, G.; McNulty, S.; Nadelhoffer, K.; Ollinger, S.; Ross, D.; Rueth, H.; Rustad, L.; Schaberg, P.; Schiff, S.; Schleppei, P.; Spoelstra, J.; Wessel, W. 2006. **Regional assessment of N saturation using foliar and root $\delta^{15}\text{N}$.** Biogeochemistry. 80 (2): 143-171.
- Peterjohn, W.T.; Adams, M.B.; Gilliam, F.S. 1996. **Symptoms of nitrogen saturation in two central Appalachian hardwood forest ecosystems.** Biogeochemistry. 35: 507-522.
- Pregitzer, K.S.; Burton, A.J.; King, J.S.; Zak, D.R. 2008. **Soil respiration, root biomass, and root turnover following long-term exposure of northern forests to elevated atmospheric CO_2 and tropospheric O_3 .** New Phytologist. 180 (1): 153-161.
- Pregitzer, K.S.; Zak, D.R.; Burton, A.J.; Ashby, J.A.; MacDonald, N.W. 2004. **Chronic nitrate additions dramatically increase the export of carbon and nitrogen from northern hardwood ecosystems.** Biogeochemistry. 68 (2): 179-197.
- Schaberg, P.G.; DeHayes, D.H.; Hawley, G.J.; Murakami, P.F.; Strimbeck, G.R.; McNulty, S.G. 2002. **Effects of chronic N fertilization on foliar membranes, cold tolerance, and carbon storage in montane red spruce.** Canadian Journal of Forest Research. 32: 1351-1359.
- Showman, R.E.; Long, R.P. 1992. **Lichen studies along a wet sulfate deposition gradient in Pennsylvania.** The Bryologist. 95 (2): 166-170.
- Smiley, D.; George, C.J. 1974. **Photographic documentation of lichen decline in the Shawangunk Mountains of New York.** The Bryologist. 77: 179-187.
- Stoddard, J.L. 1994. **Long-term changes in watershed retention of nitrogen.** In: Baker, L.A., ed. Environmental chemistry of lakes and reservoirs, advances in chemistry series, Vol. 237. Washington, DC: American Chemical Society: 223-284.
- Sutton, M.A.; Simpson, D.; Levy, P.E.; Smith, R.I.; Reis, S.; van Oijen, M.; deVries, W. 2008. **Uncertainties in the relationship between atmospheric nitrogen deposition and forest carbon sequestration.** Global Change Biology. 14: 1-7.
- Thomas, R.Q.; Canham, C.D.; Weathers, K.C.; Goodale, C.L. 2010. **Increased tree carbon storage in response to nitrogen deposition in the US.** Nature Geoscience. 3: 13-17.
- van Diepen, L.T.A. 2008. **The role and diversity of arbuscular mycorrhizal fungi in *Acer saccharum* dominated forest ecosystems under natural and N-amended conditions.** Houghton, MI: Michigan Technological University. 99 p. PhD dissertation.
- van Diepen, L.T.A.; Lilleskov, E.A.; Pregitzer, K.S.; Miller, R.M. 2007. **Decline of arbuscular mycorrhizal fungi in northern hardwood forests exposed to chronic nitrogen additions.** New Phytologist. 176: 175-183.
- van Diepen, L.T.A.; Lilleskov, E.A.; Pregitzer, K.S.; Miller R.M. 2010. **Simulated nitrogen deposition causes a decline of intra- and extraradical abundance of arbuscular mycorrhizal fungi and changes in microbial community structure in northern hardwood forests.** Ecosystems. 13: 683-695.
- Wallace, Z.P.; Lovett, G.M.; Hart, J.E.; Machona, B. 2007. **Effects of nitrogen saturation on tree growth and death in a mixed-oak forest.** Forest Ecology and Management. 243: 210-218.

Wallenstein, M.D.; McNulty, S.; Fernandez, I.J.; Boggs, J.; Schlesinger, W.H. 2006. **Nitrogen fertilization decreases forest soil fungal and bacterial biomass in three long-term experiments.** *Forest Ecology and Management*. 222(1-3): 459-468.

Zak, D.R.; Holmes, W.E.; Tomlinson, M.J.; Pregitzer, K.S.; Burton, A.J. 2006. **Microbial cycling of C and**

N in northern hardwood forests receiving chronic atmospheric NO_3^- . *Ecosystems*. 9(2): 242-253.

Zak, D.R.; Pregitzer, K.S.; Holmes, W.E.; Burton, A.J.; Zogg, G.P. 2004. **Anthropogenic N deposition and the fate of $^{15}\text{NO}_3^-$ in a northern hardwood ecosystem.** *Biogeochemistry*. 69(2): 143-157.