

FOREST BIOGEOCHEMISTRY AND PRIMARY PRODUCTION ALTERED BY NITROGEN SATURATION

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Abstract Results from four intensive site-level manipulations and one extensive field survey in northern temperate and boreal forests show a consistent set of responses to chronic N additions. These include 1) initial and often large increase in net N mineralization followed by **decreases**, 2) increases in net **nitrification**, 3) increases in N **concentration** in foliage, and 4) decreased Mg:N and **Ca:Al** ratios, and declining tree growth and vigor in all evergreen stands. These results are synthesized into a set of proposed summary relationships that define the temporal pattern of responses of **N-limited** systems to N additions.

Keywords: **NPP**, **N Leaching**, **Element Ratios**, **Nitrification**, **Mineralization**

1. Introduction

Continuing concerns over the potential **effects** of **long-term**, chronic nitrogen deposition to sensitive forest ecosystems has led to the initiation of several field experiments examining the interactions between N deposition and forest ecosystem function (e.g. Wright and van **Breeman**, 1995; **Kahl et al.**, 1993; **Magill et al.**, 1995a,b). Results confirm **that**, in those systems where increased additions lead to increased nitrate mobility, this will be accompanied by losses of nutrient cations and increases in soil and water acidity (e.g. **Emmett et al.**, 1995; **Boxman et al.**, 1995; **Kahl et al.**, 1993; **McNulty and Aber**, 1993a). Data have also been presented suggesting that excess N availability can lead to nutrient **imbalances** in trees, expressed as root or foliar element ratios, especially **Ca:Al** and Mg:N. Such imbalances have been linked to reductions in net photosynthesis, **photosynthetic** N use **efficiency**, forest **growth**, and even to tree mortality (**Schulze**, 1989; **Shortle and Smith**, 1988; **Richter et al.**, 1992; **Friedland et al.**, 1988; **McNulty and Aber**, 1993; **Cronan and Grigal**, 1995).

These responses have been embedded within the concept of nitrogen **saturation**, a term which can be defined in several ways (e.g. **Stoddard**, 1994; **Aber et al.**, 1989, 1992; **Agren and Bosatta**, 1988), but can be considered most generally as a temporal series of changes in ecosystem function in response to the alleviation of N limitations on **plant**, **microbial**, and perhaps abiotic soil processes.

A series of hypotheses regarding nitrogen saturation (**Aber et al.**, 1989) were used to frame a set of intensive, plot-level and extensive, regional-level experiments (**McNulty et al.**, 1990, 1991, 1995; **McNulty and Aber**, 1993; **Aber et al.**, 1993; **Magill et al.**, 1995a,b) which are parallel **with**, and complementary to, the **NITREX** experiments in Europe (e.g. Wright and van **Breeman**, 1995; **Emmett et al.**, 1995, **Boxman et al.**, 1995; Wright and **Tietema**, 1995; **Gundersen and Rasmussen**, 1995). The purpose of this paper is to synthesize the results of the first 7 years of results from these experiments.

2. Methods

2.1. Study Sites

Four study **site/stand** combinations were **selected** for intensive experimental manipulation and measurement (Table I). Two of these stands are at the Harvard Forest and are part of the U.S. National Science Foundation's **Long-Term Ecological Research (LTER)** program (**Aber et al.**, 1993). The Bear Brook external, intensive study plots were manipulated as part of the U.S. Environmental Protection **Agency's** Watershed Manipulation Project (**Kahl et al.**, 1993; **Rustad et al.**, 1993). The Mt. **Ascutney** site was selected as a mature, healthy spruce-fir system to complement a series of 161 stands in 11 sites across New England which were sampled for easily-measured indicators of change in **biogeochemical** cycling (**McNulty et al.**, 1990, 1991).

2.2. Treatments

N amendments differed between **study** sites (Table I). Duration of treatments has varied from 4 to 7 years. Applications are continuing at the Harvard Forest and Mt. Ascutney. The transect sites were located along a **naturally-occurring** N deposition gradient.

2.3. Sample Collection and Analysis

Measurements made at all sites included: Dnet annual nitrogen mineralization

Table 1. Study Sites used in the **nitrogen** saturation experiments summarized in this paper.

Location	Forest Type	Treatments	Duration	References
Harvard Forest Petersham, MA 42°30'N, 72°10'W	Oak-Maple (natural)	Control, +50, +150 kg N/ha yr NH ₄ NO ₃	1988-	Aber <i>et al.</i> , 1993 Magill <i>et al.</i> , 1995a
Harvard Forest Petersham, MA 42° 30'N, 72°10'W	Red Pine (plantation)	Control, +50, +150 kg N/ha yr NH ₄ NO ₃	1988-	Aber <i>et al.</i> , 1993 Magill <i>et al.</i> , 1995a
Bear Brook Beddington, ME 44°52'N, 68°06'W	Beech-Maple (natural)	Control, +28, +56 kg N/ha yr HNO ₃	1988-1991	Nadelhoffer <i>et al.</i> , 1995 Magill <i>et al.</i> , 1995b Rustad <i>et al.</i> , 1993
Mt Ascutney Ascutney, VT 43°26'N, 72°27'W	Spruce-Fir (natural)	Control, +15.7, +19.8, 25.6, 31.4 kg N/ha yr NH ₄ , NO ₃ mixtures	1988-	McNulty and Aber, 1993
New York-Maine Transect	Spruce-Fir	Ambient N depo- sition gradient		McNulty <i>et al.</i> , 1990, 1991

and nitrification (Pastor *et al.*, 1984; Nadelhoffer *et al.*, 1983; McNulty *et al.*, 1990), 2) foliar N concentration and N:Mg and Ca:Al ratios, 3) Wood and foliar NPP or basal area **increment** (except on spruce-fir transect). N leaching losses were measured at the Harvard Forest and Bear Brook sites with tension **lysimeters** placed below the rooting zone. As this was not possible in the shallow, stony soil at Mt. **Ascutney**, resin bags were used to assess relative rates of cation and **anion** movement below the rooting zone. Foliar N, Mg, **Ca** and **Al** concentrations were measured on samples collected in mid-summer from all sites (see references in Table I for more detailed descriptions).

3. Results and Discussion

Several measured responses to chronic N additions are consistent across all sites and studies (Table II). For brevity, we present here only the differences between control and high N amended plots for the final year of the **treatment**, with the exception of the transect data for which the highest and lowest N deposition sites are presented. Results are discussed in terms of a restatement of the initial hypotheses (Figure 1, *cf.* **Aber et al.**, 1989).

All studies showed initial and often large increases in net N mineralization. **We** attribute this to rapid initial **immobilization/sorption** of added N followed by

Table 2. Comparison of **results** from five stand **type/treatment** combinations. See **Table 1** for description of sites. See **text** for comparison of methods used at **different sites**. All data are for the last year of treatment and for control and highest N **additions**, except for the transect data which are from the highest and lowest N deposition **sites**. Foliar data are for the dominant species on each site.

Site Treatment	Foliar			Soil Nitrogen			Plant NPP	
	N %	Mg:N	Ca:Al	Mineral. ¹ kg N ha ⁻¹ yr ⁻¹	Nitrif. %	Leach. %	Wood kg ha ⁻¹ yr ⁻¹	Total kg ha ⁻¹ yr ⁻¹
Harvard Forest - Red Oak								
Control	2.20	.16	115	80	<1	0	4476	7348
HighN	2.75	.11	60	195	8	0	6479	9731
Harvard Forest - Red Pine								
Control	1.05	.20	20	81	17	<1	3338	6498
HighN	1.70	.12	25	98(1.5)	48	25?	2017	6099
Bear Brook - American Beech								
Control	1.98	.082	307	75	3	<1	6007	10003
HighN	2.25	.072	199	59 (1.3)	16	5?	6822	11309
ML Ascutney - Red Spruce				mg N kg ⁻¹			Bas. Area (m ² ha ⁻¹ yr ⁻¹)	
Control	0.85	.068	103	50	0	low	+ 0.7	
High N	1.47	.037	82	39 (4.0)	0.7	high	- 0.8	
Transect - Red Spruce							% Mortality	
East (Acadia)	0.84	.13	78	24	.02	-	Low	
WesKWhiteface)	1.07	.075	31	21 (2.0)	2.5	-	High	

* Values in parentheses show the maximal fractional increase in measured N mineralization rate during the period of N amendments (expressed as rates in high N **plots/control**), or highest rate along transect relative to **Acadia**.

reminerzalization/desorption during the incubation period in the buried bag. Field measurements showing **no** detectable increase in soil **CO₂ efflux** during periods of very rapid **NH₄** and **NO₃** disappearance from soil solutions (Micks, 1994) suggest the potential importance of either abiotic **sorption/desorption** reactions or rapid microbial assimilation in the absence of biomass production (Micks, 1994). Short-term increases in N mineralization ranged from 1.3 to 4.0 times control values (Table II). Longer term responses in 3 of the 4 intensive study sites show actual decreases in net N mineralization from early peak rates (cf. Baath *et al.*, 1981; Soderstrom *et al.*, 1983) supporting the theory that increased incorporation of N into soil organic matter increases the randomization of bond structure in humus and actually decreases **decomposability** (e.g. Berg, 1986). Only the Harvard Forest oak-maple site, which was the most **N-limited** initially, failed to show increased nitrification and N leaching. Both the Mt. Ascutney and transect data yield a linear and highly significant relationship **between** soil C:N ratio and the fraction of mineralized N nitrified (McNulty *et al.*, 1995). A similar relationship is apparent in data summarized from the **NITREX** sites (Tietema and Beier, 1995).

All sites showed increases in foliar N concentration, with the largest proportional changes in the Harvard Forest pine and Mt. Ascutney stands. Not surprisingly, this was accompanied by decreasing Mg:N ratios in all sites. Decreases in foliar **Ca:Al** ratios also occur in all but one site, most likely resulting from increased **anion** mobility, leading to increased cation leaching losses **and** increased soil acidification. These **results** are also **consistent** with those from the **NITREX** experiments (Dise and Wright, 1995). As forest decline has occasionally been linked to **Ca:Al** imbalances (e.g. Shortle and Smith, 1988), the finding that this condition can be induced by excess N availability alone may provide a unifying principle in forest decline research.

Finally, both evergreen stands (Harvard Forest pine and Mt. Ascutney) and the transect sites show declining tree growth or increased tree mortality with increasing N additions. Increased mortality at Mt. Ascutney is significantly and positively correlated with both N addition rate and foliar **Ca:Al** ratio (McNulty *et al.*, 1995).

We have combined these results into a set of proposed summary relationships that define the response of temperate zone forests to accumulated N deposition (Figure 1). The different positions of the letters representing each site suggest where along this sequence each of the study sites was at the beginning of the treatment (or before significant N deposition occurred for the transect sites). The arrows suggest how far each site has moved toward saturation and possible decline. The stages are taken from Smith (1974) and Bormann (1982) as summarized in our previous paper (Aber *et al.*, 1989). The first stage is **pre-treatment** and assumes strong nitrogen limitations on **growth**. **HFP** and **BBW** stands were relatively **N-rich** before treatments **began**, as indicated by the occurrence of net nitrification (and nitrate leaching at **BBW**). We hypothesize that the initial nitrogen status of each site is the result of previous land use histories.

Variation in the responses of different stands to N additions suggests some important questions which still need to be **answered**. **First**, the different stands did not all move to saturation during **treatment**. **HFHW**, which was the most N limited initially,

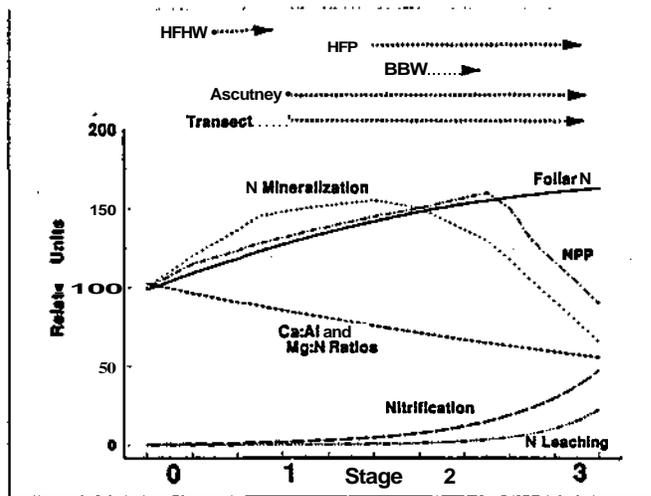


Fig. 1. Schematic summary of changes in nitrogen cycling and forest production with **long-term** chronic N additions for temperate forest ecosystems. Letters represent the initial position of each study site along this synthetic N saturation gradient HFHW and HFP are Harvard Forest hardwood and pine stands respectively. BBW is Bear Brook stand. Ascutey is Mt Ascutey site and TRANSECT is for the set of 161 native spruce-fir stands sampled across the northeastern U.S.

has **absorbed** over 900 kg N/ha without the initiation of significant nitrification or nitrate **leaching**. However, the very high N mineralization rate measured in year 6, **much** higher than the N assimilation potential of the **vegetation**, suggests that **nitrification may** begin **soon**. Despite the presence of some nitrification and N leaching in **control stands**, the BBW **deciduous** forest also exhibited fairly high rates of N **retention** (Magill *et al.*, 1995b). **Does this** suggest that greater cumulative inputs of N are required to induce N saturation in deciduous forests? Does the lack of any reduction in growth rates in deciduous stands mean that N saturation **does not** pose a problem for forest health in these forest types, or only that higher N **retention** rates will allow a delay in the onset of decline?

In **contrast**, all conifer sites and stands show large changes in nitrification and N leaching, and indications of reduced growth or increased mortality. This is especially pronounced in the spruce-fir stands at Mt Ascutey, where relatively small additions of N have resulted in large reductions in **biomass** accumulation. Does this suggest that long-term N deposition has played a significant role in causing spruce decline across **the** northeastern U.S.?

The greatest remaining challenge **in** the study of N saturation of forests is to understand the mechanisms by which large amounts of N are incorporated into **forest** soils, and to develop a method for **predicting** N retention capacity. Rapid incorporation of NH_4 and NO_3 with no parallel increase in CO_2 efflux suggests that traditional **microbial immobilization** through biomass production is not the dominant process **involved**. Are these processes then strictly abiotic, or do they represent microbial assimilation in the absence of biomass production? If microbial assimilation is **involved**, how is the assimilated N **transferred** to the stable soil humus pool? For predicting the

future **state** of N saturation in forests and the associated changes in tree growth and water quality, we need to increase our quantitative understanding of the kinetics and capacity of these reactions.

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