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Nitrogen availability and forest productivity along a climosequence on Whiteface Mountain, New York

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Abstract

We studied broadleaf and needle-leaf forests along an elevation gradient (600–1200 m) at Whiteface Mountain, New York, to determine relationships among temperature, mineral N availability, and aboveground net primary productivity (ANPP) and controls on the latter two variables. We measured net N mineralization during the growing season, annual litterfall quantity and quality, aboveground woody biomass accumulation, and soil organic matter quality. Inorganic N deposition from cloudwater markedly increases mineral N availability above 1000 m in this region. Consequently, mineral N availability across the climosequence remains relatively constant because N mineralization decreases with increasing elevation. Across this climosequence, air temperature (as growing season degree-days) exerted the most control on ANPP. Nitrogen mineralization was most strongly related to soil growing season degree-days and less so to lignin to N ratios in litter. ANPP was correlated with N mineralization but not with mineral N availability. Combining our data with those from similar studies in other boreal and cool temperate forests shows that N mineralization and ANPP are correlated at local, regional, and interbiome scales. Regarding the persistent question concerning cause and effect in the N mineralization – forest productivity relationship, our data provide evidence that at least in this case, forest productivity is a control on N mineralization.

Comments

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Abstract: We studied broadleaf and needle-leaf forests along an elevation gradient (600–1200 m) at Whiteface Mountain, New York, to determine relationships among temperature, mineral N availability, and aboveground net primary productivity (ANPP) and controls on the latter two variables. We measured net N mineralization during the growing season, annual litterfall quantity and quality, aboveground woody biomass accumulation, and soil organic matter quality. Inorganic N deposition from cloudwater markedly increases mineral N availability above 1000 m in this region. Consequently, mineral N availability across the climosequence remains relatively constant because N mineralization decreases with increasing elevation. Across this climosequence, air temperature (as growing season degree-days) exerted the most control on ANPP. Nitrogen mineralization was most strongly related to soil growing season degree-days and less so to lignin to N ratios in litter. ANPP was correlated with N mineralization but not with mineral N availability. Combining our data with those from similar studies in other boreal and cool temperate forests shows that N mineralization and ANPP are correlated at local, regional, and interbiome scales. Regarding the persistent question concerning cause and effect in the N mineralization – forest productivity relationship, our data provide evidence that at least in this case, forest productivity is a control on N mineralization.

Résumé : Nous avons étudié des forêts de feuillus et de résineux le long d'un gradient altitudinal (600–1200 m) à Whiteface Mountain dans l'État de New York pour déterminer les relations entre la température, la disponibilité en azote minéral, la productivité primaire nette aérienne (PPNA) et les facteurs contrôlant ces deux dernières variables. Nous avons mesuré la minéralisation nette de l'azote pendant la saison de croissance, la quantité annuelle de litière et sa qualité, le cumul de biomasse ligneuse aérienne et la qualité de matière organique du sol. Dans cette région, les dépôts d'azote inorganique provenant de l'eau des nuages augmentent de façon marquée la disponibilité en azote minéral au-dessus de 1000 m. De cette façon, la disponibilité en azote minéral dans la climoséquence reste relativement constante parce que la minéralisation de l'azote diminue avec l'altitude. Le long de cette climoséquence, la température de l'air (exprimée en degrés-jours pendant la saison de croissance) exerce le contrôle le plus important sur la PPNA. La minéralisation de l'azote est la plus fortement reliée aux degrés-jours dans le sol pendant la saison de croissance et moins au rapport lignine:azote dans la litière. La PPNA est corrélée avec la minéralisation de l'azote mais pas avec la disponibilité en azote minéral. La combinaison de nos données avec celles d'autres études semblables effectuées dans d'autres forêts boréales et tempérées froides montre que la minéralisation de l'azote et la PPNA sont corrélées aux échelles locales, régionale et entre les biomes. A propos de la question persistante concernant les liens de cause à effet entre la minéralisation de l'azote et la productivité forestière, nos données fournissent la preuve qu'au moins dans le cas présent la productivité forestière exerce un contrôle sur la minéralisation de l'azote.

[Traduit par la Rédaction]

Introduction

Over the last several decades, nutrient cycling studies have identified N as the nutrient most likely limiting aboveground net primary productivity (ANPP) in temperate forests (e.g., Mitchell and Chandler 1939; Vitousek et al. 1982;

Vitousek and Howarth 1991; Melillo et al. 1993; Reich et al. 1997). At a regional scale, several studies have shown a strong positive relationship between N mineralization and productivity (Pastor et al. 1984; Nadelhoffer et al. 1985; Zak et al. 1989; Reich et al. 1997). Other studies have identified climatic and soil moisture characteristics as good predictors of both N mineralization and forest productivity (Post and Curtis 1970; Pastor and Post 1986; Grigal and Homann 1994).

During the past two decades, many authors researching the relationship between N cycling and forest productivity in cool temperate forests have emphasized the importance of mineral N availability in controlling forest productivity. This represents a departure from the way many forest scientists viewed controls on site quality previously. Consider the contrasting views represented by the results of the following

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two regional-scale studies of cool temperate forests done across similar gradients of climate and soil characteristics.

Reich et al. (1997) compiled N mineralization and productivity data for 50 broadleaf and needle-leaf stands in Wisconsin and Minnesota. They found a highly significant correlation between net N mineralization and ANPP. Their N mineralization based model yielded an R^2 value of 0.54, and they concluded that N mineralization was probably an important control on ANPP, accounting for more than half of the variance in their regional-scale data. In their study, N mineralization was related to total litterfall, mean annual temperature, and soil texture.

Post and Curtis (1970) examined the relationship between site index (a height- and age-based measure of productivity) and soil-based variables and climate variables at 78 northern hardwood stands growing on a wide variety of soils from southern to northern Vermont. Their climate-based model related site index to variables reflecting temperature (latitude, elevation, and aspect) and soil moisture (soil depth and drainage class) without significant independent contributions from soil nutrients ($R^2 = 0.62$).

The correlations among temperature, moisture, community types, and N mineralization confound the interpretation of cause and effect and hinder the determination of proximal controls on ANPP (Pastor et al. 1984; Reich et al. 1997; Scott and Binkley 1997). A significant, direct relation between temperature and N mineralization has been observed in some, but not all, studies (Powers 1990; Boone 1992; Kim et al. 1995; Stottleyer et al. 1995; Sveinbjornsson et al. 1995; Reich et al. 1997). Other studies have found a significant relationship between soil silt plus clay content (a surrogate for soil moisture holding capacity) and N mineralization (Pastor et al. 1984; Stottleyer et al. 1995; Reich et al. 1997). Community types, often controlled by temperature and soil moisture conditions, contribute to differences in N mineralization through their influence on lignin to N ratios of litter (Scott and Binkley 1997).

It is difficult to choose between two interpretations of the empirical ANPP data collected in cool temperate North American forests: (i) temperature and (or) moisture availability could independently control both ANPP and N mineralization without N mineralization controlling ANPP or (ii) temperature and moisture may control N mineralization, which in turn is the primary control on ANPP. While these two possibilities are widely acknowledged, the current paradigms favor mineral N as the proximal control on ANPP.

We initiated this study on Whiteface Mountain, New York, because prior research at this site led us to expect that we could separate the effects of temperature and mineral N availability on productivity. On a global scale, Whiteface Mt. receives very high levels of anthropogenic mineral N input via the atmosphere (Lovett 1992; Miller et al. 1993; Friedland and Miller 1999). In the forests of the region, differences in mineral N availability are controlled by both N mineralization and N input from the atmosphere. Previous research in these forests suggested that a decrease in N mineralization with increasing elevation would be mostly offset by increased N deposition in clouds and rainfall.

We sought to examine potential controls on N mineralization, determining the degree to which stand-level ANPP was related to growing season length and temperature and assess-

ing whether mineral N availability explained a significant fraction of the variance in ANPP with or without accounting for the effects of growing season temperatures.

Site description

Whiteface Mountain (summit elevation 1483 m) is located in Essex County near the town of Wilmington, New York; it lies in the northeast section of the Adirondack Mountains within the boundaries of the Adirondack Park and its 2.5 million acre Forest Preserve (Adirondack Park Agency, Ray Brook, N.Y.). With the exception of the lowest elevation site (600 m), which burned in 1908, the study area has not been disturbed by fire or logging in recent history (the past 115 years) (Lindberg et al. 1992). All of the stands that we sampled are considered mature forest (Battles et al. 1992).

Regional transport of pollutants to Whiteface Mountain is predominantly from the west and south (Husain and Dutkiewicz 1990). Atmospheric N deposition at Whiteface Mountain varies with elevation, ranging from 15 to 30 kg·ha⁻¹·year⁻¹, depending largely on rainfall and cloud-water interception rates (Friedland et al. 1991; Lovett 1992; Miller et al. 1993). Nitrogen deposited from the atmosphere between 1986 and 1995 exceeded N accumulated in biomass by sixfold, and midelevation forests on Whiteface Mountain monitored since 1986 leak mineral N at rates up to 6.2 kg·ha⁻¹·year⁻¹ (Friedland and Miller 1999). Estimates of N mineralization in Whiteface Mountain forests range from 40 to >100 kg·ha⁻¹·year⁻¹ (Sasser and Binkley 1989; Friedland et al. 1991). Accordingly, we did not expect mineral N availability to limit ANPP.

Average annual precipitation at the mountain base is 98 cm, increasing at higher elevations to >130 cm, at least 30% of which falls as snow. Mean annual temperature ranges from 5 °C at the base to <2 °C at the summit; persistent cloud cover above 1000 m adds significantly to the moisture and mineral N supply (Witty 1968; Friedland et al. 1991; Friedland and Miller 1999). Mean summer temperature ranges from approximately 16 °C at the base to 12 °C at the summit (E.K. Miller, unpublished data). Airflow at the study area is dominated by westerly and northwesterly upslope winds (Lindberg et al. 1992). The growing season spans May through early September (Miller et al. 1993).

The bedrock of the study area is primarily Precambrian anorthosite (the northeastern portion of the Adirondack Anorthosite Massif; Bird 1963). Soils are differentiated by temperature and organic matter content as Typic Cryohumods, Typic Cryorthods, or Typic Haplorthods (Table 1; Witty 1968). The average depth to bedrock varies from >1 m in areas of well-developed spodosols to places where organic mats with little or no mineral soil development overlie anorthosite boulders (Witty 1968; Lindberg et al. 1992). Deeper soils are normally found at lower elevations. Soils are fine textured and soil organic matter is abundant. Given the low evapotranspiration demand and abundant rainfall, moisture is unlikely to be limiting in most years.

Methods

From May 1998 to May 1999, across this climosequence (with elevation providing the change in climate), we measured net N mineralization during the growing season, an-

Table 1. Study site characteristics (soil type data from Witty 1968; air temperature data from IFS towers), Whiteface Mountain, N.Y.

Elevation (m)	Location	Soil type, average depth of soil (cm)	Dominant vegetation	Basal area (m ² ·ha ⁻¹) (SE)	Biomass (Mg·ha ⁻¹) (SE)	Average tree age (years)	Air GSDD	Soil GSDD	Average (max./min.) summer temperatures (°C)
600	44°23'N, 73°54'W	Typic Haplorrhods, 15.6	Northern hardwood forest: mountain paper birch (<i>Betula papyrifera</i> var. <i>cordifolia</i> (Regel)), striped maple (<i>Acer pennsylvanicum</i> L.), sugar maple (<i>Acer saccharinum</i> Marsh. var. <i>saccharum</i>), and American beech (<i>Fagus grandifolia</i> Ehrh.)	33.3 (4.1)	230.6 (39.5)	78.8	2168	1781	16.20 (18/15)
800	44°23'N, 73°54'W	Typic Haplorrhods, 22.1	Northern hardwood forest (as at the 600-m site) as well as balsam fir (<i>Abies balsamea</i> (L.) and red spruce (<i>Picea rubens</i> Sarg.))	34.8 (5.1)	254.7 (29.5)	65.4	2079	1552	15.75 (14/17)
1000	44°23'N, 73°54'W	Typic Cryohumods, 11.6	Northern Hardwood Forest (as at the 600-m site) as well as balsam fir and red spruce	38.7 (2.5)	189.3 (53.0)	66.9	1962	1355	14.46 (12/16)
1200	44°23'N, 73°54'W	Typic Cryohumods, 7.7	Conifer forest: balsam fir and red spruce	51.8 (5.9)	128.7 (4.8)	41.9	1634	1262	11.95 (10/14)
1200 EL	44°23'N, 73°54'W	Typic Cryohumods, 10.1	Conifer forest: small, wind-exposed balsam fir	33.1 (1.1)	110.3 (4.0)	65.7	1634	1357	11.95 (10/14)

Note: Study sites were named for their elevation; at 1200-m elevation, two sites were set up, one of which was exposure limited (EL). GSDD, growing season degree-days.

nual litterfall quantity, litter and soil organic matter quality (C, N, and lignin), ambient air temperature, soil temperature, soil moisture, and bole diameter increment.

The study area is located on a north-south transect along the flank of Esther Mountain (at 44°23'N, 73°54'W; summit elevation 1292 m), the northeastern peak of the Whiteface massif. In June 1997, five study sites were established at four elevations (see Table 1) along this transect. Two sites were used at the highest elevation to better represent the range of environments at the upper elevations caused by an increase in exposure. One site was a sheltered stand with a closed canopy; the other site was judged to be exposure limited (EL), where exposure to winter wind was expected to be the main force controlling growth form and productivity through needle loss (Sprugel and Bormann 1981). At each study site, four 100-m² square plots were constructed, and all sampling took place within or immediately adjacent to these 20 plots. Northern hardwood forest dominates the 600-m site. The 800- and 1000-m sites are characterized by hardwood-fir-spruce transition forests; two of the four plots at the 1000-m site were established within broadleaf-dominated vegetation, and the other two plots were established within conifer-dominated vegetation. At one of the 1200-m sites, fir-spruce vegetation dominated. The 1200-m EL site consisted of small balsam fir (*Abies balsamea* (L.)) trees with wind-pruned branches on the windward side (these characters are summarized in Table 1).

At each plot, plant species and soil characteristics were determined in the summer of 1997 (see Joshi 2001). All plants were identified; diameter at breast height (1.4 m) was measured for all live and dead-standing individuals >1.4 m in height. Height was measured for the five to seven tallest and (or) largest diameter trees in the plot. Soil bulk density (grams per cubic centimetre) was calculated using a square corer to remove soil from two quantitative 10 cm × 10 cm × 10 cm soil pits located adjacent to opposite corners of each plot. Depth of the quantitative soil pit was measured in five different locations so as to increase the accuracy of the sample volume determination. The soil was air-dried to constant mass, passed through a 2-mm mesh sieve, weighed, and bulk density calculated.

Environmental variables

At each of the five sites, two electronic data loggers recorded soil temperature hourly and soil moisture at noon and midnight; these were measured at 5 cm depth. Above-canopy air temperatures were derived from sampling towers at elevations of 720, 1150, 1250, and 1350 m. Air temperatures were recorded hourly.

To examine the effects of climate on productivity and N mineralization, mean daily air temperature and growing season length were combined at each site into one index value, growing season degree-days (GSDD), calculated as the mean daily temperature multiplied by the number of days with a mean temperature >0 °C (O'Neill and DeAngelis 1981). Due to the high specific heat of wet versus dry soil, differences in soil moisture content and drainage class may result in situations where air and soil temperatures are not well correlated. Consequently, we calculated soil GSDD as a potentially better predictor of soil-based processes, particularly N mineralization.

Productivity

To determine plot age and estimate wood production, the five to seven tallest and (or) largest diameter trees in each plot were sampled through the center with a 4.5-mm increment borer. Plot age was estimated based on the ring count from these cores. Smaller cores (approximately 3 cm long) were collected from a minimum of 10 and a maximum of all small canopy and (or) subcanopy trees. Using all cores, the widths of the youngest 10 rings were measured and used with allometric equations (Whittaker et al. 1974; Tritton and Hornbeck 1982) to estimate annual woody biomass increment. To estimate litterfall, four 1385-cm² litter traps were randomly located in each plot. Traps were emptied monthly during the summer and fall (June–November 1998) and once at the end of winter (May 1999); these samples were combined into one litterfall sample per plot per collection period and oven-dried at 80 °C to constant mass. ANPP was estimated as the biomass represented by 1 year’s wood and litter production.

Mineral N availability

Mineral N availability at Whiteface Mountain consists of atmospheric inorganic N input and net N mineralization. Atmospheric N input to the area of our midelevation plots (1000 m) was measured and modeled by Friedland et al. (1991) and Lovett (1992), and atmospheric N input along the elevational gradient that encompassed the plots was modeled by Miller et al. (1993). We estimated atmospheric N input for this study using the average of the results published by these authors. These results are shown in Table 2; the highest elevation experiences about four times more N input than the lowest.

Net N mineralization was monitored just before and during the length of the 1998 growing season as determined by bud-break and the onset of autumn senescence (May–September). Net N mineralization in the top 10 cm of soil (this typically included the O horizon and a portion of the A horizon) at each site was estimated using the in situ resin core method (after DiStefano and Gholz 1986). Atmospheric N input to the cores was minimized from June through September by covering the cores with ion-exchange resin bags to trap incoming NH₄ and NO₃ in the precipitation, preventing the ions from entering the incubating soils. Ion-exchange resin bags were also placed at the bottom of all of the cores to retain leached NH₄ and NO₃.

Ion-exchange resin bags were prepared by sealing approximately 14 mL of strongly acidic cation-exchange or strongly basic anion-exchange resins (Dowex 50WX and Dowex 1X, respectively) between two small (36 cm²) square pieces of polyester fusible interfacing fabric that had been rinsed multiple times with deionized water. The edges of the square were then trimmed to create a circular ion-exchange resin bag 5 cm in diameter. The anion-exchange (with about 18 mmol ion charge (mmol_c) per bag) and cation-exchange (28 mmol_c per bag) resin bags were stacked together at the top and bottom of the cores.

Several techniques have been used to measure net N mineralization in the field. Each method has its own limitations and there is no consensus on a “best” method (Powers 1990; Binkley et al. 1992; Zou et al. 1992; Subler et al. 1995; Jensen et al. 1996). In light of the inherent difficulty in mea-

Table 2. Productivity and N flux data (mean (SE)) for five study sites at Whiteface Mountain.

Elevation (m)	ANPP (Mg·ha ⁻¹ ·year ⁻¹)	Woody growth (Mg·ha ⁻¹ ·year ⁻¹)	Litterfall quantity (Mg·ha ⁻¹ ·year ⁻¹)	Mineral N availability (kg·ha ⁻¹ ·year ⁻¹)	Atmospheric N input (kg·ha ⁻¹ ·year ⁻¹)	Net N mineralized (kg·ha ⁻¹ ·year ⁻¹)	Net NO ₃ produced (kg·ha ⁻¹ ·year ⁻¹)	NH ₄ leached (kg·ha ⁻¹ ·year ⁻¹)	NO ₃ leached (kg·ha ⁻¹ ·year ⁻¹)
600	4.0	0.9	3.1 (0.4)	44.3	7.0	37.3 (1.19)	14.29 (1.39)	6.40 (1.06)	9.68 (1.10)
800	4.1	0.8	3.4 (0.4)	41.2	12.2	28.99 (4.48)	12.88 (0.24)	5.64 (0.60)	9.28 (0.22)
1000	3.3	0.6	2.7 (0.2)	37.9	16.1	21.82 (3.95)	4.62 (0.58)	6.58 (1.43)	2.40 (0.73)
1200	2.9	1.0	1.9 (0.1)	53.3	28.0	25.29 (1.44)	0.63 (0.49)	7.05 (0.96)	0.70 (0.34)
1200 EL	1.7	0.3	1.4 (0.2)	47.9	28.0	19.85 (2.59)	5.27 (1.95)	6.04 (0.65)	4.24 (0.82)

Note: Mineral N availability is the sum of atmospheric N input (data from Friedland et al. 1991; Lovett 1992; Miller et al. 1993) and net N mineralized. NH₄ and NO₃ leached are derived from recovery of these ions from resin bags at the end of monthly N mineralization incubations. ANPP, annual aboveground net primary productivity, the sum of annual woody growth and litterfall quantity.

suring absolute net N mineralization, it should be kept in mind that present methods used to assess N mineralization yield only indices (Binkley and Hart 1989).

At the beginning of each incubation period, in each plot, six pairs of ABS plastic tubes (10 cm long, 5 cm in diameter) were installed at random locations, avoiding only large roots, tree trunks, and rocks. Loose surface forest floor material was set aside and tubes were inserted into the soil. One core from each pair was removed from the ground and the soil retained. These samples were kept refrigerated until being processed (within 48 h) and then analyzed to determine initial inorganic N levels. The second core was gently removed, ion-exchange resin bags were placed at the bottom of the core, and then the unit was replaced into the hole. Ion-exchange resin bags and loose litter were placed on top of the core.

Each incubation period was approximately 4 weeks; there were a total of four incubation periods. At the end of each period, we removed all cores from the ground and collected the incubated soil as well as the bottom ion-exchange resin bags. The upper bags were either reused once after regeneration or replaced with fresh bags. Collected soil and bottom ion-exchange bags were immediately refrigerated until they were processed in a laboratory at the Department of Earth and Environmental Science, University of Pennsylvania, 2–4 days after collection.

Soil and resin bag analysis

Each soil sample was passed through a 2-mm mesh sieve to remove rocks and coarse organic matter and to homogenize the soil. An 8- to 12-g (fresh mass) subsample was removed from the sieved material; the remainder was air-dried and weighed to determine soil water content. Each subsample was extracted with 50 mL of 2 N KCl and filtered. Storage and handling of the cation- and anion-exchange resin bags were similar to that used for the soils. Each bottom resin bag was extracted individually with 30 mL of 2 N KCl; resin extracts were centrifuged (to remove escaped resin and residue soil) and refrigerated until analysis. This extraction procedure has been shown to recover essentially all of the NH_4 and NO_3 from soils, and at least 80%–85% of the ions from the resin bags, as determined by recovery of standard additions to resins by Binkley et al. (1994) and confirmed in our laboratory. All extracts were preserved with the addition of 3 mL of chloroform and refrigerated until analysis. The NH_4 and NO_3 concentrations of all extracts were determined colorimetrically on a Technicon Auto Analyzer II (Technicon Industrial Systems, Tarrytown, N.Y.) at the University of Pennsylvania using standard procedures (Technicon Industrial Systems manual) with slight modifications.

Soil core results are reported in kilograms per hectare of surface to 10 cm depth soil for both initial extractable and net production values for NH_4 and NO_3 ; resin bag results are reported as kilograms of NH_4 or NO_3 leached per hectare of surface to 10 cm depth soil. Net N mineralization was calculated on a plot by plot basis as the average postincubation quantity of NH_4 and NO_3 in both the soil and resin bags minus the initial quantity of NH_4 and NO_3 in the preincubation soils. A negative difference between postincubation and preincubation N concentrations indicates net N immobilization.

Annual net N mineralization was estimated as the sum of the amounts of N mineralized in each incubation period during the growing season. Much prior research has shown winter N mineralization to be negligible (usually <10% of annual net N mineralized) (e.g., Pastor et al. 1984; Strader et al. 1989; Stump and Binkley 1993; Pérez et al. 1998; Schaffers 2000).

Litterfall and soil organic matter quality

Oven-dried litterfall samples were ground in a Wiley mill to pass a 1-mm mesh and analyzed for C, N, and lignin content. The six soil cores sampled to determine initial preincubation inorganic N levels were air-dried and subsampled (an equal percentage of soil was subsampled from each core in a plot) and combined into one sample so as to form one soil sample per plot per incubation period. These soils were air-dried, finely ground using a mortar and pestle, and analyzed for C and N content. Soils from the beginning, middle, and end of the growing season were analyzed for lignin content. An elemental analyzer (Carlo-Erba NA 1500 C/N analyzer; Fisons Instruments, Beverly, Mass.) was used to determine C and N content for soil and litter samples. Acid (H_2SO_4) detergent fiber analysis and further H_2SO_4 digestion at the University of Maine (B. Hoskins, University of Maine, personal communication) were used to determine lignin content for both soil and litter samples.

Statistical techniques

Pearson product moment correlation analysis was used to explore correlations among variables. Regression analysis was used to test hypotheses concerning driving variables and their effect on productivity and N mineralization. Stepwise multiple linear regression was used to examine the relative importance of GSDD and net N mineralization on ANPP and its components. ANOVA and Tukey's test were used to determine differences in major variables among different elevations.

Analyses were performed on a plot by plot ($n = 20$) basis to assess small-scale effects at each sampling location. Large-scale effects (e.g., climate) were assessed on a site by site basis ($n = 5$). Some variables were \log_{10} transformed when needed to satisfy normality requirements for regression analyses; when transformation was necessary, this is specified in the results.

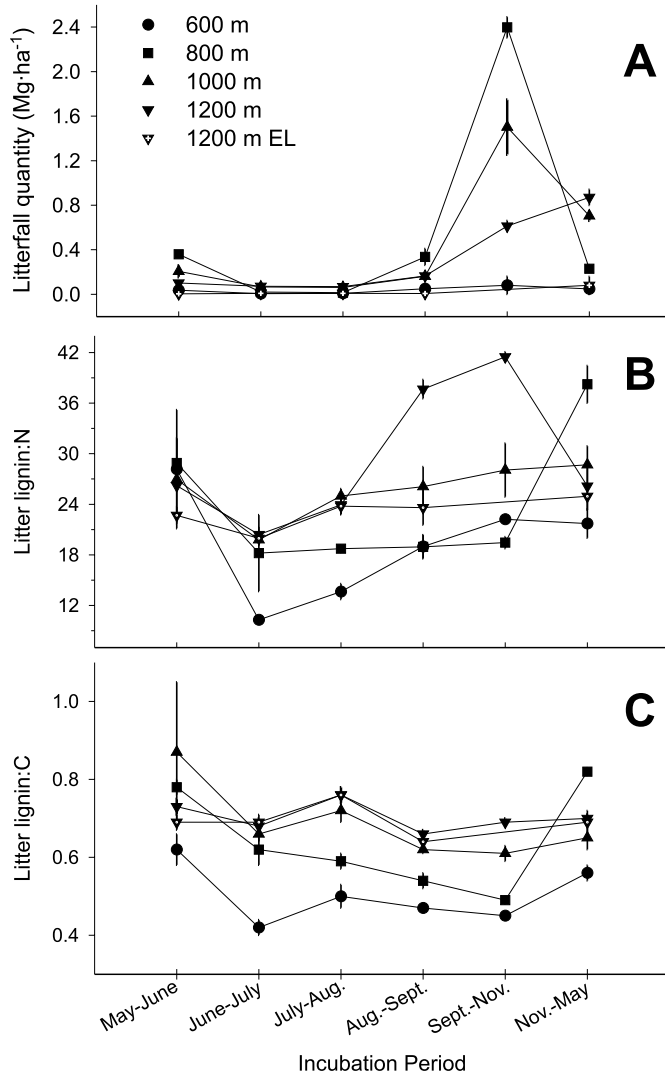
Results

Litterfall quantity and quality

Monthly litterfall quantities are shown in Fig. 1A. Summer litterfall patterns were essentially identical at all forests; however, winter litterfall patterns were, not surprisingly, different between the broadleaf and needle-leaf forests. Maximum litter was shed in the broadleaf forests during autumn, from September through November, while maximum litter was shed during winter in the needle-leaf forests.

Litter lignin:N over 1 year is shown in Fig. 1B. All sites except the 800-m site showed roughly similar patterns in changing lignin:N over the year, although patterns of change were expressed most strongly at 1200 and 600 m. Lignin:N fell early in the summer, rose steadily through the summer reaching a maximum in the fall (September–November), and

Fig. 1. Patterns in (A) litterfall quantity, (B) litter lignin:N, and (C) lignin:C over 1 year at five forests along an elevational gradient on Whiteface Mountain, N.Y. Standard error bars are shown.



then fell again in winter. The litter lignin:N at the 800-m site showed the same early summer drop but then did not change appreciably throughout the summer and rose in winter. Litter lignin:N values at the 1000- and 1200-m EL sites were similar and were significantly lower in the late summer and fall than those at 1200 m. All sites above 600 m contained *A. balsamea* as a major component of the canopy, which increased the lignin content of the litter.

All sites dominated by needle-leaf trees (1000, 1200, and 1200 m EL) showed essentially the same litter lignin:C (ANOVA and Tukey's test on log₁₀-transformed data: $p > 0.1$, $n = 20$) (Fig. 1C). The broadleaf sites showed lower lignin:C, but the difference was only significant at the 600-m site (ANOVA and Tukey's test on log₁₀-transformed data: $p < 0.01$, $n = 20$). The 600-m site followed a seasonal pattern of change in litter lignin:C that was similar to the pattern seen in the upper-elevation sites; the 800-m site followed a somewhat different seasonal pattern compared with

the upper-elevation sites, with lignin:C declining over the summer and peaking with autumn leaf fall.

Soil variables

Results for the measured soil parameters are shown in Table 3. No seasonal patterns were observed in the soil quality variables (data not shown), so the values shown are the mean of the three measurements made over the season. Water content was similar across all plots; variations during the season were small and showed no pattern. A trend toward increases in lignin, C, and N with elevation is apparent, but the 800-m site was anomalous in this regard, so the trend was not significant.

Nitrogen mineralization

For the growing season (May–September) at the five study sites on Whiteface Mountain, net N mineralization (ammonification plus nitrification) and net nitrification are listed in Table 2. In general, net N mineralization decreased as elevation increased. The 600-m site showed significantly more N mineralization than did the 1000-m site ($p < 0.05$), the 1200-m site ($p < 0.1$), and the 1200-m EL site ($p < 0.01$). Although the average amount of N mineralized at the 1200-m EL site was always less than at the other sites, the difference was only significant for comparisons between the 1200-m EL plot and either the 600- or the 800-m plot (t tests: $p < 0.005$). Seasonal patterns in inorganic N concentrations are shown in Fig. 2. All five sites showed similar trends, with N mineralization steadily increasing from early spring through summer, reaching a maximum during July and August, and subsequently decreasing. When separated by vegetation type, broadleaf forests mineralized and nitrified more N than did needle-leaf forests (t test: $p < 0.001$).

Considerable nitrification (>20% of total N mineralization) was observed at all sites except 1200 m (Fig. 3); more nitrification occurred at lower elevations. Seasonal and elevational patterns in nitrification paralleled those in net N mineralization. If atmospherically derived inorganic N is included, mineral N availability (sum of N mineralization and atmospheric N deposition) did not differ significantly across the five forest sites ($p > 0.1$); however, the 1200-m site had significantly more available mineral N than the 1000- and 800-m sites (ANOVA with Tukey's test: $p < 0.05$ and $p < 0.1$, respectively, $n = 20$). Maximum mineral N availability, approximately 53 kg·ha⁻¹·year⁻¹, is at 1200 m and minimum mineral N availability, approximately 38 kg·ha⁻¹·year⁻¹, is at 1000 m (Fig. 3).

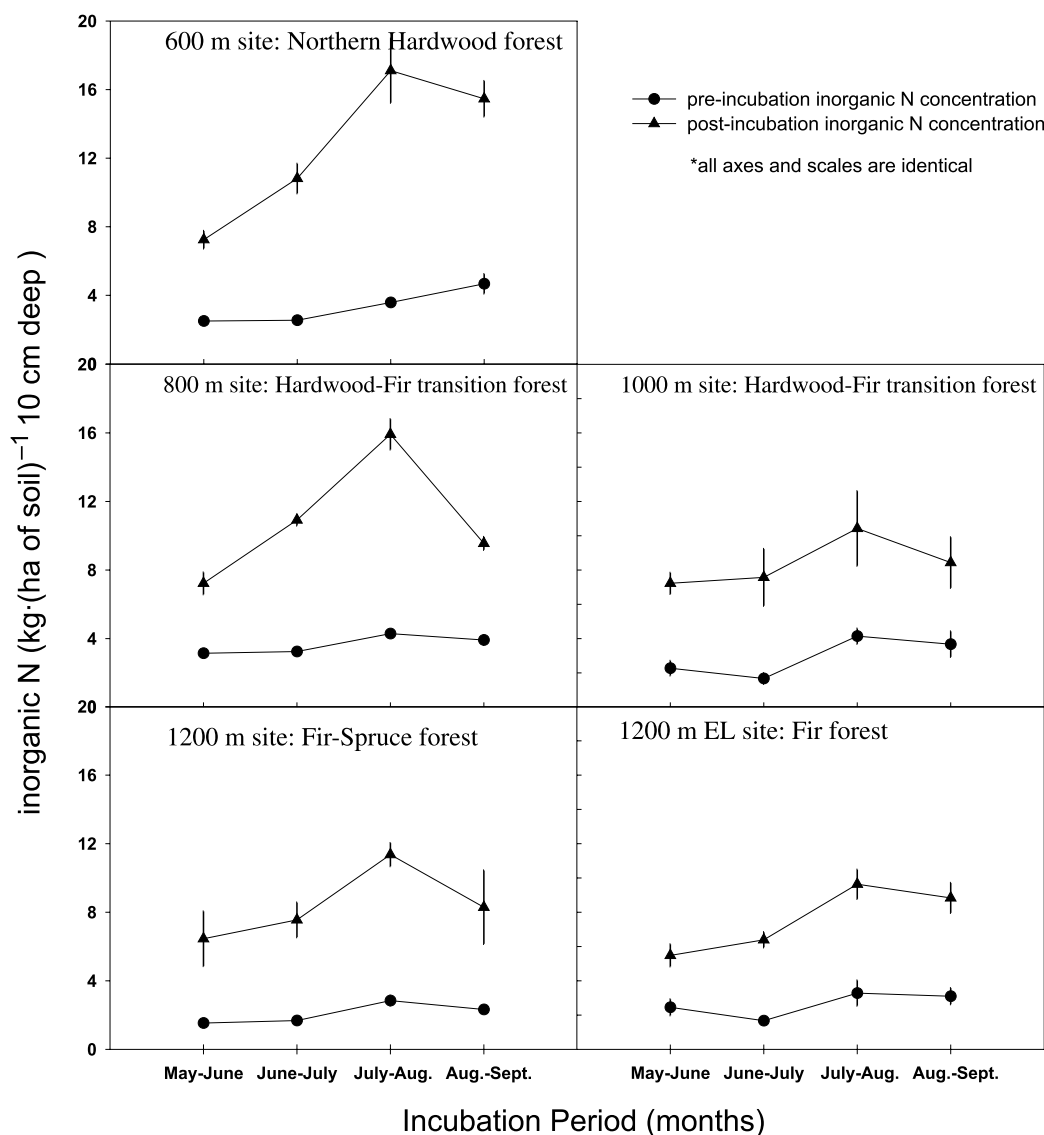
Coefficients of determination and probability values from linear regressions between N mineralization rates, nitrification rates, soil and litter quality parameters, and measured environmental variables, including soil and air GSDD, are shown in Table 4. Soil GSDD explained more of the variation in N mineralization ($R^2 = 0.469$, $p < 0.001$) and nitrification ($R^2 = 0.754$, $p < 0.001$) than did any other variable. Air GSDD could account for some of the variation in net N mineralization ($R^2 = 0.323$, $p < 0.01$) and nitrification ($R^2 = 0.656$, $p < 0.001$). Substrate quality variables did not explain as much variance in net N mineralization as they did for net nitrification. In a linear regression, litter lignin:N indicated a small but significant effect on net N mineralization ($R^2 = 0.293$, $p < 0.05$); soil C:N did not explain any of the vari-

Table 3. Soil properties along an elevational gradient at Whiteface Mountain.

Elevation (m)	Lignin content (mg·g ⁻¹)	C content (mg·g ⁻¹)	N content (mg·g ⁻¹)	Water content (g·g ⁻¹)	Bulk density (g·cm ⁻³)
600	183.2±13.1	229.7±12.5	11.5±0.5	2.45 (2.59/2.29)	0.28 (0.70/0.13)
800	303.4±1.9	361.7±9.9	16.1±0.3	2.39 (2.61/2.21)	0.17 (0.27/0.13)
1000	213.5±10.3	309.0±15.9	13.8±0.6	2.34 (2.52/2.24)	0.14 (0.25/0.07)
1200	235.0±16.2	302.5±14.2	13.2±0.7	2.59 (2.68/2.53)	0.11 (0.15/0.08)
1200 EL	219.6±21.5	313.6±13.5	15.2±0.5	2.21 (2.31/2.13)	0.14 (0.30/0.07)

Note: All values shown are on a soil dry mass basis and are presented as are mean ± SE or mean (max./min.).

Fig. 2. Change in inorganic N (NO₃ and NH₄) concentrations over the growing season on Whiteface Mountain as measured by the in situ resin core method of estimating N mineralization. Preincubation concentrations represent the inorganic N in the soil prior to installing incubations; postincubation concentrations represent the amount of inorganic N accumulated and leached from the incubation after approximately 1 month. Standard error bars are shown. The difference between pre- and post-incubation concentrations represents the amount of N mineralized during that period.



ance in net N mineralization. However, litter lignin:N produced a better regression with net nitrification ($R^2 = 0.512$, $p < 0.001$); soil C:N also produced a significant correlation with nitrification ($R^2 = 0.209$, $p < 0.05$). Litter N content and

soil lignin content did not account for any variation in either process ($p > 0.1$). Foliar production and ANPP explained 29% ($p < 0.01$) and 23% ($p < 0.05$) of the variation in N mineralization, respectively. No additional variance in net N

Fig. 3. Inorganic N availability at five forest sites on Whiteface Mountain. Bars show estimated annual net ammonification and nitrification (net N mineralization is the sum of these). Points represent total mineral N available at forest sites; total mineral N available is the sum of mineralized N plus atmospherically deposited mineral N.

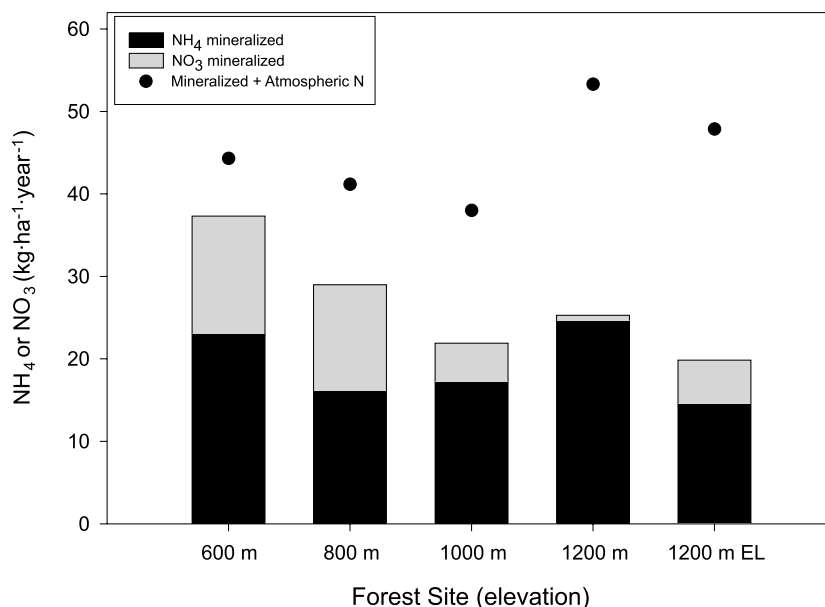


Table 4. Coefficients of determination and probability values from linear regressions between N mineralization and possible driving variables ($n = 20$).

Independent axis	Dependent axis							
	Total N mineralized	Nitrification	Litter N content	Litter lignin:N	% soil moisture	Soil GSDD	Air GSDD	Soil C:N
Nitrification	0.418**	x	x	x	x	x	x	x
% litter N	0.019	0.003	x	x	x	x	x	x
Litter lignin:N	0.293*	0.512***	na	x	x	x	x	x
% soil moisture	0.17	0.439**	0.13	0.185*	x	x	x	x
Soil GSDD	0.469***	0.754***	0.009	0.597	0.387*** ^a	x	x	x
Air GSDD	0.323*** ^a	0.656***	0.045	0.388**	0.478***	0.702***	x	x
Soil C:N	0.07	0.209*	0.001	0.155	0.322**	0.147*	0.042	x
% SOM lignin	0.005	0.003	0.164	0.008	0.384**	0	0	0.313**

Note: GSDD, growing season degree-days. “na” means that the regression would be meaningless, as the variables being tested were autocorrelated. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; x, no test; SOM, soil organic matter.

^aData failed normality test, even after various transformations.

mineralization was explained by any variable in multiple linear regressions with productivity variables.

Productivity

ANPP, represented by litterfall quantity and wood production, is reported for each site in Table 2. ANPP generally decreased with increasing elevation, although there was little difference between 600 and 800 m and between 1000 and 1200 m. The least productivity occurred at the 1200-m EL site. Litterfall accounted for 66%–84% of ANPP. As expected, air GSDD explained the most variance in ANPP ($R^2 = 0.671$, $p < 0.001$) (Fig. 4A); soil GSDD produced a significant regression as well ($R^2 = 0.356$, $p < 0.01$). Air GSDD was the best predictor of litterfall ($R^2 = 0.784$). Multiple regressions using soil variables in combination with air GSDD did not improve the R^2 values.

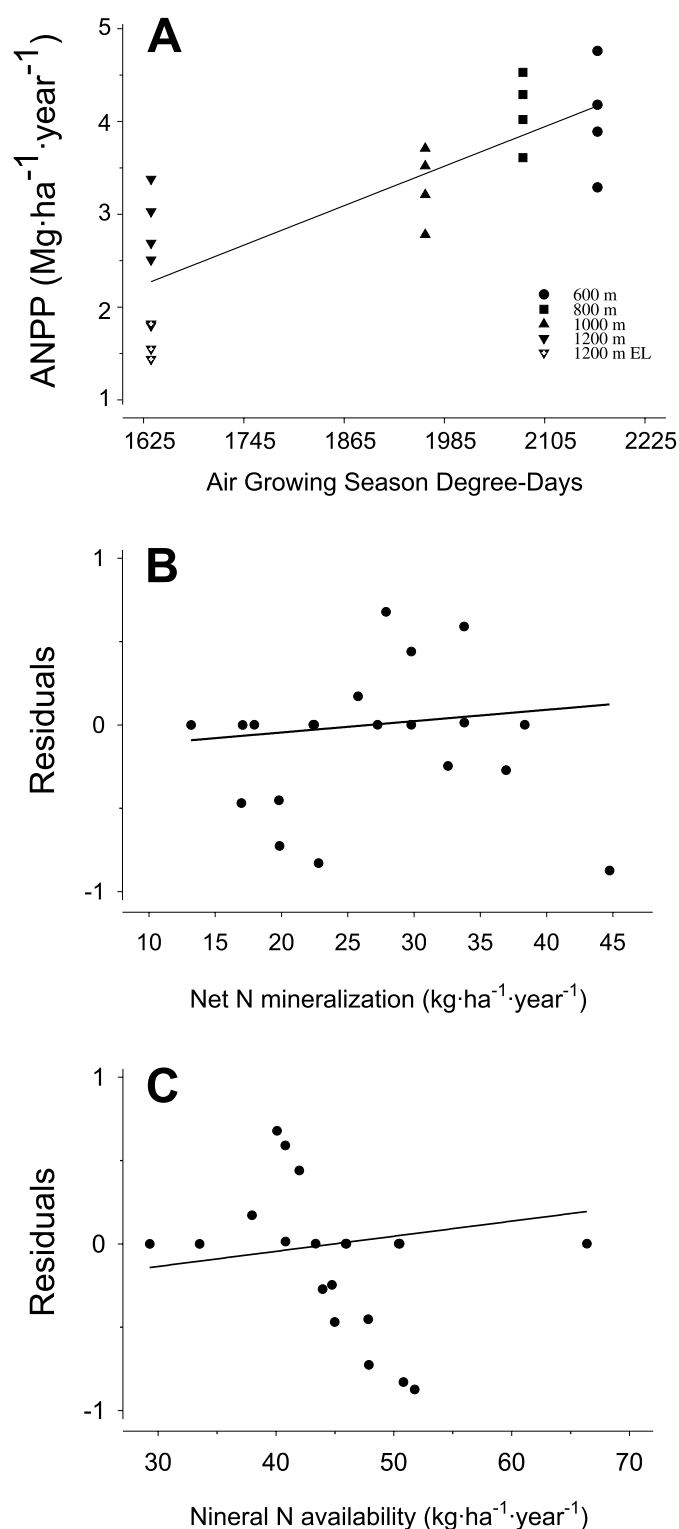
Total annual litterfall was correlated with net N mineralization (Pearson $R = 0.57$, $p < 0.01$) and net nitrification ($R = 0.67$, $p < 0.001$), but mineral N availability (the sum of net N mineralization and atmospheric N deposition) was not correlated with ANPP or any of its components ($p > 0.1$). Residuals from a regression between air GSDD and ANPP did not correlate with either net N mineralization or mineral N availability (Figs. 4B and 4C).

Discussion

Measurements of net N mineralization

Our estimates of net N mineralization along an elevational gradient on Whiteface Mountain are similar to the 40 kg·ha⁻¹·year⁻¹ estimate reported using the buried-bag method by Friedland et al. (1991) at nearby sites on Whiteface Mountain and lower than the values estimated by Sasser

Fig. 4. (A) Relationship between annual ANPP and growing season heat-sum (air GSDD) across an elevational gradient on Whiteface Mountain. The line represents the linear regression ($R^2 = 0.671$, $p < 0.001$). Regressions between the residuals from this regression and other variables failed to explain any additional variance ($R^2 < 0.02$, not significant). Residuals versus two variables representing N availability are shown: (B) net N mineralization and (C) mineral N availability, the sum of extractable NH_4 and NO_3 .



and Binkley (1989) who measured 33–54 kg N·ha⁻¹ in balsam fir dominated forests over a 2-month period. The net N mineralization estimates are generally comparable with the N mineralization estimates using buried bags and measuring over a 28-day period (6.4 kg·ha⁻¹ in a spruce–fir forest in Maine and approximately 16–18 kg·ha⁻¹ in the northern hardwood forests in New Hampshire of Federer (1983)). Nitrification in these earlier studies (Federer 1983; Friedland et al. 1991) was essentially zero, whereas we measured approximately 5 kg·ha⁻¹·year⁻¹ in the conifer forests and approximately 13.5 kg·ha⁻¹·year⁻¹ in the broadleaf forests (Table 2). McNulty et al. (1996) did find the nitrification potential at the higher elevations on Whiteface Mountain to be about 22% of mineralization, very similar to the findings of this study.

Influences on net N mineralization

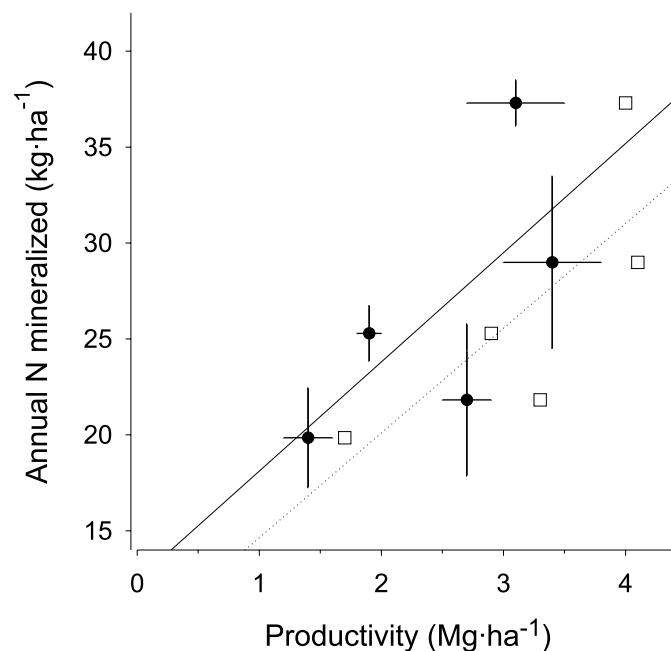
Soil temperature (soil GSDD) explained about half of the variance in net N mineralization. Increasing N mineralization rates correlating with increasing soil temperatures is consistent with the findings of several studies (e.g., Matson and Boone 1984; Powers 1990; Boone 1992; Kim et al. 1995; Stottlemeyer et al. 1995; Sveinbjornsson et al. 1995). The effect of temperature on community species composition and the resultant changes in litter quality and decomposition rates are routes whereby temperature can influence N mineralization rates (Matson and Boone 1984; Nadelhoffer et al. 1991; Bale and Charley 1994; Fan et al. 1998). In this study, substrate quality and N mineralization were correlated with each other, and with temperature, so the impact of temperature on N mineralization may be both direct and indirect. Both foliar and total productivity explained variance in N mineralization, and these variables were correlated with air and soil temperatures. In sum, N mineralization along this climosequence was related to the expected suite of factors: temperature, litter quality, and litter production. Soil moisture did not explain a significant amount of the variance in N mineralization; we speculate that this is because microorganisms in these cool, moist soils are seldom water limited (Table 3).

Influences on net nitrification

Linear regressions showed that soil GSDD explained variance in net nitrification rates better than that in net N mineralization rates ($R^2 = 0.76$ compared with $R^2 = 0.47$). Soil C:N had no significant effect on net N mineralization but did on net nitrification ($R^2 = 0.21$). These results agree with those of Powers (1990) who examined relations between substrate quality, soil temperature, N mineralization, and nitrification along an altitudinal gradient. In addition to finding more nitrification in warmer soils, Powers (1990) also found no influence of soil C:N on net N mineralization but did find an influence on net nitrification.

The decreasing soil temperatures and increasing lignin:N associated with increasing elevation explain measurements showing decreasing nitrification with elevation as well as the different rates of nitrification at the two 1200-m sites. Higher soil temperatures explain the higher rate of NO_3 production at the 1200-m EL site compared with the closed-canopy site ($R^2 = 0.644$, $p < 0.01$, $n = 8$); the addition of litter lignin:N explains an additional approximately 10% of the

Fig. 5. Relationship between productivity and mineralized N. Total annual litterfall compared with mineralization is shown with black circles; standard error bars are shown. The solid line represents the regression equation for litter versus N mineralized ($R^2 = 0.47$, $p < 0.05$). Open squares denote the calculated value for ANPP, the sum of annual litterfall total and an estimate of the annual wood increment. The dotted line is the estimated regression for the latter data ($R^2 = 0.49$, $p < 0.05$).



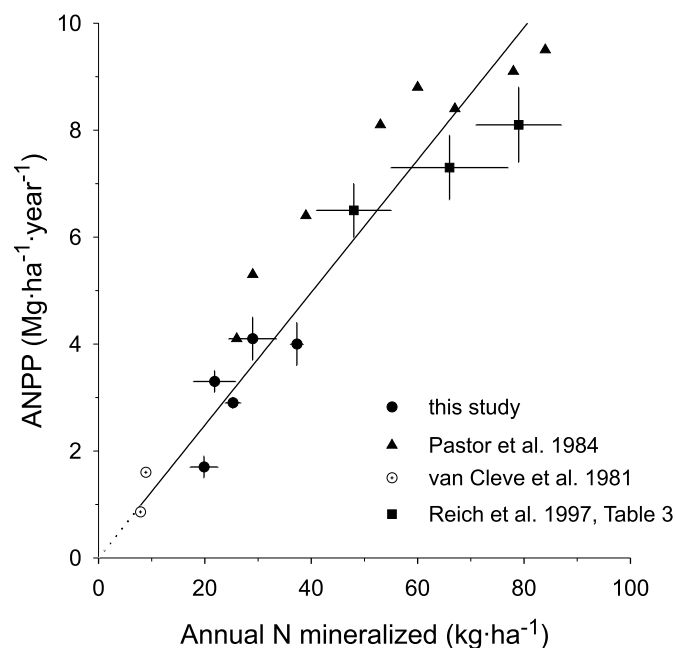
variance (multiple $R^2 = 0.738$, $p < 0.05$), despite the negative correlation between litter lignin:N and soil temperature (Pearson's $R = -0.775$, $p < 0.001$). The 1200-m EL site had warmer soils than the 1200-m site, presumably because there is less canopy cover at the EL site.

ANPP

Climate variables explained the most variance in productivity: as air GSDD increased, ANPP increased. Total mineral N availability, which includes atmospheric deposition of inorganic N, was not related to ANPP or any of its components. This finding suggests that ANPP along this climosequence was not limited by mineral N availability. This was expected given the large amounts of mineral N that have been measured in N mineralization studies and in lysimeters at the bottom of the root zone (Friedland and Miller 1999).

Figure 5 shows that N mineralization and productivity are correlated at the Whiteface sites, as has been found in other studies. Assessing cause and effect given the correlation between N mineralization and productivity across the Whiteface climosequence is facilitated by the fact that temperature and mineral N availability are not correlated. The increase in mineral N contributed by atmospheric deposition ($7\text{--}28 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) has not increased ANPP by the $1\text{--}3 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ implied by Fig. 5. A similar observation was made by Friedland and Miller (1999). Clearly, productivity is not controlled by mineral N availability in the Whiteface forests (Fig. 4). Although N mineralization can be a good predictor of ANPP across many forest types, it was not an important control on ANPP in this study. Rather, the

Fig. 6. ANPP compared with N mineralization rates for cool temperate forests across a wide range of productivity. Values are derived from four studies as noted on the figure.

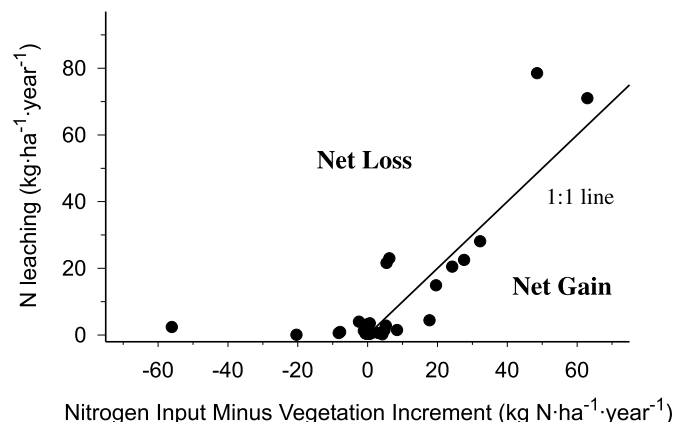


reverse is supported by the data in Fig. 5: productivity exerts some control on N mineralization. Logically, decreasing litter production with increasing elevation across the climosequence influences the amount of mineralizable N available for soil microbes as well as influencing their environment through effects on soil conditions such as moisture holding and cation-exchange capacity.

In Fig. 6, we plot the Whiteface data in the context of other studies of N mineralization and forest productivity conducted in northern coniferous and broadleaf forests using similar methods (Pastor et al. 1984; van Cleve et al. 1993; Reich et al. 1997). Nitrogen mineralization over the range of $5\text{--}90 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ has a remarkably good correlation with ANPP (Pearson's $R = 0.97$, $p \ll 0.001$). The results of many years of forest fertilization experiments have shown that moderate rates of growth increase ($15\text{--}20\%$) typically require application rates in excess of $100 \text{ kg}\cdot\text{ha}^{-1}$, substantially in excess of the total amount used by the trees and the rates of mineralization seen in natural ecosystems. Studies of the fate of atmospheric N deposition in forests suggest that substantial quantities of the added N leach from many forests (see Fig. 7 and the review by Johnson and Lindberg 1992); substantial proportions of mineral N leached from the active soil in this study as well (Table 2). These observations indicate that addition of mineral N at rates on the order of $30 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ will not lead to the $3 \text{ Mg}\cdot\text{ha}^{-1}$ increase in ANPP implied by Fig. 6. The data from this study suggest that across even modest gradients in climate, a correlation between N mineralization and ANPP should not be considered strong evidence that mineral N availability controls ANPP.

Compared with this study, atmospheric deposition of N was less substantial in most of the previous studies that found a correlation between ANPP and N mineralization. In those studies, the variance in mineral N availability was

Fig. 7. Inorganic N input less forest N increment compared with quantity of N leaching from these forests. Values above the 1:1 line imply net loss of N from the soil; values below the line imply net retention. Redrawn from Johnson and Lindberg (1992).



dominated by the variance in N mineralization, the principal source of mineral N. Those authors concluded that the correlation between ANPP and mineral N availability indicated that ANPP is controlled by N availability mediated by N mineralization. In the present study, we have separated mineral N availability from N mineralization. At Whiteface Mountain, significant variation in atmospheric deposition creates a situation where mineral N availability and N mineralization are uncorrelated (apparently independent). Under these conditions, we do not find evidence that ANPP depends on mineral N availability. Instead, the correlation between N mineralization and ANPP in the present study seems more reasonably interpreted as evidence that ANPP (specifically foliage production) influences the N mineralization rate through its determination of the supply of fresh, readily digestible substrate for soil microbes and the effect of litter on soil moisture and cation-exchange capacity. The observed correlations between N mineralization and temperature variables reflect both the well-understood constraints of temperature on microbial metabolism and the dependence of substrate supply (ANPP) on temperature.

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