NITROGEN DYNAMICS IN OAK FOREST SOILS ALONG A HISTORICAL DEPOSITION GRADIENT

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Abstract: This study quantified soil nutrient status and N mineralization/nitrification potentials in soils of oak-dominated, unmanaged forest stands in seven experimental forests ranging along a historical and current acidic deposition gradient from southern Illinois to central West Virginia, U.S.A. Among these seven sites (that spanned 8.5° of longitude) soil pH and Ca^{2+} decreased and soil organic C and extractable Al^{3+} increased from west to east. In general, initial soil solution NO_3^-, total N mineralization potential and net NO_3^- accumulation over 30 days of incubation (as measured by aerobic laboratory incubations) also decreased from west to east, whereas initial soil solution NH_4^+ was uncorrelated with longitude. The Fernow Experimental Forest (W.Va.), the eastern-most site, was the exception to this trend. Soils from the Fernow had the highest concentrations of both NO_3^- and NH_4^+ in the soil solution, and the greatest N mineralization potential. Stepwise regressions of N mineralization rate, net NO_3^- accumulation, and proportional nitrification on initial soil properties produced models with overall r^2 of 0.705, 0.772, and 0.708, respectively. Rates of N turnover were positively correlated with initial NO_3^-, pH, and Ca:Al ratio and negatively correlated with extractable Al^{3+} concentrations. Differences in oak growth and mortality may be related to the differences in soil chemical status and soil N dynamics among these seven experimental forests.

INTRODUCTION

Most mature, upland forests of eastern North America are nitrogen (N) limited (Aber et al. 1989). In such ecosystems, the processes that regulate the availability of inorganic N to roots and soil microbes are those involved in the mineralization of low molecular weight organic compounds containing N (e.g. amino acids, polypeptides, nucleotides) to NH_4^+ (i.e. ammonification or N mineralization) and, in some cases, subsequently to NO_3^- (i.e. nitrification). Once the N is in inorganic form, it is subject to competition between roots and microbes, both of which result in the inorganic N being reconverted to biomass N.

Rates of nitrogen mineralization and nitrification are affected by a variety of environmental factors, including soil solution pH, temperature, and moisture (Plymale et al. 1987; Robertson 1982), as well as the rate at which nitrogenous substrates are supplied. Thus, modification of soils by anthropogenically-generated deposition has the potential to alter the rates and patterns of organic N turnover in forest soils, and thereby, to alter the basic functioning of the forests those soils support (Bondietti and McLaughlin 1992).

Over the last 50 years, some forest soils in eastern North America have experienced decreases in pH, increases in NO_3^- deposition and soil solution concentration, increased soil solution Fe^{3+} and Al^{3+} concentrations, and lowered Ca:Al ratio (Bondietti and McLaughlin 1992), all of which have the potential to affect key ecosystem processes (Aber et al. 1989). In N-poor ecosystems, the activity of autotrophic nitrifiers may be inhibited and soil NO_3^- concentrations remain low because of a number of factors, including the inability of such bacteria to compete well against plant roots and heterotrophic soil microbes for NH_4^+ and the direct inhibition by low pH (van Miegrot et al. 1992) and relatively high Fe^{3+} and Al^{3+} availability (Liang and Tabatabai 1978). Although the activity of heterotrophic N-mineralizing bacteria and fungi may not be as sensitive to changes in soil chemistry as that of autotrophic nitrifiers (Legge and Crowther 1987), N-mineralization rates are generally lower on acidified soils (Plymale et al. 1987).

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N-limited forest ecosystems (i.e. ones with low rates of mineralization and little nitrification) are typically dominated by tree species which are dependent on ectomycorrhizae (Vogt et al. 1991) such as oaks (*Quercus* spp.), pines (*Pinus* spp.), and spruces (*Picea* spp.). Because of the ability of their ectomycorrhizae (ECM) to forage for NH_4^+, reduce NO_3^-, and degrade low molecular weight organic N substrates, these tree species can maintain growth even under very low N conditions (France and Reid 1983, Jansen 1991). Heavy, chronic N deposition may greatly alter the N status of forest soils, through its effect on leaching of Ca^{2+}, mobilization of Al^{3+}, and removal of N limitation for tree growth. Under such conditions, ECM-dependent species may decline and be replaced by tree species dependent on vesicular-arbuscular mycorrhizae (VAM) more typical of N-rich forest sites (Jansen 1991; Arnolds 1991) (e.g. maples, *Acer* spp. and yellow-poplar, *Liriodendron tulipifera*). Thus acidic deposition with a significant N component has the potential to affect eastern forest ecosystems over the long term, both in soil chemical status and in tree species composition.

As part of a larger study of the relationship between forest management, tree drought responses/mortality, historical deposition rates, and ecosystem function along the Ohio River Valley of eastern North America, this study was specifically designed to: (1) measure potentials for conversion of organic nitrogen to inorganic forms by soil microbial assemblages in forest soils differing in their historical deposition rates and in site quality; (2) determine relationships between differences in nitrogen mineralization/nitrification potentials and other soil properties (including both static properties such as texture and deposition-related properties such as Ca:Al ratio); and, (3) relate forest soil ecosystem processes such as the ones measured here to variations in tree crown condition, mortality, and drought response among these forests sites. This paper discusses the results of our analyses of the first two of those three objectives.

METHODS

Study Sites and Field Sampling

Seven experimental forests located in the Ohio River Valley were selected for study (Figure 1). These seven sites spanned 8.5° of longitude (Table 1) along a gradient of historical atmospheric deposition which increased from west to east (Work Group One 1983, Lovett 1992). In each experimental forest, two unmanaged, oak-dominated plots on NW-NE facing 15%-25% slopes on non-calcareous substrates were selected. In each plot we established two random quadrats, and took seven random soil samples from each quadrat along a transect running parallel to the contour of the slope during a ten day period in July 1993. Before taking a sample, the forest floor (litter + unconsolidated humus) was cleared from the mineral soil surface over an area of approximately 0.25 m^2. A 2 cm soil corer was then used to extract A-horizon cores of 5-20 cm in length, depending on the forest site. Each sample was a composite of 5-15 such A-horizon cores totalling at least 200 g fresh mass of soil. We limited our sampling to the A-horizon because rates of N-mineralization and nitrification are typically much greater in the A-horizon than in the B-horizon and unconsolidated litter (Boerner and Koslowsky 1989). All samples were transported to the laboratory under refrigeration.

Table 1. Experimental Forest study site names, abbreviations, and locations.

Name (Abbrev.)	State	Latitude	Longitude	Elevation Range
Kaskaskia (KAS)	Illinois	37°32' N	88°20' W	460-500'
Bald Rock (BDR)	Kentucky	36°59' N	84°16' W	1060-1080'
McKee (MCK)	Kentucky	37°27' N	83°59' W	1180-1270'
Robinson (ROB)	Kentucky	37°15' N	83°20' W	1050-1150'
Mead (MEX)	Ohio	39°15' N	83°00' W	760-800'
Raccoon (RAC)	Ohio	39°10' N	82°23' W	790-860'
Fernow (FER)	West Virginia	39°03' N	79°41' W	2650-2730'

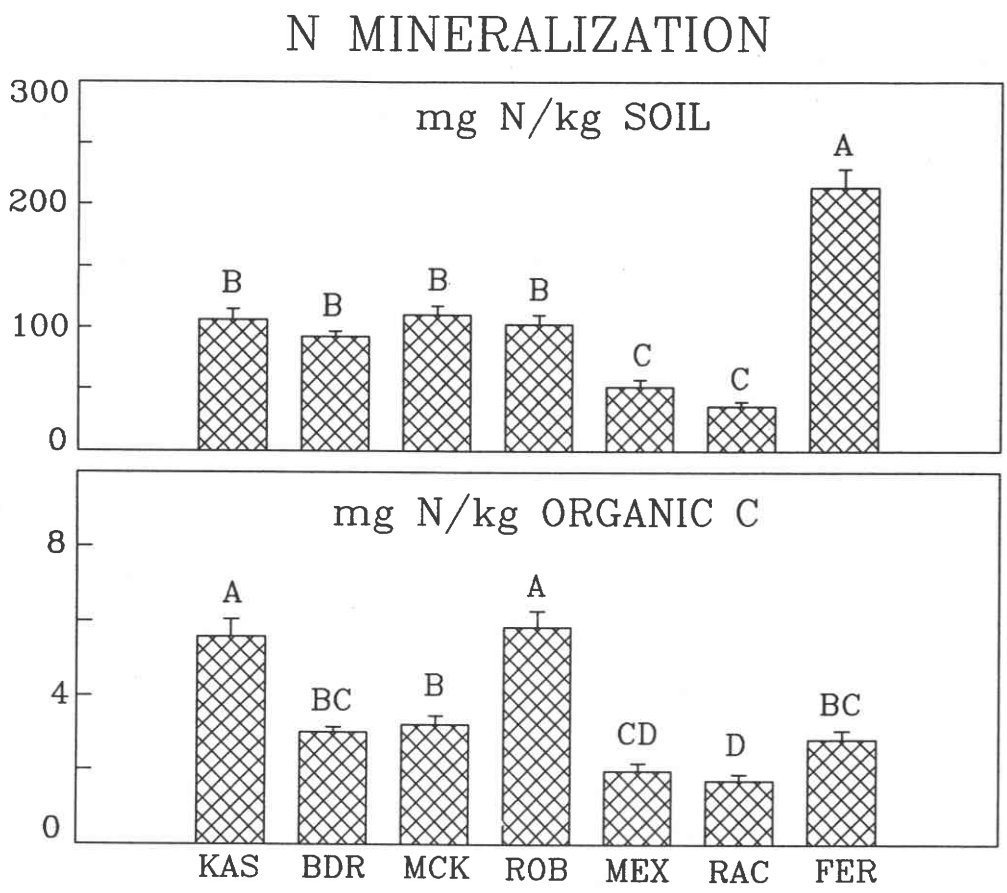

Figure 1. A-horizon N mineralization on a mass basis (mg N/kg dry soil) and on an organic matter basis (mg N/kg organic C), in soils from seven experimental forests along the Ohio River corridor. Forests are arrayed from west to east along the x-axis. Histogram bars represent the mean of N=14, and the error bars represent one standard error of the mean. Bars with the same lower case letter were not significantly different at $p<0.05$ following analysis of variance and Ryan-Einot-Gabriel-Welsch Modified F Test. Forest codes follow Table 1.

Laboratory Methods

Each sample was subdivided into two subsamples. One was sent to Micro-Macro International, Inc., Athens, GA for analysis of soil texture by hydrometer, pH in water, Ca^{2+}, Mg^{2+}, K^{+}, and Na^{+} in 1 M NH_4OAc extracts, and NO_3^{-}, PO_4^{3-}, and Al^{3+} in 1 M KCl extracts. Methods followed Jones (1992). The second subsample was air-dried for 10-14 days, then analyzed for organic C content by Walkley-Black wet oxidation (Allison 1965).

The third subsample was then subdivided into two portions. One portion of approximately 10 g was extracted with 1 M KCl and the extract frozen pending analysis. The second portion was air-dried for 10-14 days, then passed through a 6 mm sieve to remove stones, roots, and leaf fragments. Approximately 100 g of the sieved soil was weighed, placed in a 300 ml styrofoam cup, and brought to 70% of field capacity with "Hubbard Brook Recipe" artificial rainwater (Lee and Weber 1979). We used artifical rainwater rather than deionized water to better simulate field conditions and to prevent the excessive leaching of the soil samples that might occur if deionized water were used throughout the incubation period.

All samples were incubated under aerobic laboratory conditions for 30 days at 23-28° C. Samples were weighed every 2-3 days, and were maintained at 50-70% of field capacity by adding artifical rainwater as needed. At the end of the incubation period, approximately 10 g (dry mass) of soil was taken from each incubated sample and extracted as above.

NH_4^+ and NO_3^- concentrations of each initial and final sample extract were determined colorimetrically on a LaChat QuikChem Autoanalyzer. Relative nitrogen mineralization was calculated as the difference between total inorganic N (i.e. $NH_4^+ + NO_3^-$) in the initial vs final extracts, less the N added in the rainwater solution. Net NO_3^- accumulation was calculated as the difference between initial and final NO_3^- concentrations in each sample. To correct for differences in soil organic matter content among forest sites, we expressed both N mineralization and net NO_3^- accumulation as mg N/g organic C. Percent nitrification was calculated as the percent of the total nitrogen mineralized which was converted to NO_3^- during the incubation period (Campbell et al. 1993).

Initial soil parameters and rates of N turnover were compared among experimental forests, stands within forests, and sample plots within stands by analysis of variance, using the Ryan-Einot-Gabriel-Welsch Modified F Test to post-test differences among means (SAS 1985). Regression models of N turnover rates as a function of initial soil conditions were constructed by maximum-r^2, forward selection stepwise regression (SAS 1985). Significant differences were at $p<0.05$ except where otherwise indicated.

RESULTS

Soil Physical and Chemical Properties

Five of the seven soil chemical parameters we measured varied linearly with longitude (Table 2). Organic carbon content, NH_4^+ and Al^{3+} all increased from west to east, whereas pH and the molar Ca:Al ratio decreased from west to east (Table 2). In contrast, Ca^{2+} was significantly greater in soils from the Kaskaskia E.F. (IL) and Robinson E.F. (KY) than in soils from the other five sites, and NO_3^- concentration was greatest in the two sites at the ends of our longitude gradient, Kaskaskia (IL) and Fernow (WV).

There was no consistent variation in soil texture with longitude (Table 3). The soils of the Mead (OH) E.F. had the greatest proportion of clay of the seven sites sampled, and there was little variation in clay content among the soils of the other six sites. The percentage of sand varied more than did the clay fraction, with the soils of the Fernow E.F. (WV), Bald Rock E.F. (KY), and McKee E.F. (KY) having greater relative sand content than the soils of the Mead E.F. (OH), Raccoon E.F. (OH) or Kaskaskia E.F. (IL) E.F.s. The dominant textural classes ranged from silty clay through silty clay loam and clay loam.

Nitrogen Mineralization and Nitrification

Without considering the Fernow E.F., total N mineralization decreased linearly from west to east, with the soils from the Raccoon E.F. (OH) and the Mead E.F. (OH) mineralizing significantly less ($p<0.0001$) total organic N per unit soil mass than the soils from the four sites to the west (Figure 1). On a mass basis, soils from the Fernow E.F. mineralized >2X as much N over 30 days as did the soils from any of the six other sites, and did not fit the linear longitudinal pattern of the other six sites. When N mineralization was adjusted for the differences in initial soil organic C among sites, the rate of N mineralization at the Fernow E.F. was no longer greater than those from the sites to the west. The lowest rates of total N mineralization/g organic C were still recorded at the Raccoon E.F. (OH) and the Mead E.F. (OH).

Net NO_3^- accumulation on a mass basis was significantly greater at the Kaskaskia E.F. and the Fernow E.F. than at the other five sites (Figure 2). The soils from the other five experimental forests accumulated an order of magnitude less NO_3^-, and did not differ significantly from each other in NO_3^- accumulation rate. When NO_3^- accumulation rate was adjusted for difference in organic C content, the rate observed in the soils from the Fernow E.F. became more similar

Table 2. Chemical properties of A-horizon soils from unmanaged, oak-dominated forest plots in seven experimental forests. Within a column, means followed by the same lower case letter were not significantly different at $p<0.05$. N=28 for each experimental forest and standard errors of the means are given in parentheses. All parameters except pH and organic carbon (%) are in mg/kg dry soil. Experimental forests are listed from west to east.

Experimental Forest	pH	Org. Carbon	NO_3^-	NH_4^+	Ca^{2+}	Al^{3+}	Ca:Al Molar Ratio
Kaskaskia (IL)	5.14a	1.91cd	17.33b	22.42c	683.5a	10.5e	136.20a
	(0.18)	(0.30)	(2.28)	(1.78)	(48.1)	(3.3)	(22.65)
Bald Rock (KY)	4.50b	3.08bc	0.59c	26.58bc	70.6b	147.4c	0.32c
	(0.17)	(0.30)	(0.16)	(1.70)	(8.8)	(9.7)	(0.05)
McKee (KY)	4.28b	3.42b	2.34c	25.41bc	64.3b	190.9bc	0.23c
	(0.06)	(0.52)	(0.32)	(1.90)	(4.4)	(15.2)	(0.03)
Robinson (KY)	4.88a	1.76d	1.96c	24.12c	345.4a	83.8d	27.20b
	(0.11)	(0.05)	(0.48)	(1.53)	(42.0)	(22.4)	(12.00)
Mead (OH)	4.25bc	2.64bcd	0.51c	33.91b	113.3b	311.3a	0.27c
	(0.03)	(0.27)	(0.13)	(2.58)	(14.3)	(17.9)	(0.06)
Raccoon (OH)	4.07c	2.10bcd	0.39c	24.01c	59.7b	212.5b	0.19c
	(0.07)	(0.32)	(0.06)	(1.85)	(7.8)	(11.3)	(0.03)
Fernow (WV)	3.79d	5.59a	50.57a	50.58a	146.3b	244.3a	0.48c
	(0.06)	(0.31)	(6.94)	(3.97)	(19.2)	(13.5)	(0.14)

to, though still significantly different from, those at the five intermediate sites (Figure 2). The percent of total N mineralization which was subsequently nitrified to NO_3^- followed the same pattern (Figure 2).

If one does not consider the Fernow E.F., two general patterns emerged: (1) on a mass basis, total N mineralization decreased 66% over 8.5° of longitude from west to east, and (2) nitrification, measured either as net NO_3^- accumulation or percent of newly mineralized N nitrified, was significantly greater in the site with Ca:Al ratio >135 than in the other five sites. When N turnover rates were adjusted for initial organic C content of the soils, the east-west trend of decreasing total N mineralization existed among all seven sites, including the Fernow E.F.; however, even when differences in organic C were accounted for, the soils from the Fernow E.F. (WV) still accumulated significantly more NO_3^- and nitrified a significantly greater percentage of NH_4^+ than would be predicted by longitude.

Regression Analysis of N Turnover Rates

Because of the inherent weakness in assuming that field plots such as those analyzed here are truly replicates, one must interpret the results of analyses of variance with considerable caution. Given the large variation in initial soil conditions among sites, we felt a multiple regression approach which explicitly addressed the differences among study sites would be a more effective inferential tool in analyzing situations such as this one.

Table 3. Texture of A-horizon soils from unmanaged, oak-dominated forest plots in seven experimental forests. Within a column, means followed by the same lower case letter were not significantly different at $p<0.05$. N=28 for each experimental forest and standard errors of the means are given in parentheses. Experimental forests are listed from west to east.

Experimental Forest	Sand (%)	Silt (%)	Clay (%)	Prevalent Texture
Kaskaskia (IL)	12.0d (1.1)	64.8a (2.2)	23.1b (1.8)	Silty Clay Loam
Bald Rock (KY)	48.8ab (2.5)	27.5c (2.0)	23.7b (0.8)	Clay Loam
McKee (KY)	43.8b (3.5)	31.9cd (2.6)	24.3b (1.2)	Clay Loam
Robinson (KY)	35.3c (3.6)	35.6c (2.5)	29.2ab (1.7)	Clay Loam
Mead (OH)	18.0d (1.9)	47.2b (1.4)	34.8a (1.0)	Silty Clay
Raccoon (OH)	18.9d (1.5)	54.5b (1.2)	26.6b (0.8)	Silty Clay Loam
Fernow (WV)	56.9a (1.7)	21.8e (2.0)	21.3b (1.3)	Clay Loam

Regression of the rate of N mineralization per unit soil mass on the soil chemical and physical properties analyzed produced a linear model significant at $p<0.0001$ with overall model $r^2=0.705$ (Table 4). This model attributed the variance in N mineralization rates among samples and sites to, in declining order, initial NO_3^- concentration in the soils, soil texture, and soil pH, with initial NO_3^- and pH having positive slope coefficients and silt+clay content a negative sign. The robustness of the model can be appreciated when one considers that the highest N mineralization rates were recorded at the Fernow E.F., the site with the lowest pH and silt+clay content of the soil. Without the Fernow E.F. in the model, the r^2 would improve considerably. Organic carbon content was not a significant variance component in this regression, and a similar regression done on mineralization rate per unit organic matter produced essentially identical results.

Regression of the net rate of NO_3^- accumulation on soil properties produced a linear model with equal signficance ($p<0.0001$) and even closer fit ($r^2=0.772$) (Table 4). In this model, the initial concentration of NO_3^- and the Ca:Al molar ratio contributed the largest partial r^2 to the model, both with positive sign for the slope coefficient. Thus, net NO_3^- accumulation increased with increasing initial NO_3^- and Ca:Al ratio. Soil pH (+), initial Al^{3+} concentration (-), and silt+clay content (+) contributed less, but still significantly to model fit. The percent of newly mineralized N which was subsequently nitrified during the 30 day incubation period was also directly proportional to initial NO_3^- concentration and the Ca:Al ratio (Table 4). Adding in initial soil Al^{3+} concentration (-) and silt+clay content produced a linear model with $r^2=0.708$.

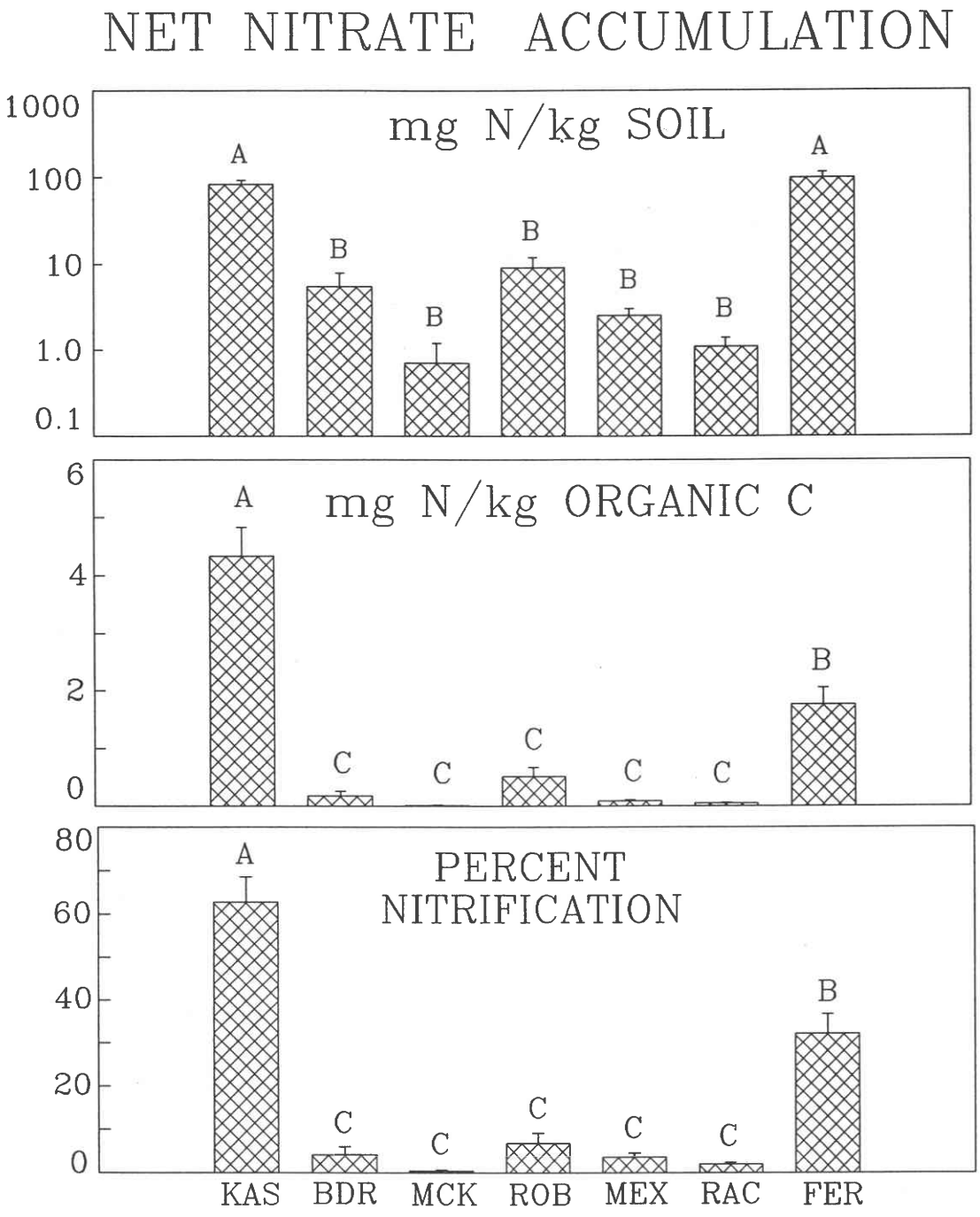

Figure 2. NO_3^- accumulation on a mass basis (mg NO_3^--N/kg dry soil) and on an organic matter basis (mg NO_3^--N/kg organic C), and percent nitrification of mineralized N in soils from seven experimental forests along the Ohio River corridor. Note the logarithmic y-axis for the two NO_3^- plots. Forests are arrayed from west to east along the x-axis. Format follows Figure 1.

Table 4. Forward selection, maximum r^2 regression of N turnover components on initial soil parameters. All independent variables with slope components significantly different from 0 at $p<0.05$ are given, and variables are listed in declining contribution to the total model r^2. N=167 for each regression.

Independent Variable	Slope Coefficient/ Significance of Slope
N Mineralization (mg N/kg soil), total model r^2=0.705, p<0.0001	
Initial NO_3^-	+2.10 p<0.0001
% Silt+Clay	-1.36 p<0.0001
pH	+12.76 p<0.026
Net NO3 Accumulation (mg N/kg soil), total model r^2=0.772, p<0.0001	
Initial NO_3^-	+1.94 p<0.0001
Ca:Al Ratio	+0.26 p<0.0001
pH	+7.83 p<0.048
Al	-0.07 p<0.014
% Silt+Clay	+0.27 p<0.048
Percent Nitrification, total model r^2=0.708, p<0.0001	
Initial NO_3^-	+0.66 p<0.0001
Ca:Al Ratio	+0.18 p<0.0001
Al	-0.05 p<0.0007
% Silt+Clay	+0.24 p<0.0019

Thus, all three measures of organic N turnover were directly proportional to and strongly affected by the initial NO_3^- concentration in the soil samples. Soil texture was also a significant variance component for all three measures of N turnover; however, N mineralization was inversely proportional to the silt+clay content of the soil whereas net NO_3^- accumulation and percent nitrification were directly proportional to that property. Total N mineralization was not affected by Al^{3+} or Ca:Al molar ratio; in contrast both net NO_3^- accumulation and percent nitrification were directly proportional to Ca:Al ratio and inversely proportional to Al^{3+} concentration.

DISCUSSION

As a result of changes in the patterns of fossil fuel use over the last two decades, the relative proportions of NO_3^- and SO_4^{2-} in precipitation and dry deposition have shifted away from predominatly S deposition to relatively greater deposition of N. Currently, upper elevations of the Appalachian Mountains receive as much as 27 kg N/ha/yr in precipitation (Lovett 1992), a level almost an order of magnitude greater than that in pristine precipitation (Aber et al. 1989; Lovett 1992). The geographic range of our seven study sites was designed to encompass a gradient of historical deposition of NO_3^-, SO_4^{2-}, and H^+ increasing from west to east, and a more recent NO_3^- deposition gradient increasing from 2.7-5.6 kg N/ha/yr in Illinois to 13.5-18.1 kg N/ha/yr in West Virginia (Work Group One 1983).

Chronic NO_3^- deposition can have a range of effects on forest soils, including enhanced leaching of Ca^{2+}, increased Al^{3+} solubility, and decreased Ca:Al ratio (Aber et al. 1989; Foster et al 1989). This pattern emerged clearly among our six study sites west of the Appalachian Plateau (i.e. excluding the Fernow Experimental Forest, West Virginia): Ca^{2+} decreased, Al^{3+} increased, and Ca:Al ratio decreased by two orders of magnitude between southern Illinois and southern Ohio. This spatial pattern was consistent with the temporal pattern of change in soil and leachate chemistry

reported from a sugar maple (*Acer saccharum*) forest in Ontario over 1981-1986 caused presumably by heavy N deposition in acidic precipitation (Foster et al. 1989).

Aber et al. (1989) hypothesized that chronic high NO_3^- deposition could reduce microbial activity and, thereby, reduce the rates of N mineralization and nitrification. Although this hypothesis was supported by the rates we observed in our six study sites west of the Appalachian Plateau, the longitudinal patterns of variation in N mineralization and nitrification differed. N mineralization decreased gradually and linearly with longitude, and the pattern of change correlated most strongly with pH. Over the 8.5° of longitude represented by our gradient, the rate of N mineralization decreased by 66%. In contrast, nitrification was significant only in the two study sites in which the Ca:Al ratio was >20; in all other sites nitrification was negligible. These data were consistent with *in vitro* studies demonstrating strong inhibition of nitrification by Al^{3+} and Fe^{3+}, even in the presence of high NH_4^+ concentrations (Liang and Tabatabai 1978), and supported the notion that nitrification is more susceptible to inhibition by low pH and high Al^{3+} than is N mineralization (Legge and Crowther 1987).

The soils of the Fernow Experimental Forest (WV) departed in a number of respects from the patterns which emerged among the other six sites. Extractable NO_3^- and NH_4^+ concentrations and organic matter content were greatest in this site. The greater organic matter accumulation may have been a function of the of higher elevation (therefore lower mean temperature) of this site. Similarly, the higher concentrations of inorganic N in the A-horizon may have been a function of greater mean annual precipitation, higher elevation (therefore lower primary productivity), and differences in the concentration of N in precipitation.

The rate of N mineralization per unit soil mass at the Fernow E.F. was considerably greater than those we observed in soils from the other six sites. However, this appears to have been primarily a function of differences in organic matter content. When N mineralization was expressed on a per unit organic matter basis, the activity of the soils of the Fernow became consistent with the longitudinal pattern suggested by the other six sites. This was not true, however, for either net NO_3^- accumulation or proportional nitrification: both remained higher than would be predicted on the basis of longitude even when expressed on an organic matter basis. This greater production and accumulation of NO_3^- indicates that the degree to which mineralization of organic N to NH_4^+ exceeded uptake by plants, fungi, and bacteria was greater at the Fernow than at all of the other study sites except Kaskaskia. Again, this is likely due to the higher elevation and cooler climate of Fernow producing lower uptake demands. Thus, we feel the departure of the soils of the Fernow from some of the longitudinal patterns we observed among the other six sites was the result of direct and indirect effects of differences in elevation.

Both mineralization and nitrification were strongly correlated with initial soil NO_3^- concentrations. This may have been the result of a simple feedback loop: soils which support high rates of mineralization are likely to produce sufficient NH_4^+ to allow for significant NO_3^- production production. Thus, high rates of mineralization correlate well with high concentrations of the products of prior mineralization (i.e. NO_3^- and NH_4^+). Thus, we feel our finding of strong correlations between organic N turnover and soil pH, Ca:Al ratio, and soluble Al^{3+} have greater significance than does the demonstration of the autocorrelation between activity rates and product accumulation.

The ramifications of these changes in soil N turnover may have significant effects on oak growth and mortality. Oaks, like many other ectomycorrhiza-dependent species, dominate N-poor and N-limited ecosystems (Vogt et al. 1991). Although these tree species may lack the ability to reduce significant amounts of NO_3^- to amine for protein biosynthesis, they can dominate in strongly N-limited conditions because of the ability of their ectomycorrhizal symbionts to forage actively for NH_4^+ and readily mineralizable, low molecular weight N compounds and because of the ability of ectomycorrhizae (ECM) to reduce modest amounts of NO_3^-. Under N-enriched conditions, where P may be as limiting as N, or more so, species of trees which rely on vesicular-arbuscular mycorrhizae (VAM) and which are capable of much greater relative growth rates, such as maples and yellow poplar, may assume dominance (Vogt et al. 1991). Thus, any process which shifts the balance of inorganic N in the soil solution towards a greater NO_3^-:NH_4^+ ratio and increases overall N availability, may negatively affect the competitive ability of oaks and other ECM-dependent species. Furthermore, if the low Ca:Al ratio and high soluble Al^{3+} concentrations we observed in the eastern portion of our gradient can affect ECM fungi directly, then the ECM-dependent oaks would be at even a

greater disadvantage. This sequence of events has been implicated in the decline of ECM-dependent spruces and pines in Europe (e.g. Jansen 1991; Arnolds 1991). Further experimental analysis of the linkages between organic N turnover, soil solution NO_3^-:NH_4^+ ratio, Ca:Al ratio, ECM fungi, and oak growth/mortality in the eastern U.S. is clearly warranted.

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