

Nitrogen mineralization, groundwater dynamics, and forest growth on a Minnesota outwash landscape

DAVID F. GRIGAL^{1*} & PETER S. HOMANN²

¹*Department of Soil Science, University of Minnesota, 439 Borlaug Hall, St. Paul, MN 55108, USA (*author for correspondence);* ²*Department of Forest Science, Oregon State University, Corvallis, OR 97331, USA*

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Abstract. We measured aboveground biomass and aboveground net primary productivity (ANPP), groundwater depth and fluctuation, and *in situ* nitrogen (N) mineralization in 13 upland and 4 wetland forest stands at Cedar Creek Natural History Area (CCNHA). The area, in east central Minnesota (45°25' N, 93°10' W), is on well-sorted glacial outwash of very uniform fine sand. Uplands are interspersed with peatlands and the area has shallow groundwater. Stands were aggregated into six ecosystem types based on overstory composition: oak, pine-oak, mesic hardwoods, northern white-cedar, lowland hardwoods, and savanna. Aboveground overstory biomass ranged from 35 to 250 Mg ha⁻¹; lowest in the savanna and highest in the pine-oak. The ANPP ranged from about 2 to 7.5 Mg ha⁻¹; also lowest in the savanna but highest in the white-cedar. Over all types, the annual aboveground uptake of N was poorly related to available N measured by *in situ* mineralization ($r^2 = 0.01$), but the relationship was better ($r^2 = 0.88$) if N availability in the wetland stands was assumed to be a fixed proportion of N in the surface soil (1.5%). Over all types, *in situ* N mineralization was poorly related to ANPP ($r^2 = 0.05$) and biomass ($r^2 = 0.38$). Both ANPP and overstory biomass were more closely related to groundwater fluctuation ($r^2 = 0.87$ and 0.28, respectively) than to depth ($r^2 = 0.01$ and 0.21, respectively). The strength of all relationships varied with the inclusion or exclusion of data from the wetland types or the savanna. Total soil N and rates of mineralization were inversely related ($r^2 = 0.42$) because of data from wetland stands. Results demonstrate that the positive relationships between aboveground productivity and measured *in situ* N mineralization observed in upland forests are not valid for the landscape that includes wetland forests either because *in situ* measurements do not indicate N availability in wetlands or because of the presence of other limiting factors. The north temperate landscape includes an abundance of wetland forests with potentially strong linkages to uplands. This study suggests that the commonly-used measure of N availability provides inconsistent information about controls on ecosystems processes in this diverse landscape.

Abbreviations: ANPP – aboveground net primary productivity; CCNHA – Cedar Creek National History Area

Introduction

Landscapes are complexes of ecosystems differing in floristic composition and in the processes regulating nutrient availability and loss (Vitousek et al. 1982; Pastor et al. 1984; Zak et al. 1989). Terrestrial ecosystems are often linked through the transfer of energy and nutrients; ecosystems in upslope

positions typically contribute water, nutrients, and organic matter to those downslope. Differences in nutrient cycling along topographic gradients can result from the influence of temperature, moisture, and substrate availability on microbial activity (Davidson & Swank 1987; Groffman & Tiedje 1980; Zak & Grigal 1991).

One of the dominant paradigms of ecology is the premise that productivity in temperate forests is primarily limited by availability of nitrogen (N) (Dyck et al. 1986). This paradigm is supported by studies that relate productivity to rates of *in situ* N mineralization (Pastor et al. 1984; Zak et al. 1989), and by the significant increases in productivity of forest stands in response to N fertilization (Allen 1987). Many studies that have related rates of N mineralization to productivity have deliberately used sampling designs that attempted to minimize variation due to factors other than N, and were usually carried out on well-drained sites (e.g. Vitousek et al. 1982). Similarly, syntheses of the literature concerning N dynamics often restrict data to those from uplands (Vitousek 1982).

Productivity is clearly a function of the growth potential of the species under consideration, the availability of resources such as light, nutrients and water, and the efficiency of resource use. Because resources are inter-related, it is difficult to discern their individual effects. Differences in N dynamics of ecosystems are related to differences in other properties, frequently soil parent material, and hence to differences in the resulting complex of positive and negative feedbacks from that important property (Anderson 1988). For example, N mineralization is often positively correlated with soil water-holding properties (Pastor et al. 1982). Data derived solely from well-drained sites have led to the generality that N availability as measured by *in situ* N mineralization directly influences productivity over most sites.

In the subtle topography of east-central Minnesota (USA), the regional water table lies near the soil surface and links upland and wetland ecosystems. Although mineral soils are very uniform in texture, relatively small differences in elevation and hence in depth to the water table are associated with differences in plant species, edaphic conditions, and soil N dynamics (Zak & Grigal 1991). On upland sites in the area, aboveground productivity of grasses and herbs is limited by N (Tilman 1986). We sought to explore the relationship of N dynamics and primary productivity in both upland and wetland forests of this landscape.

Our null hypothesis was that variation in forest productivity over a mosaic of forest ecosystems, including uplands and wetlands, would be well explained by variation in N availability as measured by *in situ* mineralization techniques. Our alternative hypothesis, lack of a good relationship, could occur if either:

(a) the *in situ* techniques do not adequately reflect N availability, or (b) other resources are more important than N.

Methods

Study site

The study was conducted at Cedar Creek Natural History Area (CCNHA), a Long Term Ecological Research site. Cedar Creek is located in the Anoka Sand Plain in east central Minnesota (45°25' N, 93°10' W). Soils are derived from deep (20 m) well-sorted glacial outwash of very uniform fine sand (>90% sand). Slopes are gentle, usually less than 15 percent, and local relief ranges up to about 5 m. The regional water table is at or near the soil surface in low-lying areas and is only several meters below the surface in the highest elevations. Due to this hydrology, the subtle topography, and permeable soil materials, the study area is composed of numerous wetland and upland ecosystems that lie in proximity to one another. Only a few meters of horizontal distance often separate upland oak forests or old fields from adjacent wetlands.

Dominant upland soils at CCNHA are mapped as Alfic Udipsamments (Zimmerman series) and Typic Udipsamments (Sartell series). Dominant organic soils are mapped as Typic Borohemists (Rifle series) and Typic Borosaprists (Lupton series). Nearly 40% of CCNHA is wet mineral or organic soils (Grigal et al. 1974). The area has a continental climate and receives 660 mm of annual precipitation; mean annual temperature is 6 °C (Grigal et al. 1974). These climatic properties interact with the sandy soils to create typically dry upland sites. Prior to European settlement, a large proportion of the study area was either prairie or savanna, and many of the present ecosystems have developed following agricultural abandonment.

We established long-term monitoring plots in 13 upland and 4 wetland forest stands, chosen to represent the range of forest types at CCNHA. In each plot we measured overstory biomass, litterfall and woody increment; understory foliage mass; rates of net N mineralization and nitrification; forest floor and surface soil N; and water table depth and fluctuation.

Sampling and analysis

Each plot was 23 m in diameter. All trees on a plot were identified by species and diameters at breast height were measured. Overstory biomass was based on allometric equations (Alemdag 1983, 1984). Woody biomass increment was determined by coring and measuring annual growth for 10 years prior to the time of sampling (1990) from a subsample of trees on the plots (ranging

from 25 to 100%). For each plot, an empirical model of tree growth (Miner et al. 1988) was calibrated with the measured annual growth. The calibrated model was then used to simulate annual growth and mortality for all trees on the plots.

Overstory litter production on each plot was measured by five 920-cm² litter traps. Litter was collected six to eight times annually from September 1988 to August 1991, oven-dried (70 °C), sorted into components (broadleaf foliage, conifer foliage, woody tissue, and other material), and weighed. All material of each component from a plot was combined for the entire year, ground (40 mesh), and analyzed for N on a Carlo Erba CN analyzer. Understory foliar production was determined by harvesting non-woody tissue in five circular 0.48 m² subplots on the perimeter of each plot. Sampling was conducted in early August 1989. Aboveground net primary production (ANPP) was considered to include annual total litterfall, woody increment, and understory foliage production. Annual aboveground N uptake included N in annual litterfall plus N in understory foliage.

Within each understory subplot on upland sites, a 30 × 30 cm section of O horizon was cut with a steel knife and removed; the surface mineral soil to a depth of 15 cm was also collected. On wetland sites, the surface peat plus mineral soil to a combined depth of 10 cm was collected. Samples of understory, O horizon, and peat were oven-dried (70 °C), weighed, ground (40 mesh) and analyzed for N on the CN analyzer. The mineral soil samples were also dried and analyzed for N. Additional soil samples were collected to determine bulk density.

In June, 1989, a monitoring well was established in each plot, extending approximately 50 cm below the groundwater surface. Groundwater depth was measured periodically (ca. monthly) through October 1991. Mean groundwater depth over that sampling period and its fluctuation (the difference between maximum and minimum depths) were recorded for each plot.

In situ net N mineralization and nitrification were measured in the surface 15 cm of mineral soil in the upland stands and the surface 10 cm of peat plus mineral soil in the wetland stands. The root-free, loose O horizon was not included in the incubation. Measurements were made monthly between 19 June and 23 October 1989 (5 replications per plot), and between 24 April and 25 June 1990 (10 replications per plot). The *in situ* tube method (Zak & Grigal 1991) was used except in the wetland plots during 1990 when the buried bag method (Eno 1960) was used. Initial and final samples were extracted with 1 M KCl. Extracts were frozen and later analyzed on an Alpkem autoanalyzer for NH₄⁺ and NO₃⁻.

Monthly net N mineralization was the difference in NH₄⁺ plus NO₃⁻-N between initial and final samples. Monthly net nitrification was the difference

in NO_3^- -N between initial and final samples. Annual net N mineralization and nitrification were the sums of the monthly measurements. Samples were not incubated from late-October to April; less than 1% of annual N mineralization and nitrification occurs during this period at CCNHA (Zak et al. 1990).

Statistical analysis

Two quantitative classification techniques, agglomerative clustering and kmeans (Wilkinson 1986), were used to aggregate the 17 sampled stands into ecosystem types. Classification was based on overstory dominance as measured by basal area of the 13 most common tree species or species groups. Our primary interest was in the ecosystem types, not in individual stands within types; stands were considered to be replicates. One-way analyses of variance (Snedecor & Cochran 1967) was used to determine significance of differences in variables among types; mean separation was by Bayes least significant difference (Smith 1978). Relationships among variables were explored by regression based on means for each type (Wilkinson 1986).

Results and discussion

Classification

The two classification techniques produced similar results, and yielded six well-defined ecosystem types: oak (primarily *Quercus ellipsoidalis* E.J. Hill and *Q. macrocarpa* Michx. var. *olivaeformis* (Michx. f.) A. Gray), pine-oak (including oak, *Pinus strobus* L. and *P. resinosa* Ait.), mesic hardwoods (*Tilia americana* L., *Quercus borealis*, and *Acer saccharum* Marsh.), northern white-cedar (*Thuja occidentalis* L.), lowland hardwoods (*Fraxinus nigra* Marsh., *Betula papyrifera* Marsh., and *Acer rubrum* L.), and savanna (primarily *Quercus ellipsoidalis* and *Q. macrocarpa*) (Table 1). Oak is the areally dominant ecosystem type at CCNHA, and that type was represented by seven stands; two stands represented each of the remainder of the types. The oak ecosystem, in part because of its areal dominance, has a range of compositions from nearly pure oak to admixtures with most species listed above.

Groundwater

Groundwater depth ranged from at or near the surface in wetlands to over 6 m in the pine-oak type (Table 2). Similarly, groundwater fluctuations ranged from about 0.2 m to over 1 m (Table 2). The depth to the water table and its fluctuations were weakly related ($r^2 = 0.14$, $p > 0.2$), with a tendency for less fluctuation on the wetter sites (Table 2).

Table 1. Basal area composition of forest ecosystem types studied at Cedar Creek Natural History Area. Species listed by relative dominance over all studied stands. Each type represented by two stands except oak (seven stands).

Species	Ecosystem type					
	Oak	Pine-Oak	Mesic Hdwds	White-Cedar	Lowland Hdwds	Savanna
	(m ² ha ⁻¹)					
<i>Quercus borealis</i> / <i>Q. ellipsoidalis</i>	20.9	10.0	9.9	0	0	7.6
<i>Pinus strobus</i>	2.3	21.5	0.4	7.9	0	0
<i>Thuja occidentalis</i>	0.2	0		36.4	0.2	0
<i>Fraxinus nigra</i>	0	0	0	0.3	14.9	0
<i>Acer rubrum</i>	2.4	4.2	0.1	0.1	1.1	0
<i>Tilia americana</i>	0	0	12.7	0	0	0
<i>Quercus alba</i> / <i>Q. macrocarpa</i>	2.4	0	1.8	0	0	1.4
<i>Pinus resinosa</i> / <i>P. banksiana</i>	0.5	7.6	0	0	0.1	0
<i>Betula papyrifera</i>	0.5	0.5	3.6	1.3	2.8	0
<i>Acer saccharum</i>	0.1	0	5.2	0	0.1	0
Total ¹	29.4	43.9	33.7	52.7	23.0	9.0

¹ Including other minor species

N mineralization

Annual N mineralization, as measured by the *in situ* incubations, ranged from virtually nothing to nearly 70 kg ha⁻¹ yr⁻¹ (Table 2). For upland types, N mineralization was higher in June and July than earlier or later in the year. For lowland types, rates over time were low and erratic. For comparison, Zak & Grigal (1991) found the highest rate in May–June for savanna and in June–July for oak at CCNHA.

The annual rates are intermediate with respect to those previously reported for the same ecosystem types, but not the same locations, in CCNHA (Fig. 1). Rates from Pastor et al. (1987) cannot be quantitatively compared because of lack of measures of uncertainty, but the rates from Zak et al. (1990) and Zak & Grigal (1991) can be compared with those we measured. Where rates were measured on comparable systems, they only differed in the savanna ($s_p = 4.7$ kg ha⁻¹ yr⁻¹, $t = 3.40$, 2 d.f., $p < 0.05$), not in the lowland hardwood

Table 2. Properties of the ecosystem types studied at Cedar Creek Natural History Area.

Property	Units	Types					Anova results				
		Oak	Pine Oak	Mesic Hdwds	White-Cedar Hdwds	Lowland Hdwds	Savanna	S_p^1	F^2	p^3	LSD ⁴
Overstory biomass	Mg ha ⁻¹	174.6	241.7	168.2	183.0	82.9	34.9	33.6	10.4	0.000	68.8
Basal area	m ² ha ⁻¹	29.4	43.9	33.7	52.7	23.0	9.0	6.0	13.2	0.000	12.1
Stocking	stems ha ⁻¹	505	480	815	1605	890	210	230	9.85	0.001	470
Understory foliage	Mg ha ⁻¹	0.43	0.35	0.30	0.21	1.44	1.13	0.28	6.94	0.004	0.60
Overstory litterfall	Mg ha ⁻¹ yr ⁻¹	3.71	4.85	3.90	5.66	3.70	0.49	0.59	17.1	0.000	1.17
Overstory wood increment	Mg ha ⁻¹ yr ⁻¹	1.74	2.10	2.78	1.59	1.33	0.41	0.35	10.1	0.001	0.72
Soil N (O + mineral)	Mg ha ⁻¹	2.18	2.08	2.16	3.18	4.67	1.62	0.73	4.92	0.013	1.61
Initial mineral N	kg ha ⁻¹	8.6	11.4	6.9	2.3	3.7	3.8	2.3	5.26	0.010	5.1
Net N mineralization	kg ha ⁻¹ yr ⁻¹	56.6	66.2	50.1	1.0	16.2	18.7	17.9	5.33	0.010	39.2
Nitrification	% of min.	50	68	18	31	52	58	22	1.35	0.31	N.D. ⁵
Groundwater depth	m	4.64	6.24	5.13	0.06	0.01	3.61	0.11	13.4	0.000	0.22
Groundwater fluctuation	m	0.57	0.39	0.37	0.21	0.17	1.14	0.02	11.4	0.000	0.03
Groundwater NO ₃ ⁻	mg L ⁻¹	0.50	0.26	0.17	0.04	0.02	0.11	0.32	1.29	0.34	N.D.

¹ Based on one-way analysis of variance, comparing differences among ecosystem types.

² F -statistic from one-way analysis of variance with 5 and 11 degrees of freedom.

³ Probability of significantly larger F -statistic.

⁴ Bayes least significant difference (Smith 1978).

⁵ Not determined.

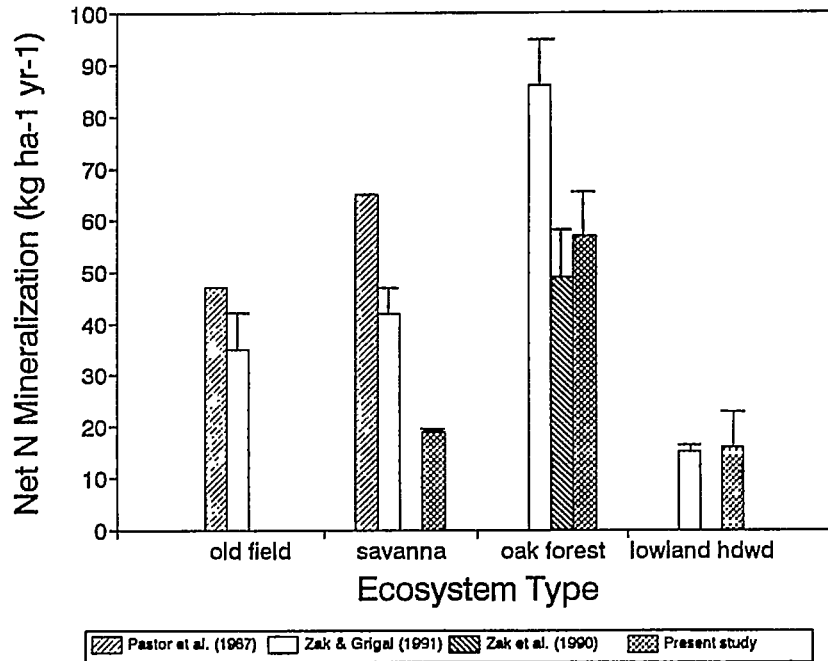


Fig. 1. Annual rates of N mineralization from *in situ* incubations in four ecosystem types at Cedar Creek Natural History Area; present study compared to previous reports. Incubations carried out in same types but not identical locations in 1984 (Pastor et al. 1987), 1987 (Zak & Grigal 1991), mid 1987 to mid 1988 (Zak et al. 1990), and mid 1989 to mid 1990 (present study). Standard error indicated.

($s_p = 7.4 \text{ kg ha}^{-1} \text{ yr}^{-1}$, $t = 0.14$, 2 d.f., $p > 0.5$) nor oak forest ($s_p = 20.5 \text{ kg ha}^{-1} \text{ yr}^{-1}$, $F(2,10) = 0.91$, $p > 0.25$) (Fig. 1).

The reported rates do not reflect the annual climatic differences during the three studies. Precipitation differed substantially during the periods; 430 mm during Zak & Grigal's (1991) incubations, 320 mm during those of Zak et al. (1990); and 700 mm during our incubations; while growing degree days were less variable; 2140, 2420, and 2270, respectively (base 4.5 °C). Despite large differences in mean rates, especially for the oak forest, significance of those differences is negated by the high pooled variance (Fig. 1). Causes of differences include microclimate differences among sites, differences in litter quality (Pastor et al. 1984), and by historical factors such as differences in stand age and associated time since disturbance (Zak et al. 1990). The rates that we measured are at the lower end of the range of other rates reported from forests in the Great Lakes States (Nadelhoffer et al. 1983; Pastor et al.

1984; Zak et al. 1989; Gower & Son 1992). The low rates are consistent with the xeric low-N environment of CCNHA (Tilman 1986).

Between 50 and 70% of the mineralized N was converted to NO_3^- except in the mesic hardwoods and the cedar types (Table 2). The low rate of nitrification in the cedar is not surprising, but the low rate in the mesic hardwoods is surprising because of the abundant data on high rates of nitrification in other mesic forests in the eastern US (Pastor et al. 1984; Mladenoff 1987; Zak et al. 1989). In general, the proportion of nitrification that we measured is very similar to that reported by Zak & Grigal (1991) for CCNHA. The rate of nitrification expressed as mass per unit area was related to the NO_3^- concentration in groundwater beneath the stands (average of three samples collected during one year) ($r^2 = 0.47$, $p < 0.15$, Table 2). Although weak, this demonstrates one of the linkages between ecosystems and groundwater.

Annual *in situ* mineralization was related to 'initial' mineral N, or the average NH_4^+ -N plus NO_3^- -N in all pre-incubation cores taken over the entire sample period ($r^2 = 0.94$, $p < 0.01$, Fig. 2a). This simpler measure ranks the ecosystem types in the same order as does the more painstaking *in situ* incubations, and could be used in broader surveys of relative N dynamics over our landscape. Similarly, Gower & Son (1992) reported *in situ* N mineralization to be positively correlated with initial NO_3^- -N; the relationship with initial mineral N including NH_4^+ -N was not reported. Measured mineralization was also related to water table depth ($r^2 = 0.82$, $p < 0.02$, Fig. 2b), but not to its fluctuation ($r^2 = 0.00$, $p > 0.5$, Fig. 2c). The strength of the former relationship is strongly influenced by the very low mineralization rates in the wetland types (Fig. 2b).

As reported in many studies (Nadelhoffer et al. 1983; Pastor et al. 1984; Zak et al. 1989; Gower & Son 1992), *in situ* N mineralization was poorly related to the sum of N in forest floor and surface mineral soil ($r^2 = 0.42$, $p > 0.2$). In our case, this relationship was inverse because of low mineralization rates but high soil N in the wetland types (Table 2). Mineralization expressed as a percent of soil N differed significantly among ecosystem types ($s_p = 0.8\%$, $F(5,11) = 6.22$, $p = 0.006$). Proportional mineralization was highest in pine-oak type (3.2%) and lowest in the wetlands (near 0). Pastor et al. (1987) reported a significant relationship between *in situ* mineralization and soil N in old-fields and a savanna at CCNHA, about 3%. Although the data from Zak & Grigal (1991) at CCNHA indicate no consistent relationship, mineralization was also about 3% of soil N in the savanna, and was 6% in the oak forest and 0.4% in the lowland hardwood type. Our data for those same ecosystem types are 1.2%, 2.2%, and 0.3% respectively.

The rates of *in situ* N mineralization in the upland ecosystems are well related to annual aboveground N uptake as measured by N in annual litterfall

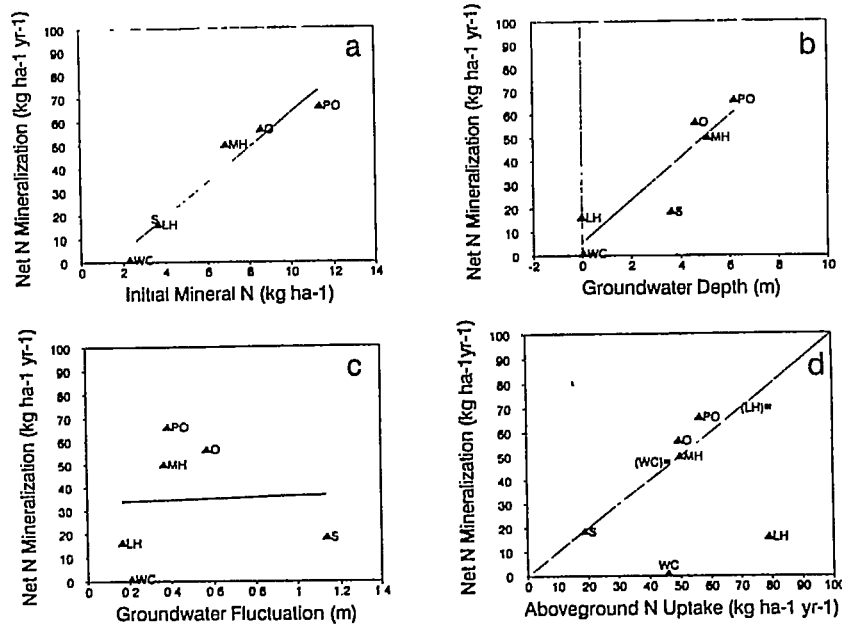


Fig. 2. Comparison of *in situ* rates of N mineralization in six forest ecosystem types in Cedar Creek Natural History Area with: (a) initial mineral N (NH_4^+ plus NO_3^-) measured at the beginning of all incubation periods, $r^2 = 0.94$; (b) mean depth of groundwater during the measurement period, $r^2 = 0.82$; (c) total fluctuation in groundwater depth over a two-year measurement period, $r^2 = 0.00$; and (d) annual aboveground N uptake in the forests as measured by N in overstory litterfall and understory foliage (triangles). In (d), N mineralization in wetland stands also estimated as a fixed proportion (1.5%) of the periodically aerated peat soil (squares), and the indicated line is 1:1. Types include O = oak, PO = pine-oak, MH = mesic hardwoods, WC = white-cedar, LH = lowland hardwoods, and S = savanna.

and understory foliage (Fig. 2d). Conversely, the *in situ* rates in the wetland ecosystems are poorly related to annual N uptake (Fig. 2d). Because of the wetlands, the overall relationship is poor ($r^2 = 0.01$, $p > 0.5$, Fig. 2d). The very low rates of measured mineralization in the wetlands deserve scrutiny because of the poor relationship to annual N uptake. If the *in situ* technique correctly measures N mineralization, then vegetation in wetlands must rely on other sources of the N. One potential source may be the groundwater, with N in solution moving to the wetland vegetation via both convection and diffusion. Under that hypothesis, the low concentrations of N in groundwater in the wetlands are related to its continual uptake by plants. An alternative explanation of our observations in the wetlands is that the *in situ* techniques that we used do not correctly measure N mineralization, and are not appropriate for soils that are periodically inundated (Binkley & Hart 1989).

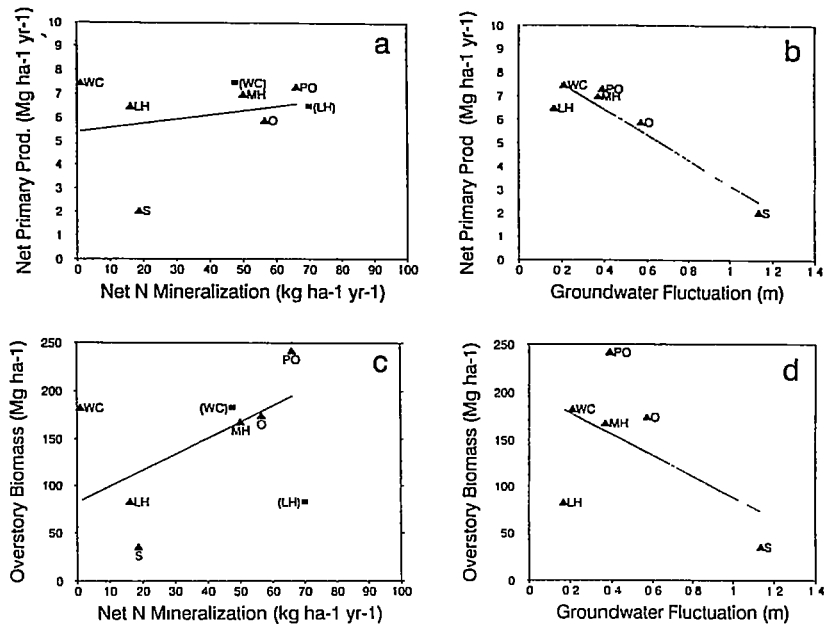


Fig. 3. Relationship of aboveground net primary productivity in six forest ecosystem types in Cedar Creek Natural History Area with (a) *in situ* rates of N mineralization, $r^2 = 0.05$, and (b) total fluctuation in groundwater depth over two year measurement period, $r^2 = 0.87$, and relationship of aboveground total overstory biomass with (c) measured rates of N mineralization, $r^2 = 0.38$, and (d) with total fluctuation in groundwater depth, $r^2 = 0.28$. In (a) and (c), N mineralization in wetland stands also estimated as a fixed proportion (1.5%) of the periodically aerated peat soil (squares). Types include O = oak, PO = pine-oak, MH = mesic hardwoods, WC = white-cedar, LH = lowland hardwoods, and S = savanna.

In previous work in wetland (bog) forests in Minnesota, Grigal (1991) concluded that approximately 1.5% of the N in the periodically aerated layer of surface peat was annually mineralized. When that proportion is applied to the approximate mean depth of water table fluctuation on the wetland sites (15 cm), these alternative estimates of N mineralization are much more closely related to N uptake ($r^2 = 0.88$, $p < 0.01$, Fig. 2d). It is clear that the *in situ* mineralization technique that we used, though reproducible in wetlands (Fig. 1), does not reflect N availability in those sites.

Productivity and biomass

Across all ecosystem types, measured *in situ* N mineralization was not related to either ANPP nor to total aboveground overstory biomass (Table 3, Fig. 3). Both ANPP and biomass were poorly related to water table depth (Table 3). Although biomass was also poorly related to water table fluctuation, ANPP

Table 3. Correlation coefficients (Pearson's 'r') between ANPP or aboveground biomass and measures of N mineralization or groundwater. *In situ* mineralization measured over one year, adjusted mineralization equal to *in situ* rates in uplands and estimated as 1.5% yr⁻¹ of the N in the periodically aerated peat soil in wetlands. Total number of types = 6, of forests (no savanna) = 5, of uplands (no wetlands) = 4, and of upland forests = 3.

Variable	Independent	All types	All forests (no savanna)	All uplands (no wetlands)	Upland forests (no savanna, wetlands)
ANPP	<i>In situ</i> N-mineralization	+0.22	-0.26	+0.94	+0.32
	Adjusted N-mineralization	+0.81	-0.27	na ¹	na
	Grdwater depth	-0.08	-0.07	+0.90	+0.86
	Grdwater fluctuation	-0.93	-0.51	-0.99	-0.96
Biomass	<i>In situ</i> N-mineralization	+0.62	+0.62	+0.99	+0.95
	Adjusted N-mineralization	+0.58	-0.23	na	na
	Grdwater depth	+0.46	+0.74	+0.94	+0.93
	Grdwater fluctuation	-0.52	+0.55	-0.93	-0.35
Significance criterion ²		0.73	0.88	0.95	0.99

¹ Not applicable.

² For 90% probability that slope not = 0, r must be > criterion.

was more strongly and inversely related (Table 3, Fig. 3). In most cases, the strength of the relationships among the environmental measures and productivity are influenced by the data from one or two ecosystem types, and often by those from the savanna (Fig. 3). Various combinations of data, including consideration of all ecosystem types, all upland types (excluding wetlands), all upland forests (excluding savannas), and all upland and wetland forests (excluding savanna), produce varying degrees of relationship (Table 3). Strong and significant relationships only exist among very contrasting ecosystems, much weaker relationships exist among similar ecosystems. This may be an example of hierarchical controls on production and biomass accumulation.

Many data collected in upland forests in the Great Lakes States report close relationships between *in situ* N mineralization and both ANPP and overstory biomass (Pastor et al. 1984; Zak et al. 1989). Our data, including both wetlands and savanna (Table 3), do not support extending those relationships to the full moisture gradient.

Conclusions

Our results demonstrate that N mineralization measured with commonly-used *in situ* techniques is not well related to productivity over a range of upland and wetland forests; we have rejected our null hypothesis. Although the results support previous conclusions about positive relationships between aboveground productivity and *in situ* N mineralization in upland ecosystems, this relationship does not appear to be valid for the landscape including wetland forests. This reflects either the failure of current *in situ* methodologies to determine N availability in periodically inundated forests, or the fact that other limiting factors are important. The north temperate landscape includes an abundance of wetland forests with potentially strong linkages to uplands. This study suggests that the commonly-used measure of N availability provides inconsistent information about controls on ecosystems processes in this diverse landscape.

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