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ORIGINAL PAPER

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Using soil temperature and moisture to predict forest soil nitrogen mineralization

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Abstract Due to the importance of N in forest productivity ecosystem and nutrient cycling research often includes measurement of soil N transformation rates as indices of potential availability and ecosystem losses of N. We examined the feasibility of using soil temperature and moisture content to predict soil N mineralization rates (Nmin) at the Coweeta Hydrologic Laboratory in the southern Appalachians. We conducted seasonal laboratory incubations of A and AB horizon soils from three sites with mixed-oak vegetation using temperature and moisture levels characteristic of the season in which the soils were collected. The incubations showed that temperature and temperature-moisture interactions significantly affected net soil Nmin. We used the laboratory data to generate equations relating net Nmin to soil temperature and moisture data. Using field-collected temperature and moisture data we then calculated Nmin on similar forest sites and compared predicted rates with in situ, closed-core Nmin measurements. The comparison showed that the in situ Nmin was greater than rates predicted from laboratory generated equations (slope =3.22; r^2=0.89). Our study suggests that while climatic factors have a significant effect on soil Nmin, other factors also influence rates measured in the laboratory and in situ.

Keywords Nitrogen mineralization rates · Laboratory incubation · In situ incubation

Introduction

Although total forest soil nitrogen (N) pools can be quite large, N availability often limits forest growth and productivity (Keeney 1980). For example, the upper 10 cm of soil in forests of the southern Appalachians contain from 750 kg N ha^{-1} in xeric mixed-oak pine sites to 3,780 kg N ha^{-1} in high-elevation northern hardwood forests. On these two site types, net N mineralization rates (Nmin), often used as an index of N availability, average 1.4 and 17.9 kg N ha^{-1} each 28 days during the growing season (Knoepp and Swank 1998). Ecosystem and nutrient cycling research often includes measurement of soil N transformation rates as indices of potential plant uptake and ecosystem loss. In temperate soils, Nmin displays a seasonal pattern; rates are greatest in summer or fall when soil temperatures are highest (Nadelhoffer et al. 1984; Strader et al. 1989; Bonilla and Roda 1992). Adams and Attiwill (1986a) and Polglase et al. (1992) found that seasonal patterns were only present when using in situ measurements of Nmin. Soils incubated in the laboratory did not show any seasonal patterns, presumably due to high incubation temperatures.

Many studies have sought to characterize the response of soil Nmin to temperature and moisture. Often, the objective is to identify the optimum temperature or soil moisture content for individual soils at which N mineralization occurs. Maximum Nmin normally occurs when soil temperatures are between 25 and 35°C (Nicolardot et al. 1994; Stark and Firestone 1996) and soil moisture is near field capacity (Stanford and Epstein 1974). Data from these studies are used in simulation models to predict actual N availability or potential N mineralization under climate change conditions. However, optimal conditions are rarely encountered in the field. In a study of soil fungi from northern hardwood forests in Rhode Island, Carreiro and Koske (1992) found that different fungal species have different optimum temperatures. The fungal species they isolated from these soils differed depending on the temperature used for incubation in the laboratory.

We conducted seasonal laboratory incubations under soil temperatures and moisture conditions found in situ. We hypothesized that responses to temperature or moisture would vary with sampling season. For example, temperature responses would be greatest in the winter and moisture responses would be greatest in the fall. We proposed to use the laboratory data to predict net in situ

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Nmin using field-collected soil temperature and moisture data. These relationships would improve our ability to predict soil N availability in nutrient cycling and forest productivity models.

Materials and methods

Site description

We conducted our study at the Coweeta Hydrologic Laboratory, a 2,180-ha USDA Forest Service facility in the southern Appalachian mountains of western North Carolina. An average of 1,900 mm precipitation is received annually with most months receiving at least 100 mm. The growing season extends from early May to early October. Mean monthly temperatures are highest in June to August (20°C) and lowest in December to January (5°C).

The three sites sampled represent the mixed-oak hardwood community, the major forest type in the Coweeta basin, occupying 50–60% of the area. All sample sites are on reference watersheds and included: a low-elevation north-facing site, 865-m elevation with 15° aspect and 34° slope; a high-elevation northeast-facing site, 1,001-m elevation with 75° aspect and 33° slope; and a low-elevation south-facing site, 739-m elevation, facing 180° with a 31° slope. Soils on the three sites differ, representing both the Inceptisol and Ultisol orders. The Trimont soil series – a fine-loamy, mixed, mesic Humic Hapludults – occupies the low-elevation north-facing site. The Chandler series – a coarse-loamy, micaceous, mesic Typic Dystrochrepts – is found on the high-elevation north-facing site. Finally, the Fannin series – a fine-loamy, micaceous, mesic Typic Hapludults – occupies the south-facing low-elevation site.

Soil sample collection and incubations

We collected soil samples on dates representing plant phenological seasons; dormant season, bud break, growing season, and abscission layer formation. Samples (>1 kg) were collected from the two surface horizons, usually A and AB horizons, of four shallow soil pits on each site. We put the samples on ice and returned them to the laboratory. The four individual samples were mixed thoroughly and sieved to <6 mm, yielding a composite sample representative of the A and AB horizons on each site. All A horizon soils are gravelly loam or sandy loam in texture. AB horizon textures include sandy clay loam, loam and fine sandy loam. Seasonal soil incubation conditions, temperature and moisture content, were determined from long-term soil temperature and moisture data sets measured at Coweeta. Temperatures were determined from a soil temperature model developed by Vose and Swank (1991) with data from the Coweeta basin. The median temperature and temperature range are representative of each season. Soil moisture levels corresponded with mean monthly values determined over 6 years of measurement by Helvey and Hewlett (1962); high and low moisture levels were plus and minus 10%. Laboratory temperature and soil moisture incubation conditions for each season are shown in Table 1.

Three replicate samples of each temperature/moisture treatment were prepared by weighing 50 g of each composite soil into a 0.94-L glass-canning jar. We covered jars containing soil with 0.01-mm thick plastic film and placed them in incubators at the appropriate temperature, within 24 h of collection (t=0). Three 50-g sub samples of each soil were oven dried (105°C) overnight to determine percent moisture. We added the appropriate amount of water to obtain the desired soil moisture content on day 1. Soils collected in the winter were wetter than the lowest percent moisture. These soils were incubated at the appropriate temperature without plastic film to allow drying, until the correct moisture content was obtained, determined by weighing soil jars daily (4–5 days), after which jars were covered with plastic film. We weighed covered soil plus jars weekly and adjusted moisture content as necessary throughout the 28-day incubation.

Time zero NH_4^+ and NO_3^--N concentrations were determined in the composite soil sample from each site and each horizon. Each sample was extracted in triplicate with 2 M KCl. Five grams of fresh soil were shaken for 1 h at a 1:4 soil /KCl ratio, then centrifuged at 3,715 *g* (6,000 rpm) for 15 min. Soil NH_4^+ and NO_3^- concentrations were determined again after 28 days for all samples at each temperature and moisture combination. Extractable NH_4^+-N and NO_3^--N were determined in the supernatant on an autoanalyzer (Technicon Instruments, Tarryton, N.Y.) using alkaline phenol (Technicon Instruments, 1971) and hydrazine sulfate reduction(USEPA 1983), respectively. Net N mineralization rates were calculated as the change in NH_4^+ plus NO_3^- from time zero to 28 days. All soil N data are reported on an oven-dry weight basis.

Data analysis

Data were analyzed using a split-plot experimental design with seasons representing plots. Statistical analyses were conducted using site means of each moisture/temperature combination. We

Table 2 Analysis of variance for laboratory incubation net nitrogen mineralization rates showing effects of sample site (*Site*); season of the year when soil was collected (*Season*) as plots; high, median, and low incubation temperature (*T*), and high, median, and low incubated soil moisture content (H_2O). Effects of Season and Site were tested using the Site*Season mean square as the error term. Data from A horizon soils are shown; means of the three replicates of each temperature and soil moisture combination for each site were analyzed as a split plot experimental design

Source	*df*	Mean square	F-value	Prob>F
Site	2	13.69	7.18	0.02
Season	3	4.44	2.33	0.17
Site*Season	6	1.91	4.06	<0.01
T	2	16.21	34.53	<0.01
H_2O	2	0.96	2.05	0.14
T*H_2O	4	1.42	3.03	0.02
T*Season	6	2.71	5.76	<0.01
H_2O*Season	6	0.58	1.23	0.30
T*H_2O*Season	12	0.25	0.53	0.89
Error	64	0.47		

Table 1 Soil moisture and temperature values used in laboratory incubation of A and AB horizon soils

Season	Phenological stage	Julian day	Temperature (°C)			Moisture content (g H_2O g soil^{-1})		
Winter	Dormant	31	0[a]	5	10	0.23	0.33	0.43
Spring	Bud break	115	5	10	15	0.25	0.35	0.45
Summer	Growing season	200	12	17	22	0.25	0.35	0.45
Fall	Abscission layer formation	272	5	15	25	0.20	0.30	0.40

[a] AB horizon soils were not incubated at 0°C

used the GLM Procedure of SAS (SAS 1985) to conduct analysis of variance on laboratory N mineralization rates for each soil horizon (Table 2; SAS 1985). Significant effects of site and season were tested using the Site × Season mean square as the error term. Effects of soil temperature and moisture levels were determined using low, median, and high designations (n =3) within each season (n =108 for A horizon soils).

Prediction and validation

We used the non-linear regression procedure (Proc NLIN) of SAS (SAS 1985) to develop a predictive equation relating net rates of N mineralization to soil incubation temperature and moisture content. An exponential relationship with temperature was used based on the finding of Van't Hoff (Rodrigo et al. 1997). The A and AB horizon soil equations were generated separately. Equations generated for each season were not significantly different, so all data were combined. The equation for A horizon soils [Nmin =0.92*H*exp (0.102T)] included a soil moisture correction term. The relationship in the AB horizon equation [Nmin =0.114*exp (0.102T)] was not significantly improved by including soil moisture.

The predictive capability of the A horizon equation was tested using in situ measurements of N mineralization rates made between 1991 and 1996 on four forested sites within the Coweeta basin (Knoepp and Swank 1998). Two were sites used for the laboratory incubation study: the north facing low- and high-elevation sites. We also included a south-facing mixed oak-pine site and a mesic north-facing mixed cove hardwood site to expand the soil temperature and moisture range. A modified closed core in situ method was used (Adams and Attiwill 1986b); see Knoepp and Swank (1998) for details. The time zero soil moisture content, measured for all in situ samples, was used in the prediction equation. Temperature data were the mean monthly values from measurements taken every 5 min on each of the four plots. Comparisons between predicted and measured Nmin were made using the Regression Procedure from SAS (SAS 1985).

Results and discussion

Laboratory soil incubations

Temperature significantly affected net Nmin rates of laboratory incubated A and AB horizon soils (P <0.01; Table 2). Nmin rates were greatest at the highest incubation temperature for both A (Fig. 1) and AB horizon soils. In A horizon soils, there was also a significant interaction between incubation temperature and soil moisture content (Table 2). This is evident in the trend toward greater Nmin rates as soil moisture content increased in soils incubated at the highest temperature in both the fall and summer incubations. Temperature and H_2O interactions were not significant in AB horizon soils.

We used soil temperature and moisture values characteristic of the sampling season; this allowed us to measure the response of organisms active at that time of year. The importance of incubation temperature was noted by Carreiro and Koske (1992) in a study of fungi in the northern hardwood forests of Rhode Island. They found that the fungal species isolated differed with incubation temperature suggesting that microbial species or varieties function optimally at different soil temperatures. High Nmin measured under non-limiting temperature and moisture conditions with added NH_4^+ or organic N may be measuring the activity of microbial populations that typically would not be active under field conditions (Carreiro and Koske 1992). In Powers' (1990) study of Nmin patterns along an elevation gradient, us-

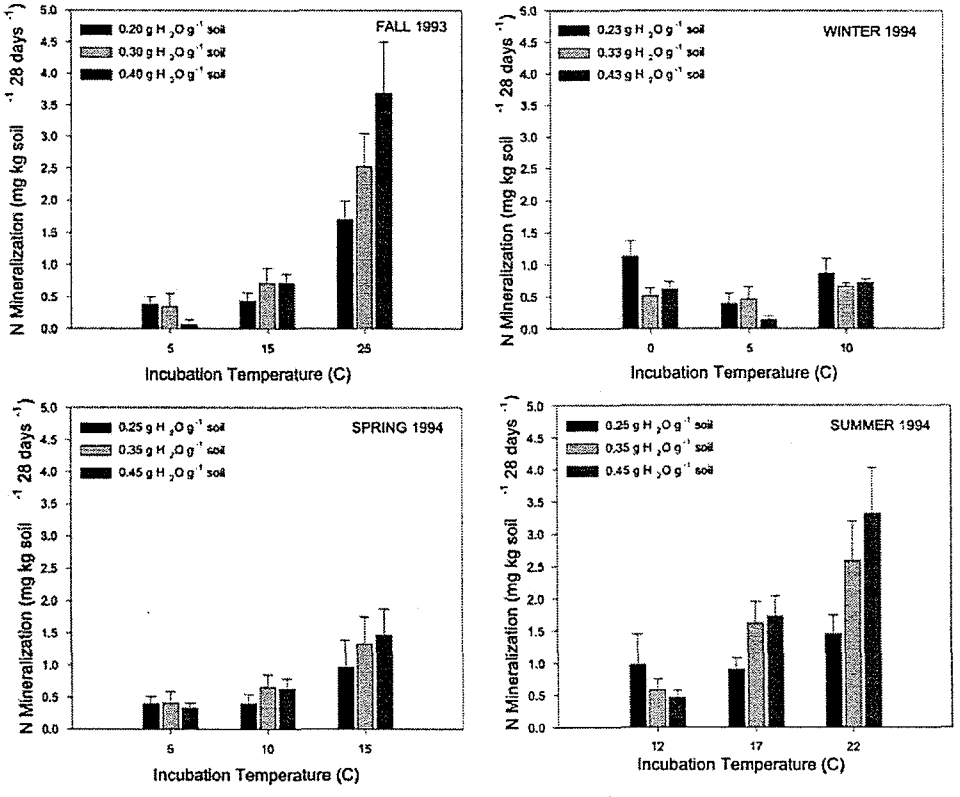

Fig. 1 Nitrogen mineralization rates of A horizon soils during laboratory incubation at three incubation temperatures and levels of soil moisture. Data shown are seasonal means of three sites (n =9). *Bars* represent standard errors

ing aerobic and anaerobic in situ soil incubations, he concluded that soil moisture limited mineralization in low-elevation sites, while temperature was most limiting at high-elevation sites. In an Alaskan chronosequence, Klingensmith and Van Cleve (1993), found that while temperature limited N mineralization in all successional stages, soil moisture was significant only in the late successional sites.

Laboratory incubation experiments examining temperature and moisture effects on Nmin are often seeking optimal conditions. For example, Nicolardot et al. (1994) measured temperature effects on the movement of labeled C and N through microbial biomass; maximum mineralization rates occurred between 20–28°C. Stanford and Epstein (1974) examined the relationships between soil moisture and Nmin for nine different soil types. Maximum mineralization rates occurred at soil matric potentials between 0.3 and 0.1 MPa; about 10–35% moisture by weight. This optimal soil moisture range held true for all soil types tested. The optimal temperatures identified by Nicolardot et al. (1994) were approximately equal to the maximum incubation temperature we used for our summer and fall incubations (22–25°C), where our maximum rates were measured. On the other hand, the range of soil moisture values we used (15–38% by volume) did not include those (<10%) found by Stanford and Epstein (1974; #2224) to be limiting. Our data show significant interaction between incubation temperature and soil moisture content. This is evident in the summer and fall, when Nmin is greatest. However, data show that when temperature is limiting (i.e. during the dormant season), increasing soil moisture content had little effect (Fig. 1). Response differences could be due to seasonal changes in soil microbial populations, in terms of either numbers or the dominant species present.

Nmin varied significantly among sites (P <0.01; Table 2). Rates were greatest on the south-facing low-elevation site and least on the north-facing high-elevation site (Fig. 2). The warmer south-facing site could have microbial populations more responsive to increased incubation temperatures. Casals et al. (1995) found that Nmin, used as an index of N supply, did not differ between aspects or plots in the oak forests they studied. On the other hand, Garten et al. (1994) studied spatial patterns of Nmin in Walker Branch Watershed, a southern mixed-oak watershed. They found that Nmin in valleys, where vegetation differed, was significantly greater than side slopes and ridges.

Our laboratory data did not show significant seasonal effects on Nmin (Table 2). However, we measured maximum Nmin rates in the summer and fall when temperatures were highest; 3.5 mg N kg soil^{-1} 28 days^{-1} in the A horizon (Fig. 1) and 2.0 mg N kg soil^{-1} 28 days^{-1} in AB horizon (data not shown). Rates were very low during winter and spring incubations, <1.5 mg N kg soil^{-1} in both A and AB horizons. This suggests that in soils with greater Nmin potential laboratory incubations may detect seasonal patterns when seasonally appropriate temperature and moisture conditions are used. Many researchers

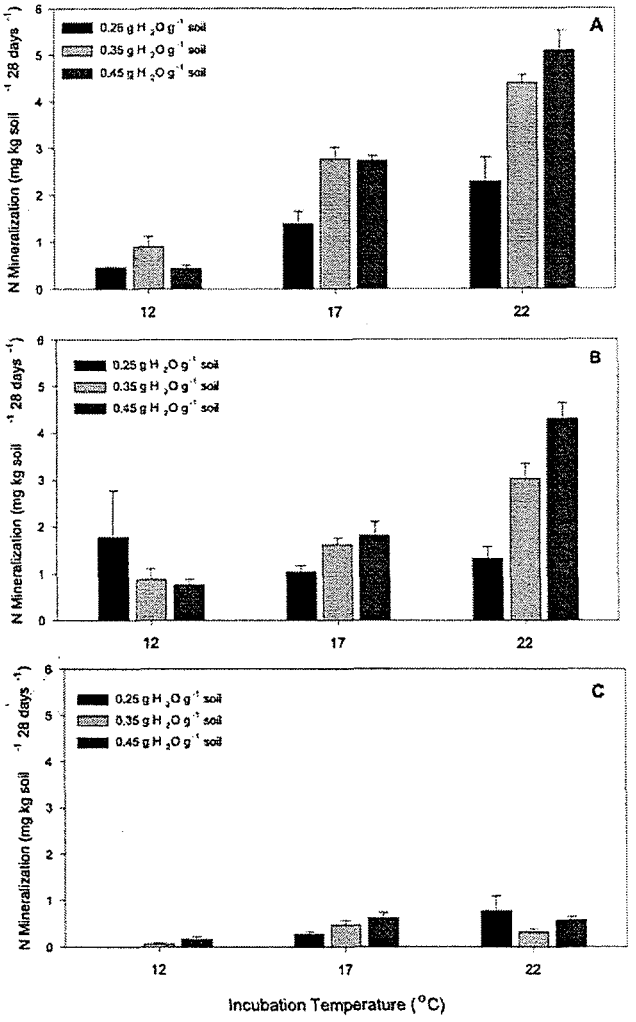

Fig. 2A–C Nitrogen mineralization rates of A horizon soils collected in summer 1994. Data show mean values for each incubation temperature and soil moisture combination for **A** south-facing low-elevation, **B** north-facing low-elevation and **C** north-facing high-elevation sites (n =3). *Bars* represent standard errors

have noted seasonal patterns in Nmin using in situ methods. Studies in temperate regions of the world find that rates are greatest when soil temperatures are high, in summer and in fall (Virzo De Santo et al. 1982; Nadelhoffer et al. 1984; Adams and Attiwill 1986a; Strader et al. 1989; Son and Lee 1997; Knoepp and Swank 1998). However, the temporal responses can vary due to other climatic influences. For example, Diaz-Ravina et al. (1993) studied soil microbial populations in Spain, a Mediterranean climate. They found that populations were lowest in the summer and winter, presumably due to limiting moisture in summer and limiting temperature in winter. In tropical forest soils, where temperature is not limiting, Wong and Nortcliff (1995) found that soil moisture fluctuations between wet and dry seasons largely regulate Nmin rates.

Prediction of in situ rates and validation

We developed an exponential relationship between Nmin and temperature based on the finding of Van't Hoff (Rodrigo et al. 1997). The equation for A horizon soils was significantly improved by the inclusion of a soil moisture correction term [Nmin =0.92*H*exp (0.102T)]. Including a soil moisture term did not improve the AB horizon equation [Nmin =0.114*exp (0.102T)]. Rodrigo et al. (1997) examined nine models developed to simulate temperature and moisture effects on Nmin. Most models used either the Van't Hoff or Arrhenius temperature functions. The Van't Hoff function describes the exponential increase in Nmin with temperature using a Q_{10} constant to represent the temperature increase. The Arrhenius function relates the natural log of Nmin and the reciprocal of the absolute temperature. The thermodynamic basis of the Arrhenius method results in Q_{10} changes as temperature increases. This suggests it may not be useful in biologically diverse soils where each microbial group has its own temperature response. Both methods overestimate microbial process rates at high temperatures and because microbial activity is zero at temperatures of 0°C neither is completely adequate in describing the response of soil microorganisms over the range of soil temperatures.

We included soil water content (cm H_2O cm^{-3} soil) in Nmin prediction equations due to the significant interactions between incubation temperature and soil moisture in A horizon soils (Table 2). Soil moisture acts as a correction term for the exponential response of Nmin to temperature. Researchers studying the effects of soil water content on Nmin have used water potentials ranging from insufficient to sufficient water content. The Nmin response to soil water is modeled as either a linear function with water content (cm H_2O cm^{-3} soil; Stanford and Epstein 1974), or a logarithmic response with water potential (kPa; Rodrigo et al. 1997). Some studies examining the combined effects of moisture and temperature used linear combinations of the variables, reducing Nmin at less-than-optimal soil moisture levels (Rodrigo et al. 1997). Models of temperature and moisture interactions may not include second-order terms adding errors due to nonlinear temperature responses. When examining these relationships one must also consider the reference temperature and moisture content used, which have a major influence on Nmin estimates.

We found that Nmin rates predicted using laboratory generated equations with field measurements of soil temperature and soil moisture underestimated in situ measured Nmin. Comparison of predicted versus in situ measurements of Nmin using 5 years of seasonal means for each of the four sites (n =16) had a slope of 3.22 and r^2=0.89 (Fig. 3). Other studies have compared laboratory and in situ Nmin measurements with varied results. Greater laboratory rates have been attributed to increased soil disturbance via sieving (Stenger et al. 1995) plus the laboratory optimization of soil temperature and moisture (Adams and Attiwill 1986b), which rarely occurs in situ.

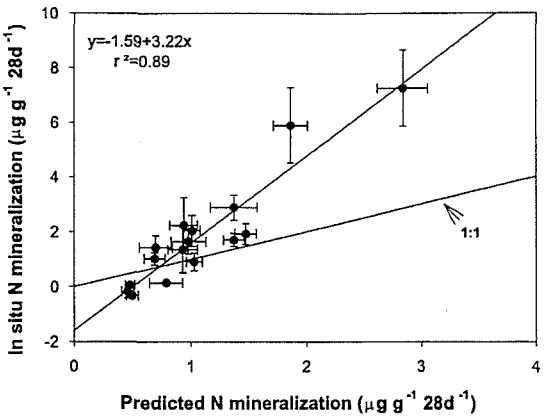

Fig. 3 Relationship between N mineralization rates predicted from field soil temperature and soil moisture data using the equation generated from laboratory incubation data (A horizon soil only) and seasonal means of in situ N mineralization measurements (0–10 cm) collected from 1991 to 1995. The regression equation and r^2 are shown; *bars* represent standard errors for both predicted and in situ data

Polglase et al. (1992) used anaerobic incubations in the laboratory and found poor relationships with in situ data. The laboratory data failed to identify significant seasonal differences that in situ measurements indicated. Adams and Attiwill (1986a) found good agreement between in situ and laboratory rates in their ability to identify site differences in Nmin. A methods comparison by Knoepp and Swank 1995 on prescribed burn sites showed no difference between lab and in situ measurements; both methods found significant treatment effects. However, both temperatures in situ and in the laboratory were similar, 20 and 25°C.

Underestimates of in situ Nmin based on laboratory prediction may result from several factors. In our experiment, in situ temperatures did not extend over the same range as the laboratory incubations. Using a small portion of the prediction curve may increase the likelihood of error. Mean monthly temperatures fell at or above the mid-level temperature used in the lab, while maximum field temperatures during in situ incubations were often greater than the lab maximum. In situ temperature fluctuations ranged from 5 to 15°C and were greatest in the spring and winter. Temperature fluctuations may stimulate Nmin, even though mean temperatures are below optimum. Soil moisture content was a secondary controlling factor in laboratory rates of Nmin; this may not be the case in situ. Examination of 6 years of in situ Nmin data across an environmental gradient showed that interannual variability was related to monthly precipitation patterns, not air temperature (Knoepp and Swank 1998). The range of in situ soil moisture content was narrow compared to laboratory values. For example, spring soil moisture ranged from 0.25 to 0.45 g H_2O g $soil^{-1}$ in the lab, and 0.29 to 0.35 g H_2O g $soil^{-1}$ in situ. Soil disturbance through sieving may stimulate short-term microbial activity, but may also alter the effective soil moisture

content. Sieving changes soil structure and aggregate arrangement effectively decreasing large pore space. The removal of roots and the removal and disturbance of soil insects may also impact Nmin rates measured in situ. Stenger et al. (Stenger et al. 1996) found that in agricultural soils N is released from severed roots after an initial period of immobilization. Soil insects directly and indirectly impact Nmin due to their role in soil structure maintenance and decomposition and nutrient cycling rates (Linden et al. 1994; Powers et al. 1998).

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