Biogeochemistry 2: 281–297 (1986)

Seasonal and annual variation in nitrogen mineralization and nitrification along an elevational gradient in New Mexico

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Key words: nitrogen mineralization, nitrification, nitrogen cycling, forest ecosystem, disturbance

Abstract. Patterns and amounts of nitrogen loss from disturbed ecosystems vary widely. The mineralization of organic nitrogen to ammonium and then nitrification to nitrate are important processes regulating nitrogen cycling rates and nitrogen losses. Nitrification is a significant process because of the production of the nitrate anion which is easily leached or denitrified. Most studies of these processes do not evaluate their seasonal and yearly variations. This study demonstrates that marked seasonal and yearly variations can occur in these processes in different ecosystems and suggests that nitrogen loss or other system properties correlated with one arbitrarily selected collection can be misleading. Spruce-fir and ponderosa pine ecosystems demonstrated little actual or potential nitrification. Aspen and mixed conifer ecosystems demonstrated distinct seasonal patterns with increased rates of mineralization and nitrification during spring and summer months and a precipitous decline in both rates coincident with autumn foliage litterfall.

The relative availability of soil nitrogen along with the amount of nitrogen circulating annually in litterfall prior to disturbance are useful predictors of the *potential* for nitrate production and loss following disturbance. However, other controls, including regulation by organic compounds, appear important in determining seasonal and annual variation in actual nitrification rates.

Introduction

Loss of nutrients from ecosystems, particularily nitrogen, has received intensive research in recent years. Studies have documented large ranges of nitrogen losses following disturbance (Vitousek and Melillo 1979), as well as large ranges of nitrogen cycling rates in undisturbed conditions (Gosz 1981; Vitousek et al. 1982, Pastor et al. 1984). Vitousek et al. (1982) have reported a direct relationship between the amount of nitrogen circulating annually in undisturbed forests (i.e. litterfall N) and the proportion of the forest floor nitrogen which could be mineralized and subsequently nitrified (which could be lost following disturbance). They also demonstrated a significant positive correlation between the mean annual concentration of mineral nitrogen in undisturbed forest floor or soil horizons and the rate of nitrification during incubation in the laboratory. The lag time prior to the onset of nitrification during incubation was negatively correlated with mean mineral nitrogen concentration of all field collections. Also, annual litterfall

nitrogen was correlated with laboratory mineralization potentials for forest floor and mineral soil samples from one collection in one season (August). However, a number of reports describe large seasonal and yearly variations in mineral nitrogen concentrations and evolution (Gosz 1978, Olsen and Reiners 1983, Pastor et al. 1984, Nadelhoffer et al. 1983, 1984), and mean concentrations during several arbitrarily selected periods may be very different. Thus, the general correlations described by Vitousek et al. (1982) must be reevaluated with respect to the natural seasonal and yearly variations that occur.

Vitousek et al. (1982) did describe seasonal patterns of available N for trenched versus control plots. Their objective was to identify forest ecosystems which demonstrated the potential for loss of nitrogen after disturbance in which the cessation of plant uptake is a significant component. By trenching intact sections of soil, plant roots were severed and further plant uptake was eliminated by weeding. The trenched plots then simulated disturbed areas where plant uptake of mineralized nitrogen would be minimized in contrast to nearby areas (controls) with intact vegetation without the confounding effects of canopy removal and soil disturbance. The seasonal data on extractable nitrogen levels were expressed as the difference between trenched and control plot values. This was a useful measure to evaluate the effects of plant uptake on the availability of inorganic nitrogen, but one which hides the true seasonal patterns of available nitrogen.

Our objectives were to document seasonal variation in actual nitrogen availability over an elevational gradient in New Mexico using trenched and control plots, and to measure the potential mineralization rates of the organic substrate collected at various times to determine actual changes in mineralization potentials. The measurements would allow us to evaluate whether low available nitrogen levels in the control plots resulted from low rates of production or from high rates of plant uptake, leaching, or volatilization.

Study sites

The study sites are located in the Tesuque Watershed Study Area in the Sangre de Cristo Mountains of New Mexico. A number of vegetational zones occur in this area as a result of temperature and moisture gradients over the elevational range (2408–3740 m). The 4 forest communities studied were ponderosa pine (*Pinus ponderosa* Laws.); mixed-conifer dominated by Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco) and white fir (*Abies concolor* [Gord. & Glend.] Hoopes); aspen (*Populus tremuloides* Michx.); and spruce-fir (*Picea engelmanii* Parry, *Abies lasiocarpa* var. *arizonica* [Merriam] Lemm.). Table 1 contains specific site data. Additional information on topography, climate, geology, hydrology, productivity, and soils is available (Gosz 1975, 1977, 1978, 1980a, 1980b, Gosz et al. 1983, Graustein 1981, Vitousek et al. 1982).

Table 1. Site characteristics for study areas along an elevational gradient in New Mexico (modified from Vitousek et al. 1982)

	Dominant age (yr)	Annual Litterfall (kg/ha)	Litterfall N (kg/ha)	Soil Subgroup	Aspect	Slope	Elevation (m)	Precipitation (cm)
Poderosa pine	200	2320	6.4	Typic Ustorthent	SW	12%	2740	45–65
Mixed conifer	200	3900	18.0	Typic Udorthent	SW	10%	2720	45–65
Aspen	60	2530	15.0	Typic Cryochrept	WSW	10%	3110	49–75
Spruce-fir	300	1106	5.6	Dystric Cryochrept	W	15%	3415	55–85

Vitousek et al. (1982) reported on nitrification rates from field trenching and laboratory incubation studies as well as litterfall nitrogen values on these sites. Those results showed consistant patterns in the magnitude of estimated nitrogen cycling rates (e.g., mineralization, nitrification, and litterfall) in the order: aspen > mixed conifer ⩾ ponderosa pine > spruce-fir. Noteably, the annual litterfall nitrogen values of these sites were markedly lower than most of the other sites reported on by Vitousek et al. (1982).

Methods

Field extractions

At each site, ten replicate samples of forest floor and 0–10 cm depth mineral soil (hereafter referred to as soil) were collected as described below. Each replicate was sieved to remove large roots and rocks and separated into two equal portions. One portion was placed in pre-weighed bottles containing 100 ml of 2*N* KCl with PMA and the second portion was placed in a pre-weighed soil can. Both the bottle and soil can with contents were weighed after return to the laboratory. The soil can was placed in the oven and dried at 105 °C for 24 hours. The % weight loss of the soil can was then applied to the total soil weight of the bottle to obtain a dry weight for the extracted sample. The bottle with soil was decanted and the solution was analyzed for nitrate and ammonium by the Technicon Auto Analyzer methods described below.

Mineralization-nitrification incubation

Undisturbed areas adjacent to control sites used in earlier field trenching experiments (Vitousek et al. 1982) were used for the collection of forest floor and 0–10 cm depth mineral soil. A total of 10 samples were collected at approximately 1 m intervals at each site. Each forest floor sample contained the entire forest floor from a 10 by 10 cm area. The 0–10 cm soil sample was taken with a 2.5 cm diameter corer after the forest floor was removed. The ten replicate samples of either forest floor or soil were composited in a single plastic bag and placed on ice in a cooler. The samples were kept refrigerated until they could be prepared for incubation (approximately 7 days). The composited samples were sieved through a 4.0 mm sieve and the > 4.0 mm material was discarded. Live roots were removed by hand. The samples were thoroughly mixed and a small portion removed to determine moisture content (weight loss upon heating at 105 °C to constant weight). The appropriate amount of demineralized water was added to the plastic bag containing the composited sample to achieve a moisture content of −0.1 bars (Vitousek et al. 1982). The sample was well mixed and proportioned into weighed plastic cups. Each cup contained 12 g of mineral soil or 4 g of forest floor. The cups were sealed with a lid which contained

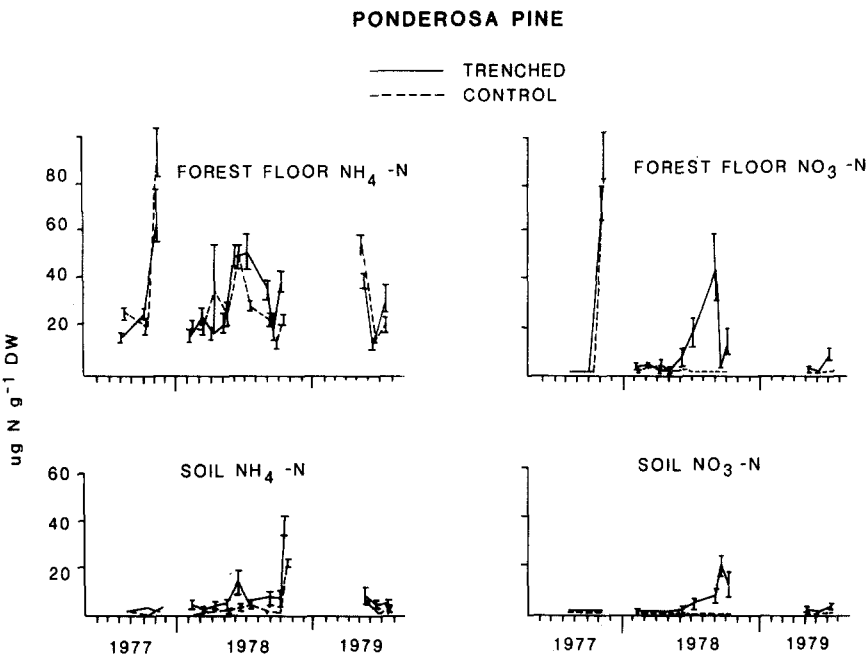

Figure 1. Responses of extractable NH_4-N and NO_3-N to trenching in forest floor and mineral soil (0–15 cm) in the aspen site (trenching strated in Nov. 1976 and completed in Feb. 1977). Values are means (+ SE).

a small hole for air exchange. Six subsamples were extracted immediately with 100 ml of 2*N* KCl (preserved with phenylmercuric acetate, PMA). The rest of the subsamples were incubated at 20 °C. Moisture lost during incubation was replenished weekly. On weekly intervals throughout the 10-week incubation, six subsamples were extracted with 100 ml of 2*N* KCl (added directly to the cup). The contents were thoroughly mixed and allowed to settle for 24 hours. The clarified supernatant was decanted into a plastic bottle and analyzed for nitrate and ammonium. Nitrate was analyzed by the cadmium reduction method on Technicon AutoAnalyzer (Vitousek et al. 1982). Ammonium was analyzed on a Technicon AutoAnalyzer by the modified alkaline phenol method of White and Gosz (1981).

^{15}N method

Heavy nitrogen was used to evaluate the importance of gaseous loss versus immobilization of the available nitrogen during incubation. A known amount of ^{15}N as NH_4Cl or KNO_3 was added to each sample contained in an incubation cup. After the incubation period, recovery of ^{15}N was determined on the entire cup sample. The sample was kjeldahl-digested (Schuman et al. 1973) and steam distilled following neutralization and the addition of MgO (the ammonium distillation method of Bremner 1965). The distillate was

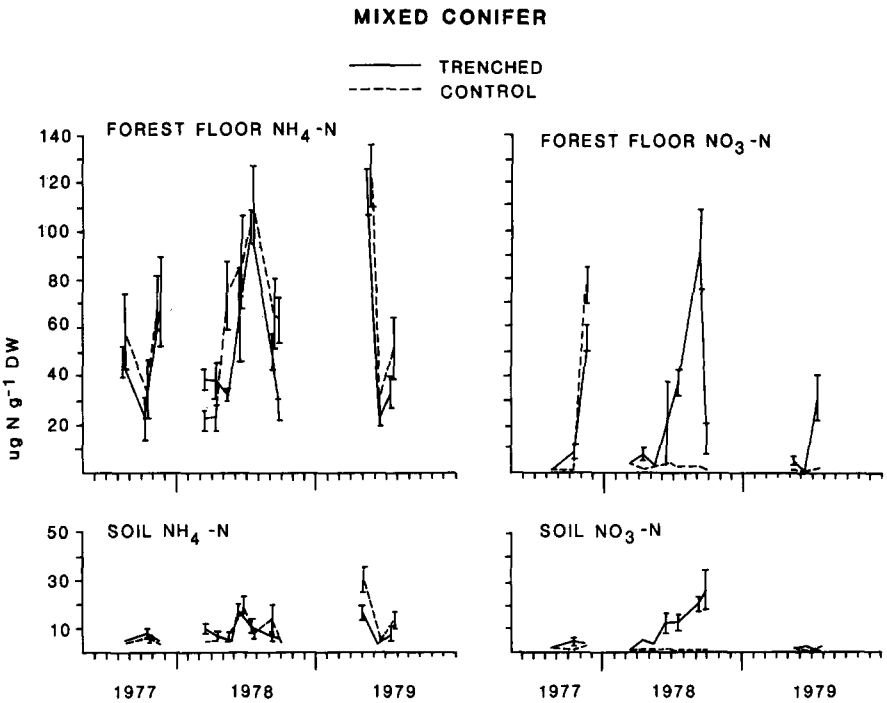

Figure 2. Responses of extractable NH_4-N and NO_3-N to trenching in forest floor and mineral soil (0–15 cm) in the mixed conifer site (site was trenched in May 1977). Values are means (+ SE).

collected in 0.01 *N* HCl. This method analyzes total organic N plus NH_4-N. The distillates were sent to Los Alamos National Laboratory for analysis of ^{15}N by a mass spectrometer isotope ratio method.

Results

Extractable NH_4-N and NO_3-N

Patterns of extractable NH_4-N and NO_3-N concentrations in samples from trenched and control plots demonstrated marked seasonal and yearly variations (Figures 1–4). Forest floors and soils were frozen and snow covered during the winter months preventing sample collection. This interval of snow cover was greater during the 1978–79 winter because of a larger snow pack accumulation that winter. The difference in snow accumulation between years was greatest at the lower elevations (ponderosa pine and mixed conifer sites), and may have been responsible for some of the yearly differences in extractable nitrogen concentrations discussed below. Based on the difference between trenched and control plots, Vitousek et al. (1982) reported the greatest response to trenching on these sites generally occurred

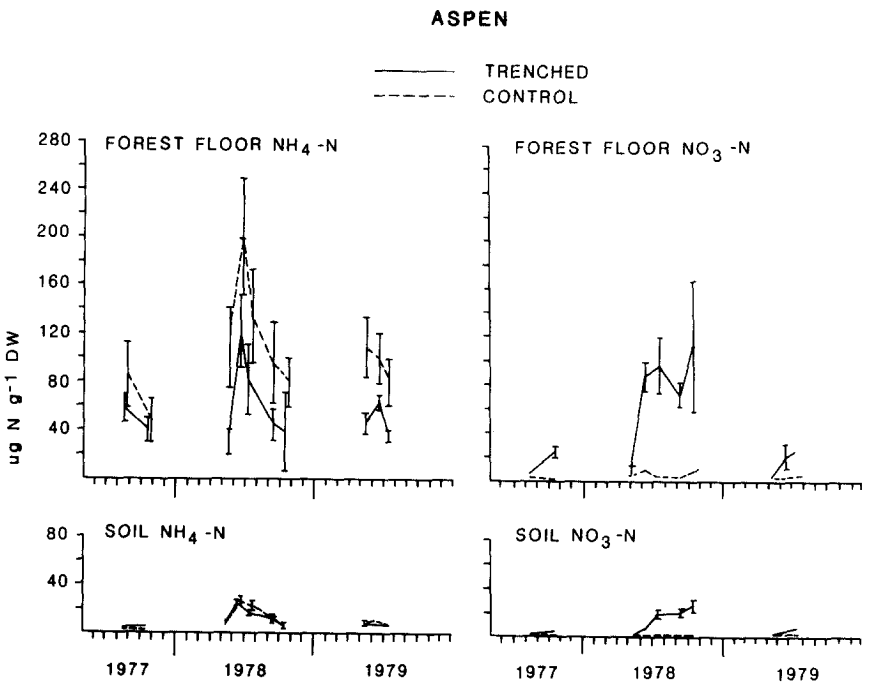

Figure 3. Responses of extractable NH_4-N and NO_3-N to trenching in forest floor and mineral soil (0–15 cm) in the ponderosa pine site (site was trenched in May 1977). Values are means (+ SE).

during the second season after trenching with trenched plot nitrate levels higher than control (i.e. aspen, mixed conifer and ponderosa pine sites). The spruce-fir site did not respond to trenching until the third season. The plots of actual extractable nitrogen concentrations (as shown in Figures 1–4) show that NO_3-N levels (i.e. nitrification) can be relatively high in both trenched and control plots before there is a difference between them.

The aspen site, which had the greatest annual N circulation in litterfall (Vitousek et al. 1982), accumulated nitrate in forest floor and soil from the trenched plots during the second year following trenching (Figure 3). This occurred although NH_4-N patterns and values were similar between trenched and control plots during the three years. The mixed conifer site, which had the next greatest annual N circulation, showed peak NO_3-N values in both trenched and control plots forest floors during the first year (Figure 2) but very low NO_3-N levels in control plots during years 2 and 3. The soils of the mixed conifer site (Figure 2) accumulated NO_3-N early within the second year after trenching. The ponderosa pine site (Figure 3) had high NH_4-N and NO_3-N values in both control and trenched forest floor in the first year following trenching. However, nitrate concentrations of trenched and control plots did not differ significantly until the second year. Surprisingly, the soil

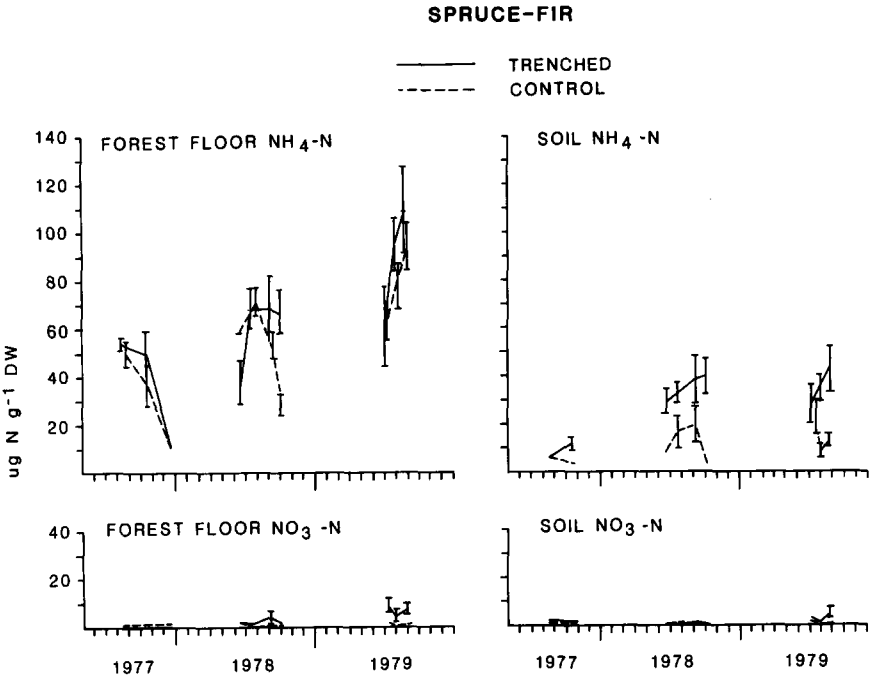

Figure 4. Responses of extractable NH_4-N and NO_3-N to trenching in forest floor and mineral soil (0–15 cm) in the spruce-fir site (site was trenched in Nov. 1976). Values are means (+ SE).

of the pine site showed a reverse pattern with no nitrate produced in the first year (Figure 3). The spruce-fir site, which had the least annual N circulation in litterfall, never accumulated nitrate in trenched plots (Figure 4). Although NH_4-N values changed seasonally, between years, and between trenched and control plots (i.e. for soils, Figure 4), NO_3-N levels were always low. The fact that NH_4-N concentrations were as high or higher than those of sites where nitrate readily accumulated suggests a factor other than substrate limitation inhibited nitrification.

Mineralization, nitrification potentials: control plots

Laboratory incubations were made of forest floor and soil from control plots for mineralization and nitrification potentials. These potential measurements, performed with favorable moisture and temperature regimes, would determine potential mineralization and nitrification rates in the control plots in the absence of plant uptake. The aspen site demonstrated the greatest mineralization and nitrification potentials followed by mixed conifer, pine, and spruce-fir. Lags in nitrate production were shortest in aspen and longest in spruce-fir (Figure 5). Although the nitrification lags were longer in forest floor than in soil samples, the highest rates of NO_3-N production during the

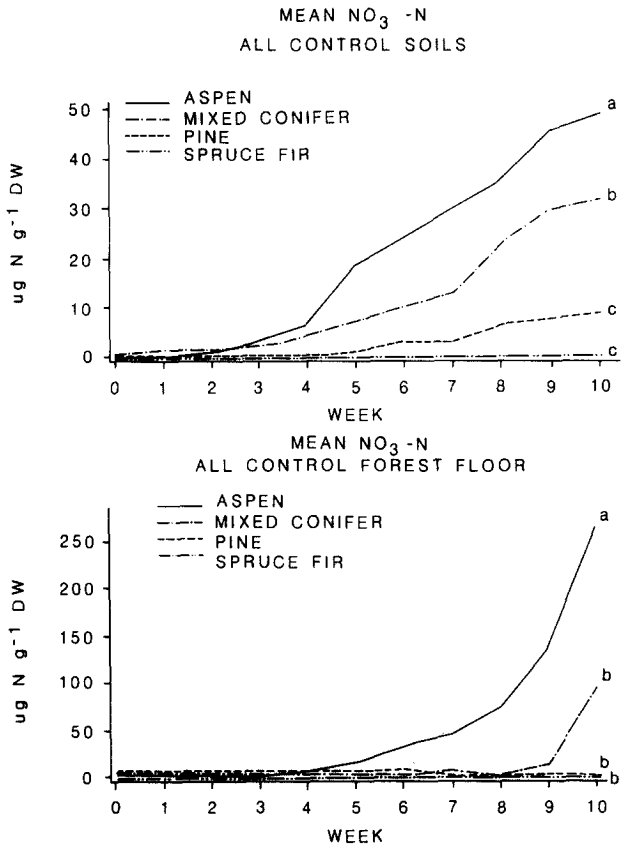

Figure 5. Extractable NO_3-N at weekly intervals during 10-week aerobic incubations (20 °C) of forest floor and mineral soil (0–15 cm) from aspen, mixed conifer, ponderosa pine (pine), and spruce-fir sites. Plots are means of all seasonal collections. Values at week 10 followed by different letters are significantly different ($P < 0.05$).

10-week incubations occurred in the forest floor. The lower rates of NO_3-N production in the soil were probably the result of their lower organic matter content (i.e. a dilution effect by mineral matter).

There were marked seasonal patterns in mineralization and nitrification potentials of each site (Table 2). Peak NH_4-N mineralization potentials occurred during late spring and summer months for forest floor and soil collections at all sites. Peak nitrification potentials in forest floor samples of the aspen and mixed conifer sites occurred in summer collections with a marked drop in October collections. The October collections coincided with the dominant leaf litterfall period at those sites. The patterns for the soils from aspen and mixed conifer were similar but less marked. All collections of the forest floor from ponderosa pine and spruce-fir showed little nitrification, even though field samples of the forest floor from ponderosa

Table 2. Mineralization and nitrification potentials for forest floor and soil collections from control areas of 4 sites in New Mexico. Values are NH_4-N or NO_3-N ($\mu g\, g^{-1}$) after 10-week incubation unless noted. Values in subgroup columns followed by different letters are significantly different ($P < 0.05$)

Collection Date (month-year)	Forest Floor		Collection Date (month-year)	Soil	
	NH_4-N	NO_3-N		NH_4-N	NO_3-N
		Ponderosa Pine			
1-79*	24.4	0.39	1-79*	13.3	1.18
4-79	34.3 b	0.00 b	4-79	14.2 a	2.13 c
8-79	54.0 a	0.00 b	8-79	6.2 bc	10.2 b
10-79	44.0 ab	0.00 b	10-79	3.6 c	20.9 a
5-80	27.4 b	0.07 a	6-80	8.8 b	1.23 c
		Mixed Conifer			
4-79	85.7 a	0.06 c	4-79	10.2 a	31.9 b
8-79	83.2 a	434. a	8-79**	5.0	41.6
10-79	44.7 c	2.45 c	10-79	1.72 b	24.2 c
10-80	20.4 d	15.1 b	10-80	1.85 b	24.6 c
12-80	62.2 b	0.56 c	12-80	2.81 b	45.3 a
		Aspen			
5-79	122. a	19.1 b	5-79	14.0 b	76.8 a
8-79	68.0 b	481. a	10-79	13.6 b	58.4 b
10-79	69.6 b	152. b	3-80	48.3 a	10.3 c
1-80	64.7 b	283. ab			
4-80	85.7 b	456. a			
		Spruce-Fir			
6-79**	169.	0.00	6-79**	32.3	0.00
9-79	56.0 c	0.00 b	9-79	4.8 a	0.00 a
1-80	166. a	0.31 a	1-80	5.9 a	0.00 a
7-80	98.7 b	0.00 b	7-80	11.3 a	0.00 a

*Seven-week incubation, not included in statistical analyses.
**Nine-week incbuation, not included in statistical analyses.

pine showed high nitrate levels shortly after trenching (material from that collection was not incubated for nitrification potential). In the soils from the pine site, peak nitrification occurred in the October collection prior to the dominant litterfall period in November. Soils from the Spruce-fir site never produced large quantities of nitrate.

Despite variation in total nitrification between sites, there was a consistent and marked drop in nitrification potential in the autumn coincident with foliage litterfall (Table 2). These differences in nitrification potentials demonstrate that the low nitrate levels in the control plots at this period were probably due to low rates of production and not due to high uptake or loss as is more likely the case during spring and summer when nitrification potentials were higher. The changes in nitrification potentials suggest that there were changes in substrate quantity, quality or microbial populations for samples collected at different collection dates. The NH_4-N concentrations (Table 2) do not appear different enough to support the explanation of insufficient NH_4-N substrate for nitrifiers (Lamb 1980, Robertson 1982).

Table 3. $^{15}NH_4^+$ additions to forest floor and soil samples to identify immobilization and gaseous loss potentials in laboratory incubations. Values are mean (standard error) % ^{15}N of 6 replicates at time 0 and after 4 weeks. The natural % ^{15}N is 0.0370 (0.004)

	% ^{15}N	
	week 0	week 4
Pine:		
Forest Floor		
Control	0.369 (0.004)	0.371 (0.001)
+ $^{15}NH_4$	0.879 (0.027)	0.828 (0.009)
+ $^{15}NH_4$ (sterilized)	0.830 (0.006)	0.815 (0.007)
Soil:		
Control	0.374 (0.0002)	0.391 (0.012)
+ $^{15}NH_4$	1.371 (0.012)	1.334 (0.012)
+ $^{15}NH_4$ (sterilized)	1.331 (0.009)	1.313 (0.013)
Spruce-fir:		
Forest Floor		
Control	0.368 (0.001)	0.376 (0.002)
+ $^{15}NH_4$	0.755 (0.009)	0.755 (0.002)
+ $^{15}NH_4$ (sterilized)	0.727 (0.003)	0.740 (0.001)
Aspen:		
Forest Floor		
Control	0.369	0.373 (n = 1)
+ $^{15}NH_4$	0.722 (0.005)	0.713 (0.006)
+ $^{15}NH_4$ (sterilized)	0.727 (0.004)	0.712 (0.004)

Since the low nitrification rates occured in samples collected in the autumn months which followed periods of very high nitrification rates in some sites, it is unlikely that low production rates could be the result of low nitrifier populations. Changes in substrate quality and/or the presence of inhibitors of nitrification appear the most likely explanations (Rice 1979). However, this information alone is not sufficient to enable one to identify causal effects.

Gaseous loss versus immobilization

Many of our mineralization-nitrification potential incubations demonstated an immediate decrease in extractable NH_4-N and NO_3-N which could be a result of immobilization, gaseous loss, or some combination. We performed ^{15}N additions to test for gaseous loss versus immobilization. In the first experiment, $^{15}NH_4Cl$ was used in forest floor collections from pine, aspen, spruce-fir, and soil collections from pine (these materials showed the greatest decrease in NH_4-N during early stages of incubation). These collections were treated in the following ways: (1) fresh material (control); (2) fresh material plus $^{15}NH_4Cl$ to achieve at least a doubling in the natural ^{15}N abundance (0.370%); (3) sterilized material plus $^{15}NH_4Cl$ to at least double the natural abundance (sterilization by autoclaving was expected to separate physical-chemical processes of gaseous loss from biological processes of gaseous loss). The samples were incubated for 4 weeks, a period when most of the

Table 4. $^{15}NO_3$ additions to forest floor samples to identify NO_3^- immobilization potentials in laboratory incubations. $^{15}NO_3$-N was added to achieve 0.750 % ^{15}N in the total sample at time 0. Kjeldahl digestion analyses (which do not analyze NO_3^-) at time 0 were not expected to detect added $^{15}NO_3$. Kjeldahl digestion analyses at 4 weeks of 0.750 % ^{15}N indicate 100% recovery (immobilization of added $^{15}N)_3$

		week 0	*week 4*	
Aspen				
replicate	1	0.370	0.701	
	2	0.369	0.667	
	3	0.372	0.698	
	4	0.371	0.651	
	5	0.370	0.703	
	6		0.662	
	$\bar{x}$	0.370	0.680 = 81.6% $^{15}NO_3$	
std. error		0.001	0.023	recovery
Mixed-Conifer				
replicate	1	0.370	0.743	
	2	0.371	0.730	
	3	0.369	0.733	
	4	0.469	0.739	
	5	0.481	0.716	
	6	0.477	0.745	
	$\bar{x}$	0.427	0.734 = 95.8% $^{15}NO_3$	
std. error		0.062	0.011	recovery

immobilization or gaseous loss occurs but before significant nitrate is formed. A total kjeldahl nitrogen analysis was performed (organic NH_3 + NH_4-N). The results (Table 3) demonstrate that virtually no gaseous loss occurred during the 4-week period. There were no statistically significant decreases in recovered ^{15}N in any of the treatments. There were downward trends, most pronounced in the unsterilized pine litter and soil experiments. These could indicate some volatile loss or some nitrification since $^{15}NO_3$-N would not be detected with this analysis. However, these results support immobilization as the dominant process reducing the available NH_4-N pool during the first weeks of incubation.

Another experiment was performed to test for the immobilization of NO_3-N or loss of NO_3-N by denitrification. Nitrogen as $K^{15}NO_3$ was added to increased the natural ^{15}N abundance from 0.370 to 0.750%. A kjeldahl digestion was performed at week 0 and after 4 weeks of incubation and analyzed for ^{15}N (Table 4). Since nitrate is not detected with this analysis, the week 0 value for ^{15}N should be 0.370 (natural abundance). If immobilization occurred during the incubation (i.e. reduced to organic NH_3 or NH_4-N), the abundance should approach 0.750%. The values (Table 4) show that 81.6% of the $^{15}NO_3$ was immobilized in aspen forest floor and 95.8% immobilized in mixed conifer forest floor. The time 0 analysis for mixed conifer was very interesting. By the time the sample could be digested (about 1 hour), a portion of the $^{15}NO_3$-N was already immobilized in several replicates. Clearly, these results demonstate rapid and high immobilization rates for NO_3-N in these samples.

Discussion

Studies which elaborate on factors controlling mineralization and nitrification are popular because of the recognized importance of nitrification in patterns of nutrient loss (Likens et al. 1970). Two explanations are generally used in hypotheses about low nitrification rates or lags in nitrification; 1) the poor affinity of nitrifying bacteria for ammonium (Jones and Richards 1977) could lead to low populations in sites with low ammonium availability, and 2) low nutrient availability could cause plants to produce and release polyphenols and other compounds which might inhibit microbial activity or complex substrate making it unavailable (Rice 1979). More specifically, organics may depress nitrifying populations and cause lags in nitrification. The onset of nitrate production may depend on the breakdown or removal (i.e. leaching, volatilization) of those organics as well as the time required for population growth. It is also possible that certain organics could inhibit the activity of an existing population, but not inhibit its number. In that case the lag would be dependent on the breakdown or removal of the organic compounds. The subsequent nitrification would not be delayed by a population growth period. That possibility is at odds with the contention that autrophic nitrifier populations cannot withstand stressful periods (Alexander 1976, Belser 1979).

Another possibility is that the organics present are not necessarily inhibitory but are simply not useable as energy sources by nitrifiers. The nitrifiers in our systems would have to be mostly heterotrophic for this possibility. Flanagan and Van Cleve (1983) reported microbial activity was greatly enhanced by energy-rich carbon additions regardless of whether or not N was added. Baath et al. (1978) and Foster et al. (1980) showed that nitrogen mineralization was less sensitive to total C/N ratios than to available-carbon/available-nitrogen ratios. The enhancement of microbial acitivty by energy-rich carbon additions provides another possibility for inhibition of nitrification since nitrifiers may be depressed by high CO_2 concentrations (Keeney et al. 1985). High microbial activity and its resultant nitrogen mineralization (production of NH_4-N) could be the cause of nitrification inhbition through high O_2 consumption (Schmidt 1982) and high CO_2 production (Keeney et al. 1985).

Our results indicate that the period associated with autumn litterfall profoundly influences nitrification rates. Litter production is a key process in the cycling of nutrients in ecosystems. The quantity and quality of litter influences decomposition, mineralization, and nitrification. These processes influence nutrient availability which in turn affects plant production and litter quality (Gosz 1981, Vitousek et al. 1982, Flanagan and Van Cleve 1983, Nadelhoffer et al. 1983, Pastor et al. 1984). Vitousek et al. (1982) reported a significant relationship between the N content of annual litterfall and nitrogen availability as measured by net nitrogen mineralization potentials in laboratory incubations of collections in August. Figure 6 shows

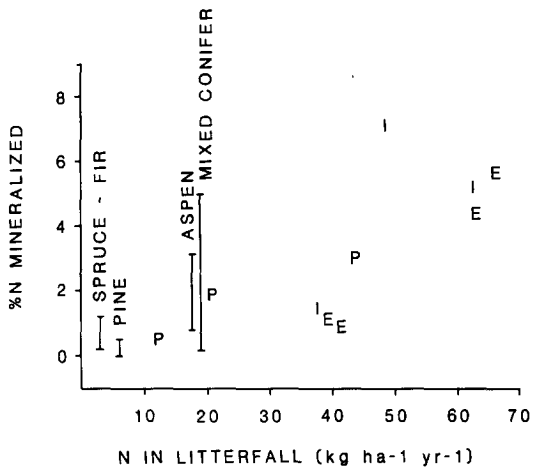

Figure 6. The relationship between the amount of nitrogen in annual litterfall and the proportion of forest floor nitrogen mineralized in 8-week aerobic incubations (from Vitousek et al., 1982) showing the range of values obtained at our sites in New Mexico. The symbols are: E = New England; I = Indiana; P = Pacific Northwest.

that relationship for a number of sites across the United States but also includes the range of nitrogen mineralization potentials from seasonal collections at each of our sites. We must modify the interpretation of Vitousek et al. (1982) to say that in sites with high amounts of nitrogen in litterfall, net mineralization and nitrification *can* be high during *certain* seasons. The relationship disappears for laboratory incubations of samples collected in the autumn following litterfall (the minimum values at each of our sites in Figure 6). Similarly, the relationship between nitrate production in laboratory incubations and *mean* mineral nitrogen concentrations (NH_4-N plus NO_3-N) in the forest floor or soil reported in Vitousek et al. (1982) disappears for the collections in certain seasons. The data of Table 2 and Figure 1–4 show that, considering all collections, there is little relationship between standing amounts of KCl extractable nitrogen in the field (mostly NH_4-N) and the nitrification potential of the material in that collection. As suggested by Vitousek et al. (1982), field collections having at least 60–90 μg of available N per g forest floor are those which can have significant nitrate production. It is not always predictive, however. This is due to the seasonal differences in nitrification which appear to be independent of available NH_4-N.

We feel the laboratory nitrification potential method is an accurate bioassay of substrate quality. Our data suggests that substrate quality changes with time and is a prime factor affecting the nitrification process. In certain sites (i.e. spruce-fir) the organic quality effectively prohibits net nitrification during all seasons, although ammonium levels apparently are high enough to not limit nitrification. If heterotrophic nitrifiers are present, they could be

limited by low levels of available carbon (Flanagan and Van Cleve 1983, Gosz 1981). It is possible that another factor (e.g. P, Mo limitation) interacts with energy-limitation also preventing heterotrophic nitrification. If nitrifiers are poor competitors for P or Mo, etc. (Purchase 1974), the energy of NH_4-N would not be useable by these organisms. Inhibition of chemolithotrophic nitrifiers by organic allelochemics can not be excluded by our results. Other sites reported by Vitousek et al. (1982) which demonstrated low levels of nitrate accumulation in trenched plots have been investigated with regard to inhibition by organic compounds. Olsen and Reiners (1983) and Baldwin et al. (1983) found inhibition of nitrification by water-insoluble tannins.

Even in sites which have higher N cycling rates (e.g. mixed conifer, aspen) where nitrification rates often were more pronounced and closely followed NH_4-N levels, certain collection times demonstrated possible inhibition of nitrification. The longer nitrification lag times in laboratory incubations of certain collections may reflect the presence of organic inhibitors which cannot be altered or rapidly removed by typical biotic/abiotic processes. It is possible that there is very high microbial activity associated with energy-rich carbon supplies at those times (i.e. litterfall) and high CO_2 levels may be depressing nitrifiers. It is less likely that these sites are energy limited because of the generally higher decomposition rates found there (Gosz 1980a).

We agree with the conclusion of Vitousek et al. (1982) that the amount of nitrogen circulating annually in litterfall and the relative availability of that nitrogen prior to disturbance are useful predictors of the potential for nitrate loss following disturbance. We did not find significant nitrification in any case with low mineralization rates or low levels of available NH_4-N. While high levels of available NH_4-N may predict the potential for nitrate production and loss, in fact, it may not occur. Other controls, primarily organic, appear important in controlling the nitrification process in our sites.

In summary, plant uptake, N return in litterfall and its mineralization, and organic matter quality all appear to exert some control on nitrate production and subsequent loss. The relative importance of each factor varies from stand to stand and from season to season.

Acknowledgements

We thank Douglas I Moore, Clifford N. Dahm, J.W. Fitzgerald, John Pastor, and two anonymous reviewers for comments on earlier drafts of this paper. Financial suport was provided by NSF grants DEB-7617425 and DEB-7811171.

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