ELSEVIER

Forest Ecology and Management 176 (2003) 509–518

Forest Ecology and Management

www.elsevier.com/locate/foreco

N mineralization, nitrification, and N uptake across a 100-year chronosequence of upland hardwood forests

Travis W. Idol[a,*,1], Phillip E. Pope[b], Felix Ponder Jr.[c]

[a]*Department of Land, Air, and Water Resources, University of California-Davis, One Shields Avenue, Davis, CA 95616, USA*
[b]*Department of Forestry and Natural Resources, Purdue University, 1159 Forestry Building, West Lafayette, IN 47907, USA*
[c]*USDA Forest Service, North Central Research Station, 208 Foster Hall, Chestnut Street, Lincoln University, Jefferson City, MO 65102, USA*

Received 3 March 2002; accepted 3 June 2002

Abstract

Net N mineralization, nitrification, and N uptake were monitored in the A (0–8 cm) and B (8–30 cm) soil horizons from 1997 to 1999 across a chronosequence of upland hardwood forest stands in southern Indiana, USA. Stand ages were 1, 6, 12, 31, and 80–100 years at the beginning of the study. Contrary to previous studies, there was no apparent stimulation of N mineralization due to harvesting. The highest rates of N mineralization, nitrification, and N uptake were in the mature forest stand. Rates of N cycling were greater in the A than the B horizon by concentration (g kg^{-1}), but the greater depth and bulk density of the B horizon led to insignificant differences by area (kg ha^{-1}). N mineralization, nitrification, and N uptake all correlated significantly with each other, and average annual rates of N mineralization balanced well with N uptake in most stands of the chronosequence. N cycling seemed to be subject to strong internal regulation at all stages of stand development. Analyses of the spatial and temporal variability in N cycling properties or processes would provide further insights in the effects of harvesting on N cycling in these forest stands.

Keywords: Chronosequence; Forest harvesting; Nitrogen mineralization; Nitrification; Nitrogen uptake; Soil horizon

1. Introduction

The effects of harvesting on forest productivity and soil quality have been of concern for decades (Tamm, 1979; Powers and Morrison, 1996) and are the subject of a national research program being conducted by the US Forest Service (Tiarks et al., 1997). Monitoring of nutrient cycling processes is one of the recommended ways to assess overall soil quality (Karlen et al., 1997; Morris and Boerner, 1998) and may be useful for understanding the effects of harvesting on long-term soil and forest productivity.

In order to study the effects of forest harvesting on nutrient cycling, it is important to consider the major nutrient pools, rates of transfer among the pools, and the internal and external controls over the pool sizes and transfer rates. In upland temperate forests, the major ecosystem N pools and transfers have been identified and modeled (Aber et al., 1991; Schimel et al., 1996). The major pools include plant biomass, forest floor and belowground litter, soil organic matter,

---

[*] Corresponding author. Tel.: +1-808-956-7508; fax: +1-808-956-6539.
E-mail address: idol@hawaii.edu (T.W. Idol).
[1] Present address: Natural Resources and Environmental Management University of Hawaii-Manoa, 1910 East West Road, Honolulu HI 96822, USA.

0378-1127/02/$ – see front matter © 2002 Elsevier Science B.V. All rights reserved.
PII: S0378-1127(02)00232-3

the soil microbial biomass, and available inorganic N. The major processes involved in the movement of N through these various pools include plant productivity and litter production, litter decomposition and humification, litter and soil organic N mineralization, microbial immobilization of organic and inorganic N, nitrification, N leaching and denitrification, atmospheric deposition, N_2-fixation, and plant N uptake. The most influential external controls over N cycling rates include soil moisture and temperature (Kladivko and Keeney, 1987; Powers, 1990) and pH (Hankinson and Schmidt, 1984; Thorne and Hamburg, 1985). Internal controls include N availability (Robertson, 1982), net N mineralization (Reich et al., 1997), and organic substrate characteristics, e.g. C:N ratio (Piatek and Allen, 1999).

In many forest ecosystems, the effects of harvesting on various aspects of nutrient cycling have been explored (Matson and Vitousek, 1981; Gholz et al., 1985; Frazer et al., 1990; Crow et al., 1991; Browaldh, 1997; Marques et al., 1997; Holmes and Zak, 1999; Schilling et al., 1999). Only a few of these studies, however, have looked simultaneously at differences in nutrient pool sizes, process rates, and the major influences on these components of nutrient cycling with forest stand age (e.g. Piatek and Allen, 1999). General conclusions from these studies are that N availability, net N mineralization, and nitrification tend to increase after harvest (Matson and Vitousek, 1981; Frazer et al., 1990; Knoepp and Swank, 1997; Prescott, 1997) and decline with increasing stand age (Piatek and Allen, 1999), although trends may vary by forest type (Ryan et al., 1997). Reasons cited for these trends include changes in soil moisture or temperature (Frazer et al., 1990; Prescott, 1997) and changes in soil C:N levels (Piatek and Allen, 1999). N uptake is generally depressed for the first few years due to reduced plant biomass (Gholz et al., 1985), but rapid vegetation growth can lead to N uptake that exceeds preharvest rates within 4–5 years (Hendrickson, 1988; Crow et al., 1991).

The limitation of many of these studies is the lack of data on potential long-term trends. The effects of harvesting are generally determined only for the first 5–10 years after harvest (Matson and Vitousek, 1981; Gholz et al., 1985; Crow et al., 1991; Prescott, 1997; Schilling et al., 1999) or are determined by a comparison of recently harvested (5–10 years) to mature or old-growth (80+ years) forest stands. There have been several studies that have investigated nutrient cycling across a range of stand ages from harvest to maturity (Frazer et al., 1990; Hughes and Fahey, 1994; Marques et al., 1997), but none of these studies has been conducted in the deciduous forests of the central US.

The purpose of our overall research program was to monitor N cycling from litter production and decomposition to N mineralization and uptake at different stages of forest development. The study described here focuses specifically upon N mineralization, nitrification, and N uptake in forest stands at different stages of development following harvesting. Rates were measured across different soil horizons and in different years because of the potential differences in N cycling rates associated with these variables. Finally, we were interested in the coupling of these N cycling processes and their relationship with environmental conditions such as soil water and temperature.

2. Materials and methods

2.1. Study site descriptions

We employed the chronosequence approach in this study, selecting five upland hardwood forest stands in the central hardwoods region of the US that represented different stages of stand development. All stands are located within a 1 mile radius of each other at the Southern Indiana Purdue Agricultural Center in Dubois County, IN. Each age stand is approximately 5–10 ha in size. All stands are located on soils of the Gilpin-Wellston complex, classified as fine-silty, mixed, mesic Ultic Hapludalfs and Typic Hapludults (Soil Survey Staff, 1980). All plots were located in areas with 10–20% slopes and south- to southwest-facing aspects. Overstory plant species composition is a mix of deciduous hardwood species, typically dominated by oak (*Quercus*) and hickory (*Carya*) at maturity. Four of the five stands were subjected to commercial harvesting followed by clear-felling of remaining overstory trees. Regeneration was allowed to proceed naturally. Vigorous regrowth of herbaceous plants, seed-dispersed pioneer trees, and tree stump and root sprouts is common on sites in this region (Matson and Vitousek, 1981). Four years after harvest, seedling density may exceed 75,000 stems ha^{-1} and sapling density may exceed 90,000 stems ha^{-1} (Idol et al., 2000). Site 1 (1–3 years old) was harvested in 1996. Site 2 (6–8 years pld) was harvested in 1991. Site 3 (12–14 years old) was harvested in 1985. Site 4 (31–33 years old) was harvested in 1966. Site 5 (80–100 years old) is a mature stand dominated by white oak (*Quercus alba* L.) in the overstory with a site index of 20 m at 50 years for white oak (Kaczmarek, 1995). The average annual precipitation is 1170 mm and is evenly distributed throughout the year, although mid- and late-summer droughts are not uncommon. The mean annual air temperature is 12.0 °C, which ranges from a low of −2.3 °C in January to a high of 24 °C in July.

2.2. N mineralization, nitrification, and N uptake

Three 0.5 ha plots were established in sites 1–3 and 5. Only two plots with suitable soil and physiographic characteristics could be established in site 4. Rates of in situ net N mineralization, nitrification, and N uptake were assessed using the field incubation core technique (Adams et al., 1989; Becquer et al., 1990) over three growing seasons, beginning in May 1997. Three open-topped PVC cores approximately 5 cm in diameter were driven 30 cm deep into the soil within each plot at the beginning of the study. Additionally, three 30 cm deep bulk samples of soil were collected within each plot. After approximately 30 days, the field-incubated cores were collected, new cores were placed in the field, and new bulk soil samples were collected. Monthly core and bulk samples were taken from 25 May to 20 December 1997, 25 April–5 December 1998, and 1 April–2 September 1999.

Cores were left open in order to incorporate the natural soil water flux. This allows for the movement of water through the soil column inside the core, meaning that N may move from A to B horizon, or that N may be added to the core via atmospheric deposition or leave the core via leaching. Historic N deposition rates (wet + dry) are approximately 6.5 kg N ha^{-1} per year (Armentano and Loucks, 1990 as cited in Kuperman, 1999). Preliminary work using porous cup lysimeters suggested leaching of N in these stands was <5 kg ha^{-1} per year (unpublished data). However, without plant uptake of added or mineralized N, leaching from inside the cores may lead to underestimates of N cycling rates.

Bulk and core samples were separated into A and B horizon samples according to natural horizon differences (e.g. color, structure, and texture). Soil from each horizon from bulk and core soil samples was then analyzed for inorganic N. Approximately 25 g of soil was extracted in 80 ml solution of 2 mol l^{-1} KCl on a shaker table for 1 h. A separate set of subsamples was taken for the determination of soil water content (via oven drying) so that a dry soil weight could be calculated. After shaking, the extraction samples were centrifuged to separate the soil and the extract. Fifteen milliliters of the extract was then analyzed separately for ammonium (NH_4^+) and nitrate (NO_3^-) via steam distillation and back-titration (Keeney and Nelson, 1982). Rates of net N mineralization, nitrification, and N uptake were calculated as differences in either total N or nitrate-N between monthly bulk and core samples (Becquer et al., 1990).

2.3. Environmental measurements

At the beginning of the study, six to nine soil samples from A and B horizons were taken from a single location within the individual sites to determine soil water content at water potentials ranging from −0.3 to −1.5 MPa. Three bulk density core samples per horizon were taken within each plot to determine water retention at −0.03 and −0.1 MPa. Additionally, type K thermocouple wires were attached to plastic stakes at 5 and 20 cm depths. Three stakes were driven into the soil at different locations within each plot. At 2-week intervals during the 1997–1999 study periods, soil water content (w/w) in the A and the B horizons was measured gravimetrically and converted to soil water potential using water retention curves derived from the pressure plate extractions. Soil temperature was measured in the A (5 cm depth) and the B (20 cm depth) horizons within each plot using a digital thermometer.

Growing degree days (GDDs) were calculated based upon daily air temperature data recorded at a weather station at the study site. The daily mean temperature was subtracted from a base level of 10 °C, and positive values were summed across months and over the year to obtain cumulative GDD. Actual evapotranspiration (AET) in millimeters was calculated according to the methods of Thornthwaite (1948). Variables used in the calculation of AET include monthly average air temperature (°C), cumulative precipitation (mm), soil water-holding capacity (mm), and day length (hours of photoactive radiation). This method is only an estimate of evapotranspiration, since it makes assumptions about forest cover type in order to derive AET rates. However, it has proven useful in estimating regional litter decomposition rates (Meentemeyer, 1978), plant net primary productivity, and nutrient cycling (Schimel et al., 1996).

2.4. Statistics

Because of the unique nature of the chronosequence, there is no true replication of stand age. Although study plots were physically separated by logging roads or intervening forest blocks, they were grouped by stand age, and thus do not meet the requirements for a randomized experimental design. Thus, the use of inferential statistics to compare stand ages is subject to the error of pseudo-replication (Hurlbert, 1984). Only trends in the data by stand age can be discussed.

Within each age stand, the average daily rates of N mineralization, nitrification, and N uptake were compared by soil horizon and year using analysis of variance (ANOVA) in SAS (SAS Institute, Inc., 1989) with a Type I error rate (α-level) of 0.05. Rates were calculated in mg N kg^{-1} of soil and g N ha^{-1} due to the different depths and bulk densities of the A and B horizons. Where the ANOVA indicated a significant difference by year ($P < 0.05$), means were separated using Duncan's multiple range test.

In order to investigate the internal and external controls over N cycling rates, monthly rates of N mineralization, nitrification, and N uptake were correlated with soil temperature, soil water potential, AET, GDD, and with each other using Pearson's correlation coefficient, R. Only relationships which were significant at $P < 0.10$ were considered significant.

3. Results

N mineralization averaged across 1997–1999 was the highest in site 5, the mature forest stand, at 689 g ha^{-1} per day, and the lowest in site 4, the 30–35-year-old stand, at 256 g ha^{-1} per day (Table 1). Nitrification seemed to decline with stand age from 226 g ha^{-1} per day in site 1 to 112 g ha^{-1} per day in site 4, but was the highest in site 5 at 234 g ha^{-1} per day. N uptake was also the highest in site 5 at 676 g ha^{-1} per day and was similar among the other sites, approximately 430 g ha^{-1} per day.

Table 1
Average daily rates (g ha^{-1} per day) of N mineralization (Min), nitrification (Nit) and N uptake (Upt) across a 100-year chronosequence of upland hardwood forest stands

Site	Min	Nit	Upt	Nit/Min	Upt/Min
1	388	226	450	0.58	1.16
2	431	166	429	0.38	1.00
3	351	139	399	0.40	1.14
4	256	112	462	0.44	1.81
5	689	234	676	0.34	0.98

Nitrification as a proportion of N mineralization also varied by stand age. In the recently harvested stand (site 1), nitrification was 0.58 of N mineralization. For sites 2–4 (aged 8–33 years), nitrification was approximately 0.40 of N mineralization. In the mature forest stand, nitrification was approximately 0.34 of N mineralization. N uptake was approximately equal to N mineralization in most stands of the chronosequence. Only in site 4 was there a striking disparity in the rates of N mineralization and N uptake. In this stand, average N uptake was 81% greater than average N mineralization. In all other stands, the difference between N mineralization and N uptake was less than 20%.

Differences in rates of N cycling between A and B horizons were generally significant when measured by concentration (mg kg^{-1} per day), but the greater depth and bulk density of the B horizon led to mostly insignificant differences by area (g ha^{-1} per day) (Table 2). There were also differences in N cycling rates from year to year (Fig. 1). For sites 1 and 2 (the stands <10 years post-harvest) rates of N mineralization, nitrification, and N uptake during 1997 were typically one-half to one-third of those in 1998 and 1999. However, these differences were not always significant. In site 4, N mineralization and nitrification during 1999 were significantly less than during 1997 or 1998. During 1999, there was virtually no net N mineralization or nitrification in this stand, whereas N mineralization averaged 350 g ha^{-1} per day and nitrification averaged 164 g ha^{-1} per day from 1997 to 1998. For site 5, variation in N cycling rates from year to year was generally small.

The relationships between monthly soil N cycling rates and selected environmental variables—soil water

Table 2
ANOVA for effect of soil horizon and year on rates of N mineralization (Min), nitrification (Nit), and N uptake (Upt) across a 100-year chronosequence of upland hardwood forests

Source	d.f.	$P > F$					
		g ha^{-1} per day			mg kg^{-1} per day		
		Min	Nit	Upt	Min	Nit	Upt
Site 1							
Horizon	1	ns[a]	0.06	ns	<0.01	<0.01	<0.01
Year	2	0.01	0.05	ns	0.03	ns	ns
H × Y	2	ns	ns	ns	ns	ns	ns
Site 2							
Horizon	1	ns	0.02	ns	<0.01	<0.01	<0.01
Year	2	0.09	ns	0.03	ns	ns	0.03
H × Y	2	ns	ns	ns	ns	ns	ns
Site 3							
Horizon	1	ns	ns	ns	ns	<0.01	ns
Year	2	ns	ns	ns	ns	<0.01	ns
H × Y	2	ns	ns	ns	ns	ns	ns
Site 4							
Horizon	1	ns	0.04	ns	0.01	<0.01	0.02
Year	2	<0.01	<0.01	ns	0.01	<0.01	ns
H × Y	2	ns	ns	ns	0.06	0.02	ns
Site 5							
Horizon	1	ns	0.07	ns	<0.01	<0.01	<0.01
Year	2	ns	0.06	ns	ns	0.02	ns
H × Y	2	ns	ns	ns	ns	0.07	ns

[a] Not significant.

Table 3
Correlation (Pearson's correlation coefficient, R) between N mineralization (Min), nitrification (Nit), and N uptake (Upt) across a 100-year chronosequence of upland hardwood forests

	A horizon			B horizon			A + B horizon		
	Min	Nit	Upt	Min	Nit	Upt	Min	Nit	Upt
Site 1									
Min		0.80	0.68		0.75	0.62		0.63	0.44
Nit			0.80			ns[a]			ns
Site 2									
Min		0.71	0.83		0.79	ns		0.71	ns
Nit			ns			ns			ns
Site 3									
Min		0.60	0.51		0.72	0.76		0.65	0.699
Nit			ns			ns			ns
Site 4									
Min		0.74	ns		0.91	0.61		0.84	ns
Nit			ns			0.57			ns
Site 5									
Min		0.51	0.76		0.77	0.67		0.67	ns
Nit			ns			0.58			ns

[a] Not significant.

potential, soil temperature, AET or GDD—were generally insignificant (data not shown). However, relationships among N mineralization, nitrification, and N uptake on a monthly basis were significant in many cases (Table 3). In general, relationships were stronger between N mineralization and nitrification than between N mineralization and N uptake or nitrification and N uptake. Relationships were also generally stronger within A or B horizon than when compared across the horizons. The strength of these relationships showed no apparent trends by stand age.

4. Discussion

4.1. N mineralization

Patterns of N mineralization varied by year and soil horizon, but mean values of N mineralization were consistently higher in the 80–100-year-old forest stand (site 5) than in the regenerating stands (Fig. 1). In several earlier studies, N mineralization increased after harvest (Bormann and Likens, 1979; Frazer et al., 1990; Prescott, 1997). Simulation of harvesting effects suggests that this period of increase lasts only 1–3 years before returning to levels at or below preharvest N mineralization rates (Aber et al., 1991). Harvesting can lead to increases in soil temperature and water availability, which would tend to increase microbial decomposition and nutrient release from decaying litter and organic matter. Coupled with a massive increase in litter inputs due to the addition of logging residues (treetops, dying root systems, etc.) and the mixing of litter and mineral soil, N mineralization may be expected to increase significantly in harvested stands.

This explanation, however, assumes that N mineralization in mature forest stands is significantly limited by soil environmental conditions or substrate availability. Both soil temperature and soil water potential were favorable for microbial and plant activity throughout the measurement periods in all stands. Soil pH was actually less acidic in the younger forest

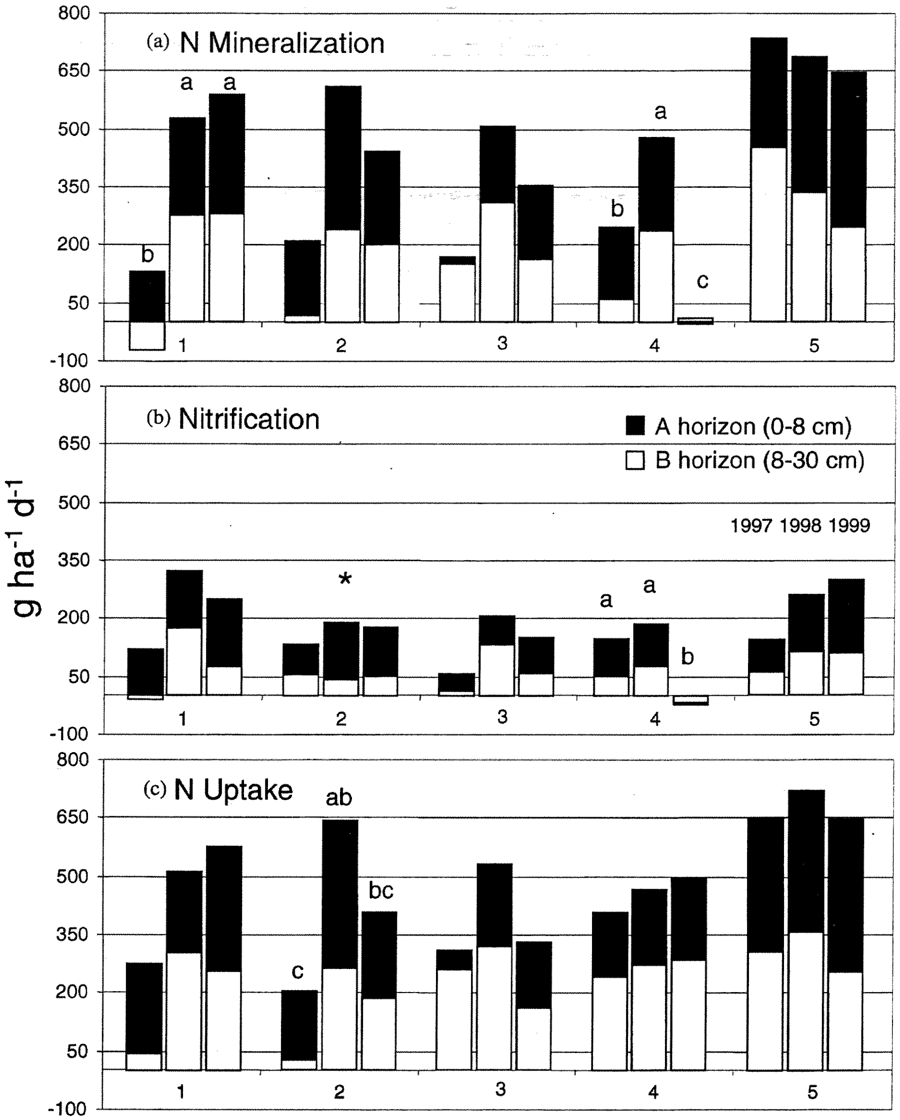

Fig. 1. Average N cycling rates during 1997–1999 across a 100-year chronosequence of upland hardwood forests. *X*-axis = site. (a) N mineralization; (b) nitrification; (c) N uptake. Bars within a site followed by a different letter differ significantly at $P < 0.05$. $*$ indicates a significant difference by horizon (see methods for description of statistics).

stands, which should have favored greater microbial activity (data not shown). Fine root growth and turnover is generally higher in the younger forest stands (Idol et al., 2000), providing high levels of substrate inputs.

Although our methods were not designed to test the hypothesis, it is possible that large inputs of logging debris, the mixing of fresh forest floor litter, and the death of coarse root systems in the recently harvested stands led to increases in net N *immobilization* due to the generally high C:N ratio of woody debris (Idol et al., 2001) and other forest litter. This would then be expected to appear as increased soil microbial N in recently harvested stands. In site 1, N mineralization during 1997 was significantly lower than during 1998 or 1999, but microbial N was higher than in any other stand (Idol et al., 2002). Thus in these forest stands, soil microbes may immobilize the flush of available N after harvesting. Mineralization of this N would then occur after the microbial N requirement was satisfied or as the microbial community turned over.

4.2. N uptake

In contrast to N mineralization, harvesting may lead to a significant decline in total stand N uptake. In a Pacific Northwest Douglas-fir (*Pseudotsuga menziesii* Mirb. (Franco)) forest, Gholz et al. (1985) found a 92% decline in N uptake after 1 year. After 3 years, uptake was 50% of preharvest levels. After 5 years, N uptake in regenerating northern hardwood (Crow et al., 1991) and mixed wood (Hendrickson, 1988) forests exceeded preharvest levels. The explanation for these results is straightforward. Harvesting removes most of the active plant biomass from the forest. Thus, with harvest, plant demands for N on an area basis should decline. With an open canopy and sufficient water and nutrients, vegetative regrowth should be rapid, and within several years after harvest, plant demands for soil resources, including N, should increase rapidly, perhaps up to or exceeding preharvest levels.

We found increasing N uptake rates in the recently harvested stand (site 1) from 1997 to 1999, but differences were not significant (Fig. 1). As with N mineralization, though, N uptake rates were consistently the highest in the mature forest stand. If N were limiting to plant growth and productivity in a forest, then it would be expected that N uptake would be limited mainly by the rate at which N is made available, i.e. by the N mineralization rate. Since the results of this study suggest that N mineralization rates after harvesting are less than or equal to preharvest levels, then it would be expected that N uptake rates would also remain below or near preharvest N uptake rates. Thus, despite a possibly higher potential for N uptake by the regenerating vegetation, actual N uptake rates may have been constrained by the rate at which soil N became available for plant uptake.

4.3. Nitrification

Harvesting typically leads to greater nitrification rates or at least greater nitrification as a proportion of N mineralization because soil available ammonium is typically the most important factor limiting nitrification rates in terrestrial ecosystems (Robertson, 1982; Donaldson and Henderson, 1990). Soon after a harvest, declines in the amount of N taken up by plants may allow nitrifying bacteria greater access to the available pool of ammonium. Thus, nitrification may be expected to increase soon after harvest. After 5–10 years of regeneration, plant growth rates and N uptake may increase competition for soil N, reducing nitrification rates.

Results from the present study generally support these trends. Nitrification rates declined with stand age from site 1 to site 4, and nitrification as a proportion of N mineralization was also the highest in site 1 (Table 1). However, nitrification rates were still slightly higher in site 5, most likely due to the high rates of N mineralization.

4.4. Soil horizons

Higher rates of N cycling by concentration (mg kg^{-1} per day) in the A as compared to the B horizon are to be expected. However, it was unknown how stand development would affect the relative importance of the A and the B horizons to overall N cycling. In site 2, 6–8 years post-harvest, the proportion of total N mineralization, nitrification, or N uptake in the A horizon exceeded 60%. However, in site 3, 10–12 years post-harvest, the opposite pattern was found (Fig. 1). It is uncertain why these changes by soil horizon occurred, but they are generally consistent with data on above- and belowground litter nutrient inputs. Idol et al. (1998) found that N return from litterfall was 2–3 times higher in a 4-year-old stand (site 2 in the present study) than in stands aged 10 and 30 years post-harvest (sites 3 and 4, respectively). Conversely, the proportion of fine root growth, mortality, and N return in the B horizon was greater in the 10-year-old stand (Idol et al., 1998, 2000). Thus, N cycling in regenerating stands seems to mirror changes in the quantity and distribution of litter inputs and fine root activity.

4.5. Correlation analysis

Monthly rates of N mineralization were significant predictors of nitrification and N uptake in all sites for both the A and the B horizons. This strong internal regulation suggests that harvesting does not significantly disrupt the basic processes underlying N availability and N cycling. Harvesting may alter many of the soil properties important for N cycling, e.g. soil temperature, soil water availability, soil pH, fine root biomass, litter inputs, and litter chemistry. This would be expected to affect rates of N cycling but not necessarily disrupt the basic relationships among N mineralization, nitrification, and N uptake. The lack of strong relationships across the A + B horizons emphasizes the need to analyze these horizons separately in studies of nutrient cycling.

It was surprising to find that none of the environmental variables measured was strongly correlated with monthly rates of N cycling. The timing of different biological events that influence rates of N cycling are likely responsible for this lack of correlation within the year. For example, N uptake in these stands during 1998, when measurements were made from April to December, was generally the highest during April–June and declined until December (data not shown). This corresponds well to levels of plant growth rates (e.g. leaf expansion and branch growth) but not to soil temperature or soil water availability, AET, or GDD. N mineralization rates are influenced not only by water and temperature but also litter inputs, litter quality, fine root activity, and predation on soil bacteria and fungi by soil micro- and mesofauna. Over longer time periods or stronger inter-site gradients of water and temperature, such relationships between environmental conditions and nutrient cycling can become apparent (Powers, 1990; Schimel et al., 1996). However, within a climatic region it is likely more difficult to detect differences in N cycling rates associated with changes in the soil microclimate.

4.6. Implications for long-term soil productivity

Do the lower post-harvest rates of N cycling, even at 30+ years, indicate long-term declines in soil or site productivity? Tree sapling and overstory density and growth was adequate on all harvested sites; thus, there does not seem to be a post-harvest decline in site index, a common measure of forest productivity. The typical rotation length for these sites is greater than 50 years; thus, our chronosequence does not cover the entire range of stand ages within a rotation. Finally, it is not known how limiting N is to plant productivity in these stands. Because these soils are classified as highly weathered Alfisols grading into true Ultisols, other soil nutrients may be as much if not more limiting to plant growth, e.g. Ca or P. At the very least, N cycling rates do not seem to have recovered fully after 30+ years of regeneration; thus rotation lengths longer than 30 years seem necessary to maintain long-term rates of N cycling.

4.7. Study limitations

There are three important limitations to the present study. The first involves the unique nature of the chronosequence of stands. Because the stands were harvested in physically separate blocks, replicates of stand age were not randomly located. Thus, plot location is confounded with stand age. A more regional assessment of harvesting effects could be conducted on multiple stands across a range of age classes, but this would inevitably require a grouping of different forest species compositions, soil types, and years of harvest. Even so, only the simplest types of comparisons are generally possible with such a meta-analysis, e.g. changes in total soil C and N (Johnson and Curtis, 2001).

The second is the difficulty of accurately measuring average rates of N cycling in stands with a high degree of seasonal and spatial variability in soil processes. It may be more informative in such cases to characterize this variability using geostatistical analyses rather than attempting to find differences in mean values using traditional univariate statistics (Rossi et al., 1992). The drawbacks to this approach are the intensity of sampling required and the limitation of such analyses to mainly soil properties, not dynamic processes.

The final limitation concerns the use of open-topped cores to assess in situ N cycling rates. Without plant uptake of soil water and N, microbial N transformations inside soil cores (open or closed) are likely to be greater than in the bulk soil. Since the soil cores used in this study were open to both atmospheric deposition and leaching, elevated rates of nitrification inside the cores may have led to higher than normal rates of N leaching, especially during months with heavy precipitation. Although N leaching was not measured in the present study, previous work suggests N leaching outside the soil cores is less than 5 kg ha^{-1} per year in sites 2–5 (data not shown). It was assumed with relatively low rates of N leaching and a 30-day incubation period that N cycling rates could be adequately assessed using this method; however, it remains unknown if this assumption is justified. Open-topped cores can be modified so that an ion-exchange resin bag is inserted at the bottom of the core to capture any leached N (Binkley and Vitousek, 1991). Although this is generally considered to be an improvement over cores without resin bags, it does require a simultaneous assessment of N leaching to prevent overestimation of N mineralization or N uptake.

5. Summary

Overall, results from this study did not agree with results from previous research on the effects of harvesting on N cycling. Previous research suggests that N mineralization and nitrification are the highest in the first few years after harvest and N uptake is the highest 5–10 years after harvest. In the present study, N mineralization, nitrification, and N uptake were the highest in the 80–100-year-old stand. Nitrification as a proportion of N mineralization, however, was the highest in the 1–3-year-old stand and the lowest in the 80–100-year-old stand. By concentration (mg kg^{-1} per day), N cycling rates in the A horizon were higher than in the B horizon, but differences by area (g ha^{-1} per day) were generally insignificant. Annual variations in average N cycling rates were significant in some cases, especially in the 31–34-year-old stand. N mineralization, nitrification, and N uptake were significantly correlated in all age stands, suggesting strong internal regulation of N cycling processes. Although plant productivity in the harvested stands appears to be vigorous, there does not appear to be full recovery of N cycling rates after 30 years of regeneration. Given the variability inherent in these stands, greater insight may be achieved with an analysis of the spatial and temporal patterns of N cycling properties and processes.

Acknowledgements

The authors wish to thank Ron Rathfon, the late Frank Burgess, and Keith Hawkins for assistance with site selection and data collection from the field, the many undergraduate assistants who helped with field sample collection and laboratory analysis, and Judy Santini for assistance with statistical analyses. This research was supported by the USDA Forest Service, grant no. 23-97-02-RJVA.

References

Aber, J.D., Melillo, J.M., Nadelhoffer, K.J., Pastor, J., Boone, R.D., 1991. Factors controlling nitrogen cycling and nitrogen saturation in northern temperate forest ecosystems. Ecol. Appl. 1, 303–315.

Adams, M.A., Polglase, P.A., Attiwill, P.M., Weston, C.J., 1989. In situ studies of nitrogen mineralization and uptake in forest soils some comments on methodology. Soil Biol. Biochem. 21, 423–429.

Armentano, T., Loucks, O., 1990. Spatial patterns of S and N deposition in the midwestern hardwoods region. In: Loucks, O. (Ed.), Air Pollutants and Forest Response: The Ohio Corridor Study: Year-4 Annual Report. Miami University, Holcomb Research Institute, Oxford, OH, pp. 54–84.

Becquer, T., Merlet, D., Boudot, J.-P., Rouiller, J., Gras, F., 1990. Nitrification and nitrate uptake: leaching balance in a declined forest ecosystem in France. Plant Soil 125, 95–107.

Binkley, D., Vitousek, P., 1991. Soil nutrient availability. In: Pearcy, R.W., Ehleringer, J.R., Mooney, H.A., Rundel, P.W. (Eds.), Plant Physiological Ecology: Field Methods and Instrumentation. Chapman & Hall, New York, pp. 75–96.

Bormann, F.H., Likens, G.E., 1979. Pattern and Process in a Forested Ecosystem. Springer, New York.

Browaldh, M., 1997. Change in soil mineral nitrogen and respiration following tree harvesting from an agrisilvicultural system in Sweden. Agrofor. Syst. 35, 131–138.

Crow, T.R., Mroz, G.D., Gale, M.R., 1991. Regrowth and nutrient accumulations following whole-tree harvesting of a maple–oak forest. Can. J. For. Res. 21, 1305–1315.

Donaldson, J.M., Henderson, G.S., 1990. Nitrification potential of secondary-succession upland oak forests. II. Regulation of ammonium-oxidizing bacteria populations. Soil Sci. Soc. Am. J. 54, 898–902.

Frazer, D.W., McColl, J.G., Powers, R.F., 1990. Soil nitrogen mineralization in a clearcutting chronosequence in a northern California conifer forest. Soil Sci. Soc. Am. J. 54, 1145–1152.

Gholz, H.L., Hawk, G.M., Campbell, A., Cromack Jr., K., Brown, A.T., 1985. Early vegetation recovery and element cycles on a clear-cut watershed in western Oregon. Can. J. For. Res. 15, 400–409.

Hankinson, T.R., Schmidt, E.L., 1984. Examination of an acid forest soil for ammonia- and nitrite-oxidizing autotrophic bacteria. Can. J. Microbiol. 30, 1125–1132.

Hendrickson, Q.Q., 1988. Biomass and nutrients in regenerating woody vegetation following whole-tree and conventional harvest in a northern mixed forest. Can. J. For. Res. 18, 1427–1436.

Holmes, W.E., Zak, D.R., 1999. Soil microbial control of nitrogen loss following clear-cut harvest in northern hardwood ecosystems. Ecol. Appl. 9, 202–215.

Hughes, J.W., Fahey, T.J., 1994. Litterfall dynamics and ecosystem recovery during forest development. For. Ecol. Manage. 63, 181–198.

Hurlbert, S.H., 1984. Pseudoreplication and the design of field experiments. Ecol. Monogr. 54, 187–211.

Idol, T.W., Pope, P.E., Tucker, J., Ponder Jr., F., 1998. The role of fine root dynamics in the N and P cycles of regenerating upland oak–hickory forests. In: Waldrop, T.A. (Ed.), Proceedings of the Ninth Biennial Southern Silvicultural Research Conference. General Technology Report SRS-20. USDA Forest Service, pp. 136–140.

Idol, T.W., Pope, P.E., Ponder Jr., F., 2000. Fine root dynamics across a chronosequence of upland oak–hickory forests. For. Ecol. Manage. 127, 153–167.

Idol, T.W., Pope, P.E., Figler, R.A., Ponder Jr., F., 2001. Characterization of coarse woody debris across a 100-year chronosequence of upland oak–hickory forests. For. Ecol. Manage. 149, 153–161.

Idol, T.W., Pope, P.E., Ponder Jr., F., 2002. Changes in microbial-nitrogen across a 100-year chronosequence of upland hardwood forests. Soil Sci. Soc. Am. J. 66, 1662–1668.

Johnson, D.W., Curtis, P.S., 2001. Effects of forest management on soil C and N storage: meta-analysis. For. Ecol. Manage. 140, 227–238.

Kaczmarek, D.J., 1995. Nutrient pools and patterns of nutrient availability and use in oak–hickory dominated forests. Ph.D. Thesis. Purdue University, West Lafayette, IN.

Karlen, D.L., Mausbach, M.J., Doran, J.W., Cline, R.G., Harris, R.F., Schuman, G.E., 1997. Soil quality: a concept, definition, and framework for evaluation (a guest editorial). Soil Sci. Soc. Am. J. 61, 4–10.

Keeney, D.R., Nelson, D.W., 1982. Nitrogen-inorganic forms. In: Page, A.L. (Ed.), Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties, 2nd Edition. American Society of Agronomy, Madison, WI, pp. 643–698.

Kladivko, E.J., Keeney, D.R., 1987. Soil nitrogen mineralization as affected by water and temperature interactions. Biol. Fert. Soils 5, 248–252.

Knoepp, J.D., Swank, W.T., 1997. Forest management effects on surface soil carbon and nitrogen. Soil Sci. Soc. Am. J. 61, 928–935.

Kuperman, R.G., 1999. Litter decomposition and nutrient dynamics in oak–hickory forests along a historic gradient of nitrogen and sulfur deposition. Soil Biol. Biochem. 31, 237–244.

Marques, R., Ranger, J., Villette, S., Granier, A., 1997. Nutrient dynamics in a chronosequence of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands on the Beaujolais Mounts (France). 2. Quantitative approach. For. Ecol. Manage. 92, 167–197.

Matson, P.A., Vitousek, P.M., 1981. Nitrogen mineralization and nitrification potentials following clearcutting in the Hoosier National Forest, IN. For. Sci. 27, 81–91.

Meentemeyer, V., 1978. Microclimate and lignin control of litter decomposition rates. Ecology 59, 465–472.

Morris, S.J., Boerner, R.E.J., 1998. Interactive influences of silvicultural management and soil chemistry upon soil microbial abundance and nitrogen mineralization. For. Ecol. Manage. 103, 129–139.

Piatek, K.B., Allen, H.L., 1999. Nitrogen mineralization in a pine plantation 15 years after harvesting and site preparation. Soil Sci. Soc. Am. J. 63, 990–998.

Powers, R.F., 1990. Nitrogen mineralization along an altitudinal gradient: interactions of soil temperature, moisture, and substrate quality. For. Ecol. Manage. 30, 19–29.

Powers, R.F., Morrison, I.K., 1996. Soil and sustainable forest productivity: a preamble. Soil Sci. Soc. Am. J. 60, 1613.

Prescott, C.E., 1997. Effects of clearcutting and alternative silvicultural systems on rates of decomposition and nitrogen mineralization in a coastal montane coniferous forest. For. Ecol. Manage. 95, 253–260.

Reich, P.B., Grigal, D.F., Aber, J.D., Gower, S.T., 1997. Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. Ecology 78, 335–347.

Robertson, G.P., 1982. Factors regulating nitrification in primary and secondary succession. Ecology 63, 1561–1573.

Rossi, R.E., Mulla, D.J., Journel, A.G., Franz, E.H., 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. Ecol. Monogr. 62, 277–314.

Ryan, M.G., Binkley, D., Fownes, J.H., 1997. Age-related decline in forest productivity: pattern and process. Adv. Ecol. Res. 27, 213–262.

SAS Institute, Inc., 1989. SAS for Windows, Version 6.10. SAS Institute, Inc., Cary, NC.

Schilling, E.B., Lockaby, B.G., Rummer, R., 1999. Belowground nutrient dynamics following three harvest intensities on the Pearl River Floodplain, Mississippi. Soil Sci. Soc. Am. J. 63, 1856–1868.

Schimel, D.S., Braswell, B.H., McKeown, R., Ojima, D.S., Parton, W.J., Pullian, W., 1996. Climate and nitrogen controls on the geography and timescales of terrestrial biogeochemical cycling. Global Biogeochem. Cycles 10, 677–692.

Soil Survey Staff, 1980. Soil Survey of Dubois County, Indiana. US Department of Agriculture, Soil Conservation Service, Washington, DC.

Tamm, C.O., 1979. Nutrient cycling and productivity of forest ecosystems. In: Leaf, A.L. (Ed.), Proceedings of the Impact of Intensive Harvesting on Forest Nutrient Cycling. US Department of Agriculture, Forest Service, Northeast Forest Experiment Station, Broomall, PA, pp. 2–21.

Thorne, J.F., Hamburg, S.P., 1985. Nitrification potentials of an old-field chronosequence in Campton, New Hampshire. Ecology 66, 1333–1338.

Thornthwaite, C.W., 1948. An approach to a rational classification of climate. Geogr. Rev. 38, 55–94.

Tiarks, A.E., Buford, M.A., Powers, R.F., Ragus, J.F., Page-Dumroese, D.S., Ponder Jr., F., Stone, D.M., 1997. North American long-term soil productivity research program. In: Proceedings of the National Silviculture Workshop. General Technology Report NE-238. US Department of Agriculture, Forest Service, pp. 140–147.