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Long-Term Effects of Nitrogen Fertilization on Nitrogen Availability in Coastal Douglas-Fir Forest Floors

H. N. Chappell, C. E. Prescott,* and L. Vesterdal

ABSTRACT

It has been suggested that a long-term increase in N availability could be achieved by repeated N fertilization of forests, and that the increase in N availability would be greatest at initially N-rich sites. The aim of this study was to determine if N availability was elevated 8 to 12 yr after repeated N fertilization, and if the effects of N fertilization were related to the soil N capital. Rates of N cycling in control and fertilized plots of Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] were compared by measuring net N mineralization rates in forest floors and by estimating rates of N turnover from the litterfall/forest floor ratio. Litterfall N contents, litter N concentrations, and rates of N turnover increased along the gradient in soil N capital in both control and fertilized stands. Fertilization did not affect litterfall N content, but C/N ratios of litter and forest floors were significantly lower in fertilized stands along the gradient. Turnover rates of N in the forest floors were not higher in fertilized plots than in control plots, nor were rates of net N mineralization affected by fertilization. Net nitrification rates were higher in some of the plots that received 1120 kg N ha⁻¹ than in control plots. We conclude that N fertilization did not result in a sustained increase in N cycling and N availability analogous to a higher site N capital, and that the effect of N fertilization was not related to the initial soil N capital of these sites.

IT HAS BEEN SUGGESTED that a long-term increase in N availability could be achieved by N fertilization because of more rapid recycling of N through litter. Trees in fertilized forests produce litter of higher quality (lower C/N ratio), which will decompose more rapidly and release more N, thereby prolonging the fertilization effect (Gosz, 1981; Vitousek et al., 1982). However, largely as a result of immobilization of N in the soil (Binkley, 1986), tree growth responses and higher soil N concentrations usually persist for only a few years after N fertilization (Miller, 1988). Snowdon and Khanna (1989) suggested that frequent and large N applications could permanently increase the rate of N cycling and site quality. Sustained growth response and increased N availability have been reported more than

15 years after a single N application of 470 kg ha⁻¹ to a Douglas-fir stand in southeastern Washington (Binkley and Reid, 1985; Strader and Binkley, 1989). Prescott et al. (1995a) also found higher N availability in forest floors of jack pine (*Pinus banksiana* Lambert) 20 yr after they received 672 kg N ha⁻¹ in six applications. Conversely, Prescott et al. (1993b) found no evidence of more rapid turnover of N in litter in coastal Douglas-fir forests that received repeated applications of N fertilizer or sewage sludge equivalent to one-half and twice the estimated soil capital of N. This was attributed to the poor site, so presumably most of the added N was immobilized in the soil. They hypothesized that a long-term enhancement of N cycling might occur on sites initially richer in N, where less of the added N would be immobilized in the soil. Feger (1992) added N to Norway spruce [*Picea abies* (L.) Karst.] forests on a site rich in N and a site poor in N, and found that most of the N was immobilized in soil on the poor site, whereas on the rich site much was converted to NO₃ and leached. In Rocky Mountain forests, greater rates of N mineralization were found 4 yr after addition of N, but only on sites that were initially relatively rich in N (Prescott et al., 1992).

In this study, we compared N availability in control and repeatedly fertilized plots in coastal Douglas-fir stands across a natural range of soil N capital 8 to 12 yr after the last N addition. Our objective was to test the hypothesis that fertilization will induce a sustained increase in N availability in coastal Douglas-fir forests as a result of faster recycling of N. Further, our aim was to determine if a sustained increase in N availability occurred to the same extent at N-poor and N-rich sites. The indices of N cycling measured were the amounts of N in litterfall, and rates of N turnover and net N mineralization in the forest floors.

MATERIALS AND METHODS

Study Sites

Nine coastal Douglas-fir stands of widely different site index were selected to represent a gradient in N availability, based on the established relationship between N availability and productivity (Chappell et al., 1991). Eight stands were located in coastal Washington and one was in coastal Oregon. Characteristics of the nine sites are summarized in Table 1. Soil N capital ranged from 2.5 to 12.1 Mg ha⁻¹ and was significantly

H.N. Chappell, College of Forest Resources, Univ. of Washington, Seattle, WA 98195. Current address: Potlatch Corp., P.O. Box 390, Warren, AR 71671; C.E. Prescott, Faculty of Forestry, Univ. of British Columbia, 2424 Main Mall, Vancouver, BC V6T 1Z4, Canada; L. Vesterdal, Dep. of Forest Ecology, Danish Forest and Landscape Research Institute, Hørsholm Kongevej 11, DK-2970 Hørsholm, Denmark. Received 3 Sept. 1998. *Corresponding author (cpres@interchange.ubc.ca).

Table 1. Characteristics for the nine sites. Sites are listed according to increasing soil N capital.

Site†	USDA soil suborder	Parent material	Aspect	Slope	Elevation	Precipitation cm yr ⁻¹	Soil N capital‡
				%	m		Mg ha ⁻¹
Skykomish (43)	Haplorthod	Granite	NW	10	457	—	2.53
White Chuck Mountain (110)	Fragiorthod	Meta-igneous shale	SE	60	945	292	3.28
Cedar Falls Powerline (5)	Xerochrept	Glacial till	E	10	274	178	4.06
Cedar Falls (1)	Durochrept	Glacial till	level	5	344	203	4.50
Little Ohop Creek (117)	Haploxeralf	Sandstone	SE	20	671	152	7.00
Headquarter Camp (57)	Haplohumult	Igneous	level	10	536	165	8.50
Middle Fork Satsop River (77)	Haplorthod	Glacial till	level	10	162	229	9.68
Deep Creek (20)	Haplumbrept	Glacial sediments	SE	10	373	178	10.54
Camp Grisdale (53)	Haplumbrept	Glacial till	W	15	421	292	12.10

† Stand Management Cooperative installation numbers in parentheses.

‡ Mineral soil N capital in the entire soil profiles prior to fertilization.

correlated with site index (Prescott et al., 1999). Total N contents in the mineral soils are from profiles ranging from 63 to 152 cm in depth. The differences in profile depth were not related to soil N capital and were assumed to be of little importance due to very low concentrations of N in the deep soil horizons.

The fully stocked second growth stands were part of a fertilization trial established in 1969 and 1970 as part of Phase I of the Regional Forest Nutrition Research Project (now the Stand Management Cooperative). There were six plots 0.04 ha or larger plus a treated buffer at each site, which received single or multiple applications of urea, as well as a control that received no fertilizer (for more information about initial treatment design, see Hazard and Peterson, 1984). Stands were 18 to 46 yr old at the time of the initial fertilization. For this study, we sampled the control plot and the plot that had received the maximum cumulative amount of N at each site (a total of 896 or 1120 kg N ha⁻¹ in four or five applications between 1969 and 1985). The initial fertilizer application was 448 kg N ha⁻¹ at plot establishment in 1969 (except for White Chuck Mountain which received 224 kg ha⁻¹), with an additional 224 kg N ha⁻¹ applied after each of 8, 12, and 16 yr. Two installations, Skykomish and Cedar Falls, did not receive the 16-yr fertilization. The cumulative N applications amounted to between 10 and 35% of the initial soil N capitals. Stand characteristics at the time of sampling in 1993 and total N applications for the nine sites are shown in Table 2.

Sampling and Analyses

The following measurements were made in each plot: (i) N concentration in needle litter and annual litterfall mass, (ii) N concentration and mass of the forest floor, and (iii) net N mineralization in the forest floor. All sampling was done within

the two (control and fertilized) 0.04-ha measurement plots in each stand. Samples were taken 8 yr after the last fertilizer application at seven sites and after 12 yr at Skykomish and Cedar Falls. Increases in growth and N availability generally last less than 8 yr after fertilization (Strader and Binkley, 1989), so differences in N cycling between control and fertilized stands after 8 yr should indicate sustained responses to the fertilization treatment.

To estimate the N content of litterfall, ten 0.135-m² plastic trays with fiberglass screens in the bottom and holes for drainage were randomly placed in each measurement plot in April 1993. Fallen litter was collected from each tray at ≈2-mo intervals for 1 yr; dried at 70°C; sorted into brown needles, green needles and other material; and weighed. Only brown needles having undergone senescence and abscission were measured since these would best represent the nutritional conditions of the site. Green needles were excluded because they were mostly attached to branches broken off during windstorms. Concentrations of C and N were measured in litter collected in October following the annual peak in litterfall, using a CHN analyzer (Perkin Elmer Series II CHNS/O Analyzer 2400, Perkin Elmer, Norwalk, CT). The total amounts of C and N in annual litterfall were estimated by multiplying the mass of litter in each tray by the concentration of C or N.

The mass of the forest floors were estimated from five 0.093-m² samples of the Oi, Oe, and Oa layers collected from each plot in October 1993. Samples were dried at 70°C and weighed, and concentrations of total C and N were measured with the CHN analyzer. The total amounts of C and N in the forest floors were estimated by multiplying the masses of the forest floors by the concentration of C or N.

The rate of turnover of forest floor at each site was estimated using the litterfall/forest floor mass ratio method (Olson, 1963). The fractional annual losses of C and N from

Table 2. Stand characteristics for the nine sites at the time of sampling in 1993. Sites are listed according to increasing soil N capital.

Site	Age	Site index	Control plots†			Fertilized plots†				N applied‡
			Stem number	Volume	Annual increment	Stem number	Volume	Annual increment	Increment response‡	
	yr	m	ha ⁻¹	m ³ ha ⁻¹	m ³ ha ⁻¹ yr ⁻¹	ha ⁻¹	m ³ ha ⁻¹	m ³ ha ⁻¹ yr ⁻¹		kg ha ⁻¹
Skykomish	70	26	1960	923	18.4	1304	1109	23.7	5.3	896
White Chuck Mountain	42	35	1235	672	26.6	1353	676	26.9	0.3	896
Cedar Falls Powerline	62	31	872	613	13.7	827	767	18.6	4.9	1120
Cedar Falls	67	35	472	781	11.8	615	865	13.4	1.6	896
Little Ohop Creek	51	40	1111	944	20.7	983	752	16.1	-4.6	1120
Headquarter Camp	59	40	474	1018	23.0	551	1197	28.4	5.4	1120
Middle Fork Satsop River	46	38	1383	613	24.4	1160	575	23.0	-1.4	1120
Deep Creek	56	42	630	844	16.8	464	948	22.7	5.9	1120
Camp Grisdale	52	37	751	878	24.6	793	1031	28.8	4.2	1120

† Stocking data for 1993, and annual increment applies to the preceding 24-yr period following fertilization. Stocking data for Middle Fork Satsop River are from 1989 and annual increment applies to a 20-yr period only.

‡ Increment response for the 24-yr period (20 yr for Middle Fork Satsop River).

§ Cumulative N application. For differences see text.

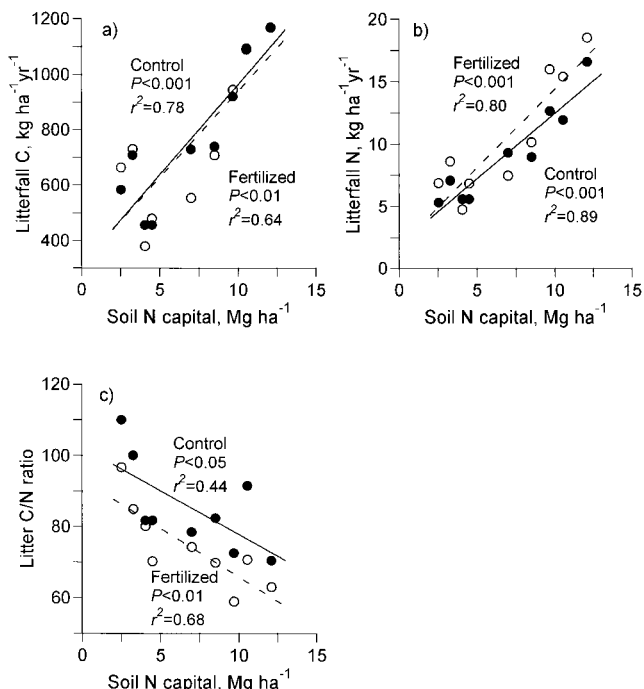


Fig. 1. Aboveground litterfall C and N in control (closed circles, solid regression line) and fertilized stands (open circles, dashed regression line) along the gradient in soil N capital: (a) C contents, (b) N contents, and (c) C/N ratios. In (a) the values for the fertilized plots at the two sites with highest N capital are the same as those for the control plots.

the forest floor were calculated by dividing the annual inputs of C and N in litter by the total amounts of C and N in the forest floor (Gosz et al., 1976). Turnover estimates were based on brown needle litter and all forest floor material except woody debris >1 cm.

Potential rates of net N mineralization in the forest floor were estimated from the amounts of $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ produced during 24-d aerobic incubations in the laboratory (Vitousek et al., 1982). Temperature and moisture conditions were standardized so that differences in mineralization rates would reflect changes in the forest floor substrate rather than climatic influences. Ten samples of the Oe and Oa layers in each plot were collected in October 1993 separately from the forest floor samples described above. A 5-g subsample (dry weight equivalent) was extracted with 50 mL of 2 M KCl, and concentrations of $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ were measured on an Alpkem RFA 300 AutoAnalyzer (Alpkem Corp., Wilsonville, OR; Page et al., 1982). A second 10-g subsample (dry weight equivalent) was placed in a 60-cm³ glass jar. Distilled water was sprayed into each subsample to bring the moisture contents to 75% (wet weight basis), and the jars were incubated in the dark at $\approx 20^\circ\text{C}$. Each week, the jars were opened to outside air for 15 min. After 24 d, each sample was extracted with 2 M KCl. Differences between the amounts of extractable N before and after incubation were used to estimate net N mineralization in each forest floor sample.

Data Analysis

Relationships between the N availability indices and soil N capital within control and fertilized plots were tested by simple linear regression. Forest floor N content data and net N mineralization data were log-transformed prior to analysis in order to homogenize the variances, but transformation of other data were not necessary. The effect of fertilization along the gradi-

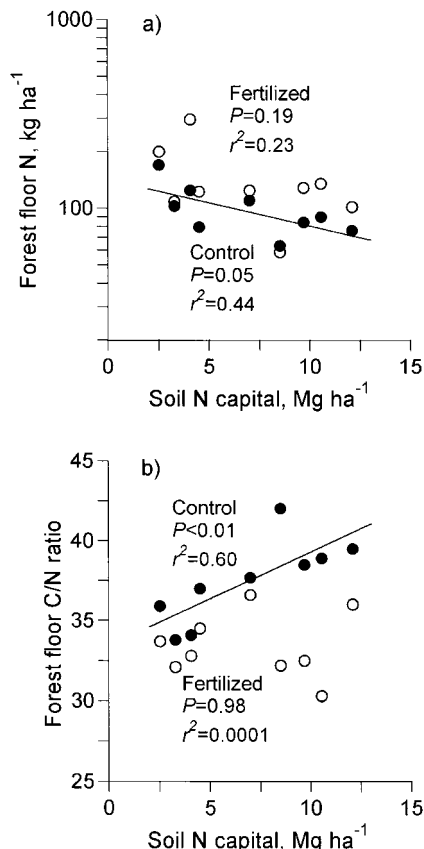


Fig. 2. Forest floor C and N in control (closed circles, solid regression line) and fertilized stands (open circles, dashed regression line) along the gradient in soil N capital: (a) N contents and (b) C/N ratios. Note the logarithmic y-axis.

ent in soil N was tested by analysis of covariance using treatment (control, fertilization) as the class variable, soil N capital as the covariate, and the interaction term for treatment and soil N capital. Fertilization effects were tested by comparing the means for treatments adjusted to common levels of soil N capital (least-square means). The influence of soil N capital on fertilization effects, that is, the interaction effect, was tested by comparing the slopes of the regression lines for control and fertilized plots. All analyses were carried out using the GLM procedure in SAS (SAS Institute, 1993).

RESULTS

Litterfall C and N contents were significantly correlated with soil N capital in both control and fertilized plots (Fig. 1a and 1b). Fertilization did not change litterfall C and N content along the soil N gradient, as neither the levels nor the slopes of the regression lines were significantly different between control and fertilized plots. Litter C/N ratios were negatively correlated with soil N capital in both treatments (Fig. 1c), and fertilized plots had lower litter C/N ratios than control plots ($P < 0.01$). Litter in fertilized plots had C/N ratio least square means of 74 compared with 85 in control plots. The litter C/N ratios of control and fertilized plots declined similarly along the gradient, as indicated by the similar slopes of the two regression lines (Fig. 1c).

Forest floor N contents decreased significantly along

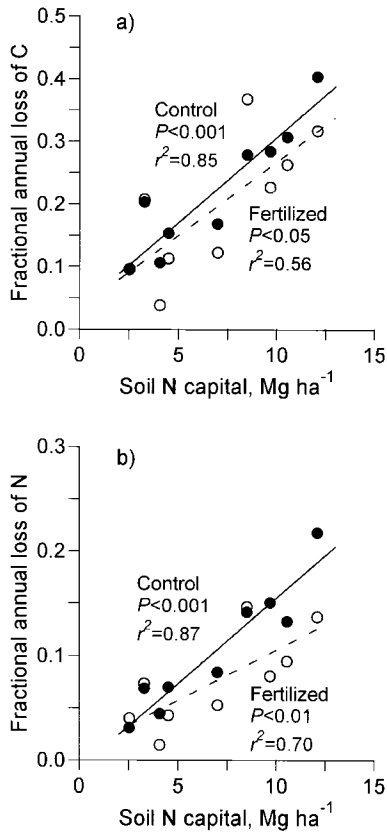


Fig. 3. Fractional annual losses of C and N (annual input of senesced needle litter/forest floor mass) in forest floors of control (closed circles, solid regression line) and fertilized stands (open circles, dashed regression line) along the gradient in soil N capital: (a) C loss and (b) N loss. In (a) the value for the fertilized plots at the site with the lowest N capital is the same as that for the control plot.

the soil N gradient in control plots but did not decrease significantly in fertilized plots (Fig. 2a). There was a tendency for fertilized forest floors to have greater N contents (least significant means of 130 vs. 96 kg ha⁻¹ in control plots, *P* = 0.07). Forest floor C/N ratios were lower in fertilized plots than in control plots (means of 33 vs. 37, *P* < 0.001) (Fig. 2b). Forest floor C/N ratios in control plots were weakly positively correlated with the gradient in soil N capital, whereas C/N ratios in fertilized plots were not correlated with soil N.

Fractional annual losses of C and N increased significantly along the soil N gradient in both control and fertilized plots (Fig. 3). Fractional annual losses of C and N tended to be lower in fertilized plots, but the levels of the regression lines for control and fertilized plots were not significantly different.

Fertilization did not significantly affect rates of net N mineralization in the forest floors (Fig. 4). Net N mineralization generally declined with increasing soil N capital; this relationship was significant in fertilized plots but not in control plots. Mineralization rates expressed on a per hectare basis also showed no effect of fertilization, because there was no significant difference in forest floor mass between control and fertilized plots. Rates of net nitrification in the forest floors were negligible in the control plots and in most of the fertilized plots

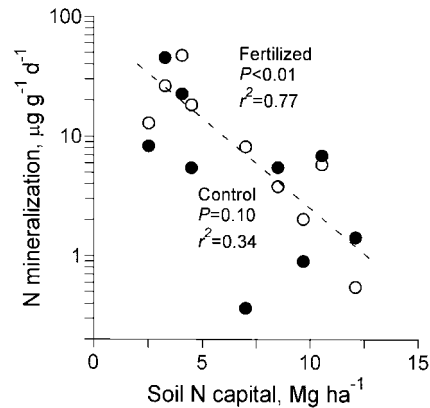


Fig. 4. Net nitrogen mineralization rates in forest floors from control (closed circles, solid regression line) and fertilized stands (open circles, dashed regression line) along the gradient in soil N capital during a 24-d laboratory incubation in control and fertilized plots. Note the logarithmic y-axis.

(Fig. 5). There were higher rates of nitrification in three of the fertilized plots (Sites 5, 17, and 57); these were among the six plots that received the larger amount of N fertilizer (1120 kg ha⁻¹). Nitrification rates in the forest floors were not related to the gradient in soil N.

DISCUSSION

Repeated applications of N totaling 896 or 1120 kg ha⁻¹ did not result in a sustained increase in N availability in Douglas-fir forests in this study. Although the N concentrations of litter increased, the amounts of litterfall C were unchanged in fertilized plots 8 to 12 yr after fertilization, and the amounts of N returned annually in aboveground litterfall were not significantly higher in fertilized plots. The C/N ratio of the forest floors was lower in fertilized plots, but fractional annual loss of N from the forest floor was not faster in fertilized plots. In fact, there was a trend for slower turnover in fertilized forest floors. Rates of net N mineralization were similar in control and fertilized forest floors, and nitrification rates increased in only three of the nine fertilized plots. These results do not support the hypothesis that repeated N fertilization results in higher miner-

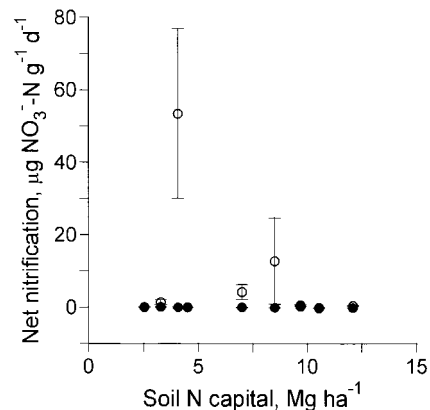


Fig. 5. Net nitrification rates in forest floors from control (closed circles, solid regression line) and fertilized stands (open circles, dashed regression line) along the gradient in soil N capital during a 24-d laboratory incubation. Bars indicate standard errors.

alization rates and greater N cycling through litterfall (Gosz, 1981; Vitousek et al., 1982).

Nitrogen concentrations in litter were higher in fertilized plots than in control plots 8 to 12 yr after the last application of N. Increased litter N concentrations have often been reported in the first few years following fertilization or concurrent with chronic N applications (Miller et al., 1976; Theodorou and Bowen, 1990; Gundersen, 1998). Sustained increases in litter N concentrations persisting for 6, 10, and 18 yr have been reported as a result of N application to Douglas-fir forests (Trofy-mow et al., 1991; Prescott et al., 1993b; Binkley and Reid, 1985, respectively). Litterfall N content (either measured or inferred from leaf area measurements) also increased in some of these studies. The lack of fertilization effect on needle litter mass in this study indicates that any increases in foliage production had subsided at least 4 yr prior to this study (four being the usual number of needle age classes for coastal Douglas-fir). Thus, any changes in N cycling that we detect in this study should be indicative of long-term effects of fertilization.

Based on the ratio of litterfall N to forest floor N, we found no evidence of faster N turnover in the forest floor due to N fertilization. Although fractional annual loss of N was slightly slower in fertilized plots due to larger forest floor N contents, neither of these differences were significant. Estimation of turnover rates by the litterfall/forest floor ratio method assumes that the stands are in steady state, in other words, that annual decomposition in the forest floor equals annual litter input. Although the stands were more than 40 yr old, and closed canopies many years earlier, steady state conditions cannot be assumed for these stands. Nevertheless, comparing the ratios of litterfall to forest floor mass in control and fertilized plots at the same site should identify any substantial change in decomposition and N turnover as a consequence of fertilization. Turnover rates may have been underestimated in fertilized forest floors, which may carry the legacy of greater inputs of litter in the past. There may also be more green needle and branch input in fertilized plots, although there was no such trend during the year that we collected litter. Comparing forest floor mass with input of brown needles 8 to 12 yr after fertilization could lead to underestimation of forest floor turnover rates in fertilized plots. We used brown needle mass because the rates of input would be less variable than inputs of branches and green needles and so would provide a better indication of site N status and litter turnover rates.

The lower C/N ratios of forest floors in fertilized plots might be expected to result in greater rates of net N mineralization and nitrification. However, as in an earlier study in Douglas-fir (Prescott et al., 1993b), we did not detect any long-term differences in rates of net N mineralization in the forest floors. In contrast, Strader and Binkley (1989) and Binkley and Reid (1985) reported increased rates of net N mineralization and increased amounts of mineral N in a Douglas-fir forest, and Prescott et al. (1995a) found increased net N mineralization in a jack pine forest, both 22 yr after fertiliza-

tion. Increased rates of nitrification in fertilized plots were only observed at three of the nine sites in this study. This included three of the six plots that received the highest N additions (1120 kg ha^{-1}), but none of the three sites that received the lesser amount of N (896 kg ha^{-1}). This suggests that repeated N additions totaling more than 896 kg ha^{-1} (equivalent to $56 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) are necessary to induce net nitrification in these forest floors. Rates of net nitrification in the mineral soil may have been even greater (White et al., 1988), but were not measured, nor was NO_3 leaching. As Johnson (1992) points out, increases in NO_3 leaching are more likely to follow small, frequent doses of N than single, large doses. However, even in forests subject to chronic N addition, increased nitrification rates are often temporary or highly variable (McNulty and Aber, 1993; Gundersen, 1998). Recent studies have demonstrated that rates of net nitrification in coniferous forests are largely controlled by microbial assimilation of NO_3 (Stark and Hart, 1997), which depends on C availability. Rates of net N mineralization are also closely linked to C availability (Hart et al., 1994). It is therefore not surprising that manipulation of N availability alone does not have a consistent effect on rates of net N mineralization and nitrification.

Results from other studies suggest that the effects of N fertilization on N cycling might be different at N-rich and N-poor sites (Feger, 1992; Prescott et al., 1993b). At N-poor sites, a larger portion of the applied N may be immobilized in the soil (Preston et al., 1990; Johnson, 1992) or recycled within the trees (Miller, 1988), whereas at more N-rich sites, more of the applied N may remain in the pools that are actively recycled. The sites used in this study comprised a natural gradient in soil N capital, and the amount of N circulating in litter and the rate of N turnover in the forest floor increased along the gradient (Prescott et al., 1999). However, the effects of repeated N additions on these indices of N cycling did not differ along the N gradient, indicating that the effects of fertilization on N cycling were not related to site N capital.

As outlined by Gosz (1981), coniferous forests on rich sites produce litter with high N concentrations and low amounts of phenolics, leading to rapid decomposition and mineralization of N. On N-poor sites, the litter has low N concentrations and higher amounts of phenolics, decomposes slowly and mineralizes the N slowly. These differences in litter chemistry among sites thus create a feedback that increases N availability on rich sites but decreases it on poor sites. Support for this hypothesis has come from a study of N cycling along a N-availability gradient in Wisconsin forests, which reported increases in litter N concentrations and N return in litter, with increasing N availability (Pastor et al., 1984). In the control stands used in this study, Prescott et al. (1999) found greater N return in litter and faster N turnover with increasing soil N capital. It is therefore conceivable that increasing N availability through the addition of N fertilizer would increase the rate of N cycling. Repeated or continuous N additions would be particularly likely to induce this change in N cycling. However, with a

few notable exceptions (Binkley and Reid, 1985), most studies have shown the effect of N addition to be fleeting, with N availability and tree growth response returning to prefertilization levels within a few years (Binkley, 1986). Why does N fertilization of coniferous forest not result in a sustained improvement in N availability?

Many of the studies that have shown greater N cycling at N-rich sites were along N-availability gradients in which the tree species composition changed, with species that produce higher quality litter replacing others as N availability increased (Pastor et al., 1984; Reich et al., 1997). It may be that N additions must be substantial enough to change the tree species composition of the forest before there will be a sustained increase in litter quality, turnover, and N availability. Changes in the composition of ground vegetation have been reported in response to fertilization (Kellner and Marshagen, 1991; Prescott et al., 1993a), and this may influence rates of N cycling. A long-term increase in forest floor N mineralization rates in N-fertilized jack pine forests was associated with a major shift in ground vegetation from ericaceous species, such as sheep laurel (*Kalmia angustifolia* L.) and lowbush blueberry (*Vaccinium angustifolium* Ait.), to nitrophilous species, including threeseeded sedge (*Carex trisperma* Dewey) and elderberry [*Sambucus canadensis* (L.) R. Bolli] (Prescott et al., 1995b). Differences in the composition of ground vegetation in fertilized plots were apparent at some of the sites in this study, but apparently their effect was not sufficient to significantly increase N availability in fertilized plots.

Another reason for the lack of sustained change in N cycling in N-fertilized forests is that increasing the availability of N may not increase the rate of litter decomposition. Although the N concentration of litter is often correlated with the rate of decomposition of different litter types, increasing the N concentration within a litter type may not increase its rate of decay. Rates of litter decomposition in fertilized forest floors are often the same (Prescott, 1995) or slower (Titus and Malcolm, 1987) than in unfertilized forest floors. Nitrogen-enriched Scots pine (*Pinus sylvestris* L.) litter decomposed faster than control litter initially, but then slower, so that rates were comparable after 4 yr (Berg et al., 1987). We found an indication of faster turnover on N-rich sites, but no indication of faster turnover in fertilized plots. This suggests that site factors other than N availability contribute to faster litter turnover on N-rich sites.

Natural gradients in soil N capital are usually associated with changes in other site factors such as climate, soils, and vegetation, all of which may influence rates of N cycling. The radiata pine (*Pinus radiata* D. Don) stands studied by Lamb (1975) that displayed different N cycling rates were on different soil types. The N mineralization gradients studied by Reich et al. (1997) and Pastor et al. (1984) included diverse soils and forest types. The N capital gradient in this study was associated with differences in soil texture, with greatest N capitals occurring on finer-textured soils. Prescott et al. (1999) concluded that although N capital appeared to be the

proximate control of N cycling in these stands, soil texture may ultimately control N availability by controlling the productivity and the buildup of soil N capital on these sites. Additions of N in fertilizer may temporarily increase N availability, but do not change the other site factors that govern productivity and N cycling. Therefore, it is unlikely that a sustained increase in N availability analogous to an increase in soil N capital can be achieved through fertilization.

In conclusion, we found higher rates of N cycling along a natural gradient in soil N capital, but no effect of repeated N fertilization on N cycling in the forest floor on N-rich or N-poor sites. These results indicate that a sustained increase in forest floor N availability analogous to a higher site N capital was not achieved by repeated N fertilization.

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