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Factors influencing the availability of nitrogen in thinned and unthinned Douglas-fir stands in the central Oregon Cascades

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Abstract

Soil N mineralized during 7-day anaerobic incubation at 40°C ('available' N) was compared at two soil depths and correlated to soil and site factors in Douglas-fir stands with different combinations of thinning and multinutrient fertilization. Available N expressed either on an area basis (kg ha^{-1}) or on a concentration basis (mg kg^{-1}) at the two depths did not vary significantly by stocking density, treatment, or density–treatment interaction. There was a significant difference between the soil depths, averaging 39 mg kg^{-1} at 0–20 cm depth, and 20 mg kg^{-1} at 20–40 cm depth. Available N was positively correlated with total soil N, exchangeable Ca, and adjusted aspect (the former two factors accounting for 46% of the total variation), and negatively with rock content and slope steepness. Stand density had no effect. © 1997 Elsevier Science B.V.

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1. Introduction

Nutrient availability in forest ecosystems depends on the interaction of soil, vegetation, and environmental processes (Jenny, 1941). Forest productivity, like that of most terrestrial ecosystems, is generally nitrogen limited (Myrold, 1987), and N is recognized as the most limiting element for forest growth in the Pacific Northwest (Johnson et al., 1982). Because of its degree of limitation, there has been search for an adequate index of N availability (Keeney, 1980; Powers, 1980, 1984).

An index that has proved to be a reliable indicator

of N availability, at least for some tree species, is the rate at which nitrogen is mineralized. Mineralizable N, determined either aerobically or anaerobically, has been found to correlate reasonably well with growth response to fertilization (Shumway and Atkinson, 1978; Powers, 1980; Radwan and Shumway, 1984), aboveground primary production (Nadelhoffer et al., 1983; Pastor et al., 1984; Binkley et al., 1986), growth efficiency (Velazquez Martinez et al., 1992), and site index (Powers, 1980; Kabzems and Klinka, 1987). Anaerobically-determined mineralizable N is considered to index the pool of readily available N in soils (Waring and Bremner, 1964; Powers, 1980), and correlates closely with nitrogen contained in microbial biomass (Myrold, 1987; Binkley and Hart, 1989).

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Understanding the factors that influence nitrogen availability yields insights into controls over primary productivity. Researchers have examined relationships between N mineralization and soil characteristics such as pH, temperature, water content, and soil organic matter (SOM) (Stanford and Epstein, 1974; Nadelhoffer et al., 1983; Hart and Binkley, 1985; Warren and Whitehead, 1988). The objectives of the present study were: (1) to compare available N, as indexed by anaerobic mineralization, among Douglas-fir plantations with different combinations of thinning and multinutrient fertilization; (2) to examine the influence of soil nutrients and topography on available N across a range of sites on the H.J. Andrews Experimental Forest, Oregon.

2. Methods

The study was conducted in the H.J. Andrews Experimental Forest, located in the west-central Cascade Mountains, 80 km east of Eugene, Oregon (44°15'N, 122°10'W). The Experimental Forest is wet and fairly mild in winter and warm and dry in summer (Bierlmaier and McKee, 1989). Average yearly temperature (recorded at 426 m elevation) is 8.5°C. At lower elevations of the forest, the mean temperature of the coldest month is 2.3°C, and 26.6°C in the hottest (Rothacher et al., 1967). Extreme temperatures range from -18 to 38°C. Average annual precipitation is about 2300 mm at lower elevations and may reach more than 2500 mm on some higher ridges (Dyrness et al., 1974).

The most prevalent soils are Inceptisols, although there are some Alfisols (Brown and Parson, 1973). Soils are formed primarily from igneous bedrock, particularly andesites. Because of their high porosity, these soils permit rapid absorption of water and

provide storage for 30–40 cm of water (Bierlmaier and McKee, 1989).

The study was located in four Douglas-fir plantations in the western hemlock zone (Franklin and Dyrness, 1973). Established by planting following clearcutting and slash burning, plantations ranged from 21 to 27 years of age in 1987 (the time of sampling). Elevations, slopes, aspects, and soil rock contents are shown for each site in Table 1. No soil survey has been done on the H.J. Andrews; however, in nearby locales that have been surveyed, sites with temperatures, precipitation, and topography similar to our study sites have soils classified as Klickitat or Bohannon (SCS, 1989). These are deep and well drained, with a dark brown stony or gravely loam surface layer and a brown to dark brown cobbly loam subsoil. Depth to bedrock ranges from 50 to 150 cm.

Plantations were manually thinned in 1981 to three levels: heavily thinned (average spacing 5.5 m), moderately thinned (average spacing 3.6 m), and unthinned. Felled trees were left on site. In 1987, leaf area index (LAI) averaged 2.8 m² m⁻², 4.4 m² m⁻², and 10.7 m² m⁻² in heavily thinned, moderately thinned, and unthinned, respectively. Each level of thinning was represented by one randomly selected block within each plantation. Each thinning block was subdivided into four subplots which were either pruned, fertilized with multinutrient tabs, pruned and fertilized, or left untreated (controls), giving a total of 48 subplots in the entire study. Subplots contained a similar number of trees (45–50), and varied in size depending on stocking density. Subplots were separated from one another and from stand edges by 10 m buffers. Average and ranges of slope and aspect were calculated from five random points per subplot (aspect by compass and slope by clinometer). Density was determined from plots of

Table 1
Mean and range of topographic variables for the study sites

Site	Elevation (m)	Soil rock content (%)		Slope (%)		Aspect (deg.)	
	Mean	Mean	Range	Mean	Range	Mean	Range
L107	705	11.2	5.2–18.3	41	12–75	168	0–360
L111	732	8.4	2.7–20.5	43	25–65	277	200–360
L405	854	6.6	1.9–15.7	23	12–50	182	155–215
L701	854	14.6	7.6–27.0	42	12–63	166	100–252

known area within each subplot. Procedures for pruning and fertilizing are given in Velazquez Martinez et al. (1992). Fertilizer tabs contained 4.2 g N, 2.1 g P, 1.0 g K, 0.55 g Ca, 0.34 g S, and 0.07 g Fe in the following compounds: urea formaldehyde, calcium phosphate, and potassium, calcium, and ferrous sulfates. Each tree was given one tab per 1.2 cm diameter at breast height (DBH), buried at 15–20 cm depth evenly around the tree at the crown drip line.

Available N was determined in 1987 (6 years after thinning) for two soil depths. Three randomly selected soil samples were extracted from the top 0–20 cm of mineral soil and one from 20–40 cm depth in each subplot during mid summer 1988. All samples were collected within 10 days. Samples were placed in plastic bags and stored in walk-in coolers no longer than 3 days before analysis. After sieving to 4 mm and homogenizing in a splitter, a 50 g subsample was taken from each sample and incubated anaerobically for 7 days at 40°C (Waring and Bremner, 1964). Prior to and following incubation, NH_4^+ was extracted with 2 N KCl and analyzed using an Alphen Rapid Flow Analyzer. Available N was calculated as the difference in NH_4^+ between initial and final samples.

Available N in the 0–20 cm depth was expressed both on a concentration basis (mg kg^{-1}) and on an area basis (kg ha^{-1}), the latter calculated using soil rock content (Velazquez Martinez et al., 1992). Soils were analyzed to determine exchangeable K, Ca, and

Mg, using the ammonium acetate method (Knudsen et al., 1982; Lanyon and Heald, 1982). Total soil nitrogen and phosphorus concentrations were determined using the standard microKjeldahl technique (Bremner and Mulvaney, 1982) and pH was determined using both distilled water and 1 N KCl solution. Leaf area index was estimated from sapwood area using the equation presented by Waring et al. (1982). For regression, aspect was adjusted as $180 - |180 - \text{aspect}| = \text{adjusted aspect}$.

2.1. Statistical analysis

ANOVAs and the Tukey test were used to investigate treatment effects on available N (Steel and Torrie, 1980). A *t*-test was used to compare available N expressed on a concentration basis in the two sampled soil depths. Stepwise regression (Statistical Analysis Systems Institute Inc., 1985) was used to examine the relationship between available N from the top 0–20 cm of mineral soil, topsoil characteristics, and 1987 leaf area index. Prior to ANOVA and regression, nutrient data were log transformed to improve the normality of distributions. The model selected by backwards stepwise regression was checked for collinearity using variance inflation and condition index, and was additionally verified using forwards stepwise regression (Statistical Analysis Systems Institute Inc., 1985). All three procedures showed the model free of significant collinearity.

Table 2
Averaged soil and physiographic characteristics of Douglas-fir plantations at different stand densities

Variable	Stand density		
	High	Medium	Low
Total soil N (mg kg^{-1})	2000 (120)a	2100 (130)a	2200 (110)a
Total soil P (mg kg^{-1})	1400 (140)a	2000 (210)a	1700 (200)a
Exch. soil Ca (meq per 100 g)	16.7 (1.46)a	10.5 (1.06)b	10.6 (1.16)b
Exch. soil Mg (meq per 100 g)	4.6 (0.56)a	2.5 (0.38)b	2.8 (0.39)b
Exch. soil K (meq per 100 g)	506.0 (43.6)a	397.0 (26.0)b	387.0 (36.8)b
Soil Ca/Mg ratio	3.9 (0.28)a	4.8 (0.43)a	4.2 (0.26)a
pH	5.9 (.034)a	6.0 (.049)a	5.9 (0.52)a
Rock content (%)	7.1 (0.72)b	11.7 (1.64)a	11.8 (1.53)a
Slope (%)	44.0 (4.9)a	34.7 (4.3)a	33.2 (4.2)a
Aspect (deg.)	195.0 (19.7)a	197.0 (27.3)a	202.0 (23.4)a

Standard errors are given in parentheses. Within a row, means followed by the same letter are not significantly different at $\alpha = 0.05$.

3. Results

Soil nutrient and physiographic characteristics are summarized in Table 2. In most cases there were no significant differences among stand densities and treatments for the measured variables. However, exchangeable Ca, Mg, and K were highest in soils of high density plots, and rock content was higher in both medium and low than in high density plots.

Available N, expressed either on an area basis (kg ha^{-1}) or on a concentration basis (mg kg^{-1}) did not vary significantly by stocking density, treatment or density-treatment interaction (Tables 3 and 4). Available N varied among sites when expressed on an area basis, but not when expressed as a concentration. Expressed on a concentration basis, available N averaged 39 mg kg^{-1} at 0–20 cm depth and 20 mg kg^{-1} at 20–40 cm depth (significant at $P < 0.05$; Fig. 1). On an area basis, available N in the 0–20 cm depth averaged 47 kg ha^{-1} (Fig. 1).

Because available N did not vary significantly among densities or treatments (Tables 3 and 4), we combined data from all plots in a stepwise regression

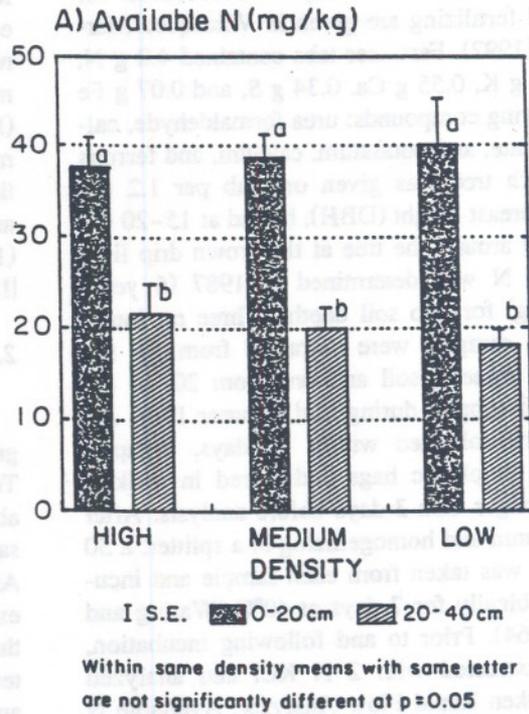
Table 3
ANOVA for Ln (available N) in kg ha^{-1} at 0–20 cm soil depth

Source	d.f.	Mean square	F-value	Pr > F
Site	3	0.63770	3.59	0.0857
Density	2	0.00534	0.03	0.9705
Error (a)	6	0.17774		
Treatment	3	0.02388	0.24	0.8691
Dens × Trt	6	0.12408	1.24	0.3193
Error (b)	27	0.10038		
Total	47			

Table 4
ANOVA for Ln (available N) in mg kg^{-1} at two soil depths

Source	d.f.		Mean square		F-value		Pr > F	
	I	II	I	II	I	II	I	II
Site	3	3	0.25629	0.66491	1.28	5.39	0.3642	0.0387
Density	2	2	0.01024	0.09654	0.05	1.72	0.3642	0.2560
Error (a)	6	6	0.20007	0.15035				
Treatment	3	3	0.04053	0.25810	0.39	1.54	0.7646	0.2298
Dens × Trt	6	6	0.09905	0.33447	0.94	1.62	0.4824	0.1870
Error (b)	27	23	0.10526	0.20657				
Total	47	43						

I, 0–20 cm; II, 20–40 cm.



B) Available N (kg ha^{-1})

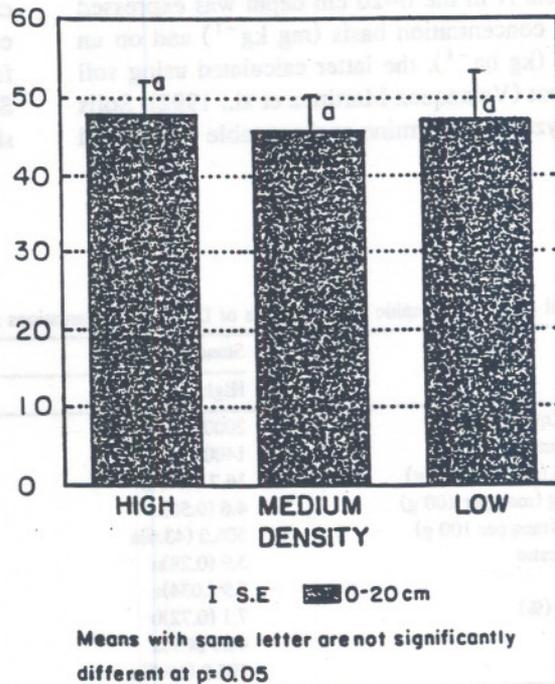


Fig. 1. Available nitrogen at two soil depths in plots with different tree densities: (A) mg kg^{-1} ; (B) kg ha^{-1} .

Table 5

Model of Ln (available N) in kg ha⁻¹

Variable entered	Model R ²	F	Pr > F
Step 1: Total soil N (N)	0.23	13.6	0.0006
Step 2: Exchangeable Ca (Ca)	0.46	19.7	0.0001
Step 3: Adjusted aspect ^a (Asp)	0.60	15.7	0.0003
Step 4: Rock content (Rock)	0.67	8.6	0.0053
Step 5: Slope (Slp)	0.71	5.5	0.0240
Model: Ln (Min. N) = 4.88 + 1.087 Ln (N) + 0.29 Ln (Ca) + 0.0021 (Asp) - 0.017 (Rock) - 0.0044 (Slp)			
SE = (0.317) (0.155) (0.078) (0.155) (0.0065) (0.0018)			

^a Adjusted aspect = 180 - |180 - aspect|. This variable, rather than an absolute value for aspect, was used in regression.

procedure. Available N (kg ha⁻¹) in the top 0–20 cm of mineral soil was regressed against topsoil variables and 1987 LAI. The resulting model (Table 5) explained 71% of the variation, available N correlating positively with total soil N, exchangeable Ca, and adjusted aspect (i.e. it was higher on south than on north aspects), and negatively with rock content and slope steepness. Total soil N and exchangeable Ca accounted for 46% of the total variation.

To explore the relationships among the independent variables used in regression, we performed principal component analysis (Table 6). The first two principal components (PCs) accounted for 55% of the total variation among the measured variables. Exchangeable Ca and Mg and total P loaded strongly on the first PC (Ca and Mg correlating negatively with the first component, and P correlating positively), while total N and adjusted aspect loaded

strongly on the second PC (the former correlating positively and the latter negatively).

4. Discussion

Anaerobically determined mineralizable N is believed to measure three components of the soil N pool: ammonium, microbial-N, and N contained in nonmicrobial but labile SOM (Binkley and Hart, 1989). Estimates of the proportion of variability explained by microbial biomass range from 25 to 78% (Paul et al., 1986; Myrold, 1987). In an old-growth Douglas-fir forest on the H.J. Andrews Experimental Forest, 60% of variation in available N was explained by microbial biomass (T.E. Bell, D.D. Myrold, and D.A. Perry, unpublished data, 1990). Smith et al. (1985) found that estimates of microbial biomass in several forest soils correlated strongly ($r^2 > 0.9$) with CO₂ evolved during anaerobic incubations, supporting the hypothesis that nitrogen released during anaerobic incubations primarily reflects microbial biomass (Binkley and Hart, 1989).

Since soil microbes live on the carbon supplied by plants, their biomass reflects both total amounts of soil organic matter and the rate at which it is decomposed and converted to microbial cells. A number of factors influence decomposition rates, including substrate quality, moisture, temperature, and the degree of processing by soil animals (Witkamp and Van der Drift, 1961; Fogel and Cromack, 1977; Melillo et al., 1982; Paul, 1984; Meentemeyer and Berg, 1986; Pastor and Post, 1986). In our study, 46% of the variation in available N was explained by total N and exchangeable Ca. We believe this pattern accurately

Table 6

Results of principal components analysis on soil and site variables in all plots

	Loadings ^a			
	PC1	PC2	PC3	PC4
Total soil P	0.80272	0.23029	-0.23287	0.05759
Soil Ca/Mg ratio	0.79089	0.14827	0.04798	0.34643
Rock content	0.62624	-0.19568	0.39330	-0.04483
Exchangeable Ca	-0.82414	0.19641	0.05579	0.30176
Exchangeable Mg	-0.92944	0.08667	0.13214	0.10898
Total soil N	0.24421	0.84123	-0.12579	-0.01866
Adjusted aspect	-0.18814	-0.74394	-0.43503	-0.10353
Percent slope	-0.45170	0.07814	0.73605	0.01237
pH	0.46922	-0.41014	0.28967	0.66167
Exchangeable K	-0.46309	0.11840	-0.46839	0.56569

^a Loadings listed are simple correlations of the original variables with the new principal components.

reflects soil processes on our sites, i.e. results were not biased by inadvertent sampling of fertilizer tabs. If enough of our soil samples had contained fertilizer tabs to affect the results, we should have seen significant positive correlations among all nutrients contained within the tabs. However, we did not. Total N and exchangeable Ca, for example, had no correlation with one another ($r = -0.07$). Exchangeable Ca and soil P correlated negatively ($r = -0.59$). Moreover, exchangeable Ca correlated strongly with exchangeable Mg, even though the latter was not contained in the tabs.

The relation between total and available N is not surprising and has been shown by others (Powers, 1980; Lea and Ballard, 1982; Radwan and Shumway, 1983, 1984; McNabb et al., 1986; Miller et al., 1989). To our knowledge, a relationship between exchangeable Ca and available N has not been previously reported; however, lime added to conifer soils speeds decomposition and stimulates biological activity, including the activity free-living N-fixers (Lutz and Chandler, 1947; Williams, 1972; Jones and Richards, 1977; Lohm et al., 1984; Weier and Gilliam, 1986). The effect of Ca on microbial biomass, especially when added as lime, is often attributed to increased pH. However, this did not appear to be the case on our study sites as pH had a weak negative correlation with both exchangeable Ca ($r = -0.27$, $\alpha = 0.07$) and available N ($r = -0.26$, $\alpha = 0.08$).

Ca is required in rather high amounts by some microbes and soil animals. For example, Ca content in decomposer organisms ranges from 0.07 to 14% of dry weight (Swift et al., 1979), hence limitation in Ca supply may in turn limit decomposer activity. Through factors such as comminution of litter and mutualistic associations with microbes, macro- and mesofauna (including Ca-demanding taxa such as earthworms and oribatid mites) enhance decomposition, thereby increasing microbial biomass and other forms of available N (Edwards et al., 1970; Hole, 1981; Anderson et al., 1983; Spiers et al., 1986; Lavelle et al., 1993). It is plausible to hypothesize that N availability in our stands is indirectly limited by exchangeable Ca via the latter's effects on soil animals. Additionally, Ca promotes granulation in soils (Lutz and Chandler, 1947). Soils rich in lime usually have better physical condition than soils of

the same texture but which are poor in lime, perhaps because of increased activity on the part of soil fauna (Lutz and Chandler, 1947). Ca also has been found to enhance conifer root growth (Lyle and Adams, 1971; Matzner et al., 1986), which should in turn increase the biomass of rhizosphere microbes within soil.

The relationship with adjusted aspect indicates that available N is greater on southerly than on northerly aspects, even though total soil N tended to be higher on the latter. This may be related to higher soil temperatures on southerly slopes. Powers (1980) and Addiscott (1983) have reported a linear dependence of N mineralization on soil temperature. Microbial activity increases directly with temperature in the range common to forest soils (Brock, 1970). Although our incubations were all conducted at the same temperature, the fact that they were initiated (by flooding soils and killing all aerobes) within 3 days of soil collection suggests that the results largely reflect the biomass of aerobic organisms at the time of collection.

The negative correlation of available N with slope steepness may indicate water shortage. Several studies have shown that N mineralization is related to site moisture status (Stanford and Epstein, 1974; Nadelhoffer et al., 1983; Pastor et al., 1982, 1984; Plymale et al., 1987; Zak et al., 1989; Powers, 1990).

Available N on our sites is within the range of values reported for coniferous forest soils (Shumway and Atkinson, 1978; Powers, 1980; Smith et al., 1981; Boyle, 1982; Radwan and Shumway, 1983; Binkley and Reid, 1985; McNabb et al., 1986; Myrold, 1987). The differences that we found between soil depths are similar to those reported by Powers (1980) in forest soils of northern California, where the difference in available N between 5–15 cm and 25–35 cm depth was 46%. In our stands, the average difference between 0–20 cm and 20–40 cm was 51%. Powers (1980), Powers (1984) recommended that soil sampling for available N be confined to the top 0–15 cm.

In contrast to our results, there are various reasons to expect that thinning would increase available N. Trees in thinned plots had significantly higher N concentrations in new and 1-year-old foliage than trees in unthinned plots (Velazquez Martinez et al.,

1992), suggesting a more readily decomposable substrate in the former. However, the highest foliar N concentration in low density plots was 1.15%, and because of translocation, the older needles that compose litterfall were likely to contain 40–60% less N than new needles (Sollins et al., 1980; Fife and Nambiar, 1982; Powers, 1984). Therefore, needle litter even in low density plots would have had C:N ratios greater than 60:1, a marginal level for producing mineralization. Staaf and Berg (1977) found that N was mineralized from Scots pine needles at a C:N ratio of 67:1. The large pulse of organic matter from thinned trees, which occurred 6 years before our measurements, added substrate with a range of C:N ratios (e.g. needles, fine roots, coarse roots, branches and stems), some of which would have been relatively labile (new needles, fine roots and mycorrhizal hyphae) and would have produced a pulse of increased N mineralization (Bosatta and Berendse, 1984). In the 6 years since thinning, however, decomposition of higher C:N branches and coarse roots is likely to have proceeded sufficiently to create a sink for N released from the more labile tissues. Might potential differences in available N among density levels of our study have been masked by differing site conditions among replications? Mean values for available N differed little among density treatments, and standard errors were relatively small (Fig. 1), i.e. replicates responded consistently. However, high density plots had significantly lower rock content and higher exchangeable cations than the other density levels (Table 2). According to regression, higher exchangeable Ca and lower rock content would increase available N, hence could have biased our estimates of available N in high density plots upwards. The direct effect of soil rock content can be determined by looking at available N on a concentration basis (Fig. 1(A)); expressed in that way, high density plots do average slightly lower levels of available N than medium and low density plots, but differences are not statistically significant. We conclude that the lower average rock content in high density plots did not significantly bias our results. To test the effect of exchangeable calcium, we analyzed the data after deleting the high range of calcium values, which involved dropping eight high density subplots, two medium density, and one low density, producing a data set in which exchangeable Ca did

not differ among density levels. Available N did not differ among density levels in the reduced data set, which is consistent with what we saw in the full data set. Therefore, we conclude that our inability to show a difference in available N among density levels was not an artifact of differing levels of exchangeable Ca. (Note: we cannot rule out the possibility that lower rock content and higher exchangeable Ca in high density plots were an effect of density, rather than an underlying site effect independent of density.)

Collinearity analysis, as well as simple pairwise correlation coefficients, showed the independent variables in our regression equation—total soil N, exchangeable Ca, aspect, slope, and rock content—were not correlated among themselves, hence they comprise an orthogonal set defining a complex mosaic of available N across the low and mid-elevation landscape of the H.J. Andrews Experimental Forest. Leaf area and aboveground biomass growth on the plots of this study correlate positively with available N, especially in moderate and high density plots (Velazquez Martinez, 1990; Velazquez Martinez and Perry, 1997), which also varies in a mosaic across the landscape. For these forest types, and probably most others as well, improved knowledge of landscape patterns in nitrogen availability will contribute to a better understanding of spatial variation in primary productivity.

References

- Addiscott, T.M., 1983. Kinetics and temperature relationships of mineralization and nitrification in Rothamsted soils with different stories. *J. Soil Sci.*, 34: 343–353.
- Anderson, J.M., Ineson, P. and Huish, S.A., 1983. Nitrogen and cation mobilization by soil fauna feeding on leaf litter and soil organic matter from deciduous woodlands. *Soil Biol. Biochem.*, 15: 463–467.
- Bierlmaier, F.A. and McKee, A., 1989. Climatic summaries and documentation for the primary meteorological station, H.J. Andrews Experimental Forest, 1972 to 1984. Gen. Tech. Rep. PNW-GTR-242, Pacific NW Research Station, USDA Forest Service, 56 pp.
- Binkley, D. and Hart, S.C., 1989. The components of nitrogen availability assessments. I. Forest soils. *Adv. Soil Sci.*, 10: 57–112.
- Binkley, D. and Reid, P., 1985. Long-term increase of nitrogen availability, from fertilization of Douglas-fir. *Can. J. For. Res.*, 15: 723–724.

- Binkley, D., Aber, J., Pastor, J. and Nadelhoffer, K., 1986. Nitrogen availability in some Wisconsin forests: comparisons of resin bags and on-site incubations. *Biol. Fertil. Soils*, 2: 77–82.
- Bosatta, E. and Berendse, F., 1984. Energy or nutrient regulation of decomposition: implications for the mineralization immobilization response to perturbations. *Soil Biol. Biochem.*, 16: 63–67.
- Boyle, J.R., 1982. Mineralizable nitrogen: variability in the Oregon Coast Range soils. *Agron. Abstr.* 1982, p. 261.
- Bremner, J.M. and Mulvaney, C.S., 1982. Nitrogen-Total. In: A.L. Page (Ed.), *Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties. Agronomy Series Number 9 (Part 2).* American Society of Agronomy, Inc., Soil Science Society of America, Inc. Madison, Wisconsin, USA, pp. 595–624.
- Brock, T.D., 1970. *Biology of Microorganisms.* Prentice Hall, Englewood Cliffs, NJ.
- Brown, R.B. and Parson, R.B., 1973. Soils of the reference stands. Oregon IBP. Coniferous Biome Intern. Rep. 128, University of Washington, Seattle, WA, 76 pp.
- Dymess, C.T., Franklin, J.F. and Moir, W.H., 1974. A preliminary classification of forest communities in the central portion of the western cascades in Oregon. *Bull. No. 4, Coniferous Forest Biome Ecosystem Analysis Studies.* US/Int. Biol. Program, University of Washington, Seattle, WA, 123 pp.
- Edwards, C.A., Reichle, D.E. and Crossley, Jr., D.A., 1970. The role of soil invertebrates in turnover of organic matter and nutrients. In: D.E. Reichle (Editor), *Temperate Forest Ecosystems.* Springer, New York, pp. 147–172.
- Fife, D.N. and Nambiar, E.K.S., 1982. Accumulation and retranslocation of mineral nutrients in developing needles in relation to seasonal growth of young radiata pine trees. *Ann. Bot.*, 50: 817–829.
- Fogel, R. and Cromack, Jr., K., 1977. Effect of habitat and substrate quality on Douglas-fir litter decomposition in western Oregon. *Can. J. Bot.*, 55: 1632–1640.
- Franklin, J.F. and Dymess, C.T., 1973. *Natural vegetation of Oregon and Washington. Gen. Tech. Rep. PNW-8,* Pacific NW Forestry and Range Experiment Station, Portland, OR. USDA Forest Service, 417 pp.
- Hart, S.C. and Binkley, D., 1985. Correlation among indices of forest soil nutrient availability in fertilized and unfertilized loblolly pine plantations. *Plant Soil*, 85: 11–21.
- Hole, F.D., 1981. Effects of animals on soil. *Geoderma*, 25: 75–112.
- Jenny, H., 1941. *Factors of Soil Formation.* McGraw-Hill, New York.
- Johnson, D.W., Cole, D.W., Bledsoe, C.S., Cromack, Jr., K., Edmonds, R.L., Gessel, S.P., Grier, C.C., Richards, B.N. and Vogt, K.A., 1982. Nutrient cycling of forest of the Pacific Northwest. In: R.L. Edmonds (Editor), *Analysis of Coniferous Forest Ecosystems in the Western United States. US/IBP Synthesis Series 14,* pp. 186–232.
- Jones, J.M. and Richards, B.N., 1977. Effect of reforestation on turnover of ¹⁵N-labelled nitrate and ammonium in relation to changes in soil microflora. *Soil Biol. Biochem.*, 9: 383–392.
- Kabzems, R.D. and Klinka, K., 1987. Initial quantitative characterization of soil nutrient regimes. II. Relationships among soils, vegetation, and site index. *Can. J. For. Res.*, 17: 1565–1571.
- Keeney, D.R., 1980. Prediction of soil nitrogen availability in forest ecosystems: a literature review. *For. Sci.*, 26: 159–171.
- Knudsen, D., Peterson, G.A. and Pratt, P.F., 1982. Lithium, sodium, and potassium. In: A.L. Page (Ed.), *Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties. Agronomy Series Number 9 (Part 2).* American Society of Agronomy, Inc., Soil Science Society of America, Inc. Madison, Wisconsin, USA, pp. 225–246.
- Lanyon, L.E. and Heald, W.R., 1982. Magnesium, calcium, strontium and barium. In: A.L. Page, R.H. Miller and D.R. Keeney (Editors), *Methods of Soil Analysis. Part 2.* American Society of Agronomy, Madison, WI, pp. 247–274.
- Lavelle, P., Blanchart, E., Martin, A., Martin, S., Spain, A., Totain, F., Barois, I. and Schaefer, R., 1993. A hierarchical model for decomposition in terrestrial ecosystems: application to soils of the humid tropics. *Biotropica*, 25: 130–150.
- Lea, R. and Ballard, R., 1982. Predicting loblolly pine growth from N fertilizer, using soil N availability indices. *Soil Sci. Soc. Am. J.*, 46: 1096–1099.
- Lohm, U., Larsson, K. and Nommik, H., 1984. Acidification and liming of coniferous forest soil: long-term effects on turnover rates of carbon and nitrogen during an incubation experiment. *Soil Biol. Biochem.*, 16: 343–346.
- Lutz, H.J. and Chandler, Jr., R.F., 1947. *Forest Soils.* John Wiley, New York, 514 pp.
- Lyle, Jr., E.S. and Adams, F., 1971. Effect of available soil calcium on taproot elongation of Loblolly pine (*Pinus taeda*) seedlings. *Soil Sci. Soc. Am. Proc.*, 35: 800–805.
- Matzner, E., Murach, D. and Fortmann, H., 1986. Soil acidity and its relationship to root growth in declining forest stands in Germany. *Water, Air, Soil Pollut.*, 31: 273–282.
- McNabb, D.H., Cromack, Jr., K. and Fredricksen, R.L., 1986. Variability of nitrogen and carbon in surface soils of six forest types in the Oregon Cascades. *Soil Sci. Soc. Am. J.*, 50: 1037–1041.
- Meentemeyer, V. and Berg, B., 1986. Regional variation in rate of mass loss of *Pinus sylvestris* needle litter in Swedish pine forests as influenced by climate and litter quality. *Scand. J. For. Res.*, 1: 167–180.
- Melillo, J.M., Aber, J.D. and Muratore, J.F., 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology*, 63: 621–626.
- Miller, R.E., McNabb, D.H. and Hazard, J., 1989. Predicting Douglas-fir growth and response to nitrogen fertilization in Western Oregon. *Soil Sci. Soc. Am. J.*, 53: 1552–1560.
- Myrold, D.D., 1987. Relationship between microbial biomass nitrogen and a nitrogen availability index. *Soil Sci. Soc. Am. J.*, 1047–1049.
- Nadelhoffer, K.J., Aber, J.D. and Melillo, J.M., 1983. Leaf-litter production and soil organic matter dynamics along a nitrogen-availability gradient in Southern Wisconsin (U.S.A.). *Can. J. For. Res.*, 13: 12–21.
- Pastor, J. and Post, W.M., 1986. Influence of climate, soil mois-

- ture, and succession on forest carbon and nitrogen cycles. *Biogeochemistry*, 2: 3–27.
- Pastor, J., Aber, J.D., McClaugherty, C.A. and Melillo, J.M., 1982. Geology, soils and vegetation of Blackhawk Island, Wisconsin. *Am. Midl. Nat.*, 108: 266–277.
- Pastor, J., Aber, J.D., McClaugherty, C.A. and Melillo, J.M., 1984. Aboveground production and N and P cycling along a N mineralization gradient on Blackhawk Island, Wisconsin. *Ecology*, 65: 265–268.
- Paul, E.A., 1984. Dynamics of organic matter in soils. *Plant Soil*, 76: 275–285.
- Paul, E.A., Smith, J.L. and Norton, J.M., 1986. The decomposition of ¹⁴N- and ¹⁵N-labelled cells in soil under anaerobic conditions. *Agron. Abstr.* 1986, p. 186.
- Plymale, A.E., Boerner, R.E.J. and Logan, T.J., 1987. Relative nitrogen mineralization and nitrification in soils of two contrasting hardwood forests: effects of site microclimate and initial soil chemistry. *For. Ecol. Manage.*, 21: 21–36.
- Powers, R.F., 1980. Mineralizable nitrogen as an index of nitrogen availability to forest trees. *Soil Sci. Soc. Am. J.*, 44: 1314–1320.
- Powers, R.F., 1984. Estimating soil nitrogen availability through soil and foliar analysis. In: E.L. Stone (Editor), *Forest Soils and Treatment Impacts*. Proc. 6th North American Forest Soils Conference, The University of Tennessee, Knoxville, pp. 353–379.
- Powers, R.F., 1990. Nitrogen mineralization along an altitudinal gradient: interactions of soil temperature, moisture, and substrate quality. *For. Ecol. Manage.*, 30: 19–29.
- Radwan, M.A. and Shumway, J.S., 1983. Soil nitrogen, sulfur, and phosphorus in relation to growth response of western hemlock to nitrogen fertilization. *For. Sci.*, 29: 469–477.
- Radwan, M.A. and Shumway, J.S., 1984. Site index and selected soil properties in relation to response of Douglas-fir and western hemlock to nitrogen fertilizer. In: E.L. Stone (Editor), *Forest Soils and Treatment Impacts*. Proc. 6th North American Forest Soils Conference, The University of Tennessee, Knoxville, pp. 89–104.
- Rothacher, J., Dymess, C.T. and Fredriksen, R.L., 1967. Hydrologic and related characteristics of three small watersheds in the Oregon Cascades. Misc. Pap. Pacific NW Forest and Range Experiment Station, USDA Forest Service, 54 pp.
- Shumway, J.S. and Atkinson, W.A., 1978. Predicting nitrogen fertilizer response in unthinned stands of Douglas-fir. *Commun. Soil Sci. Plant Anal.*, 9: 529–539.
- Smith, J.L., McNeal, B.L., Owens, E.J. and Klock, G.O., 1981. Comparison of nitrogen mineralized under anaerobic and aerobic conditions for some agricultural and forest soils of Washington. *Commun. Soil Sci. Plant Anal.*, 12: 997–1009.
- Smith, J.L., Norton, J. and Paul, E.A., 1985. Microbial biomass estimation. In: J.L. Smith and E.A. Paul (Editors), *Process Controls and Nitrogen Transformations in Terrestrial Ecosystems*. Department of Plant and Soil Biology, University of California, Berkeley, CA, pp. 94–108.
- Sollins, P., Grier, C.C., McCorison, F.M., 1980. The internal element cycles of an old-growth Douglas-fir ecosystem in western Oregon. *Ecol. Monogr.*, 50: 261–285.
- Spiers, G.A., Gagnon, D., Nason, G.E., et al., 1986. Effects and importance of indigenous earthworms on decomposition and nutrient cycling in coastal forest ecosystems. *Can. J. For. Res.*, 16: 983–989.
- Staaf, H. and Berg, B., 1977. Mobilization of plant nutrients in a Scots pine forest moor in central Sweden. *Silva. Fenn.* 11: 210–217.
- Stanford, G. and Epstein, E., 1974. Nitrogen mineralization–water relations in soils. *Soil Sci. Soc. Am. Proc.*, 38: 103–107.
- Statistical Analysis Systems Institute Inc., 1985. *SAS/STAT Guide for Personal Computers*, Version 6. Vol. 2. SAS Institute Inc., Cary, NC, 378 pp.
- Steel, R.G.D. and Torrie, J.H., 1980. *Principles and Procedures of Statistics. A Biometrical Approach*, 2nd edn. McGraw-Hill, New York, 633 pp.
- Swift, M.J.S., Heal, O.W. and Anderson, J.M., 1979. *Decomposition in Terrestrial Ecosystems Studies in Ecology*, Vol. 5. University of California Press, Berkeley/Los Angeles, CA, 372 pp.
- Velazquez Martinez, A., 1990. Interacting effects of stand density, site factors, and nutrients on productivity and productive efficiency of Douglas-fir plantations in the Oregon Cascades. Ph.D. Thesis, Oregon State University, 142 pp.
- Velazquez Martinez, A. and Perry, D.A., 1997. Nutrient and topographic factors influence in growth efficiency and leaf area in Douglas-fir plantations in the central Oregon cascades, U.S.A. *Terra*, in press.
- Velazquez Martinez, A., Perry, D.A. and Bell, T.E., 1992. Response of aboveground biomass increment, growth efficiency, and foliar nutrients to thinning, fertilization, and pruning in young Douglas-fir plantations in the central Oregon Cascades. *Can. For. Res.*, 22: 1278–1289.
- Waring, R.H., Schroeder, P.E. and Oren, R., 1982. Application of the pipe model theory to predict canopy leaf area. *Can. J. For. Res.*, 12: 556–560.
- Waring, S.A. and Bremner, J.M., 1964. Ammonium production in soil under waterlogged conditions as an index of nitrogen availability. *Nature*, 201: 951–952.
- Warren, G.P. and Whitehead, D.C., 1988. Available soil nitrogen in relation to fractions of soil nitrogen and other soil properties. *Plant Soil*, 112: 155–165.
- Weier, K.L. and Gilliam, J.W., 1986. Effect of acidity on nitrogen mineralization and nitrification in Atlantic coastal sandy soils. *Soil Sci. Soc. Am. J.*, 50: 1210–1214.
- Williams, B.L., 1972. Nitrogen mineralization and organic matter decomposition in Scots pine humus. *Forestry*, 45: 177–188.
- Witkamp, M. and van der Drift, J., 1961. Breakdown of forest litter in relation to environmental factors. *Plant Soil*, 15: 295–311.
- Zak, D.R., Host, G.E. and Pregitzer, K.S., 1989. Regional variability in nitrogen mineralization, nitrification, and overstory biomass in northern lower Michigan. *Can. J. For. Res.*, 19: 1521–1526.

