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Mineralizable Soil Nitrogen as an Index of Nitrogen Availability to Forest Trees[1]

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ABSTRACT

Soil N mineralized during 14-day anaerobic incubation at 30°C is evaluated as an index of forest soil fertility and site productivity. Mineralizable soil N determined under standard conditions correlates significantly with N mineralized anaerobically for 6 months in the field, with site index and yield potential of *Pinus ponderosa* L. growing on volcanic, metavolcanic, and metasedimentary soils, and with foliar concentrations of N. Soils testing less than 12 ppm of mineralizable N are judged clearly deficient, but stands of pine and fir on soils testing as high as 16 ppm of N still may respond well to fertilization. Absolute variability in mineralizable soil N decreases with soil depth and increases with the magnitude of the soil test mean, but relative variability is constant. Comparing ammonium produced during laboratory incubation with that mineralized over 6 months in the field shows that field soil temperature has a strong bearing on the interpretation of the laboratory test.

Additional Index Words: **soil testing, soil variability, site productivity, foliar analysis, ponderosa pine, fertilization.**

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EXPANDING DEMAND for wood products, coupled with a shrinking forest base, create a need for a clearer understanding of forest soil fertility and practicable means for assessing it. Recently, emphasis in soil N testing has shifted from static measures (chemical extraction, total Kjeldahl N) to organic pathways of N release (Dahnke and Vasey, 1973). In forestry, soil incubation methods have produced N values correlating well with tree growth properties, but reports are scattered and few.

In France, Le Tacon (1972) found that N quantities mineralized during incubation of Al horizon soil samples correlated well with site index and foliar N concentrations in *Picea,* but soil nitrate and total N contents did not. In Bavarian forests of *Picea* and *Pinus,* N mineralized from humus correlated strongly with both tree growth and foliar N concentration (Zöttle, 1960). Shumway and Atkinson (1978), studying *Pseudotsuga menziesii* (Mirb.) Franco in the Pacific Northwest, found that growth response to N fertilization could be predicted from N mineralized in the 0- to 15-cm soil depth zone and relative stand density.

Soil incubation shows promise in developing indices of soil N availability to forest trees. But before a particular procedure is adopted, questions concerning variability of the method, its validity in differing ecosystems, and its relationship to biological properties of interest should be considered. In this study, a variant of Waring and Bremner's (1964) anaerobic index of soil N availability was chosen for its simplicity and evaluated for the following characteristics: spatial variability within and between forest stands, correlation with biotic and abiotic site variables, and potential in predicting forest tree performance and site productivity.

MATERIALS AND METHODS

Experiment 1

To study vertical variability in mineralizable N, soil samples were taken at 23 random locations in a 0.5-ha conifer plantation on Sites soil series (clayey, kaolinitic, mesic, Xeric Haplohumults) in northern California. Samples were taken from the 5- to 15-, 25- to 35-, 45- to 55-, 65- to 75-, and 85- to 95-cm depth zones in the soil profile. Following air-drying, soils were sieved to 2 mm and analyzed for mineralizable N as follows. Soil samples weighing 5.00 g were added to 16 by 150-mm test tubes containing 12.5 ± 1 ml of distilled H_2O. Soil was added gradually to ensure thorough wetting so that air pockets would not develop in the soil column. Tubes were sealed with rubber stoppers and incubated 14 days in the dark at 30 ± 1.5°C. (Subsequent tests here and by Keeney and Bremner (1966) showed that 7 days of incubation at 40°C gives similar results.) Distilled water blanks were included.

Following incubation, tubes were shaken vigorously for 15 sec and the contents transferred to a 150-ml distillation flask using three rinsings for a total of 12.5 ml of 4*N* KCl. To the flask was added 0.25 ± 0.05 g of carbonate-free MgO. The flask was attached immediately to the distillation apparatus and the contents distilled with steam until 25 ml of distillate had been

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trapped in 5 ml of boric acid mixed-indicator solution. Contents were titrated with 0.01N HCl. Results, corrected for distilled water blanks and adjusted for oven-dry weights, were reported as ppm mineralizable N.

Unlike the Waring and Bremner procedure, results were not reduced by the initial amounts of mineral N present, because I considered initial mineral N to be part of the N pool potentially available. Also, I have found that combining extractable ammonium with that mineralized during incubation counters the storage effects noted by Keeney and Bremner (1966). When extractable ammonium is included, air-dry soils may be stored at least a year without significant changes in mineralizable N.

Five species of free-growing conifer saplings were examined in the same plantation to see if their root distributions paralleled distribution of soil N. For each of 50 trees, one 10-cm diam soil core was extracted from the surface to a depth of 100 cm beneath the crown drip line. Cores were separated into 10-cm depth segments for the first 40 cm and into 20-cm segments thereafter. Samples were screened and washed, and roots of herbaceous species were discarded. Total lengths of conifer roots to a minimum diameter of about 1 mm were measured to the nearest 5 mm within each depth zone. Differences in root distributions between species and depth zones were tested on arc sine transformations of percentages using factorial ANOVA and Scheffé mean comparisons.

To examine horizontal variability in mineralizable N, soils were sampled randomly from the 18- to 22-cm depth zone in 25 stands covering a wide variety of forest types, sites, and disturbance conditions in northern California. Study sites were relatively homogenous units ranging between 0.2 and 30 ha in area. Between 10 and 78 samples were taken at each site, depending on the size and apparent variability of the unit. Samples were prepared and analyzed for mineralizable N using the procedure described previously. Standard deviation in mineralizable N was calculated for each sample site, and data were examined for trends.

Experiment 2

To investigate how well soil N mineralized in a standardized laboratory test might relate to N mineralized over longer periods under varying temperatures in the field, five plots were established in distinct forest types along an elevational and climatic transect of common timber soils of volcanic origin. Soils were classed to family using standard procedures (Soil Survey Staff, 1975). At each site, potential productivity—mean annual cubic volume increment (MAI) at 50 years—was estimated using heights and ages of dominant trees and appropriate yield tables.

Bulk soil samples were drawn from composites of the 18- to 22-cm depth zone, air-dried, sieved, and subsamples analyzed for mineralizable N, KCl extractable N, total N by macro-Kjeldahl (Bremner 1965), and organic C by loss on combustion (Ball 1964). Twenty replicate 5-g samples of each soil were placed into test tubes containing 12.5 ml of distilled water and sealed with rubber stoppers. Samples were sorted into sets of four, which were then assigned randomly to each of the five field sites. Each group of 20 tubes was placed in a plastic container to which sand was added to insulate the tubes and to hold them firmly upright.

Tube sets were refrigerated at 3°C in darkness until the first day of spring 1978, when they were taken to each field site and buried with soil column midpoints at depths of 20 cm. Soil temperatures at 20 cm were measured on that date and at monthly intervals thereafter. On the first day of autumn 1978, tube sets were removed and returned to the lab, where their ammonium contents were determined through distillation and titration. Quantities of N mineralized were determined by subtracting N extracted by KCl before field incubation. Means of all measured plot variables were compared using tests of simple linear correlation. Treatment effects on N mineralized in the field were tested by factorial ANOVA. Field results were compared by regression with results from standard laboratory incubations.

Experiment 3

To study the relationship between mineralizable soil N and forest growth within a climatic zone, natural and planted stands of *Pinus ponderosa* Laws., ranging in size from sapling to young sawtimber, were examined at 57 locations in the interior Coast Range, Klamath Mountains, Sierra Nevada, and Cascade Mountains of California and southern Oregon. Locations were chosen to span the range of timber site qualities found in nature. Soils at study sites were acid Ultisols, Alfisols, and Inceptisols, primarily of volcanic, metavolcanic, and metasedimentary origin, though nine sites were on granitics and six on ultramafics. All soils fell within the mesic temperature regime. Sampling was not restricted to a particular season.

Sample trees were chosen from well-formed dominants judged from crown, bole, and branch whorl appearance to be free of significant past injury or suppression. Site index was estimated for each tree either conventionally or by using height intercept adjusted for degree of soil development (Powers and Oliver, 1978). Mineral soil was collected with a bucket auger and composited from the 18- to 22-cm depth zone at three points spaced equally around each tree approximately at crown drip line. Recently matured needles were collected from three to five branches in the upper third of crowns of trees ranging from 2 to 20 m tall and were composited for each tree.

To extend the range of the foliar data, treated and untreated trees were sampled in seven extra stands that had been fertilized with N 3 to 5 years before. Collections also were taken from four stands of *Pinus jeffreyi* (Grev.) Balf.—a species similar in many ways to *P. ponderosa* L. A total of 183 trees were sampled. An average of five trees were selected at each location. Because sample trees often were scatterd widly, no formal "plots" existed other than the individual tree. Foliar samples were dried, ground to pass through a 40-mesh screen, and analyzed for total N by micro-Kjeldahl (Jackson, 1958). Site indices for 102 trees growing on volcanic and metasedimentary soils were used in predicting MAI projected for 50-year-old stands grown at a 3 by 3 m spacing (Oliver and Powers, 1978). To avoid bias, site index was not estimated in fertilized stands or for *P. jeffreyi*, because no site classification system exists separately for this species. Data were stratified by soil parent material type, and mineralizable N values were compared with site index, MAI, and foliar N concentrations through regression for all field data pairs. A total of 272 tree and soil pairs were examined.

An important use of soil nutrient tests is screening stands for their probability of response to fertilization. To study this, I reviewed all California N fertilizer trials in pine and true fir known to me. Of these, 13 met the criteria of adequate experimental design and at least 3 years of growth since treatment. Fertilizer rates were between 224 and 448 kg N/ha, with urea as the usual fertilizer form.

Depending on plot size (0.04–0.12 ha), from one to five composite soil samples were drawn from the 18- to 22-cm depth zone in all control plots. Samples were analyzed for mineralizable N, and results were averaged to characterize each site. Measurements were made of heights, diameters, or both for trees on control and fertilized plots and compared with measurements recorded at the beginning of each study. Volumes were estimated for trees of pole size and larger using appropriate equations (MacLean and Berger, 1976; Oliver and Powers, 1978). Treatment effects on periodic increment were examined statistically for each site using ANOVA or regression and analysis of covariance, depending on experimental design and stand conditions.

RESULTS AND DISCUSSION

Experiment 1

Concentration of mineralizable N decreased exponentially with soil depth (Table 1), paralleling the usual distribution of organic N in residual forest soils (Zinke, 1960), but possibly reflecting a greater proportion of easily-refracted organic N compounds near the surface. Absolute variability decreased similarly with depth, but no trend was apparent in coefficients of sample variation (C.V.). Standard deviations within depth zones averaged 46% of the mineralizable N mean concentration in that zone. Fitting an exponential model to the mean values in Table 1 produced the following depth function:

$$N = 401\ D^{-0.88}$$
$$r^2 = 0.99$$

where N is mineralizable soil N in ppm, D is soil depth

Table 1—Means ($\overline{X}$), standard deviations (SD), and coefficients of variation (C.V.), for mineralizable N at five depths in a 6-year-old conifer plantation, Sites soil series.

Soil depth	Mineralizable soil N $\overline{X}$	SD	C.V.
cm	ppm		%
5–15	50.6	23.1	46
25–35	23.1	12.3	53
45–55	12.1	5.2	43
65–75	9.4	5.3	56
85–95	7.7	2.5	32

in cm, and r^2 is the coefficient of determination. Root distribution (Table 2) followed the trend reported elsewhere (Safford and Bell, 1972, Eis, 1974, Kimmins and Hawkes, 1978), with the bulk of the root system concentrated near the surface.

No statistically significant differences were found between species in the proportional distribution of their root system. However, root densities were significantly greater in the 0- to 10- and 10- to 20-cm depth zones than in any other portion of the soil profile. Primarily, these were fine feeder roots. For each species, more than one fifth the length of the measured root system was found in the top 10 cm, one third in the top 20, and over one half in the top 30. Limited sampling of root systems in dissimilar soils and size classes of trees have produced similar results.

Shumway and Atkinson (1978) found that C.V. for mineralizable soil N increased with increasing soil depth and recommended that sampling be confined to the top 0 to 15 cm. Although results here show somewhat greater variation in the 25- to 35-cm depth zone, no particular trend was apparent overall. Sampling a few centimeters beneath the soil surface reduces absolute variability, however, while remaining in a zone of high root density. Avoiding surface soil also reduces the problem of undecomposed organic material floating to the top of the soil suspension during incubation, creating both aerobic and anaerobic conditions within the tube and causing underestimates of mineralizable N (Keeney and Bremner, 1966). Accordingly, I choose the 18- to 22-cm depth zone as the standard depth for all subsequent sampling.

Standard deviations in mineralizable N of samples from 25 separate stands plotted against their means increase directly with the magnitude of the mean at a rate of 0.449 (Fig. 1). The relationship was unrelated to recency of disturbance. No simple cause is apparent in explaining the positions of outliers. With the use of $(0.449N)^2$ as an estimate of sample variance, two equations can be derived for determining sampling intensity needed or estimating population means within given levels of precision. For absolute precision:

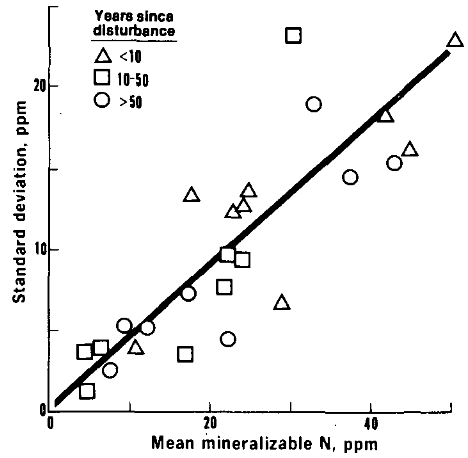

Fig. 1—Variation in mineralizable N increased with the magnitude of the sample mean, regardless of recency of site disturbance. Means are based on 10 to 78 forest soil samples, 18- to 22-cm depth zone.

$$n = \frac{t^2\,(0.449\,\overline{N})^2}{E^2_{\text{ppm}}}. \qquad [1]$$

For relative precision:

$$n = 2016\ t^2/E^2_{\%} \qquad [2]$$

where n is the number of samples, t is Student's t for a given probability, $\overline{N}$ is the expected mean concentration of mineralizable N in ppm, and E is the precision desired, either in absolute (ppm) or relative (%) units. For the range of conditions tested, between 2 and 75 samples would be needed to estimate the mean within 5 ppm at 95% probability (Eq. 1) and a constant 21 samples to estimate the mean within 20% (Eq. 2).

Experiment 2

Sites selected in the transect study covered a broad span in biotic and abiotic diversity (Table 3). Differences between the lowest and highest values for each of the nine variables measured varied by factors between 2.2 (mean summer soil temperature) and 5.8 (elevation). Testing for interrelationships between study site variables showed that five variable pairs were correlated linearly at $\alpha = 0.10$, eight at $\alpha = 0.05$, and four at $\alpha = 0.01$ (Table 4).

Ammonium mineralized during 6 months anaerobic incubation in the field increased directly with mean summer soil temperature at 20 cm and inversely with elevation—not particularly surprising, since elevation and soil temperature were highly (and inversely) correlated, and since microbial activity increases directly

Table 2—Proportional distribution of roots by length to 100-cm soil depth in a 6-year-old mixed-conifer plantation on Sites soil series. Column averages not sharing a common letter differ at $\alpha = 0.05$.

Tree species	Mean height	Root distribution in depth zone, cm 0–10	10–20	20–30	30–40	40–60	60–80	80–100
	cm	%						
Abies concolor	62	20.3	15.3	15.1	9.3	14.5	15.3	10.1
Libocedrus decurrens	108	20.9	22.2	12.8	8.8	12.1	12.7	10.5
P. lambertiana	84	23.9	19.3	11.3	8.3	16.3	10.2	10.6
P. ponderosa	132	21.3	17.5	14.4	10.1	14.4	11.1	11.1
Pseudotsuga menziesii	63	20.1	25.5	11.5	8.9	12.1	11.2	10.6
Average	89.8	21.3a	20.0a	13.0bc	9.1c	13.9b	13.1bc	10.6c

Table 3—Physical and chemical characteristics of N transect study plots. Temperature and chemical data are for the 18- to 22-cm soil depth zone.

Forest type	Soil family	MAI	Elev.	Annual ppt.	Summer soil temp.	Soil C	Total soil N	KCl N	Mineralized N Lab	Mineralized N Field
		m³/ha	m	mm	°C	%	ppm	ppm	ppm	ppm
Deciduous oak (*Quercus kelloggii*)	Loamy, mixed, mesic Ultic Haploxeralfs	3	80	1,675	20	2.6	1,374	10.9	30.9	63.5
Westside pine (*P. ponderosa*)	Clayey, mixed, mesic Xeric Haplohumults	10	670	890	19	1.8	784	6.9	20.9	51.0
Mixed conifer (*A. concolor, L. decurrens, P. lambertiana, P. ponderosa, Pseudotsuga menziesii*)	Loamy, mixed, mesic Ultic Haploxeralfs	15	1,245	1,090	14	3.1	1,478	7.1	27.9	41.0
Eastside pine (*P. jeffreyi*)	Cindery, frigid Typic Dystrandepts	6	1,440	710	12	1.3	545	2.8	10.5	17.3
Red fir (*A. magnifica*)	Cindery, Typic Cryandepts	9	2,195	1,880	9	1.7	737	3.1	9.2	10.1

with temperature in the range common to forest soils (Brock, 1970).

A similar but weaker correlation exists for KCl-extractable N, indicating that site conditions promoting N mineralization also increase extractable N. Both KCl-extractable and mineralizable N from laboratory incubation correlated directly and significantly with N mineralized at original field sites, but total soil N did not. Both KCl-extractable and mineralizable N were correlated directly and significantly with total soil N and inversely with C/N ratio. Correlations with soil C were significant for mineralizable and total soil N at $\alpha = 0.10$ and 0.01, respectively. No variable showed a significant linear correlation with MAI.

If it is assumed that N mineralized anaerobically during 6-month field incubation is related to actual N availability in the course of a growing season, the simplest N test correlating well with this would seem the best method to use in a standard test. On this basis, KCl-N appears the best choice. However, recent work here has shown high temporal variability in KCl-extractable N. Samples collected from identical locations at five sites in the fall of back-to-back drought years showed average differences of 89% for KCl-extractable N but only 29% for mineralizable N. Replicate samples taken on a given collection date had C.V.'s averaging two-thirds greater for KCl-N than for mineralizable N. Thus, mineralizable N measured through laboratory incubation seems a better potential predictor of N mineralized in the field.

Mineralizable N correlated weakly with field soil temperature because mineralization occurred under standard laboratory conditions. However, temperature directly affects both mineralization rates in the field (Table 5) and subsqeuent ammonium additions to exchange sites as reflected in KCl-extractable N. Factorial analysis showed that N quantities mineralized in the field were affected strongly by conditions at both original and transplant locations and that these conditions interacted significantly.

The interaction effect can be seen in Q_{10} values determined from N mineralized in the field between 9 and 19°C for the five respective soils. Q_{10} values averaged 1.9 for the three mesic soils and ranged well within the limits reported for agricultural soils incubated aerobically over a broader temperature span (Stanford et al., 1973). Yet, soils taken from both frigid and cryic sites showed little or no response to increasing soil temperature.

At least two factors may explain this response. The

Table 4—Coefficients of linear correlation between variables associated with N transect study plots.

	MAI	Elev.	Ppt.	Soil temp.	Soil C	C/N	Total N	KCl N	Min. N lab
Min. N field	−0.15	−0.95**	−0.02	0.96***	0.60	−0.76	0.66	0.96***	0.91**
Min. N lab	0.06	−0.81*	0.07	0.78	0.87*	−0.89**	0.91**	0.95**	
KCl N	−0.20	−0.89**	−0.22	0.87*	0.72	−0.91**	0.79*		
Total N	0.23	−0.46	0.29	0.45	0.99***	−0.89**			
C/N	0.22	0.62	−0.44	−0.60	−0.81*				
Soil C	0.39	−0.38	0.23	0.37					
Soil temp.	−0.28	−0.98***	−0.14						
Ppt.	−0.25	0.23							
Elev.	0.31								

*,**,*** Significance of r at $\alpha = 0.10, 0.05$, and 0.01, respectively.

Table 5—Nitrogen mineralized at transplant sites during 6-month field incubation.

Collection site	Soil temperature regime	N mineralized in 6 months beneath: Red fir (9°C)	Eastside pine (12°C)	Mixed conifer (14°C)	Westside pine (19°C)	Deciduous oak (20°C)	Q_{10}
		ppm	ppm	ppm	ppm	ppm	
Deciduous oak	Mesic	30.9	42.7	56.6	63.4	63.5	2.1
Westside pine	Mesic	25.9	40.2	40.4	51.0	51.3	2.0
Mixed conifer	Mesic	34.9	41.5	41.0	56.3	56.4	1.6
Eastside pine	Frigid	17.0	17.3	20.6	18.8	21.4	1.1
Red fir	Cryic	10.1	9.9	10.1	10.0	10.8	1.0

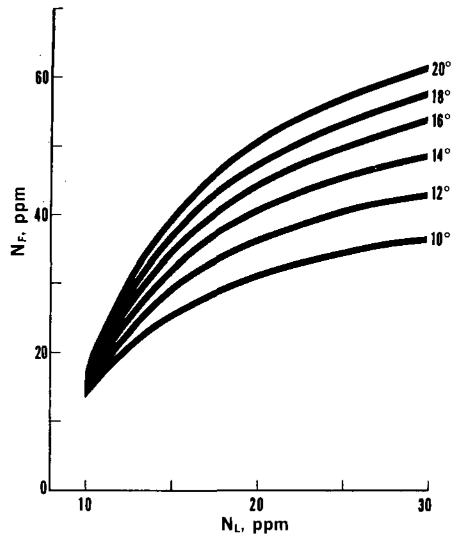

Fig. 2—Relation of field soil temperature and mineralizable soil N determined by laboratory incubation (N_L) to N mineralized anaerobically in the field (N_F) over a 6-month spring to fall period.

first may stem from an artifact of the technique, in that psychrophilic anaerobes may be absent in frigid and colder soils; or if present, psychrophiles may be adapted so narrowly that warmer temperatures do not increase their activity. A second possibility concerns the relative balance of degradable and resistant soil N fractions—a balance affected strongly by both environment and origin of the parent substance (Wollum and Davey, 1975). Low quantities of N mineralized under standard conditions may reflect complete mineralization of very low pools of potentially degradable N. These pools may be so low that complete mineralization in the field is reached at relatively low temperatures, so that Q_{10} is nearer 1 than 2.

Neither hypothesis can be tested with data from this experiment. However, data from Tables 4 and 5 form the basis for a general predictive model for testing future hypotheses:

$$N_F = 52.5 \ln T + \frac{789.9 - 488.8 \ln T}{N_L} - 73.1$$
$$R^2 = 0.98$$

where N_F is N in ppm mineralized during 6 months (spring through fall) anaerobic field incubation, T is mean soil temperature for that period at incubation depth, N_L is mineralizable N in ppm as determined through standard laboratory incubation, and R is the coefficient of multiple determination. This trend (Fig. 2) shows that the mineralizable N laboratory test yields results correlating closely with N mineralized during field incubation but that field temperature bears strongly on the test's interpretation. For a given mineralizable N value determined in the laboratory, field N availability would be less in frigid soils than mesic. Temperature effects increase with increasing values of mineralizable N but weaken as soil temperatures increase.

Experiment 3

On volcanic, metavolcanic, and metasedimentary soils of mesic temperatures, mineralizable soil N

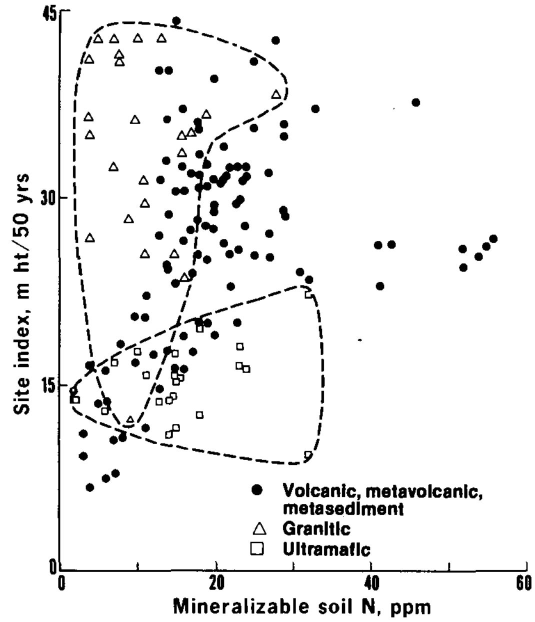

Fig. 3—*P. ponderosa* site index increased with mineralizable soil N to 12 ppm of N on volcanic, metavolcanic, and metasedimentary soils. No trends were apparent on granitic or ultramafic soils.

ranged as high as 56 ppm, with most sites testing between 14 and 24 ppm. Site index of westside *P. ponderosa* on these soils increased directly with mineralizable N between 0 and 12 ppm of N (Fig. 3). Variation in site index is minimal within this range [standard deviation from regression ($S_{y.x}$) = 3.84] but increases greatly thereafter. This suggests (but does not prove) that N availability as estimated by the anaerobic incubation technique strongly controls potential productivity on soils testing 12 ppm of N and less, has lessening influence between 12 and 20 ppm, and ceases to be a limiting factor thereafter. Presumably, absolute N availability would decrease with increasing soil gravel content. However, stratifying the data by skeletal and nonskeletal soils had no effect on variation or the trend. Between 0 and 20 ppm of mineralizable N, site index can be estimated as 7.17 + 1.22 mineralizable N ($r^2 = 0.46$, $\alpha < 0.01$, $S_{y.x} = 6.81$).

Site indices of trees growing on soils from ultramafic parent materials were universally low and related poorly to mineralizable soil *N* ($r^2 = 0.04$, regression slope not significantly different from 0), reflecting the Ca/Mg imbalances that usually are the primary limiting factors rather than N availability. On granitic soils, site indices were relatively high. Yet, most granitic sites tested less than 12 ppm of mineralizable N, and no clear calibration trend is apparent.

Keeney and Bremner (1966) noted erratic results of mineralizable N tests whenever the odor of H_2S was detected in incubated samples. The source of the H_2S is soil sulfate that serves as an electron acceptor for sulfate-reducing bacteria when ferric and manganic ions are not available for reduction (Takai and Kamura, 1966). Compared with volcanic soils and many metasedimentaries, granitic soils test relatively low in Fe and Mn. Thus, ferric and manganic electron acceptors would be depleted rapidly during anaerobic incubation of granitic soils. Low solution potential then might trigger activity of sulfate-reducing bacteria,

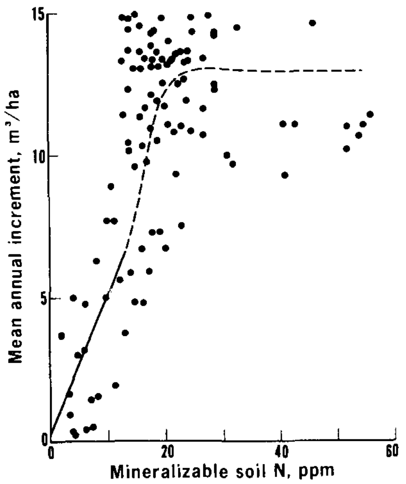

Fig. 4—Potential mean annual increment of *P. ponderosa* stands growing on volcanic, metavolcanic, and metasedimentary soils in respect to mineralizable soil N. Solid curve shows linear trend calculated between 0 and 12 ppm; dashed curve shows probable trend beyond.

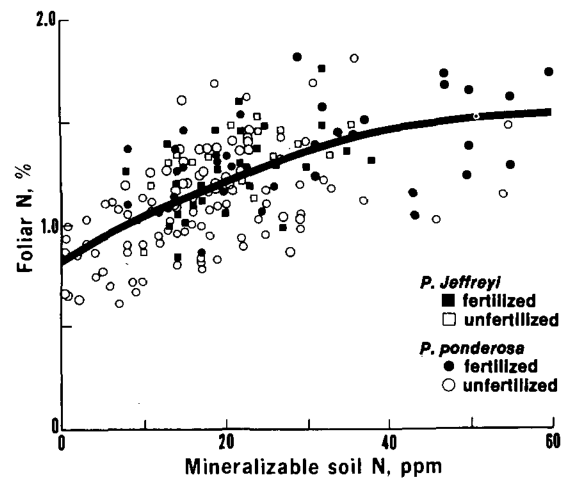

Fig. 5—Relation of foliar N concentration in fertilized and unfertilized *P. jeffreyi* and *P. ponderosa* trees to mineralizable soil N.

causing H_2S production and countering the effect of distilled ammonia on boric acid indicator.

To check if this phenomenon might account for apparently low mineralizable N results in granitics, 10 samples each of typical granitic and volcanic soils were incubated anaerobically. Samples were split and analyzed for ammonia content using the standard procedure and the ammonia-specific electrode (Banwart et al., 1972), which would not be influenced by H_2S or sulfide ion content. Analysis of paired samples by *t* test detected no differences between analytic methods at $\alpha = 0.10$ and confirmed that granitic soils generally test lower in mineralizable N than volcanics of comparable productivity.

Possibly, low values of mineralizable N associated with highly productive granitic soils may relate to soil physical properties. Because restrictive horizons generally are absent in coarse-textured granitics, roots and mineralizable N may be distributed more uniformly throughout the profile than in finely textured soils. No particular horizon need be especially rich in mineralizable N to satisfy rapid growth needs.

The relationship between site index and yield is sigmoid rather than linear (Oliver and Powers, 1978). Thus, MAI provides a more direct measure of site productivity than site index alone. The relationship of mineralizable soil N with MAI was determined for stands of *P. ponderosa* growing on volcanic, metavolcanic, and metasedimentary soils (Fig. 4). Applying the Cate-Nelson (1971) iterative procedure to define a critical level produces a maximum r^2 of 0.59 at 12 ppm. Within the range of 0 to 12 ppm of N, MAI may be estimated as 0.18 + 0.49 mineralizable N ($S_{y.x} = 2.20$, $\alpha < 0.01$).

Foliar N concentration in recently matured needles of *P. jeffreyi* and *P. ponderosa* is related curvilinearly to mineralizable soil N, regardless of fertilization history (Fig. 5). The fit is surprisingly good ($r^2 = 0.37$, $\alpha < 0.01$) considering that sampling covered all seasons. Apparently, restricting foliar samples to upper crown needles of similar physiological maturity reduced some of the seasonal variation.

Leaf (1973), summarizing data for many coniferous species, suggested that N was deficient when current, upper crown needles collected in autumn tested less than 1.0 to 1.1% N. In Fig. 5, this corresponds to soils testing between 10 and 15 ppm of mineralizable N, suporting the premise that a critical soil test level falls within this range. For *P. ponderosa,* an N concentration of 0.85% for current needles collected late

Table 6—Relationship of mineralizable soil N to growth responses of trees on volcanic or metasedimentary soils fertilized with 224 to 448 kg N/ha.

Species	Size class	Soil temp. regime	Min. N	Growth response†	α‡	Response variable	Growth period
			ppm	%			years
Ponderosa pine	Seedlings	Mesic	35	−6	0.3	Height	3
White fir	Seedlings	Mesic	35	3	0.5	Height	3
Jeffrey pine	Poles	Mesic	30	0	>0.5	Volume	5
Ponderosa pine	Saplings	Mesic	24	3	0.2	Height	4
Ponderosa pine	Poles	Mesic	19	8	>0.5	Volume	5
Jeffrey pine	Poles	Frigid	16	41	<0.01	Volume	6
Ponderosa pine	Poles	Frigid	15	31	<0.01	Volume	6
Red fir	Sawtimber	Frigid	14	69	0.1	Diameter	4
Red fir	Seedlings	Frigid	13	37	0.1	Height	3
Ponderosa pine	Saplings	Mesic	9	25	0.1	Height	3
Red fir	Saplings	Frigid	8	78	<0.01	Height	5
Ponderosa pine	Saplings	Mesic	6	80	<0.01	Height	3
Red fir	Poles	Frigid	5	47	0.05	Volume	3

† Percentage growth increase caused by N fertilization.
‡ Probability that growth response is due to chance.

in the growing season, or 1.0% for those collected during dormancy is regarded as a critical level (Powers and Jackson, 1978). Had the sampling portrayed in Fig. 5 been confined to late summer, foliar N concentrations generally would have been lower. Concentration of N in fully matured current needles may be estimated by the equation

$$y = 0.821 + 0.024X - 0.0002X^2$$

where y is the foliar N concentration in percent, and X is mineralizable soil N in ppm, with $S_{y \cdot x} = 0.20$.

Analyses of 3- to 5-year results of fertilization trials show no significant treatment responses by pine or true fir on sites testing 19 ppm of more mineralizable soil N (Table 6). However, growth increased significantly on all soils testing 16 ppm and less. Interestingly, all nonresponding sites had mesic soil temperatures, whereas all responding sites testing between 13 and 16 ppm were frigid. Presumably, stands would respond to fertilization at higher values of mineralizable N on frigid soils than on mesic because actual rates of N mineralization are much lower there (Fig. 2).

SUMMARY

Mineralizable soil N as measured by anaerobic incubation is a promising index of N availability to forest trees on volcanic, metavolcanic, and metasedimentary soils. Its variability is predictable, and its distribution in soil is similar to that of total N, concentrating near the surface where fine roots are abundant and decreasing with depth. Quantities of N mineralized in the laboratory correlate well with those mineralized anaerobically for 6 months in the field, though field temperature strongly influences the relationship. Mineralizable N measured in the 18- to 22-cm depth zone of mesic temperature soils correlates linearly with productive potential of *P. ponderosa* to soil test values of 12 ppm of N. The correlation found between mineralizable soil N and foliar N shows that the soil test may be useful in supplementing foliar analysis and offers an alternative to foliar sampling in very tall trees. Calibrating the trend for summer or autumn sampling probably would improve the correlation. Pine and fir in variety of size classes respond well to N fertilization on soils testing at least as high as 9 ppm of mineralizable N on mesic sites and 16 ppm on frigid.

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