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Soil Nitrogen Mineralization in a Clearcutting Chronosequence in a Northern California Conifer Forest

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ABSTRACT

Soil ammonification, nitrification, and N mobility were studied for 1 yr in three Sierra Nevada (USA) mixed-conifer stands to examine the long-term influence of timber harvesting on soil N dynamics. Clearcutting had a persistent effect on soil N mineralization, detectable by in situ incubation but not by conventional low-tension lysimetry. Mineralization rates were greater in 5- and 17-yr-old regenerated clearcuts than in an adjacent 100-yr-old uncut forest. Annual rates of N mineralization averaged 12 kg ha^{-1} for the uncut forest, and 49 and 31 kg ha^{-1} for the 5- and 17-yr-old clearcuts, respectively. Mineralization continued throughout the summer, even when soil matric potentials were < -1500 kPa. Soil solution NO_3 concentrations were much higher in the younger clearcut than in either the older clearcut or the uncut forest. Sustained effects of clearcutting seem due largely to higher substrate availability and to moisture and temperature conditions favoring microbial activity. Chemical inhibition of nitrification may become important as the forest floor develops.

THE MAIN FACTORS controlling ammonification and nitrification in forested ecosystems are moisture, temperature, and substrate availability (Gadgil and Gadgil, 1978; Vitousek, 1981). Ammonification rates generally are low enough that NH_4 is cycled efficiently into vegetation and microbial biomass, producing a closed N cycle (Miller et al., 1979; Cole, 1981). Consequently, the scarcity of NH_4 limits NO_3 production in well-stocked, uncut forests (Vitousek, 1981; Robertson, 1982). Yet, disturbances such as fire or timber harvest generally accelerate nitrification, and attention has centered on this process because NO_3 can be leached from the ecosystem if not immobilized biologically.

Timber harvesting usually increases ammonification and nitrification by altering the main controlling factors. Harvesting increases summer soil temperatures from direct solar radiation. Soil moisture rises because transpirational losses are reduced. Furthermore, logging adds labile organic matter to the soil in slash and roots. All of these favor increased microbial activity, ammonification, and nitrification. How long this effect lasts is not known, and the answer may vary with the measurement technique.

Nitrate losses commonly are measured through the analysis of soil solutions collected in lysimeters placed below the rooting depth (Vitousek et al., 1979; Dyck et al., 1983), or through the analysis of stream-water samples collected below the harvested site (Likens et al., 1969; Brown et al., 1973; Aubertin and Patric, 1974). After harvesting, NO_3 concentration usually increases, but the magnitude varies. For instance, Aubertin and Patric (1974) noted only minor increases in the loss of NO_3 from a clearcut in West Virginia, but Likens et al. (1969) found that N losses from a clearcut and experimentally devegetated New Hampshire watershed were 100 times greater than those from an adjacent forested watershed.

Although soil-solution techniques are effective in estimating net losses of soluble N from forest ecosystems, they have limited value in broader or more intensive studies of N mineralization processes. Tension lysimetry requires continual or frequent suction and solution collection. Watershed studies involve comparison of small watersheds with water-tight bedrock and with similar drainage streams, soil, relief, vegetation, and area, differing only in one of the above factors of interest or in a superimposed, management treatment. Both techniques focus only on the solution phase of the N cycle and are difficult to apply to remote sites or to sites lacking appreciable surface drainage. For these reasons, recent field work on soil N dynamics has favored small-plot incubation techniques using buried bags (Federer, 1983), ion exchange resins (Binkley and Matson, 1983), intact soil cores (Adams and Attiwill, 1986; Raison et al., 1987), or combinations thereof (Hart and Firestone, 1989; Powers, 1990).

Field estimates of organic N mineralization rates in temperate forest soils vary between net immobilization and 78 mg N m^{-1} d^{-1}, depending on site and season (Table 1). Rates generally are greater in the summer than in the winter. To date, most estimates are for undisturbed, natural ecosystems, rather than for forests managed intensively for timber production. Except for Australian work (Adams and Attiwill, 1986; Edmonds and McColl, 1983, 1989), field studies generally reflect climatic conditions differing markedly from California's hot, dry summers and cool, wet winters. Irrespective of climatic differences, the edaphic and vegetative diversity of California raise questions as to how well findings from other regions might apply.

Some forest soil N mineralization studies have been reported for California. Field anaerobic incubations of soils transplanted reciprocally along a mean annual soil temperature gradient between 9 and 20 °C showed a mineralization of Q_{10} of nearly 2 (Powers, 1990). (The Q_{10} is the ratio of the reaction rate constant for two temperatures differing by 10° [Williams and Williams, 1967].) Aerobic field mineralization studies are limited to those by Hart and Firestone (1989) and Powers (1990). Hart and Firestone (1989) found that intact cores in polyethylene and those in PVC cylinders capped with ion-exchange resin bags yielded similar mineralization rates. However, rates were greater in a young-growth forest than in an adjacent old-growth forest on similar soil (Table 1). Powers (1980), also using intact soil cores and ion exchange resins,

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Table 1. Areal N mineralization rates as determined under field conditions in seven different studies.

Study	Location	Site	In situ incubation technique	Study period	Rate of mineralization
Edmonds and McColl (1983)	Australia	Pine	Cylinder, 4–6 wk	Summer and fall	2.9
Ellis (1974)	Canada	Maple woodlot	Vial, 2 wk	2 yr	78†
		Pine			19†
Federer (1983)	New England	Deciduous forest	Bag, 28 d	Summer	23–65
Hart and Firestone (1989)	California	Mixed confier:			
		Old growth	Bag, 6 wk	10 mo	3.4
		Young growth	Bag, 6 wk		11.2
		Old growth	Cylinder with ion exchange resin bags	10 mo	6.3
		Young growth			11.6
Matson and Boone (1984)	Oregon	Hemlock:	Bag, 10 wk	Summer	
		Bare areas			3.6
		Old growth			7.7
Powers (1990)	California	Mixed oak:			
		Forest floor	Cylinder with resin, 210 d	Wet season‡	7.9
		15 cm soil			4.6
		Forest floor	Cylinder with resin, 155 d	Dry season‡	6.4
		15 cm soil			7.5
		Mixed conifer:			
		Forest floor	Cylinder with resin, 210 d	Wet season	4.5
		15 cm soil			8.1
		Forest floor	Cylinder with resin, 155 d	Dry season	5.6
		15 cm soil			15.1
		Red fir:			
		Forest floor	Cylinder with resin, 210 d	Wet season	5.4
		15 cm soil			1.7
		Forest floor	Cylinder with resin, 155 d	Dry season	4.7
		15 cm soil			−1.6
Rapp et al. (1979)	France	Pine forest	Cylinder, 2–12 wk	1 yr	3.1

† Assuming bulk density of 1.3 Mg m^{-3}.
‡ Wet season was November–June; dry season was June–October.

minimized initial organic soil N differences between sites by reporting N mineralization per unit of total soil N (Table 1). Once standardized, mineralization was judged to be greater in midelevation mixed-conifer forests (where climate is relatively mild) than at higher elevations (cold soil temperatures) or lower elevations (droughty soil conditions). Nitrification occurred at all sites, but was reduced where soil temperatures or NH_4 substrate were low.

Our study was conducted in a managed, highly productive, mixed-conifer forest of northern California's Sierra Nevada to further our understanding of the relatively long-term effects of timber harvest on soil N mineralization and mobility. Using a chronosequence approach and the same site and plots studied previously (McColl and Powers, 1984; Powers and McColl, 1984), we addressed the following questions:

1. Does clearcutting affect long-term changes in soil N mineralization in a Mediterranean climate forest ecosystem?
2. Do ammonification and nitrification proceed under droughty soil conditions?
3. What are the probable factors controlling field mineralization?

MATERIALS AND METHODS

Site Characteristics

We conducted our study between September 1983 and July 1984 at the Challenge Experimental Forest of the USDA Forest Service Pacific Southwest Experiment Station in the western foothills of the Sierra Nevada (39°29′N, 121°13′E). Elevation of the site is 790 m and slope is <5%. Mean air temperatures average 4 °C in January and 24 °C in July. Annual precipitation averages 1600 mm and occurs mainly as rain from October to April. The soil is a very productive, deep, reddish-brown, fine-loamy, mixed, mesic, Ultic Haploxeralf weathered from diorite.

The mixed-conifer forest at Challenge is dominated by *Pinus ponderosa* Dougl. ex P. Lawson & C. Laws., *Pinus lambertiana* Dougl., *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr., *Pseudotsuga menziesii* (Mirb.) Franco, and *Libocedrus decurrens* Torr. Subordinate tree species include *Lithocarpus densiflora* (Hook. & Arn) Rehd., *Quercus kelloggii* Newb., *Cornus occidentalis* (Torr. & A. Gray) Coville, and *Arbutus menziesii* Pursh. Understory species include *Symphoricarpos* and *Pyrola* spp. In open areas the vegetation consists primarily of *Ceanothus lemmonii* Parry, *Pteridium aquilinum* (L.) Kuhn, and various annuals.

Three adjacent 1.5- to 4-ha stand units representing a clearcutting chronosequence were chosen for study. One, the Forest Control, was an uncut, second-growth, closed-canopy forest ~100 yr old, with a site index of 25 m at 50 years and an average basal area stocking of 53 m^2 ha^{-1}. Forest-floor thickness averaged 30 to 120 mm. A second unit, called the Clearcut, was harvested in spring 1978 using crawler tractors. Slash was piled into windrows and burned that winter, and the unit was planted with *P. ponderosa* the following spring. Logging and windrowing of slash disrupted the forest floor considerably, but topsoil displacement was minimal. During this study, five growing seasons after planting, the thickness of the forest floor in the Clearcut ranged from 0 to 10 mm, and the planted trees were 0.9 to 1.7 m tall.

A third stand, the Regeneration unit, was clearcut in 1966 and regenerated naturally to *P. ponderosa* within 2 yr of harvesting. Slash was treated in the same way as in the more recent Clearcut. The tallest trees were 17 yr old and averaged 10 m tall, with about 40% canopy closure. The forest floor varied in both composition and depth. Pine needles decomposing under the larger trees formed a forest floor similar to, but thinner than, that found in the Forest Control unit. Litterfall from the predominantly *Ceanothus* and *Pteridium* understory formed a discontinuous forest floor of about 20-mm thickness, but some soil remained exposed.

Field Work

General Soil Measurements. A central plot measuring 5 by 30 m was established away from windrows in each adjacent unit for studying soil N dynamics. Within each plot, single (triplicate for bulk density) samples of 0 to 70 and 70 to 140 mm soil depths were collected at four positions and composited by depth. These depths are known to be the zones of greatest N mineralization rates and root activity in Challenge Experimental Forest soils (Powers, 1980). Samples were air dried, sieved to <2 mm, and analyzed in duplicate for total C by Walkley-Black (Nelson and Sommers, 1982) and Kjeldahl N (Bremner and Mulvaney, 1982) methods. Bulk densities for each depth increment were estimated from triplicate samples taken horizontally from a single soil pit in each sampling unit using a steel cylinder of 70 mm inside diameter.

Field soil temperatures were estimated from thermocouple measurements taken continuously at 35 and 105 mm depths in a cleared and forested unit at the Forest Service La Porte Ranger Station located 2.5 km north of the study area. These soil depths represent midpoints of those used in the mineralization study. Periodic measurements at the study site confirmed that soil temperatures there corresponded closely with those at the Ranger Station.

Moisture contents of the mineral soil and forest floor were determined gravimetrically at the beginning and end of each incubation period using steel incubation cylinders described below. Gravimetric moisture values were converted to matric potentials using moisture retention curves from previous equilibrations at −30, −100, −500, and −1500 kPa (Richards, 1965).

In Situ Nitrogen Mineralization. An intact soil core field incubation technique (Rapp et al., 1979) was used to chart net N mineralization within the soil from September 1983 through July 1984. Six pairs of steel cylinders measuring 53 mm i.d. and either 260 or 390 mm in length were driven to a depth of 180 mm at 5- to 9-m intervals in plots of each of the three units. The longer cylinders were used in the Forest Control, to allow for the thickness of the forest floor. Cylinders in each pair were positioned 250 mm apart. For each pair, one cylinder and its intact soil core was removed immediately, refrigerated, and transported to the laboratory. The remaining cylinder and encased soil core was left to incubate in place. After ~1 mo, each cylinder and incubated soil core was removed and transported to the laboratory; new cylinder pairs were installed, and the process was repeated. During field incubations, all cylinders were capped lightly with styrofoam cups to prevent leaching in the event of precipitation. Each cylinder had two holes drilled near the top to provide further aeration.

In the laboratory, soil cores were extruded and separated into 0 to 70 mm (surface) and 70 to 140 mm (subsoil) sections. The relatively thick forest floor in the Forest Control allowed us to separate this horizon as well, but the Clearcut and Regeneration units had insufficient material for meaningful separation. Following extraction, large roots and gravel were discarded. Residual material was mixed thoroughly for each section, refrigerated at 5 °C, and analyzed within 24 h. Materials were weighed and subsampled for moisture content, and mineral N was extracted from 10-g samples by shaking 1 hr in 50 mL of 2 *M* KCl, followed by paper filtration or centrifugation to produce clear extracts. Debris was discarded and extracts were stored at −18 °C for up to 6 mo. Ammonium and NO_3 concentrations were determined with a QuickChem System IV (Lachat Instruments, Milwaukee, WI) autoanalyzer, using the colorimetric phenate method for NH_4 and Cd reduction for NO_3 (U.S. Environmental Production Agency, 1979). Findings were converted to a whole-soil basis, and net mineralization was expressed as the change in mineral N content before and after field incubation.

Solution-Phase Nitrogen. Standard, porous ceramic-cup soil-moisture extraction tubes (Soil Moisture Equipment Co., Santa Barbara, CA) were used to measure soil N mobility in the soil solution between September 1983 and July 1984. Three pairs of tubes selected for similar draw rates were installed centrally in each mineralization plot. One tube of each pair had its cup placed at 0.25 m below the soil surface, and the other at 1.00 m. The shallow tube measured 0.4 m long, and the deeper tube measured 1.1 m. Each month, −50 kPA suction were applied to each tube, and solutions collected over that period were refrigerated and transported to the laboratory for storage at −18 °C until analysis for NH_4 and NO_3 as described above.

Controlled Laboratory Incubation

Additional soil and forest floor samples were collected in December 1984 for studying N mineralization under controlled conditions in the laboratory. Samples of soil were collected randomly from three locations in each of the chronosequence units: Forest Control, Clearcut, and Regeneration. Samples were obtained from the litter, the surface soil (0–70 mm), and subsoil (70–140 mm) layers by pressing a 354-mm-diameter steel cylinder into the soil. The large diameter of the cylinder provided enough material for separate incubations of the litter layer and two mineral soil depth sections (0–70 mm and 70–140 mm). Stones and roots >10 mm diameter were discarded. Each section was mixed by gentle shaking in a plastic bag, weighed, and stored at 5 °C until further analysis.

To estimate aerobic N mineralization potentials, 30 g of the mineral soil samples were incubated in the laboratory for 20 d in capped, 20-mL polypropylene vials (Cunningham, 1962). Caps were perforated to permit gas exchange. Ten grams of forest floor material was incubated in polyethylene bags, opened weekly to improve aeration beyond that occurring through the polyethylene (Bremner and Douglas, 1971). Water contents were maintained near field capacity by weekly weighings and additions as needed. As in the field study, net mineralization rates were estimated from the difference in mineral N content of the soil before and after incubation. Subsamples from each depth were incubated at 6, 18, and 30 °C (corresponding to the mean winter low soil temperature for all treatment units, and the mean summer highs for the Forest Control and Clearcut, respectively). Following incubation, NH_4 and NO_3 were extracted and determined as described previously. Net mineralization potential was determined after subtracting the mineral N present initially, and was adjusted to an areal basis through weight adjustment and the known surface area of the sampling cylinder.

RESULTS

Field Study

Soil Properties

Relevant properties of soil from the three chronosequence units and for the two depth classes are given

in Table 2. Bulk densities were similar between units, showing little evidence of a persistent clearcutting effect. Bulk density in the Clearcut remained relatively low—probably because of cumulative frost action, and because organic residues were incorporated into the surface soil during harvesting and site preparation (as indicated by greater C concentrations). Total N concentrations also were higher in the Clearcut for both soil depth classes, again reflecting the mixing of harvesting residues with soil. However, C/N ratios did not differ appreciably between units.

In Situ Mineralization

Cumulative plots of net N-mineralization in the field show major differences between chronosequence units (Fig. 1). Most mineralization occurred in the surface soil (0–70 mm) depth and was greatest in the Clearcut, where disturbance and incorporation or organic residues were most recent. Immobilization occurred throughout the winter for the 70- to 140-mm-depth subsoil, but by March there was a net gain in mineral N for the Clearcut and Forest Control. Mineralization rates for September through July for combined depths averaged 13.7, 8.0 and 0.8 mg N m^{-2} d^{-1} for the Clearcut, Regeneration, and Forest Control units, respectively, which is comparable to rates reported for other coniferous forests (Table 1). Although spatial variability seemed relatively high, coefficients of variation (CV) in the subsoil (Table 3) actually reflect low mineralization means, rather than high absolute variability.

Ammonification and nitrification rates appeared to be greater in the Clearcut than in the other units; the Regeneration unit was intermediate, but appeared more like the Forest Control (Fig. 2). Nitrification rates peaked during the winter on the Forest Control, but were high from October through March in the Clearcut. Rates were minimal in all units by July. Although the field incubation study lasted nearly a year, both NH_4 and NO_3 production was much less at the end of the period than at the beginning, regardless of treatment.

Table 2. Soil properties by chronosequence unit and depth class in fall 1983.

Soil property	Soil depth	Chronosequence unit: Clearcut (cut in 1978)	Regeneration (cut in 1966)	Forest Control (uncut)
	mm			
Bulk density, Mg m^{-3}	0–70	0.8	0.9	0.9
	70–140	1.0	1.0	1.1
Total C,† g kg^{-1}	0–70	90	64	73
	70–140	35	26	26
Total N,† g kg^{-1}	0–70	2.0	1.6	1.5
	70–140	1.3	1.0	1.0
Total N, kg ha^{-1}	0–140	2 030	1 708	1 715
Absolute N-mineralization rate (Sept.–July), kg ha^{-1}	0–140	49	31	12
Specific N-mineralization rate (Sept.–July), g N mineralized kg^{-1} total N	0–140	24	18	7
C/N Ratio	0–70	45	41	50
	70–140	27	26	27

† Total C was analyzed by the Walkley-Black method, and Total N by Kjeldahl.

Soil Physical Conditions

Based on calibrated measurements at the Challenge Ranger Station, soil temperatures were higher in the Clearcut than in the Forest Control in the fall and spring, but the same in winter (Fig. 3). During July, temperatures averaged 12 °C warmer in the Clearcut than in the Forest Control, and were not cold enough

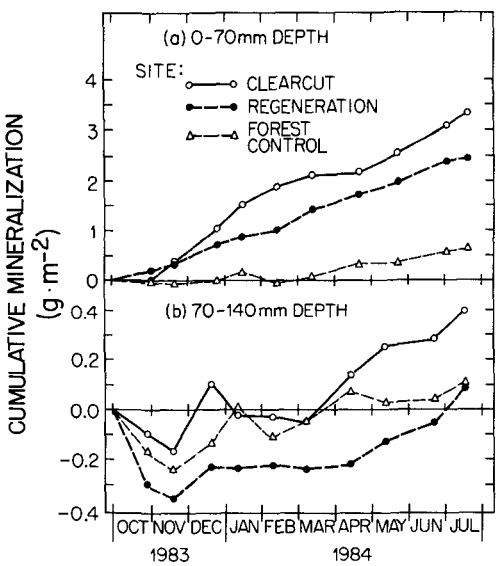

Fig. 1. Cumulative N mineralization in three chronosequence units soil at depths of (a) 0–70 and (b) 70–140 mm.

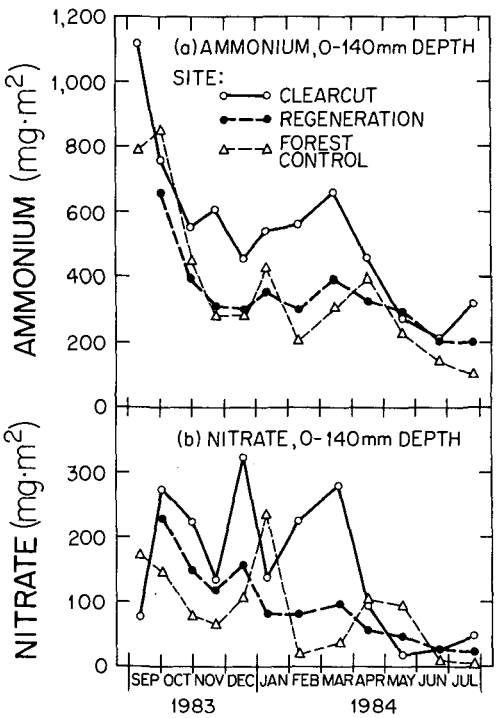

Fig. 2. Ammonium and NO_3 content of soil in three chronosequence units to a depth of 140 mm.

in any unit to preclude microbial activity (Stanford et al., 1973). Surface soils tended to be drier in the Clearcut and Regeneration units than in the control during summer and autumn (Fig. 4), but wetter in the winter (presumably, because of greater crown interception and transpiration in the Forest Control). Subsoils of the Clearcut and Regeneration units tended to be wetter than the Forest Control throughout the winter (presumably, because of lower transpirational demand), but there was no apparent difference between sites at other times (Fig. 4). Between November and March, soil matric potentials in the Clearcut unit were much more favorable for N mineralization (Stanford and Epstein, 1974) than were those for the Regeneration or Forest Control units.

Nitrogen Concentrations in Soil Solutions

Soil solution could not be collected until mid-December, when the soil had become moist enough for extraction, and collection ceased again in the early summer, as soil matric potentials dried below −50 kPa. The magnitude of the differences in solution N concentrations at 0.25 and 1.00 m depths for a given chronosequence unit were minor (Fig. 5). Few fine roots occur at 1-m depth on similar soils nearby (Powers, 1980); thus, we assume that most NO_3 at this depth will be lost to groundwater. Nitrate concentrations were consistently higher in the Clearcut than in the Regeneration and Forest Control units, but there were no appreciable differences between the latter two units. Nitrate concentrations decreased as the season progressed. Ammonium concentrations were very low (Table 4) and usually were close to the limit of detection.

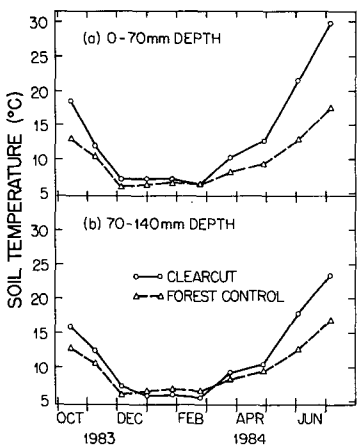

Fig. 3. Soil temperatures in the Clearcut and Forest Control units soil at depths of (a) 0–70 and (b) 70–140 mm.

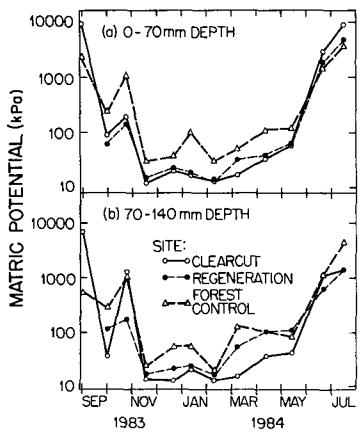

Fig. 4. Soil matric potential in three chronosequence units soil at depths of (a) 0–70 and (b) 70–140 mm.

Laboratory Incubation

Mineralization rates in the laboratory under constant moisture and 30 °C temperature were higher for

Table 3. Average coefficient of variation (n = 6) by soil depth for groups of subsamples collected from each chronosequence unit for October through July.

Chronosequence unit	Soil depth	CV: Initial NH_4 conc.	CV: Initial NO_3 conc.	CV: Net mineralization
	mm	%	%	%
Clearcut	0–70	47	98	273
	70–140	43	76	2925
Regeneration	0–70	54	100	111
	70–140	51	135	773
Forest Control	Forest floor	57	82	317
	0–70	62	108	217
	70–140	50	139	359

Table 4. Mean NO_3 and NH_4 concentrations in soil solutions for October through July.

Soil depth	Chronosequence unit	NO_3	NH_4
m		mg L^{-1}	mg L^{-1}
0.25	Clearcut	1.03	0.12
	Regeneration	0.25	0.01
	Forest Control	0.14	0.01
1.00	Clearcut	0.97	0.04
	Regeneration	0.10	0.03
	Forest Control	0.19	0.04

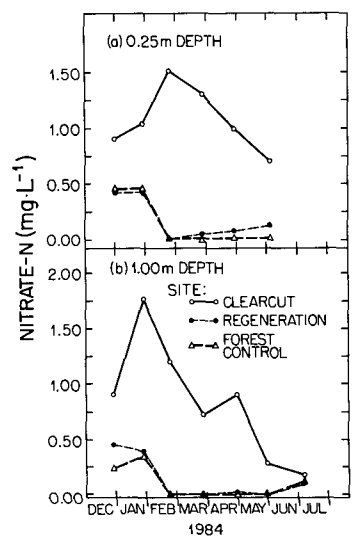

Fig. 5. Nitrate concentration in soil solutions of the three chronosequence units soil at depths of (a) 0.25 and (b) 1.00 m.

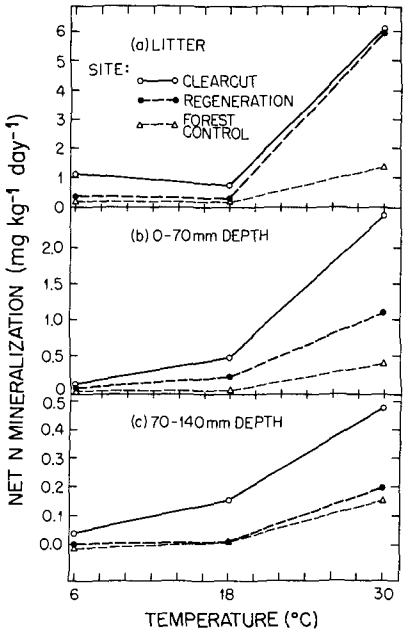

Fig. 6. Net N mineralization from (a) litter, (b) 0–70 mm soil depth, and (c) 70–140 mm soil depth during laboratory incubations of samples from three chronosequence units.

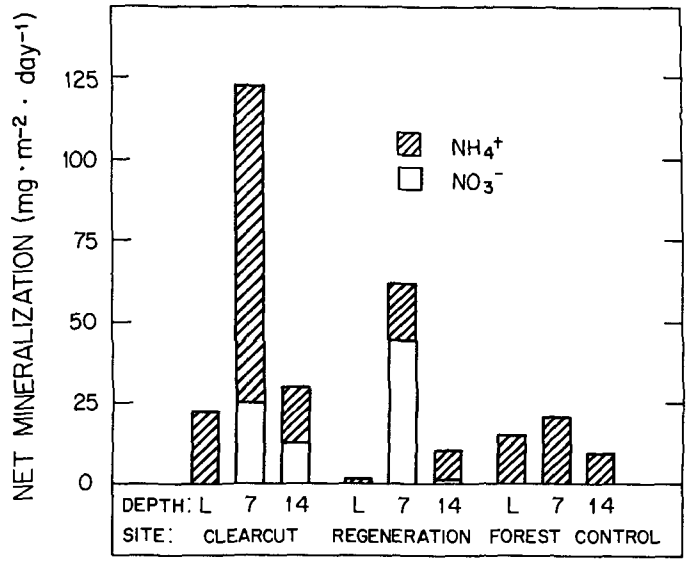

Fig. 7. Net N mineralization of NH_4 and NO_3 produced at 30 °C in litter (L), 0–70-mm (7), and 70–140-mm (14) soil depths during laboratory incubations of samples from three chronosequence units.

the Clearcut and Regeneration units than for the Forest Control, particularly for the litter and 0- to 70-mm soil depth (Fig. 6). Differences between units were generally less at the lowest incubation temperature. No nitrification occurred in litter incubations for any of the field units, nor at any soil depth for the Forest Control, even under the warmest laboratory conditions (Fig. 7).

DISCUSSION

Our chronosequence units (stand-age classes) were neither replicated nor randomized. This precludes our using inferential statistics, because we cannot conclusively separate positional effects from those due solely to treatment (Hurlbert, 1984). However, we have examined stand structure and soil properties, and monitored soil-solution chemistry in the Forest Control (uncut) and the Clearcut (cut in 1978) for an 18-month period before clearcutting, and have found the units to be similar in all measured characteristics (Powers and McColl, 1984). Also, the older Regeneration unit (cut in 1966) is adjacent to the Forest Control and the Clearcut, with similar soil and topography. Thus, all three units were assumed to have come from a common preharvest population. Evidence that follows also supports the validity of our findings as indicators of the sequential effects of clearcutting on N mineralization at this site.

Total Kjeldahl N for each of the chronosequence units is expressed as both g kg^{-1} of soil for each sampling depth, and in kg ha^{-1} for the combined depth of 0–140 mm (Table 2). The amounts for the combined depth indicate that total N was essentially the same in the Forest Control and Regeneration units, and 18% greater in the Clearcut. The N mineralization rates for the combined depths in the Clearcut, Regeneration, and Forest Control units of 13.7, 8.0, and 0.8 mg m^{-2} d^{-1} correspond to 49, 31, and 12 kg ha^{-1}, respectively (Table 2). If the *specific rate* of N mineralization is calculated as the amount of N mineralized per unit of total N (Powers, 1990), the amount for the Clearcut is 343% greater than that of the Forest Control unit, and for the Regeneration unit is 257% greater. Thus, specific rates of mineralization are far out of proportion to simple differences in total soil N. In our professional judgment, the differences in N mineralization rates between chronosequence units are due to clearcutting effects, and are not merely due to differences in total soil N found 5 and 17 yr after clearcutting.

Although soil temperatures were similar among all units throughout the winter (Fig. 3), cumulative mineralization rates in the surface (0–70 mm) soil were greatest in the Clearcut, intermediate in the Regeneration, and least in the Forest Control unit (Fig. 1). In the subsoil (70–140 mm), cumulative mineralization rates were much greater in the Clearcut than in the Regeneration and Forest Control units, but from April to July rates were greater in the Forest Control unit than in the Regeneration unit. This is attributable in part to higher substrate concentrations in the Clearcut that persisted 5 yr after logging (Table 2), but equally important is the fact that soil moisture was higher and more favorable for mineralization in the Clearcut and Regeneration units than in the Forest Control during the winter (Fig. 4). Presumably, this was due to a combination of greater crown interception and transpiration in the Forest Control.

Possibly, soil in incubation tubes experiences a different microclimate than adjacent soil, enough to affect N mineralization rates. Edmonds and McColl (1989) reported that soil moisture and temperature in incubation tubes were very similar to those in adjacent soil, although in surface soil in an exposed clearcut both moisture and temperature were slightly elevated (probably by severing of roots and reduced evaporation, and by heat transfer down the metal tube, respectively). Raison et al. (1987) also observed slight

temperature differences. However, we agree with Edmonds and McColl (1989) that artifacts due to conditions within the tubes are minor, compared with effects due to treatments.

While soil solution analysis indicates NO_3 mobility is a winter and spring event in soils of this Mediterranean climate (Fig. 5), both ammonification and nitrification do occur during the summer and autumn months (Fig. 1 and 2) if soil matric potentials are adequate (Fig. 4). Sollins et al. (1984) have shown that the most readily mineralized N compounds are sequestered within soil microaggregates, which may retain appreciable moisture after low-tension gravimetric water has drained from larger pores. Judging from moisture trends in Fig. 4, soil microaggregates of the Clearcut unit probably remained moist enough to continue ammonification and nitrification much later in the dry season than did those of the Forest Control. A prolonged period of favorable soil moisture (because of lower transpirational demand) and of low uptake (because of low stocking density), coupled with consistently more favorable soil temperatures and higher substrate levels, helps explain why the Clearcut unit showed positive net mineralization throughout the spring and early summer.

Nitrogen mineralization rates were much greater in all treatment units at the beginning of the field study in September than at its conclusion in July (Fig. 2). This phenomenon cannot be attributed to soil moisture or temperature differences between September 1983 and July 1984, because these were minor (Fig. 3 and 4). However, by August at Challenge Experimental Forest tree growth is negligible (Powers, 1981). Possibly, increased net mineralization in September and October reflects either or both of (i) a 2-month period free of N uptake and (ii) a gradual accumulation of labile organic N from root decay of annual plants dying during the summer.

In an earlier study, Powers and McColl (1984) showed that soil solution NO_3 concentrations in the Regeneration unit remained elevated for 13 yr before declining to Forest Control levels. In the present study, NO_3 concentrations of soil solutions remained at Forest Control levels 17 yr after harvesting, but N-mineralization rates still were higher than those in the uncut Forest Control. In short, our results suggest that the persistent effect of clearcutting on nitrification is evident through in situ mineralization, but would not have been detected using conventional lysimetry. In New England, Marks and Bormann (1972) attributed reduced leaching losses of NO_3 in a revegetated clearcut to increased N uptake. We assume that additional N mineralized in our Regeneration unit was routed into accumulating perennial plant biomass.

Net mineralization rates in our laboratory study (Fig. 6 and 7) far exceeded those of the same soil in the field, because laboratory temperatures and moisture conditions were more ideal. This illustrates the dangers of using such laboratory results to predict field behavior. We recommend that such laboratory results be used only as a measure of potential N mineralization. Estimates of N mineralization that most closely represent those of real conditions can only be obtained from field incubation.

In a laboratory incubation study similar to ours, Matson and Vitousek (1981) found that mineralization rates declined to normal levels within 7 yr of timber harvest. Our findings suggest that rates are elevated for at least 17 yr. Results from our laboratory study show higher mineralization potential of the Clearcut unit for ammonification and nitrification (Fig. 6 and 7). Part of the reason for negligible nitrification in the Forest Control soil may be lack of NH_4 substrate. Total N concentrations in soil without incubation were lower in the Forest Control than in other units (Table 2). Extractable NH_4 concentrations in surface soil collections taken in September 1983 also were lowest in the Forest Control (1.1 mg N kg^{-1}, compared with 1.7 and 4.5 mg N kg^{-1} in the Regeneration and Clearcut units, respectively). Consistently low concentrations of NH_4 substrate in field soils can keep nitrifier populations low, leading to a lag in the production of NO_3 when NH_4 supply is increased.

Another factor potentially controlling nitrifier activity in the Forest Control are nitrification-inhibiting chemicals present in the forest litter (Baldwin et al., 1983; Olson and Reiners, 1983). Pohlman and McColl (1988), examining litter extracts from the Forest Control, have identified several free-organic acids known to suppress nitrification. Using soil column studies under controlled conditions, Powers (1982, unpublished data) found that water-soluble extracts (presumably phenolics) from understory plants at our Challenge site have a strong suppressive effect on nitrification.

CONCLUSIONS

Although we cannot attach statistical significance to our conclusions, we believe that this chronosequence analysis reflects a logical progression of changes in soil N mobility due to harvesting, site preparation, and the emergence of a new forest. Results support Powers and McColl's earlier (1984) hypothesis that temperature, moisture, and lack of available NH_4 are the principal factors controlling nitrification on this Mediterranean climate site, and that removing these constraints leads to increased nitrification. Chemical inhibition of nitrification from forest-floor leachates could have an additional effect as a new forest floor develops.

For the period September through July, soil N mineralization rates averaged 13.7 mg m^{-2} d^{-1} for the Clearcut unit (i.e., 5-yr-old clearcut), 8.0 for the Regeneration unit (17-yr-old clearcut), and 0.8 for the Forest Control unit, corresponding to 49, 31, and 12 kg ha^{-1}, respectively. Both ammonification and nitrification occurred throughout the summer, when soils were too dry for soil-solution collection by conventional low-tension lysimetry. This indicates that treatment effects persisted for at least 17 yr beyond harvesting, despite rapid reforestation. We infer that additional N made available by sustained rates of high mineralization is incorporated into rapidly growing vegetation.

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