Nitrogen dynamics in conifer-dominated forests with and without hardwoods

D. A. PERRY[1] AND C. CHOQUETTE

Department of Forest Science, College of Forestry, Oregon State University, Corvallis, OR, U.S.A. 97331

AND

P. SCHROEDER

Environmental Protection Agency, Corvallis, OR, U.S.A. 97331

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Nitrogen and carbon in the surface 12 cm of mineral soil, N in leaf litterfall, anaerobic N mineralization rates in the soil and forest floor, and root and N accretion to sand traps placed in surface soil layers were compared in forests with hardwoods either completely or partially removed during a conifer thinning 3 years before. An adjacent unthinned conifer–hardwood stand was also included. Conifer stocking did not differ between thinned stands with and without hardwoods. Stands without hardwoods averaged 520 kg/ha more N in mineral soil ($p < 0.001$), 20% more N mineralized from soil during 7-day incubations ($p < 0.001$), and lower soil C:N ratio ($p = 0.02$) than stands with hardwoods. These variables did not differ between thinned and unthinned mixed stands. Soil N did not correlate with the number of hardwoods removed. Weight of forest floor and rate of N mineralization from the forest floor did not differ between mixed and pure stands. However, stands with hardwoods returned about 10 $kg \cdot ha^{-1} \cdot year^{-1}$ more N in leaf litter (due to higher N concentration in conifer litter as well as the presence of high-N hardwood litter); stands without hardwoods accreted about 10 $kg \cdot ha^{-1} \cdot year^{-1}$ more N in sand traps. Soil N mineralization in mixed stands correlated positively with N mineralization in the forest floor but not with N accretion to sand traps, while the opposite was true in pure conifer stands. Although pretreatment variability among stands cannot be ruled out, the replicated treatments within a relatively uniform area make it appear likely that differences were related to the presence or absence of hardwoods. This was not a simple additive effect, however, but a community-level phenomenon, that is, conifers cycled N differently when mixed with hardwoods than when in pure stands.

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Dans les forêts où les essences feuillues ont été complètement ou partiellement enlevées au cours de coupes d'éclaircie trois ans auparavant, les auteurs ont comparé l'azote et le carbone dans les 12 cm de surface du sol, N dans la litière de feuilles, les taux de minéralisation anaérobie de N dans le sol et la couverture morte, ainsi que l'accrétion des racines et de N dans des trappes de salle placées dans les horizons de surface du sol. On a aussi inclus un peuplement adjacent, non éclairci, de conifères et feuilles. Le stock de conifères était le même dans les peuplements éclaircis, avec ou sans feuillus. Les peuplements sans feuillus avaient en moyenne 520 kg/ha de N en plus dans le sol minéral ($p < 0{,}001$), 20% plus de N minéralisé du sol durant des incubations de 7 jours ($p < 0{,}001$) et un ratio C:N plus faible ($p = 0{,}02$) que les peuplements avec feuillus. Ces variables n'ont pas présenté de différences entre les peuplements mixtes éclaircis et non éclaircis. L'azote du sol n'était pas corrélé avec le nombre de feuillus enlevés. La masse de la couverture morte et le taux de minéralisation de N dans la couverture morte n'ont pas varié entre les peuplements mixtes et les peuplements purs. Cependant, les peuplements avec feuillus ont restitué environ 10 $kg\ N \cdot ha^{-1} \cdot an^{-1}$ de plus dans la litière de feuilles (dû à une plus forte concentration de N dans la litière de conifères et à la présence de litière de feuillus riche en N); les peuplements sans feuillus ont eu une accrétion additionnelle de N dans les trappes de sable de l'ordre de 10 $kg \cdot ha^{-1} \cdot an^{-1}$. La minéralisation de N dans les peuplements mixtes était corrélée positivement avec la minéralisation de N dans la couverture morte mais pas avec l'accrétion de N dans les trappes de sable, alors que l'inverse a été observé dans les peuplements purs de conifères. Bien que la variabilité de prétraitement entre les peuplements ne puisse être écartée, les traitements répliqués à l'intérieur d'une aire de surface relativement uniforme portent à croire que les différences observées étaient reliées à la présence ou à l'absence des feuillus. Cependant, il ne s'agit pas d'un simple effet additif, mais d'un phénomène se situant au niveau de la communauté végétale, à savoir que les conifères ont un cycle de N différent lorsqu'ils sont mélangés aux feuillus, comparé à des peuplements purs.

[Traduit par la revue]

Introduction

Because of generally higher nutrient content, lower lignin and other polyphenolics, and a higher proportion of surface area to mass, deciduous leaves often decompose more readily than conifer needles. Turnover of forest-floor organic matter averaged more than four times longer, and turnover of nitrogen more than three times longer, in 13 temperate conifer stands than in 14 temperate deciduous stands (IBP data set, Cole and Rapp 1981). These comparisons are confounded by environmental differences; however, in the Oregon Coast Range, Fried (1985) found similar differences between areas dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) or bigleaf maple (*Acer macrophyllum* Pursh). The generally faster cycling associated with deciduous trees has led to speculation that a deciduous component may increase nutrient turnover and thereby enhance productivity of conifer stands (Assman 1970; Perry 1978). Tappeiner and Alm (1975) provided evidence that deciduous understory plants accelerated nutrient cycling in red pine forests.

In 1980, the Forest Engineering Department of Oregon State University thinned a large area of mixed conifer–hardwood forest. Conifers were felled with all or only a portion of hardwoods, creating either pure conifer stands or mixed stands. In this study, we compare pure conifer and conifer–hardwood stands with respect to soil nitrogen (N) and anaerobic N mineral-

[1]Author to whom correspondence should be sent.

ization rates, weight and N content of leaf litterfall, weight and N mineralization rate of forest floor, and N accretion in below-ground sand traps. We hypothesized that (*i*) because of loss of their more rapidly cycling litter, removing hardwoods would reduce N mineralization rates in both soil and forest floor and (*ii*) without a concomitant increase in total site N (which there was no reason to expect), reduced N mineralization rate in stands without hardwoods would result in lower N content of leaf litterfall (reflecting reduced N availability). Although the hypothesized decrease in N cycling rate could eventually lead to shifts in total N from soil to litter components, we did not expect to detect changes in either within the time frame of this experiment.

Methods

Study sites and thinning procedure

The study area was a 28-ha tract of the Paul Dunn Forest (owned by the College of Forestry, Oregon State University) on the eastern slopes of the Oregon Coast Range (44°40′ N; 123°20′ W). The area, in the western hemlock zone of Franklin and Dyrness (1973), averages 130 cm precipitation yearly, roughly 80% of which falls as winter rain, and has a 165- to 200-day frost-free season (Knezevich 1975). Temperatures are mild, averaging 10°C. Soils, Pachic Ultic Argixerolls, are silty clay loams derived from weathered basalts (Knezevich 1975). Slopes are gentle, seldom exceeding 20%. Elevation ranges from 250 to 300 m.

The 25- to 35-year-old forests are dominated by Douglas-fir but include a few grand fir (*Abies grandis* (Dougl.) Lindl.) and a significant hardwood component, primarily bigleaf maple, Pacific madrone (*Arbutus menziesii* Pursh), Pacific dogwood (*Cornus nuttallii* Aud.), and bitter cherry (*Prunus emarginata* Dougl.). Before thinning, the stands averaged 910 conifers and 340 hardwoods per hectare. Stem volumes of conifers and hardwoods with 15 cm or greater dbh averaged 47 m^3/ha and 17 m^3/ha, respectively (Loren Kellogg, Oregon State University Department of Forest Engineering, personal communication).

The stands were thinned with a skyline system. For the engineering study, a total of 36 corridors (strips 3 m wide, 100 to 250 m long, and approximately 60 m apart) were cleared of trees. A cable from small, mobile yarders was run down each strip and felled trees were winched to the corridor from either side, then up the corridor to the yarder. Hardwood removal and other logging treatments were randomly assigned to corridors. We randomly selected 15 of these corridors, 5 from each of the treatments described below, for the N cycling study. As control blocks, five areas from an adjacent unthinned area were selected to contain a hardwood–conifer mix similar to that of the stands before thinning. Arrangement of the 15 corridors and 5 control blocks used for this study is shown in Fig. 1.

Trees were felled, limbed, and yarded during the summer of 1980. Conifer and hardwood residues greater than 1 m long and 6 cm in midpoint diameter were bundled and yarded from some hardwood removal corridors. After thinning, conifers averaged 500/ha; hardwoods, 218/ha; or there were no hardwoods, depending on which of three treatments were given: (*i*) conifers thinned, some hardwoods retained, residue retained; (*ii*) conifers thinned, hardwoods completely removed, residue retained; or (*iii*) conifers thinned, hardwoods completely removed, residue removed.

Plot layout and data collection

Three 9.10 × 15.15 m plots were installed within each control block and along each selected corridor. Plots were located randomly with the following constraints: each had to be at least 5 m from the central cleared strip of a corridor and at least 20 m from adjacent treatments. Number and dbh of trees on each plot were tallied, and recent stumps were counted in order to reconstruct prethinning density and species composition.

After plot installation but before soil and litter measurements, trespassing firewood cutters disrupted one conifer–hardwood plot and one control plot; therefore, these were dropped from the study, leaving 14 thinned plots and 14 control plots.

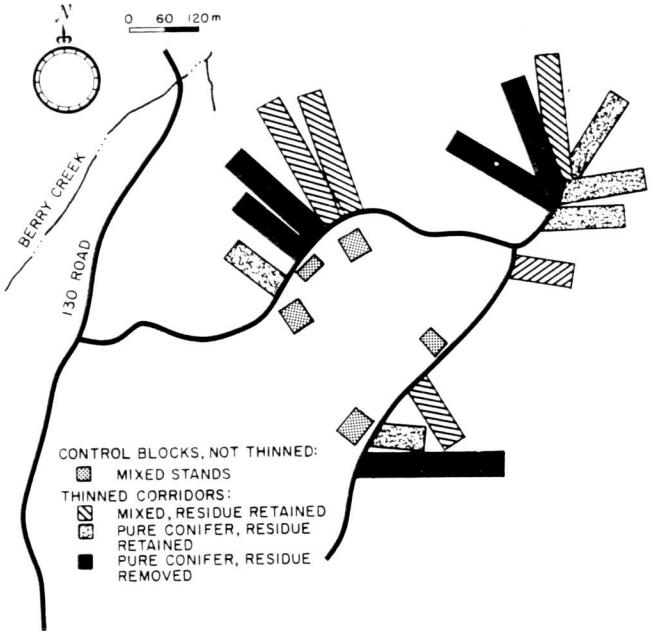

FIG. 1. Location of thinning corridors and control blocks used in the study. Control areas were unthinned, mixed stands. Conifers were thinned on each of the 15 corridors receiving different treatment of hardwoods and residues.

Soil and forest-floor sampling

The forest floor and soil were sampled in March and April, 1983, at five permanent points systematically located within each plot. L, F, and H layers were lifted from one 10 × 10 cm area adjacent to each of the five sampling points. Mineral soil to 12 cm was extracted at each point with a soil corer. (Points were offset to avoid logs when necessary.) Soil was passed through a 2-mm sieve, and soil and litter from the five sampling points were thoroughly mixed to give one soil and one litter composite per plot.

Nitrogen concentration in the soil and leaf litterfall was determined by micro-Kjeldahl technique and soil carbon with a Leco carbon analyzer. We measured pH on 20-g subsamples of soil to which 40 mL of distilled water was added, and on 3-g subsamples of litter to which 68 mL of distilled water was added. Samples were shaken by hand and allowed to stand for 1 h before measurement. Bulk density was determined for each plot from five cores taken with a 7.5 cm diameter soil corer designed to minimize compaction (Matson and Boone 1984). Cores were extracted to 15 cm; then the top 3 cm was removed, leaving 331 cm^3 on which bulk density was determined.

Mineralizable N was estimated anaerobically within 1 month of sample collection (Waring and Bremner 1964). Samples were stored at 2°C until incubation. After thorough mixing, six 20-g subsamples were taken from each of the composite samples described earlier; two subsamples were for gravimetric moisture determination, two for initial ammonium (NH_4) extraction, and two for 7 days of anaerobic incubation at 40°C. NH_4 was extracted by adding 30 mL of 1 *N* KCl to samples in a 50-mL centrifuge tube, shaking them 1 h on an Eberbach shaker table, then centrifuging them for 5 min at 5000 rpm. Three-millilitre aliquots were drawn from tubes and initial NH_4 concentration was measured on an autoanalyzer. Mineralizable N was calculated as the difference between initial and final NH_4 concentrations.

Litterfall

Litterfall was collected in conifer–hardwood plots (both thinned and control) and in pure conifer plots with residue removed. Two litter traps (3600 cm^2 and 2600 cm^2, the sizes available) were placed in each plot in early August 1983. Litter was collected twice during the fall of 1983: on October 22 before winter rains and on November 22 after some rainfall. Litter was separated into conifer and hardwood, dried at 70°C for 4 days, then weighed. Subsamples from six to nine plots per

TABLE 1. Number of hardwoods and conifers per hectare (and standard error) before and after thinning, by treatment

Treatment	Before thinning		After thinning	
	Conifers	Hardwoods	Conifers	Hardwoods
Hardwoods retained				
Unthinned (n = 14)	880(184)*a*	399(106)*a*	880(184)*a*	399(106)*a*
Thinned (n = 14)	880(107)*a*	341(79)*a*	490(52)*b*	191(42)*b*
Hardwoods removed				
Residue removed (n = 15)	971(97)*a*	266(71)*a*	435(35)*b*	0
Residue retained (n = 15)	860(71)*a*	406(94)*a*	435(37)*b*	0

NOTE: Within a column, values followed by the same letter do not differ significantly at $p = 0.05$.

TABLE 2. Nitrogen, carbon, C:N ratio, bulk density, and pH of the forest soil, by treatment

Treatment	Nitrogen		Carbon (kg/ha)	C:N	Bulk density (g/cm^3)	pH
	Total (kg/ha)	Mineralizable ($\mu g/g$)				
Hardwoods retained						
Unthinned (n = 14)	2940(120)*a*	41(2)*a*	66 970(2400)*a*	23(1)*a*	0.94(0.02)*ac*	5.3(0.06)*a*
Thinned (n = 14)	2750(140)*a*	41(2)*a*	58 800(3750)*b*	22(2)*ac*	0.99(0.02)*b*	5.4(0.04)*b*
Hardwoods removed						
Thinned, residue removed (n = 15)	3460(70)*b*	47(2)*b*	66 170(2410)*ab*	19(1)*b*	0.97(0.01)*bc*	5.4(0.03)*b*
Thinned, residue retained (n = 15)	3260(80)*b*	51(3)*b*	65 420(1990)*ab*	20(1)*bc*	0.89(0.02)*d*	5.4(0.06)*b*
LSD (0.05)	300	6	7560	3	0.04	0.1
Probability that mixed and pure conifer plots will not differ	<0.001	<0.001	0.294	0.023	0.086	0.163

NOTE: Two levels of statistical comparison are shown. LSD values are calculated from one-way analysis of variance of the three treatments and control. Probabilities given at the bottom are from a simple t-test of differences between plots with hardwoods (controls and thinned plots) and plots without hardwoods. Within a column, means followed by the same letter do not differ significantly at $p = 0.05$.

treatment were ground in a 20-mesh Wiley mill, and N was determined by the micro-Kjeldahl technique.

Sand traps

Sand traps were placed in the plots in which litterfall was collected. In spring 1983, one mineral soil core (7.5 cm diameter × 12 cm deep) was extracted in each plot. The holes were filled with washed silica sand in cheesecloth (which did not last and is not recommended). Sand was extracted in spring 1985. Roots were removed by hand, dried, and weighed. Nitrogen was measured with micro-Kjeldahl procedures, but with 3-g samples in order to compensate for low concentrations. Average values for duplicate Kjeldahl samples were within 10% of one another; therefore we consider them reliable. No N was detected in sand before it was placed in the field.

Statistical analyses

All variables were subjected to both nested (corridors within treatments) and one-way analysis of variance, in which variances associated with corridors within treatments and plots within corridors were combined into a single error term. Except for soil mineralizable N and litter pH, measured variables for corridors within a given treatment did not differ significantly, and values for least significant difference were calculated from one-way analysis of variance (Anonymous 1984). Differences between pure conifer plots and mixed plots (both thinned and unthinned) were tested with a t-test. Correlation between variables was examined with a Pearson correlation matrix and stepwise regression (Anonymous 1984).

Results

Pre- and post-thinning stocking

Prethinning stocking of conifers (mean 898 stems/ha) and hardwoods (mean 353 stems/ha) did not differ significantly among treatments (Table 1), nor did postthinning conifer density (mean 490 stems/ha). An average 191 hardwood stems/ha remained on mixed conifer–hardwood plots after thinning, but although the proportions of hardwoods in thinned and unthinned stands were similar (45 and 38%, respectively), their composition differed. On control plots, an average 48% of hardwood stems were madrone and 28% were maple; on thinned plots, 81% were maple and only 5% were madrone. (This may reflect a prethinning difference as well; however, madrone is a favored fuelwood and may have been cut preferentially.)

Soil nitrogen, carbon, and pH

Contrary to our expectation, average total soil N was 520 kg/ha higher and mineralizable N 20% higher in pure conifer plots than in mixed plots ($p < 0.001$; Table 2). These variables did not differ between the two treatments without hardwoods, or between the thinned mixed stands and the controls. The amount of soil N did not correlate with either the number of hardwoods or the number of conifers removed during thinning, which suggests that the different levels of soil N beneath the different species groups were not due to differences in decomposition of dead roots.

Mixed, thinned plots averaged from 10 to 12% less soil C than plots receiving other treatments, but differed significantly at $p = 0.05$ only from controls. The C:N ratio was significantly lower in pure conifer plots than in mixed plots ($p = 0.023$; Table 2). Soil pH did not differ among thinned plots regardless

TABLE 3. Forest-floor weight, mineralizable nitrogen, and pH by treatment

Treatment	Weight (kg/ha)	Mineralizable N (μg/g)	pH
Hardwoods retained			
Unthinned (n = 14)	12 840(620)a	306(51)a	6.0(0.06)a
Thinned (n = 14)	13 380(660)a	436(83)a*	6.0(0.03)a
Hardwoods removed			
Thinned, residue removed (n = 15)	11 690(1210)a	388(59)a	5.8(0.03)b
Thinned, residue retained (n = 15)	13 340(1390)a	444(72)a†	6.0(0.03)a
LSD	295	192	0.1

NOTE: Within a column, values followed by the same letter do not differ significantly at $p = 0.05$.
*n = 13.
†n = 14.

of whether hardwoods were removed or not; however, it was slightly but significantly higher in all thinned plots than in control plots (Table 2).

Bulk density ranged from 0.89 in thinned, pure conifer plots with residue retained to 0.99 in thinned, mixed plots. Control plot values were intermediate at 0.94. Soils in pure conifer plots without residue were significantly denser than those with residue, perhaps because of compaction associated with residue removal. Bulk density was the only measured variable that differed between the two hardwood-removal treatments.

Forest-floor weight and nitrogen mineralization

Neither weight nor N mineralization rates of the forest floor differed among treatments (Table 3), nor was N mineralization correlated with N concentration of litterfall ($r^2 = 0.004$). The forest floor of pure conifer plots without residue had slightly but significantly lower pH.

Weight and nitrogen content of leaf litterfall

The weight of conifer leaf litter on thinned and control plots did not differ; however, the weight of hardwood leaf litter was 35% lower on the thinned, mixed plots than on controls ($p = 0.06$; Table 4). N concentration of shed hardwood leaves was uniformly higher than that of conifers on all mixed plots except those in which madrone was the dominant hardwood, where N concentration of conifer and hardwood leaf litter did not differ. Except for conifer litter collected in November, N concentrations in both conifer and hardwood leaf litter were higher on thinned, mixed plots than on control plots. Differences in hardwood litter probably reflected the higher proportion of maples and lower proportion of madrone on thinned plots.

Total N in leaf litterfall averaged 22.6 kg/ha in control and thinned, mixed plots, and 11.5 kg/ha in thinned, pure conifer plots. The difference was not due solely to hardwood litter; conifer leaf fall contained 25% more N in thinned, mixed plots than in pure conifer plots ($p < 0.10$), a function of higher N concentration rather than differences in mass. The amount of N returned to the forest floor in leaf litterfall on all plots correlated negatively with total soil N ($r^2 = 0.36$, $p = 0.002$; Fig. 2).

Root growth and nitrogen accretion in sand traps

Pure conifer plots had the greatest average root weight in sand traps, and thinned, mixed plots the least ($p < 0.09$; Table 5). Nitrogen accretion in sand traps followed the same pattern, averaging 32 kg/ha in pure conifer plots and 23 kg/ha in thinned, mixed plots ($p < 0.025$). Control plot values for both variables were intermediate. Many of the sand traps were densely occupied by fungal hyphae, probably from mycorrhizae, and an unknown fraction of N accreted in traps was contained in these rather than in dead organic matter.

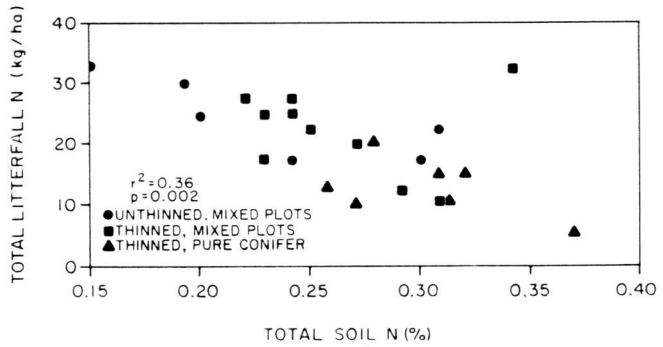

FIG. 2. The amount of nitrogen cycled to the forest floor, from leaves shed on all plots, in relation to total soil nitrogen.

Factors influencing nitrogen mineralization rates

Anaerobic mineralizable N in soil correlated positively with total soil N in all thinned plots (r^2 values ranged from 0.24 to 0.51), but correlated not at all in control plots (Fig. 3). Mineralizable N did not correlate with soil C:N ratio either linearly or logarithmically. (Evidence in the C:N data for complicated higher order patterns will not be discussed here.)

To estimate the relative influence of aboveground and belowground N input on soil mineralizable N, we regressed soil mineralizable N against the rate of forest-floor N mineralization and the accretion of N in sand traps. We assumed that mineralization in the forest floor is an index of nitrogenous compounds leaching into the upper soil, and that N in sand traps primarily reflects input associated with roots rather than with leaching from above (sand trap N did not correlate with forest-floor mineralization). Again, plots receiving different treatments were quite different. Mineralizable N in soils of pure conifer plots correlated positively with sand trap N ($p = 0.007$) and not with forest-floor mineralization, while that in soils of thinned, mixed plots correlated positively with forest-floor mineralization ($p = 0.012$) but not with sand trap N. This pattern suggests that substrates for soil mineralizable N were derived primarily from roots in pure conifer plots and from the forest floor in thinned, mixed plots. In contrast to thinned plots, soil mineralizable N in the control plots correlated with neither accretion of N in sand traps nor the rate of forest-floor N mineralization.

TABLE 4. Weight and nitrogen concentration of leaf litterfall by treatment

Stand type	n	Weight (kg/ha)		n	Nitrogen concentration (%)				Nitrogen content (kg/ha)		
					Conifer		Hardwood				
		Conifer	Hardwood		October	November	October	November	Hardwood	Conifer	Total
Unthinned, mixed (control)	14	1850(120)*a*	1270(260)*a**	9	0.67(0.03)*a*	0.61(0.02)*a*	0.88(0.08)*a*	0.72(0.02)*a*	10.1(1.8)*a*	12.2(1.0)*a*	22.3(1.94)*a*
Thinned, mixed	14	1960(160)*a*	830(120)*a*	8	0.74(0.03)*b*	0.67(0.03)*a*	1.27(0.19)*b*	0.85(0.02)*b*	8.6(1.0)*a*	14.3(2.4)*a*	23.0(2.34)*a*
Thinned, pure conifer	15	1990(170)*a*	10(5)*b*	11	0.69(0.02)*ab*	0.64(0.02)*a*	—	—	0.1(0.1)*b*	11.4(1.6)*a*	11.5(1.58)*b*
LSD (0.05)		450	450		0.07	0.07	0.29	0.06	2.7	3.4	4.3

NOTE: Within a column, values followed by the same letter do not differ significantly at $p = 0.05$.
*Weight of hardwood litter differs between control and thinned, mixed plots at $p = 0.06$.

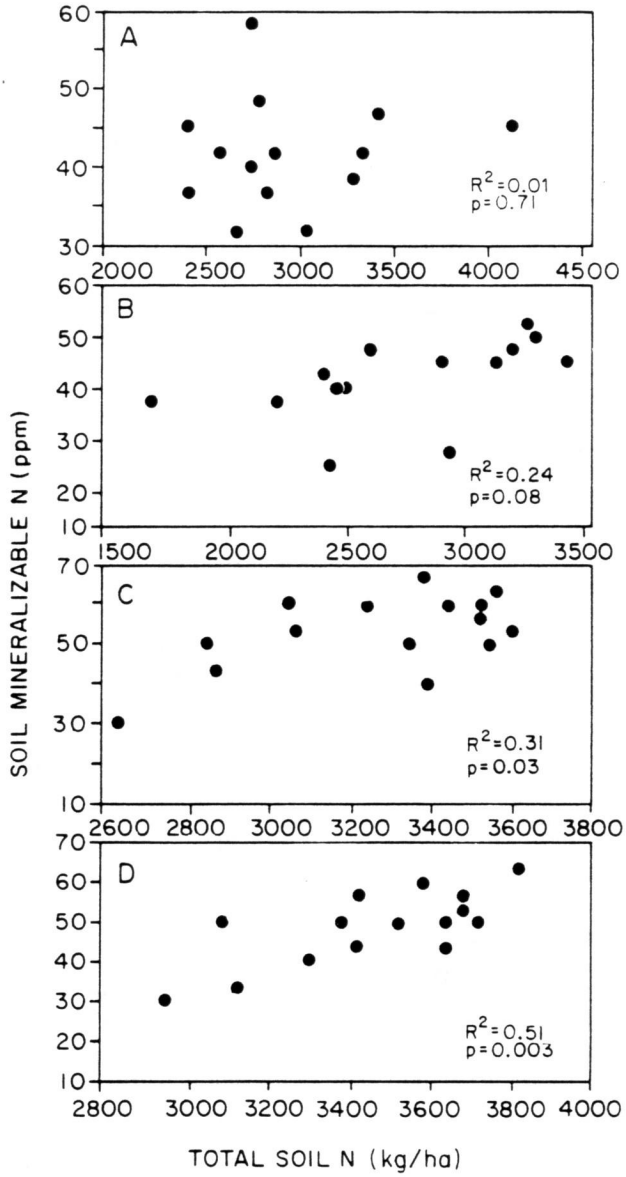

FIG. 3. The relationship between mineralizable nitrogen and total nitrogen in the soil by treatment: (A) unthinned, mixed plots; (B) thinned, mixed plots; (C) thinned, pure conifer plots, residue left; (D) thinned, pure conifer plots, residue removed.

Discussion

Contrary to our hypotheses, stands without hardwoods averaged 520 kg/ha more N in the top 12 cm of mineral soil, a 20% greater rate of anaerobic soil N mineralization, and a lower soil C:N ratio than stands with hardwoods. None of these factors varied significantly within the mixed group or the pure conifer group. Although we have no pretreatment measurements and cannot rule out the possibility of inherent site differences, the magnitude of difference between treatments, general consistency among randomly located corridors within treatments, and relative uniformity of environment and soil type within the study area suggest that differences are related to hardwood removal.

Similar patterns have been shown elsewhere. In Minnesota, the top 10 cm of mineral soil contain from 160 to 430 kg/ha more N in coniferous forests than in aspen forests, probably because of differences in N distribution within the system rather than in total system N (Alban 1982). Southern pines also accum-

TABLE 5. Weight of roots and accretion of nitrogen in sand traps

Stand type	n	Root weight (g)	Nitrogen ($\mu g/g$)	Nitrogen accretion ($kg \cdot ha^{-1} \cdot year^{-1}$)
Unthinned, mixed (control)	14	1.12(0.06)*a*	48.6(2.7)*ab*	29
Thinned, mixed	14	1.02(0.10)*a**	38.7(2.0)*a*	23
Thinned, pure conifer	15	1.30(0.14)*a*	53.2(5.6)*b*	32
LSD (0.05)		0.32	11.4	

NOTE: Within a column, values followed by the same letter do not differ significantly at $p = 0.05$.
*Root weight differs between thinned, mixed and thinned, pure conifer plots at $p = 0.09$.

ulate a higher proportion of total nutrients in their roots than do associated hardwoods (McGinty 1976). However, Nadelhoffer et al. (1985) found no consistent difference between hardwood and conifer forests in the relative allocation of N to fine roots and leaf litter.

If the patterns we detected in fact developed in the 3 years since thinning, the annual N flux in the top 12 cm of soil exceeded 150 kg/ha, or about 5% of total N in that portion of the soil profile. Rapid, large changes in soil properties have been noted before in conjunction with vigorous forests (Sanchez et al. 1985). In Nigeria, 6-year-old *Gmelina arborea* plantations have nearly twice as much N concentrated in surface soils as do 3-year-old plantations (Chijike 1980, cited in Sanchez et al. 1985), an absolute difference of more than 1000 kg/ha. *Gmelina* is not a known N fixer. In our study, such rapid change must be explained by redistribution of N in the system after hardwood removal, more N input to the pure conifer stands, or a combination of these factors.

Litterfall and sand trap data at least partially support the hypothesis of differential N distribution. If we assume that litterfall N correlates with total canopy N, stands with hardwoods accumulate relatively more N in foliage, while sand trap data indicate that stands without hardwoods accrete more N in the soil, at least in the top 12 cm. Moreover, the difference in N accretion to sand traps in thinned plots with and without hardwoods is similar to the difference in leaf litter N (both about $10 kg \cdot ha^{-1} \cdot year^{-1}$), suggesting that N is transferred from the foliage compartment to the soil compartment after hardwoods are removed. We do not know what fraction of the total yearly litterfall the collections from August through late November represent, but it is likely to be on the order of 70 to 80%. In their recent literature review, Vogt et al. (1986) concluded that deciduous species carry only about one-half of the root biomass of evergreens.

The shift of N from leaf to root explains only a small portion of differences in soil N of stands with and without hardwoods, but N may also be moved from lower to upper soil layers after hardwood removal. Conifers fix significant amounts of carbon during the mild, wet winters in the Oregon Coast Range (Emmingham and Waring 1977), while deciduous hardwoods such as maple, cherry, and dogwood must photosynthesize during the dry summers. Hence it is likely that deciduous trees root deeper than evergreens in order to maintain a favorable water balance during physiologically active periods, and the apparent gain in soil N that we measured in plots without hardwoods may reflect an upward shift in root activity. In California, where seasonal precipitation patterns are similar to those in Oregon, soils beneath evergreen oaks have significantly more total N and higher rates of nitrification than soils under deciduous oaks (Billows 1986). This interpretation of the data is confounded, however, by the fact that conifer stocking did not differ in pure and mixed thinned stands; hence, the fact that hardwoods may root deeper than conifers, or produce smaller root systems, is not in itself sufficient to explain differences between treatments. It is possible that conifers associated with hardwoods produce fewer roots, or root deeper, than they do in pure stands. Allelochemicals leached from forest litter have been shown to reduce the formation of some mycorrhizal types on Douglas-fir (Schoenberger and Perry 1982; Rose et al. 1983). This effect varies widely with litter type and could conceivably be a greater factor in mixed than in pure stands.

What about the possibility of different N input in plots with and without hardwoods? More dead hardwood roots decomposed in soils in pure stands than in mixed stands, and small roots had probably decomposed sufficiently in the 3 years since thinning to add most of their N to the soil pool that we measured. Soil N on a given plot did not correlate with the number of hardwoods removed during thinning; but number alone, without accounting for tree size, may not fairly indicate hardwood importance. If differences in decomposition of dead hardwood roots are to account for the apparent differences in soil N, hardwoods would have to have tied up large amounts of N in roots and, contrary to our previous arguments, roots would have to be growing in the top soil layers.

In the absence of symbiotic N-fixing plants (none were present on the study sites), known N input is quite low in this area. Precipitation adds less than $0.2 g \cdot m^{-2} \cdot year^{-1}$, and fixation by free-living organisms in litter adds roughly the same (Heath 1985). N impaction on foliage has not been measured in this area, but as the air is relatively clean, probably only small amounts are added in this way. Even if amounts were significant, there is no reason to expect that the input would differ between stands with or without hardwoods. Conifers may be more efficient atmospheric "rakes," but conifer stocking did not differ among the thinned plots. One possible source of N might well differ, however. Nitrogenase activity has been detected in association with belowground ectomycorrhizal fruiting bodies (Li and Castellano 1985) and within the rhizosphere of ectomycorrhizal conifers, including Douglas-fir (Florence and Cook 1984; M. P. Amaranthus, C. Y. Li, and D. A. Perry, submitted for publication). We do not know how much N soils receive through mycorrhizal-associated fixation, but such fixation is probably stimulated by the greater rooting activity in plots without hardwoods.

For whatever reason, it is clear that the upper soil layers of these pure conifer stands have significantly more N, at a lower C:N ratio, and higher rates of anaerobic N mineralization than the conifer–hardwood stands. Unlike the buried-bag technique

(e.g., Federer 1983; Nadelhoffer et al. 1985), anaerobic mineralization provides a comparative index that does not purport to measure actual amounts of N released in the field. However, the anaerobic test is a good predictor of fertilizer response in western conifers and is considered to be a reliable index of N available for tree growth (Shumway and Atkinson 1978; Keeney 1980; Powers 1980).

Not only did the rate of anaerobic N mineralization differ on plots with and without hardwoods, but also the source of substrate for N mineralization. On pure conifer plots, soil N mineralization correlated positively with N accretion in sand traps and either weakly or not at all with the mineralization rate in the forest floor. The opposite was true in conifer–hardwood plots. Exactly what N substrates are measured in the anaerobic technique remains unclear, but microbial biomass is probably an important one (Paul 1984). If we assume that N accreted to sand traps was derived directly or indirectly from root activity (as it did not correlate with forest-floor mineralization), the data suggest that the two forest types differ in the source of energy for soil microbes. In pure conifer plots, substrates for N mineralization (hence, soil microbes) are derived from roots and mycorrhizae, probably from a combination of sloughing, exudation, and perhaps biological fixation. Mixed plots appear to incorporate a forest floor to soil path, in which substrates derived from decomposition in the forest floor move downward into upper soil layers. The latter is consistent with the well-known tendency of hardwood forests to develop mull-type humus, in which forest floor and mineral soil are intimately mixed (Pritchett 1979).

Ulrich et al. (1981) hypothesize that root sloughing is an important mechanism for returning nutrient elements and organic matter to temperate forest soils and stabilizing nutrients in seasonal environments. Root input to soil is rich and varied, however, and besides sloughed tissues includes organic exudations, which account for 10 to 40% of the total carbon fixed by plants (Reid and Mexal 1977; Whipps and Lynch 1986), and mycorrhiza-associated tissues (mostly hyphae but also truffles and microorganisms that derive energy from hyphal exudations). In a Douglas-fir forest similar to the one we studied, 73% of total net primary production was invested in roots and mycorrhizae, and mycorrhizae accounted for more than 90% of N cycled from trees to soil (Fogel and Hunt 1983). Much of the N accreted in our sand traps may have been derived from mycorrhizae or mycorrhizal hyphae; therefore differences in accretion between pure conifer and mixed stands may reflect not only rooting depth but also the lower proportion of ectomycorrhizal species in mixed stands. Conifers and madrone are ectomycorrhizal; maple, cherry, and dogwood have vesicular–arbuscular mycorrhizae, which produce fewer tissues external to the root (Harley and Smith 1983).

N not only limits productivity of many ecosystems, it is a key element in global biogeochemical cycles because of its control of the strength of the biotic sink for atmospheric CO_2 in many ecosystems and because of the importance of various gaseous N compounds in the chemical and radiative properties of the atmosphere (National Research Council 1983). Understanding the N storage and cycling characteristics of forests is essential to understanding the biogeochemistry of the global ecosystem; however, as Stone (1975) and Sanchez et al. (1985) point out and as this study emphasizes, much is left to be learned. Some established ideas about the effect of different plant species on soils and the N cycle need reexamination. Nutrient dynamics in mixed species communities may not be successfully explained as a simple additive function of the individual species. In our study, differences in N cycling characteristics between pure conifer and mixed forests were a phenomenon of the community as a whole and not of the hardwood component alone.

Three years after thinning, stands of this study were probably still rapidly changing in response to altered site conditions. The poor correlation between mineralizable N and soil properties in unthinned stands suggests that at least some of the pattern we detected was influenced by thinning, and the forest floor was unlikely to be in steady state after the recent alteration in density and species composition. Ultimately, therefore, the soil properties and N cycling characteristics of these plots may be different than those we have measured.

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