Forest soil characteristics in a chronosequence of harvested Douglas-fir forests[1]

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Abstract: This study was designed to measure the microbiological and chemical characteristics of forest soils in a chronosequence of harvested Douglas-fir (*Pseusotsuga menziesii* (Mirb.) Franco) stands in different climatic settings. Mineral soil samples were collected along transects running from old-growth (OG) forests into harvested stands of ages 5, 15, and 40 years (5YS, 15YS, and 40YS, respectively) in the H.J. Andrews Experimental Forest in the central Oregon Cascade Mountains. We took litter depth measurements and cores to test for the presence of mycorrhizal mats at each sampling location. Denitrification potential was significantly lower in OG than in 5YS, and litter depth, forest floor respiration rate, and concentration of ectomycorrhizal mats were significantly greater in OG than in 5YS. Values were intermediate in 15YS and similar to those measured in OG in 40YS. No significant stand-age differences occurred in soil organic matter, soil moisture, pH, mineralizable N, laboratory soil respiration rate, or extractable ammonium. Sample variability was generally lowest in OG forests and highest in 5YS, and no consistent autocorrelations were observed for any of the variables at lags of 5 m or greater. We found no second-level interactions between stand age and location in ANOVA analyses, suggesting that, within the limits of this study, climate did not influence soil response to disturbance and subsequent recovery; however, several soil properties were affected by site location and, therefore, climate.

Résumé : Cette étude a été conçue pour mesurer les caractéristiques chimiques et microbiologiques des sols forestiers dans une chronoséquence de peuplements récoltés de douglas de Menzies (*Pseusotsuga menziesii* (Mirb.) Franco) soumis à différentes conditions climatiques. Des échantillons de sol minéral ont été collectés le long de transects allant de vieilles forêts (VF) jusque dans des peuplements récoltés et âgés de 5, 15 et 40 ans (5YS, 15YS et 40YS) dans la forêt expérimentale H.J. Andrews située dans la partie centrale de la chaîne des Cascades en Oregon. Nous avons mesuré l'épaisseur de la litière et prélevé des carottes pour vérifier la présence de manchons d'ectomycorhizes à chaque point d'échantillonnage. La capacité de dénitrification était significativement plus faible dans les VF que dans les 5YS et l'épaisseur de la litière, le taux de respiration dans le parterre forestier, ainsi que la concentration de manchons d'ectomycorhizes étaient significativement plus grands dans les VF que dans les 5YS. Les valeurs étaient intermédiaires dans les 15YS et semblables à celles des VF dans les 40YS. Il n'y avait pas de différences importantes selon l'âge des peuplements dans la matière organique du sol, l'humidité du sol, le pH, l'azote minéralisable, le taux de respiration du sol en laboratoire ou l'ammonium extractible. La variation entre les échantillons était généralement la plus faible dans les VF et la plus forte dans les 5YS et aucune autocorrélation significative n'a été observée pour aucuns des intervalles de 5 m ou plus. Nous n'avons observé aucune interaction du second degré entre les peuplements de différents âges et les stations dans les analyses ANOVA; ce qui indique que, dans le cadre de cette étude, le climat n'a pas influencé la réaction du sol aux perturbations et à la récupération subséquente. Cependant, plusieurs propriétés du sol étaient affectées par la localisation du site et par conséquent par le climat.

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Introduction

Forest managers have considerable interest in the influences of clear-cutting old-growth forests on geochemical processes in forest soils and the sequence of events that take place during subsequent stand reestablishment. Although numerous studies examine the effects of clear-cutting, relatively little is known about effects on forest floor geochemical cycles and other soil properties that potentially impact long-term site productivity and the biodiversity of soil organisms. A number of studies document changes in soil C and N cycling (Bormann and Likens 1979; Covington 1981; Gholz et al. 1985; Bradley et al. 1998) in harvested old-growth forests. Because of differences in both experimental design and vegetation present before and after harvest, inconsistent conclusions have been drawn from many of these studies (Likens et al. 1969; Aubertin and Patric 1974).

The effects of clear-cutting on N cycling have been of particular interest because of potential impacts on water quality and long-term site productivity. Increases in N mineralization rates and nitrification (Matson et al. 1987; Frazer et al. 1990) and decreases in plant N uptake (Vitousek and

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Matson 1985) are common after clearcuts in temperate forests. Clear-cutting also results in a net loss of C from the system in the form of timber removal, slash burning, and increased forest floor respiration rates (Harmon et al. 1986, 1990).

This study was designed to expand our understanding of how soils change over time in coniferous forests that have been clear-cut. Of particular interest in stand recovery is the point at which N losses resulting from clear-cutting become equal to levels found in old-growth forests and at which ectomycorrhizal mats, an important component of nutrient cycling (Perry et al. 1987; Griffiths et al. 1994), return to predisturbance levels. In addition, this study was designed to determine how climate might influence the rate at which forest soils return to predisturbance levels and to test the hypothesis that spatial variability of soil processes in old-growth stands might be higher than that found in recently harvested stands.

Nitrogen is the primary limiting nutrient in these forests; thus, N retention is critical for long-term productivity (Perry 1994). Because of interest in the loss of mineralized N from disturbed forest ecosystems, we included measurements of denitrification potential (Stenberg 1998). Field respiration rates were measured as a relative indicator of stand primary productivity (Ellis 1969; Coleman 1973; Fung et al. 1987; Raich 1998; Law et al. 1999). In addition, because of the importance of ectomycorrhizal fungi in forest productivity (Pankow et al. 1991; Read 1991), we examined effects of clear-cutting and subsequent forest regeneration on the presence of ectomycorrhizal mats in forest soils. These effects have implications for understanding forest recovery and productivity after disturbance (Harvey et al. 1980; Parke et al. 1984; Perry et al. 1987).

We also investigated changes in C stored in the forest floor as harvested stands recover over time. Although a number of studies examine the effects of clear-cutting on total N and C, no studies to our knowledge examine the effects on labile or biologically active N and C pools. These are the pools that are most likely to be impacted by changes in vegetation. This information can provide forest managers additional data with which to determine the influence of forest practices on the ability of forests to sequester C, thereby contributing to management of global C fluxes (Harmon et al. 1990).

Methods and materials

Site descriptions

The Mediterranean climate at the H.J. Andrews Experimental Forest has been described by Greenland (1994). Soils are derived from volcanic parent materials and are classified as Typic Distrochrepts (Sollins et al. 1980). Mineral soil samples were collected at 27 sites along 1 transect per site. Transects were 150 m long and ran along a contour from old-growth forest (OG) into harvested stands of different ages. Each transect extended 75 m on either side of the stand edge, and soil samples were taken every 5 m from 75 to 15 m from the edge. Between 15 and 1 m on either side of the edge, samples were taken at 1-m intervals, allowing us to test for spatial variability at both 1- and 5-m intervals.

The old-growth forests were dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), as described by Franklin and Dyrness (1988). The harvested stands used in this study had been commercially harvested, i.e., in each case, old growth was cut, and slash and debris were subjected to a light burn, thus leaving burned stumps and old, decayed logs. Douglas-fir seedlings were typically replanted within 2 years of harvest and represented the majority of trees present in all age-classes.

The experimental design consisted of 3 stand ages and 3 location types, each of which was replicated 3 times for a total of 27 transects. Each of the transects was located in a different stand. The three stand ages were those harvested approximately 5, 15, and 40 years prior to this study. Nine transects of each age-class were sampled. Of these nine transects, three transects were located in low-elevation (646–800 m), flat sites; three were located in high-elevation (1000–1262 m), south-facing sites; and three were in high-elevation (800–1338 m), north-facing sites.

The 5-year-old stands (5YS) generally consisted of early successional herbs and shrubs with large gaps between young trees, which were usually <2 m in height. Vegetation was sparse over much of the ground. Stands ca. 15 years old (15YS) still had gaps between trees but contained only small areas that were not covered with trees or shrubs; few herbs were present. Most of the trees were Douglas-fir, generally <5 m in height. The 40-year-old stands (40YS) had closed Douglas-fir canopies (most >15 m in height), with relatively little understory vegetation.

Sample collection and storage

Mineral soil samples were collected with a trowel to a depth of 10 cm and transported to the laboratory in an ice chest. Soils were stored at 15°C until the initiation of analyses, within 16 h of their receipt. Field respiration rates and air temperatures were measured once in November. Soil temperatures were measured in August and November. All other variables were measured in August.

Field measurements

Field (forest floor) respiration rate was measured with a nondispersive, infrared CO_2 analyzer (LI-6200; LI-COR, Lincoln, Nebr.). Measurements were made over a period of 1 min after the chamber gas reached ambient CO_2 concentration. The instrument was calibrated on site against a known standard at each location. A Q_{10} adjustment was made for ambient soil temperature. Soil and air temperatures were measured by electronic thermometers calibrated at 0°C with ice water. For soil temperatures, the probes were inserted into the mineral soil to a depth of 10 cm. Air temperatures were measured by placing the probe, elevated 10 cm from the soil surface, in the shade for a period of at least 10 min. Temperature measurements were made at the same time (early morning) and locations as the respiration rate determinations.

The distribution of ectomycorrhizal mats was determined visually in the field by inspecting the relative abundance of mats in 4.5 × 10 cm cores. Two distinct mat types were scored: (*i*) mats similar to those of the genus *Hysterangium* and (*ii*) mats similar to those of the genus *Gautieria*. This approach has been used successfully in the past to document ectomycorrhizal mat distribution patterns in coniferous forests of the Pacific Northwest (Griffiths et al. 1996). Litter depth was measured three times at each sampling location. The litter depth included all litter above the mineral soil.

Laboratory analyses

In preparation for laboratory analysis, all soils were sieved through a 2-mm sieve. Soil pH was measured in 1:10 (soil : distilled water) slurries of ovendried (100°C) soil. These slurries were shaken for 1 h prior to reading pH values with a Sigma model E4753 electrode. Soil organic matter (SOM) was measured by loss-on-ignition at 550°C for 6 h after oven-drying at 100°C. Soil moisture was measured gravimetrically by subtracting the mass of ovendried soil (100°C for >8 h) from the mass of field-moist soil and then dividing by the mass of dried soil.

Denitrification potential was measured according to a method similar to that used by Groffman and Tiedje (1989). This assay

measured denitrification enzyme activity (DEA), which has been shown to correlate with mineralized N and N mineralization in soils (Melillo et al. 1983; Schipper et al. 1993; Griffiths et al. 1998; Stenberg 1998). Each reaction vessel (25-mL Erlenmeyer flask) contained 5 g of <2 mm, field-moist soil. Flasks were sealed with rubber serum bottle stoppers and purged with Ar to displace O_2 in the headspace gas. After purging with Ar, 2 mL of a 1 mM solution of glucose and NO_3^- were added to each flask. Flasks were subsequently incubated at 25°C for 1 h. This preincubation period was used because time-series experiments on representative soils showed a lag in N_2O production during this period. The same experiments showed linear N_2O production rates during the following 2–4 h (data not shown). After the preincubation period, 0.5 mL of headspace gas was removed from the reaction vessel and injected into a gas chromatograph (GC) fitted with an electron capture detector (Hewlett Packard model 5890 GC, fitted with Hewlett Packard model 3396 integrator). The integrator was calibrated by the external calibration method with known gas standards.

A second headspace N_2O analysis was made after an additional 2-h incubation at 25°C. The net N_2O released over this 2-h period was used to estimate N_2O production rate. Acetylene was not routinely added to the headspace to prevent the conversion of N_2O to N_2, because results of assays with a 10% acetylene atmosphere on randomly selected samples (10% of the total) indicated no significant differences between N_2O production rates with and without acetylene. Christensen et al. (1990) took the same approach and found that, in soils of low pH, most of the end product of denitrification is N_2O; therefore, the acetylene block is not necessary to estimate denitrification rate by N_2O production rate.

Laboratory respiration measurements, used to measure labile organic C (Anderson 1982; Zibilske 1994), were made on field-moist, sieved soils (4 g dry mass). Soils were brought to 75% moisture content by the addition of enough sterile deionized water to equal 3 g water per 25-mL Erlenmeyer flask. Once sealed with serum bottle stoppers, the flasks were incubated for 14 days at 24°C and analyzed for headspace CO_2 by gas chromatography with the same GC and integrator as were used for measuring N_2O. A flame ionization detector and a methanizer in series were used to measure CO_2.

Extractable ammonium was determined by shaking 10 g of field-moist soil with 50 mL 2 M KCl for 1 h (Keeney and Nelson 1982), adding 0.3 mL 10 M NaOH to the slurry, and measuring ammonium concentration with an Orion model 95-12 ammonium electrode (Orion Research Inc., Boston, Mass.). Mineralizable N was measured by the waterlogged technique of Keeney and Bremner (1966). This assay measured labile or readily degradable organic N (Bundy and Meisinger 1994). For each analysis, 10 g of field-moist soil were added to 53 mL of distilled water in a 20 × 125 mm screw-cap test tube and incubated at 40°C for 7 days. Then 53 mL of 4 M KCl were added to the slurry, and ammonium concentration was determined with the ammonium electrode. Mineralizable N was calculated as the difference between initial and final ammonium concentrations.

Statistical analyses

All statistical analyses were conducted with the PC program STATGRAPHICS (Statistical Graphics Corp., Rockville, Md.). The ANOVAs were computed on the means of all values for each transect. Significance of differences between mean values was determined with Fisher's protected least significant difference ($p \leq 0.05$). The exceptions are noted in the text. Coefficients of variability were calculated as the mean/SD.

Results

Significant differences were found in many of the properties of OG soils and those of adjacent harvested stands (Table 1). Summer soil temperatures were lower in OG and 40YS than in the younger stands. Denitrification potentials were significantly higher in the younger stands than in the older stands, with approximately sixfold higher values in 5YS and 15YS than in OG and 40YS. In addition, the occurrence of ectomycorrhizal mats differed dramatically among harvested stands. The percent cover for all mats was a factor of 50 lower in 5YS than in OG. In 15YS, mat coverage increased, although not significantly, mainly as a result of increases in *Hysterangium*-like mats. The total coverage of mats in 40YS was about half that in OG. We found no statistically significant stand-age differences in soil pH, moisture, air temperature, SOM, extractable ammonium, mineralizable N, or laboratory respiration, although both extractable ammonium and laboratory respiration were higher in OG than in the most recently harvested stands.

For most soil properties, coefficients of variability were lower in OG than in the youngest stands. These differences were statistically significant ($p \leq 0.05$) for soil moisture, summer soil temperatures, litter depth, and ectomycorrhizal mats (Table 2). At the $p \leq 0.08$ level, the coefficients of variability were also significantly lower for SOM and laboratory respiration in OG forests.

Results of the ANOVA indicated no significant interactions between stand age and location but significant location differences in several variables (Table 3). Air temperature and fall soil temperatures were significantly ($p \leq 0.05$) higher in the low-elevation sites than in the high-elevation, north-facing sites. Mineralizable N was also higher in the low-elevation sites but was only significant at the $p \leq 0.09$ level. Soil organic matter and extractable ammonium were significantly lower in low-elevation sites than in north-facing, high-elevation sites. Soil pH, mineralizable N, and denitrification potential were all significantly higher at low-elevation, flat sites than at high-elevation, north-facing sites.

Discussion

Stand-age effects

As reported in other studies (Chen et al. 1993), soil temperatures were higher in young stands than in OG and 40YS (Table 1). This was expected in summer, when the absence of foliage in younger stands allows solar radiation to directly warm exposed soils; this effect was not seen in closed-canopied 40YS. This temperature difference was not seen later in the fall, when air temperatures were much lower and solar energy was greatly reduced because of cloud cover. We did not see significant stand-age effects on soil moisture, which differs from results reported by other researchers (Bethlahmy 1963; Hendrickson et al. 1989; Weber 1990) (Table 1). Nonetheless, our results are substantiated by an earlier study in the Andrews Experimental Forest (Adams et al. 1991). When comparing old-growth and clear-cut soil moisture seasonally, Adams et al. (1991) found an initial increase in moisture in harvested stands during the first 2 years post-harvest. After that brief period, they found either no difference between the two treatments or a reduction in moisture in the harvested units as vegetation became reestablished.

A reduction in litter depth as a result of stand harvest was also observed (Table 1), a phenomenon most likely driven by

Table 1. Means of variables measured in old-growth (OG) and in harvested stands, 40, 15, and 5 years after harvest (40YS, 15YS, and 5YS, respectively) in the central Oregon Cascades.

	Treatment			
Variable	OG	40YS	15YS	5YS
Soil moisture (%)	41.3	40.6	40.5	45.6
Soil temperature (°C)				
Summer	14.2*b*	14.1*b*	16.1*a*	17.4*a*
Fall	8.0	8.1	7.8	7.0
Air temperature (°C)	9.74	9.23	9.33	10.14
pH	5.15	5.37	5.29	5.38
Soil organic matter (%)	24.4	23.8	24.2	24.0
Litter depth (cm)	3.76*a*	2.76*ab*	1.20*b*	2.14*b*
Extractable ammonium (μg N·g dry mass^{-1})	3.80	3.62	3.96	3.34
Mineralizable N (μg N·g dry mass^{-1})	135	169	120	113
Field respiration (g·m^{-2}·day^{-1})	10.7*a*	9.2*ab*	8.0*b*	6.8*b*
Laboratory respiration (mg C·g dry mass^{-1})	0.89	0.99	0.56	0.79
Denitrification potential (nmol N·g dry mass^{-1}·h^{-1})	1.10*b*	0.87*b*	6.13*a*	6.41*a*
Ectomycorrhizal mat cover (%)				
Hysterangium-like	19.2*a*	13.4*a*	3.6*b*	0.3*b*
Gautieria-like	10.8*a*	2.5*b*	0.6*b*	0.2*b*
Total*	31.3*a*	16.1*b*	4.4*c*	0.6*c*

Note: Means followed by different letters differ significantly ($p \leq 0.05$). All measurements were made in July–August 1995, with the exception of fall soil temperature and field respiration, which were made in November 1995.

*Includes all ectomycorrhizal mats present.

Table 2. Coefficients of variability of variables measured in old-growth (OG) and in harvested stands, 40, 15, and 5 years after harvest (40YS, 15YS, and 5YS, respectively) in the central Oregon Cascades.

	Treatment			
Variable	OG	40YS	15YS	5YS
Soil moisture	0.33*ab*	0.23*b*	0.29*ab*	0.47*a*
Soil temperature				
Summer	0.07*b*	0.06*b*	0.10*a*	0.12*a*
Fall	0.11	0.12	0.19	0.26
Air temperature	0.10	0.09	0.09	0.09
pH	0.70	0.70	0.67	0.66
Soil organic matter*	0.23*b*	0.27*ab*	0.25*ab*	0.34*a*
Litter depth	0.70*b*	1.13*a*	1.14*a*	1.37*a*
Extractable ammonium	0.52	0.67	0.56	0.74
Mineralizable N	0.52	0.66	0.72	0.66
Field respiration	0.48	0.45	0.53	0.60
Laboratory respiration*	0.88*b*	0.83*b*	0.97*ab*	1.15*a*
Denitrification potential	1.39	1.26	1.64	1.33
Ectomycorrhizal mat cover				
Hysterangium-like	1.37*b*	1.87*b*	2.40*a*	2.44*a*
Gautieria-like	2.24*b*	3.66*a*	3.38*a*	3.49*a*
Total†	1.07*c*	1.75*b*	2.01*b*	2.97*a*

Note: Values followed by different letters differ significantly ($p \leq 0.05$). Variables with asterisks differ at $p \leq 0.08$.

†Includes all ectomycorrhizal mats present.

post-harvest site preparation and a subsequent reduced input of litter produced by early successional plants. The maximum difference in litter depth was observed between OG and 15YS, with litter depths between these two extremes in both 5YS and 40YS. This is essentially the same pattern seen by Covington (1981) in his study of the effects of clear-cutting on forest floor material in 14 northern hardwood forests and by Black and Harden (1994) in a study of mixed conifer forests in California. As in our study, Black and Harden (1994) found the lowest litter levels in 17YS, with both OG and 7YS showing greater depths. In another recent study in similar Oregon forests, litter depth was found to be significantly lower in 60- to 100-year-old stands when compared to OG stands, suggesting that the reestablishment of predisturbance litter levels could take considerable time (R.P. Griffiths, unpublished data).

Reduced forest floor organic matter, however, did not result in the reduction of SOM, a trend also observed in slash pine plantations (Gholz et al. 1985) and in mixed conifer and hardwood stands (Hendrickson et al. 1989) (Table 1). In a review of the effects of forest management on SOM, Johnson (1992) concludes that, unless a stand has been severely burned, SOM is seldom reduced as a result of clear-cutting. Results from a recently developed, long-term, post-disturbance, C stores model predict that, because of the relative recalcitrance of C pools in SOM, many years of reduced litter input may be required before a change in SOM values is observed (M.E. Harmon, personal communication). As was the case with SOM, clear-cutting did not reduce the more labile forms of organic N and C: mineralizable N and laboratory respiration, respectively.

In contrast, clear-cutting resulted in reduced field respiration rates. As expected, this response was greatest in the youngest stands, was less pronounced in 15YS, and was close to OG values by 40 years (Table 1). Other researchers have measured similar responses to clear-cutting. Weber

Table 3. Means of variables measured along old-growth–harvested stand transects in flat (low elevation), south-facing (high elevation), and north-facing (high elevation) sites.

	Site aspect		
Variable	Flat	South-facing	North-facing
Soil moisture (%)	40.7	45.0	40.8
Soil temperature (°C)			
Summer	15.8	14.3	15.0
Fall	10.6*a*	8.7*b*	4.3*c*
Air temperature (°C)	12.4*a*	10.6*a*	5.5*b*
pH	5.38*a*	5.27*ab*	5.09*b*
Soil organic matter (%)	21.7*b*	28.0*a*	24.7*ab*
Litter depth (cm)	3.04	2.67	2.93
Extractable ammonium (μg N·g dry mass^{-1})	2.60*b*	4.89*a*	3.80*ab*
Mineralizable N (μg N·g dry mass^{-1})	184*a*	128*ab*	96*b*
Field respiration (g·m^{-2}·day^{-1})	10.0	9.25	8.26
Laboratory respiration (mg C·g dry mass^{-1})	0.84	1.02	0.67
Denitrification potential (nmol N·g dry mass^{-1}·h^{-1})	3.26*a*	4.37*a*	0.50*b*
Ectomycorrhizal mat cover (%)			
Hysterangium-like	14.1	12.4	11.0
Gautieria-like	4.94	5.57	7.40
Total*	19.1	18.8	19.5

Note: Means with different letters differ significantly ($p \leq 0.05$), except for mineralizable N, which differs at $p \leq 0.09$.

*Includes all ectomycorrhizal mats present.

(1990) observed reductions in forest floor respiration in cut, immature aspen stands soon after harvest. These rates were restored to control levels within 3 years, as vegetation returned to the sites. A similar pattern was reported by Frazer et al. (1990) in studies of mixed conifer forests on three Sierra Nevada (U.S.A.) sites.

The reduced field respiration rates could be caused by a reduction in microbial activity (i.e., decomposition rates) and (or) root respiration. Studies of the soil microbial response to both clear-cutting (Lundgren 1982) and burning have shown reductions in microbial populations in northern coniferous forests (Baath et al. 1995; Bradley et al. 1998). This may explain, in part, the reduced field respiration rates we measured in harvested stands. In a recent study of soil properties in 9-year-old, 50-m tree-fall gaps, we found reduced α-glucosidase activities in the gap center, suggesting that, under conditions somewhat analogous to those in this study, microbial activities were indeed lower (R.P. Griffiths, unpublished data).

Reduced soil respiration rates after clear-cutting may also be the result of reduced root respiration (Ewell et al. 1987). Edwards and Ross-Todd (1983), in a study of harvesting in a mixed deciduous eastern (U.S.A.) forest, measured greater forest floor respiration rates in the uncut control forests than in the harvested stands approximately 5 months after harvest. Because laboratory soil respiration rates were actually higher for the harvested stands, they concluded that the reduction in forest floor respiration after harvest was the result of reduced root respiration. The laboratory respiration experiments we conducted did not indicate any significant differences by stand age. These experiments were, however, conducted under laboratory conditions in which soils were brought up to a 75% moisture content and incubated at 24°C.

Another consequence of harvesting trees is the loss of mycorrhizal hosts and the associated loss of mycorrhizal fungi (Perry et al. 1987). Seedling greenhouse studies have shown that soils from recently clear-cut or burned sites may have higher (Amaranthus and Perry 1987; Brainerd 1988) or lower (Perry et al. 1982; Parke et al. 1984) inoculum potentials than soils collected from nearby undisturbed forests. Even though the inoculum potential may remain high in clear-cut forests, the ability to take up and cycle plant nutrients is radically reduced when the host tree is cut (Read 1991).

In this study, the loss of mycorrhizal fungi is reflected in a specialized subset of these fungi, represented by two morphotypes of ectomycorrhizal mats: one set similar to those formed by species in the genus *Hysterangium*, and the other set similar to the genus *Gautieria*. *Hysterangium* mats have higher enzyme activities than *Gautieria* mats and, thus, are relatively more suited for extracting N by breaking down litter and SOM (Griffiths et al. 1990, 1991; Aquilera and Griffiths 1993). In contrast, *Gautieria* mats have higher levels of organic acids than *Hysterangium* mats and are relatively better adapted for weathering mineral soils for plant nutrients (Griffiths et al. 1994). Both mat types were essentially absent in stands that had been recently clear-cut (Table 1). Of all variables measured, ectomycorrhizal mats were the only variables that showed a significant difference between OG and 40YS. In a recent study of the effects of stand age on ectomycorrhizal mat distribution patterns, the area covered by *Gautieria* mats in 80-years-old stands was only half that in OG stands (Griffiths et al. 1996), suggesting that these important forest features are very slow to recover after clear-cutting.

Many studies have documented the loss of inorganic N, both as nitrate and as nitrous oxide, in leachates and ground-

water from recent clear-cuts (Vitousek et al. 1979; Vitousek and Matson 1985; Bowden and Bormann 1986). This loss can be influenced by both living and dead biomass left on the site after harvest, which suggests that loss of inorganic N after harvest is controlled by a balance between sources (decomposition of litter, fine roots, and mycorrhizal fungi) and sinks (plant and mycorrhizal uptake, microbial immobilization, and denitrification) of mineralized N (Vitousek and Matson 1985). The reduction in all mycorrhizae as a result of clear-cutting could reduce the ability of the plant community to take up inorganic N and P (Pankow et al. 1991), and transfer N, P, and other elements among plants (Simard 1993; Read 1994). While studying the effects of clear-cutting on N cycling in hemlock forests of British Columbia, Bradley et al. (1998) found a reduction of the gross nitrate consumption rate in clear-cuts when compared with old-growth forests. This suggests that the sink for nitrate has been reduced in clear-cut forest soils.

One of the effects of clear-cutting was a dramatic increase in denitrification potential, a relative indicator of mineralized N availability in forest soils. The link between denitrification potential and relative availability of mineralized N is as follows: denitrification potential as we measured it actually measures soil DEA (Tiedje 1982). Denitrifying enzyme activity increases as the number and activity of denitrifiers increase in soils. The primary factors influencing DEA in soils are the availability of nitrate and soil moisture (Davidson and Swank 1986; Tiedje et al. 1989; Drury et al. 1991). Available C can also be a factor where nitrate is not limiting (Drury et al. 1991), but this was not found to be the case during a study of factors limiting denitrification in Douglas-fir forest soils of the central Oregon Cascades (Griffiths et al. 1998). If, as in this study, there were no significant soil moisture changes with stand age, this leaves nitrate availability as the most likely driver for the differences in denitrification potential. Evidence in the literature supports this idea. In fertilization experiments, DEA and field denitrification rates increase when N in various forms is added to soils (Priha and Smolander 1999; Simek and Hopkins 1999). This relationship has also been observed in filter belts adjacent to agricultural soils with high N loadings (Lowrance 1992; Verchot et al. 1998). Denitrification potentials have also been correlated with nitrification potential (Griffiths et al. 1998), nitrate concentrations (Melillo et al. 1983; Schipper et al. 1993), in situ denitrification (Schipper et al. 1993), and annual denitrification loss of mineralized N in forest soils (Groffman and Tiedje 1989).

Denitrification rates were much higher in 5YS and 15YS than in OG and 40YS (Table 1). From this we conclude that nitrate losses are greater in the younger stands, but that, after 40 years, these losses are essentially at the same level as that observed in OG. A similar observation was made by Berg and Staaf (1980) in studies of nutrient losses from litter. They found the greatest N losses in the youngest stands and the smallest losses in the oldest stands. In contrast to denitrification potential, no treatment effects were observed in either mineralizable N (anaerobic incubation) or extractable ammonium. Similar results have been reported for both mineralizable N (Ross et al. 1995) and extractable ammonium (Vitousek and Matson 1985).

Sample and spatial heterogeneity

Before conducting this study, we hypothesized that 40YS would show the lowest sample variability, and that 5YS would show the highest. We reasoned that 40YS, which were plantations of almost pure Douglas-fir with relatively low horizontal heterogeneity, would have relatively little belowground sample variability when compared with 5YS, where vegetation was not as well established. We thought that, because high structural and biological diversity is found in OG forests, sample variability would be high in these stands as well.

As predicted, 5YS soils showed the highest variability, but OG soils unexpectedly showed the lowest variability for most soil properties, although these differences were not consistently statistically significant (Table 2). The relatively low variability in OG soils data likely reflects a more homogeneous belowground component, even though structural and species heterogeneity are high in the aboveground vegetation. We suspect that, over hundreds of years, OG vegetation has totally colonized forest soils with their roots and associated mycorrhizae, resulting in lower belowground sample variability. This phenomenon was graphically demonstrated in our study of mycorrhizal mat distribution patterns (Griffiths et al. 1996).

We analyzed for spatial variability according to a geostatistical approach with data collected along transects with both 1- and 5-m sampling resolutions. We hypothesized that, because many were 400–600 years old, the OG trees would imprint on the soil an autocorrelation lag of approximately 15 m, which is the typical crown width for these trees. In addition, we expected that much smaller lags would be found in the harvested stands with smaller, younger trees. An autocorrelation analysis at the 5-m scale showed no consistent autocorrelations for any of the variables except soil temperature. At the 1-m scale, autocorrelations at lags of 1–2 m were observed for individual transects for some variables; however, these trends were not consistent, and no trends by stand age were observed (data not shown). Stand age, therefore, did not appear to consistently affect spatial patterns of belowground processes as we had originally hypothesized. This suggests that, on these scales and regardless of age, individual trees did not impart consistent spatial patterns on forest soil properties.

Aspect and elevation effects

Relatively large climatic gradients are generated by differences in elevation and aspect across the Andrews Experimental Forest. One of our site-selection criteria was to maximize climate extremes to optimize potential higher level ANOVA interactions between climate (different location types) and stand age (Table 3). An equal number of treatment types was represented in each of the three location types. The multivariate ANOVA showed no second-level interactions by stand age and location but did show location differences independent of stand age. Not surprisingly, we found location differences in air and soil temperatures during the November sampling period, with the lowest temperatures in the north-facing, high-elevation sites. The higher SOM at the higher elevation, north-facing sites was expected, because of the cooler conditions typically found in

these soils (Parton et al. 1987). Griffiths observed similar patterns between SOM and elevation in an earlier study in which soils were collected from a synoptic grid of 184 sites throughout Andrews Experimental Forest (unpublished data). Considering reports of climate effects on terrestrial C stores (Schlesinger 1984; Schimel et al. 1994), we anticipated that litter depth would also increase with elevation, but that trend was not observed.

Conclusions

Many soil properties were influenced by harvesting old-growth forests. Recently harvested stands had significantly higher denitrification rates and lower litter depth, forest floor respiration, and ectomycorrhizal mat coverage than old-growth forests. With increasing time after harvest, variables tended to shift closer to old-growth values, with most variables in 40YS showing no significant differences from those in OG. This suggests that, with the exception of ectomycorrhizal mat distribution patterns, the soil properties that we studied returned to essentially old-growth values within 40 years after clear-cutting.

Sample variability in OG soils was typically lower than in recent clear-cut stands, suggesting greater belowground homogeneity in OG soils. This relative homogeneity did not, however, translate into consistent spatial patterns that resulted in significant autocorrelations at the scales studied. The ANOVA showed no higher level interactions between stand age and location; however, many variables were influenced by location (elevation and aspect) and, thus, climate.

Results of this study may serve to guide forest managers concerned with the long-term effects of clear-cutting on the properties of the forest floor and mineral soil. No significant changes were observed in SOM or labile C at any time after clear-cutting. Nonetheless, litter depth and field respiration data suggest that net primary productivity may not have recovered fully, even after 40 years. Although the differences between OG and 40YS values were not significant, the trends over time were consistent. Low denitrification potentials after 40 years may reflect the establishment of an effective belowground grid of roots and mycorrhizal fungi that prevent the loss of mineralized N from the forest floor.

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