An Abstract of the Thesis of

Jeffrey G. Borchers for the degree of Doctor of Philosophy in Forest Science presented on March 1, 1990.

Title: Physical Processes Affecting Soil Biotic and Abiotic Responses to Disturbance in Forest Ecosystems of Southwestern Oregon.

Abstract approved: _____
David A. Perry

The effect of physical factors such as soil structure, bulk density, parent material, and topographic variables on soil C and N dynamics and ectomycorrhizal inoculum potential in forests of southwest Oregon were investigated. In the high-elevation white fir (Abies concolor (Gord. & Glend.) Lindl.) zone, two old poorly-vegetated clearcuts with different soil textures (sandy loam and silt loam) were compared with adjacent uncut areas. Significant differences in soil C and N were not detected at either site, but the site with silt loam soil had 20-25% lower C and N concentrations in several particle size fractions. Compared to adjacent forests, anaerobically mineralizable N (N_{min}) was lower only in the clearcut with sandy loam soil. A larger pool of physically-stabilized but chemically labile N probably sustained N_{min} levels on the clearcut with finer-textured soil. In another investigation on

these sites, Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) seedlings were used to bioassay six soil particle-size fractions for ectomycorrhiza (EM) formation. Six major EM types were found to be heterogeneously distributed among size fractions. Increased colonization by one EM type following mechanical disaggregation of soil from a clearcut indicated propagules had a "clumpy" distribution in soil or had been suppressed by actinomycete activity. A separate investigation in a lower elevation vegetation zone (the mixed evergreen zone) of southwest Oregon compared soil and forest floor C and N in forests and 5-year-old clearcuts that had been broadcast-burned (BB) or hand piled-and-burned (PB). Total C and N, and N_{min} were determined variously in litter, F-layer, 0-5 cm soil, and 5-15 cm soil. In clearcuts, decreases in C and N stored in these layers exceeded amounts typically removed by harvest. BB clearcuts had significantly lower N_{min} levels in the 0-5 cm layer compared to adjacent forests. The disappearance of F layers from BB and PB clearcuts represented the largest loss of N from the layers we sampled. The proportion of N lost from these layers was related by regression to C:N ratios of the two soil layers. This proportion and both C:N ratios were in turn correlated with slope, aspect, and soil bulk density. We incorporated the relationships into a conceptual model depicting a complex topographic influence on N losses following forest disturbance.

Physical Processes Affecting Soil Biotic and Abiotic Responses to Disturbance in Forest Ecosystems of Southwestern Oregon

by

Jeffrey G. Borchers

A Thesis

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I have a feeling
That through the hole in reason's ceiling
We can fly to knowledge
Without ever going to college.

Patrick Kavanagh, Poems

Approved:

Professor of Forest Science in charge of major

Head of Department of Forest Science

Dean of the Graduate School

Date thesis presented March 1, 1990

Acknowledgements

It is one thing to have a thought, but quite another to recognize the school from which it springs. In a sense, each of the people that has influenced the work that is the thesis and the work that is me, are schools of thought. I have attended many, flunked a few, but owe them all:

Among my friends I count the members of my committee: As my major advisor, Dave Perry had the patience of a saint as I tried on thesis topics like neckties until I found a match. He precipitated many brainstorms (the alchemy of it all), said little when most appropriate, and filled my sails in the doldrums. Many thanks to Phil Sollins for his candid appraisals of me and my work, for such lessons are as rare and valuable gems. Dave Myrold dutifully provided detailed (and necessary) attention in reviewing these chapters. Kermit Cromack, Jr. contributed in the planning stages of research conducted in chapter III. Also, thanks to Bob Griffiths for joining this committee at the 11th hour.

Many others aided in the logistics of research. Special thanks are owed to Randy Molina, the blues root man extraordinaire; I profited greatly from his cooperation with Dave Perry's group. While in his labs, I pestered many people for information, especially Mike Castellano, Dan Luoma, Steve Miller, and Dave Janos. In Phil Sollins'

lab Carol Glassman was always ready with practical ideas that so often elude graduate students. In the field, there were many other soil-stained hands besides mine, but Greg Koerper gave most on the dusty Siskiyou trail. Financial support for this research was derived mainly from the Forestry Intensive Research program. Mel Greenup, Tom Atzet, and others with the Siskiyou National Forest were helpful, especially in the initial stages of the work.

I owe much to my friends; they know who they are and made the way more important than the destination. For showing me the Way, I also thank sensei Tsutomu Ohshima. I hope I can pass it on, straight and true.

From my heart, for my heart, I thank my family. The support from my parents was beyond the call of duty. This is your work as much as mine.

Last and most, my wife Susan didn't type this thesis. But without her love, friendship, and partnership there would have been nothing to type. Here's to our future.

Contribution of Authors

Chapter III of this thesis was a large study requiring the input of several individuals. Greg Koerper contributed significantly to planning and conducting field and lab work. Phil Sollins and Kermit Cromack, Jr. were frequently consulted on experimental design and techniques. As my major advisor, Dave Perry was a collaborator in all the research reported herein.

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$$P_j = \sum_{i}^{6} N_{ij} \; / \; \sum_{ij}^{67} N_{ij}$$

where P_j=the proportion of short roots mycorrhizal with type j and N=short roots in i=1,2,..,6 size fractions and of j=1,2,...,6 types. The columns labeled "p" contain significance probability values associated with t-tests of intact and disaggregated soil means.

Physical Processes Affecting Soil Biotic and Abiotic Responses to Disturbance in Forest Ecosystems of Southwestern Oregon

Chapter I.

General Introduction

To study forest ecosystems is to study how they change. Whether it be molecules or landslides, nothing is static within its confines. Still, ecosystem scientists subjectively differentiate among changes that occur at different scales of time and space. When events are perceived to upset ecosystem "stability" or "equilibrium" (usually occurring rapidly over large areas), they are referred to as disturbance. The events may be of natural or human origin, distinctions that are also somewhat arbitrary.

Nevertheless these categories elicit a fundamental question about ecosystem stewardship: How does the disturbance regime imposed on forests by humans compare with "natural" historical patterns of disturbance? The difficulties of this question become apparent if one views the current state of ecosystems (organisms and processes) as an integrated record of past disturbances and other more subtle events. This natural history is in many cases extremely difficult to reconstruct, but would properly be

the standard by which forest management practices are assessed.

The order imposed by forest managers has brought great success at increasing certain ecosystem outputs such as wood products. However, unpredictable "natural" events (fire, insects, pathogens, erosion) may still confound our wishes for sustainable ecosystem productivity. Sustaining "what", and at what level, further complicate the issue. Ideally, the effects of forest management practices on sustainability can be assessed only by comparing planned and unplanned future events with historical patterns of disturbance. In practice, however, research focuses on several key ecosystem processes and organisms that are most affected by disturbance. In a sense, Liebig's "law" of the minimum (Odum 1971) serves as Occam's razor to simplify ecosystem studies.

Frequently, processes and organisms that limit ecosystem recovery following disturbance are linked to the soil. One branch of ecosystem ecology has traditionally focused on the flow of matter and energy (McIntosh 1985), i.e., the abiotic or process approach. But organisms mediate much of that flow and can greatly alter patterns of nutrient cycling and energy flow, e.g., symbiotic fungi that form mycorrhizae (Richards 1987). For this reason a biotic approach to explaining ecosystem behavior is often

simpler. But neither element in this "dual organization" of ecosystems should be ignored (O'Neill et al. 1986).

The research described in this thesis takes both a biotic and abiotic approach to disturbance ecology. It examines how selected nutrient cycling processes and soil organisms respond to forest harvesting and prescribed burning. The work was conducted in southwest Oregon on the Siskiyou National Forest. Its rugged, deeply dissected terrain is geologically and floristically complex with hot, dry summers and cool, wet winters (Franklin and Dyrness 1973). The uniquely variable soils and geology of the region prompted a special attention to physical attributes of sites, particularly soil structure.

Chapter II examines soil C and N dynamics in a case study of two, old poorly-vegetated clearcuts. Forest ecosystem production is frequently limited by the availability of N (Gosz 1981, Johnson et al. 1982), which may be a function of litter and soil organic matter decomposition (Waring and Schlesinger 1985). Decomposition is in turn regulated by numerous attributes of the substrate and its environment, in particular the size distribution of soil particles. These particles form organo-mineral complexes (Paul 1984) that may ultimately affect organic matter decomposition rates and plant available N.

Chapter III also deals with C and N cycling, but focuses on the effect of prescribed burning on young clearcuts. A concern for sustaining long-term site productivity (Ford 1983) prompted this study of standard harvest and site preparation practices. Although short-term increases in productivity from prescribed burning are possible (Johansen 1975), so are significant N losses by convection, volatilization, erosion, and leaching (Dunn and DeBano 1977; Raison et al. 1985; Sollins et al. 1981).

Chapter IV takes a habitat approach to investigating ectomycorrhizal fungi in the same locale described in chapter II. Forest harvesting and site preparation usually have unpredictable effects on ectomycorrhiza formation and tree seedling performance. In extreme environments, ectomycorrhiza formation may limit both performance and survival of regenerating tree seedlings (Amaranthus and Perry 1987; Parke et al. 1984). But other studies have shown that disturbance does not always have negative effects (Perry et al. 1987). Our knowledge of the mechanisms contributing to this variability is quite limited, especially below ground where tree and fungus life cycles intercept. This study was a first approximation to describing the soil as habitat for ectomycorrhizal fungi. As with plant ecology, such a description is a necessary prelude to understanding how organisms interact with each

other and their environment. The approach taken was to bioassay various soil habitats for ectomycorrhizal fungi using a range of particle size fractions. Previous investigations using this approach have yielded information about the spatial distribution of microorganisms, enzymes, and nutrients in soil (Hattori 1988; Mateos and Carcedo 1985; Christensen 1986).

Chapter II.

Carbon and Nitrogen Dynamics in Particle Size Fractions of Forest Soils from Southwest Oregon Clearcuts

Introduction

Sustained productivity of managed forest ecosystems depends to a great extent on the maintenance of soil fertility under various harvesting and site preparation regimes (Ballard 1978, Glass 1976, Keeves 1966). Ecosystem production is frequently limited by N availability (Gosz 1981, Johnson et al. 1982), which may be a function of litter and soil organic matter (SOM) decomposition (Waring and Schlesinger 1985). Decomposition is regulated by numerous physical and chemical attributes of the substrate and its environment. For example, Paul (1984) emphasized soil organo-mineral complexes in regulating C and N dynamics.

Few studies have examined the role of organo-mineral complexes in forest soil C and N dynamics. Bruckert and Kilbertus (1980) used physical and chemical fractionation to characterize forms of humus and organo-mineral complexes in forest and steppe soils. Young and Spycher (1979) studied the distribution of C and N in density and size fractions of forest and cultivated soils. Sollins et al. (1984) found linear relationships between C:N ratio and %

mineralizable N in density fractions of several soil types, but not in unfractionated soils.

Our objective was a case study comparison of two forest ecosystems where the major difference was parent material and soil texture. We hypothesized that the textural difference influences long-term C and N turnover following disturbance. We assessed the status of C and N among particle size fractions of soils from old, poorly vegetated clearcuts and their adjacent forests. Analysis of particle size fractions can distinguish the labile portion of total SOM that is a "more sensitive and early indicator of management effects on soil fertility" (Dalal and Mayer 1987). Another early indicator of management effects, anaerobically mineralizable N, indexes N availability to plants (Powers 1980).

Methods and Materials

Site Characteristics

The rugged, deeply dissected terrain of southwest Oregon is geologically and floristically complex with hot, dry summers and cool, wet winters (Franklin and Dyrness 1973). We selected two sites for this study, each consisting of a clearcut paired with an adjacent forest (Table II-1). The sites were similar in many respects, but occurred on different geological substrates. The first (Cedar Camp), has coarse-textured soil formed from quartz diorite, whereas the second (Holcomb Peak) has finer-textured soil derived from metavolcanic rocks (Ramp 1979). The Cedar Camp clearcut is dominated by annual grasses with a few scattered shrubs, and several attempts at forest regeneration have failed. Woody plants represent a larger component of the clearcut vegetation at Holcomb Peak, but a large portion remain understocked with tree seedlings. Soils from both clearcuts have lost most large aggregates (2.0-9.5 mm) since harvest (Borchers and Perry 1990).

Soil and Litter Sampling

Five sampling points were established at 15-m intervals along each member of a pair of randomly located, parallel transects in each clearcut. Sample spacing in forests was the same, but transects were shaped into an

irregular grid because of limited area. Soils were sampled twice, in June of 1987 and 1988. Two samples were collected 3 m upslope and downslope from each point to a 15-cm depth. Soil was transferred to a 5°C cooler within 48h. For both samplings, pairs from each point were composited yielding 10 replications per unit (n=10). For the fractionation procedure, soil (1988 sampling) from adjacent sampling points was further composited to yield five replications per unit (n=5).

Soil Fractionation

The procedure for quantitatively obtaining five particle size fractions of soil was modified from Anderson et al. (1981). Chilled tap water (2° C) was added to approximately 150 g of <2 mm soil (1988 sampling, n=5) to make a 200 ml volume. The soil-water mixtures were then placed on ice and sonicated (200 W, 20 MHz) for 12 min. (=720 J/ml) using a Heat Systems-Ultrasonics W-370. The sand fraction (>53 um) was separated by wet-sieving and contained most of the low density organic debris. Coarse silt (5-53 um) and fine silt (2-5 um) fractions were separated by repeated sedimentation and decantation (12 cycles), then dried at 105°C. The remaining slurry of coarse clay (0.2-2 um) and fine clay (<0.2 um) was concentrated by repeated sedimentation and decantation (12 cycles) after adding $CaCl_2$ to make a 0.2 M solution.

(During sedimentation only minute quantities of floating organic particles were detected). Clays were then dispersed with NaCl (0.7 M) and centrifuged to separate the coarse clay fraction. Slurries of coarse and fine clay were dried at 70°C. We assumed that losses of C and N in solution during particle size separation were small relative to total amounts. Average recovery of starting mass for all soils exceeded 98%.

Soil Chemical and Physical Analyses

Because recovery of particle size fractions was quantitative, their relative distribution in soil was determined by weighing oven-dried material. To determine soil C and N concentrations, subsamples of fractions (1988 sampling, n=5) and <2mm unfractionated soil (1987 sampling, n=10) were ground to pass a 40-mesh sieve. Carbon concentration was obtained by combustion in an induction furnace (Leco WR-12 Automatic Carbon Analyzer). Nitrogen was determined by automated colorimetry (Alpchem RFA-300) on semimicro-Kjeldahl digests (350°C).

An anaerobic index of N availability in unfractionated soil was obtained by modifying the procedure of Waring and Bremner (1964a). Triplicate 10-g soil subsamples (n=10) were placed in 30 ml dH_2O. One sample was used to determine initial NH_4^+ and NO_3^- contents. Another was sonicated (3 min. @ 100 W = 600 J/ml) to disrupt soil

aggregates. This sample and the third, unsonicated sample were then incubated for 7 days at 40°C. Net mineralizable N (N_{min}) was calculated as the difference between the initial 1N KCl-extractable NH_4^+ and the amount extracted following incubation.

Statistical Analyses and Variables

Data were subjected to analysis of variance (ANOVA) for pairwise comparisons of forests and clearcuts and to compare sonication treatment effects on N_{min}. Correlations among variables were examined with a Pearson correlation matrix. All analyses were performed using SAS (SAS Institute, Inc. 1985).

C and N in particle size fractions were expressed as (1) concentration (g C or N in fraction/g dry wt. fraction X 100), and (2) relative concentration (g C or N in fraction/g dry wt. whole soil X 100). Relative concentrations were calculated using measured concentrations and particle size distributions.

Results

Particle size distribution

Cedar Camp and Holcomb Peak soils differed greatly in texture, especially the relative proportions of sand and silt fractions (Table II-2). Whereas Cedar Camp soil had nearly 70% sand, Holcomb Peak sand content was half that. The reverse was true for the other size fractions: Holcomb Peak soils had about twice the amount of coarse silt, fine silt, coarse clay, and fine clay. Total clay content for Cedar Camp and Holcomb Peak soils averaged 7.0% and 14.3%, respectively.

Carbon and nitrogen in size fractions

Generally, C and N concentrations increased with decreasing particle size, except at Cedar Camp where C values in fine silt and clay fractions were about the same (Table II-2). Relative to sand fractions, the fine clay fractions were enriched in C and N by a factor of ten.

There were large differences in C concentrations of size fractions between Holcomb Peak forest and clearcut (Table II-2). Carbon concentrations in silt and clay fractions were 15-27% lower in the clearcut than in the forest, but at Cedar Camp only sand fraction C concentration differed by as much. Silt and clay fractions

from the Holcomb Peak clearcut also had lower average N concentrations than the forest, but only fine silt was significantly different (-23%; p=0.084). At Cedar Camp the data suggested higher N concentrations in several of the fractions from clearcuts, but only fine clay differed significantly with a 10% increase (p=0.059).

The relative contribution of each size fraction to amounts and differences in whole soil C and N was assessed by examining relative concentrations (Fig. II-1a,b,c,d). (The use of relative concentration is similar to expressing C and N as a distribution among fractions, but values have been indexed to whole soil C and N concentrations. This allows comparison of fractions between sites having widely differing whole soil C and N concentrations). At both sites the largest proportion of the whole soil C was contained in the coarse silt fraction, nevertheless clay fractions made the greatest contribution to whole soil C differences between forests and clearcuts. Also important were the sand fraction at Cedar Camp and possibly silt fractions at Holcomb Peak. Most of the whole soil N of both sites was contained in coarse silt and coarse clay, but clay fractions contributed most to differences between forests and clearcuts. However, at Cedar Camp there was less certainty with the fine clay N difference (p=0.111).

C:N ratios generally were lower in smaller particle size classes and were little changed between clearcuts and

forest pairs (Table II-2). The major exception was the Cedar Camp clearcut where sand fraction C depletion resulted in a lower C:N ratio.

Whole soil carbon and nitrogen

No significant difference in whole soil C or N concentrations associated with clearcutting was detected by analysis of variance in a randomized block design. Clearcut and forest whole soil C and N concentrations also did not differ when compared by site (Table II-2).

Mineralizable nitrogen

Anaerobic incubations of unsonicated soil from forest and clearcut at Holcomb Peak produced similar N_{min} levels, 53.1 and 48.9 mg N/kg, respectively ($p=0.383$; Fig. II-2). However, N_{min} levels at the Cedar Camp clearcut were 38% lower than in the adjacent forest ($p=0.044$), where the concentration was 55.3 mg N/kg. With sonicated soil, N_{min} did not differ between forest and clearcut at either site ($p=0.648$ and $p=0.323$ for Cedar Camp and Holcomb Peak, respectively). However, the sonication response was nearly twice as large at Holcomb Peak than at Cedar Camp.

The proportions of whole soil N that were mineralized in all incubations ranged from 1.2% to 4.3% (Table II-3). With unsonicated soil the proportion was lower at Holcomb

Peak than at Cedar Camp, but the reverse was true with sonicated soil.

Sonication significantly altered mineralizable N correlations with C:N ratio and C and N concentrations in particle size fractions (Table II-4; Fig. II-3a,b). In Holcomb Peak soil, significant correlations ($p<0.10$) of N_{min} (unsonicated) and dN_{min} (where $dN_{min}=N_{min}$(sonicated)-N_{min}(unsonicated) vs. C and N concentrations were generally restricted to fractions smaller than sand (Table II-4; Fig. II-3b). However, dN_{min} correlations were much stronger. N_{min} (unsonicated) and dN_{min} were also strongly correlated with Holcomb Peak soil ($r=+0.79$; $p<0.001$) (Fig. II-4), indicating that the magnitude of the sonication response, dN_{min}, was directly related to the amount of N mineralized without sonication.

At Cedar Camp, N_{min} (unsonicated) correlated positively with C and N concentrations of sand and C:N ratio of fine clay (Table II-4; Fig. II-3a). Unlike Holcomb Peak, correlations were not strengthened by sonication, but the pattern of size fractions involved in significant correlations were noticeably altered. The range of N_{min} (unsonicated) and dN_{min} values at Cedar Camp were similar to Holcomb Peak, but poorly correlated ($r=-0.22$; $p=0.344$) (Fig. II-4).

Discussion

C and N concentrations in Cedar Camp and Holcomb Peak soils peaked in the fine clay fraction, a trend sometimes seen in soils with low clay contents (See Dalal and Mayer 1986, Turchenek and Oades 1979, and Young and Spycher 1979). Soils low in clays generally have fewer total exchange sites, hence clay fractions may be more completely saturated with organic matter.

The significantly different C and N concentrations in various particle size fractions from clearcuts and forests were not apparent in the analysis of whole soil. This underscores the sensitivity of the particle size fractionation method in detecting changes in labile soil fractions (Dalal and Mayer 1987). Tiessen and Stewart (1983) found that fine clay organic matter and sand fraction "floatable" materials had lower C and N concentrations than other fractions following long periods of cultivation. Hence they were regarded as more labile and important to soil fertility. From this perspective, Cedar Camp sand fraction and Holcomb Peak silts and clays contribute most to fertility. But the pattern of relative C and N concentrations reveals a different picture. Differences in C and N concentrations of the clay fractions from clearcuts and forests were generally larger than in silt fractions, indicating that the relative quantity of a

substrate is just as important as its lability when considering soil fertility.

Mineralizable N as measured by anaerobic incubations reflects microbial biomass N in some instances (Myrold 1987; Paul 1984). It also correlates well with N availability in the field and is useful in predicting potential productivity (Powers 1980). The similar unsonicated N_{min} levels and site indices (Table II-1) in Cedar Camp and Holcomb Peak forests suggest that they have similar productivities.

Significantly lower unsonicated N_{min} levels on the Cedar Camp clearcut may signify a trend toward decreased productivity. Still, this level of mineralizable N was high relative to other studies (Powers 1980; Radwan and Shumway 1984; Pilz and Perry 1984; Schoenberger and Perry 1982) and not in the range of N deficiency (Powers 1980).

The significance of greater N mineralization following sonication (dN_{min}) rests in the interpretation that it represents a discrete pool of physically stabilized, but otherwise labile, N. Similar increases in mineralization or respiration have been observed after sieving (Waring and Bremner 1964b) and grinding (Craswell and Waring 1972, Elliott 1986, Powlson 1980). Physical protection of labile substrates (e.g., by soil aggregation) may create a pool of organic matter having an intermediate turnover time

(Jenkinson and Rayner 1977) that dampens fluctuations in nutrient availability after disturbance (Anderson 1979, Anderson and Paul 1984).

The smaller sonication response (dN_{min}) of Cedar Camp soil relative to Holcomb Peak soil (Fig. II-2) can be attributed to either greater chemical recalcitrance of physically stabilized N or smaller quantities of stabilized, but equally labile N. To some degree the substrate is more chemically recalcitrant at Cedar Camp, because smaller proportions of whole soil N were mineralized after sonication (Table II-3). But this small effect cannot nearly account for the large difference in sonication response between the two sites. Hence, the amount of physically stabilized N is probably greater at Holcomb Peak.

This large contrast in quantities of physically stabilized N is probably a result of greater silt and clay contents of Holcomb Peak soil. The relationship between unsonicated N_{min} and dN_{min} (Fig. II-4) suggests that Cedar Camp soil has a constant amount of physically protected, mineralizable N regardless of the quantities of unsonicated N_{min}. This constant may represent a maximum level of physical protection possible given the low silt and clay contents of this soil.

At Holcomb Peak the magnitude of the physically

protected N pool (dN_{min}) does not appear to be limited by low silt or clay contents, because dN_{min} varies widely and in direct proportion to N_{min} (unsonicated). The correlations of dN_{min} and N_{min} (unsonicated) with C and N in silt and clay fractions suggests that N was mineralized from similar particle size fractions regardless of sonication treatment, i.e., the quantity rather than the source of substrate was most affected by sonication. The apparently even distribution of physically protected N across silt and clay fractions from Holcomb Peak parallels the somewhat uniform pattern of post-harvest C and N losses from these fractions.

The foregoing relationships were not evident at Cedar Camp, signifying that soil aggregation plays a lesser role in C and N dynamics there. Low silt and clay contents preclude the formation of significantly large physically stabilized N pools. Similar N_{min} (unsonicated) levels on the Holcomb Peak forest and clearcut are probably sustained at the cost of C and N depletions from silt and clay fractions from the clearcut. Soil from the Cedar Camp clearcut had smaller C and N losses from these size fractions, hence N_{min} (unsonicated) levels were lower in the clearcut than in the forest.

Figure II-1. Relative concentrations of C and N in particle size fractions from (a,b) Cedar Camp and (c,d) Holcomb Peak forests and clearcuts. Lines above bars represent one standard error and values above bars are probabilities from t-tests comparing forest and clearcut.

Figure II-1a

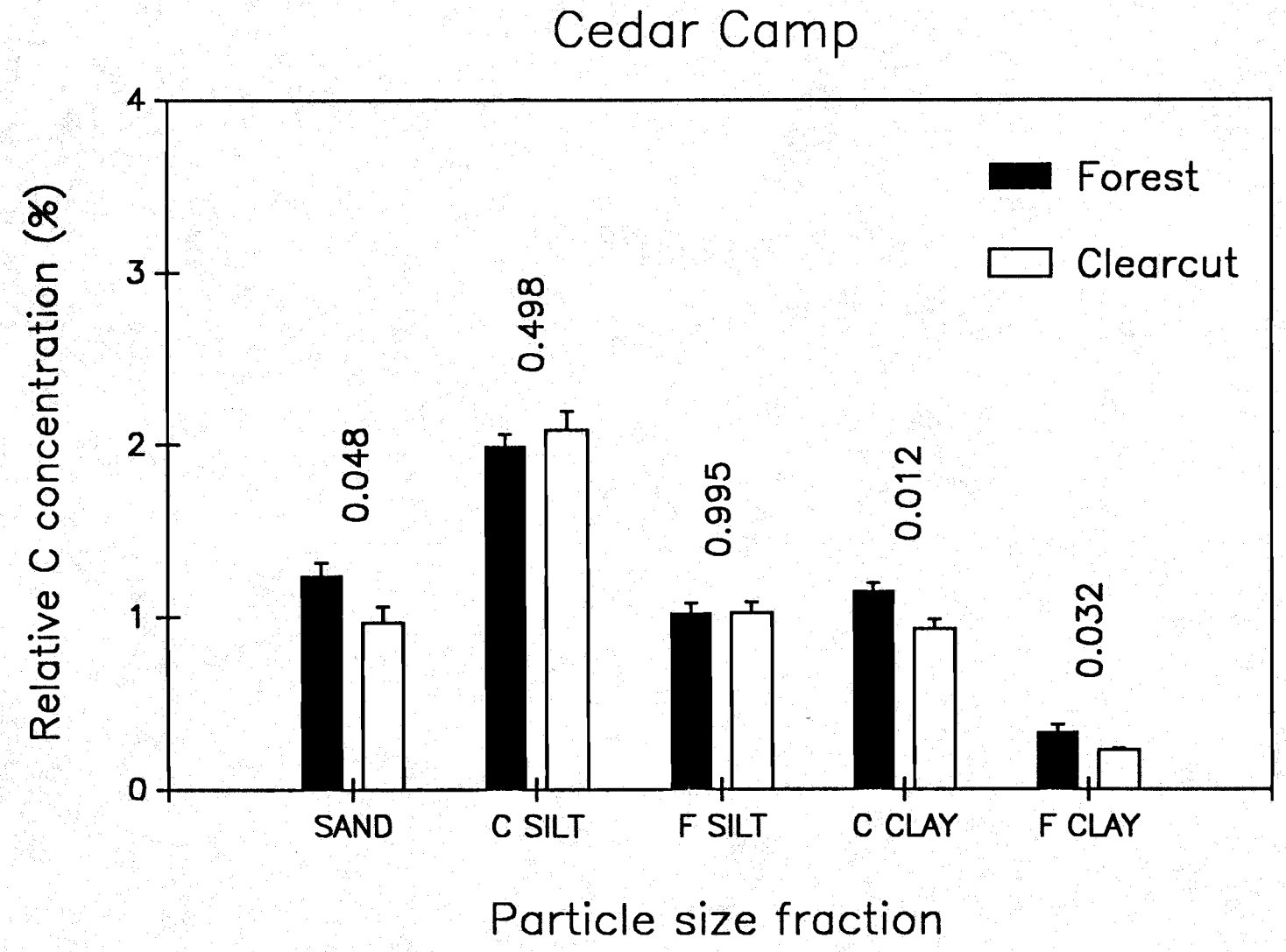
Cedar Camp
Relative C concentration (%)
4
3
2
1
0
Forest
Clearcut
0.048
0.498
0.995
0.012
0.032
SAND
C SILT
F SILT
C CLAY
F CLAY
Particle size fraction

Figure II-1b

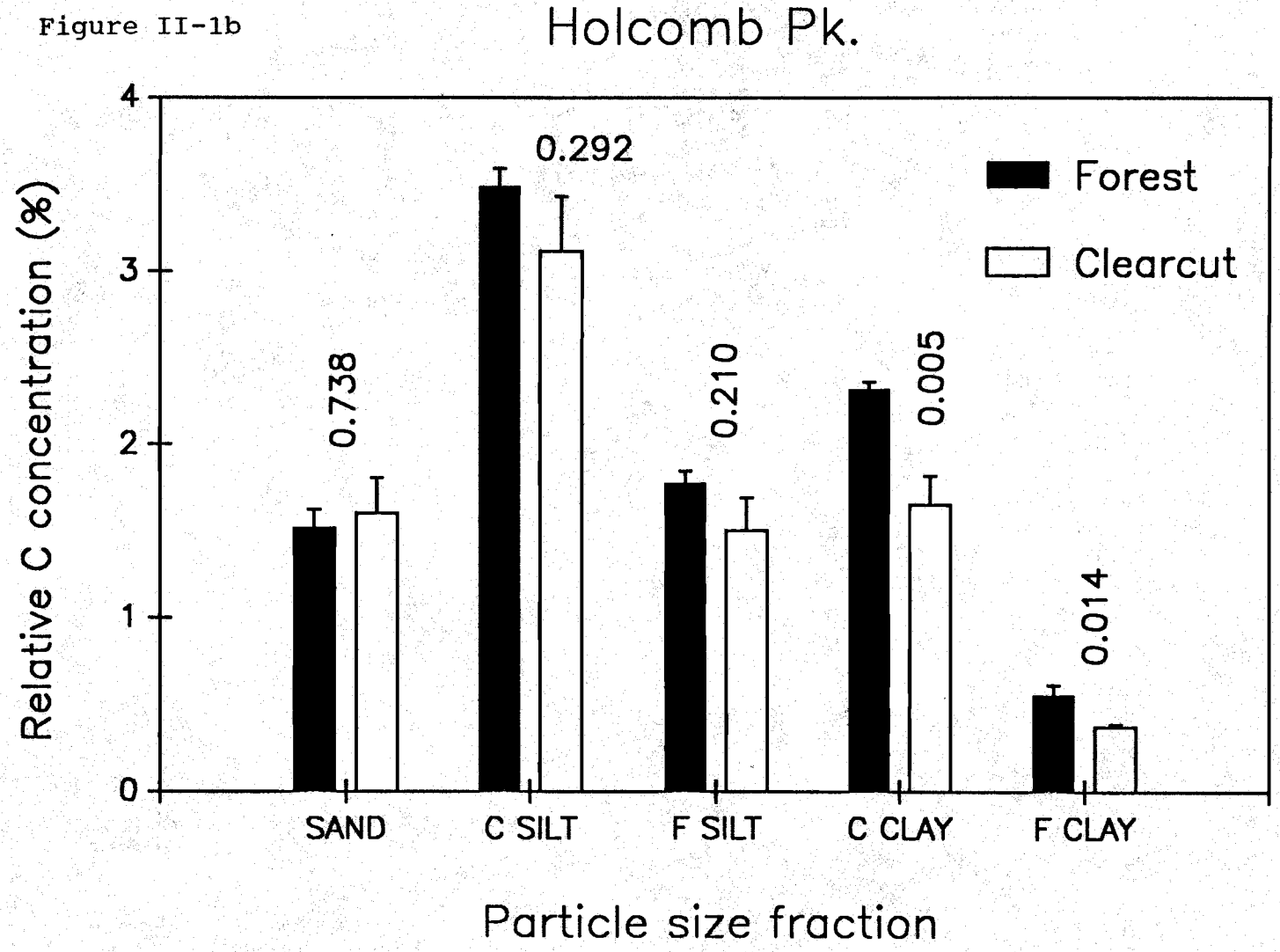
Holcomb Pk.
Relative C concentration (%)
4
3
2
1
0
0.738
0.292
0.210
0.005
0.014
Forest
Clearcut
SAND
C SILT
F SILT
C CLAY
F CLAY
Particle size fraction

Figure II-1c

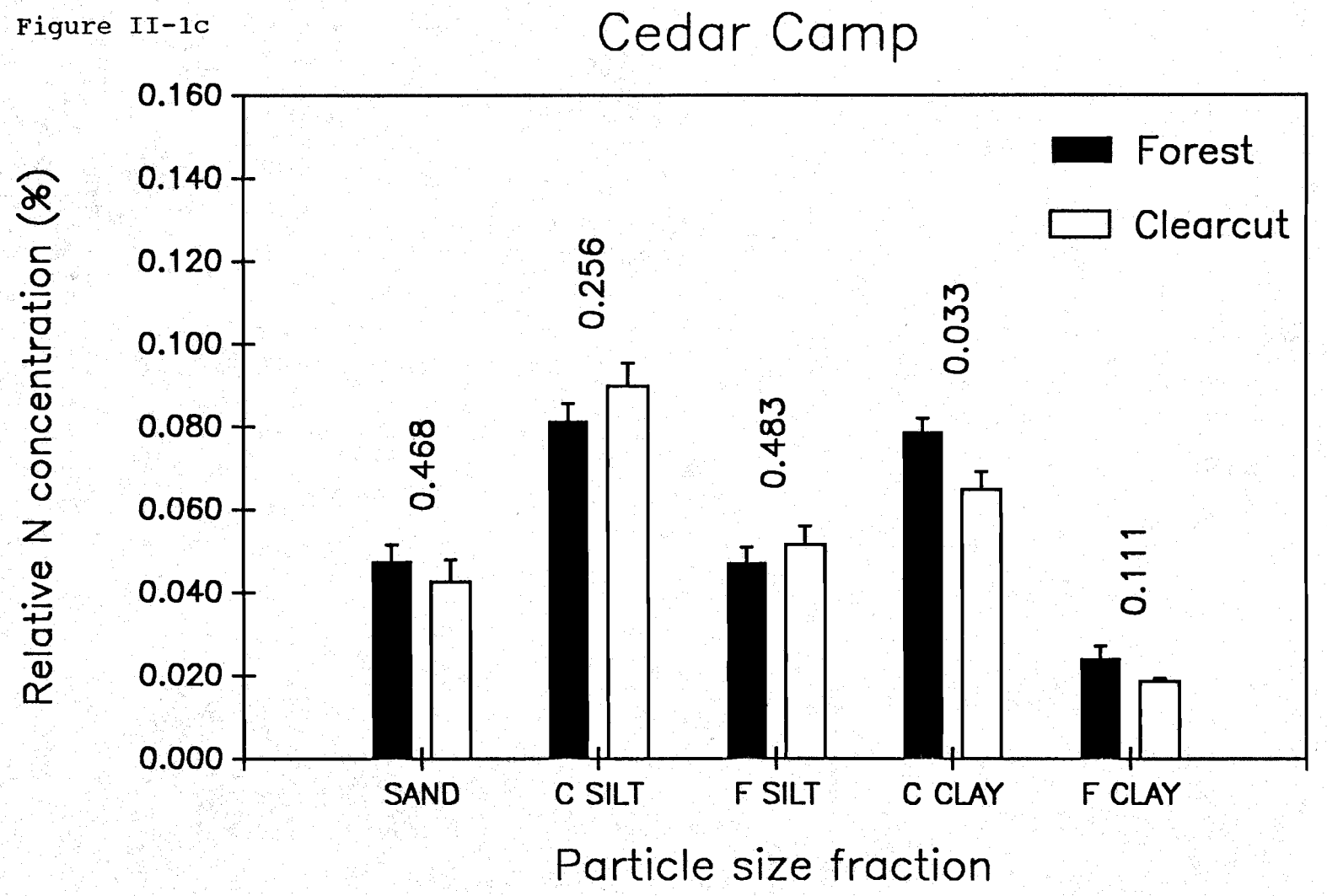
Cedar Camp
Forest
Clearcut
Relative N concentration (%)
0.160
0.140
0.120
0.100
0.080
0.060
0.040
0.020
0.000
0.468
0.256
0.483
0.033
0.111
SAND
C SILT
F SILT
C CLAY
F CLAY
Particle size fraction

Figure II-1d

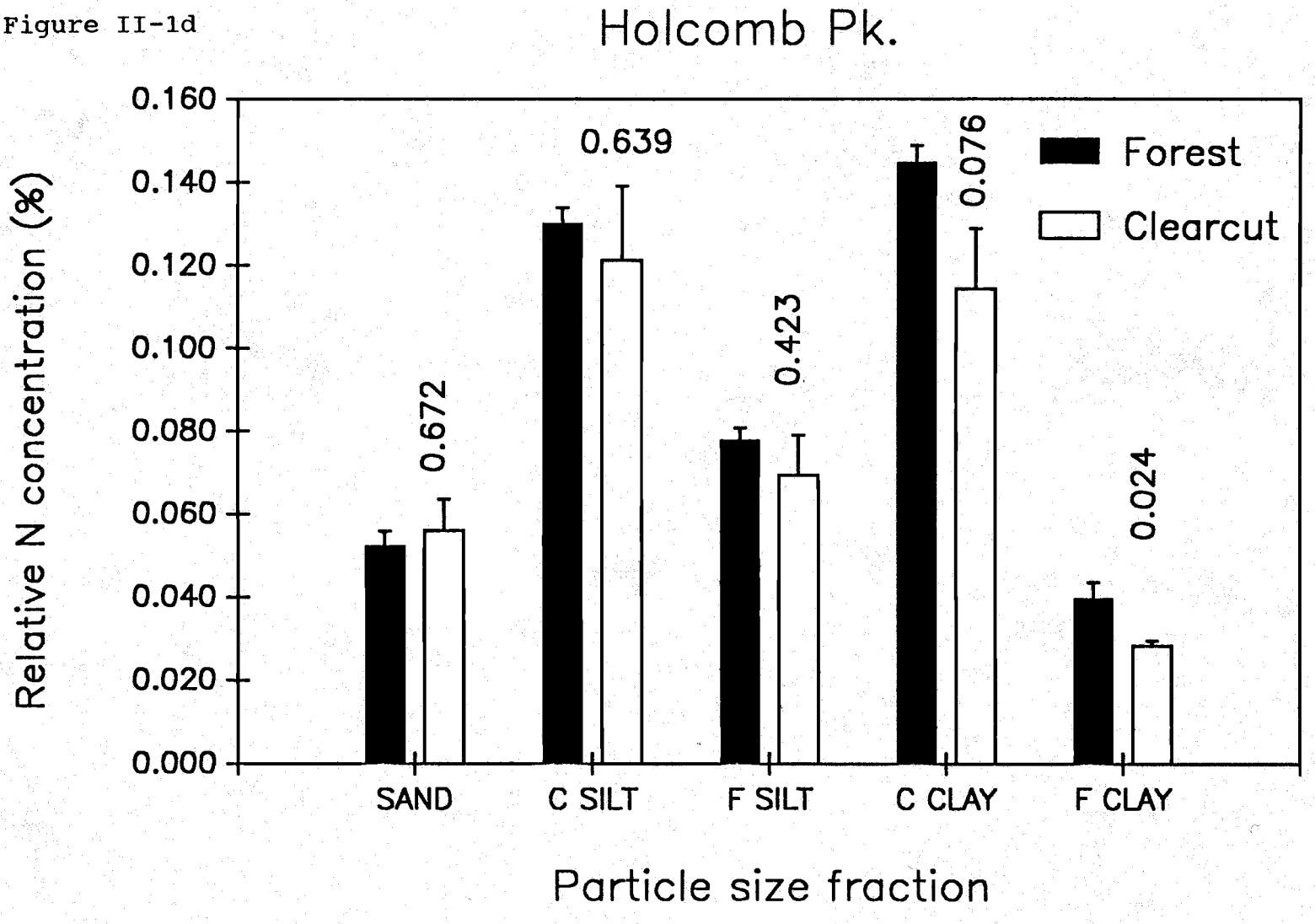
Holcomb Pk.
Relative N concentration (%)
0.160
0.140
0.120
0.100
0.080
0.060
0.040
0.020
0.000
0.672
0.639
0.423
0.076
0.024
Forest
Clearcut
SAND
C SILT
F SILT
C CLAY
F CLAY
Particle size fraction

Figure II-2. Net N mineralized with and without sonication in forest and clearcut soil from Cedar Camp and Holcomb Peak. Lines above bars represent one standard error and values above bars are significance probability levels from t-tests comparing sonication treatments.

Figure II-2

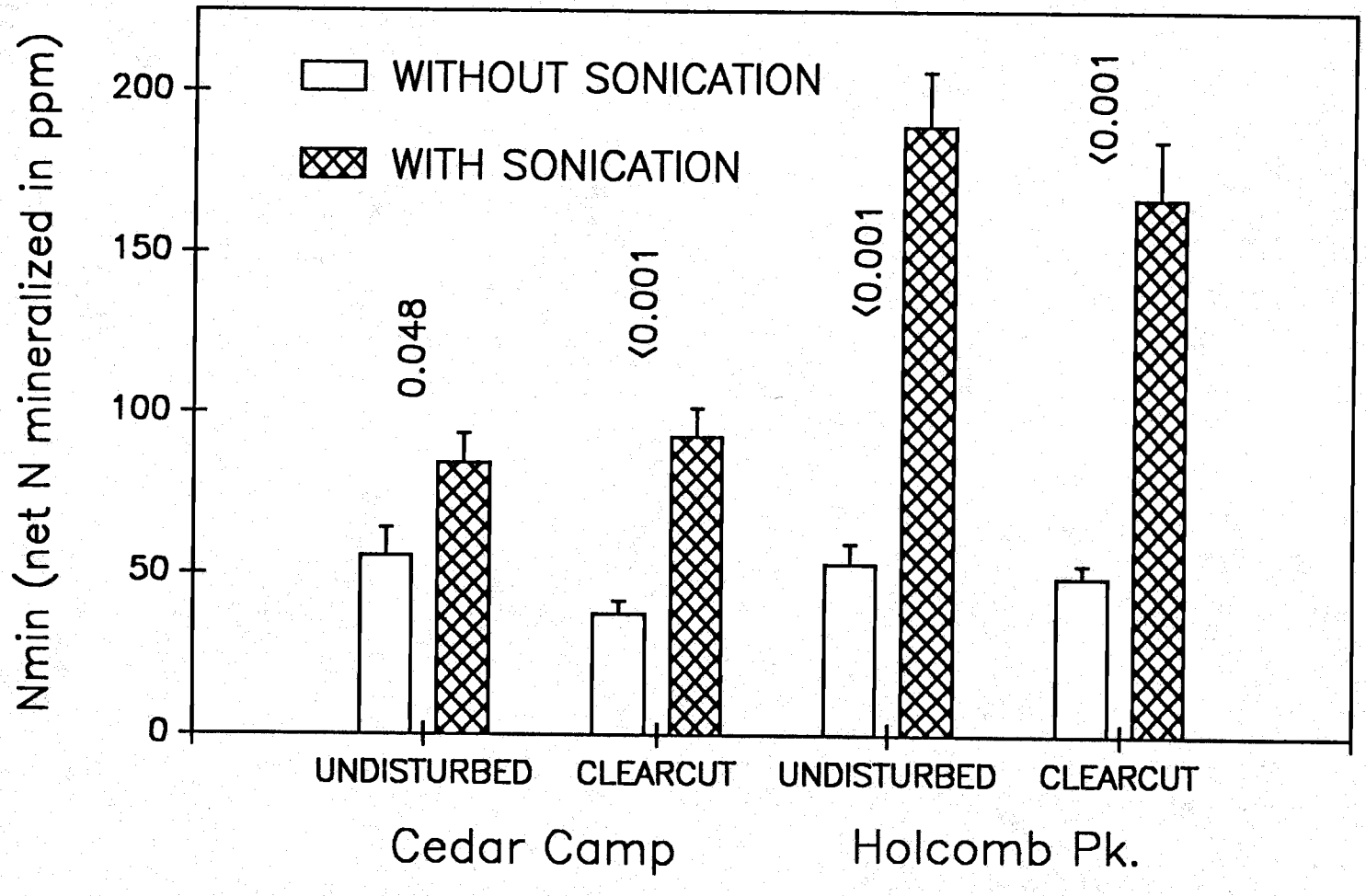
Nmin (net N mineralized in ppm)
200
150
100
50
0
WITHOUT SONICATION
WITH SONICATION
0.048
<0.001
<0.001
<0.001
UNDISTURBED
CLEARCUT
UNDISTURBED
CLEARCUT
Cedar Camp
Holcomb Pk.

Figure II-3. Scatter plots of coefficients obtained by two correlation analyses: dN_{min} (y axis) and unsonicated N_{min} (x axis) vs. C and N concentrations and C:N ratios in particle size fractions. We define dN_{min} as N_{min}(sonicated)-N_{min}(unsonicated). 1=sand; 2=coarse silt; 3=fine silt; 4=coarse clay; 5=fine clay; C=%C; N=%N; CN=C:N ratio. (a) Cedar Camp, (b) Holcomb Peak.

Figure II-3a

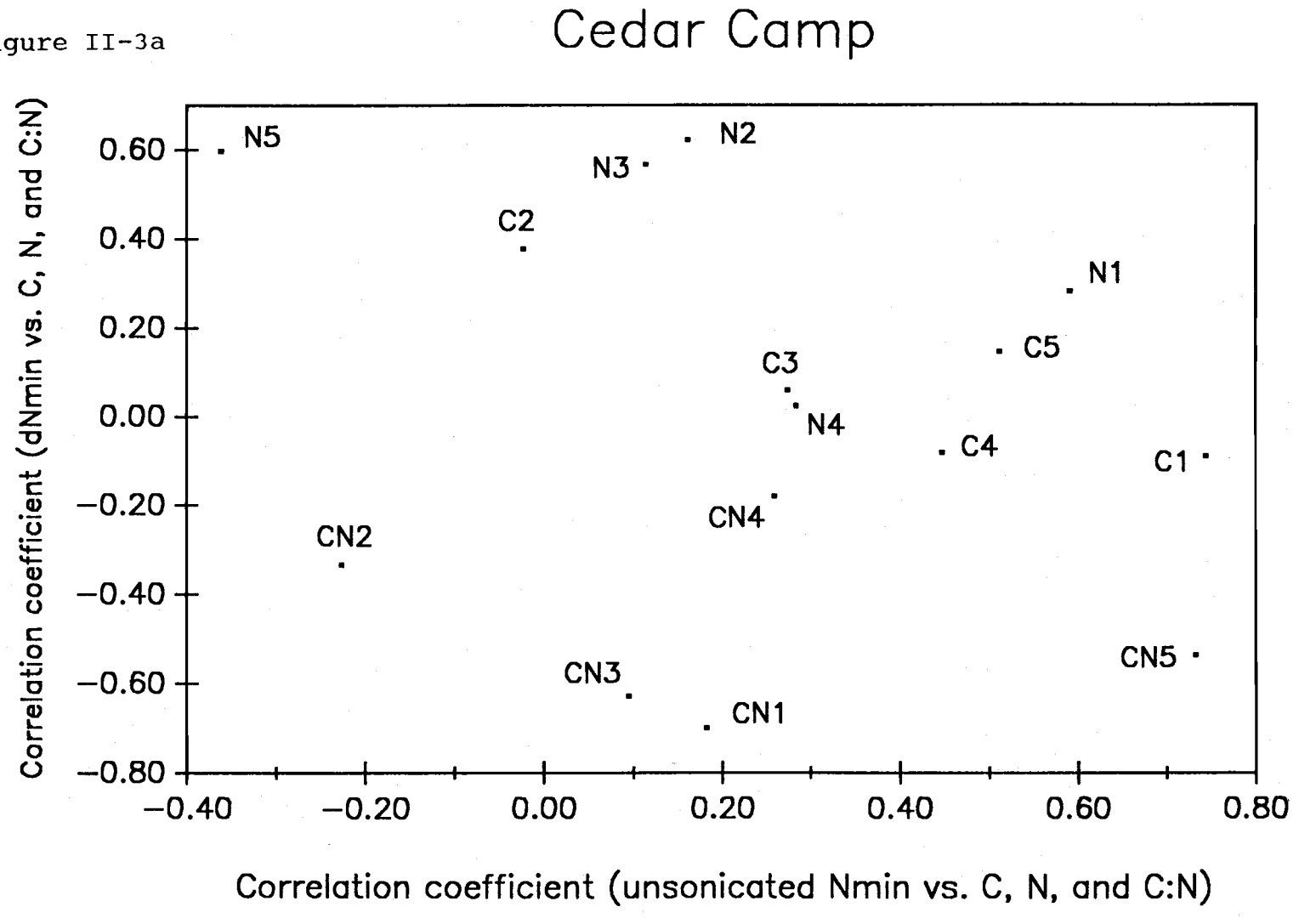
Cedar Camp
Correlation coefficient (dNmin vs. C, N, and C:N)
0.60
0.40
0.20
0.00
−0.20
−0.40
−0.60
−0.80
N5
N2
N3
C2
N1
C5
C3
N4
C4
C1
CN4
CN2
CN5
CN3
CN1
−0.40
−0.20
0.00
0.20
0.40
0.60
0.80
Correlation coefficient (unsonicated Nmin vs. C, N, and C:N)

Figure II-3b

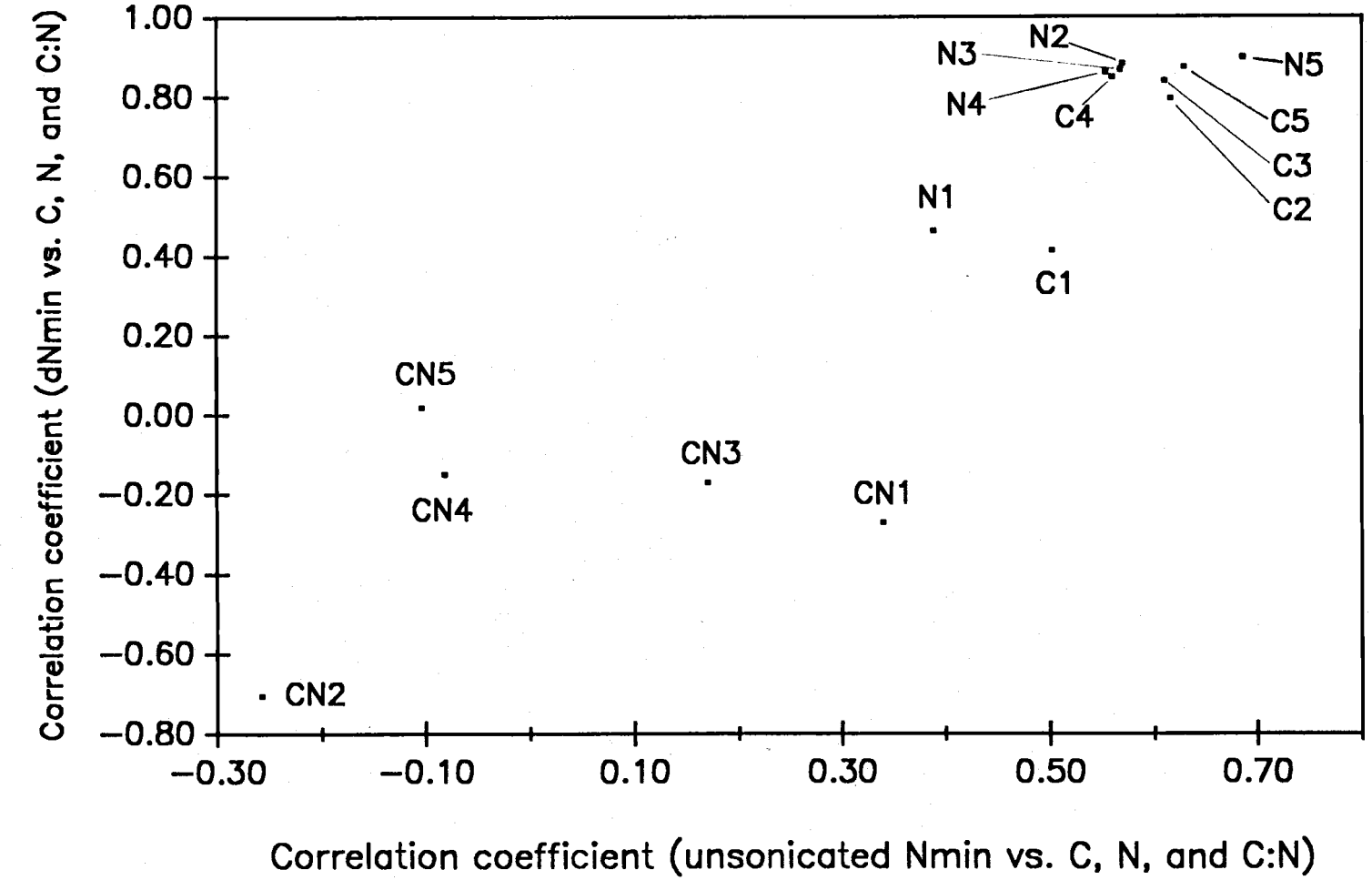
Holcomb Pk.
Correlation coefficient (dNmin vs. C, N, and C:N)
1.00
0.80
0.60
0.40
0.20
0.00
−0.20
−0.40
−0.60
−0.80
−0.30
−0.10
0.10
0.30
0.50
0.70
Correlation coefficient (unsonicated Nmin vs. C, N, and C:N)
N2
N3
N4
N5
C4
C5
C3
C2
N1
C1
CN5
CN3
CN1
CN4
CN2

Figure II-4. Scatter plot of dN_{min} (sonicated N_{min} - unsonicated N_{min}) vs. unsonicated N_{min} for sample values from clearcut and forest at Cedar Camp and Holcomb Peak.

Figure II-4

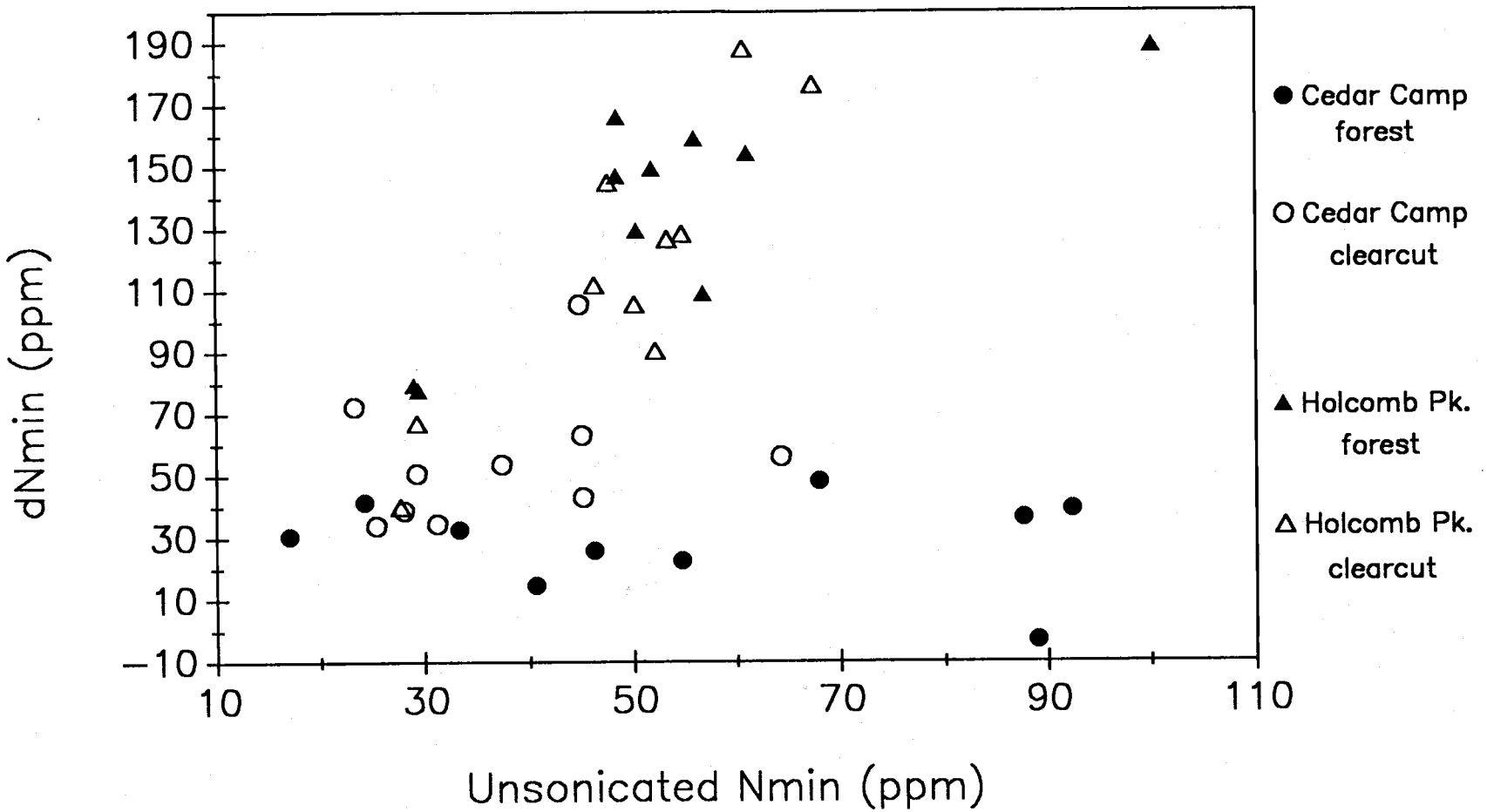
190
170
150
130
110
90
70
50
30
10
−10
dNmin (ppm)
10
30
50
70
90
110
Unsonicated Nmin (ppm)
Cedar Camp forest
Cedar Camp clearcut
Holcomb Pk. forest
Holcomb Pk. clearcut

Table II-1. Characteristics of forest and clearcut study sites (Klamath Geological province, southwest Oregon).

Table II-1

Characteristics	Cedar Camp	Holcomb Peak
Soil parent material	Quartz diorite	Metavolcanic
Soil classification (1)	Loamy-skeletal, mixed Entic Cryumbrept	Loamy-skeletal, mixed, frigid Lithic Xerumbrept
Soil texture	Sandy loam	Silt loam
Elevation, aspect slope	1720 m, SW, 50%	1520 m, SW, 40%
Precipitation	173 cm (map) 165 cm (gauge)	123 cm (map)
Plant association (adjacent, undisturbed forest)	ABCO-ABMAS/SYMO (2)	ABMAS-ABCO/RIBES (2)

(1) Soil Conservation Service, 1983.

(2) ABCO-ABMAS/SYMO, Abies concolor/Abies magnifica var. shastensis/Symphoricarpus mollis; ABMAS-ABCO/RIBES, Abies concolor-Abies magnifica var. shastensis/Ribes spp.

(3) White fir, Abies concolor (Gordon & Glend.)Hildebr.; shasta red fir, Abies magnifica shastensis Lemm.; Douglas-fir, Pseudotsuga menziesii (Mirb.) Franco; Bracken fern, Pteridium auilinium (L.) Kuhn.; red elderberry, Sambucus racemosa L.; greenleaf manzanita, Arctostaphylos patula Greene; currant. Ribes spp., creeping snowberry, Symphoricarpos mollis Nutt.

Table II-1 (continued)

Characteristics	Cedar Camp	Holcomb Peak
Vegetation (3)		
Clearcut	Primarily annual grasses; occasional herbs, bracken fern, red elderberry, greenleaf manzanita	Annual grasses, currant, greanleaf manzanita, creeping snowberry, Douglas-fir
Undisturbed forest	White fir, Douglas-fir, Shasta red fir	Shasta red fir, white fir, Douglas-fir
Site index (ht. in ft. at 100 years)	110	110
Management history		
Clearcut	1969	1971
Broadcast-burned	1975	1972

(1) Soil Conservation Service, 1983.

(2) ABCO-ABMAS/SYMO, Abies concolor/Abies magnifica var. shastensis/Symphoricarpus mollis; ABMAS-ABCO/RIBES, Abies concolor-Abies magnifica var. shastensis/Ribes spp.

(3) White fir, Abies concolor (Gordon & Glend.)Hildebr.; shasta red fir, Abies magnifica shastensis Lemm.; Douglas-fir, Pseudotsuga menziesii (Mirb.) Franco; Bracken fern, Pteridium auilinium (L.) Kuhn.; red elderberry, Sambucus racemosa L.; greenleaf manzanita, Arctostaphylos patula Greene; currant. Ribes spp., creeping snowberry, Symphoricarpos mollis Nutt.

Table II-2. Particle size distribution, C and N concentrations, and C:N ratios of particle size fractions and whole soil from Cedar Camp and Holcomb Peak test sites.

Table II-2

		Cedar Camp					
		Undisturbed	s.e.	Clearcut	s.e.	p (2)	% differencee
Particle size Distribution (%)	Sand	0.68	0.013	0.70	0.013	0.655	2.4
	Coarse silt	0.19	0.008	0.19	0.007	0.556	-2.3
	Fine silt	0.05	0.002	0.05	0.003	0.792	2.9
	Coarse clay	0.06	0.003	0.05	0.002	0.034 **	-13.9
	Fine clay	0.02	0.002	0.01	0.000	0.035 **	-28.4
C concentration (%)	Whole soil	5.0	0.2	5.4	0.4	0.475	6.3
	Whole soil (summation) (1)	5.7	0.1	5.2	0.3	0.114	-9.0
	Sand	1.8	0.1	1.4	0.1	0.047 **	-23.5
	Coarse silt	10.4	0.5	11.2	0.6	0.335	7.7
	Fine silt	21.0	0.7	20.6	0.5	0.671	-1.8
	Coarse clay	19.0	0.7	17.9	0.6	0.259	-5.9
	Fine clay	21.7	0.1	21.1	0.6	0.347	-3.0
N concentration (%)	Whole soil	0.25	0.02	0.27	0.02	0.412	9.7
	Whole soil (summation) (1)	0.28	0.01	0.27	0.02	0.596	-4.2
	Sand	0.07	0.01	0.06	0.01	0.431	-11.9
	Coarse silt	0.42	0.02	0.48	0.03	0.123	14.2
	Fine silt	0.97	0.04	1.04	0.04	0.290	7.1
	Coarse clay	1.30	0.05	1.25	0.05	0.488	-4.0
	Fine clay	1.57	0.03	1.72	0.06	0.059 *	9.6
C:N ratio	Whole soil	20.9	0.7	20.1	0.4	0.306	-3.9
	Whole soil (summation) (1)	20.7	0.5	19.6	0.6	0.219	-4.9
	Sand	26.0	1.3	22.6	0.7	0.048 **	-13.1
	Coarse silt	24.6	0.7	23.2	1.4	0.456	-5.7
	Fine silt	21.7	0.7	19.9	0.5	0.064 *	-8.3
	Coarse clay	14.6	0.3	14.3	0.3	0.507	-1.9
	Fine clay	13.8	0.2	12.2	0.2	0.001 **	-11.4

1. Total concentration of C and N estimated by summing relative concentrations of size fractions (1988 sampling). When these estimates were compared with those obtained from whole soil (1987 sampling), there were significantly different estimates of C concentration in soil from forests at Holcomb Peak ($p=0.081$) and Cedar Camp ($p=0.055$).

2. Probability value from t-test of differences between undisturbed forest and clearcut. Probability values have one asterisk if $0.05>p<0.10$ and two asterisks if $p<0.05$.

Table II-2 (continued)

		Holcomb Peak					
		Undisturbed	s.e.	Clearcut	s.e.	p(2)	% difference
Particle size Distribution (%)	Sand	0.39	0.006	0.31	0.020	0.010 **	-18.4
	Coarse silt	0.35	0.005	0.42	0.008	<0.001 **	19.5
	Fine silt	0.11	0.002	0.13	0.003	0.002 **	15.4
	Coarse clay	0.13	0.003	0.12	0.003	0.073 *	-7.6
	Fine clay	0.02	0.002	0.02	0.001	0.077 *	-20.6
C concentration (%)	Whole soil	8.6	0.4	7.9	0.8	0.456	-8.2
	Whole soil (summation)(1)	9.7	0.3	8.2	0.9	0.163	-14.7
	Sand	4.0	0.3	5.1	0.5	0.113	27.2
	Coarse silt	10.1	0.4	7.5	0.8	0.024 **	-25.4
	Fine silt	16.0	0.4	11.8	1.6	0.032 **	-26.5
	Coarse clay	18.1	0.2	14.0	1.7	0.041 **	-22.7
	Fine clay	24.9	0.5	21.2	1.6	0.060 *	-14.7
N concentration (%)	Whole soil	0.48	0.03	0.40	0.05	0.178	-16.8
	Whole soil (summation)(1)	0.45	0.02	0.39	0.05	0.316	-12.5
	Sand	0.14	0.01	0.18	0.02	0.102	29.1
	Coarse silt	0.38	0.01	0.29	0.05	0.120	-22.0
	Fine silt	0.70	0.02	0.54	0.08	0.084 *	-22.7
	Coarse clay	1.13	0.02	0.97	0.14	0.291	-14.2
	Fine clay	1.78	0.05	1.62	0.13	0.283	-9.1
C:N ratio	Whole soil	18.0	0.5	20.2	0.7	0.026	12.1
	Whole soil (summation)(1)	21.7	0.3	21.5	0.8	0.803	-1.0
	Sand	29.1	1.1	28.6	0.9	0.831	-1.5
	Coarse silt	26.8	0.6	25.6	1.7	0.914	-4.4
	Fine silt	22.8	0.5	21.7	0.4	0.165	-4.9
	Coarse clay	16.0	0.2	14.4	0.5	0.025 **	-10.0
	Fine clay	14.0	0.3	13.1	0.3	0.098 *	-6.1

1. Total concentration of C and N estimated by summing relative concentrations of size fractions (1988 sampling). When these estimates were compared with those obtained from whole soil (1987 sampling), there were significantly different estimates of C concentration in soil from forests at Holcomb Peak ($p=0.081$) and Cedar Camp ($p=0.055$).

2. Probability value from t-test of differences between undisturbed forest and clearcut. Probability values have one asterisk if $0.05>p<0.10$ and two asterisks if $p<0.05$.

Table II-3. Proportion of whole soil N mineralized in anaerobic incubations of soil from Cedar Camp and Holcomb Peak test sites.

Table II-3.

N mineralized as % of total N (1)	Forest				Clearcut			
	Unsonicated		Sonicated		Unsonicated		Sonicated	
	mean	s.e.	mean	s.e	mean	s.e	mean	s.e
Cedar Camp	1.98	0.30	3.01	0.32	1.40	0.15	3.44	0.26
Holcomb Peak	1.20	0.14	4.27	0.40	1.30	0.12	4.29	0.34
p (2)	0.030		0.024		0.596		0.062	

(1) Total N estimated from sum of relative concentrations (table II-2.

(2) Significance probability levels from t-test between mean ratios from Cedar Camp and Holcomb Peak, n=10.

Table II-4. Coefficients and probabilities for correlations of mineralizable N with C and N concentrations and C:N ratios in particle size fractions of Cedar Camp and Holcomb Peak soils (clearcut and forest combined, n=10). For sonicated soil the variable used was dN_{min}, the increase in N_{min} due to sonication. Here, $dN_{min}=N_{min}(sonicated)-N_{min}(unsonicated)$. Only correlations with $p<0.10$ are shown.

Table II-4.

Cedar Camp

	Sand	Coarse silt	Fine silt	Coarse clay	Fine clay
Unsonicated N_{min}					
C concentration	0.74 0.013	-	-	-	-
N concentration	0.59 0.072	-	-	-	-
C:N ratio	-	-	-	-	0.73 0.016
dN_{min}					
C concentration	-	-	-	-	-
N concentration	-	0.62 0.055	0.57 0.087	-	0.60 0.069
C:N ratio	-0.70 0.025	-	-0.63 0.052	-	-0.54 0.110

Holcomb Peak

	Sand	Coarse silt	Fine silt	Coarse clay	Fine clay
Unsonicated N_{min}					
C concentration	-	0.62 0.058	0.61 0.061	0.56 0.093	0.63 0.051
N concentration	-	0.57 0.086	0.57 0.087	-	0.69 0.028
C:N ratio	-	-	-	-	-
dN_{min}					
C concentration	-	0.79 0.006	0.84 0.002	0.85 0.002	0.87 <.001
N concentration	-	0.88 <.001	0.87 0.001	0.86 0.001	0.90 <.001
C:N ratio	-	-0.71 0.023	-	-	-

Chapter III.

Effects of Harvesting and Burning on Carbon and Nitrogen Status in Soil and Forest Floor Layers: Implications for Long-term Site Productivity

Introduction

Forest managers require new information to predict the consequences of their decisions. Concerns for long-term site productivity (Ford 1983), reductions in the productive forest landbase (Alig et al. 1983), and possible future climate changes (Pastor and Post 1988) complicate the task. Standard practices such as clearcutting and prescribed burning must be reassessed from a long-term perspective.

Southwest Oregon is a productive region for several coniferous species but is subject to environmental extremes that limit reforestation success and crop tree performance. Clearcutting is common, often followed by either broadcast burning or burning hand-piled slash. Slash disposal by these methods reduces future fire hazard, controls competing vegetation, and creates favorable seedbed conditions (McNabb 1988). Short-term increases in productivity from prescribed burning are possible (Johansen 1975), but decreases are also possible such as when N is lost from sites by convection, volatilization, erosion, and leaching (Dunn and DeBano 1977; Raison et al. 1985; Sollins et al. 1981).

Our objective was to measure the how forests respond to clearcutting and two different prescribed burning treatments. We focused on C and N because 1) N frequently limits growth in Pacific Northwest forests (Gosz 1981; Johnson et al. 1982); 2) C and N dynamics are interrelated (McGill and Cole 1981); and 3) forest soil and biomass store a large proportion of the world's terrestrial C stores (Post 1982; Schlesinger 1983). Estimates of plant available N were also emphasized because of its strong correlation with site index (Powers 1980) and fertilizer response (Shumway and Atkinson 1978).

Methods and Materials

Site Characteristics

This study was conducted in the Galice Ranger District of Siskiyou National Forest, part of the southwest Oregon Klamath geological province. The rugged, deeply dissected terrain is geologically and floristically complex with hot, dry summers and cool, wet winters (Franklin and Dyrness 1973). Twenty sites were selected forming five distinct site groups located within 8 km of each other (Table III-1). Every group consisted of two clearcuts each paired with an adjacent uncut forest. Clearcuts were all harvested in 1978 or 1979 followed by removal of unmerchantable material (larger than 30.5 cm X 3 m). Prescribed burning occurred between 1980 and 1982. Each site group contained two clearcuts that had been either broadcast-burned (BB) or hand-piled-and-burned (PB). Generally, within-group clearcuts were physiographically similar (Table III-1). Soils have developed on metasediments of the Galice formation (Ramp 1979), but one group was influenced by metavolcanics of the same formation. Dominant overstory vegetation on uncut sites was Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) with minor components of tanoak (Lithocarpus densiflorus (Hook. & Arn.) Rehd.), Pacific madrone (Arbutus menziesii Pursh.), sugar pine (Pinus lambertiana Dougl.), and incense-cedar (Calocedrus decurrens (Torr.) Florin.).

Ground vegetation, forest floor, and soil sampling

Two parallel transects (20 m apart) each with five plots spaced at 15 m were established on each site. Occasionally the shape or size of sites would result in deviations from this pattern, but these spacings were still maintained. Transects were established randomly, but at least 15 m away from clearcut edges. Four points were established 2.5 m from plot centers at 90 degree increments aligned with the transect, but usually only two of the four were sampled. Most sampling occurred at the two points perpendicular to the transect where foot traffic was minimal. On one uncut-clearcut pair only six plots were established because of limited area. Therefore, extra sampling points were randomly assigned to four of the six plots to maintain a 20 point sampling intensity.

On PB sites, burned areas represented a small proportion of the site and were not sampled. These sites resemble unburned clearcuts except that larger woody debris had been removed from unburned areas for piling and burning.

Most sampling took place in summer and fall 1985. Ground vegetation (mosses, annuals, and perennials) was collected using 0.25-m^2 quadrats (two points per plot) on all sites but two: Waters-BB (0.5 m^2) and Bear-BB (0.08 m^2

or 1 m^2). Forest floor (litter and F layer) was sampled using 0.25-m^2 quadrats. All plant and forest floor materials were oven-dried (70° C) for at least 24 h and weighed. Soil was sampled at 0-5 cm and 5-15 cm for carbon (C) and N analyses and stored field-moist at 5° C.

In spring 1986, soil and F layer were re-sampled adjacent to previous collection points for available N estimation. This occurred over a one-week period with storage on ice within 8 h of collection. Field-moist samples were maintained at 5° C until analysis.

Samples for bulk density determination were taken in summer 1987 adjacent to previous collection points. On most sites soil volumes were removed by sampling within a 15-cm by 20-cm template to fixed vertical depths (0-5 cm or 5-15 cm). Slope angles at the template were measured with a clinometer for use in bulk density calculations and estimating mean slope angle for each site. Where soils had low rock content (Onion sites) samples were taken to the same depths using 7.6 cm dia. cores.

Chemical and Physical Analyses

Anaerobic mineralizable N (N_{min} concentration) (Waring and Bremner 1964a) and gravimetric moisture content were estimated with F layer and soil subsamples (<2mm fraction). Initial ammonium concentration (NH_4^+) of 10 g subsamples

was determined by extraction with 50 ml 1 N NaCl. 20 g subsamples were anaerobically incubated in 80 ml de-ionized H_2O for 7 days at 40° C. NH_4^+ was extracted as before. NH_4^+ concentrations were determined with an autoanalyzer after filtration. Anaerobic mineralizable N was calculated as the difference between initial and incubation NH_4^+ concentrations. For analysis, it was expressed in three ways: (1) N_{min} concentration (ug N mineralized/g dry soil, i.e., ppm), (2) N_{min}:N (g N mineralized/g N in dry soil X 100, i.e., %), and (3) N_{min} content (kg N mineralized/ha).

Of the available samples, only half were analyzed for total C and N. To get a representative selection, we selected alternate samples from a list of plots obtained by ranking N_{min} concentration values. N concentration in plant, litter, F layer, and soil material was determined by micro-Kjeldahl technique (Bremner 1965) using an autoanalyzer. Carbon concentration in F layer and soil were measured with a Leco C analyzer.

Bulk density of the <2 mm dia. fraction was determined using sample weight, sampling area and depth, coarse fragment content, and gravimetric water content.

Variables and statistical analyses

Several analyses of variance (ANOVAs) were performed. The assumption of normality and homogeneity of variance

were tested using the W-test (Shapiro and Wilk 1982) and Levene's test (Levene 1960). When either assumption could not be met, response variables were transformed using the maximum likelihood method of Box and Cox (1964).

In the comparison of uncut sites, all variables were subjected to one-way analysis of variance (ANOVA). Because of extreme heteroscedasticity, ground vegetation data were subjected to a rank transformation prior to analysis (Conover and Iman 1981). The effects of management treatment were tested with ANOVA in a randomized block design and Fisher's least-significant-difference test.

Correlation between variables was examined with a Pearson correlation matrix. All analyses were performed using SAS (SAS Institute, Inc. 1985).

Results

Comparison of uncut sites

Forested sites fell into three distinct groups with regard to C and N contents of soil, F layer and litter (Fig. III-1a,b). Total N stores of most sites were between 1000 and 2000 kg/ha. The two forests in the Ramsey group were lower, averaging 806 kg/ha, but the two in the Onion group were considerably higher, between 4000 and 4500 kg/ha. C and N_{min} contents (kg mineralizable N/ha; Fig. III-1c) also were greatest at Onion sites, but Ramsey sites did not rank lowest as they did with N content.

High C, N, and N_{min} contents of soil and forest floor on Onion sites were due to two factors: Greater bulk density of <2 mm soil (BD2) and a relatively large F layer mass (Table III-2; Fig. III-1a,b,c). BD2 at both depths was strongly correlated with C, N, and N_{min} contents ($r>0.93$; $p<0.001$). Low total N contents (i.e., forest floor and soil summed) at Ramsey sites were primarily due to low BD2, especially at 5-15 cm (Table III-2).

C, N, and N_{min} concentrations of soil and forest floor were generally less variable, but patterns among the site groups were evident (Table III-2). N_{min} concentration was highest and N concentration lowest in 5-15 cm soil from Ramsey sites. At Onion sites where soil N_{min} contents ranked highest, N_{min} concentrations were among the lowest.

N_{min}:N, a index of N lability, was greater in the F layer than in soil except on Ramsey and Bear sites. N in Ramsey soil may be significantly more labile because such high proportions were mineralized, especially at 5-15 cm (Table III-2).

BD2 at both depths were strongly correlated with site index in these forests ($r=0.98$ and $p<0.001$ for both). But correlations of site index with total site C, N, and N_{min} contents also were strong ($p>0.88$; $p<0.001$), reflecting the role of bulk density in determining soil nutrient stores and availability. Correlations of site index with N_{min} concentration were negative and much weaker ($r=-0.59$ $p=0.094$ and $r=-0.54$ $p=0.109$ for 0-5 cm and 5-15 cm, respectively).

Effects of harvesting and burning

Sites varied widely with regard to the effects of clearcutting on C and N stores in soil and forest floor (Fig. III-1a,b). Forests, PB clearcuts, and BB clearcuts averaged 1793, 1643, and 1553 kg N/ha, respectively (Table III-3). Some individual sites had significant losses of total N content, up to 1000 kg/ha (Fig. III-1b). For example, soil and forest floor of Waters-PB, Bear-BB, and Ramsey-PB had a third to two-thirds the total N content of adjacent forests. Mass and N content of F layers were

sharply lower in clearcuts than in forests ($p=0.014$), but only on burned sites was the difference in litter N statistically significant (Table III-3). Soil C and N contents on clearcuts did not differ significantly from those of forests at either soil depth, nor did BD2 (Table III-3; Table III-2). Herbaceous vegetation on clearcuts contained 6-7 kg N/ha (Table III-3), far below the several hundred kg N/ha typically removed by harvest (Perry and Norgren 1983; Cromack et al. 1978; Feller and Kimmins 1984).

Anaerobic mineralizable N is generally a good predictor of conifer response to fertilization (Shumway and Atkinson 1978), and is thought to reflect labile N pools such as microbial biomass (Paul 1984, Myrold 1987). The F layer accounted for a high proportion of mineralizable N in our forested sites, more than three times the concentration of 0-5 cm soil (Table III-4). However, N_{min} contents of the F layer averaged only a third of soil values (Table III-3).

Both N_{min} concentration and content in 0-5 cm soil of BB clearcuts were about half that of PB clearcuts and uncut forests (Tables III-3, III-4). The large decrease in N_{min} concentration on broadcast-burned clearcut soil at 0-5 cm was mostly because of changes at Ramsey and Slate (Fig. III-2a). These clearcuts also ranked among the largest in loss of total N_{min} contents (Fig. III-1c).

Clearcutting the N-rich Onion sites produced the greatest absolute decreases in total N_{min} contents (Fig. III-1c), primarily losses from the F layer. Even when expressed as a proportion of the total N_{min} contents of adjacent forests, the decreases were substantial relative to other sites.

We regressed the proportion of total site N lost from harvesting activities (N_{change}) against soil and forest floor variables from forest sites using stepwise regression. The regression model explained 89% of the total variation among forest sites (Table III-5):

$$N_{change} = 166 + 4.86\ (CN5) - 2.40\ (CN15) + 7.82\ (\text{C concentration at 0-5 cm})$$

where CN5 and CN15 are soil C:N ratios at 0-5 cm and 5-15 cm, respectively. Most of the variation (50%) was associated with the first predictor, CN5. The remaining variables accounted for another 39% of the total variation.

There were numerous correlations suggesting how N_{change} might ultimately be influenced by physical site factors. For example, CN5 from the above regression equation was weakly related to N concentration ($r=-0.57$; $p=0.086$). Nitrogen concentration was more strongly correlated with slope ($r=+0.72$; $p=0.020$) (Table III-6).

Slope, along with aspect and bulk density, were significantly related to a number of other variables (Table III-6). Slope was correlated with F layer mass ($r=-0.76$; $p=0.012$), the proportion of total N stored in the F layer ($r=-0.63$; $p=0.051$), and F layer N concentration ($r=-0.83$; $p=0.003$). At 0-5 cm, N_{min} was also associated with slope ($r=+0.64$; $p=0.045$). Aspect was correlated with the F layer mass ($r=+0.71$; $p=0.021$), F layer C concentration ($r=+0.71$; $p=0.021$), F layer N concentration ($r=+0.67$; $p=0.034$), N_{min} at 5-15 cm ($r=-0.69$; $p=0.027$), and N_{min}:N at 0-5 cm ($r=-0.83$; $p=0.003$). A similar set of relationships emerged for bulk density variables. BD2 (0-5 cm) was related to F layer mass ($r=+0.78$; $p=0.007$), F layer C concentration ($r=+0.84$; $p=0.002$) and N concentration ($r=+0.70$; $p=0.026$), and N_{min}:N ($r=-0.67$; $p=0.033$). BD at 5-15 cm correlated significantly with the proportion of total N stored at 0-5 cm ($r=+0.64$; $p=0.045$) and CN5 ($r=-0.67$; $p=0.033$).

Discussion

Comparison of uncut sites

The pattern of C, N, and N_{min} contents among forest sites were due primarily to variations in bulk density. Expressing nutrient stores on a mass-per-area basis may improve data interpretation, especially where large differences in bulk density and coarse fragment content exist (Mehlich 1980; McNabb et al. 1986). Soil N_{min} content was better correlated with site index than N_{min} concentration because it may have better portrayed differences in plant available N. Powers (1980) found good correlations between site index and N_{min} concentration on several soil types in northern California. The exceptions were highly productive granitic soils that nevertheless had low N_{min} concentrations. He attributed this to an absence of restrictive soil horizons (i.e., deeper soils). Observations such as these relating soil physical properties to tree productivity are common to many soil-site studies (Steinbrenner 1978).

Effects of harvesting and burning

The decreases of C and N stores in soil and forest floor layers on clearcuts exceeded amounts typically removed by harvest. For example, Feller and Kimmins (1984) measured 234 kg/ha removed in logs from a western hemlock-

Douglas fir forest.

Decreases in litter N contents were not as large as those measured by Little and Ohman (1988), but litter N contents in southwest Oregon are typically lower than in other western Oregon forest types (McNabb 1988). Of the two burning treatments, PB clearcuts had greater litter N contents reflecting the influence of unburned harvest residue.

Anaerobic N_{min} concentration averages for 0-5 cm soil from forests and clearcuts were large relative to measurements taken at greater depths (e.g., Powers 1980; Radwan and Shumway 1984; Pilz and Perry 1984). Even BB clearcuts had values well above the range considered N deficient (Powers 1980; Shumway and Atkinson 1978). N_{min} concentration values at 5-15 cm were somewhat low, but still above the 12-16 ppm limit for deficiency suggested by Powers (1980). Weighted averages of N_{min} concentrations at both depths were more in line with these other studies. But evaluating available N at 0-5 cm provided a sensitive indicator for disturbance because this layer was enriched in N.

The largest average loss of N in this study was from the F layer (Table III-3). On some sites the F layer represented over 20% of the total N content. The fate of this material is not known, but losses on BB and PB

clearcuts were similar, suggesting that other factors (e.g., decomposition, erosion, incorporation into mineral soil) were as important as combustion in its disappearance. On PB clearcuts more F layer C and N may have been retained and eventually incorporated into soil. There is some evidence for this since PB clearcuts had larger average C, N, and N_{min} concentrations compared to forests (Table III-4). However, these differences were not statistically significant. Thus, lower N_{min} in 0-5 cm soil from BB clearcuts may reflect not only volatilization losses, but also the absence of residual forest floor. This material represents an important source of N for developing stands (Gessel 1974; Pritchett and Wells 1978).

A conceptual model

The relationship between N_{change} and soil C:N ratios is reminiscent of work by Sollins et al. (1984). They depicted linear relationships between C:N ratios and N_{min}:N in density fractions of several soil types, demonstrating how the quality (C:N ratio) of some simplified substrates can influence the proportion of N mineralized. In the present study, N_{change} was positively related to C:N at 0-5 cm, but negatively related at 5-15 cm. Thus, the qualitative nature of the soil at these two depths may differ sufficiently to create distinct patterns of decomposition across sites.

The pattern of correlations (Table III-6) suggests some mechanisms that may explain why C:N ratio apparently has an opposite effect on N_{change} at 0-5 cm and 5-15 cm (Table III-5). Our conceptual model of these interacting processes (Fig. III-3) depicts a scenario whereby aspect, slope, and bulk density influence F layer accumulation and incorporation, soil N concentration, and eventually the C:N ratios that predict N_{change}. Several processes may affect F layer dynamics: 1) Colluvial processes on steeper slopes mix organic layers into mineral layers; 2) on southerly aspects, decomposition rates of litter and F layer may be limited by moisture availability (Fogel and Cromack 1977) during the hot, dry summers; 3) coarser soil textures (or lower BD2) may allow organic matter to eluviate more deeply (Birkeland 1984). For example at Ramsey forest sites, where BD2 was lowest, 5-15 cm soil was very similar to 0-5 cm soil, particularly N_{min}:N and C:N ratio (Table III-2).

The effects of these processes were most apparent in the 0-5 cm soil layer where N_{min}:N (0-5 cm) and N_{change} appeared to behave independently. For instance, on steeper, more northerly sites, F layer accumulations were smaller. Its rapid incorporation into mineral layers especially affects 0-5 cm soil: F layer N is probably more labile than soil N (i.e., N_{min}:N is larger; Table III-2), and N_{min}:N for the two layers are most similar where slopes are steepest. Notably, N_{min}:N (0-5 cm) was correlated with

C:N of the F layer, but not with C:N of 0-5 cm soil. Rapid incorporation of F layer (and litter) material into soil imparts higher N concentrations, more labile N (larger N_{min}:N), and a lower C:N ratio. But according to the regression model, N_{change} would be least when C:N ratio at 0-5 cm is lowest, that is, we would expect a lower proportion of soil and forest floor N to be lost when N at 0-5 cm is most labile. This apparent paradox is resolved when one recalls that there are substantial stores of N in the forest floor, material which is subject to erosion or burning following harvest. Hence, rapid incorporation of forest floor material enriches soil layers and, at the same time, may protect N stores from disturbance. This is most likely on steeper sites where soils are generally shallower, ecosystems less productive, and nutrient retention more critical.

To a certain extent the pattern of N_{change} suggests where our concerns for long-term site productivity should be focused. But to properly assess the impact of human disturbance on long-term site productivity, the historical disturbance regime and potential for recovery of the ecosystem must be considered along with its current and past productivity (Klock and Grier 1979; McNabb 1988; Graumlich et al. 1989). In this study N losses were sometimes large as a proportion of totals, but are not necessarily irreplaceable over a single rotation. On the

other hand, long-term declines in productivity are more likely where the absolute magnitude of N losses exceed N accumulations over many rotations.

Figure III-1abc. Carbon, N, and mineralizable N contents (kg/ha) in forest floor and soil layers of southwest Oregon test sites. U=uncut forest, PB=piled-and-burned clearcut, and BB=broadcast-burned clearcut. Litter C content was estimated as 50% of litter mass. Numbers above bars are significance probability values associated with t-tests of sums between forests and clearcuts.

Figure III-1a

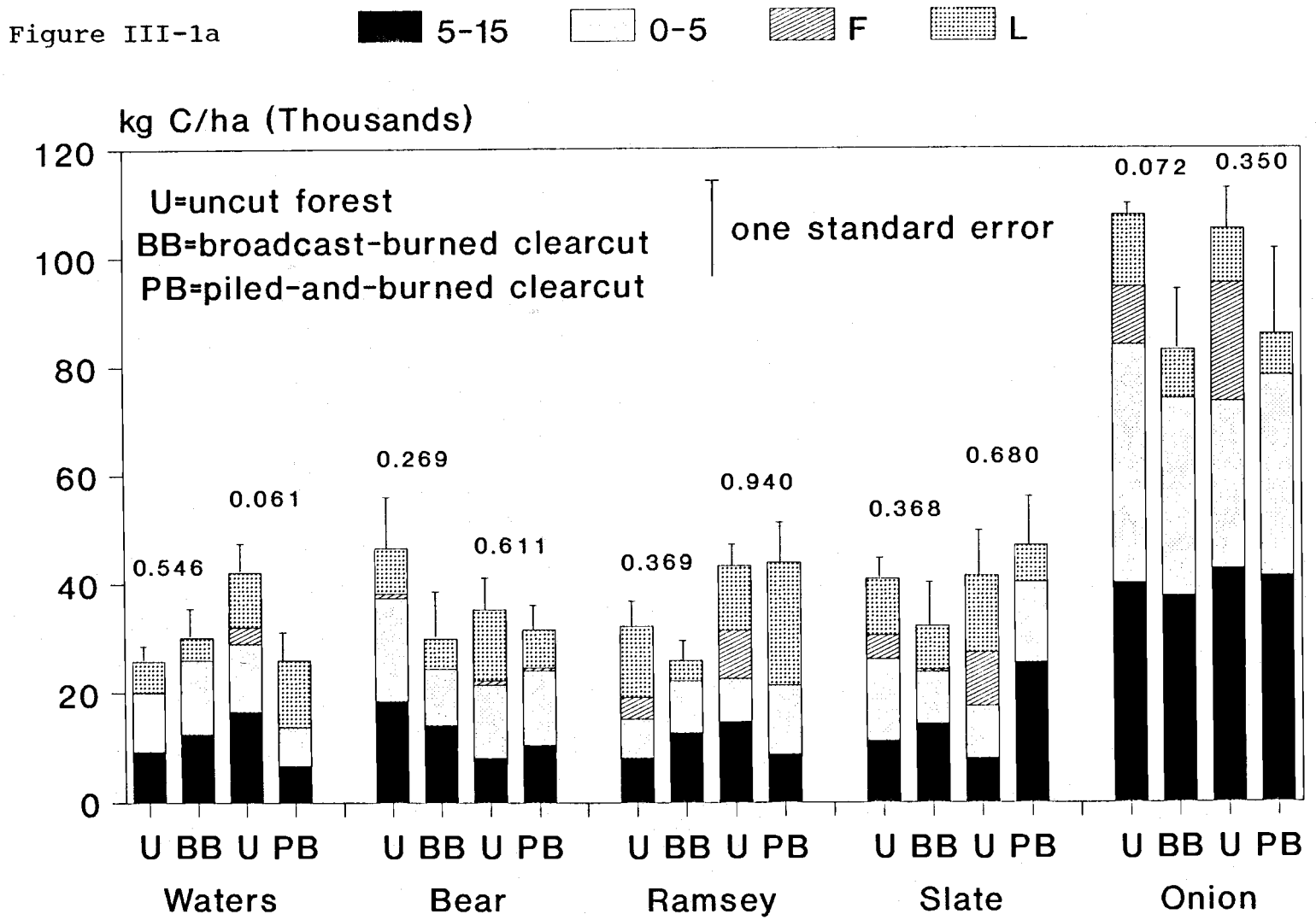

Figure III-1b

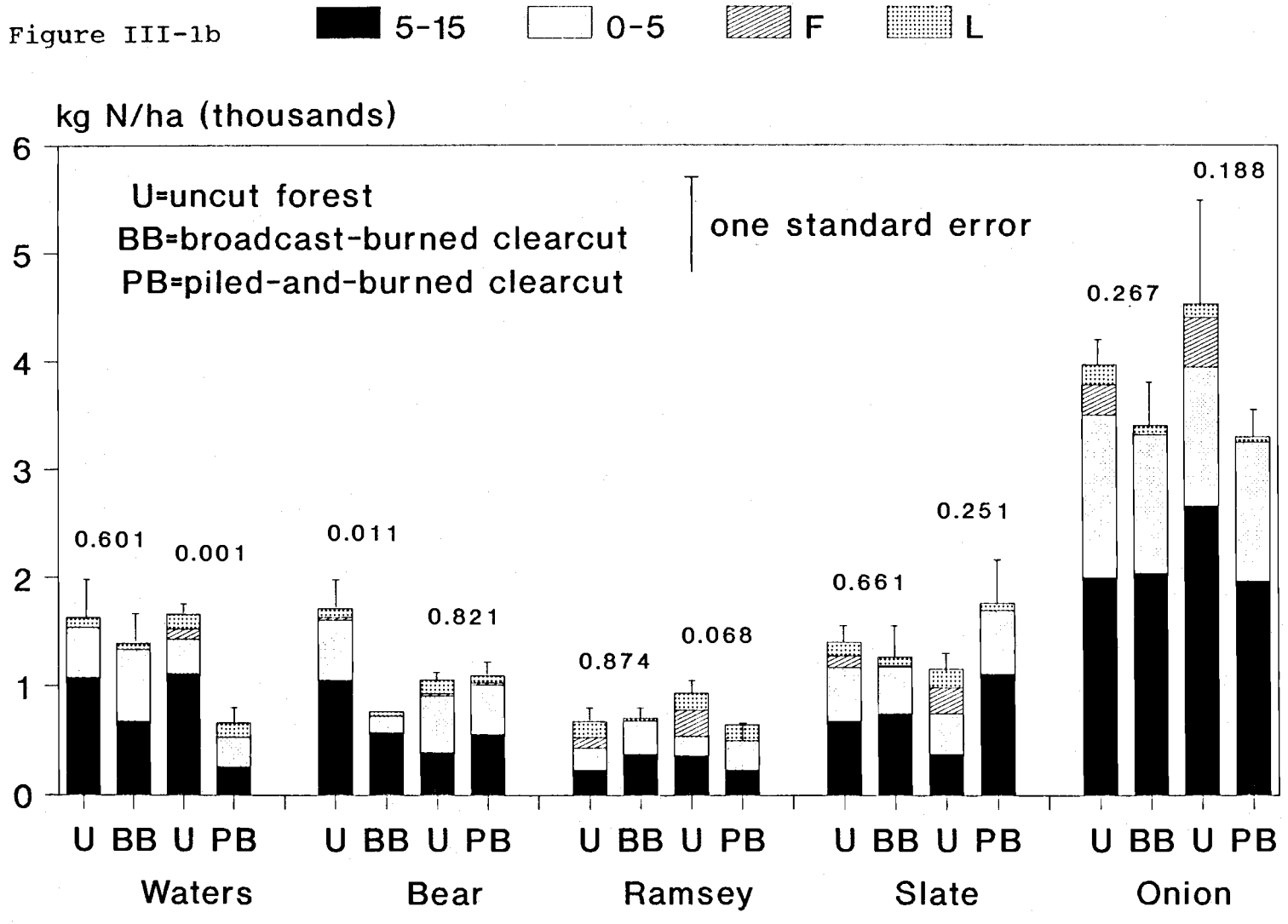

Figure III-1c

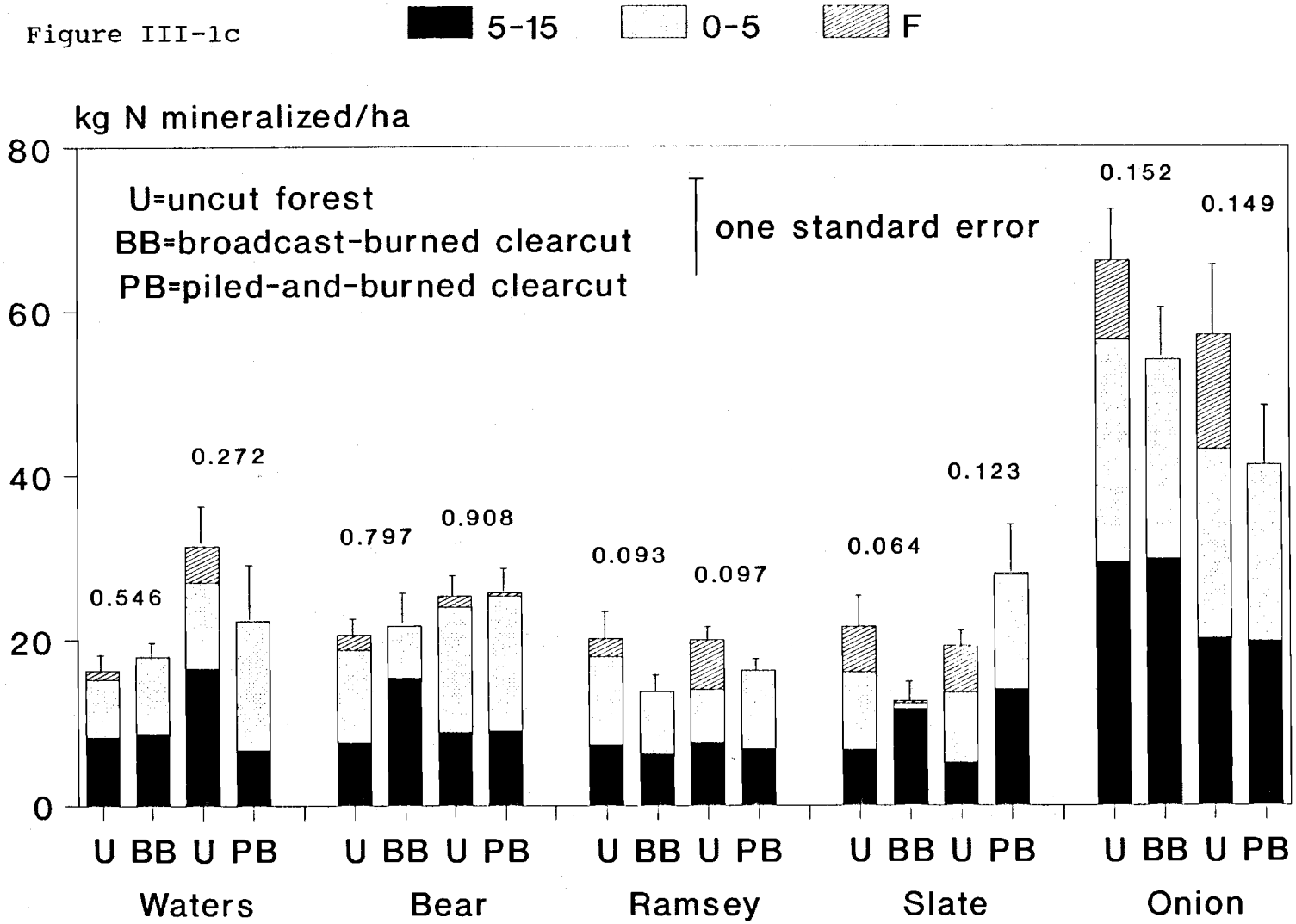

Figure III-2ab. Concentrations of mineralizable N (N_{min} concentration) in 0-5 cm and 5-15 cm soil from southwest Oregon test sites. U=uncut forest, PB=piled-and-burned clearcut, and BB=broadcast-burned clearcut. Numbers above bars are significance probability values associated with t-tests between forests and clearcuts.

Figure III-2a

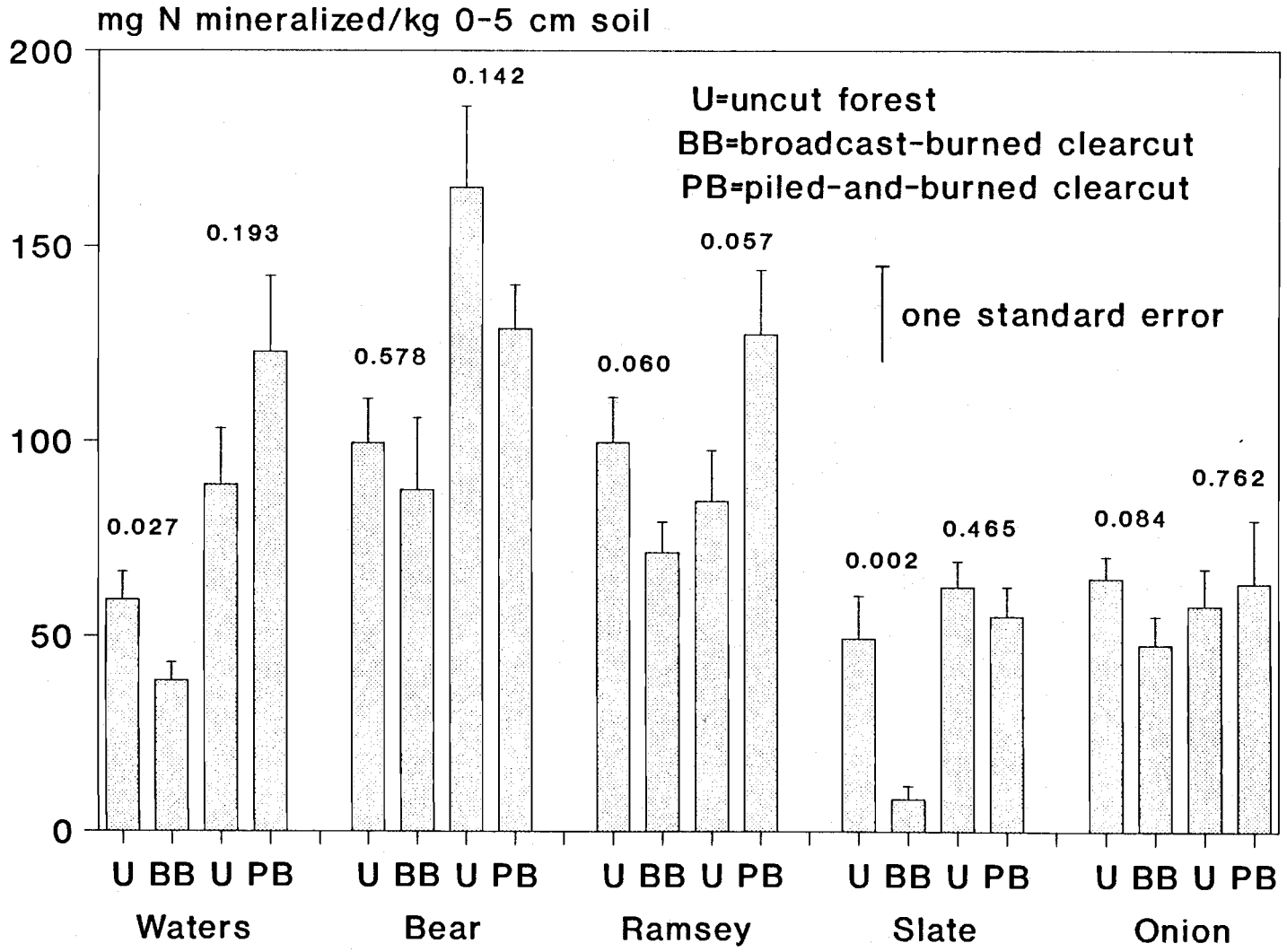

Figure III-2b

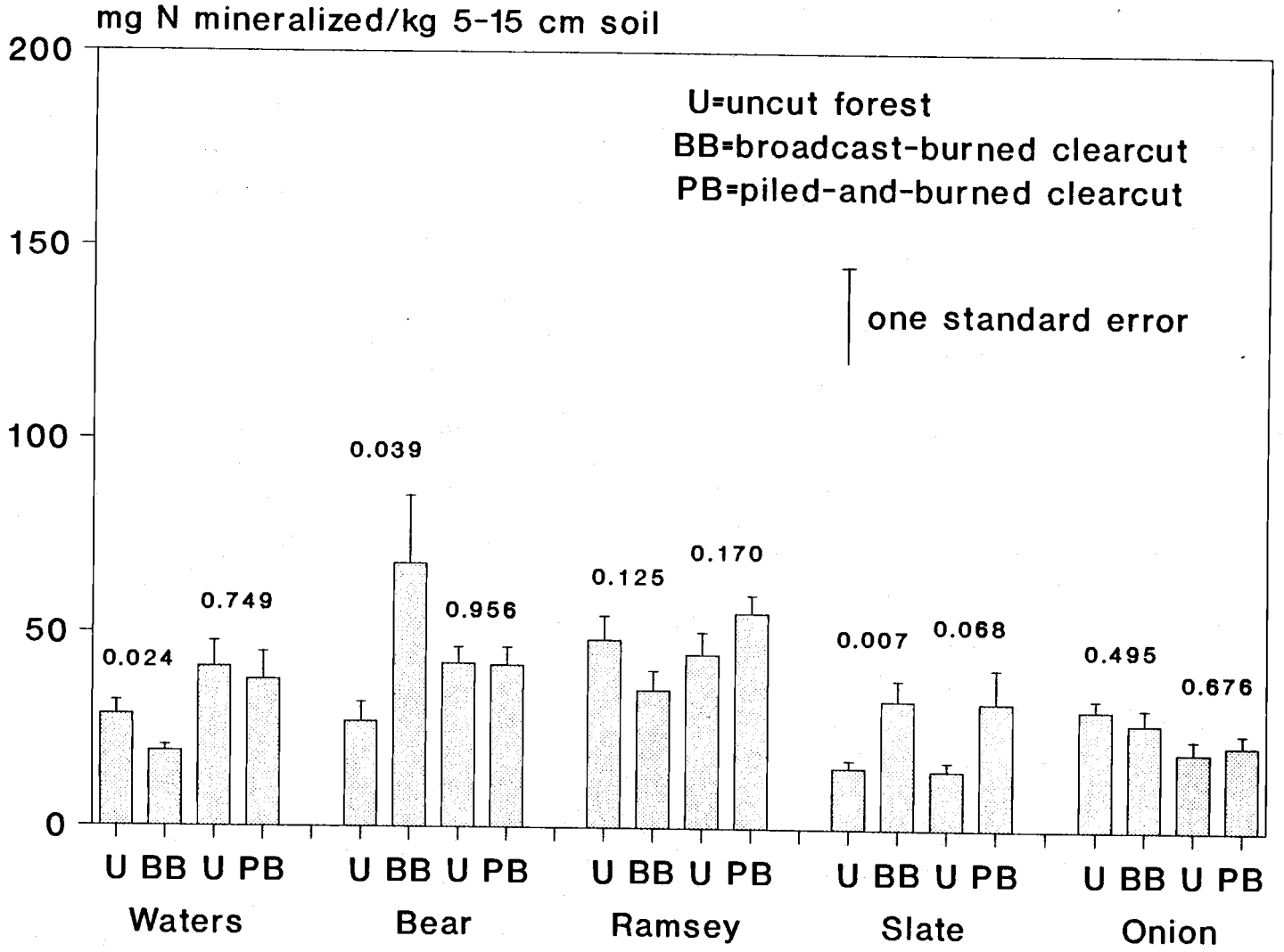

Figure III-3. Conceptual model relating slope, aspect, and bulk density to N_{change} (the relative change in total soil and forest floor N between uncut forests and clearcuts). Symbols (+,-) represent direct and inverse relationships, mostly derived from Pearson correlation coefficients.

Figure III-3

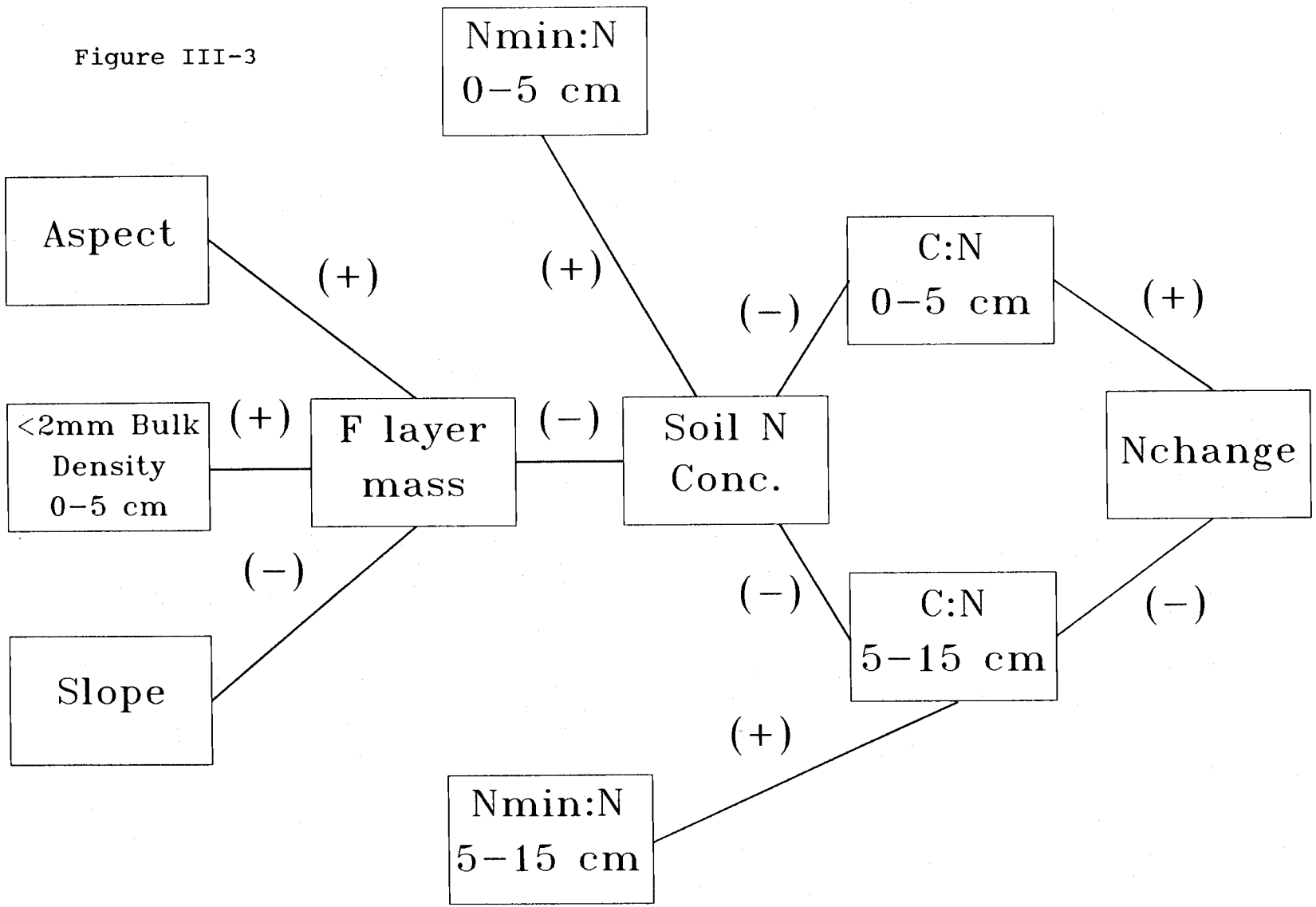
Nmin:N
0–5 cm
Aspect
(+)
(+)
C:N
0–5 cm
(–)
(+)
<2mm Bulk
Density
0–5 cm
(+)
F layer
mass
(–)
Soil N
Conc.
Nchange
(–)
(–)
C:N
5–15 cm
(–)
Slope
(+)
Nmin:N
5–15 cm

Table III-1. Site characteristics of the twenty study sites, Klamath mountain region, southwest Oregon.

Table III-1

Group	Site	Elevation (m) (3)	Aspect (degrees)	Slope (3)	Slope (calculated)	Annual Precip. (in) (1)	Summer Rainfall (in) (1)	Soil (2)	Harvest & Burn date (3)	Clearcut size (ha) (3)	Site Index (3)	Stand age (5)
Waters	UB	580	16	70	53	45	5	Typic Haploxerult			110	260
	BB	600	6	50	42	45	5	Typic Haploxerult	11-78, 5-80	1.2	110	
	UP	580	26	70	48	45	5	Typic Haploxerult			110	260
	PB	600	20	50	50	45	5	Typic Haploxerult	11-78, 10-80	1.2	110	
Bear	UB	580	45	70	58	45	5	Typic Xerochrept			110	270
	BB	600	46	50	32	45	5	Typic Xerochrept	11-78, 5-80	1.2	110	
	UP	640	82	60	59	50	5	Typic Xerochrept			100	270
	PB	600	59	60	53	50	5	Typic Xerochrept	2-79, 10-80	4.1	100	
Ramsey	UB	1030	20	70	52	60	6	Ultic Haploxeralf (4)			100	225
	BB	940	51	65	52	60	6	Ultic Haploxeralf	10-79, 4-80	1.2	100	
	UP	1030	32	70	33	60	6	Ultic Haploxeralf			100	225
	PB	1030	77	50	47	60	6	Ultic Haploxeralf	10-79, 6-80	0.8	100	
Slate	UB	730	180	65	38	55	5	Typic Xerochrept			110	240
	BB	600	193	50	32	55	5	Typic Xerochrept	11-79, 11/82	1.6	120	
	UP	760	149	50	46	55	5	Typic Xerochrept			110	240
	PB	730	151	50	53	55	5	Typic Xerochrept	11-79, 11/82	2.8	110	
Onion	UB	730	146	30	40	65	8	Typic Haploxerult			130	340
	BB	700	132	35	40	65	8	Typic Haploxerult	11-79, 4-81	3.2	130	
	UP	730	168	30	39	65	8	Typic Haploxerult			130	340
	PB	730	169	40	36	65	8	Typic Haploxerult	12-79, 3-81	3.6	130	

1. Precipitation estimated by interpolation from rainfall maps (Froehlich et al. 1982; McNabb et al. 1982). 2. Soil types from Josephine County soil survey (Soil Conservation Service 1983). 3. Obtained from Timber Resource Inventory, Siskiyou National Forest. 4. Rock type on Ramsey sites was metavolcanic; all others were metasediments. 5. Tom Atzet, unpublished data, Siskiyou National Forest.

Table III-2. Mean C, N, and mineralizable N concentrations of forest floor and soil layers from uncut forest sites. UB=uncut forest site paired with broadcast-burned clearcut; UP=uncut forest site paired with piled-and-burned clearcut. Means followed by same letter do not differ significantly at $p<0.05$, Fisher's LSD after one-way ANOVA.

Table III-2.

C concentration(2)
(%)

Site		Litter Mean	Litter s.e.		F layer Mean	F layer s.e.		0-5 cm Mean	0-5 cm s.e.		5-15 cm Mean	5-15 cm s.e.	
Waters	UB	-	-	-	32.6	1.7	bc	7.28	0.98	a	3.68	0.54	bcd
	UP	-	-	-	30.4	2.7	bc	9.50	1.82	a	3.43	0.32	bcd
Bear	UB	-	-	-	35.7	4.4	abc	13.17	3.07	a	4.13	0.85	bcd
	UP	-	-	-	28.8	3.4	c	11.81	1.55	a	4.11	0.39	abc
Ramsey	UB	-	-	-	35.4	3.4	abc	10.33	2.34	a	5.24	0.81	ab
	UP	-	-	-	33.9	3.2	bc	10.81	1.73	a	6.00	1.00	a
Slate	UB	-	-	-	36.3	2.6	abc	8.36	1.19	a	2.80	0.19	d
	UP	-	-	-	38.9	2.4	ab	7.54	0.78	a	3.52	0.47	cd
Onion	UB	-	-	-	42.9	2.6	a	9.44	1.09	a	3.96	0.40	abc
	UP	-	-	-	42.7	2.6	a	8.46	1.29	a	3.77	0.42	bcd

(1) Significance probability level for this multiple comparison was p=0.0563.
(2) Analysis of variance performed on transformed data.

Table III-2 (cont).

N concentration[2] (%)

Site		Litter Mean	Litter s.e.		F layer Mean	F layer s.e.		0-5 cm Mean	0-5 cm s.e.		5-15 cm Mean[1]	5-15 cm s.e.	
Waters	UB	0.61	0.04	a	0.84	0.07	a	0.28	0.06	bc	0.35	0.09	a
	UP	0.70	0.03	a	0.89	0.09	a	0.27	0.05	bc	0.23	0.04	abc
Bear	UB	0.57	0.04	a	0.80	0.05	a	0.37	0.06	ab	0.24	0.03	ab
	UP	0.54	0.05	a	0.85	0.10	a	0.47	0.05	a	0.21	0.02	abc
Ramsey	UB	0.60	0.05	a	0.88	0.06	a	0.31	0.05	bc	0.15	0.02	d
	UP	0.56	0.05	a	0.94	0.07	a	0.25	0.04	c	0.15	0.03	d
Slate	UB	0.60	0.02	a	0.91	0.05	a	0.28	0.02	bc	0.16	0.01	cd
	UP	0.56	0.02	a	0.93	0.08	a	0.29	0.02	bc	0.17	0.02	bcd
Onion	UB	0.63	0.03	a	0.99	0.06	a	0.32	0.03	bc	0.20	0.01	abc
	UP	0.57	0.05	a	0.96	0.06	a	0.27	0.02	bc	0.22	0.04	abc

(1) Significance probability level for this multiple comparison was p=0.0563.
(2) Analysis of variance performed on transformed data.

Table III-2 (cont).

C:N ratio

Site		Litter Mean	Litter s.e.		F layer Mean	F layer s.e.		0-5 cm Mean	0-5 cm s.e.		5-15 cm Mean	5-15 cm s.e.	
Waters	UB	-	-	-	40.4	4.0	a	33.2	7.6	a	16.5	4.6	b
	UP	-	-	-	34.4	2.3	a	40.7	8.4	a	16.1	1.8	b
Bear	UB	-	-	-	44.1	3.7	a	34.5	4.6	a	18.6	4.1	b
	UP	-	-	-	34.0	1.8	a	24.4	1.1	a	20.1	1.4	b
Ramsey	UB	-	-	-	40.3	2.4	a	32.1	2.4	a	33.7	1.9	a
	UP	-	-	-	35.7	1.0	a	44.1	2.7	a	41.3	2.3	a
Slate	UB	-	-	-	39.8	1.6	a	29.8	3.0	a	17.4	0.7	b
	UP	-	-	-	43.2	5.4	a	26.3	1.4	a	20.6	1.1	b
Onion	UB	-	-	-	43.4	2.3	a	29.9	1.9	a	20.1	1.2	b
	UP	-	-	-	45.0	2.9	a	32.6	5.7	a	18.7	2.2	b

(1) Significance probability level for this multiple comparison was p=0.0563.
(2) Analysis of variance performed on transformed data.

Table III-2 (cont).

N_{min} concentration (ppp)

Site		Litter Mean	Litter s.e.		F layer Mean	F layer s.e.		0-5 cm Mean	0-5 cm s.e.		5-15 cm Mean	5-15 cm s.e.	
Waters	UB	-	-	-	337	27	ab	59.2	7.2	cde	28.8	3.5	cd
	UP	-	-	-	393	22	a	88.8	14.4	bc	41.1	6.6	abc
Bear	UB	-	-	-	225	15	cd	99.4	11.3	b	27.0	5.1	de
	UP	-	-	-	234	18	cd	165.1	20.8	a	42.1	4.2	abc
Ramsey	UB	-	-	-	218	20	d	99.6	11.7	b	48.2	6.2	a
	UP	-	-	-	289	22	bc	84.6	13.0	bc	44.6	5.7	ab
Slate	UB	-	-	-	365	40	a	49.2	11.0	e	15.7	2.0	f
	UP	-	-	-	361	26	a	62.4	6.6	cde	15.1	2.3	f
Onion	UB	-	-	-	364	14	a	64.5	5.7	cd	30.7	2.8	bcd
	UP	-	-	-	347	17	ab	57.5	9.7	de	20.0	3.5	ef

(1) Significance probability level for this multiple comparison was p=0.0563.
(2) Analysis of variance performed on transformed data.

Table III-2 (cont).

N_{min} percent(2)
(% mineralized of N concentration)

Site		Litter Mean	Litter s.e.		F layer Mean	F layer s.e.		0-5 cm Mean	0-5 cm s.e.		5-15 cm Mean	5-15 cm s.e.	
Waters	UB	-	-	-	4.35	0.69	a	2.85	0.59	abc	1.29	0.34	de
	UP	-	-	-	4.57	0.38	a	3.77	0.69	a	2.15	0.53	bc
Bear	UB	-	-	-	2.70	0.21	de	2.87	0.35	abc	1.08	0.26	de
	UP	-	-	-	2.84	0.35	cde	3.44	0.27	ab	1.95	0.15	c
Ramsey	UB	-	-	-	2.46	0.25	e	3.50	0.26	a	3.23	0.34	a
	UP	-	-	-	3.10	0.22	bcde	3.31	0.24	abc	3.01	0.18	ab
Slate	UB	-	-	-	4.00	0.48	ab	1.77	0.30	d	0.92	0.10	e
	UP	-	-	-	3.79	0.30	abc	2.36	0.27	bcd	0.91	0.14	e
Onion	UB	-	-	-	3.79	0.27	abcd	2.13	0.13	cd	1.59	0.16	cd
	UP	-	-	-	3.68	0.16	abcd	2.26	0.43	cd	0.93	0.15	e

(1) Significance probability level for this multiple comparison was p=0.0563.
(2) Analysis of variance performed on transformed data.

Table III-2 (cont).

Bulk density <2 mm fraction(2)
(g/cm3)

Site		Litter Mean	Litter s.e.		F layer Mean	F layer s.e.		0-5 cm Mean	0-5 cm s.e.		5-15 cm Mean	5-15 cm s.e.	
Waters	UB	-	-	-	-	-	-	0.24	0.04	cd	0.20	0.02	d
	UP	-	-	-	-	-	-	0.26	0.04	c	0.29	0.04	b
Bear	UB	-	-	-	-	-	-	0.25	0.04	cd	0.22	0.03	cd
	UP	-	-	-	-	-	-	0.18	0.02	cd	0.13	0.02	e
Ramsey	UB	-	-	-	-	-	-	0.23	0.04	cd	0.10	0.01	e
	UP	-	-	-	-	-	-	0.17	0.02	d	0.12	0.02	e
Slate	UB	-	-	-	-	-	-	0.43	0.05	b	0.27	0.02	bc
	UP	-	-	-	-	-	-	0.28	0.04	c	0.21	0.01	cd
Onion	UB	-	-	-	-	-	-	0.84	0.05	a	0.64	0.03	a
	UP	-	-	-	-	-	-	0.80	0.04	a	0.70	0.03	a

(1) Significance probability level for this multiple comparison was p=0.0563.
(2) Analysis of variance performed on transformed data.

Table III-2 (cont).

Dry mass (kg/ha)

		Litter			F layer			0-5 cm			5-15 cm		
Site		Mean	s.e.		Mean	s.e.		Mean	s.e.		Mean	s.e.	
Waters	UB	22130	4222	a	3191	1012	e	-	-	-	-	-	-
	UP	20274	2858	a	10948	2188	cd	-	-	-	-	-	-
Bear	UB	22350	3882	a	8064	2171	de	-	-	-	-	-	-
	UP	24617	3584	a	5329	2132	e	-	-	-	-	-	-
Ramsey	UB	19158	2126	a	6139	1426	e	-	-	-	-	-	-
	UP	25350	1720	a	19902	1944	bc	-	-	-	-	-	-
Slate	UB	20988	1786	a	14020	2188	bcd	-	-	-	-	-	-
	UP	24944	2585	a	17379	4222	bc	-	-	-	-	-	-
Onion	UB	26969	915	a	23914	4197	ab	-	-	-	-	-	-
	UP	31354	7400	a	34064	6729	a	-	-	-	-	-	-

(1) Significance probability level for this multiple comparison was p=0.0563.
(2) Analysis of variance performed on transformed data.

Table III-3. Mean C and N contents of forest floor and soil layers, forest floor dry mass, and soil bulk density, by treatment. U=uncut forests, PB=piled-and-burned clearcuts, and BB=broadcast-burned clearcuts. Treatment means compared for each layer with one-way ANOVA followed by Fisher's LSD. Means followed by same letter do not differ significantly at $p<0.05$.

Table III-3.

N content (kg/ha)

	U	PB	BB	p
Ground vegetation	2.16 a	6.89 a	6.42 b	0.006
S.E.	1.23	1.19	0.60	
Litter	136.5 a	98.7 ab	51.8 b	0.024
S.E.	8.5	21.3	11.9	
F layer	145 a	3.9 b	0.8 b	0.014
S.E.	57.8	2.1	0.9	
Soil				
0-5 cm	589 a	675 a	582 a	0.894
S.E.	236	190	190	
5-15 cm	950 a	850 a	909 a	0.975
S.E.	417	260	271	
Total(2)	1793 a	1643 a	1553 a	0.250
S.E.	689	463	464	

N_{min} content (kg/ha)

	U	PB	BB	p
F layer	4.81 a	0.14 b	0.03 b	0.010
S.E.	1.95	0.07	0.03	
Soil				
0-5 cm	13.3 a	15.5 a	9.7 a	0.093
S.E.	4.2	2.2	3.7	
5-15 cm	11.8 a	12.0 a	14.4 a	0.609
S.E.	4.5	1.8	3.6	
Total(2)	29.9 a	27.5 a	24.3 a	0.350
S.E.	10.2	3.7	6.9	

(1) Calculated as 50% litter dry mass.

(2) Means from soil and forest floor layers do not sum to totals because totals were obtained by averaging sites having the same treatment.

Table III-3 (cont).

C content (kg/ha)

	U	PB	BB	p
Litter[1]	11981 a	15682 a	5500 a	0.237
S.E.	844	5078	911	
F layer	6091 a	124 b	33 b	0.027
S.E.	2790	73	37	
Soil				
0-5 cm	17693 a	21080 a	16346 a	0.507
S.E.	7113	5576	4716	
5-15 cm	17340 a	18747 a	19980 a	0.218
S.E.	7395	5414	5274	
Total[2]	52379 a	55118 a	42147 a	0.124
S.E.	17299	9989	10342	

Dry mass (kg/ha)

	U	PB	BB	p
Litter	23961 a	31364 a	10999 a	0.237
S.E.	1688	10155	1822	
F layer	14435 a	411 b	145 b	0.005
S.E.	5097	215	129	

Bulk Density <2 mm soil (g/cm3)

	U	PB	BB	p
Soil				
0-5 cm	0.377 a	0.388 a	0.447 a	0.493
S.E.	0.146	0.098	0.146	
5-15 cm	0.293 a	0.275 a	0.323 a	0.258
S.E.	0.124	0.082	0.100	

(1) Calculated as 50% litter dry mass.

(2) Means from soil and forest floor layers do not sum to totals because totals were obtained by averaging sites having the same treatment

Table III-4. Mean C and N concentrations of forest floor and soil layers, forest floor dry mass, and soil bulk density, by treatment. U=uncut forests, PB=piled-and-burned clearcuts, and BB=broadcast-burned clearcuts. Treatment means compared for each layer with one-way ANOVA followed by Fisher's LSD. Means followed by same letter do not differ significantly at $p<0.05$.

Table III-4.

N concentration (%)

	U	PB	BB	p
Litter	0.59 a	0.38 c	0.45 b	<0.001
S.E.	0.02	0.02	0.03	
F layer	0.90	-	-	-
S.E.	0.04 (2)			
Soil				
0-5 cm	0.31 a	0.34 a	0.27 a	0.358
S.E.	0.04	0.02	0.02	
5-15 cm	0.21 a	0.21 a	0.21 a	0.965
S.E.	0.03	0.01	0.02	

N_{min} concentration (ppm)

	U	PB	BB	p
F layer	312	-	-	-
S.E.	46 (2)			
Soil				
0-5 cm	82.8 a	96.7 a	49.8 b	0.005
S.E.	17.4	14.2	11.9	
5-15 cm	30.9 a	37.5 a	36.6 a	0.574
S.E.	6.5	4.7	7.3	

N_{min} percent
(% mineralized of N concentration)

	U	PB	BB	p
Soil				
0-5 cm	2.77 a	3.21 a	2.36 a	0.552
S.E.	0.36	0.62	0.82	
5-15 cm	1.66 a	2.02 a	1.74 a	0.703
S.E.	0.47	0.42	0.14	

(1) Analysis of variance performed on transformed data.
(2) Insufficient F layer samples for statistical analysis.

Table III-4 (cont).

C concentration (%)

	U	PB	BB	p
F layer	35.8	-	-	-
S.E.	3.1 (2)			
Soil				
0-5 cm	9.7 a	11.1 a	8.9 a	0.300
S.E.	1.0	1.3	1.2	
5-15 cm	4.1 a	5.0 a	5.0 a	0.247
S.E.	0.5	0.2	0.8	

C:N ratio

	U	PB	BB	p
Soil				
0-5 cm	32.3 a	34.8 a	43.0 a	0.876
S.E.	2.4	3.3	13.8	
5-15 cm	22.2 a	24.0 a	22.6 a	0.381
S.E.	4.7	2.1	2.3	

(1) Analysis of variance performed on transformed data.
(2) Insufficient F layer samples for statistical analysis.

Table III-5. Linear stepwise regression of N_{change} against forest floor, soil, and physiographic parameters from uncut forests. N_{change} = mean total nitrogen loss on clearcuts as a proportion of total nitrogen in uncut forest sites. Total nitrogen refers to the sum of N contents in forest floor and soil layers). N=10.

Table III-5.

Dependent variable	Independent variables	Partial R2	Regression parameters	Intercept	p
Nchange	C:N ratio (0-5 cm soil)	0.50	4.86	-166.2	0.022
	C:N ratio (5-15 cm soil)	0.20	-2.40		0.067
	C concentration	0.19	7.82		0.016
	Total R2=	0.89			

Table III-6. Correlation coefficients among topographic, forest floor, and soil variables. Paired numbers represent coefficients (top) and significance probability levels (bottom)

Table III-6

	Aspect	BD at 5-15 cm	BD(<2 mm) at 0-5 cm	CN 0-5 cm	CN 5-15 cm	C conc. 0-5 cm	C conc. 5-15 cm	C conc. F layer
BD at	0.407							
5-15 cm	0.243							
BD(<2 mm)	0.629	0.641						
at 0-5 cm	0.052	0.046						
CN	-0.386	-0.673	-0.209					
0-5 cm	0.271	0.033	0.563					
CN	-0.107	-0.289	-0.316	0.445				
5-15 cm	0.768	0.418	0.374	0.198				
C conc.	-0.375	-0.077	-0.318	0.168	0.292			
0-5 cm	0.286	0.833	0.371	0.642	0.414			
C conc.	-0.348	-0.200	-0.317	0.470	0.929	0.478		
5-15 cm	0.325	0.580	0.372	0.171	0.000	0.163		
C conc.	0.712	0.600	0.839	-0.200	-0.063	-0.331	-0.126	
F layer	0.021	0.067	0.002	0.579	0.863	0.351	0.728	
Nchange	0.395	0.285	-0.048	-0.710	0.084	-0.430	-0.081	0.200
	0.259	0.424	0.896	0.022	0.817	0.214	0.824	0.579

Table III-6 (continued)

	Aspect	BD at 5-15 cm	BD(<2 mm) at 0-5 cm	CN 0-5 cm	CN 5-15 cm	C conc. 0-5 cm	C conc. 5-15 cm	C conc. F layer	Nchange	CN F layer	% N in F layer
CN	0.462	0.675	0.600	-0.305	-0.257	-0.237	-0.233	0.850	0.175		
F layer	0.179	0.032	0.067	0.392	0.473	0.510	0.517	0.002	0.630		
% N in	0.337	-0.339	-0.097	0.306	0.757	-0.146	0.549	0.253	0.362	-0.030	
F layer	0.342	0.338	0.789	0.390	0.011	0.688	0.100	0.481	0.304	0.934	
Mass of	0.713	0.289	0.784	0.099	0.062	-0.275	-0.015	0.786	-0.014	0.442	0.427
F layer	0.021	0.418	0.007	0.785	0.865	0.442	0.968	0.007	0.969	0.201	0.218
Nmin	0.402	-0.177	0.467	0.091	-0.453	-0.767	-0.607	0.320	0.007	0.092	0.057
F layer	0.250	0.625	0.174	0.803	0.189	0.010	0.063	0.367	0.985	0.801	0.876
N conc.	0.670	0.135	0.695	0.026	0.184	-0.457	0.021	0.668	0.233	0.193	0.544
F layer	0.034	0.710	0.026	0.942	0.610	0.184	0.954	0.035	0.518	0.593	0.104
Nmin	-0.691	-0.374	-0.443	0.418	0.589	0.519	0.717	-0.565	-0.282	-0.665	0.082
5-15 cm	0.027	0.287	0.200	0.229	0.073	0.124	0.020	0.089	0.430	0.036	0.821
Nmin	-0.490	-0.075	-0.494	-0.173	0.163	0.735	0.338	-0.643	-0.039	-0.572	-0.228
0-5 cm	0.151	0.836	0.147	0.634	0.652	0.016	0.340	0.045	0.916	0.084	0.526

Table III-6 (continued)

	Aspect	BD at 5-15 cm	BD(<2 mm) at 0-5 cm	CN 0-5 cm	CN 5-15 cm	C conc. 0-5 cm	C conc. 5-15 cm	C conc. F layer	Nchange	CN F layer	% N in F layer
Nmin:N	-0.486	-0.422	-0.421	0.469	0.800	0.368	0.812	-0.405	-0.120	-0.584	0.394
5-15 cm	0.154	0.224	0.226	0.171	0.006	0.295	0.004	0.245	0.742	0.076	0.260
Nmin:N	-0.833	-0.555	-0.673	0.435	0.378	0.479	0.534	-0.749	-0.301	-0.691	0.006
0-5 cm	0.003	0.096	0.033	0.209	0.282	0.161	0.112	0.013	0.399	0.027	0.987
N conc.	-0.224	0.329	-0.210	-0.569	-0.194	0.630	-0.010	-0.360	0.116	-0.197	-0.493
0-5 cm	0.533	0.354	0.560	0.086	0.592	0.051	0.979	0.307	0.749	0.586	0.148
N conc.	-0.509	0.141	-0.016	0.013	-0.574	-0.221	-0.345	-0.215	-0.297	0.105	-0.696
5-15 cm	0.133	0.697	0.964	0.972	0.083	0.539	0.329	0.551	0.405	0.773	0.025
% N at	0.245	0.642	0.165	-0.886	-0.355	0.198	-0.305	0.028	0.441	0.095	-0.447
0-5 cm	0.495	0.045	0.650	0.001	0.315	0.584	0.391	0.940	0.203	0.793	0.195
% N at	-0.312	-0.045	0.227	0.373	-0.600	-0.101	-0.431	-0.034	-0.743	0.142	-0.637
5-15 cm	0.381	0.903	0.529	0.289	0.067	0.781	0.214	0.925	0.014	0.696	0.048
Slope	-0.634	0.133	-0.479	-0.374	-0.334	0.409	-0.101	-0.518	0.021	-0.098	-0.630
	0.049	0.714	0.162	0.288	0.346	0.241	0.781	0.125	0.954	0.787	0.051

Table III-6 (continued)

	Mass of F layer	Nmin F layer	N conc. F layer	Nmin 5-15 cm	Nmin 0-5 cm	Nmin:N 5-15 cm
Nmin	0.458					
F layer	0.183					
N conc.	0.842	0.590				
F layer	0.002	0.073				
Nmin	-0.389	-0.505	-0.203			
5-15 cm	0.266	0.136	0.574			
Nmin	-0.490	-0.700	-0.483	0.641		
0-5 cm	0.150	0.024	0.157	0.046		
Nmin:N	-0.254	-0.438	-0.011	0.928	0.432	
5-15 cm	0.480	0.206	0.976	0.000	0.213	
Nmin:N	-0.526	-0.457	-0.454	0.872	0.680	0.748
0-5 cm	0.118	0.185	0.188	0.001	0.031	0.013

Table III-6 (continued)

	Mass of F layer	Nmin F layer	N conc. F layer	Nmin 5-15 cm	Nmin 0-5 cm	Nmin:N 5-15 cm	Nmin:N 0-5 cm	N conc. 0-5 cm	N conc. 5-15 cm	% N at 0-5 cm	% N at 5-15 cm
N conc.	-0.427	-0.618	-0.475	0.222	0.839	-0.026	0.227				
0-5 cm	0.218	0.057	0.165	0.538	0.002	0.944	0.529				
N conc.	-0.311	0.141	-0.447	-0.128	-0.091	-0.376	0.060	0.049			
5-15 cm	0.382	0.697	0.195	0.724	0.802	0.285	0.869	0.893			
% N at	-0.179	-0.300	-0.129	-0.176	0.447	-0.316	-0.292	0.817	-0.032		
0-5 cm	0.622	0.399	0.722	0.626	0.196	0.373	0.413	0.004	0.930		
% N at	-0.007	0.366	-0.245	-0.181	-0.303	-0.383	-0.026	-0.228	0.753	-0.330	
5-15 cm	0.984	0.298	0.495	0.618	0.395	0.275	0.943	0.527	0.012	0.352	
Slope	-0.755	-0.564	-0.834	0.232	0.644	-0.026	0.457	0.716	0.452	0.428	0.112
	0.012	0.089	0.003	0.520	0.045	0.944	0.184	0.020	0.189	0.217	0.758

Chapter IV.

Ectomycorrhizal fungi in soil aggregates from forests and clearcuts, southwest Oregon

Introduction

Modification of the soil environment by forest harvest and site preparation may reduce ectomycorrhiza (EM) formation on regenerating tree seedlings. For example, clearcutting and broadcast burning reduced EM formation on outplanted (Amaranthus and Perry 1987) and greenhouse-grown seedlings (Parke et al. 1984). But as Perry et al. (1987) pointed out, the response to harvesting can be complex, resulting in no change or even increases in total EM formation.

These sometimes conflicting results underscore the gaps in our knowledge of the soil environment and its effect on EM formation. Fries (1987) noted that "...the very last part of the spore 'flight' for the ectomycorrhizal fungi takes place in the soil and may be very risky...", yet soil remains a poorly understood habitat for spores and other propagules. Developing a propagule ecology (e.g., Tommerup 1985) for ectomycorrhizal fungi would provide an autecological framework in which EM formation in disturbed ecosystems could be better

understood.

Our objective was a first approximation of a soil habitat description for EM fungal propagules. The discrete microhabitats that exist in soil can be characterized at the level of soil aggregates (Hattori and Hattori 1976; Kilbertus 1980) that are relatively easy to separate from whole soil. Previous investigations based on segregation of particle size fractions have yielded information about the spatial distribution of microorganisms, enzymes, and nutrients in soil (Hattori 1988; Mateos and Carcedo 1985; Christensen 1986). In the present study we bioassay soil particle size fractions taken from forests and old, poorly-revegetated clearcuts for their potential to form EM with greenhouse-grown tree seedlings.

Methods and Materials

Site Characteristics

The rugged, deeply dissected terrain of southwest Oregon is geologically and floristically complex with hot, dry summers and cool, wet winters (Franklin and Dyrness 1973). We selected two sites for this study, each consisting of a clearcut paired with an adjacent forest. The first (Cedar Camp), has coarse-textured soil formed from quartz diorite, whereas the second (Holcomb Peak) has finer-textured soil derived from metavolcanic rocks (Ramp 1979). The Cedar Camp clearcut was harvested in 1969 and is dominated by annual grasses with a few scattered shrubs. Several attempts at reforestation have been failures. At Holcomb Peak woody plants represent a larger component of the clearcut vegetation, but portions remain understocked with tree seedlings. The unit was clearcut in 1971. Soils from both clearcuts have lost most large aggregates (2.0-9.5 mm) since harvest (Borchers and Perry 1990).

Soil Sampling

In June of 1986 ten sampling points were established at 15 m intervals along two randomly located transects in each clearcut. Sample spacing in forests was the same, but transects were shaped into an irregular grid because of limited area. Two soil samples were collected and bagged

near each point (approximately 3 m upslope and downslope) to a 15 cm depth in a 20x15 cm area. Soil was transferred to a 5°C cooler within 48h. Prior to analyses, taken from pairs of adjacent sampling points was composited, yielding five replicates for each forest and clearcut.

Soil particle size fractionation

Each composite soil sample was mixed by gently rolling in an air-filled plastic bag, then sieved to 9.5 mm to remove rocks, coarse roots, and large organic debris. The <9.5 mm material was evenly split and two 975-ml samples taken. One of these was mechanically disaggregated in tap water for five minutes using a Hamilton-Beach blender tipped with surgical tubing to minimize abrasion of soil particles and microorganisms. Both intact and disaggregated soil subsamples were then wet-sieved to obtain five sand-sized particle size classes (2-9.5 mm, 1-2 mm, 0.5-1 mm, 0.25-0.5 mm, 0.05-0.25 mm) and one silt-plus-clay size fraction (<0.05 mm). Except for the 9.5 mm size fraction, these were among the values used by Tisdall and Oades (1980).

Intact soil was wet-sieved one size fraction at a time by repeatedly immersing and draining sieves into buckets of water. The resulting soil slurry was then poured into the next smallest-sized sieve to repeat the procedure. Fresh

water was added slowly to material on sieves as a final rinse. The smallest particle size class, a <0.05 mm slurry, was concentrated by vacuum filtration through Whatman no. 42 filter papers on Buchner funnels. The resulting particle size fractions were stored moist at 5° C after weighing and subsampling for moisture content. Disaggregated soil was wet-sieved in a similar fashion, but material was forced through sieves by hand and with water streams to assure complete disruption of large aggregates.

Greenhouse bioassay

Six particle size fractions as well as pasteurized and unpasteurized whole soil (<9.5 mm) were assayed for their potential to form ectomycorrhizae with greenhouse-grown Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) seedlings. For each whole soil replicate (n=5 at each forest and clearcut, Holcomb Peak and Cedar Camp) the moist equivalent of 500 g oven-dried material was divided equally among four 160-ml planting tubes. Pasteurization consisted of steam treatment at 80° C for 12 hours.

In the bioassay of six particle size fractions, 24 seedlings defined six replicates, i.e., four for each of six size fractions. The quantities of soil fractions that were used for planting were in proportion to the sample particle size distribution, such that the total amount to be distributed among 24 tubes was 500 g oven-dry weight.

Steam-pasteurized (80° C) peat and vermiculite (1:1 ratio) were mixed with each soil fraction in quantities sufficient to make a 640 ml volume for partitioning among the four 160-ml planting tubes. In addition, ten peat-vermiculite "blanks" were evenly distributed among the other planting tubes to detect airborne or seed contamination by ectomycorrhizal fungi.

Douglas-fir seeds, selected from an appropriate seed zone, were soaked overnight in running tap water, then air dried. After 30 days of cold stratification (5° C) they were planted in tubes beneath a light cover of gravel to prevent cross-contamination by water splash. Tubes were weeded to one seedling each after seedling emergence. High intensity sodium vapor lamps (150 uE) extended natural day lengths to 16 h. After one month's growth, each seedling was fertilized at monthly intervals with 5 ml of 2.50 g/L Peter's conifer grower (20:19:18 NPK).

Seedlings were grown in soils from Holcomb Peak for 4-6 months and Cedar Camp for 6-8 months, concurrently. They were harvested one replicate at a time, i.e., four seedlings. Shoots were removed, air dried, and weighed separately. Roots were washed gently in running water, then cut tranversely into 2 cm segments. Cut roots from all four seedling were then thoroughly mixed in a pan of water. One area of the pan was systematically subsampled to

yield short root counts of 200-300. We defined short roots as single root tips (mycorrhizal or non-mycorrhizal) or clusters of root tips (always mycorrhizal) that have probably arisen from a single infection point on the root. Short roots as well as root tips were tallied and classified as to mycorrhizal status. Mycorrhizal roots were classified into types based on morphology, e.g., color, texture, extramatrical hyphae, rhizomorphs. Total and subsample root weights were determined after air drying.

Statistical Analysis and Variables

In all analyses numbers of ectomycorrhizal short roots on seedlings were expressed as a proportion of the total number of short roots. In this experiment, we considered proportions to be a more accurate estimate of viable propagule density than short root numbers, because total short root numbers differed substantially among treatments.

Several analyses of variance (ANOVAs) were performed. Assumptions of normality and homogeneity of variance were evaluated using the W-test (Shapiro and Wilk 1982) and Levene's test (Levene 1960). When either assumption could not be met, a logit transformation was applied to response variables (Weisberg 1985).

Differences in seedling mycorrhizal responses between

forests and clearcuts and the effect od soil disaggreation were both evaluated using t-tests. The effect of soil disaggregation on total short roots, shoot weight, and root weight in soil size fractions was tested with separate split-plot ANOVAs of Cedar Camp and Holcomb Peak data. (Disaggregation treatment was a main-plot factor). Separate one-way ANOVAs were performed on the proportion of total EM and EM types from seedlings grown in soil particle size fractions from forests and clearcuts. Differences among means associated with various particle size fractions were evaluated using Fisher's protested LSD at $p=0.05$ (Petersen 1985). All analyses were carried out using SAS (SAS Institute, Inc. 1985).

Results

Soil size fractions

The distribution of mass with particle size reflects the sharply contrasting textures of soil from Cedar Camp and Holcomb Peak (Table IV-2). Generally, most mass was contained in the 2-9.5 mm size class. Although Cedar Camp soil was coarser-textured than Holcomb Pk (Table IV-2; <2mm dia.), there were considerably fewer coarse fragments (2-9.5 mm size class).

Ectomycorrhiza types and fungi

We observed the following types of EM on Douglas-fir:

Type 1

This EM type was formed by various fungi with abundant rhizomorphs ranging in color from tan to gray to white. The mantle was loosely sheathed with dense extramatrical hyphae of similar colors. An irregular branching habit often produced clusters of many root tips. This type was possibly formed by Rhizopogon sp. (M. Castellano, personal communication).

Type 2

Mantle appeared coarse-textured and black with rigid,

straight black hyphae projecting from surface to distances exceeding the diameter of the root tip. The fungal symbiont was Cenococcum geophilum Fr.

Type 3

Mantle was iridescent gold with sparse gold rhizomorphs. Gold color readily leached with 70% EtOH. Symbiont was possibly Alpova sp. or Melanogaster sp. (M. Castellano, personal communication).

Type 4

Mantle was smooth and brick red. Possibly symbiotic with Lactarius sp. (D. Luoma, personal communication).

Type 5

Very dark brown mantle; apex tan colored. Texture generally smooth, but somewhat wrinkled. Symbiont unknown, but resembles brown type found in previous studies (Pilz and Perry 1984; S. L. Borchers and Perry 1990; Rose and Perry, unpubl. data).

Type 6

Tan colored mantle with nearly white apex both staining blue in $FeSO_4$. Symbiont was common greenhouse

contaminant, Thelephora terrestris (M. Castellano, personal communication).

Bioassay of whole soil

Seedlings grown in unpasteurized whole soil from Holcomb Peak clearcut had a smaller total proportion of EM short roots than seedlings grown in forest soil (Fig. IV-1). This was due mainly to differences in type 1 proportions. With soil from Cedar Camp forest and clearcut, seedlings formed similar total proportions of EM short roots, though somewhat less than Holcomb Peak forest and clearcut. Type 5 EM dominated roots systems in Cedar Camp forest soil, but in clearcut soil it was relatively minor compared to type 4. This was consistent with previous observations on this site (Rose and Perry unpubl. data). Type 6, Thelephora terrestris, was prevalent on seedlings grown in Holcomb Peak soil, but nearly absent from Cedar Camp seedlings.

In pasteurized whole soil, seedlings were mycorrhizal exclusively with type 6 and usually in proportions greater than total EM in other treatments (Table IV-3). In pasteurized peat-vermiculite most seedlings were mycorrhizal exclusively with type 6. Two of the ten seedlings were non-mycorrhizal and one was slightly colonized with type 1.

Bioassay of particle size fractions

Total EM proportions in fractions (Fig. IV-2a,b) from Cedar Camp soil were generally lower than at Holcomb Peak as was the case with whole soil (Fig. IV-1). There was also more variability among fractions at Cedar Camp with greatest root colonization usually occurring in smaller size fractions. In intact soil from Cedar Camp forest, the distribution of type 6 was distinct from other EM (Fig. IV-3a). It was restricted mainly to smaller size fractions, whereas other types dominated size fractions >0.25 mm.

Type 1 was present in all treatments and ranged from less than a percent to nearly 50% of total short roots (Fig. IV-2a,b; Fig. IV-3a,b). It was most prevalent on seedlings grown in Holcomb Peak soil, although proportions varied widely among particle size fractions. In Cedar Camp clearcut soil the proportion of type 1 EM was altered by disaggregation, increasing from 7% to 23% (Table IV-4; Fig. IV-3a). Disaggregating Holcomb Peak forest soil also appeared to stimulate type 1 formation, but to a lesser extent (Table IV-4; Fig. IV-3b). The effect on Holcomb Peak clearcut soil was opposite, with type 1 proportions decreasing from 35% to 22%.

The proportion of short roots mycorrhizal with type 2 averaged less than 8% on both sites, and was associated mainly with the three largest particle size classes (Fig.

IV-3c,d). Disaggregation shifted the distribution of type 2 EM toward smaller particle size fractions.

Type 5 EM were also clustered in the larger diameter size fractions of soil from Cedar Camp forest (41% short roots colonized in the 2-9.5 mm fraction) (Fig. IV-3e; Fig. IV-2a). None were detected in Holcomb Peak soil (Fig. IV-1). Disaggregation greatly increased the quantity of material in the <0.05 mm fraction (Table IV-2), yet most type 5 mycorrhizae were found in the 0.05-0.25 mm fraction. The combined level of type 5 colonization decreased from 13% to 3% producing a similar trend in combined totals for the forest at Cedar Camp (Table IV-4).

Although type 4 EM were predominant in whole soil from Cedar Camp clearcut (Fig. IV-1), only small quantities were detected after fractionation. These were restricted to smaller-diameter size fractions (Fig. IV-3f; Table IV-4). Type 3 mycorrhizae occurred in small proportions in Holcomb Peak soil, also in smaller size fractions (Fig. IV-3g). Type 6 was common in most size fractions from all treatments (Fig. IV-2a,b).

Soil disaggregation had little effect on shoot and root mass of seedlings (Fig. IV-4a,b,c,d). However it produced more total short roots, a 38% and 27% increase at Cedar Camp and Holcomb Peak, respectively (Fig. IV-4e,f). Mean numbers of short roots were less variable across size

fractions than shoot and root weights.

Discussion

The bioassay of soil size fractions demonstrated that EM fungal propagules occupy a mosaic of distinct microhabitats that correspond to soil aggregates. Such structure actually represents a complex environmental gradient composed of many fundamental abiotic factors, e.g., nutrient, water, and O_2 availability, types of organic matter, etc. (Turchenek and Oades 1979; Sexstone et al. 1985; Shaykewich and Warkentin 1970; Foster 1985). But interactions of fungi with other soil organisms can outweigh the effect of abiotic factors such as these (Christensen 1989).

In the present study, disaggregation of soil from Cedar Camp clearcut appears to have stimulated type 1 (possibly Rhizopogon sp.) EM formation. There are at least three possible explanations. First, disaggregation may have reduced allelopathic effects of other organisms by lowering their activity, or by segregating them from EM propagules. Other evidence at Cedar Camp supports this. Friedman et al. (1990) isolated several actinomycetes from the Cedar Camp forest and clearcut soils that inhibited in vitro growth of two common EM fungi. Actinomycete activity may supress EM formation in the clearcut, since pasteurization of forest soil used as inoculum greatly increased EM formation and seedling survival in the

clearcut (Amaranthus and Perry 1987).

Alternatively, disaggregation may have simply dispersed dense clusters of type 1 propagules, thereby decreasing "competition" for uncolonized roots. A clustered distribution could arise if propagules were deposited in mammal fecal pellets. This would be most likely if type 1 EM are formed predominantly by Rhizopogon sp. The genus forms hypogeous sporocarps and may be largely dependent on small mammals for spore dispersal (Maser et al. 1978). On the clearcut there were numerous clusters of mammal fecal pellets that contained fungal spores (Gautieria sp. and possibly Rhizopogon sp.) (Borchers, pers. obs.).

A third possibility for the type 1 response to disaggregating soil from the Cedar Camp clearcut is fragmentation of type 1 hyphae creating increased numbers of viable propagules (Atlas and Bartha 1981). This seems unlikely, because for many years there have been few EM host plants on the clearcut that could potentially sustain active mycelia. Indeed, SEM revealed few hyphae in soil from the clearcut, but larger quantities in the forest (Borchers and Perry, unpubl. data).

This disaggregation effect must be cautiously interpreted, especially in view of the conflicting results with type 1 at Holcomb Peak. The effect is probably highly

site-specific and depends on numerous factors that enhance or supress EM formation (Mosse et al. 1982; Slankis 1974).

The greater abundance of type 2 EM (Cenococcum geophilum) in larger particle size fractions indicate that propagules were predominantly sclerotia and not hyphae. We frequently observed sclerotia during microscopic survey of roots, and diameters were generally greater than 0.25 mm, i.e., the sieve size for the 0.25-0.5 mm size fraction (Borchers, pers. obs.). Cenococcum geophilum is an imperfect fungus (does not form fruiting bodies) and produces abundant sclerotia in Douglas-fir and true fir forest soils (Vogt et al. 1982). The slight shift in distribution of Cenococcum geophilum EM toward smaller size fractions after disaggregation indicates that sclerotia were to some extent bound to larger diameter aggregates. The shift is probably not due to comminution of the hard sclerotia tissue during disaggregation, because a rubber-tipped blender was used for for soil disaggregation.

The distribution of type 5 EM in intact size fractions of Cedar Camp forest soil indicates that propagules were associated mainly with water-stable aggregates or organic debris 1-9.5 mm diameter. However, the shift toward the 0.05-0.25 mm size fraction after disaggregation signifies that propagules may have been even more strongly associated with smaller particles that make up large aggregates. The large decrease in type 5 activity after disaggregation

suggests that most propagules were inactivated by comminution.

Type 4 EM (possible Lactarius species) that were so prevalent in whole soil from Cedar Camp clearcut exhibited even greater sensitivity to soil disturbance as they were present only in smaller size fractions and in minute proportions. If type 4 EM were derived from wind-dispersed spores of a Lactarius species, then aggregate exteriors (i.e., larger pore spaces) would be a likely destination for spores carried into the soil profile. During wet-sieving spores would easily elute into smaller size fractions (as the type 4 distribution in size fractions indicates). This displacement from aggregate exteriors may represent the loss of a unique microhabitat, one that confers certain advantages to type 4 fungi in competition for uncolonized root tips. For example, microorganisms more tolerant of desiccation may proliferate on aggregate exteriors (Hattori and Hattori 1976). In a similar way, type 3 EM in Holcomb Peak soil size fractions were apparently not retained with larger aggregates during wet-sieving.

Greater numbers of short roots in disaggregated Cedar Camp and Holcomb Peak soil fractions were probably not a result of increased nutrient availability. Ultrasonic disaggregation increased nitrogen availability in soil from

both sites. However, the effect was significantly smaller with Cedar Camp soil (chapter II) which was where the largest short root response occurred.

In whole soil, lower total EM proportions associated with clearcutting and burning at Holcomb Peak reflect lower proportions of type 1 EM. This decrease is markedly smaller than those measured by Parke et al. (1984) who surveyed difficult-to-regenerate sites in this region. At Cedar Camp, the similar total EM proportions we obtained from forest and clearcut soil paralleled the responses obtained by Amaranthus and Perry (1987). In that study seedlings outplanted to the Cedar Camp clearcut were inoculated with soil from the adjacent forest, but total EM formation (no. of root tips) and seedling survival rates were unchanged from controls. Perry and Rose (1983) however, compared this forest and clearcut in a greenhouse bioassay and found significantly fewer EM associated with the clearcut.

Compared to Cedar Camp, seedlings formed larger proportions of total EM in Holcomb Peak soils. However, Holcomb Peak soil may have a considerably lower inoculum potential if we assume that the source of type 6 EM (Thelephora terrestris) is greenhouse contamination and not test soils. From this perspective, there were too few native EM propagules in Holcomb Peak soil to compete with

Thelephora terrestris contamination. In contrast, higher levels of native EM propagules in Cedar Camp soil precluded most Thelephora terrestris colonization.

The biological significance of EM formation in this study encompasses not only total EM formation, but also the diversity and abundance of native EM fungi (Perry et al. 1987). For example, at Cedar Camp clearcutting resulted in lower proportions of type 5 EM, but compensation by type 4 EM maintained similar levels of root colonization. However, the less diverse flora at Holcomb Peak was accompanied by a decrease in type 1 EM formation that produced lower total EM proportions. This suggests that soils with a greater diversity of native EM fungi are better able to maintain inoculum potential when disturbed. However, if the shift in EM types results in host-fungus combinations less fit for the harsh environment of a high elevation clearcut, then poor seedling survival may result.

Figure IV-1. Colonization by ectomycorrhiza type of Douglas-fir seedlings grown in whole soil from forest and clearcuts of Cedar Camp and Holcomb Peak Numbers above individual bars are standard errors of mean proportion of short roots ectomycorrhizal. Other values are significance probability values associated with t-tests of forest and clearcut means.

Figure IV-1

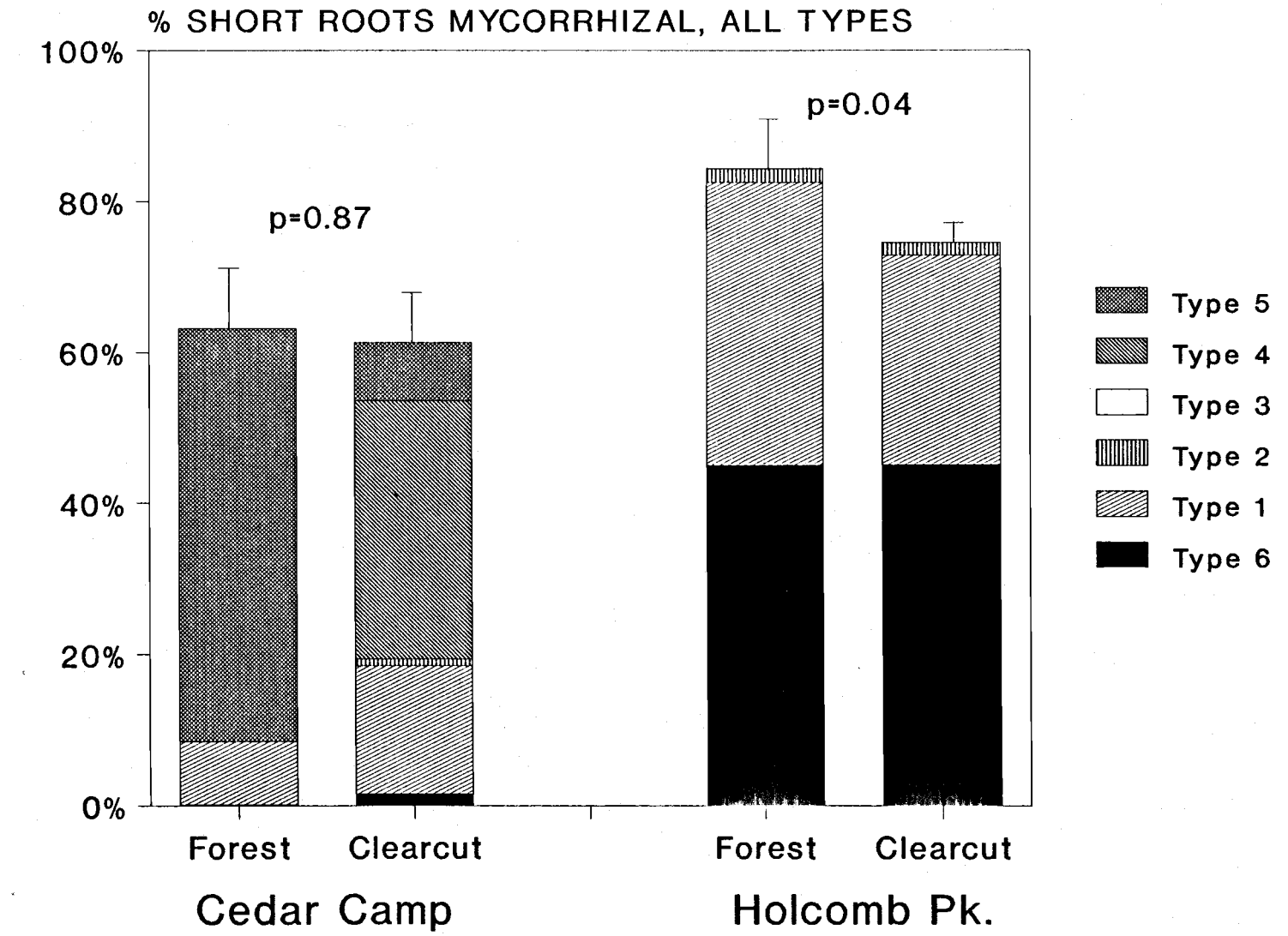
% SHORT ROOTS MYCORRHIZAL, ALL TYPES
100%
80%
60%
40%
20%
0%
p=0.87
p=0.04
Type 5
Type 4
Type 3
Type 2
Type 1
Type 6
Forest
Clearcut
Forest
Clearcut
Cedar Camp
Holcomb Pk.

Figure IV-2a,b. Total ectomycorrhiza colonization on Douglas-fir seedlings grown in six particle size fractions obtained from intact and disaggregated soil: 1 = 2-9.5 mm; 2 = 1-2 mm; 3 = 0.5-1 mm; 4 = 0.25-0.5 mm; 5 = 0.05-0.25 mm; 6 = <0.05 mm. One-way ANOVA and Fisher's protected LSD were used to separately evaluate the four groups of size fraction means. Bars with same lower case letters are not significantly different ($p \leq 0.05$).

Figure IV-2a

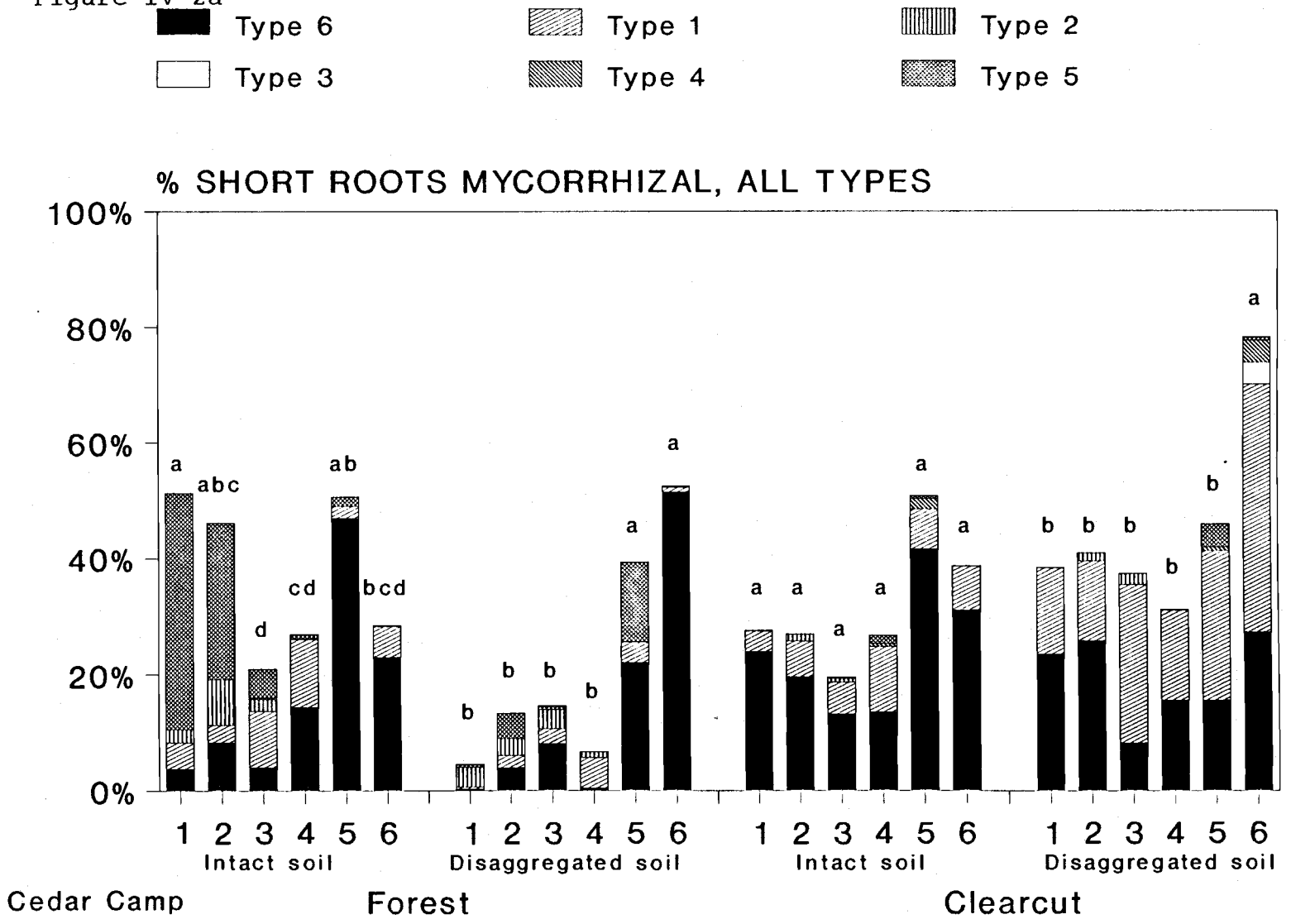
Type 6
Type 1
Type 2
Type 3
Type 4
Type 5
% SHORT ROOTS MYCORRHIZAL, ALL TYPES
100%
80%
60%
40%
20%
0%
a
abc
d
cd
ab
bcd
b
b
b
b
a
a
a
a
a
a
a
a
a
b
b
b
b
b
a
1 2 3 4 5 6
Intact soil
1 2 3 4 5 6
Disaggregated soil
1 2 3 4 5 6
Intact soil
1 2 3 4 5 6
Disaggregated soil
Cedar Camp
Forest
Clearcut

Figure IV-2b

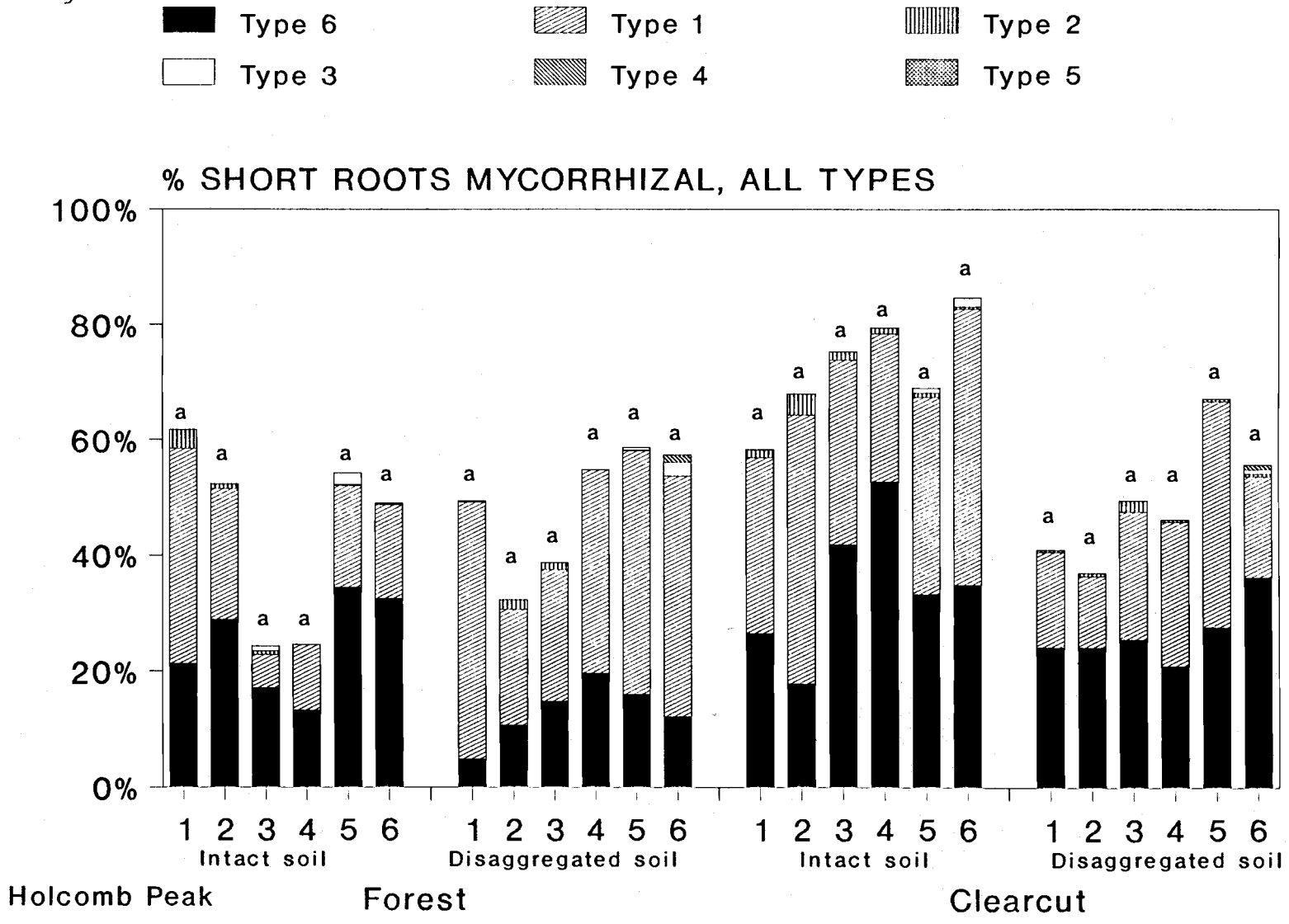
Type 6
Type 1
Type 2
Type 3
Type 4
Type 5
% SHORT ROOTS MYCORRHIZAL, ALL TYPES
100%
80%
60%
40%
20%
0%
1 2 3 4 5 6
Intact soil
Disaggregated soil
Intact soil
Disaggregated soil
Holcomb Peak
Forest
Clearcut

Figure IV-3a,b,c,d,e,f,g. Colonization by ectomycorrhiza types of Douglas-fir seedlings grown in six particle size fractions obtained from intact and disaggregated soil: 1 = 2-9.5 mm; 2 = 1-2 mm; 3 = 0.5-1 mm; 4 = 0.25-0.5 mm; 5 = 0.05-0.25 mm; 6 = <0.05 mm. One-way ANOVA and Fisher's protected LSD were used to separately evaluate the four groups of size fraction means. Bars with same lower case letters are not significantly different ($p \leq 0.05$).

Figure IV-3a

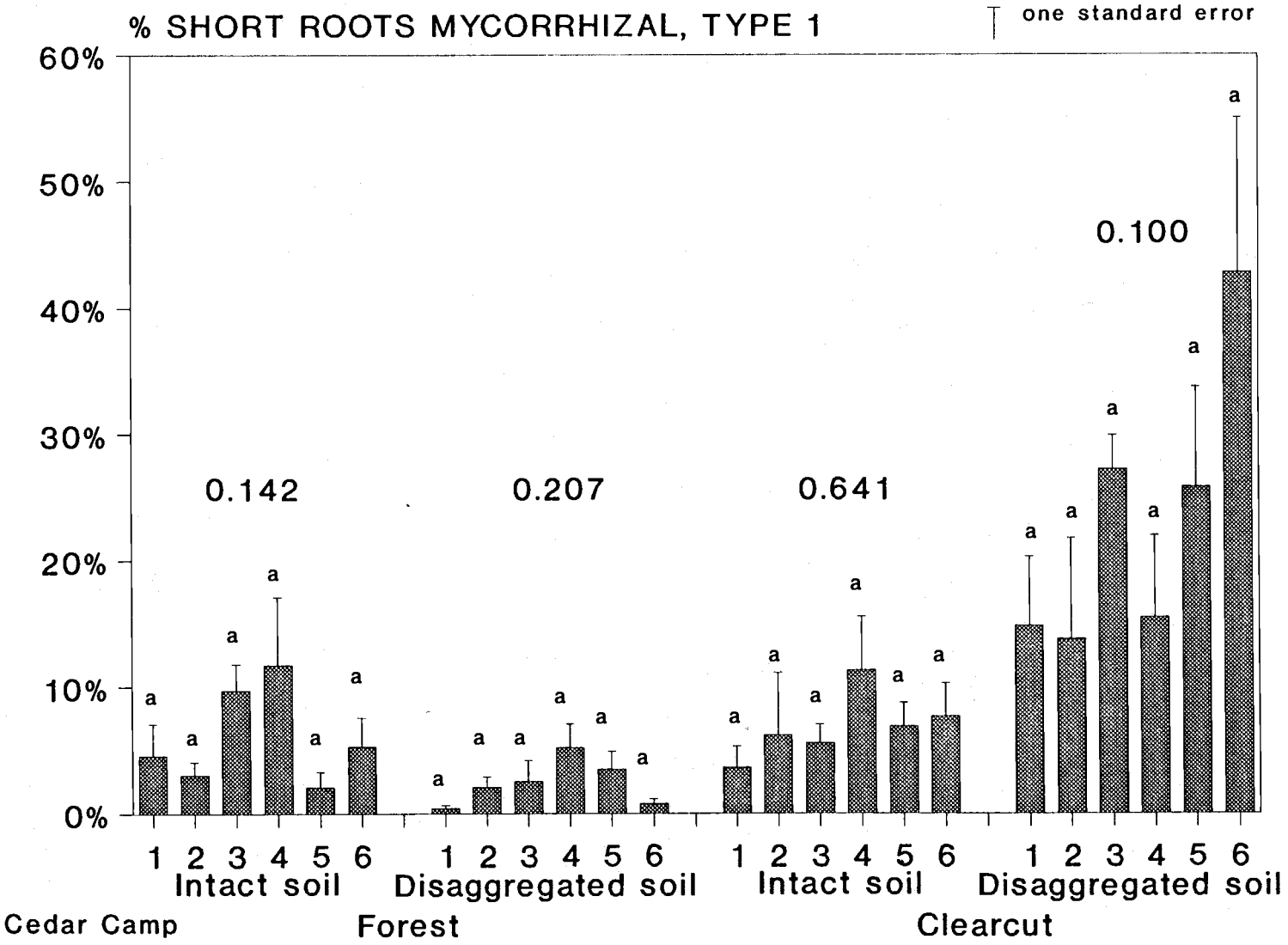
% SHORT ROOTS MYCORRHIZAL, TYPE 1
one standard error
60%
50%
40%
30%
20%
10%
0%
0.142
0.207
0.641
0.100
a
1 2 3 4 5 6
Intact soil
Disaggregated soil
Intact soil
Disaggregated soil
Cedar Camp
Forest
Clearcut

Figure IV-3b

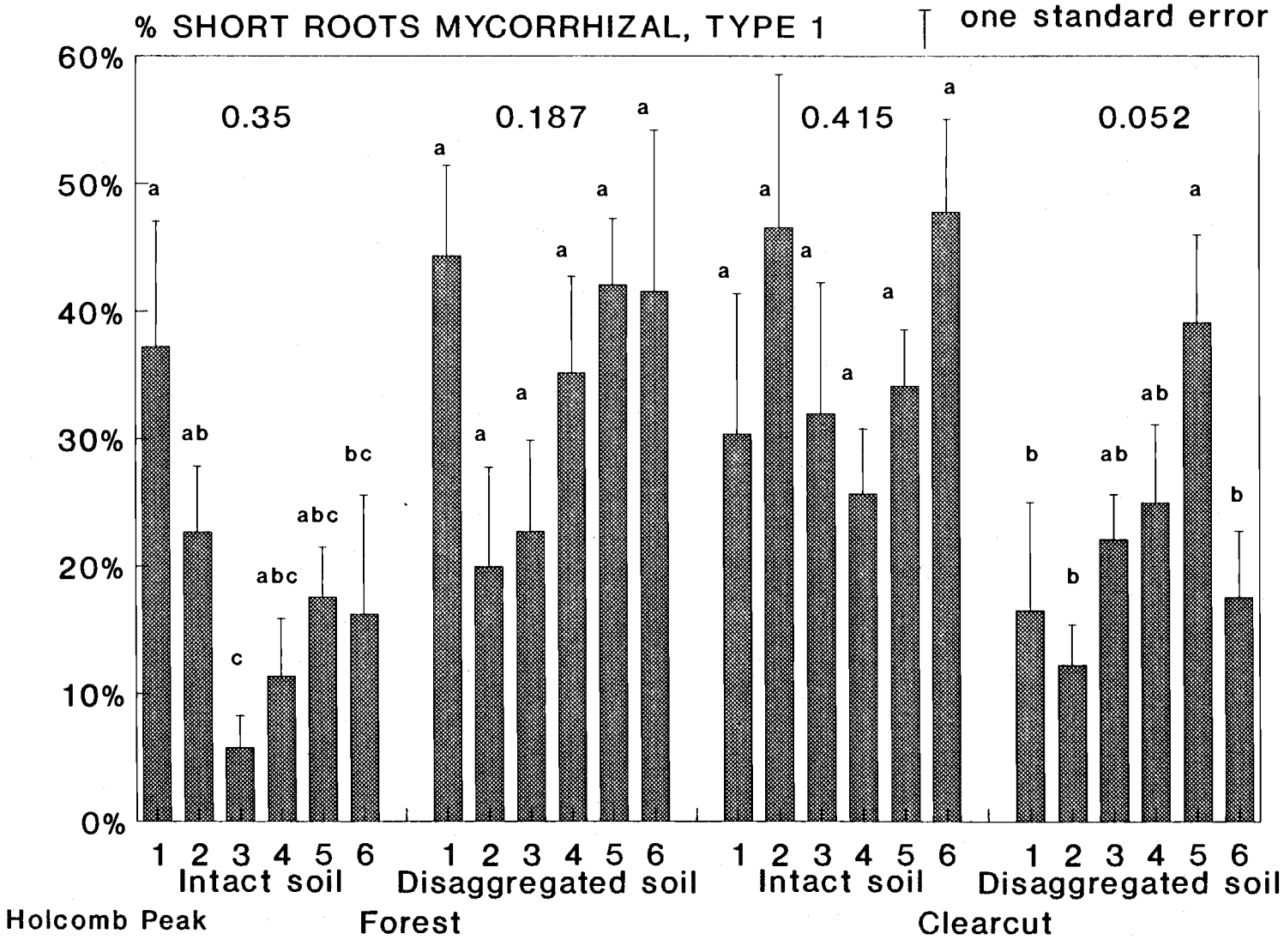
% SHORT ROOTS MYCORRHIZAL, TYPE 1
one standard error
60%
50%
40%
30%
20%
10%
0%
0.35
0.187
0.415
0.052
a
ab
c
abc
abc
bc
a
a
a
a
a
a
a
a
a
a
a
a
b
b
ab
ab
a
b
1 2 3 4 5 6
Intact soil
Disaggregated soil
Intact soil
Disaggregated soil
Holcomb Peak
Forest
Clearcut

Figure IV-3c

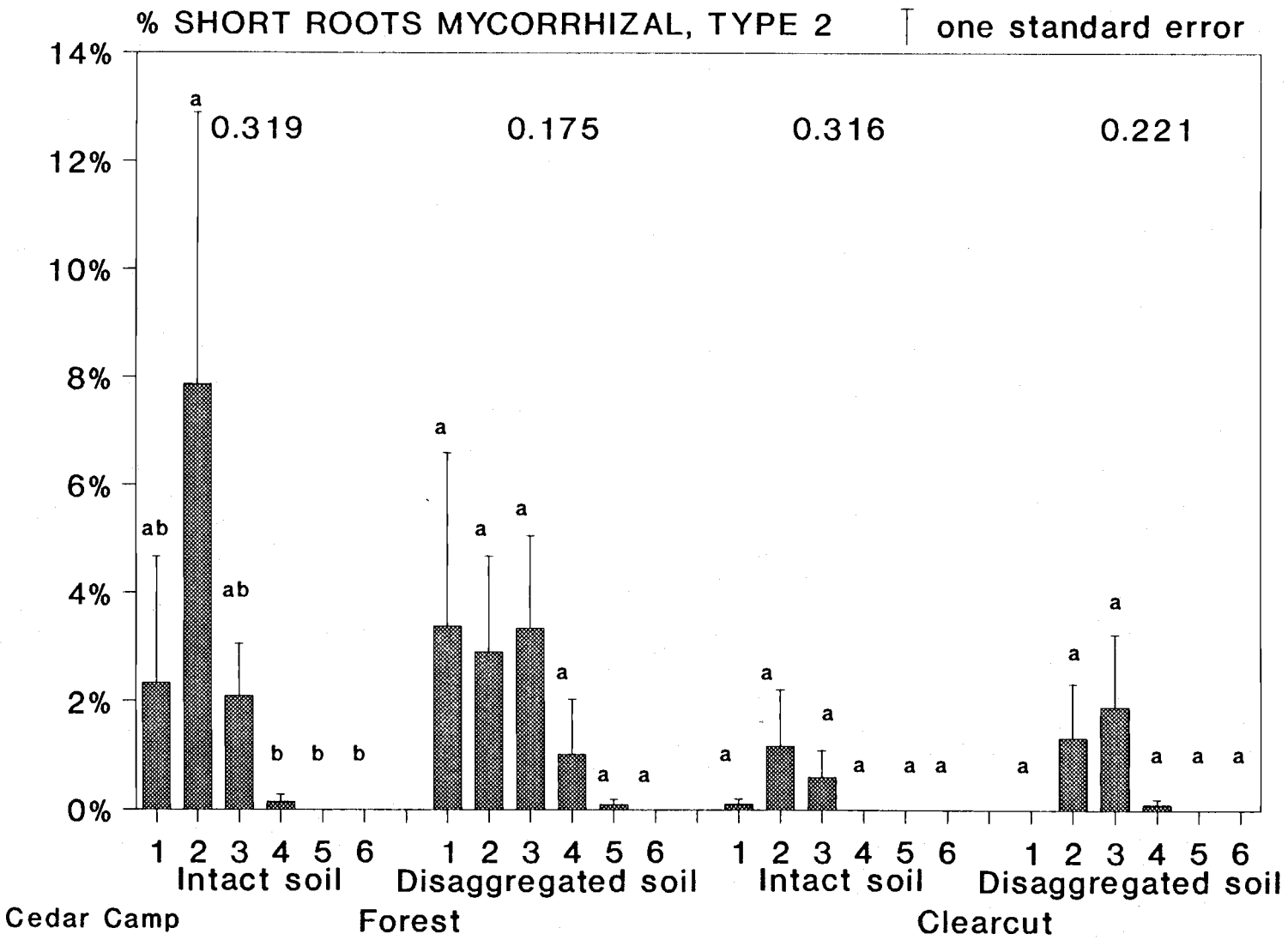
% SHORT ROOTS MYCORRHIZAL, TYPE 2
one standard error
14%
12%
10%
8%
6%
4%
2%
0%
0.319
0.175
0.316
0.221
1 2 3 4 5 6
Intact soil
Disaggregated soil
Intact soil
Disaggregated soil
Cedar Camp
Forest
Clearcut

Figure IV-3d

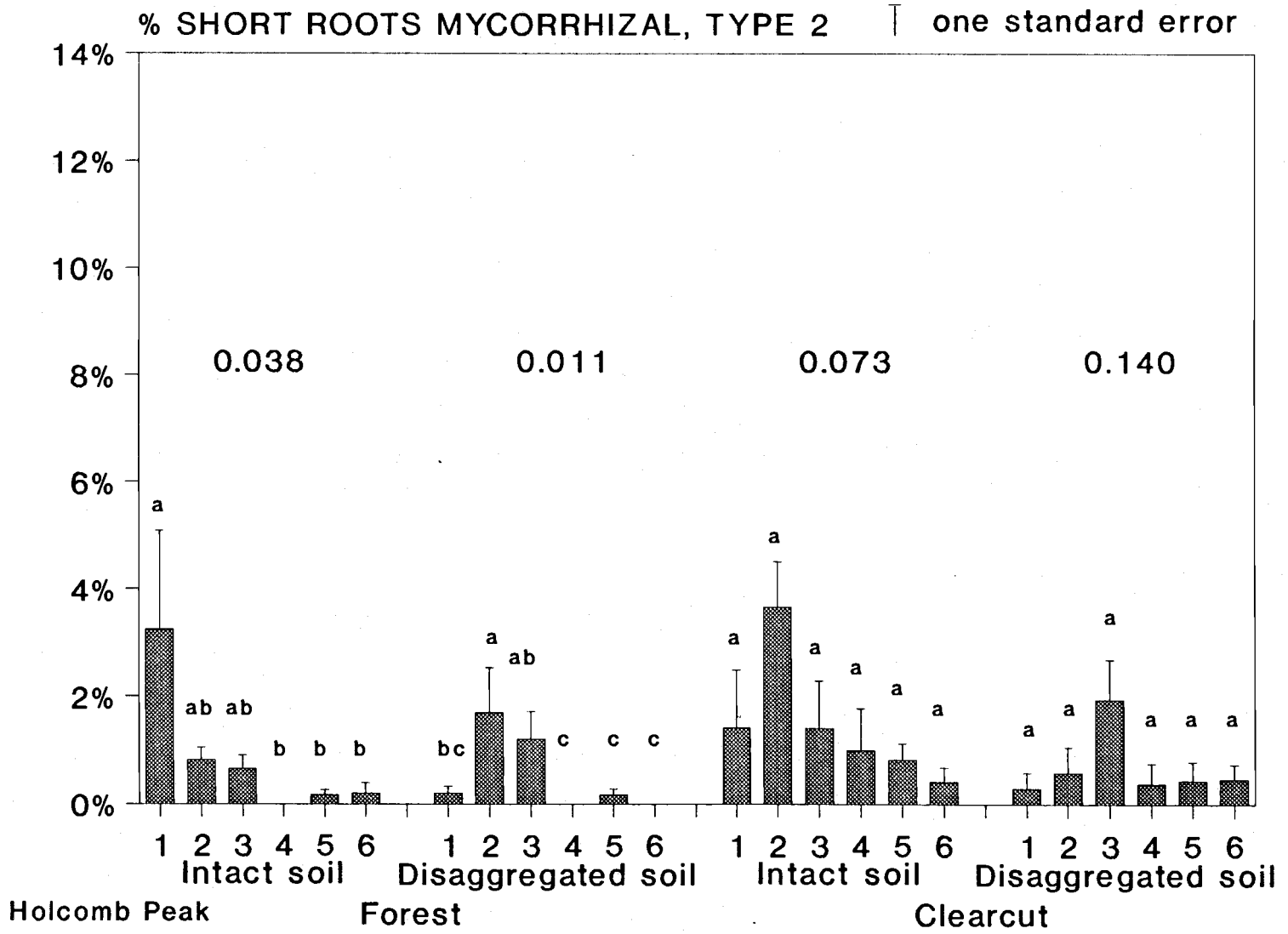
% SHORT ROOTS MYCORRHIZAL, TYPE 2
one standard error
14%
12%
10%
8%
6%
4%
2%
0%
0.038
0.011
0.073
0.140
a
ab ab
b b b
bc
a
ab
c c c
a
a
a
a
a
a
a
a
a
a
a
a
1 2 3 4 5 6
Intact soil
1 2 3 4 5 6
Disaggregated soil
1 2 3 4 5 6
Intact soil
1 2 3 4 5 6
Disaggregated soil
Holcomb Peak
Forest
Clearcut

Figure IV-3e

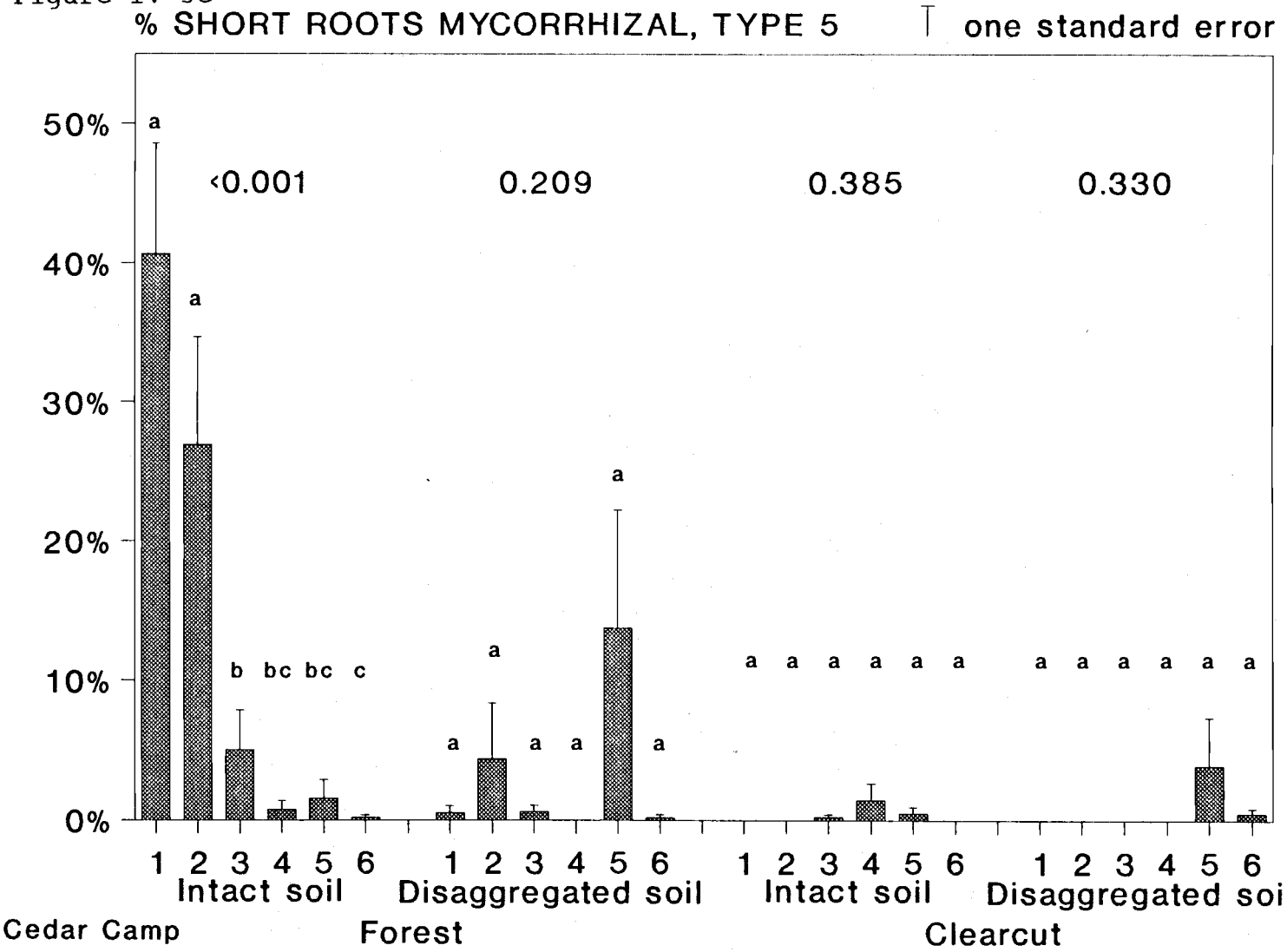
% SHORT ROOTS MYCORRHIZAL, TYPE 5
one standard error
50%
40%
30%
20%
10%
0%
<0.001
0.209
0.385
0.330
a
a
b bc bc c
a a a a
a
a a a a a a
a a a a a a
1 2 3 4 5 6
Intact soil
Disaggregated soil
Intact soil
Disaggregated soil
Cedar Camp
Forest
Clearcut

Figure IV-3f

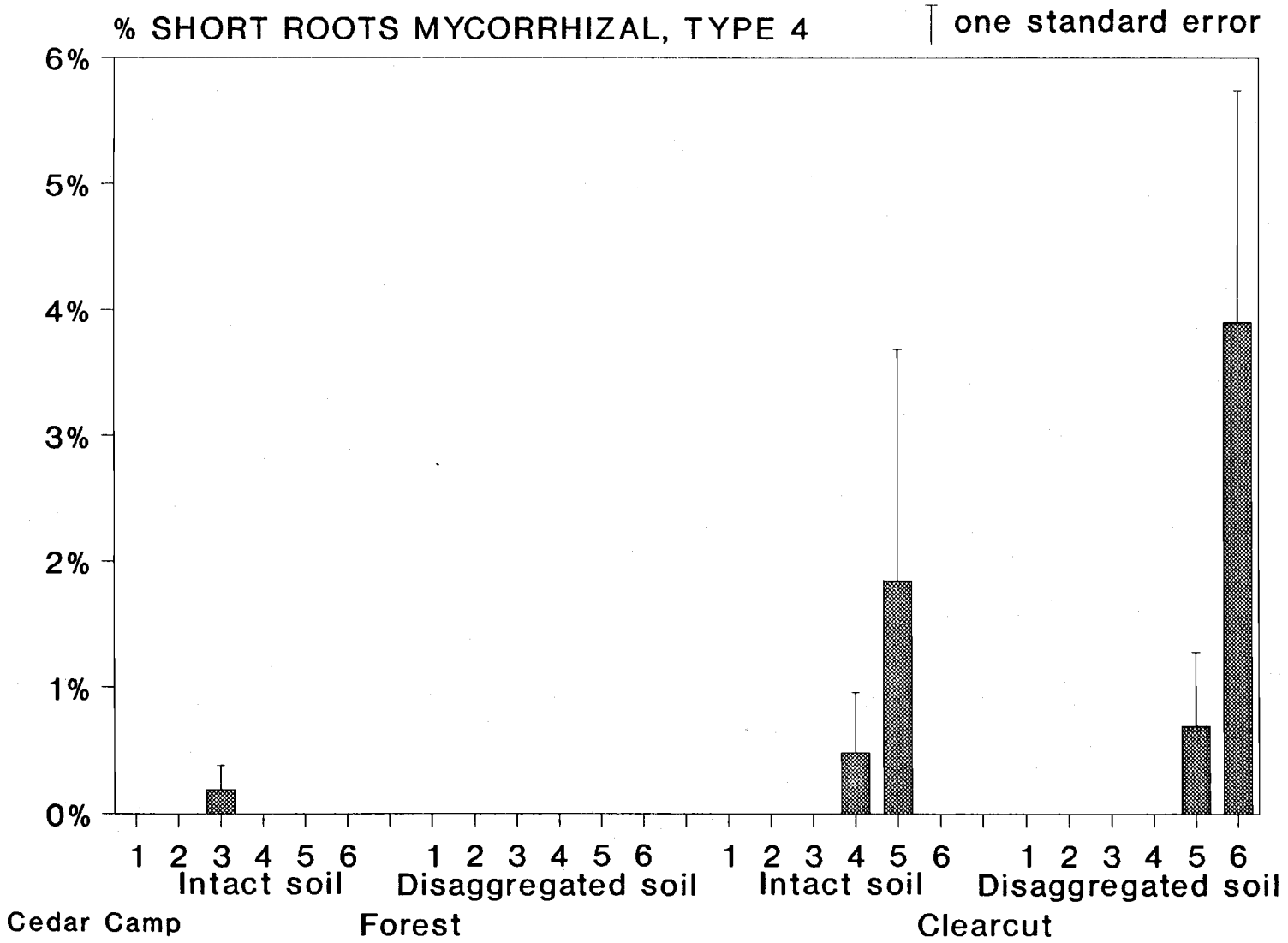
% SHORT ROOTS MYCORRHIZAL, TYPE 4
one standard error
6%
5%
4%
3%
2%
1%
0%
1 2 3 4 5 6
Intact soil
1 2 3 4 5 6
Disaggregated soil
1 2 3 4 5 6
Intact soil
1 2 3 4 5 6
Disaggregated soil
Cedar Camp
Forest
Clearcut

Figure IV-3g

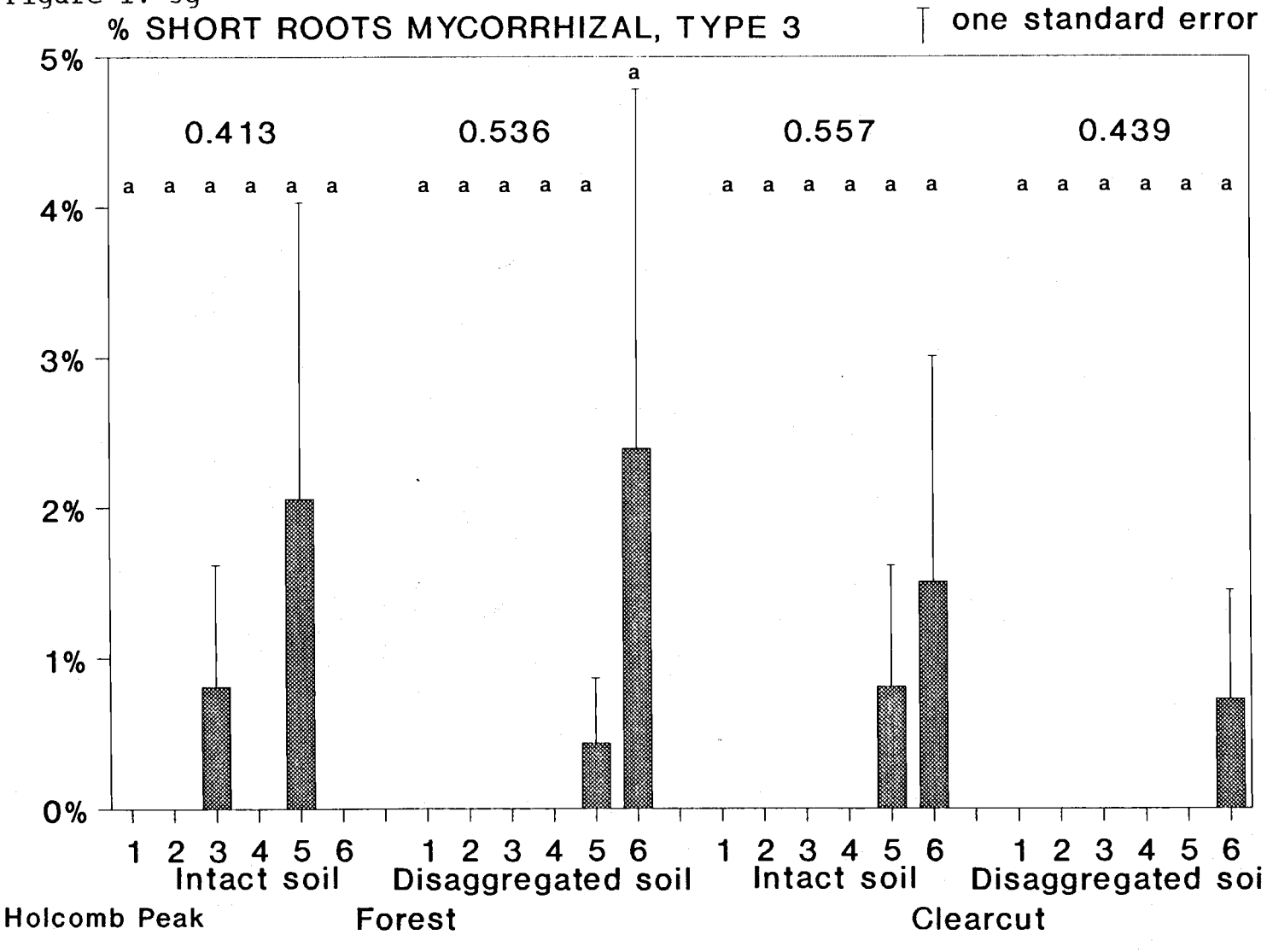
% SHORT ROOTS MYCORRHIZAL, TYPE 3
one standard error
5%
4%
3%
2%
1%
0%
0.413
0.536
0.557
0.439
a a a a a a
a a a a a a
a a a a a a
a a a a a a
a
1 2 3 4 5 6
Intact soil
Disaggregated soil
Intact soil
Disaggregated soil
Holcomb Peak
Forest
Clearcut

Figure IV-4. Mean shoot mass (a,b), root mass (c,d), and total number of short roots (e,f) per seedling from bioassay of Cedar Camp and Holcomb Peak soil. Particle size fractions on x axis given by: 1 = 2-9.5 mm; 2 = 1-2 mm; 3 = 0.5-1 mm; 4 = 0.25-0.5 mm; 5 = 0.05-0.25 mm; 6 = <0.05 mm. Significance probability values are associated with split-plot ANOVAs where disaggregation treatment was the main plot factor.

Figure IV-4a

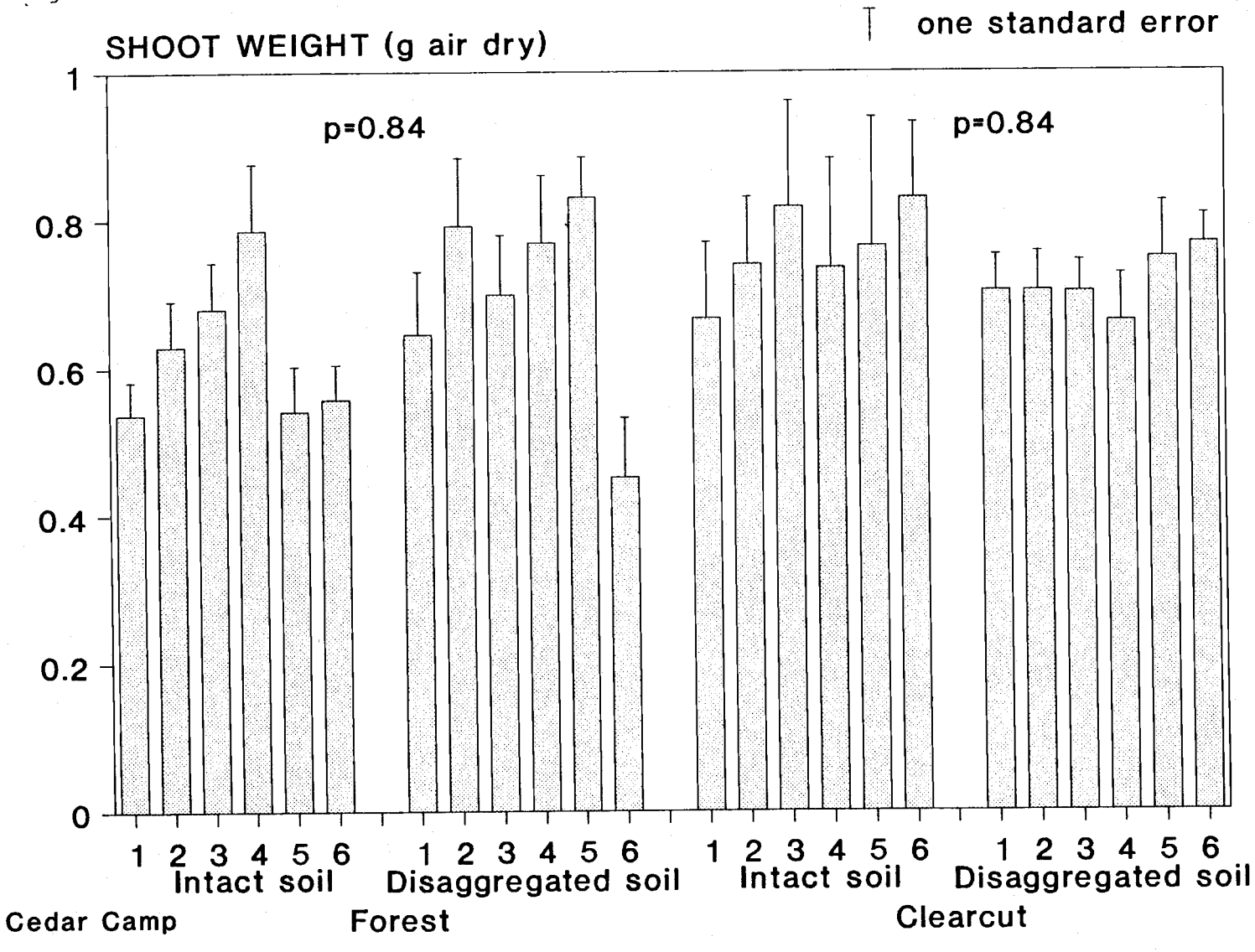
one standard error
SHOOT WEIGHT (g air dry)
1
0.8
0.6
0.4
0.2
0
p=0.84
p=0.84
1 2 3 4 5 6
1 2 3 4 5 6
1 2 3 4 5 6
1 2 3 4 5 6
Intact soil
Disaggregated soil
Intact soil
Disaggregated soil
Cedar Camp
Forest
Clearcut

Figure IV-4b

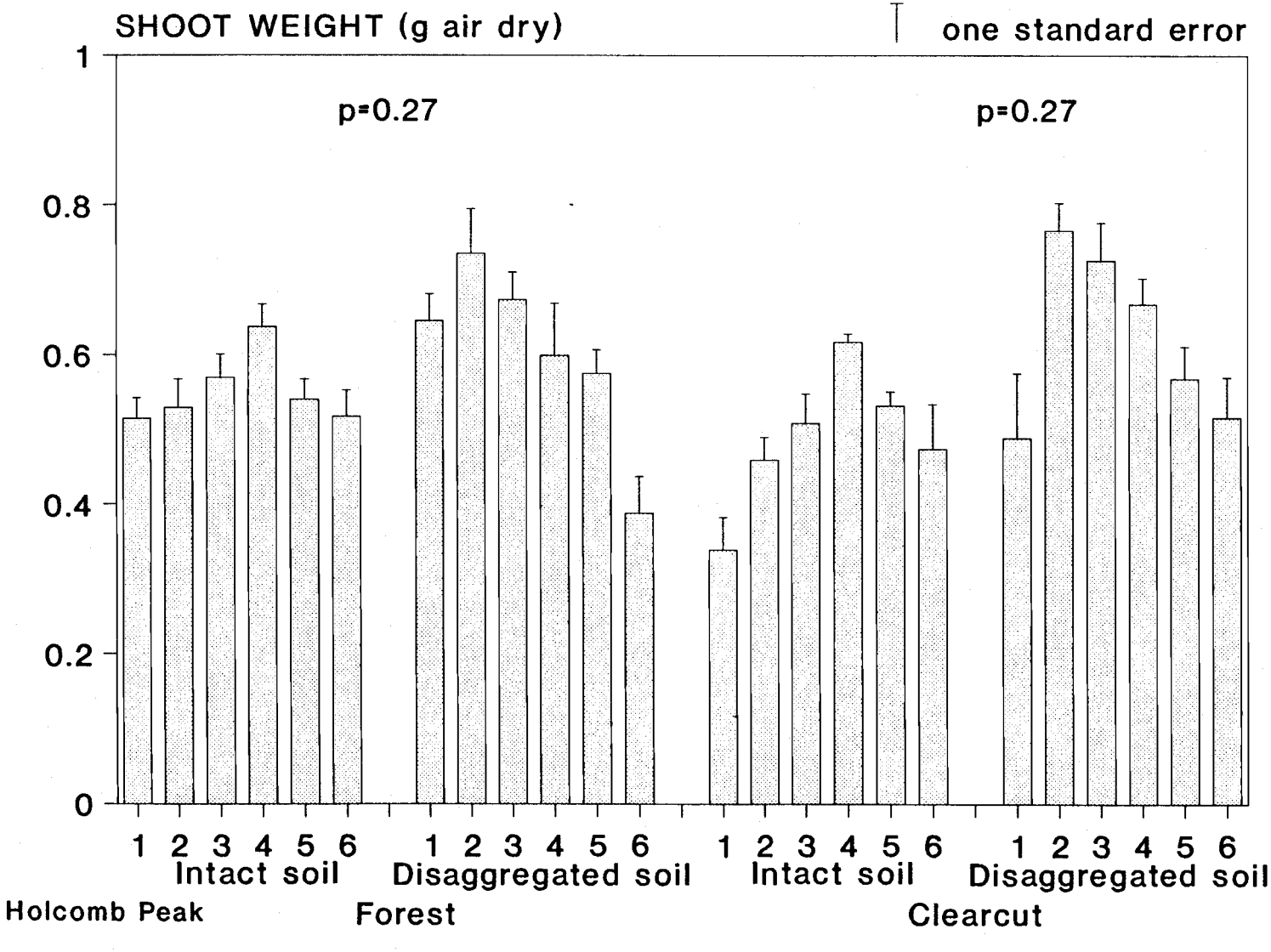
SHOOT WEIGHT (g air dry)
one standard error
1
0.8
0.6
0.4
0.2
0
p=0.27
p=0.27
1 2 3 4 5 6
Intact soil
1 2 3 4 5 6
Disaggregated soil
1 2 3 4 5 6
Intact soil
1 2 3 4 5 6
Disaggregated soil
Holcomb Peak
Forest
Clearcut

Figure IV-4c

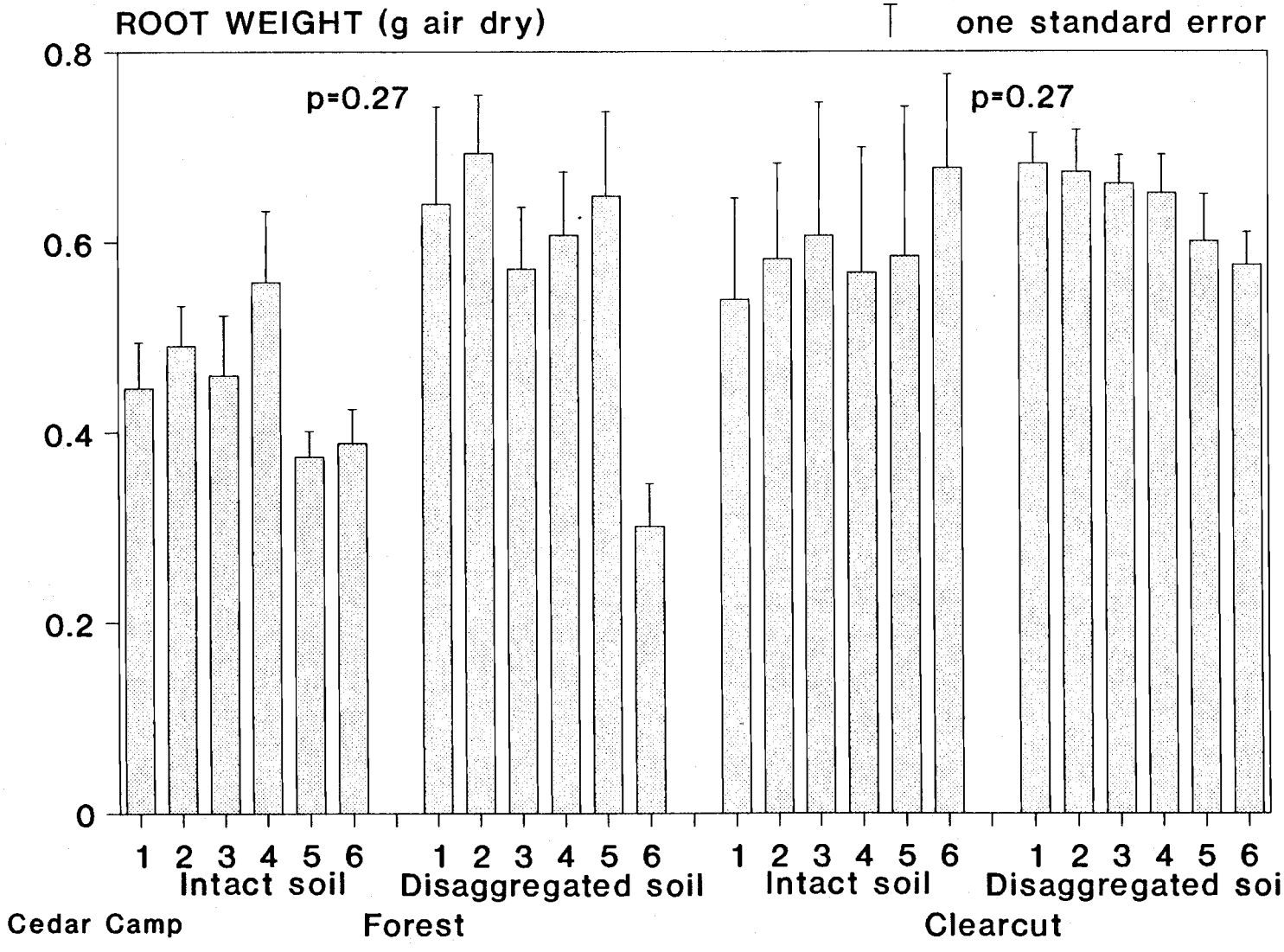
ROOT WEIGHT (g air dry)
one standard error
0.8
0.6
0.4
0.2
0
p=0.27
p=0.27
1 2 3 4 5 6
1 2 3 4 5 6
1 2 3 4 5 6
1 2 3 4 5 6
Intact soil
Disaggregated soil
Intact soil
Disaggregated soil
Cedar Camp
Forest
Clearcut

Figure IV-4d

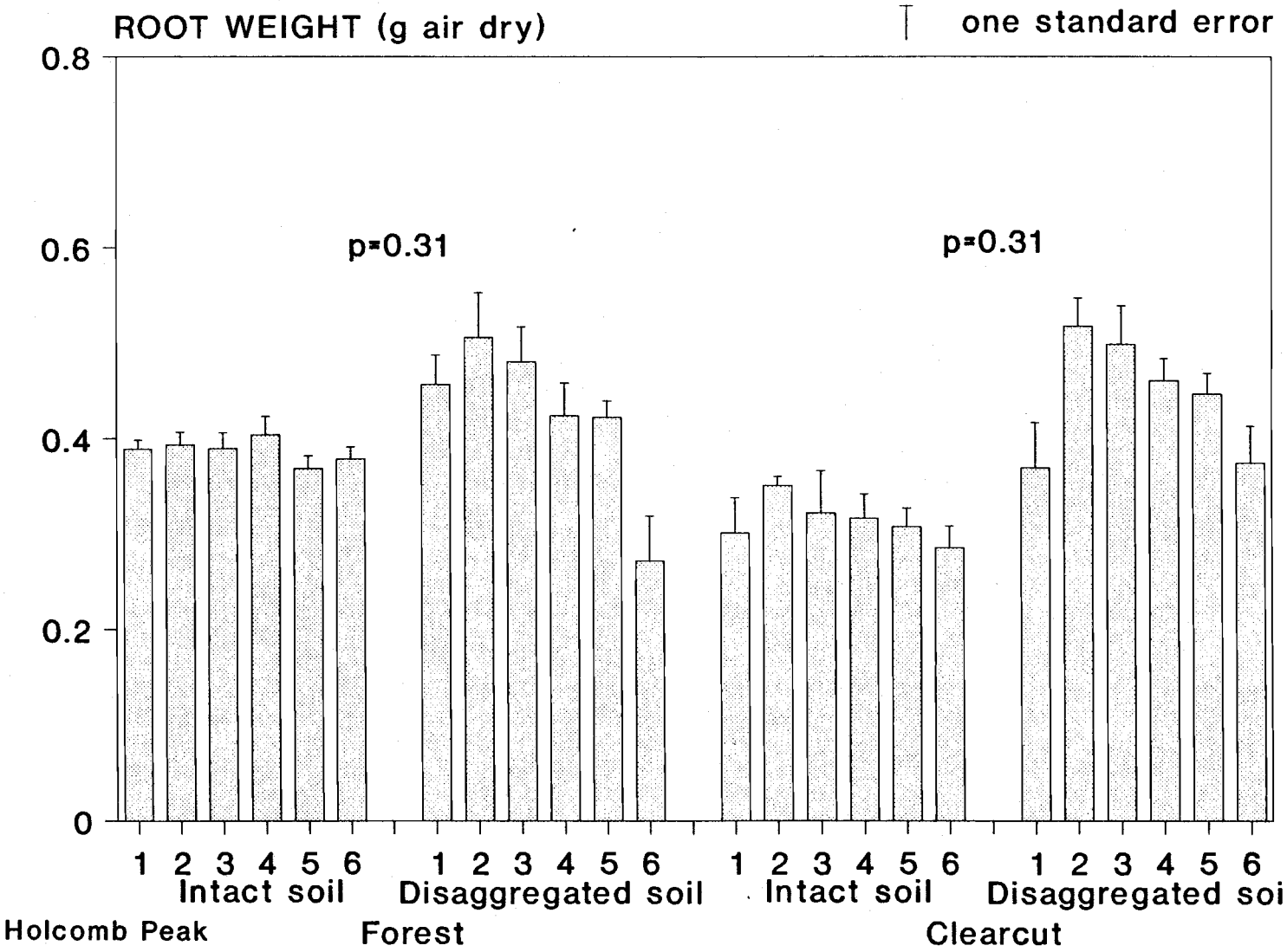
ROOT WEIGHT (g air dry)
one standard error
0.8
0.6
0.4
0.2
0
p=0.31
p=0.31
1 2 3 4 5 6
1 2 3 4 5 6
1 2 3 4 5 6
1 2 3 4 5 6
Intact soil
Disaggregated soil
Intact soil
Disaggregated soil
Holcomb Peak
Forest
Clearcut

Figure IV-4e

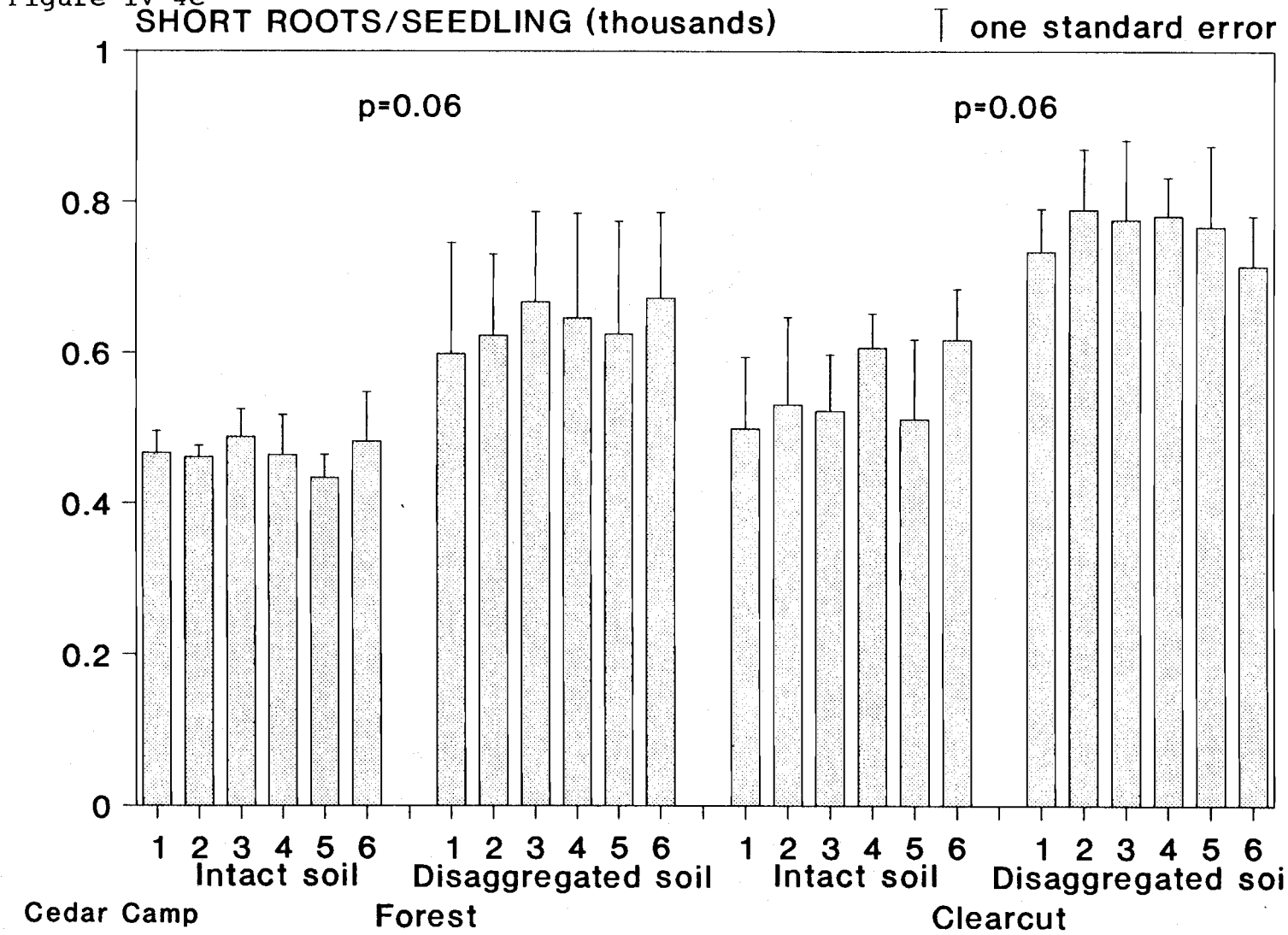
SHORT ROOTS/SEEDLING (thousands)
one standard error
1
0.8
0.6
0.4
0.2
0
p=0.06
p=0.06
1 2 3 4 5 6
1 2 3 4 5 6
1 2 3 4 5 6
1 2 3 4 5 6
Intact soil
Disaggregated soil
Intact soil
Disaggregated soil
Cedar Camp
Forest
Clearcut

Figure IV-4f

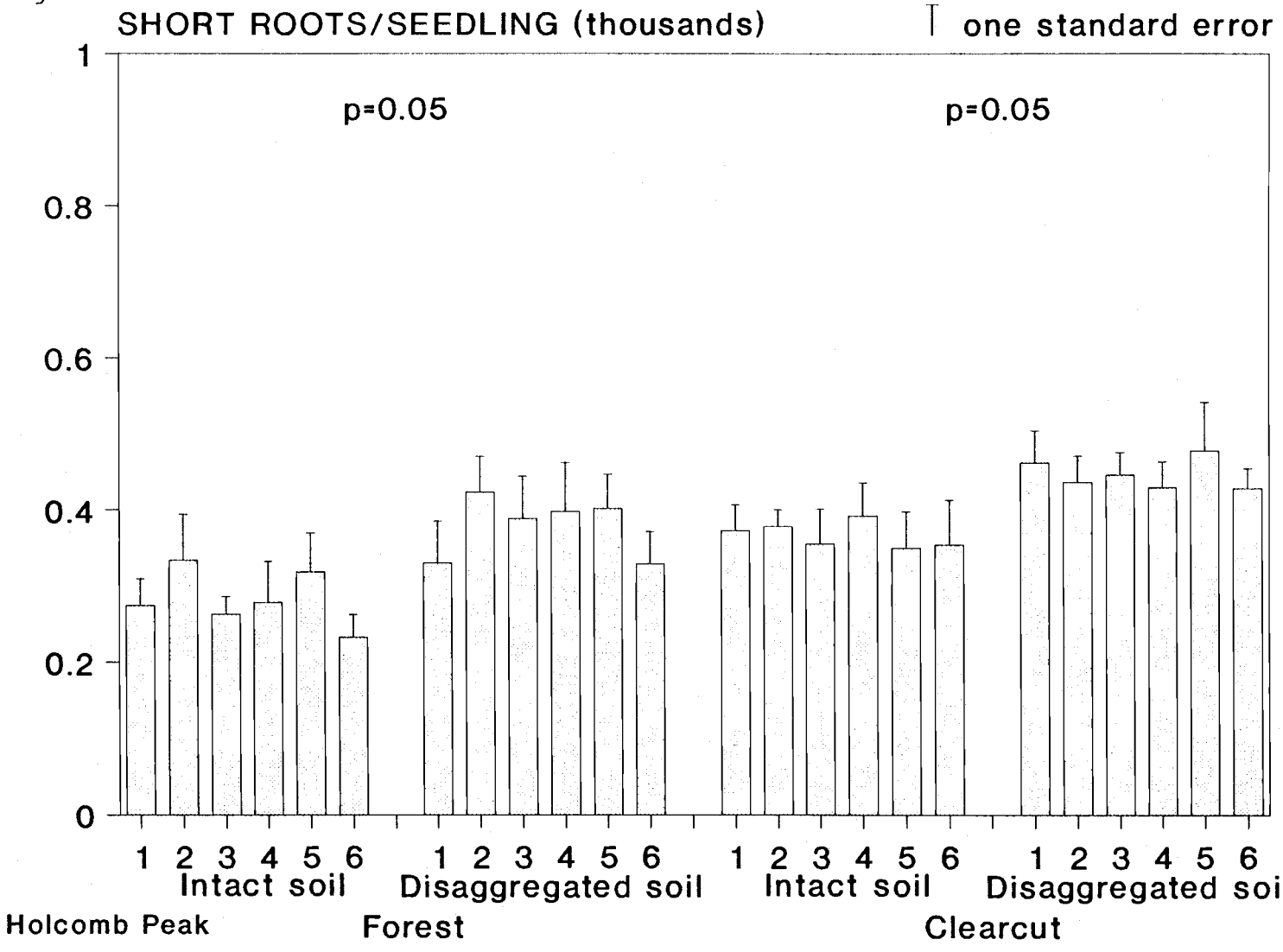
SHORT ROOTS/SEEDLING (thousands)
I one standard error
1
0.8
0.6
0.4
0.2
0
p=0.05
p=0.05
1 2 3 4 5 6
Intact soil
1 2 3 4 5 6
Disaggregated soil
1 2 3 4 5 6
Intact soil
1 2 3 4 5 6
Disaggregated soil
Holcomb Peak
Forest
Clearcut

Table IV-1. Characteristics of forest and clearcut study sites (Klamath Mountain region, southwest Oregon).

Table IV-1.

Characteristics	Cedar Camp	Holcomb Peak
Soil parent material	Quartz diorite	Metavolcanic
Soil classification (1)	Loamy-skeletal, mixed Entic Cryumbrept	Loamy-skeletal, mixed, frigid Lithic Xerumbrept
Soil texture	Sandy loam	Silt loam
Elevation, aspect slope	1720 m, SW, 50%	1520 m, SW, 40%
Precipitation	173 cm (map) 165 cm (gauge)	123 cm (map)
Plant association (adjacent, undisturbed forest)	ABCO-ABMAS/SYMO (2)	ABMAS-ABCO/RIBES (2)

(1) Soil Conservation Service, 1983.

(2) ABCO-ABMAS/SYMO, Abies concolor/Abies magnifica var. shastensis/Symphoricarpus mollis; ABMAS-ABCO/RIBES, Abies concolor-Abies magnifica var. shastensis/Ribes spp.

(3) White fir, Abies concolor (Gordon & Glend.)Hildebr.; shasta red fir, Abies magnifica shastensis Lemm.; Douglas-fir, Pseudotsuga menziesii (Mirb.) Franco; Bracken fern, Pteridium auilinium (L.) Kuhn.; red elderberry, Sambucus racemosa L.; greenleaf manzanita, Arctostaphylos patula Greene; currant. Ribes spp., creeping snowberry, Symphoricarpos mollis Nutt.

Table IV-1 (continued)

Characteristics	Cedar Camp	Holcomb Peak
Vegetation (3)		
Clearcut	Primarily annual grasses; occasional herbs, bracken fern, red elderberry, greenleaf manzanita	Annual grasses, currant, greanleaf manzanita, creeping snowberry, Douglas-fir
Undisturbed forest	White fir, Douglas-fir, Shasta red fir	Shasta red fir, white fir, Douglas-fir
Site index (ht. in ft. @100 years)	110	110
Management history		
Clearcut	1969	1971
Broadcast-burned	1975	1972

(1) Soil Conservation Service, 1983.
(2) ABCO-ABMAS/SYMO, Abies concolor/Abies magnifica var. shastensis/Symphoricarpus mollis; ABMAS-ABCO/RIBES, Abies concolor-Abies magnifica var. shastensis/Ribes spp.
(3) White fir, Abies concolor (Gordon & Glend.)Hildebr.; shasta red fir, Abies magnifica shastensis Lemm.; Douglas-fir, Pseudotsuga menziesii (Mirb.) Franco; Bracken fern, Pteridium auilinium (L.) Kuhn.; red elderberry, Sambucus racemosa L.; greenleaf manzanita, Arctostaphylos patula Greene; currant. Ribes spp., creeping snowberry, Symphoricarpos mollis Nutt.

Table IV-2. Relative distribution (%) of particle size fractions obtained from intact and mechanically disaggregated Cedar Camp and Holcomb Peak soil.

Table IV-2.

	Size fraction (mm)	Forest				Clearcut			
		Intact	se	Disrupted	se	Intact	se	Disrupted	se
Cedar Camp									
	2-9.5	38.3	0.8	31.3	2.1	23.9	1.4	21.7	1.9
	1-2	22.6	1.2	11.6	0.9	23.9	1.4	13.2	2.1
	0.5-1	11.7	0.7	11.4	0.3	14.7	0.5	13.1	0.9
	0.25-0.5	8.4	0.6	9.9	0.3	11.3	0.6	11.0	0.3
	0.05-0.25	14.4	0.7	21.8	0.9	20.1	0.8	26.5	0.6
	<0.05	4.6	0.4	14.1	1.2	6.1	0.4	14.5	0.9
Holcomb Peak									
	2-9.5	58.5	1.5	46.9	2.0	44.2	1.6	38.9	1.7
	1-2	16.3	1.1	6.8	0.7	17.4	0.8	5.9	0.6
	0.5-1	7.2	0.8	4.9	0.3	8.1	1.0	4.7	0.3
	0.25-0.5	3.7	0.4	3.6	0.3	5.3	0.1	4.2	0.3
	0.05-0.25	7.6	1.1	13.2	0.6	11.2	0.6	13.8	0.2
	<0.05	6.6	0.9	24.6	0.9	13.8	1.9	32.5	1.5

Table IV-3. Percent ectomycorrhizal colonization of control seedlings grown in pasteurized whole soil and peat-vermiculite

Table IV-3

Pasteurized whole soil

	Total EM		Type 1		Type 2		Type 6	
Cedar Camp	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.
Forest	74.3	4.5	0.0	0.0	0.0	0.0	74.3	4.5
Clearcut	78.8	2.6	0.0	0.0	0.0	0.0	78.8	2.6
Holcomb Peak								
Forest	84.6	2.2	0.0	0.0	0.1	0.1	84.5	2.3
Clearcut	85.8	3.3	0.1	0.1	0.0	0.0	85.7	3.3

Peat-vermiculite

Tube No.	Total EM	Type 1	Type 6
1	0.0	0.0	0.0
2	6.6	0.0	6.6
3	70.7	0.0	70.7
4	24.1	0.0	24.1
5	45.9	0.0	45.9
6	0.0	0.0	0.0
7	0.4	0.0	0.4
8	76.6	0.0	76.6
9	22.7	0.7	22.0
10	65.9	65.9	0.0

Table IV-4. Ectomycorrhiza colonization by type on Douglas-fir seedlings where soil size fractions have been numerically recombined to simulate a response in whole soil. This was feasible because seedlings were grown in quantities of soil fractions proportional to the sample particle size distributions (see Methods). Hence, combined proportions for each ectomycorrhiza type are given by

$$P_j = \sum_{i}^{6} N_{ij} \; / \; \sum\sum_{ij}^{67} N_{ij}$$

where P_j=the proportion of short roots mycorrhizal with type j and N=short roots in i=1,2,..,6 size fractions and of j=1,2,...,6 types. The columns labeled "p" contain significance probability values associated with t-tests of intact and disaggregated soil means.

Table IV-4.

	Forest					Clearcut				
	Intact		Disaggregated			Intact		Disaggregated		
	mean	se	mean	se	p	mean	se	mean	se	p
Cedar Camp										
Type 1	5.74	1.65	2.39	0.65	0.10	6.87	2.13	23.00	4.59	0.01
Type 2	2.28	1.41	1.83	1.09	0.81	0.31	0.15	0.61	0.45	0.55
Type 3	0.00	0.00	0.00	0.00	-	0.00	0.00	0.56	0.54	0.33
Type 4	0.03	0.03	0.00	0.00	0.35	0.39	0.30	0.72	0.37	0.50
Type 5	12.56	2.30	3.49	1.52	0.01	0.36	0.32	0.74	0.61	0.59
Type 6	16.93	5.90	16.66	3.95	0.97	23.88	4.21	19.52	5.59	0.55
Total	37.55	5.82	24.37	5.30	0.13	31.80	6.10	45.16	5.07	0.13
Holcomb Peak										
Type 1	18.06	1.60	33.30	3.63	0.00	34.71	5.13	21.93	2.20	0.05
Type 2	0.86	0.36	0.56	0.14	0.47	1.48	0.29	0.71	0.27	0.09
Type 3	0.47	0.46	0.41	0.32	0.91	0.38	0.26	0.12	0.12	0.37
Type 4	0.00	0.00	0.18	0.18	0.35	0.00	0.00	0.13	0.13	0.35
Type 5	0.00	0.00	0.00	0.00	-	0.00	0.00	0.00	0.00	-
Type 6	25.19	6.49	12.87	2.99	0.12	34.84	2.60	26.26	3.96	0.11
Total	44.58	7.78	47.32	3.43	0.75	71.41	4.37	49.15	4.66	0.01

Bibliography

Amaranthus and Perry. 1987. Effects of soil transfer on ectomycorrhiza formation and the survival and growth of conifer seedlings on old, non-reforested clearcuts. Can. J. For. Res. 17:944-950

Anderson, D. W. 1979. Processes of humus formation and transformation in soils of the Canadian Great Plains. J. Soil Science 30:77-84.

Anderson, D. W. and Paul, E. A. 1984. Organo-mineral complexes and their study by radiocarbon dating. Soil Sci. Soc. Amer. J. 48:298-301.

Anderson, D. W., Saggar, S., Bettany, J. R., and Stewart, J. W. B. 1981. Particle-size fractions and their use in studies of soil organic matter: I. The nature and distribution of forms of carbon, nitrogen, and sulfur. Soil Sci. Soc. Amer. J. 45:767-772.

Atlas, R. M. and Bartha, R. 1981. Microbial ecology. p. 90. Addison-Wesley Publishing Co., Menlo Park, CA. 560 pp.

Ballard. 1978. Effect of slash and soil removal on the productivity of second rotation radiata pine on a pumice soil. N. Z. J. For. Sci. 8:248-258.

Berg, B. and G. Ekbohm. 1983. Nitrogen immobilization in decomposing needles at variable carbon:nitrogen ratios. Ecology 64:63-67.

Birkeland, P. W. 1984. Soils and geomorphology. pp 179-181. Oxford University Press, New York, NY.

Borchers, J. G. and D. A. Perry. 1989. Organic matter content and aggregation of forest soils with different texture in southwest Oregon clearcuts. Poster abstract in: Maintaining Long Term Productivity of Pacific Northwest Forests. (Perry, D. A., R. Meurisse, B. Thomas, R. Miller, J. Boyle, J. Means, and P. Sollins, eds.). Timber Press. Portland, OR. pp. 143-157.

Borchers, S. L. and D. A. Perry. 1990. Growth and mycorrhiza formation by Douglas-fir seedlings grown in soils collected at different distances from hardwoods pioneering southwest Oregon clearcuts. Can. J. For. (In press).

Box, G. E. P., and Cox, D. R. 1964. An analysis of transformations revisited. J. Amer. Statist. Soc., Ser. B. 26:211-246.

Bremner, J. M. 1965. Total nitrogen. In Methods of soil analysis, part 2. Chemical and microbiological properties. Edited by Black, C. A. et al. Agronomy monograph no. 9 (1st ed.). Agronomy Soc. Am., Inc. Madison, WI. pp 1149-1178.

Bruckert, S. and Kilbertus, G. 1980. Fractionnement et analyse des complexes organo-mineraux de sols bruns et de chernozems. Plant and Soil 57:271-295.

Christensen, B. T. 1986. Straw incorporation and soil organic matter in macro-aggregates and particle size separates. J. Soil Science 37:125-135.

Christensen, M. 1989. A view of fungal ecology. Mycologia 81:1-19.

Craswell, E. T. and Waring, S. A. 1972. Effect of grinding on the decomposition of soil organic matter-II. Oxygen uptake and nitrogen mineralization in virgin and cultivated cracking clay soils. Soil Biol. Biochem. 4:435-442.

Cromack, K., Jr., Swanson, F. J., and Grier, C. C. 1978. A comparison of harvesting methods and their impact on soils and environment in the Pacific Northwest, pp. 449-515. In Forest soils and land use. Proc., Fifth North Amer. Forest Soils Conf., Colo. State Univ., Ft. Collins, CO.

Dalal, R. C. and Mayer, R. J. 1986. Long-term trends in fertility of soils under continuous cultivation and cereal cropping in southern Queensland. III

Distribution and kinetics of soil organic carbon in particle-size fractions. Aust. J. Soil Res. 24:293-300.

Dalal, R. C. and Mayer, R. J. 1987. Long-term trends in fertility of soils under continuous cultivation and cereal cropping in southern Queensland. VI. Loss of total nitrogen from different particle-size and density fractions. Aust. J. Soil Res. 25:83-93.

Dunn, P. H. and L. F. DeBano. 1977. Fire's effect on biological and chemical properties of chaparral soils. p. 75-84. In Proc. Symp. on the Environ. Consequences of fire and fuel management in Mediterranean ecosystems. USDA For. Serv., Washington, D. C., Gen Tech. Rep. WO-3. 498 pp.

Edmonds, R. L. 1984. Long-term decomposition and nutrient dynamics in Pacific silver fir needles in western Washington. Can. J. For. 14:395-400.

Elliott, E. T. 1986. Aggregate structure and carbon, nitrogen, and phosphorus in native and cultivated soils. Soil Sci. Soc. Amer. J. 50:627-633.

Feller, M. C. and Kimmins, J. P. 1984. Effects of clearcutting and slash burning on streamwater chemistry and watershed nutrient budgets in southwestern British Columbia. Water Resour. Res. 20:29-40.

Fogel, R. and K. Cromack, Jr. 1977. Effect of habitat and substrate quality on Douglas-fir litter decomposition in western Oregon. Can J. Bot. 75:1632-1640.

Ford, E. D. 1983. What do we need to know about forest productivity and how can we measure it? In I.U.F.R.O. Symposium on Forest Site and Continuous Productivity. Edited by R. Ballard and S. P. Gessel. USDA Forest Service Gen. Tech. Rep. PNW-163. pp. 243-251.

Foster, R. C. 1985. In situ localization of organic matter in soils. Quaestiones Entomologicae 21:609-633.

Franklin, J. F. and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. U. S. Dep. Agric. For. Serv., Gen. Tech. Rep. PNW-8.

Friedman, J, Hutchins, A., Li, C. Y., and Perry, D. A. 1990. Actinomycetes inducing phytotoxic or fungistatic activity in a Douglas-fir forest and in an adjacent area of repeated regeneration failure in southwestern Oregon. Biol. Plantarum (in press).

Fries, N. 1987. Ecological and evolutionary aspects of spore germination in the higher Basidiomycetes. Trans. Br. Mycol. Soc. 88:1-7.

Froehlich, H. A., D. H. McNabb, and F. Gaweda. 1982. Average annual precipitation, 1960-1980, in southwest Oregon. Oregon State University Extension Service, EM 82:20.

Gessel, S. P. et al. 1974. Nutrient cycling in 37- and 450-year-old Douglas-fir ecosystems. In Integrated research in the coniferous forest biome. Univ. Washington CFB Bull. 5, Seattle. pp. 21-34.

Glass, C. G., Jr. 1976. The effects from root raking on an upland Piedmont loblolly pine (Pinus taeda L.) site. North Carolina State Univ. Sch. For. Resour. Tech. Rep. 76.

Gosz, J. R. 1980. Nitrogen cycling in coniferous ecosystems. In Terrestrial nitrogen cycles. Edited by Clark, F. E. and Rosswall, T. Ecol. Bull. (Stockholm) 33:405-426.

Graumlich, L. J., L. B. Brubaker, and C. C. Grier. 1989. Long-term trends in forest net primary productivity: Cascade Mountains, Washington. Ecology 70:405-410.

Hattori, T. 1988. Soil aggreates as microhabitats of microorganisms. Rep. Inst. Agr. Res. 37:23-36.

Hattori, T. and Hattori, R. 1976. The physical environment in soil microbiology: An attempt to extend principles of microbiology to soil microorganisms.

CRC Critical Reviews in Microbiology 4:423-461.

Jenkinson, D. S. and Rayner, J. H. 1977. The turnover of soil organic matter in some Rothamsted classical experiments. Soil Science 123:298-305.

Johansen, R. W. 1975. Prescribed burning may enhance growth of young slash pine. J. For. 73:148-149.

Johnson, D. W., Cole, D. W., Bledsoe, C. S., Cromack, K., Edmonds, R. L., Gessel, S. P., Grier, C. C., Richards, B. N., and Vogt, K. A. 1982. Nutrient cycling in forests of the Pacific Northwest. In Analysis of coniferous forest ecosystems in the western United States. Edited by Edmonds, R. L. US/IBP Synthesis Series, vol. 14.

Keeves, A. 1966. Some evidence of loss of productivity with successive rotations of Pinus radiata in the south-east of South Australia. Australian Forestry 30:51-66.

Kilbertus, G. 1980. tudes des microhabitats contenus dans les agrgats du sol. Leur relation avec la biomasse bacterinne et la taille des procaryotes prsents. Rev. col. Biol. Sol 17:543-557.

Klock, G. O. and C. C. Grier. 1979. Effects of fire on the long-term maintenance of forest productivity. In Proc. Forest Fertilization Conf., College of Forest Resources. S. P. Gessel, R. M. Kenady, and W. A. Adkinson (eds.) Univ. Wash., Seattle, WA, pp. 247-250.

Levene, H. 1960. Robust tests for equality of variances. In Contributions to probability and statistics. Edited by Olkin, I. Palo Alto, CA, Stanford Univ. Press, pp 278-292.

Little, S. N. and Ohman, J. K. 1988. Estimating nitrogen lost from forest floor during prescribed fires in Douglas-fir/western hemlock clearcuts. For. Science 34:152-164.

McGill, W. B. and C. V. Cole. 1981. Comparative aspects of cycling of organic C, N, S, and P through soil organic

matter. Geoderma 26:267-286.

McIntosh, R. P. 1985. The background of ecology: Concepts and theory. Cambridge Univ. Press, New York, NY. 383 pp.

McNabb, D. H., Cromack, Jr., K., and R. L. Frederickson. 1986. Variability of nitrogen and carbon in surface soils of six forest types in the Oregon Cascades. SSSAJ 50:1037-1041.

McNabb, D. H., H. A. Froehlich, and F. Gaweda. 1982. Average dry season in southwest Oregon, May through September. Oregon State University Extension Service, EM 8226.

McNabb, D. H. 1988. Interpreting the effects of broadcast burning on forest productivity, p. 89-103. In D. J. Lousier and G. W. Still (eds.), Degradation of forested lands-Forest soils at risk, Proc., Tenth British Columbia Soil Sci. Workshop, Feb. 20-21, 1986. British Columbia Ministry of Forests and Lands, Land Management Report 56. Victoria, B. C. 331 p.

Maser, C., Trappe, J. M., and Nussbaum, R. A. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology 59:799-809.

Mateos, M. P. and Carcedo, S. G. 1985. Effect of fractionation on location of enzyme activities in soil structural units. Biol. Fert. Soils 1:153-159.

Mehlich, A. 1980. Why not use relevant data in soil-plant relationships? Soil Sci. Soc. Amer. J. 44:440-441.

Meyer, L. C. and Amaranthus, M. P. 1979. Siskiyou National Forest soil resource inventory. USDA Forest Service, Pacific Northwest Region. 258 pp.

Mosse, B., Stribley. D. P., and LeTacon, F. 1982. Ecology of mycorrhizae and Mycorrhizal fungi. Adv. Microbial Ecol. 5:137-210.

Myrold, D. D. 1987. Relationship between microbial biomass nitrogen and a nitrogen availability index. Soil Sci. Soc. Amer. J. 51:1047-1049.

Odum, E. P. 1971. Fundamentals of ecology. W. B. Saunders Co., Philadelphia, PA. 574 pp.

O'Neill, R. V., DeAngelis, D. L., Waide, J. B., and Allen, T. F. H. 1986. A hierarchical concept of ecosystems. Princeton Univ. Press, Princeton, NJ. 253 pp.

Parke, J. L., Linderman, R. G., and Trappe, J. M. 1984. Inoculum potential of ectomycorrhizal fungi in forest soils of southwest Oregon and northern California. Forest Science 30:300-304.

Pastor, P. and W. M. Post. 1988. Response of northern forests to CO_2-induced climate change. Nature 334:55-58.

Paul, E. A. 1984. Dynamics of organic matter in soil. Plant Soil 76:275-285.

Paul, E. A. and N. G. Juma. 1981. Mineralization and immobilization of soil nitrogen by microorganisms. Ecological Bulletin (Stockholm) 33:179-195.

Perry, D. A. and J. Norgren. 1983. Impact of biomass harvest on soil and nutrient loss. In Generating electricity with wood and solid wastes in southern Oregon. Edited by Perry, D. A. Res. Bull. No. 40, Oregon State Univ. School of Forestry.

Perry, D. A. and Rose, S. L. 1983. Soil biology and forest productivity: opportunities and constraints. In I.U.F.R.O. Symposium on Forest Site and Continuous Productivity. Edited by Ballard, R. B. and Gessel, S. P. USDA Forest Service Gen. Tech. Report PNW-163. 406 pp.

Perry, D. A., Molina, R., and Amaranthus, M. P. 1987. Mycorrhizae, mycorrhizospheres, and reforestation: current knowledge and research needs. Can. J. For. Res. 17:929-940.

Petersen, R. G. 1985. Design and analysis of experiments. Marcel Dekker, Inc., New York, NY. 429 pp.

Pilz, D. P. and Perry, D. A. 1984. Impact of clearcutting and slash burning on ectomycorrhizal associations of Douglas-fir seedlings. Can. J. For. Res. 14:94-100.

Post, W. M., W. R. Emanuel, P. J. Zinke, and A. G. Stangenberger. 1982. Soil carbon pools and world life zones. Nature 298:156-159.

Powers, R. F. 1980. Mineralizable soil nitrogen as an index of soil nitrogen availability to forest trees. SSSAJ 44:1314-1320.

Powlson, D. S. 1980. The effects of grinding on microbial and non-microbial organic matter in soil. J. Soil Science 31:77-85.

Pritchett, W. L. and Wells, C. G. 1978. Harvesting and site preparation increase nutrient mobilization. In Proc. symposium on principles of maintaining productivity on prepared sites. Edited by T. Tippin. Region Assoc. State Coll. & Univ. For. Resour. Organ., New Orleans, LA. pp 98-110.

Radwan, M. A. and Shumway, J. S. 1984. Site index and selected soil properties in relation to response of Douglas-fir and western hemlock to nitrogen fertilizer. In Forest soils and treatment impacts. Proceedings of the 6th North American Forest Soils Conference. Edited by E. A. Stone. pp. 89-105.

Raison, R. J., P. K. Khanna, and P. V. Woods. 1985. Mechanisms of element transfer to the atmosphere during vegetation fires. Can. J. For. Res. 15:132-140.

Ramp, L. 1979. Geologic map of Josephine County, Oregon. Bull. 100, Oregon State Dep. Geol. and Mineral Industries.

Richards, B. N. 1987. The microbiology of terrestrial ecosystems. John Wiley and Sons, New York, NY. 399 pp.

SAS Institute Inc. (1985). SAS/STAT Guide for Personal Computers, Version 6 Ed. SAS Institute Inc., Cary, NC.

Sexstone, A. J., Revsbech, N. P., Parkin, T. B., Tiedje, J. M. 1985. Direct measurement of oxygen profiles and denitrification rates in soil aggregates. Soil Science Soc. Amer. J. 49:645-651.

Schlesinger, W. H. 1983. The world carbon pool in soil organic matter: a source of atmospheric CO_2. In The role of terrestrial vegetation in the global carbon cycle: Measurement by remote sensing. SCOPE, Wiley and Sons, New York, NY.

Schoenberger, M. Meyer and Perry, D. A. 1982. The effect of soil disturbance on growth and ectomycorrhizae of Douglas-fir and western hemlock seedlings: A greenhouse bioassay. Can J. For. Res. 12:343-353.

Shapiro, S. S. and Wilke, M. B. 1982. An analysis of variance test for normality (complete samples). Biometrika 52:591-611.

Shaykewich, C. F. and Warkentin, B. P. 1970. Effects of clay content and aggregation size on availability of soil water to tomato plants. Can. J. Soil Science 50:205-217.

Shumway, J. and Atkinson, W. A. 1978. Predicting nitrogen fertilizer response in unthinned stands of Douglas-fir stands. Commun. Soil Sci. and Plant Anal. 9:529-539.

Slankis, V. 1974. Soil factors influencing formation of mycorrhizae. Ann. Rev. Phytopathol. 12:437-457.

Sollins, P., K. Cromack, Jr., F. M. McCorison, R. H. Waring, and R. D. Harr. 1981. Changes in nitrogen cycling at an old-growth Douglas-fir site after disturbance. J. Environ. Qual. 10:37-42.

Sollins, P., Spycher, G., and Glassman, C. A. 1984. Net nitrogen mineralization from light- and heavy-fraction forest soil organic matter. Soil Biol. Biochem. 16:31-37.

Steinbrenner, E. C. 1978. Forest soil productivity relationships. In Forest soils of the Douglas-fir region. Edited by P. H. Heilman, H. W. Anderson, D. M. Baumgartner. Washington State Univ. Cooperative Extension Service, Pullman, WA.

Tiessen, H. and Stewart, J. W. B. 1983. Particle-size fractions and their use in studies of soil organic matter:II. Cultivation effects on organic matter composition in size fractions. Soil Sci. Soc. Amer. J. 47:509-514.

Tisdall, J. M. and Oades, J. M. 1980. The effect of crop rotation on aggregation in a Red-brown earth. Aust. J. Soil Res. 18:423-433.

Tommerup, I. C. 1985. Population biology of VA mycorrhizal fungi: propagules behavior. In Proc. 6th North Amer. Conf. on Mycorrhizae. Edited by Molina, R. Oregon State Univ. Forest Res. Lab. 471 pp.

Turchenek, L. W. and Oades, J. M. 1979. Fractionation of organo-mineral complexes by sedimentation and density techniques. Geoderma 21:311-343.

Vogt, K. A., Grier, C. C., Meier, C. E., and Edmonds, E. L. 1982. Mycorrhizal role in net primary production and nutrient cycling in Abies amabilis (Dougl.) Forbes ecosystems in western Washington. Ecology 63:370-380.

Waring, R. H. and W. H. Schlesinger. 1985. Forest Ecosystems. Concepts and Management. Academic Press, Inc., New York, NY. 340 pp.

Waring, S. A. and J. M. Bremner. 1964a. Ammonium production in soil under waterlogged conditions as an index of nitrogen availability. Nature 201:951-952.

Waring, S. A. and J. M. Bremner. 1964b. Effect of soil mesh-size on the estimation of mineralizable nitrogen in soils. Nature 202:1141.

Weisberg, S. 1985. Applied linear regression. John Wiley and Sons, New York, NY. 324 pp.

Young, J. L. and Spycher, G. 1979. Water-dispersable soil organic-mineral particles: I. Carbon and nitrogen distribution. Soil Sci. Soc. Amer. J. 43:324-328.