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Patterns of Soil Organic Matter and Microclimate Accompanying the Death and Regeneration of a Mountain Hemlock (Tsuga mertensiana) Forest

by

Richard D. Boone

A THESIS

submitted to

Oregon State University

in partial fulfillment of the requirements for the degree of Master of Science

Completed July 30, 1982

AN ABSTRACT OF THE THESIS OF

Richard D. Boone for the degree of Master of Science in Forest Science presented on July 30, 1982.

Title: Patterns of Soil Organic Matter and Microclimate Accompanying the Death and Regeneration of a Mountain Hemlock (<u>Tsuga mertensiana</u>) Forest

Signature redacted for privacy.

Abstract approved:

Dr. Kermit Cromack, Jr. (

Soil organic matter levels, soil temperature and moisture, and vegetation properties were measured along a sequence of death and regeneration in a mountain hemlock (Tsuga mertensiana) forest. The sequence is produced by slowly moving waves of the root pathogen Phellinus weirii. While analysis of variance for all sampled soil layers indicated no change in carbon mass along the gradient, data suggested a loss of carbon in the O2 layer after stand death. Moisture in the organic layers decreased from the old growth to the young regeneration area and increased in the older regeneration area. In contrast, both moisture in the mineral soil and temperature at three profile depths increased from the old growth to the young regeneration area and decreased in the older regeneration area. Multiple regression analyses revealed that little variation in soil carbon levels was explained by variation in vegetation and soil microclimate.

Table of Contents

I.	Introduction	-
II.	Methods 3 Study site description 3 Field methods 4 Laboratory analyses 9 Statistical analyses 10	534))
III.	Results12Stand age12Stand and ground cover biomass14Temperature14Particle size analysis14Water release curve18Soil moisture18Carbon analysis18Multiple regressions26	***
IV.	Discussion	3 3 1
۷.	References) -
VI.	Appendix	r

Page

List of Tables

Table		Page
1	Ground cover biomass	16
2	Percent mass wetness for organic layers and mineral soil	21
3	Mg C/ha for all soil layers and fractions \ldots .	25
4	Multiple regression summary	27
5	Percent carbon and percent ash in organic layers	34
6	Properties of whole soil, light fraction, and heavy fraction	35

List of Figures

Figure		Page
1	Aerial view of study area	5
2	Transect with hypothetical sample points \ldots .	7
3	Stand age	13
4	Tree biomass	15
5	Soil temperature at 6cm depth	17
6	Particle size distribution	19
7	Water release curve	20
8	Mass wetness in mineral soil 0-15 cm	23
9	02 layer carbon/ha	24

ACKNOWLEDGEMENTS

I have deep gratitude for the many people who helped me during the past two years. Throughout the study I received superb technical assistance. Bill and Nadine Fender, Carol Glassman, Cindy McCain, Tom Verhoeven, and Andy Ungerer all lightened the burdens of soil pit digging, soil sieving and grinding, density fractionations, and LECO carbon analyses. Rod Slagle, Greg Koerper, and Susan Stafford helped me though the process of data management and analysis with deftness Gody Sycher proved an excellent consultant when and patience. laboratory problems or questions of statistical analysis arose. Mary Kay Amistadi of the Oregon State University Soil Testing Lab determined the water release curve and cheerfully helped me with the particle size analysis. Finally, Jeannette Emry and her word processor remained nonplussed by countless manuscript changes.

Several people deserve thanks for their strong support of my work and for giving of themselves in many aspects of the project. Steve Omi, Dan Binkley, Paula Reid, and Pam Matson gave welcome help in the field, helped keep my thoughts on course and helped convince me that I really could finish. Dick Waring gave me generous support as one of the Waldo crew, a good deal of confidence, and welcome critical review. Phil Sollins challenged me and opened my eyes to the terrestrial sea beneath us. Kermit Cromack, my advisor, deserves special thanks for guiding me through the project with great care and making possible a rich educational experience. Finally, I thank my wife, Marlene McDermott, who shared my daily triumphs and frustrations, endured the inconveniences, spent long hours in the field and lab and always demonstrated extraordinary steadfastness and love. Patterns of Soil Organic Matter and Microclimate Accompanying the Death and Regeneration of a Mountain Hemlock (Tsuga mertensiana) Forest

INTRODUCTION

Recent modelling work on the global carbon cycle has identified the need for more complete information on how levels of soil organic matter (SOM) change with forest death and regeneration (Woodwell et al. 1978; Broecker et al. 1979). Literature searches have revealed that present understanding of SOM response to forest death and regeneration is based mainly on forest floor studies in a limited number of forest types (Covington 1981; Turner and Long 1975; Bormann and DeBell 1981). Most sites studied were logged areas that were planted or experienced rapid natural regeneration. Little or no information is available for boreal forests, subalpine forests, and tropical forests and for any forest that undergoes a cycle of death and regeneration independent of man.

An unusual opportunity to assess the response of SOM levels to forest death and regeneration is provided in mountain hemlock (<u>Tsuga</u> <u>mertensiana</u> (Bong.) Carr.) forests of the Oregon Cascades. Large sections of these subalpine forests are being killed and regenerated by slowly moving waves of the root pathogen <u>Phellinus</u> (<u>Poria</u>) <u>weirii</u> (Murr.) Gilbertson (McCauley and Cook 1980). The pathogen either kills trees directly or so much weakens root systems that trees are blown down in high winds. The result of the pathogen's movement is a sequence of uninfected old growth, a narrow band of old growth infected by <u>Phellinus weirii</u>, and an 85-year age gradient of regenerating mountain hemlock and lodgepole pine (<u>Pinus contorta</u> var latifolia Engelm).

The objectives of this study were twofold: first, to document the changes in stand age, stand biomass, soil microclimate, and SOM levels that accompany the death and regeneration of the stand; and second, to determine how much variability in soil carbon levels can be explained by properties of vegetation and soil microclimate.

METHODS

Study Site

The site is located at 1770-m elevation about 2 km northwest of Waldo Lake, Oregon, within the Oakridge Ranger District of the Willamette National Forest. Vegetation consists of an old growth stand of mountain hemlock and a regeneration area composed mostly of mountain hemlock and lodgepole pine. Other tree species in the regeneration zone are Western white pine (<u>Pinus monticola</u> Dougl. ex D. Don), Pacific silver fir (<u>Abies amabilis</u> (Dougl.) Forbes), noble fir (<u>Abies procera</u> Rehd.), and subalpine fir (<u>Abies lasiocarpa</u> (Hock.) Nutt.). Grouse huckleberry (<u>Vaccinium scoparium</u> Leiberg) forms a patchy ground cover in both the old growth forest and the regeneration area.

The site is wet and within the coolest of western Oregon's forest zones (Franklin and Dyrness 1973). Though annual weather data are not available for the Waldo Lake area, data for Crater Lake suggest a 4 °C mean annual temperature and 1640 mm annual precipitation. Most precipitation falls during the winter months with only 100 mm of precipitation falling from June to August. Snowpack can accumulate to 7.5 m (Franklin and Dyrness 1973) and frequently remains from late November to early June.

The soil at the site is derived from volcanic pumice and ash deposited during the last eruption of Mt. Mazama ca. 6600 years ago. The soil is a sand classified as an Entic cryorthod in the Winopee series. The organic horizons are best described as an Ol horizon of partially decomposed litter and an O2 horizon of mor humus. The albic horizon is weakly developed, and a well defined B horizon is not usually present. Subscils are shallow to moderately deep with andesite and basalt bedrock 1-2 m beneath the surface.

Field Methods

Sampling Design.--A block design with subsampling (Steel & Torrie 1980) was selected because of the varying mixture of mountain hemlock and lodgepole pine in the regeneration area and because of the high spatial variance of both the old growth stand and the regeneration area. At the site several <u>Phellinus weirii</u> waves have merged to form what appears to be a series of scallops from an aerial view (Fig. 1). I chose to define each scallop as a block because some scallops have regeneration zones dominated by mountain hemlock while others have regeneration zones dominated by lodgepole pine. I reasoned that SOM levels might vary among blocks because of differences in annual above- and below-ground litter inputs, litter decomposability, and rate of crown closure. I chose to subsample each block because trees showed a clumping tendency.

Through each of three selected blocks a pair of randomly chosen transects were set perpendicular to the wave front and laid from the old growth to the end of the regeneration area. Three points in the old growth and seven points in the regeneration area were established along each transect at selected intervals. Short intervals were chosen for the zone just behind the wave front in order to measure the changes in SOM levels that immediately follow stand death. With the interval marks as a reference, sample points were established randomly one to five paces to the right or left of



FIGURE 1: AN AERIAL VIEW OF THE STUDY AREA SHOWING MERGED PHELLINUS WEIRII WAVES

each transect. Sample points were offset slightly if they fell within 1 m of a stump, live tree, or large woody debris. Figure 2 shows an idealized transect with its marked intervals and ten hypothetical sample points.

Vegetation sampling.--Information was gathered at each sampling point to characterize stand age, stand biomass, dead wood accumulation, and ground cover biomass. Species type, diameter, and distance to the sample point were recorded for all live trees, snags, and fallen trees greater than 1 m in height or length that were within 5 m of the sample point. If height or length was greater than 2 m, bole diameter was measured 1.5 m from the base; otherwise, bole diameter was measured at the base. Along one transect per block, cores or cross-sections were taken at breast height from the three dominant trees at each sampling point. In addition, cross-sections were taken at ground level from several small trees in the regeneration area to compare tree age at ground level with tree age at breast height. Finally, ground cover plants on the 1 m² about each sample point were clipped at the base, air-dried, and weighed. All ground cover plants were harvested in July when most were at full leaf.

Temperature measurements.--Soil temperature along each transect was measured once within a ten day period in July when skies were completely clear and air movement was negligible. Measurements with a soil thermometer were taken just beneath the Ol layer and at 6 cm and 10 cm depths in the mineral soil. Measurements along each transect began between 13:00 and 13:53 and were completed between



FIGURE 2: TRANSECT WITH TEN HYPOTHETICAL SAMPLE POINTS.

15:15 and 15:40. To adjust soil temperature for air temperature on the day of measurement, shade temperature in the old growth forest was recorded at the beginning of measurement period.

Soil sampling.--Over a rainless three-week period in July, 1981 soil pits at each sample point were dug, and samples of organic layers and mineral soil were collected. Duplicate samples of both Ol material and O2 material were collected with a 20 cm x 40 cm wooden frame. One set of samples, collected for moisture and mass measurements, was sealed in polyethylene bags and stored in a dark, cool place until processing. Another set of samples, collected for chemical analyses, was placed in paper sacks for air drying.

Because discontinuous and weakly developed horizons made horizon sampling difficult, mineral soil samples were collected from 0-15 cm and 15-30 cm depth intervals. Two 7.5 cm x 7.5 cm cores positioned midway in each depth interval were collected and composited for bulk density and moisture analysis. A grab sample across each entire 15 cm face was taken for chemical analyses. Mineral soil samples for moisture determination were handled in the same fashion as the organic layer material collected for moisture determination.

Laboratory Analyses

Moisture, bulk density, and mass.--Soil samples collected for measurement of moisture, bulk density, and mass were dried at 70 $^{\circ}$ C for 24 hours in a forced air drying oven. To estimate water potential of the mineral soil from gravimetric water content, a water release curve was determined for both an undisturbed ped and a slightly fragmented ped taken over a 2-7 cm depth interval in the mineral soil.

Particle size analysis.--One bulk density sample from the upper 15 cm of the mineral soil was randomly chosen for particle size analysis. After removal of coarse fragments larger than 2 mm, the sample was passed through graded sieves until the silt and clay fraction was collected. At each sieving step the weight of the soil left on the sieve was recorded. The pipette technique (Day 1965) was used to separate silt from clay. All size fractions were expressed as percent of fine (<2 mm) soil weight.

Chemical analyses.--Subsamples of the grab samples taken from the 0-15 cm layer of the mineral soil were separated densimetrically into a light fraction with most organic matter as fine root fragments and a heavy fraction with most organic matter absorbed to mineral surfaces. The fractionation procedure, modified from Spycher and Young (1977), uses a separation medium with a density greater than that of recent detritus. For this study a sodium chloride solution adjusted to a density of 1.2 g/cm^3 was used as the separation medium. The choice of density was based on a pilot study that showed that a

solution at 1.2 g/cm³ removed all recognizable fine root fragments from whole soil. Solutions at higher densities, e.g. 1.4 g/cm³ and 1.6 g/cm³, added excessive amounts of pumice to the light fraction.

Duplicate 50 g soil samples were stirred vigorously in 100 ml of sodium chloride solution for 25 s and then centrifuged at 5000 <u>g</u> for 5 minutes. The salt solution with floating bits of detritus (the light fraction) was decanted onto a glass filter with polycarbonate membranes (1.0 μ m pores). The procedure was repeated a second time to remove any residual detritus from the heavy fraction. All light fraction samples were washed with 150 ml of de-ionized water and weighed after oven drying at 70°C. Subsamples of each light fraction sample were heated at 550°C for 4 h to determine ash content. The heavy fraction was washed three times with 100 ml of de-ionized water and then oven dried at 70°C.

Subsamples of the organic layers, light fraction, heavy fraction, and fine mineral soil (<2 mm) from O-15 cm and 15-30 cm were collected from a splitter, ground, and analyzed for carbon content. The whole soils and the two fractions were ground with a mortar and pestle to pass a 42-mesh sieve. The organic layer material was ground through a Wiley mill with fine mesh. All material was analyzed for carbon content on a LECO 12 Carbon Analyzer.

Statistical Analyses

Analysis of variance was used to test for significant differences in stand age, stand biomass, ground cover biomass, microclimate, and carbon levels due to position along the disturbance sequence. Using the ANOVA for a block design with subsampling, I

designated the ten positions along the transects as treatments, the scallop-like disturbance areas as blocks, and the transects as subsamples. Log or natural log transformations were employed to reduce unequal variances. All the analyses were done with the MANOVA subprogram (Hohlen 1979) of SPSS.

Multiple regression analysis was used to examine the influence of vegetation and soil microclimate on levels of O2 carbon/ha and light fraction carbon/ha. The forward, stepwise procedure in SPSS (Nie et al. 1975) was chosen for selection of significant independent variables. Pools of independent variables were altered if correlation matrices indicated high collinearity.

RESULTS

Stand Age

The tree cores and cross-sections yielded the dramatic age sequence (\approx =.01) shown in Figure 3 as well as the discovery that roughly one-fourth of the dominant trees in the regeneration area had survived passage of the <u>Phellinus weirii</u> wave. Both information from the tree rings and observations at the wave front supported this finding. First, the age of the "survivor trees" ($\bar{x} = 151 \pm 26$ years), fell within the lower age range of the old growth. Second, most of the survivor trees showed a period of release that correlated well with the age of neighboring, young regeneration trees. Lastly, scattered, suppressed trees were not uncommonly found under the old growth near the wave front where the light regime in the understory is improved. Apparently, trees suppressed under the old growth trees.

In regard to the survivor trees and the stand age characterization, one point should be emphasized. Because I wanted a measure of the time elapsed since the young regeneration began to appear, I used a separate index for regeneration trees and survivor trees. If a tree was a regeneration tree, I used its true age. If a tree was a survivor tree, however, I used the time since its last major release. This convention was used in the generation of Figure 3.





Stand and Ground Cover Biomass

Dimension analysis equations for the site's six tree species (Gholz et al. 1979) were used to calculate aboveground biomass from the recorded bole diameters. The biomass values should be regarded as estimates because the equations were used for some trees with diameters below the diameter range on which the equations were based. Bole diameter at ground level was used for all trees with height less than 2 m but greater than 1 m.

The calculated stand biomass showed a highly significant difference ($\ll =.003$) along the disturbance sequence (Figure 4). The basic pattern was the same as that for stand age. Biomass dropped nearly to zero just beyond the <u>Phellinus weirii</u> wave and then increased with distance from the wave front. A log transformation helped equalize variance of the biomass means but did not markedly change the significance of their difference ($\ll =.011$).

Ground cover biomass did not change significantly along the disturbance sequence (Table 1).

Temperature

Temperature along the transects changed significantly (p < .02) at all three depths in the soil profile. All the depths showed the same pattern as that depicted in Figure 5 for the 6 cm position. Soil temperatures were generally higher in the more open, young regeneration area than in the old growth and older regeneration areas where the canopies were closed. Though shade temperature in the old growth was measured for possible use as a covariate, regression analysis showed no significant relationship (p < .10) between shade



FIGURE 4: TREE BIOMASS (kg) WITHIN 5m OF SAMPLE POINT. (GRAND MEANS ±1SE)

Sample Point	Distance From Wave Front(m)	Block 1	Block 2	Block 3	x	SE
1	- 25	49.1	8.7	20.1	26.0	12.0
2	-15	82.2	0.8	123.2	68.7	36.0
3	- 5	71.5	34.5	40.1	48.7	19.9
4	2	99.2	104.3	59.3	87.6	14.2
5	5	149.3	109.7	119.1	126.0	11.9
6	9	127.2	17.0	13.8	52.7	37.3
7	14	596.5	4.3	81.0	227.3	187.9
8	24	20.9	43.3	176.5	80.2	48.6
9	34	87.0	0	81.3	56.1	28.1
10	44	39.1	31.1	83.1	51.1	16.2

----GROUND COVER BIOMASS (g/m²)----

Table 1: Block means of ground cover biomass on the lm^2 area about each sample point.





temperature and soil temperature. Mean transect temperature actually varied very little during the ten day measurement period. As an example, the coefficient of variation for 6 cm temperature over the sampling period was only 4.67%.

Particle Size Analysis

Particle size analysis revealed that fine mineral soil (<2 mm) from the 0-15 cm depth interval was a pure sand on the textural triangle. The fine mineral soil was composed of 88% sand, 11% silt, and 1% clay (Figure 6). Coarse fragments with diameters greater than 2 mm comprised 15% of whole soil weight.

Water Release Curve

The water release curve obtained for the undisturbed soil ped is characteristic of sandy soil with poor structure. The curve indicated rapid loss of moisture from 0 to 2 bars and then gradual loss from 2 to 15 bars (Figure 7). The development of an almost identical surve for the slightly fragmented soil ped demonstrated that the soil's structure had little effect on water retention.

Soil Moisture

Different moisture patterns were found for the organic layers and the mineral soil along the disturbance sequence (Table 2). Though the means exhibited considerable heteroscedasticity, the Ol layer and O2 layer showed a decrease in mass wetness from the old growth to the young regeneration area and then an increase in the older regeneration area. After a natural log transformation was used



FIGURE 6: PARTICLE SIZE DISTRIBUTION.



FIGURE 7: WATER RELEASE CURVE FOR MINERAL SOIL 0-15cm.

Sample Point	Distance From Wave Front (m)	01 Layer	02 Layer	Mineral Soil 0-15 cm	Mineral Soil 15-30 cm
1	-25	12.7 (2.6)	26.7 (2.3)	20.9 (5.1)	27.1 (2.4)
2	-15	14.6 (1.2)	53.0 (5.6)	23.2 (1.3)	25.7 (1.2)
3	- 5	12.9 (1.3)	23.1 (13.2)	17.4 (3.1)	25.2 (3.7)
4	2	9.8 (1.7)	34.0 (12.0)	29.6 (3.4)	37.2 (3.5)
5	5	5.9 (2.9)	21.7 (5.6)	25.5 (1.9)	36.5 (1.8)
6	9	7.9 (5.6)	11.7 (7.9)	19.9 (5.2)	32.2 (2.7)
7	14	8.2 (1.5)	13.5 (1.1)	17.9 (1.0)	28.4 (2.4)
8	24	8.4 (5.2)	9.5 (0.0)	18.9 (3.9)	31.9 (5.2)
9	34	10.0 (2.7)	19.0 (6.9)	17.7 (0.8)	27.1 (1.0)
10	44	14.6 (2.8)	33.3 (17.9)	18.2 (5.0)	28.6 (3.2)

Table 2: Mean values (and standard errors) of percent mass wetness (gm water/gm soil) in organic layers and mineral soil.

to equalize variances, analysis of variance indicated a difference between Ol mass wetness means ($\alpha = .09$) and a difference between O2 mass wetness means ($\alpha = .05$).

The upper and lower mineral soil layers exhibited a moisture pattern opposite to that in the organic layers. While there was no significant difference in mass wetness means for the 0-15 cm layer, the data suggested an increase in moisture from the old growth to the young regeneration and then an increase in the older regeneration area. Analysis of variance did indicate a difference in means ($\approx =$.07) for the 15-30 cm layer, which displayed the same pattern as the upper layer (Figure 8).

Carbon Analysis

When expressed as megagrams of carbon per ha, only 02 carbon showed indication of a trend across the disturbance sequence (Figure 9 and Table 3). None of the soil layers or fractions showed a significant difference in carbon means when an analysis of variance was used. Data for the 02 layer, however, did suggest a carbon reduction from the old growth to the younger sections of the regeneration zone. In five of six cases Student's t-test indicated that 02 carbon/ha was significantly higher ($\propto = .05$) at the first two old growth points than at the first three points in the regeneration area. The t-test also indicated no significant difference in 02 carbon/ha between the last sample point in the regeneration area and either the second old growth point or the first point in the regeneration area. In part the lack of a detectable



FIGURE 8: MASS WETNESS (gm water/gm) OF MINERAL SOIL 15-30cm. (GRAND MEANS ±1SE)



FIGURE 9: O2 CARBON (Mg/ha). (GRAND MEANS ± 1 SE)

		Mineral Soil					
Sample Point	Distance From Wave Front(m)	01 Carbon <u>(Mg/ha)</u>	02 Carbon _(Mg/ha)	Carbon 0-15 cm	(Mg/ha) 15-30 cm	Light Fraction Carbon (Mg/Ha)	Heavy Fract. Carbon (mg/ha)
1	-25	5.22	15.3	25.90	12.21	11.55	10.20
2	-15	7.07	19.9	19.70	9.66	10.37	10.00
3	- 5	5.47	13.7	23.48	9.00	11.18	9.67
4	2	5.53	10.3	24.15	12.07	11.02	10.73
5	5	6.13	13.3	26.13	13.10	13.06	10.74
6	9	4.94	10.3	26.26	10.21	12.56	11.70
7	14	5.39	11.9	28.05	10.83	13.44	11.11
8	14	5.86	10.4	27.74	13.10	13.94	12.02
9	34	5.01	11.1	23.88	9.15	11.04	9.92
10	44	5.89	14.6	28.30	11.37	13.82	13.56

Table 3: Grand means of carbon per hectare for all soil samples.

difference may have been due to high variance in the older section of the regeneration zone. No transformation successfully equalized the unpredictable O2 carbon variance.

Multiple Regressions

Multiple regression analyses revealed that little of the variation in soil carbon levels was explained by variation in vegetation and soil microclimate. In only about half the conducted regressions, in fact, did any independent variable have a significant F-statistic. Furthermore, when variables were significant, they produced a small R^2 (Table 4).

Dependent Variable	Sample Points	Selected Variables	Sequential R ² Values
02C/Ha	A11	01C/HA	.07
		6 CMTEMP	.14
02C/HA	4-10	01C/HA 6 CMTEMP	.12 .14
		DWDEX	.15
Light Fraction Carbon/HA	A11	DWDEX	.12
Light Fraction	4-10	DWDEX	. 10
Carbon/HA		6CMTEMP	.11
		MIMW	.17
Light Fraction	4-10	DWDEX	. 18
Carbon/HA		STANDAGE	. 28
		6 CMTEMP	. 36

Table 4: Multiple regression equations where at least one independent variable had a significant F statistic. DWDEX is a measure of dead wood importance and is calculated as (DBH²/Distance to Sample Point²)//10. Two groups of independent variables yielded significant variables for light fraction carbon/ha at sample points 4-10.

DISCUSSION

Soil Moisture Across the Gradient

The soil moisture pattern weakens the contention that increased soil moisture is one of the factors that helps accelerate forest floor mineralization after stand removal (Marks & Bormann 1972; Bormann et al. 1974; Covington 1981). Though moisture in the lower mineral soil increased after stand death, moisture in the organic layers clearly decreased. Most likely, little decomposition actually takes place in the dry organic layers during mid-summer (Fogel & Cromack 1977). However, I suggest that, as long as the organic layers receive intense solar radiation, the same pattern will be found during late spring and early fall when rainfall and decomposition rates are higher.

The water release curve derived for the upper mineral soil (Figure 7) yields valuable information on the water potential that microbial populations may experience along the disturbance gradient. If we use the collected data for the upper mineral soil (Table 2), mass wetness ranges from about 17%, or -7 bars, in the old growth and older regeneration area to about 27%, or -0.3 bars, in the younger regeneration area. Evidence from laboratory and field experiments indicates that these changes in potential may affect carbon mineralization rates. Work by Laura (1974), involving the addition of salts to decomposing plant residues, indicates a rapid decrease in CO_2 evolution from -0.05 to -10 bars. Similarly, Sindhu and Cornfield (1967), cited by Sommers et al. (1981), found that optimum water potential for nitrogen mineralization is between -0.3 and -5 bars and decreases at -5 bars. During summer months at the Waldo

site, then, evidence suggests that the local water potentials in the upper mineral soil encourage carbon mineralization in the younger regeneration area and discourage carbon mineralization in the old growth and older regeneration area.

O2 Carbon Levels Across the Gradient

Even though the pattern is not substantiated by an analysis of variance, the trend in O2 carbon levels across the disturbance gradient supports the general principle that O2 mass declines after the death or removal of a forest stand (Aber et al. 1978; Bormann & Likens 1979). Somewhat surprising is the severe heteroscedasticity, which prevents conclusions about how the O2 carbon levels change with age of the regeneration stand. I suggest the high variance in the older regeneration area is due to a patchy crown cover that causes variation in aboveground litter inputs. Variable O2 levels at the old growth point next to the wave front may reflect irregular litter inputs from Phellinus-infected trees.

Light Fraction Carbon Levels Across the Gradient

The constancy of light fraction carbon levels across the disturbance gradient prompts new hypotheses on light fraction decomposition in a severe environment and on the fine root turnover changes that accompany stand death and regrowth. At the onset of the study I expected light fraction carbon levels to decline at some time after stand death. I reasoned that higher temperature and moisture would accelerate decomposition and that fine root inputs to the light fraction pool would decrease. Clearly, my original assumptions are inadequate to explain the results.

I suggest several reasons for the lack of a light fraction decline. First, the soil nutrient status and the quality of light fraction material make the rapid decay of light fraction highly unlikely. In a survey of fourteen Oregon soils derived from Mazama ash, Geist (1977) found low values for both total nitrogen and available nitrogen. Mean values were 0.12% for total nitrogen and 7 ppm for nitrogen released during anaerobic incubation. In a nitrogen-poor environment, microorganisms will have a difficult time mineralizing the relatively carbon-rich light fraction. Second. inputs to the light fraction pool may accelerate as dead fine root material from the former old growth is broken down. Third, the volume of fine root turnover in the most recently formed regeneration area may be high. Together these three factors may compensate for any increases in carbon mineralization rates brought about by higher soil temperature and moisture at the first points in the regeneration area.

Effect of Vegetation and Microclimate on Soil Carbon Levels

Perhaps the study's most intriguing result was that vegetation and soil microclimate patterns explained very little or none of the variation in soil carbon levels. This result is counter to the findings of Sollins et al. (Accepted with revision) that showed that vegetation properties explained up to 80% of the variability in light fraction levels at two Mt. Shasta sites. These authors proposed that light fraction mass responds to short-term changes in biological activity. For the Waldo site, this is either not the case or other factors, e.g. high fine root turnover volumes in the young regeneration area, have offset changes in biological activity.

A major point to emphasize in this context is that light fraction variability at the Mt. Shasta and Waldo Lake sites was dramatically different. As a percent of whole soil weight, light fraction carbon at the Shasta site varied widely within a range of 0.75-10%. In contrast, light fraction carbon expressed on the same basis at the Waldo site fell within the narrow range of 1.02-1.50%. That a collection of independent variables could explain any variation within this narrow range is quite surprising.

A look at the independent variables that were significant in both the light fraction regressions and O2 layer regressions for the regeneration zone suggests why the predictive power of the equations was so low. In the five regression equations where independent variables were significant, the dead wood importance index was always present. In the three regressions with light fraction as the dependent variable, the dead wood index was either the first or the only dependent variable added. The implication, I propose, is that what most controls light fraction carbon levels and O2 carbon levels in the regeneration zone is the history of the previous stand.

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APPENDIX

	01	Layer	02 Layer		
SAMPLE POINT	<u></u> ۶ ,C	₹ ASH	%_C	% ASH	
1	45.3 (12.6)	14.2 (22.2)	24.2 (11.5)	54.6 (21.5)	
2	50.3 (0.6)	5.2 (0.9)	28.8 (7.0)	45.4 (13.5)	
3	44.1 (10.0)	16.7 (18.5)	19.5 (7.9)	60.7 (12.5)	
4	48.1 (2.9)	9.2 (5.5)	25.5 (7.3)	53.2 (12.7)	
5	46.0 (5.3)	12.7 (9.0)	25.6 (12.8)	53.2 (22.5)	
6	47.9 (3.0)	15.2 (9.8)	18.6 (5.9)	63.3 (11.6)	
7	43.7 (7.2)	17.9 (11.4)	21.9 (12.5)	60.1 (22.0)	
8	44.1 (7.2)	15.8 (13.4)	19.2 (11.2)	50.1 (26.6)	
9	49.5 (2.6)	6.4 (5.3)	23.9 (11.2)	56.6 (21.1)	
10	47.4 (4.4)	10.4 (7.6)	28.0 (11.9)	54.0 (21.9)	

Table 5: Mean values (and standard deviations) of percent carbon and percent ash in organic layers.

SAMPLE POINT	% C IN LIGHT FRACTION	% ASH IN LIGHT FRACTION	% C IN HEAVY FRACTION	% C IN ₩HOLE SOIL	BULK DENSITY g/cm ³
1	10.9 (1.7)	71.6 (5.5)	1.2 (0.3)	2.7 (0.6)	0.65 (0.06)
2	10.6 (3.0)	72.7 (5.0)	1.1 (0.4)	1.9 (0.6)	0.68 (0.05)
3	9.2 (3.6)	75.7 (6.6)	1.2 (0.3)	2.4 (0.6)	0.65 (0.04)
4	11.3 (3.6)	71.3 (5.39)	1.3 (0.2)	2.5 (0.4)	0.64 (0.06
5	11.1 (3.3)	71.6 (5.5)	1.3 (0.2)	2.8 (1.1)	0.64 (0.04)
6	10.6 (1.1)	72.7 (2.0) ·	1.3 (0.4)	2.6 (0.7)	0.68 (0.09)
7	10.9 (3.7)	71.9 (5.8)	1.2 (0.2)	2.7 (0.6)	0.68 (0.08)
8	12.8 (3.3)	69.1 (5.4)	1.4 (0.2)	2.9 (0.6)	0.63 (0.08)
9	9.1 (1.0)	75.0 (0.8)	1.2 (0.1)	2.4 (0.1)	0.63 (0.05)
10	13.7 (4.5)	68.4 (6.4)	1.5 (0.2)	3.0 (0.6)	0.65 (0.08)

-MINERAL SOIL 0-15 cm-----

Table 6: Mean values (and standard deviations) for measured properties in the whole soil, light fraction, and heavy fraction.

Table 6 continued:

---MINERAL SOIL 15-30 cm---

SAMPLE POINT	% C IN WHOLE SOIL	BULK DENSITY <u>g/cm³</u>
1	1.4 (0.3)	0.58 (0.06)
2	1.1 (0.3)	0.57 (0.04)
3	1.1 (0.3)	0.55 (0.04)
4	1.4 (0.8)	0.56 (0.03)
5	1.7 (1.2)	0.53 (0.04)
6	1.3 (0.3)	0.53 (0.03)
7	1.3 (0.3)	0.56 (0.04)
8	1.5 (0.5)	0.53 (0.03)
9	1.0 (0.3)	0.53 (0.05)
10	1.3 (0.5)	0.56 (0.05)