

## STAND AND SOIL CHANGES ALONG A MOUNTAIN HEMLOCK DEATH AND REGROWTH SEQUENCE<sup>1</sup>

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**Abstract.** Stand characteristics, dead wood, and soil carbon (C) and nitrogen (N) pools were measured through a wave-regenerated sequence of mountain hemlock death and regrowth created by *Phellinus weirii*. Stem density increased along the 96-yr regrowth sequence, but was low in the 225-yr-old, mature stand. Total ecosystem C (TEC) dropped upon stand death and did not recover. Net ecosystem production (NEP) was negative just after stand death and zero thereafter.

The O2 horizon and the forest floor (O1 + O2) had greater mass, organic matter, and N capital in the mature stand than in the bare or regrowth zones. From the mature stand to the bare zone, forest-floor organic matter decreased 27% and C and N 24%. The forest-floor N decrease was offset by an equal N increase in the mineral soil at 0–15 cm depth. Mineral-soil C, as well as C and N for the sum of the forest floor + mineral soil, were constant across the death and regrowth sequence. The C/N ratio peaked for O1 material, and reached its minimum for fine roots, in the bare zone.

**Key words:** dead wood; forest floor; mountain hemlock; net ecosystem production; nitrogen; organic matter; *Phellinus weirii*; stem density; subalpine.

### INTRODUCTION

Mountain hemlock (*Tsuga mertensiana* [Bong.] Carr.) forests in the Oregon Cascade Mountains provide an unusual opportunity for examining changes in stand and soil characteristics that accompany natural forest death and regeneration. Sections of these subalpine forests are dying in waves following infection by laminated root rot (*Phellinus* [*Poria*] *weirii* [Murr.] Gilbertson) (Nelson and Hartman 1975, McCauley and Cook 1980). Spreading radially from a central infection point, the root pathogen either kills host trees directly or so much weakens root systems that infected trees are toppled by winds. A new stand develops behind the *Phellinus* wave, although some dominants survive from the original stand. McCauley and Cook (1980) found that waves in these forests advance at a mean rate of 34 cm/yr, creating in <50 m a chronosequence that spans well over 100 yr. Unlike wave-regenerated fir forests in Japan (Oshima et al. 1958, Kohyama and Fujita 1981) and the United States (Sprugel 1984), little regeneration occurs ahead of the wave front in the mountain hemlock forest at Waldo Lake. Even the

10-m band behind the wave front, an area we refer to as the "bare zone," contains few seedlings.

Previous work at Waldo Lake has focused on nitrogen (N) availability (Matson and Boone 1984) and decomposition and tree vigor (Waring et al. 1987). Here we report on changes in stand density, carbon (C) and N pools, dead wood, and net ecosystem production (NEP) that accompany dieback and regrowth in this mountain hemlock forest.

### STUDY SITE

Our study site was at 1770 m elevation  $\approx$  2 km northeast of Waldo Lake, Oregon (43°30' N, 122° W) within one of the coolest of Oregon's wet forest zones (Franklin and Dyrness 1973). Annual precipitation is 1600–2800 mm, most falling as snow during the winter. The snowpack can reach 7.5 m depth and usually persists from November to early June.

The forest site includes a relatively pure stand of mature mountain hemlock surrounding *Phellinus weirii* pockets in which hemlock shares dominance with lodgepole pine (*Pinus contorta* var. *murrayana* [Grev. & Balf.] Engelm.). Minor tree species in the regenerating stand are western white pine (*Pinus monticola* Dougl. ex. Don.), Pacific silver fir (*Abies amabilis* [Dougl.] Forbes), noble fir (*Abies procera* Rehd.), and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.). Grouse whortleberry (*Vaccinium scoparium* Leiberg) forms a patchy ground cover over the entire study area.

The soil, derived from volcanic ejecta deposited during the most recent eruption of Mt. Mazama  $\approx$  6600 yr ago, is a sandy Entic Cryorthod in the Winopee series

<sup>1</sup> Manuscript received 1 April 1986; revised 10 July 1987; accepted 21 August 1987.

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(J. Simonson, *personal communication*). It includes a mor forest floor, a discontinuous albic horizon, and a poorly defined spodic horizon. The mineral soil (<2 mm) from 0 to 15 cm depth is 88% sand, 11% silt, and 1% clay; coarse fragments (>2 mm) constitute 15% of the total soil mass. Bulk density in the mineral soil ( $\bar{X} \pm \text{SE}$ ) is low and decreases somewhat with depth from  $0.65 \pm 0.01 \text{ g/cm}^3$  at 0–15 cm depth to  $0.55 \pm 0.01 \text{ g/cm}^3$  at 15–30 cm depth), a not uncommon phenomenon for the pumice soils of the Oregon Cascade Mountains (C. T. Youngberg, *personal communication*).

#### METHODS

##### *Field sampling*

In each of three dieback areas, we randomly placed two transects that extended from 25 m ahead of the *Phellinus* wave front in the mature stand to 44 m behind the wave front in the fully regenerated area. Along each transect, we sampled at three locations in the mature stand and at seven locations in the regenerating stand. Intervals were shorter just behind the wave front in order to capture more precisely the changes that immediately follow stand death. Sampling points were placed randomly from one to five paces on either side of a transect. They were moved slightly if they fell within 1 m of a stump, live tree, or large piece of woody debris.

We recorded species and diameter of standing live and dead trees >1 m tall and fallen stems >1 m long that were within 5 m of a sampling point. Diameters of trees >2 m tall and dead stems >2 m long were measured at 1.5 m; shorter trees and stems were measured at ground level. We used allometric equations of Gholz et al. (1979) for mountain hemlock, lodgepole pine, and the two true firs to calculate aboveground tree biomass from the live-tree diameters. For western white pine, we used their pooled pine equation because a species-specific equation was not provided. Biomass of roots and stumps was not calculated.

Each fallen stem was assigned to one of five decay classes (Sollins 1982): class 1 = sound wood, bark intact, and invading roots absent; class 2 = sapwood somewhat decayed, bark mostly intact, and invading roots absent; class 3 = heartwood mostly sound, bark sloughing, and roots invading sapwood; class 4 = heartwood rotten, bark detached or absent, and roots throughout; class 5 = wood fragmented and merging with soil, bark absent, and roots throughout. Standing stems were assigned to decay class 1 or 2. Mass of dead trees (excluding foliage and roots) was calculated from the same allometric equations as for live trees; biomass in each decay class was adjusted downward by multiplying by the ratio of dead-wood density for that decay class (Sollins 1982) to live-wood density for western hemlock (United States Forest Products Laboratory 1974).

Along one transect per dieback area, the age of each of the three dominant trees within 3 m of each sampling point was determined by adding the ring count at 1.5 m height to the number of whorls below. Stand age at each sampling point in the regenerating area was defined as years since passage of the wave front. This was assumed to be equal to tree age for new growth and to the number of years since cambial growth release for survivor trees. The two measures agreed well.

In July 1981, we sampled the forest floor and mineral soil and recorded soil temperatures. We measured the thickness of the O1 and O2 horizons and collected two sample sets from each with a  $20 \times 40 \text{ cm}$  frame. One set was used for measurement of mass and moisture content, the other for chemical analyses. Dead twigs <10 mm in diameter were included in the O1 material. The mineral soil was sampled by depth intervals because the horizons were discontinuous and poorly delineated. Soil for chemical analysis was cut in columns from the walls of a soil pit at depths of 0–15 and 15–30 cm. Two cores (7.5 cm deep  $\times$  7.5 cm diameter) were collected and composited from the middle of each depth interval for determining bulk density and moisture content. By necessity, roots >10 mm in diameter were excluded from the bulk-density samples because they were not easily cut by the sampler. Prior to soil sampling the groundcover plants within a 1-m<sup>2</sup> circle around each sampling point were clipped, then air dried and weighed.

*Phellinus weirii* was recorded as present at a soil pit if roots unearthed during sampling were covered with the type of white hyphal mat found on roots of dying trees at the wave front. The mat, typical of laminated root rot (Hadfield and Johnson 1977), was confirmed as *Phellinus* by incubating hyphal pieces on a selective medium developed by Hutchins et al. (1985).

##### *Soil analysis*

Samples of the forest floor and mineral soil collected for measurement of moisture, mass, and bulk density were dried at 60°C for 48 h, and samples for chemical analyses at 70° for 6 h after being air dried for 6 wk. Roots <5 mm in diameter in the mineral soil from a 0–15 cm depth were handpicked from plant debris retained on a 2-mm sieve, then dried at 70° for 12 h and weighed. Live and dead roots were not separated. Fine roots were not removed from forest-floor samples. Duplicate 50-g subsamples of sieved soil (<2 mm diameter) were separated into light and heavy fractions as defined by Spycher et al. (1983). We altered their procedure slightly by using a sodium chloride solution of  $1.2 \text{ g/cm}^3$ , which floated all recognizable plant debris but little volcanic ash.

C and N contents were determined by a LECO 12 Carbon Analyzer (Laboratory Equipment Corporation, St. Joseph, Michigan) and a micro-Kjeldahl technique. Ash-free mass of the forest-floor horizons was determined by heating samples at 550° for 4 h.

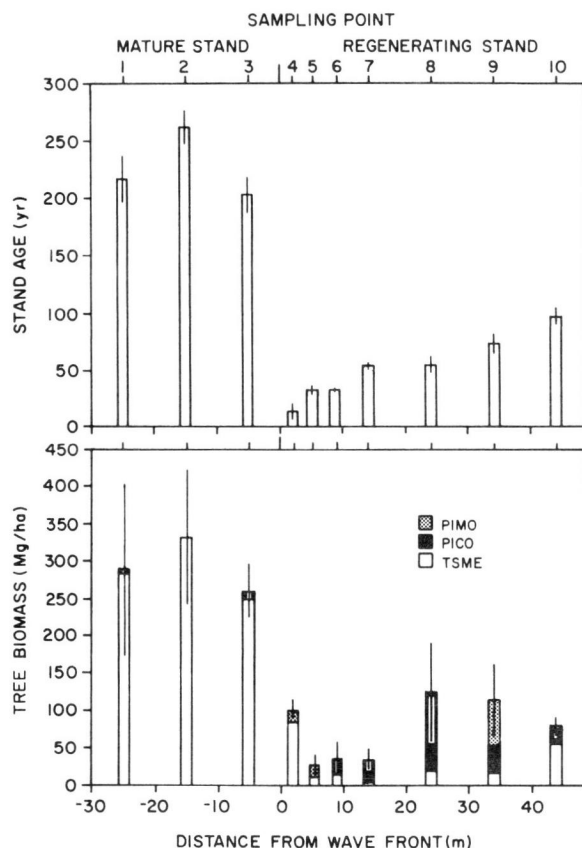


FIG. 1. Stand age and biomass along the disturbance sequence. Age in the regenerating stand is years since passage of the wave, which moves left to right. Biomass is based on dbh measurements of all trees within 5 m of a sampling point. PIMO = western white pine (*Pinus monticola*), PICO = lodgepole pine (*Pinus contorta*), TSME = mountain hemlock (*Tsuga mertensiana*). Each value is a treatment mean ( $\pm$ SE).

#### Total ecosystem carbon and net ecosystem production

Total ecosystem C (TEC) was calculated as the sum of C in aboveground biomass (including live trees, dead trees, and groundcover plants), forest floor, and the upper 30 cm of the mineral soil. Aboveground biomass was assumed to be 45% C by mass; dead trees were assumed to have no foliage. Carbon in fine roots was added to the C values for the mineral soil. Net ecosystem production (NEP) was calculated as the change in TEC during stand development. NEP in the mature stand was assumed to be zero.

#### Statistical analysis

For stand age and biomass, soil temperature and moisture, and evidence of *Phellinus weirii*, we tested for differences among sampling points (sampling-point effect) by regarding the three dieback areas as blocks and the 10 sampling points as treatments. A mixed-effects analysis of variance (ANOVA) model was used

to test the null hypothesis of no change through the death and regrowth sequence, with the block effect considered random and the treatment considered fixed. The nonparametric Kruskal-Wallis test was used to examine differences in dead tree mass because distributions were highly skewed.

For the forest floor and soil nutrient pools, the 10 sampling points were grouped into four zones on the basis of distance from the wave front and patterns for the other variables. The four zones, nearly the same as those defined by Matson and Boone (1984), were as follows: points 1, 2, 3 = mature stand zone; 4, 5, 6 = bare zone; 7, 8 = young regrowth zone; 9, 10 = old regrowth zone. The block effect was dropped from the ANOVA model if block was nonsignificant at  $P \leq .20$  (after Damon and Harvey 1986), which was true in most cases. The pooled error MSAB + MSE [(mean square of the interaction between factors A and B) + (mean square error)] was used to test zone (treatment) effect if block was significant and the block  $\times$  zone interaction was nonsignificant at  $P \leq .20$  (Lindman 1974). A block  $\times$  zone interaction was not expected a priori. All analyses of variance were made with the MANOVA subprogram of SPSS (Hull and Nie 1981). Fisher's protected LSD test (Steel and Torrie 1980) was used to compare means of zones and sampling points when ANOVA indicated a significant difference. In two cases, when the ANOVA showed no significance but a difference was expected a priori, zone or sampling-point means were compared with a simple  $t$  test.

#### RESULTS

##### Stand changes

As expected, stand age and tree biomass declined sharply at the wave front, and stand age increased at a relatively even rate through the regenerating stand

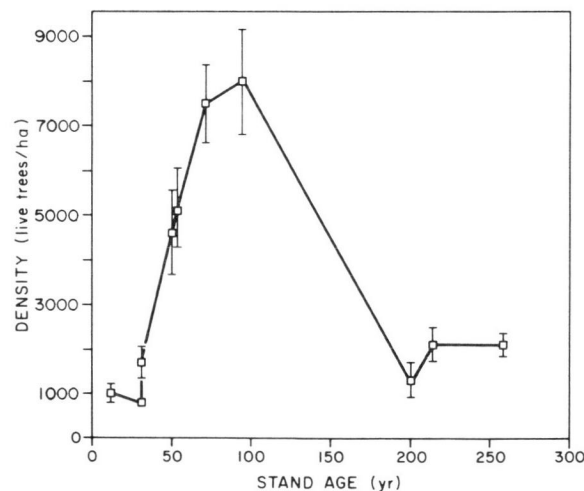


FIG. 2. Relationship between stem density ( $\bar{X} \pm$  SE) and stand age in the regrowing and mature stands. One standard error is too small to be visible.

(Fig. 1). Mean tree age in the mature stand ahead of the wave was 225 yr. Trees at sampling point 10 (44 m behind the wave front) were 96 yr old on average, yielding a mean wave speed of 0.46 m/yr. Most of the new growth was lodgepole pine. A few large hemlocks and pines survived from the previous stand and, although few in number, accounted for much of the aboveground tree biomass in the young regrowth zone.

ANOVA gave a significant ( $P < .05$ ) sampling-point (treatment) effect for all stand characteristics except groundcover mass. Tree biomass, according to the LSD test, did not vary significantly across the regenerating stand alone. Stem density increased consistently over the 96-yr regrowth sequence, where self-thinning was absent, but was low in the mature stand (Fig. 2). Mean groundcover mass ranged from 26 to 227 g/m<sup>2</sup>, with highest values from the bare zone. Dead-wood mass began to increase just ahead of the wave front and remained high into the young-regrowth zone (Fig. 3). Decay classes 3 to 5 accounted for a larger portion of the dead wood as age of the regenerating stand increased; dead-wood mass behind the wave front was lowest in the older regrowth area, 72–96 yr after trees from the former stand presumably had fallen. *Phellinus weirii*, as shown by the roots unearthed, occurred as far as 15 m ahead of the wave front, peaked in the bare zone, and then was not evident again until the oldest regenerating trees were reached.

#### Soil temperature and moisture

Temperatures in the O1 horizon and mineral soil showed the expected pattern; they were higher in the bare zone than in the mature stand or older regene-

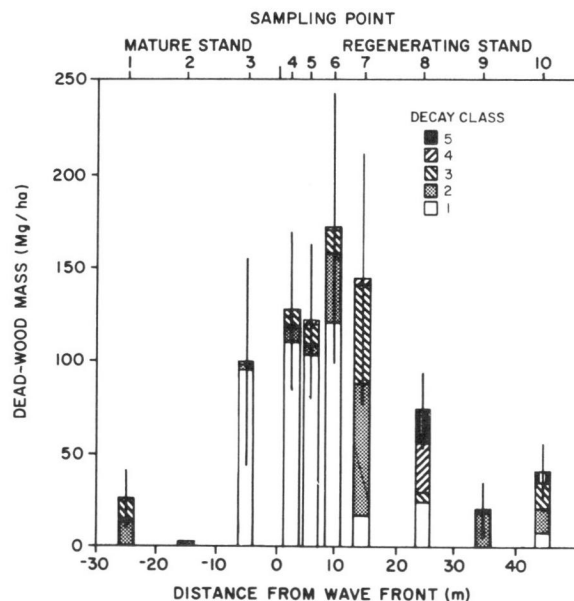


FIG. 3. Dead-wood mass ( $\bar{X} \pm \text{SE}$ ) along the disturbance sequence. Decay class 1 is least decayed, decay class 5 most decayed.

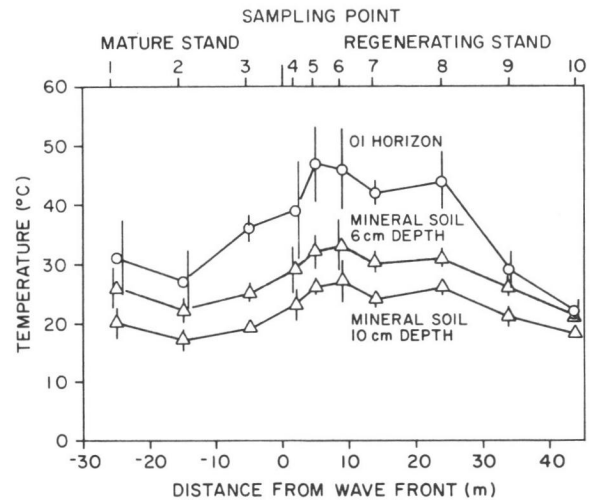


FIG. 4. Soil temperature ( $\bar{X} \pm \text{SE}$ ) just beneath the O1 horizon and at two depths in the mineral soil. Some standard errors are too small to be visible.

ation zone (Fig. 4). The bare zone also gave the lowest forest-floor and highest mineral-soil moisture contents (Fig. 5). Moisture was more variable in the O2 horizon than in the O1 horizon and mineral soil. Sampling-point effects were significant ( $P < .05$ ) for all temperatures and moisture variables, except for O1-horizon moisture.

#### Forest floor and mineral soil

Zone effects for the O2 horizon and the sum of O1 plus O2 (forest floor) were significant for mass thickness, organic matter, and N capital (Table 1). For the O1 horizon, only thickness varied significantly by zone. Comparing the mature stand with the bare zone, organic matter in the forest floor decreased by 11.6 Mg/ha (27%), and N decreased by 107 kg/ha (24%); both changes were significant by the LSD test. Forest floor N content remained low across the regrowth sequence. Although forest floor C variables showed no significant zone effect by ANOVA, a *t* test showed that C content of forest floor decreased ( $P < .05$ ) from the mature stand to the bare zone, consistent with the patterns for N and organic matter; C loss upon stand death was 5.4 Mg/ha (24%). Simple linear regression yielded no relationship at  $P \leq .10$  between the age of the regrowing stand and amounts of C and N in the forest floor.

For the 0–15 cm depth mineral soil, zone effects were significant only for N (Table 1). Comparing zone means by the LSD test, N was much lower ( $P < .05$ ) in the mature stand than in the young- and old-regrowth zones. The increase from the mature stand to the young-regrowth zone (134 kg/ha) was nearly equal to the decrease in the forest floor (133 kg/ha). There was no significant zone effect for C in the mineral soil at either depth, or for C and N in either of the density fractions. In a previous study, light-fraction C and N had cor-

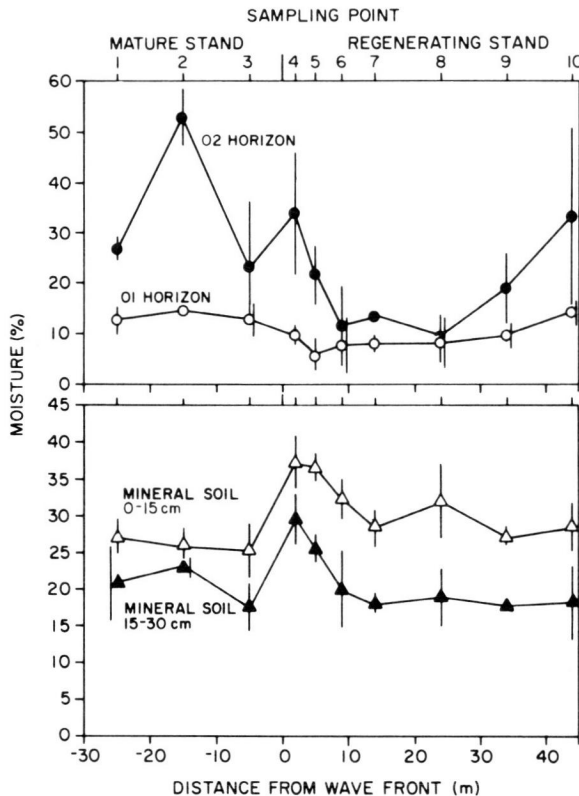


FIG. 5. Moisture content (g water/g oven-dry soil) ( $\bar{X} \pm \text{SE}$ ) for forest-floor horizons and the two depth intervals in the mineral soil. Some standard errors are too small to be visible.

related well with biomass of nearby trees (Sollins et al. 1983).

Nitrogen capital in the fine roots from the mineral soil (0–15 cm depth) increased 9 kg/ha ( $P < .05$ ) from the mature stand to the bare zone and remained high (Table 1). ANOVA showed no significant zone effect for fine-root mass, which ranged from 5 to 7 Mg/ha, or for fine root C capital, though both peaked in the old-regrowth zone.

C/N ratios (Fig. 6) peaked for the O1 horizon, and fell to a minimum for fine roots, just behind the wave front ( $P < .01$ ); C/N ratios for the O2 horizon, mineral soil (0–15 cm depth), light fraction, and heavy fraction were constant across the disturbance sequence (Fig. 6). Decrease in the C/N ratio for the fine roots was the result of both higher N concentrations and lower C concentrations, while the increase for the O1 horizon was the result of lower N concentrations alone.

#### Total ecosystem carbon and net ecosystem production

Total ecosystem C (TEC), most of which was from live vegetation, dropped from the mature stand to the bare zone and then changed little with increasing age of the regenerating stand (Fig. 7). TEC was significantly

higher ( $P < .05$ ,  $t$  test) in the mature stand than in the bare or regrowth zones. Net ecosystem production (NEP) was negative ( $P \leq .10$ ,  $t$  test) in the bare zone and not significantly different from zero in the young- and old-regrowth zones (Fig. 8).

## DISCUSSION

### Recruitment

Seedling recruitment at the Waldo Lake forest is exceedingly slow (Fig. 2), relative to temperate (Spurr 1964, Hett and Loucks 1968), tropical (Hartshorn 1978, Brokaw 1985), and even other subalpine wave-regenerated forests (Tadaki et al. 1977, Kohyama and Fujita 1981, Sprugel 1984), especially given that mountain hemlocks of seed-bearing age border the regeneration area. Causes of the delayed recruitment may be the particularly high summer temperatures in the bare zone and the extremely N-poor soil. Mid-July soil temperatures in the bare zone occasionally exceeded 54°C, a temperature lethal to many conifer seedlings (Cleary et al. 1978). Nitrogen mineralization at the site is minimal. Nitrogen mineralized during the 1982 growing season, as measured by the buried-bag technique, av-

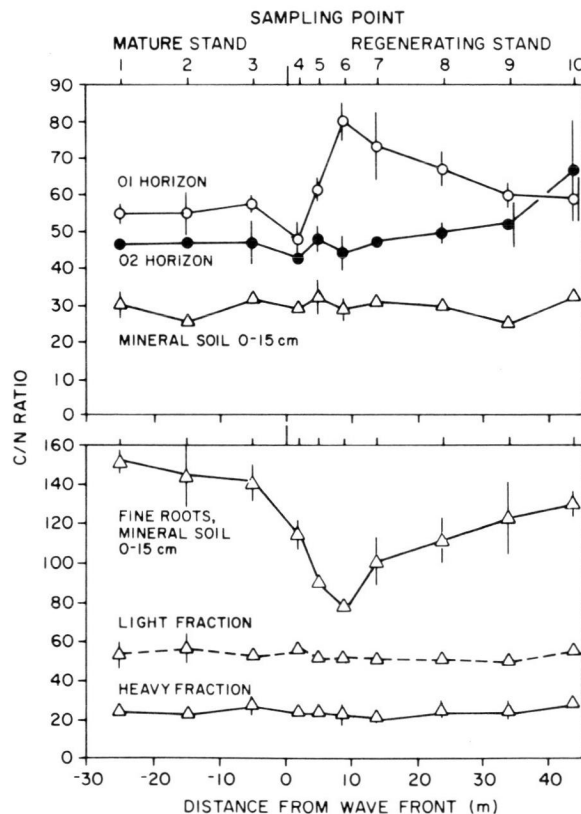


FIG. 6. C/N ratios ( $\bar{X} \pm \text{SE}$ ) for the two organic horizons, upper 15 cm of the mineral soil, the light and heavy fractions and live and dead fine roots from the upper 15 cm of mineral soil. Some standard errors are too small to be visible.



TABLE 1. Characteristics of the forest floor and mineral soil along a mountain hemlock death and regrowth sequence. Data are means  $\pm$  SE. $\ddagger$ 

| Property                | Zones of sequence           |                             |                             |                             |
|-------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|
|                         | Mature stand                | Bare zone                   | Young regrowth              | Old regrowth                |
| Mean tree age (yr)      | 225 $\pm$ 10 <sup>a</sup>   | 25 $\pm$ 3 <sup>b</sup>     | 53 $\pm$ 4 <sup>c</sup>     | 84 $\pm$ 5 <sup>d</sup>     |
| Horizon thickness (cm)  |                             |                             |                             |                             |
| O1 horizon**            | 1.1 $\pm$ 0.1 <sup>a</sup>  | 0.7 $\pm$ 0.1 <sup>b</sup>  | 0.8 $\pm$ 0.1 <sup>b</sup>  | 1.2 $\pm$ 0.2 <sup>a</sup>  |
| O2 horizon**            | 2.1 $\pm$ 0.3 <sup>a</sup>  | 1.2 $\pm$ 0.1 <sup>b</sup>  | 1.4 $\pm$ 0.3 <sup>b</sup>  | 1.3 $\pm$ 0.1 <sup>b</sup>  |
| Forest floor**          | 3.2 $\pm$ 0.3 <sup>a</sup>  | 1.9 $\pm$ 0.2 <sup>b</sup>  | 2.2 $\pm$ 0.3 <sup>b</sup>  | 2.5 $\pm$ 0.2 <sup>b</sup>  |
| Horizon mass (Mg/ha)    |                             |                             |                             |                             |
| O1 horizon              | 12.5 $\pm$ 1.1              | 11.7 $\pm$ 1.1              | 12.2 $\pm$ 2.0              | 11.1 $\pm$ 1.1              |
| O2 horizon*             | 72.4 $\pm$ 9.1 <sup>a</sup> | 50.1 $\pm$ 3.4 <sup>b</sup> | 51.0 $\pm$ 9.0 <sup>b</sup> | 49.3 $\pm$ 4.9 <sup>b</sup> |
| Forest floor*           | 84.9 $\pm$ 9.2 <sup>a</sup> | 61.8 $\pm$ 3.4 <sup>b</sup> | 63.2 $\pm$ 9.9 <sup>b</sup> | 60.4 $\pm$ 4.9 <sup>b</sup> |
| Organic matter (Mg/ha)  |                             |                             |                             |                             |
| O1 horizon              | 11.2 $\pm$ 1.2              | 10.3 $\pm$ 1.1              | 10.6 $\pm$ 1.9              | 10.3 $\pm$ 1.0              |
| O2 horizon*             | 32.1 $\pm$ 4.1 <sup>a</sup> | 21.4 $\pm$ 2.0 <sup>b</sup> | 20.0 $\pm$ 4.0 <sup>b</sup> | 21.8 $\pm$ 4.1 <sup>b</sup> |
| Forest floor $\ddagger$ | 43.3 $\pm$ 4.3 <sup>a</sup> | 31.7 $\pm$ 2.7 <sup>b</sup> | 30.6 $\pm$ 5.3 <sup>b</sup> | 32.1 $\pm$ 4.1 <sup>b</sup> |
| Carbon (Mg/ha)          |                             |                             |                             |                             |
| O1 horizon              | 5.9 $\pm$ 0.6               | 5.5 $\pm$ 0.6               | 5.6 $\pm$ 1.0               | 5.5 $\pm$ 0.6               |
| O2 horizon              | 16.3 $\pm$ 2.0              | 11.3 $\pm$ 1.1              | 11.2 $\pm$ 2.2              | 12.9 $\pm$ 2.4              |
| Forest floor            | 22.2 $\pm$ 2.1              | 16.8 $\pm$ 1.5              | 16.8 $\pm$ 2.9              | 18.4 $\pm$ 2.4              |
| Mineral soil§ 0–15 cm   | 23.0 $\pm$ 1.4              | 25.5 $\pm$ 1.6              | 27.9 $\pm$ 1.6              | 26.7 $\pm$ 1.1              |
| Light fraction          | 11.0 $\pm$ 1.0              | 12.2 $\pm$ 1.1              | 13.7 $\pm$ 1.1              | 12.4 $\pm$ 1.0              |
| Heavy fraction          | 10.0 $\pm$ 0.6              | 11.1 $\pm$ 0.6              | 11.6 $\pm$ 0.7              | 11.7 $\pm$ 0.6              |
| Mineral soil§ 15–30 cm  | 10.3 $\pm$ 2.5              | 11.9 $\pm$ 8.3              | 11.9 $\pm$ 2.6              | 10.3 $\pm$ 3.0              |
| Fine roots              | 2.8 $\pm$ 0.4               | 2.6 $\pm$ 0.3               | 2.6 $\pm$ 0.4               | 3.5 $\pm$ 0.5               |
| Total                   | 58.3 $\pm$ 2.4              | 56.8 $\pm$ 2.9              | 59.2 $\pm$ 3.1              | 58.9 $\pm$ 3.1              |
| Nitrogen (kg/ha)        |                             |                             |                             |                             |
| O1 horizon              | 107 $\pm$ 11                | 94 $\pm$ 11                 | 81 $\pm$ 14                 | 92 $\pm$ 9                  |
| O2 horizon*             | 339 $\pm$ 35 <sup>a</sup>   | 245 $\pm$ 19 <sup>b</sup>   | 232 $\pm$ 41 <sup>b</sup>   | 211 $\pm$ 27 <sup>b</sup>   |
| Forest floor*           | 446 $\pm$ 39 <sup>a</sup>   | 339 $\pm$ 25 <sup>b</sup>   | 313 $\pm$ 50 <sup>b</sup>   | 303 $\pm$ 26 <sup>b</sup>   |
| Mineral soil§ 0–15 cm   | 793 $\pm$ 28 <sup>a</sup>   | 855 $\pm$ 30 <sup>ab</sup>  | 927 $\pm$ 40 <sup>b</sup>   | 923 $\pm$ 25 <sup>b</sup>   |
| Light fraction          | 199 $\pm$ 18                | 229 $\pm$ 20                | 266 $\pm$ 21                | 227 $\pm$ 20                |
| Heavy fraction          | 441 $\pm$ 31                | 498 $\pm$ 27                | 528 $\pm$ 43                | 483 $\pm$ 36                |
| Fine roots*             | 19 $\pm$ 3 <sup>a</sup>     | 29 $\pm$ 3 <sup>b</sup>     | 25 $\pm$ 4 <sup>ab</sup>    | 28 $\pm$ 3 <sup>b</sup>     |
| Total                   | 1258 $\pm$ 47               | 1223 $\pm$ 30               | 1265 $\pm$ 35               | 1254 $\pm$ 40               |

\*  $P < .05$ , \*\*  $P < .01$ ,  $\ddagger P < .10$ ; ANOVA testing  $H_0$ : no differences among the zones of the death and regrowth sequence. $\ddagger$  Values in the same row followed by the same superscript letter are not significantly different ( $P > .05$ ), by Fisher's protected LSD test following a significant ANOVA.

§ Based on &lt;2-mm particle fraction only.

eraged 2.8 kg/ha of N in the O2 horizon and only 1.0 kg/ha in the mineral soil at 0–15 cm depth (Matson and Boone 1984).

Slow seedling recruitment, though unusual, has been reported for other coniferous stands. Peet (1981) found that tree density in the subalpine Colorado spruce–fir stands peaks once at 100 yr and again at 500 yr. Franklin and Waring (1979) noted that the uneven age structure commonly observed in old-growth stands in Oregon indicates slow establishment of new seedlings after disturbance(s). We would expect an uneven age structure for the oldest *Phellinus*-regenerated stands at Waldo Lake.

#### Tree biomass

Aboveground tree biomass for the 225-yr-old mature stand at Waldo Lake (315 Mg/ha) is low relative to other mature western subalpine stands: 445 Mg/ha for a 180-yr-old *Abies amabilis* stand at 1200 m elevation in western Washington (Grier et al. 1981) and

467 Mg/ha for a 417-yr-old *Abies amabilis*–*Tsuga mertensiana* stand at 1500 m elevation in the Coast Range of British Columbia (Krumlik and Kimmins 1976). Biomass in mature stands at Waldo Lake, however, is high relative to the mature stands adjacent to wave-regenerated fir forests: 123 Mg/ha for 60-yr-old *Abies balsamea* stands at 1484 m elevation on Whiteface Mountain, New York (Sprugel 1984), and 161 Mg/ha for 89-yr-old *Abies veitchii* stands at 2395 m elevation on Mt. Shimagare, Japan (Tadaki et al. 1977). Biomass in both wave-regenerated fir stands is limited by short lifespans of the trees: 60–80 yr on Whiteface Mountain (Sprugel 1984) and 100 to 127 yr on Mt. Shimagare (Tadaki et al. 1977). Like slow seedling recruitment, the slow biomass recovery rate at Waldo Lake has been observed in other subalpine coniferous stands (Peet 1981) but not in wave-regenerated fir forests, where biomass accumulates most rapidly between 15 and 30 yr (Whiteface Mountain: Sprugel 1984) and 10–15 yr (Mt. Shimagare: Tadaki et al. 1977).

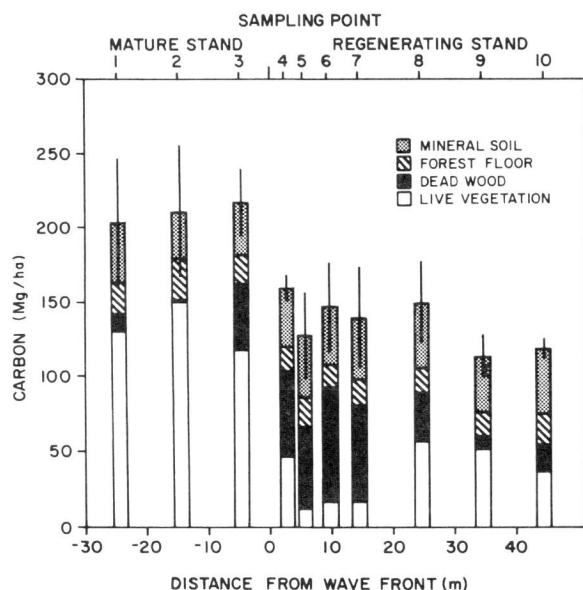


FIG. 7. Total ecosystem carbon (TEC) ( $\bar{X} \pm SE$ ) calculated from aboveground biomass (including live trees, dead trees, and groundcover plants) and carbon pools in the forest floor and upper 30 cm of the mineral soil. Values for dead trees excluded foliage; those for the forest floor and mineral soil included fine roots. Coarse roots are not included. Biomass and dead wood are assumed to be 45% carbon by mass.

#### Dead wood

The pattern of dead wood through the Waldo Lake wave sequence (Fig. 3) and the associated rate of wood decomposition is similar to that reported for other sites. Dead wood at the Waldo site peaked at year 17 after wave passage and reached its minimum at year 72 (Fig. 3). Dead wood in wave-regenerated balsam fir stands on Mt. Moosilauke, New Hampshire, peaked at about year 10 after wave passage, then declined to a minimum at about year 60. We computed a decay constant of 0.036/yr from the dead-wood maximum at sampling point 6 and the mean stand age and dead-wood mass for sampling points 9 and 10. The Waldo Lake value is very close to decay constants reported for boles of Douglas-fir in western Washington (0.028/yr: Sollins 1982), American chestnut at Cooweta, North Carolina (0.031/yr: Mitchell et al. 1975), and balsam fir on Mt. Moosilauke, New Hampshire (0.0299/yr: Lambert et al. 1980). The agreement was unexpected. Low temperatures, lack of available N, dry summers, and large bole size should limit bole decomposition at Waldo Lake.

The presence of *Phellinus*-infected roots and a large quantity of dead wood (Fig. 3) at sampling point 3 suggest that tree mortality began at least 5 m ahead of the wave front. The small increase in dead wood and presence of infected roots at sampling point 10, where the regrowing stand is 96 yr old, may herald the beginning of a second mortality wave. This is consistent

with observations (McCauley and Cook 1980) that *Phellinus* normally reinfects mountain hemlock stands near Waldo Lake after 88–165 yr.

#### Forest floor and mineral soil

The mature mountain hemlock forest has lower organic matter and N reserves in the forest floor and mineral soil than other subalpine, coniferous forests (Table 2). Limited reserves in the mineral soil at the site are the result of both low bulk density and low organic matter and N levels (percentage mass). Important factors may be the moderate age (6600 yr) and low surface area of the soil (<2% clay). Low reserves of mineral-soil N may not be unusual near the crest of the Cascade Mountains. We calculated similar values from N and bulk-density data reported by Youngberg and Dyrness (1964) for the Lapine soil series, also developed on Mazama pumice in central Oregon.

Nitrogen and carbon reserves in the soil of the subalpine mountain hemlock forest did not change significantly following death and regrowth if the organic horizons and mineral soil were regarded as one pool (Table 1). Forest-floor N and C decline after stand death, but the N decrease, at least, was offset by corresponding gains in the mineral soil.

Changes in the forest-floor thickness, mass, organic matter, and N capital at Waldo Lake suggest that the timing of forest-floor decline and recovery differs from that observed at other sites after disturbance (Sartz and Huttering 1950, Switzer and Nelson 1972, Covington 1981, Gholz and Fisher 1982). Recovery of the forest floor to predisturbance levels, if it happens at all, takes >100 yr. Comparable recovery times are 64 yr for northern hardwoods (Covington 1981) and  $\approx 10$  yr for loblolly pine plantations (Switzer and Nelson 1972). The slow forest-floor recovery at Waldo Lake probably results from a prolonged period of low litter inputs, in turn, a consequence of slow recruitment and slow tree-

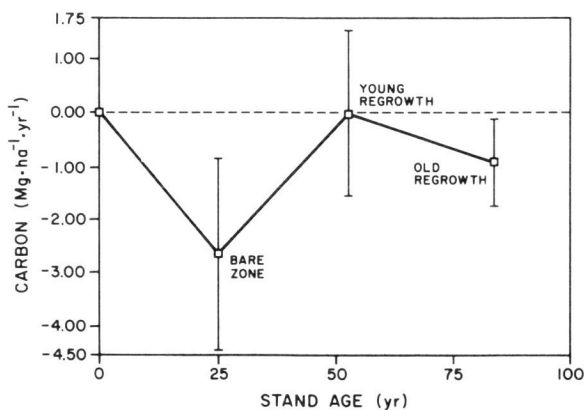


FIG. 8. Net ecosystem production (NEP) calculated from changes in total ecosystem carbon (TEC) after stand death and during stand regrowth. Each value is the grand mean ( $\pm SE$ ) of zone means for the three dieback areas.

TABLE 2. Organic matter and nitrogen (N) reserves in the forest floor and total mineral soil (0–30 cm depth) of mature, subalpine coniferous forests and of a mid-elevation Japanese hemlock forest.

| Forest type            | Reference              | Organic matter (Mg/ha) |      |              |              | Nitrogen (kg/ha) |     |              |              |
|------------------------|------------------------|------------------------|------|--------------|--------------|------------------|-----|--------------|--------------|
|                        |                        | O1                     | O2   | Forest floor | Mineral soil | O1               | O2  | Forest floor | Mineral soil |
| Mountain hemlock       | This study             | 11.2                   | 32.1 | 43.3         | 62.9†        | 107              | 339 | 446          | 1244‡        |
| Balsam fir             | Lang et al. 1981       | 75.0                   | 17.2 | 92.2         | 130          | 1800             | 500 | 2300         | 2165§        |
| Pacific silver fir     | Grier et al. 1981      |                        |      | 149.5        | 230.8        |                  |     |              |              |
| Pacific silver fir     | Turner and Singer 1976 | 13.0                   | 30.5 | 43.5         | 205.2¶       | 174              | 397 | 571          | 3555¶        |
| <i>Tsuga sieboldii</i> | Cole and Rapp 1981     |                        |      | 50.8         |              |                  |     |              |              |

† Calculated by multiplying appropriate carbon values (Table 1) by 2.22, and then correcting for coarse fragment content.

‡ Calculated by adding N value for the 0–15 cm depth (Table 1) to an estimate for the 15–30 cm depth, and then correcting for coarse fragment content.

§ Calculated from data provided by Lang et al. 1981.

|| For mineral soil from 0–38 cm depth.

¶ For mineral soil from 0–27 cm depth.

biomass recovery. By contrast, forest-floor organic matter in the wave-regenerated fir stands of New Hampshire showed no trend with respect to disturbance and stand age (Lang et al. 1981).

We have found no studies documenting increases in total mineral-soil N after forest disturbance. Factors contributing to the mineral-soil N increase at Waldo Lake are minimal N uptake by the slowly aggrading stand, low nitrification (Matson and Boone 1984), and, perhaps most likely, eluviation of particulate organic matter from the forest floor into the coarse-textured soil.

We suggest that the C/N ratio of the O1 horizon peaked in the bare zone because of increased input of woody litter from trees downed by the wave (see Fig. 3). The low C/N ratio of the fine roots (live + dead) in the bare zone, the result of lower C and higher N levels, suggests that most of the fine roots were decomposing dead roots that were immobilizing N. A possible factor is that net mineralized N (Matson and Boone 1984) also peaked in the bare zone.

#### Net ecosystem production

Net ecosystem production (NEP) may typically be negative after stand death, as decomposition exceeds organic matter inputs, positive while biomass accumulates rapidly, and near zero in a climax stand (Gorham et al. 1979, Sprugel 1985a, b). NEP rarely has been measured for a regrowth sequence, however. In one such analysis, Gholz and Fisher (1982) found that NEP was negative for 2 yr after harvest of a slash pine plantation, and positive thereafter. NEP in the pine plantation was calculated solely from changes in living biomass; harvested wood was not included, and the sum of organic matter in the forest floor and mineral soil was constant. Sprugel (1985a) developed a simulation model for biomass changes in wave-regenerated balsam fir forests and also obtained the conventionally accepted NEP pattern.

The mountain hemlock stand at Waldo Lake provides a contrast to these previous findings, in that NEP

remains near zero for nearly 100 yr of stand regrowth (Fig. 8). NEP is controlled principally by changes in live vegetation and dead wood, the forest floor and mineral soil having little effect (Fig. 7). The loss of dead wood appears to outweigh or at least balance biomass accumulation during regrowth. NEP must, of course, be positive at some point during the second century of stand growth, given the large difference in TEC between the oldest regrowth and the mature stands. The long period of near-zero NEP should be looked for at other harsh forest sites where pioneer species do not invade rapidly.

#### ACKNOWLEDGMENTS

We thank Bill Fender, Pam Matson, Steve Omi, and Gody Spycher for assistance in the field; Carol Glassman, Cindy McCain, and Andy Ungerer for contribution to the laboratory analyses; Knute Nadelhoffer, Douglas Sprugel, Peter Vitousek, and an anonymous reviewer for helpful reviews; Jo Anne Lattin for editing assistance; and Richard Waring for providing the opportunity to do this work. The Department of Forestry and Wildlife Management at the University of Massachusetts, Amherst provided additional support during manuscript preparation. We express special thanks to Marlene McDermott for overall assistance in many phases of the project. This research was supported by NSF grant DEB 81-11015. This is Paper 2051, Forest Research Laboratory, Oregon State University, Corvallis. A contribution from the H. J. Andrews Ecosystems Program.

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