Responses to Pathogen-induced Disturbance: Decomposition, Nutrient Availability, and Tree Vigour

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SUMMARY

In the Oregon subalpine zone, extensive dieback occurs in relatively pure stands of 150 to 250-year-old mountain hemlock growing on very infertile soils. Tree death is caused by a root-rot fungus, *Phellinus weirii*. Young trees that become established following death of the original forest are apparently not reinfected by the pathogen until 80–140 years later, whereon mortality occurs again. We examined the effects of this natural disturbance and subsequent regrowth on a number of ecosystem characteristics.

Decomposition rates and nitrogen availability measured by *in situ* exchange resins increased in the zones of young regrowth, but dropped to values common for old growth as the forest aged and the canopy closed. Phosphorus and potassium accumulation on exchange resins showed trends opposite to nitrogen, and may have been associated with changes in biomass. Increased nitrogen concentrations and decreased lignin concentrations in fine roots in the zone of young regrowth suggested improved tree nutrition under conditions of higher N availability and lower leaf area index. Tree vigour, estimated as wood production per unit leaf area, also was significantly increased in the zones where young forests grew. Circumstantial evidence suggests that increases in nutrient availability and light following death of the mature forest improved photosynthesis leading to increased resistance of young trees against infection by the pathogen.

INTRODUCTION

In the subalpine zone of the Cascade Mountains in Oregon, United States of America, the pathogen *Phellinus (Poria) weirii* (Murr.) Gilbertson causes the death of old-growth mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) forests as root infection progresses radially from a central point, often causing death of essentially all vegetation, including tree saplings. Young trees,

however, quickly become established on the bare soil and grow without apparent infection until they reach the age of 80–140 years, whereafter mortality begins again, providing a cyclic pattern of vegetation development (McCauley and Cook, 1980).

We were intrigued with the apparent resistance of young trees growing in an area filled with old stumps still supporting ample amounts of inoculum (Hansen, 1979; Bloomberg and Reynolds, 1981; Hadfield, 1985). In an earlier study, Matson and Waring (1984) conducted a growth room study with mountain hemlock seedlings lifted from the residual soil and later replanted · in the same. Following improvement in the availability of light or nitrogen, the transplanted seedlings increased their carbohydrate reserves and became significantly more resistant to infection to *Phellinus* than shaded or unfertilized seedlings.

In this paper we report changes in ecosystem characteristics observed across a gradient from mature 250 year-old mountain hemlock forest infected by *P. weirii* through three stages of regrowth. We associate changes in decomposition and nutrient availability with canopy leaf area, tree vigour, and fine-root chemistry that are symptomatic of changes in physiology likely to affect the resistance of trees to infection by *Phellinus* (McLaughlin and Shriner, 1980).

METHODS

The study site was in the Oak Ridge Ranger District of the Willamette National Forest in central Oregon (43° 30′N, 122° W), at 1770 m elevation. Snowpack in this area often remains from November until June or early July. The soil is an Entic Cryorthod (spodosol) derived from volcanic ash and pumice deposited ca 6600 years ago. The study site was described in detail in Matson and Boone (1984).

From three previously established transects, 70 m long, located about 500 m apart, we had data on stand age classes, July soil temperatures and moisture contents, and *in situ* and laboratory nitrogen mineralization (Boone, 1982; Matson and Boone, 1984). These same transects were used to assess alterations in canopy leaf area index, decomposition, nutrient availability, and root chemistry. We also measured an index of tree vigor found useful in predicting resistance against bark beetle attack (Waring and Pitman, 1985).

Decomposition and nutrient availability

Along each 70 m transect ten points were identified, three in the old-growth forests and the other 7 randomly placed to sample a nearly bare zone, where the only old trees were standing dead or fallen, a young regrowth area where saplings were established, and an older regrowth area where trees had made a fairly closed canopy.

Decomposition rates were estimated from weight loss of three Whatman No. 5 cellulose filter papers placed in nylon bags with 1 mm mesh. Bags were placed beneath the 02 horizon at a random distance within 5 m of either side of each transect point. The bags were installed immediately after snowmelt in early July 1982, and separate collections were made 2, 12, and 14 months later. Following collection, bags were dried at 70°C for 24hr, brushed free of adhering litter, and weighed. The filter papers were analyzed for total nitrogen using a semi-micro Kjeldahl method.

A nylon bag containing 10 g of mixed cation and anion resin beads (J. T. Baker M-614) was buried near the filter papers and collected at the same times (Binkley and Matson, 1983). Within 48 hr following collection, ions were extracted with 1 N NaCl. Ammonium, nitrate, and phosphate were determined using a Technicon Autoanalyzer. Potassium, calcium, and magnesium were analyzed using atomic absorption spectrophotometry.

Vegetation assessments

Along each of the three transects, wood cores were extracted at breast height from three trees nearest to each of the 10 sampling points. Sapwood area was determined, and leaf area estimated by assuming 0.16 m² of projected foliage area for each square cm of sapwood (a relationship derived during a previous study (Waring *et al.*, 1982). Where the sampled trees were not mountain hemlock (less than 5%), other appropriate constants were used (Waring *et al.*, 1982). Projected leaf-area index (LAI) was estimated for an area within 2 m of the transect through each of the four vegetation units by extrapolating locally determined sapwood area: total basal area relationships to all the trees found within each unit of the transect (Boone, 1982). Growth in diameter during the previous year was measured on each of the increment cores, and wood production was estimated using allometric relationships (Gholz *et al.*, 1979). The ratio of wood production per unit of leaf area was calculated as an index of vigour, as in earlier studies of host-insect interactions (Larsson *et al.*, 1983; Waring and Pitman, 1985).

Tree roots (< 5 mm diameter) were collected from the 0–15 cm soil depth at each of 10 points along the transects. Roots were dried, ground through a 40-mesh screen and analyzed for total N using semi-micro Kjeldahl and for total carbon with a LECO 12 carbon analyzer. Lignin was analyzed following the procedures of Van Soest (1963).

Statistical analyses

Sampling points along the transects were grouped into four classes based on location relative to stand age. Points 1, 2 and 3 represented old-growth; 4 and 5 the nearly bare areas with some seedlings; 6, 7 and 8 the young regrowth; and points 9 and 10 the older regrowth. These four areas were defined as treatments for analysis of variance. The three transects, located about 500 m

apart, were considered block replicates. A Fisher Protected LSD test was used to compare means of significant effects (Steel and Torrie, 1980).

RESULTS

All of the variables reported in Tables 1 and 2 varied significantly at $P < 0.05$ or 0.1 across the three transects. Soil and forest floor characteristics across the transects are summarized in Table 1. Approximately 60 per cent of cellulose paper weight was lost between late September 1982 and July 1983; snowpack was on the site for 33 of 38 weeks during this period. There were no real differences in weight loss among treatments. Nitrogen concentrations in the filter paper increased as decomposition progressed. Samples from the zone of young regrowth exhibited the highest concentrations.

Nitrogen (N) accumulation on ion exchange resins increased rapidly following mortality of the old-growth trees (Table 1). Mineral N (ammonium-N plus nitrate-N) collected by the resin over the 14 month period was four times greater in the nearly bare and young regrowth zone than in the old-growth. This agrees with the results of Matson and Boone (1984) who found that N availability (estimated by *in situ* incubations) increased in the same respective zones in both the 02 and 0–15 cm soil horizons.

TABLE 1. *Soil and litter characteristics across the four sampled zones representing various stages in development of the subalpine forest. Row means with different letters indicate significant difference at $P < 0.05$. Exceptions are denoted by an asterisk (*) where $P < 0.10$.*

Variable	Zone			
	Old growth	Bare	Young regrowth	Old regrowth
Temperature[1]				
July at 6 cm depth (°C)	24.5 a	30.8 b	31.2 b	23.5 a
Moisture content[1]				
(% dry weight)				
O_2 litter	34.3 a*	27.8 a	11.5 b	25.6 a
Soil, 15–30 cm	26.0 a	36.9 b	30.8 ab	27.8 a
Exchange resin, (µg/g)				
K	14800 a*	3020 b	7860 ab	12000 a
P	1260 a	276 b	417 b	500 ab
NO_3 N	18 a*	69 b	50 b	32 a
$NO_3 + NH_4$ N	32 a	132 b	129 b	63 a
P/N	39.4 a	2.1 b	3.2 b	7.9 b
Filter paper				
(after 14 months)				
(% weight loss)	67 a	63 a	76 a	70 a
(% N)	0.75 a	0.58 a	1.04 b	0.71 a

[1] from Boone (1982).

In contrast, phosphorus accumulation on resin was significantly less in the bare zone than in the old-growth (Table 1). Potassium accumulation on resin also varied across zones, with the lower accumulation rates occurring in the bare and young regrowth zones with higher values in the old-growth and old regrowth (Table 1). Calcium and magnesium (not tabulated) did not change significantly across zones at any sampling date, although they continued to accumulate on the resins over time.

Forest characteristics across the transects are summarized in Table 2. The canopy leaf area index reached levels in the old regrowth equivalent to the old-growth zone. The more recently colonized zones had only about half the canopy leaf area of the two more mature stages in forest development. At midday, under a uniformly overcast sky, we found that the maximum leaf area (5.6) absorbed about $89 + 3\%$ SE of all photosynthetically active radiation, as would be expected for a canopy with a light extinction coefficient of about 0.5 (Jarvis and Leverenz, 1983).

TABLE 2. *Vegetation characteristics across the four sampled zones representing various stages in forest development. Means with different letters differ significantly at $p < 0.05$.*

Variable	Zone			
	Old growth	Bare	Young regrowth	Old regrowth
Tree age (y)[1]	215 a	18 b	35 c	74 d
Leaf-area index (LAI)	5.6 a	1.9 b	2.8 b	5.2 a
Vigour Index stemwood increment per square metre of foliage (g m^{-2}y^{-1})	27 a	41 ab	63 b	30 a
Roots N (%)	0.35 a	0.45 b	0.48 b	0.38 a
C (%)	50.6 a	46.1 b	44.6 b	47.8 ab
Lignin (%)	45.5 a	40.6 b	34.3 c	35.4 c
Lignin N	130 a	90 b	72 c	93 b

[1] from Boone (1982).

Tree vigour was inversely related to canopy leaf area with values in the young regrowth reaching twice those in more mature stages. The mean values of tree vigour and canopy leaf-area index are compared graphically in Fig. 1 with changes in available soil nitrogen.

Nitrogen concentrations in small diameter roots were significantly higher in the two more recently established stands than in the older forests (Table 2). Carbon content averaged between 45–51 per cent of root dry weight with highest values in the old growth where lignin concentrations also peaked. The highest lignin nitrogen ratio was observed in the old growth with the lowest in the young regrowth (Table 2).
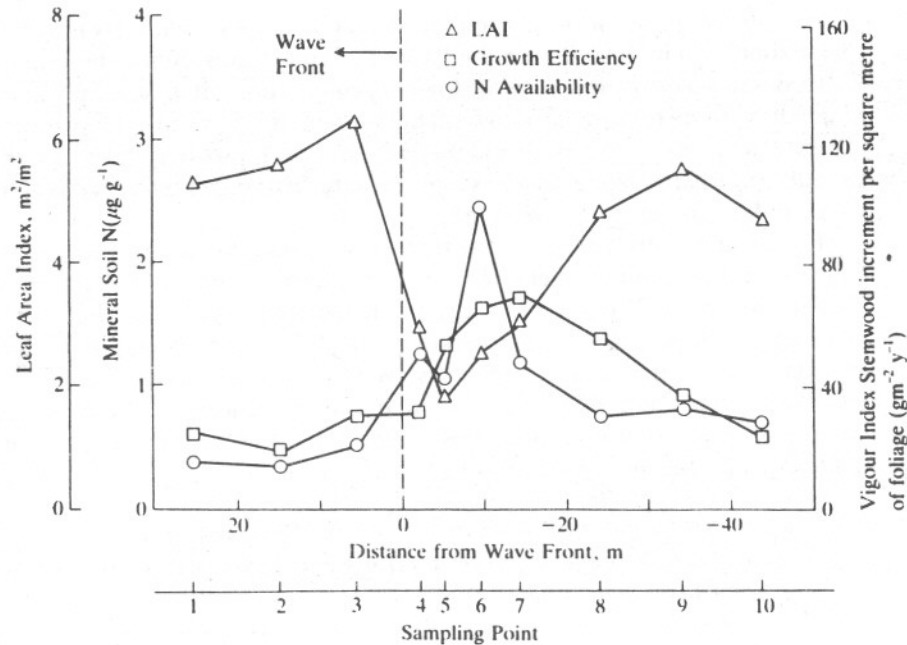
Figure 1. A transect on either side of a dieback zone (zero point) in a subalpine mountain hemlock forest. Leaf Area Index (LAI) decreases abruptly as the old growth forest is killed (0 to −10 m behind wave front). As a new forest is re-established, the canopy leaf area gradually increases again (−20 to −40 m). In conjunction with the death of the old forest, the young trees are provided more light and available nitrogen, the latter assessed by *in situ* incubation at 15–30 cm (Matson and Boone, 1984). As a result, tree vigour or growth efficiency initially improves significantly, but later decreases as the canopy again closes and nitrogen also becomes less available. We interpret increased tree vigour with resistance to the well distributed pathogen, *Phellinus weirii* and reduced vigour with susceptibility.

DISCUSSION

Subalpine mountain hemlock forests occur in a harsh environment and their ability to grow there is associated with slow growth rates and low nutrient demands. The rates at which nitrogen becomes available are among the lowest measured in the Pacific Northwest (Matson and Boone, 1984). Nevertheless, the ecosystems show distinct, measurable responses to pathogen-induced disturbance, both in terms of decomposition and nitrogen availability.

Numerous studies of the effects of forest harvesting have reported similar responses (Glavac and Koenies, 1978; Covington, 1981; Matson and Vitousek, 1981; Gordon and Van Cleve, 1983; Vitousek and Matson, 1984). These changes have been attributed in part to changes in microclimate after reduction in the canopy, as well as to changes in substrate quality. In this study, summertime temperature, soil and litter moisture contents increased in the bare and young regrowth zones (Table 1). In addition, the reduced lignin:

nitrogen ratio of fine roots suggests that they provide a more decomposable substrate in all three of the regrowth zones (Table 2).

We speculate that the relatively high concentrations of phosphorous and potassium on exchange resins under the old growth compared with the bare zone indicate that the mobility or availability of these elements is more closely tied with vegetation processes than is nitrogen mineralization. Decreased phosphorous accumulation may reflect a reduction in mycorrhizal activity in the young regenerating stands (Hintikka and Naykki, 1967; Fisher, 1972; Cromack *et al.*, 1979). Lower potassium accumulation in the bare zone in particular could reflect reduced leaching of this mobile ion from a less dense canopy.

As with soil processes, vegetation characteristics across the dieback sequence are dynamic. Tree vigour in all sequences of forest development was unusually low. In nearby areas, trees usually produce an average of 50–60 g wood per square metre of foliage at canopy leaf area indices of 5 or more (Larsson *et al.*, 1983; Waring and Pitman, 1985). In many coniferous forests, trees annually produce between 75–85 g wood per square metre of foliage (Waring and Schlesinger, 1985). Even higher values of vigour are reported in forests highly resistant to attack by various bark beetles (Mitchell *et al.*, 1983, Blanche *et al.*, 1985). In contrast, mountain hemlock trees in the stands with a leaf-area index around 5 produced annually only about 30 g wood per square metre of foliage. These values reflect the harshness of the environment, not the effects of *Phellinus weirii* infection because trees more than 100 m from any area with mortality exhibited similar vigour.

Trees in the regrowth areas were more vigorous (Fig. 1), despite the fact that the pathogen persists in dead roots (Hadfield and Johnson, 1985). Perhaps the increased decomposition of detritus associated with death of the original forest increased N availability adequately to stimulate fungi antagonistic to *P. weirii* (Nelson, 1970, 1975). The enhanced vigour and nutrient status of newly established hemlock trees is associated with increased resistance to infection by *Phellinus* as demonstrated under controlled conditions by Matson and Waring (1984).

Management implications

In the particular area we investigated, thinning and fertilization could be expected to increase the relative availability of critical resources sufficiently to improve tree vigour. A long-term experiment involving the annual addition of 50 kg of nitrogen per hectare led to trees in the regrowth zone to increase significantly their vigour and foliar nitrogen content above that of unfertilized trees (Waring and Cromack, unpublished).

Elsewhere, other factors are found to cause reduction in vigour (Marchand *et al.*, 1986). In an extreme case, excess nitrogen or imbalanced nutrition may also lead to reduced vigour and cause trees to become increasingly susceptible to disease (Matson and Waring, 1984; Entry *et al.*, 1986). The recognition

that apparently healthy trees may be physiologically incapable of resisting infection from a large dose of inoculum is well established through direct field experiments (Horntvedt *et al.*, 1983; Christiansen, 1985; Christiansen and Ericsson, 1986). This does not mean, however, that there are no silvicultural options. Presumably, improving the environmental conditions for tree growth will increase resistance to a given dose of inoculum. The results of such an experiment will be the subject of a later paper.

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