AN ABSTRACT OF THE THESIS OF

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Title: Effects of Nutrient and Light Limitation on Mountain

Hemlock: Susceptibility to Laminated Root Rot

Signature redacted for privacy.

Abstract approved: _____

Kermit Cromack, Jr.

Mountain hemlock forests in the Oregon Cascades exhibit
wave-form dieback resulting from infection by laminated root
rot (Phellinus weirii). Although Phellinus remains viable
in dead roots after the wave of dieback passes, many
regenerating mountain hemlock forests do not become
immediately reinfected. We measured at least a doubling of
nitrogen availability in the dieback and regrowth zones, and
thought that this increased availability could improve tree
resistance to the fungus. To test this hypothesis, we grew
small mountain hemlocks under nutrient and light limitations
in a growth-room, and then inoculated with the fungus.
Trees growing without added nutrients had significantly
greater foliage damage and mortality after Phellinus
inoculation than did trees growing with nutrients. Shading
significantly increased susceptibility whether or not
nutrients were added. We believe that increased nitrogen

availability and possibly increased light levels after dieback in the field act similarly to increase resistance and prevent reinfection of the regrowing stands.

Foliage damage and susceptibilty to infection were related to pool sizes of total nitrogen, phosphorus, and non-structural carbohydrates. Plants with very low nitrogen reserves (< 10 mg N per plant), or very low energy reserves (< 20 mg starch per plant), were more susceptible. It appears that resistance to Phellinus occurs via a defensive pathway that requires resources of both nutrients and carbohydrates.

Effects of Nutrient and Light Limitation

on Mountain Hemlock:

Susceptibility to Laminated Root Rot

by

Pamela A. Matson

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PREFACE

In the fall of 1980, Richard Waring, Peter Marchand, Kermit Cromack, and I proposed to test the major hypothesis that wave mortality in subalpine forests is triggered by chronic stress. We at Oregon State University chose for our study site a mature mountain hemlock forest at around 1800 m elevation in the Oregon Cascades, where tree mortality is caused by root infection with Phellinus weirii. We suggested that tree susceptibility to Phellinus is influenced by tree vigor and the status of nutrient and carbon reserves, which are in turn influenced by the environmental conditions under which the trees are growing. In these relatively open stands we found extremely low amounts of nitrogen available to trees, and originally suggested that nitrogen deficiency in these pumice soils increases tree susceptibility to Phellinus.

We proposed three kinds of experiments to test this:

1. Observations of wave-front advance following field amendments with nitrogen and carbon;

2. Observation on changes in vigor of Phellinus-infected individual trees following field additions of nitrogen, carbon, or thinning; and

3. Growth-room experiments where whole-plant carbohydrate and nutrient allocation in nutrient and light limited plants could be measured and related directly to susceptibility to Phellinus infection.

Although I was to be involved in all of these experiments, the third, relatively short-term experiment was to be considered the major portion of my Ph. D. research, and it is this research that forms the body of this thesis.

Included as Appendix 1, however, is a manuscript that establishes the major influence of wave mortality on nitrogen availability in these sites. Used in conjunction with my thesis research, it strongly suggests that the pattern of nitrogen availability is both a cause and a consequence of this wave-form disturbance.

In Appendix 3 are preliminary results from the experiments 1 and 2 described above. I was responsible for designing these field experiments and for inoculating individual trees with Phellinus-infected roots. I measured nitrogen availability before and after treatments were begun, and foliar concentrations of nitrogen, phosphorus, and starch after treatment initiation, to provide the research team with a method of evaluating treatment effectiveness relatively early in the experiments. Within another one to three years, we will measure tree vigor and actual pathogen advance to provide a field test of our major hypothesis.

EFFECTS OF NUTRIENT AND LIGHT LIMITATION

ON MOUNTAIN HEMLOCK:

SUSCEPTIBILITY TO LAMINATED ROOT ROT

INTRODUCTION

Relatively pure stands of mountain hemlock (Tsuga
mertensiana (Bong.) Carr.) in the subalpine zone of the
Oregon Cascades die back in distinct waves similar to the
fir-waves of New England (Sprugel 1976). The dieback occurs
in a radial pattern as root infection and subsequent tree
death spread outward from a central infection point (Figure
1). The pathogen (laminated root rot, Phellinus (Poria)
weirii (Murr.) Gilbertson) remains viable in dead roots and
buried stumps for 50 years or more (McCauley and Cook 1980,
Hadfield and Johnson 1977) and can reinfect trees of all
ages and sizes, so the regenerating stands can become
reinfected (Hadfield and Johnson 1977). However, in many of
these mountain hemlock stands, trees in the regrowth areas
do not exhibit symptoms of Phellinus infection, and stand-
level reinfection does not occur for 85 years or more
(McCauley and Cook 1980). This suggested to us that some
environmental factor which predisposed the trees to
infection was reduced or altered after the forest died,
allowing the regrowing vegetation to survive.

We examined several dieback areas near Waldo Lake, Oregon, where waves were advancing into 200-250 year old stands at rates of about 30 cm per year (Boone 1982). Stands were relatively open, with stocking densities well below 500 trees per hectare. Nitrogen availability, however, was very low. Matson and Boone (submitted, Appendix 1) measured potential nitrogen mineralization using anaerobic, aerobic, and in situ incubations, and found mineralizable nitrogen values of 0.5 ug/g or less in the old-growth forests. Nitrogen availability increased two to four fold in the dieback and young regrowth areas, but declined again as stands increased in age. By about 85 years, nitrogen availability was again at levels found in the old-growth. The old-growth values for nitrogen availability are lower than all of the 42 Pacific Northwest volcanic soils reported by Powers (1980), and all of the Mazama ash soils reported by Geist (1977), which indicates that these mountain hemlock stands are growing under extremely nitrogen deficient conditions. We hypothesized that nutrient limitations in the mature stands predisposed the trees to infection and spread of Phellinus, and that the improved conditions in the regrowth areas enabled the trees to resist reinfection.

Similar suggestions that environmental stresses can predispose plants to pathogen and insect attack have been made. A number of studies have demonstrated that deficiencies in nutrients result in reduced tree vigor and

increased susceptibility to diseases, especially to facultative pathogens (Hare 1966, Stakman and Harrar 1957), as well as to some insects (Mattson 1980). However, increasing nutrient availability does not always result in increased resistance (Onuff et al. 1977, Hesterburg and Jurgensen 1972). This inconsistancy may be partially attributable to different responses by different kinds of pathogens and herbivores (Mattson 1980), but also may result when only one of several limitations is alleviated by fertilization (Huber 1980, Schoeneweiss 1975). For example, Waring and Pitman (submitted) found that while thinning plus fertilization of Pinus contorta stands increased tree vigor and resistance to pine bark beetle attack, fertilization alone did not. Lambert and Turner (1977) reported that high nitrogen availability in relative excess of sulfur supply may induce sulfur deficiency and increase susceptibility of Pinus radiata to fungal pathogens. Removing a nutrient limitation may not be effective when plants are also limited by light, another nutrient, or some other factor. Under some circumstances, fertilization may even increase susceptibility.

In this study, we examined the effects of nutrient and light limitations, and the interactions of those limitations, on mountain hemlock response to Phellinus infection under controlled conditions. Because limitations of nutrients, light, and other environmental factors affect the levels of biochemical reserves which are available for

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defense (secondary compounds and morphological barriers) and repair (Bell 1981, Huber 1980, McLaughlin and Shriner 1980, Schoeneweiss 1975), we measured the pool sizes of readily-available carbohydrates as well as nitrogen and phosphorus in the trees. Our goal was to relate the status of these reserves in plants growing under limitations to the survival of the plants after Phellinus infection.

METHODS

Growth Room Experimental Design and Treatments

Dormant mountain hemlock trees (15-30 cm tall, 6-8 years old) were collected from a road-cut near the Waldo Lake dieback area. Trees were held dormant at 2 C for one month, then shipped to the Duke University Phytotron, grouped by root size, and planted into pumice soil. They were grown under a 16 hour daylength at 600 uE m^{-2} sec^{-2} PAR, with daytime temperature at 20 C and nighttime at 14 C.

Pumice soil for the growth-room experiment was collected from the 0-15 cm depth in an old-growth mountain hemlock stand adjacent to the roadside where the seedlings were collected. The soil was the same as that in the nearby dieback site; it was an Entic cryorthod in the Winopee series, derived from volcanic pumice and ash deposited in the Mazama eruption ca 6600 years ago, and was 88 per cent sand, 11 per cent silt, and 1 per cent clay.

In September, after buds had broken and growth of above-ground apical meristems was complete, trees were grouped into 10 blocks on the basis of common height, number of branches, and root size. Treatments were then applied in a split-plot design using blocks for replication. Seven nutrient and/or light combinations were the main plot treatments. Each main plot treatment was randomly applied

to groups of three trees within each block.

These treatments were designed to alter the degree of nutrient or light limitation under which the plants were growing. They originated from nutrient x sugar and nutrient x shade 2 x 2 factorials. The main plot treatments were the following: 1) a sugar addition, to stimulate uptake of nutrients by decomposers and reduce availability to the trees (Turner and Olson 1976); 2) a nutrient (NPS) fertilization; 3) a nutrient plus sugar treatment, to promote microbial activity and increase rates of decomposition, thereby acting as a priming agent for nitrogen mineralization (Baath et al. 1978); 4) the non-amended field soil control; 5) a shading treatment, to provide both nutrient and light limitation; 6) a shade plus nutrient treatment, which would provide inadequate light but adequate nutrients; and 7) a nitrogen alone treatment, to assess if this element was, as we expected, the major deficient nutrient in the soil.

Nitrogen, phosphorus, and sulfur were applied in a ratio of 100:16:8 after Ingestad and Lund (1979), and provided 10 mg N/kg dry soil, 1.6 mg P/kg, and 0.8 mg S/kg with each treatment. Sugar was added as 300 mg sucrose/kg soil, and the nitrogen alone treatment provided 10 mg N/kg. These treatments were applied in solution three times weekly, after all pots were watered to remove excess salt and to bring the pots to equal saturation. Shading with two layers of cheese cloth reduced PAR to 65 per cent of the

non-shaded. The sugar, control, shade, and shade plus
nutrient treatments were considered a priori limitation or
stress treatments. A priori comparisons were planned
between the stressed and non-stressed members within each of
the two factorials (1) control, nutrient, sugar, sugar plus
nutrient, and 2) control, nutrient, shade, shade plus
nutrient) as well as between the nutrient and nitrogen alone
treatments.

In November, after two months growth under the
limitation treatments, the subplot treatments were begun.
The three trees in each main plot treatment were assigned
randomly to inoculation treatments. One tree was grafted
with Phellinus-infected mountain hemlock roots, which had
been collected 7 days earlier from dying trees in the Waldo
Lake dieback area. The roots were covered with the white
hyphal mat characteristic of Phellinus infection (Hadfield
and Johnson 1977). Phellinus weirii was isolated from this
material on a selected media (Anita Hutchins, unpublished
data). The grafting method was similar to one recently
tested at Washington State University (Morse 1979). Trees
were partially removed from their pots, the stems just above
the first root branch were washed and sterilized with 65 per
cent ethanol, and a 2 cm long x 0.5 cm wide section of bark
and cambium was removed in each to expose the xylem.
Segments of infected roots 2.0-2.5 cm long and 1 cm in
diameter also had xylem exposed and a 0.5 cm deep x 0.5 cm
wide depression cut. Trees were placed into the groove on

the infected roots, and the exposed xylem tissues held in close contact with rubberbands. Trees were then replaced in the pots.

A second tree from each main plot group was treated in the same manner, except that each was grafted with a non-infected root from healthy mountain hemlock trees. These served as wounding controls. Finally, the third tree was harvested at the time that the others were grafted. This harvest provided the material for biomass and biochemical analyses, as it represented the response of non-wounded trees to the limitation treatments. Subplot treatments were assigned randomly.

Nutrient and light treatments were continued for an additional nine weeks until January 1982, during which time the trees were monitored for foliage yellowing and browning or leaf loss. The visual condition of the foliage was rated with scores of 1 through 5 as follows: 1=no visual foliage damage; 2= <12% foliage yellowing, browning, or loss; 3= >12% and <25% foliage damage; 4= >25% and <50% damage; and 5= >50% damage. All scores were updated twice weekly and plants attaining a score of 5 were harvested. After nine weeks, all remaining plants were harvested. The most recent, updated scores were analyzed using analysis of variance (ANOVA) for a split-plot design with only two subplot treatments included (Phellinus-inoculation and wounding control) (Figure 2). Comparisons between inoculation treatments within each limitation treatment and

between limitation treatments follow Steel and Torrie (1980, p. 381). Arcsine transformations of the score data were also done, but because the ANOVA and comparisons showed the same significant relationships, the non-transformed data is reported here.

Pieces of the inoculated stems were sent to the USFS Research Laboratory in Corvallis, Oregon for isolation and confirmation of <u>Phellinus</u>. However, stem diameters were too small for the methods then in use, and reisolation was not attempted.

Harvest Methods and Chemical Analyses

At harvest, plants were removed from the pots, and, after the root systems were carefully washed with deionized water, were separated into roots, leaves, and stems. Subsamples of leaves were weighed and specific leaf areas were measured. Root mycorrhizal cover, root lengths, and numbers of root branches were also measured on subsamples, and stem heights and diameters were recorded. Stems and remaining leaf and root tissue were quick frozen with liquid nitrogen and stored at -10 C until they could be lyophilized. After freeze drying, samples were weighed, ground to pass through a 40 mesh screen, and stored dry at -10 C until analysis.

Chemical analyses were done only for plants harvested in November. Total nitrogen and phosphorus were measured with a Technicon Autoanalyzer II after samples were digested

in a Technicon block digestor using a sulfuric acid-mercuric oxide catalyst (Technicon Instruments Corp. 1977). At least one duplicate was run in every 20 samples to ensure uniformity in the method.

Non-structural carbohydrates were measured using methods of Haissig and Dickson (1979). Tissue samples weighing .020 g were extracted in a methanol-chloroform-water (MCW) solution (6:2.5:1.5 V:V:V), with the supernatant containing soluble sugars, pigments, phenolics and other solubles (Dickson 1979). Sugars were separated from pigments and lipids by adding 3 ml water per 5 ml MCW, followed by centrifugation and separation of the water-alcohol phase from the chloroform phase. Sucrose was hydrolyzed to glucose with 0.1 N HCl, neutralized with 0.1 N NaOH, and measured as glucose by mixing 0.5 ml of diluted sample with 5 ml peroxidase glucose oxidase o-dianisidine dihydrochloride reagent (Sigma Chemical Company Bulletin 510-A). Absorbance was measured at 450 nm after 30 minutes incubation at 30 C. Only sucrose and glucose were measured because they have key roles in transport and the regulation of transport of carbon, and because sucrose is generally the sugar that varies most with season and nutrient status in conifers (Geiger 1979, Krueger and Trappe 1967).

Ater MCW extraction, the residue, which contains starch, was dried at 50 C overnight. After 0.2 ml 95% ethanol and 4 ml water were added to each sample, tubes were capped and placed in boiling water for 10 minutes. Each

tube, including water blanks, received 1 ml purified enzyme solution; tissue blanks received only buffer. The enzyme solution was a combination of purified Diazyme L-150 (alpha 1,4 glucan glucohydrolase, Miles Laboratories) and Mylase 100 (alpha-amylase, G.B. Fermentation Industries, Inc.) in concentrations of 10 mg/ml and 5 mg/ml respectively. Tubes were capped tightly, mixed, and placed in an incubator at 50 C for 24 hours. After enzymatic hydrolysis, starch was measured as glucose using the glucose oxidase method described above. Duplicates were run for two samples in each group of 20, and two to five tissue blanks, one enzyme blank, and three starch standards were included with each group.

Amino acids were analyzed for root tissues from two replicates for four of the treatments (control, nutrient, shade, and shade plus nutrient). The analyses were completed in the Department of Biochemistry at Oregon State University, and followed the procedure of Spakman, Stein and Moore (1958).

Data for the November harvest plants were analyzed with ANOVA for a randomized block design using the ANOVA procedure of the SAS statistical programs package (SAS Institute Inc. 1979). Log transformations were used when necessary to equalize variances. However, all data are reported here in the non-transformed form. In general, individual comparisons were made using Tukey's honestly significant difference test (HSD) (Steel and Torrie 1980, p.

185). In addition, a priori planned comparisons between stressed and non-stressed members of the two factorials (described above) were made using the least significant difference test (lsd), and are noted as such in the results.

Biomass data from the plants harvested in January were analyzed using ANOVA for a split-plot design. In addition, correlations were made between mean scores and mean ratios of leaf weight to stem weight for the treatments. Correlations were done using the GLM procedure of SAS.

RESULTS

Inoculation Scores

Analysis of variance for a split-plot design for the final score showed highly significant F values for both the main plot (limitation) and subplot (inoculation) treatments (Table 1). Within the limitation treatments, comparisons between scores of plants inoculated with Phellinus and scores of the wounded control indicated significant differences in four of the seven treatments (Table 2). In the control, sugar, shade, and shade plus nutrient treatments, which were our a priori stress treatments, the plants inoculated with Phellinus had more severe foliage damage and mortality than did their paired controls, apparently indicating that the damage in these plants was Phellinus-induced.

Comparisons between limitation treatments for the Phellinus-inoculated plants showed that the nutrient, sugar plus nutrient, and nitrogen treatments had significantly lower scores and apparently less susceptibility than did the stress treatments (Table 2, Figure 2). The shading treatment had the most foliage damage resulting from Phellinus infection, while the sugar alone and control treatments produced slightly less damage. The shade plus nutrient treatment had a significantly lower mean score than the other stress treatments, but a significantly higher score than the nutrient treatment.

Because scores were assigned using a visual estimate of damage, a correlation of the mean score vs. the mean ratio of leaf weight to stem weight was used to quantify the relationship. Because trees from the November harvest had approximately the same ratio regardless of treatment, variations in the ratio for the January harvest should indicate foliage loss or browning due to infection or wounding, and should therefore correlate with the assigned scores. The correlation coefficient was .74 ($p < .01$); ratios ranged from 0.6 to 1.0, and trees with higher scores had lower ratios of leaves to stems, indicating that they had more severe foliage damage.

Biomass

Plants harvested in November did not have significantly different total dry weights when analyzed by ANOVA (Table 3). Root weights, however, did differ; the nutrient treatment had significantly greater mean root weight than the other stress treatments ($p < .05$, Table 3).

Dry weights for the plants from the first harvest were compared with the wounded controls from the final harvest using ANOVA for a split-plot design. Root weights increased in the two months between harvests in all cases, but significantly so only in the sugar plus nutrient and shade plus nutrient treatments (Table 4). The ANOVAs for leaves and stems did not demonstrate any significant differences in biomass between harvests, but total dry weights were

significantly different, apparently because the root weights increased (Table 4). The fact that growth response to treatment was evident only in the roots in both harvests is not surprising considering that mountain hemlock is a determinate, slow-growing tree. Shoots did not flush during the course of the experiment.

Total Nitrogen and Phosphorus

Because plant tissue weights were not generally different for the plants harvested in November, differences in total plant tissue nutrients reflected primarily differences in tissue nutrient concentrations (Table 5, Figure 3). As expected, increasing the nitrogen supply to the roots significantly increased N concentrations and contents in all plant parts (Table 5, Figure 3). The planned comparisons between the nutrient and sugar plus nutrient treatments indicated significantly less N in the sugar plus nutrient treated plants (lsd, $p < .05$). Apparently, instead of increasing N availability to the plant through a priming effect on decomposition, the sugar plus nutrient treatment provided an accessible carbon source for the decomposers, thereby increasing their N requirement and leading to N immobilization in microbial biomass. Nitrogen allocation to plant tissues did not differ significantly between any of the treatments (Figure 3).

Although significance tests were not used for amino acids due to the small sample size, the means for two

replicates in the nutrient, shade plus nutrient, shade, and control treatments indicated that nutrient-treated plants put twice as much of their larger amino acid pool into arginine, a common storage amino acid (Van den Dreissche and Webber 1977, 1975) than did the nutrient limited plants.

Total phosphorus in individual plant tissues was not different between treatments (Figure 4). Phosphorus concentrations, however, varied significantly in stems and roots, with the nutrient treated plants generally having higher P concentrations in those tissues (Table 5). Allocation of P to plant tissues also varied significantly, with the plants growing without nutrients or nitrogen allocating more P to leaves ($p < .001$), Figure 4). Because there were no significant differences between the nutrient and nitrogen alone treatments, these differences in concentration and allocation between stressed and non-stressed plants are not caused by a direct response to P fertilization, but rather result from some relationship between N availability and P uptake and use by the plants.

Plant Starch and Sugars

As with N and P, starch quantities in plant tissues reflected starch concentrations. Plants growing without added nutrients generally accumulated significantly greater quantities of starch than did those treated with nutrients (Table 6, Figure 5). While total tissue levels were not different between treatments, concentrations of sucrose plus

glucose in leaves and roots were significantly lower in the nutrient treated plants than in those growing without nutrients (Table 6). These trends in non-structural carbohydrates are in agreement with a number of studies of both agricultural and wild plants (Shaver and Chapin 1981, Ericsson and Persson 1980, Ericsson 1979, Smith 1973, Priestly 1962), and presumably occur because without adequate nutrients for growth the carbon fixed in photosynthesis is in excess of the demands of the plant (Webb 1981, Mattson 1980).

When trees were receiving nutrients, shading significantly lowered starch accumulation (lsd $p < .05$, Figure 5). However, for plants growing without nutrients, starch accumulation with shading was not significantly different from the control.

DISCUSSION

Trees that were grown under nutrient limitations were more susceptible to <u>Phellinus</u> than trees receiving nutrients. These more susceptible plants in general had very low nutrient contents and high starch storage. The availability of stored carbohydrates suggests that the production of carbon-based secondary chemicals such as phenolics may not have been quantitatively important in defense. Phenolic levels are normally highest when low nitrogen availability limits the production of proteins, thus leaving their common precursor, phenylalanine, available for use in phenolic synthesis (Phillips and Henshaw 1977).

Shading trees which were growing without adequate nutrients resulted in even higher scores and greater susceptibiltiy to <u>Phellinus</u>. This increased susceptibiltiy under a combination of light and nutrient limitation, however, could not be related to the plant reserves measured here, as the shaded trees had nutrient and carbohydrate reserves similar to the control plants. Carbon reserves in this case were not reduced by shading, probably because when nutrients are inadequate, carbon fixation and storage is more limited by a lack of N-containing compounds like chlorophyll and RuDP carboxylase than by light availability. Qualitative as well as quantitative variations in soluble sugars, amino acids, or organic acids could be

caused by shading (Durzan 1971), and could influence
susceptibility of trees to attack by Phellinus (Li and
Bollen 1975).

Among trees receiving nutrient additions, shading
significantly increased the trees' susceptibility to the
pathogen. In this case, however, light limitation did
affect the amounts and concentrations of non-structural
carbohydrates without affecting plant nutrient levels. When
nutrients are adequate, reduction in light intensity does
influence carbon fixation and storage (Magnussen 1981,
Little and Loach 1973, Smith 1973, Priestly 1962).
Increased susceptibility under these conditions could
indicate that some lower threshold of carbon necessary for
allocation to defense or repair had been exceeded.
Alternatively, this result could suggest that an excess of N
in relation to carbon had been produced, resulting in
alterations in the biochemical components which influence
susceptibility to the pathogen. Excess N has apparently
resulted in greater susceptibility to insects and disease in
a number of studies (Hesterberg and Jurgensen 1972, Lambert
and Turner 1977, Onuf et al. 1977, Stakman and Harrar 1957).

Together, these results suggest that resistance to the
spread of Phellinus in mountain hemlock occurs via a
defensive pathway that requires adequate and balanced
resources of both nitrogen and carbon. One such pathway,
the building of morphological barriers, is a relatively
common response to wounding and invasion by decay fungi and

rusts (Bell 1981, Shigo et al. 1977, Hare 1966), and could have functioned in resistance to <u>Phellinus</u>. However, resistance may depend on many biochemical and physical components acting through one or more defensive pathways (Bell 1981, McLaughlin and Shriner 1980, Levin 1976).

Whatever the pathway of defense, our results show that plants growing without adequate nutrients were more susceptible to infection by <u>Phellinus</u> than were nutrient-treated plants. These results may explain the field observation that while mountain hemlock trees growing in the old-growth stands are susceptible to infection, trees in the regrowth zone do not show infection and mortality. We think that the increased nutrient availability after dieback leads to increased resistance and prevents reinfection of the regrowing stands (Matson and Boone submitted, see Appendix 1). Long-term experiments are now underway to test more directly the effects of nutrient and light limitations on susceptibility in both old-growth and regrowing mountain hemlock stands.

Table 1. Analysis of variance for a split-plot design, with
          limitation treatments as main plots and
          inoculation treatments (Phellinus inoculation and
          wounded control) as subplots, for the variable
          SCORE.

ANOVA for SCORE

Source	df	SS	MS	F	P
Block	9	24.5		2.71	.01
Limitation	6	65.9		10.95	.0001
Error A	53	53.2	1.00		
Inoculation	1	20.1		20.98	.0001
Limit x Inoc	6	8.9		1.55	.18
Error B	62	59.3	.96		

Table 2. Foliar damage score for <u>Phellinus</u> inoculation and wounded controls. Low scores indicate no damage, high scores indicate severe damage (see Methods). Each value is the mean (+-s.e.) of 10 replicates. Asterisks indicate significant differences between columns only (* p<.05, *** p<.001); common letters indicate no significant differences within columns.

SCORE

Treatment	Inoculation Treatment		
	Wounded Control		Phellinus
Nitrogen	1.3 (.21) [ab]		1.6 (.42) [c]
Nutrient	1.1 (.10) [a]		1.3 (.15) [c]
Shade plus Nutrient	1.4 (.40) [ab]	*	2.3 (.50) [d]
Sugar plus Nutrient	1.0 (0) [a]		1.2 (.13) [c]
Control	1.8 (.20) [ab]	*	2.7 (.45) [de]
Sugar	2.1 (.45) [b]	*	3.3 (.37) [ef]
Shade	2.2 (.29) [b]	***	3.8 (.42) [f]

Table 3. Biomass (g dry weight) for plants harvested in
          November, after two months growth under
          treatments. Each value is the mean (+- s.e.) of
          10 replicates. Comparisons of means using HSD
          were done only when the ANOVA F was significant.

Treatments	Biomass (g)			
	Total	Leaves	Stems	Roots
Nitrogen	4.06 (.63)	1.02 (.17)	1.13 (.18)	1.91 (.32)
Nutrient	4.42 (.57)	1.08 (.15)	1.01 (.15)	2.33 (.28)
Shade plus Nutrient	3.53 (.54)	.89 (.14)	.93 (.18)	1.71 (.23)
Sugar plus Nutrient	3.54 (.55)	.86 (.14)	.99 (.21)	1.69 (.21)
Control	3.15 (.36)	.79 (.09)	.88 (.10)	1.48 (.22)
Sugar	3.69 (.53)	1.00 (.18)	.99 (.14)	1.70 (.23)
Shade	3.16 (.16)	.84 (.16)	.96 (.14)	1.36 (.16)
HSD				.764
ANOVA significance	−	−	−	.001

Table 4. Total and root biomass (g dry weight) for November harvest and January harvest (wounded control only). Each value is the mean (+- s.e.) of 10 replicates. Asterisks indicate significant differences between November and January means (* p<.05, *** p<.001). Common letters within columns indicate no significant differences. Comparisons of means are according to Steel and Torrie (1980), using MSE's from ANOVA for a split-plot design.

Treatment	Biomass (g)			
	Total		Root	
	November	January	November	January
Nitrogen	ab 4.06 (.63)	a 3.92 (.44)	ab 1.91 (.32)	b 2.21 (.27)
Nutrient	b 4.42 (.57)	bc 4.88 (.67)	b 2.33 (.28)	c 2.82 (.48)
Shade plus Nutrient	a 3.53 (.54)	* b 4.48 (.58)	ab 1.71 (.23)	* bc 2.40 (.32)
Sugar plus Nutrient	a 3.54 (.55)	*** c 5.49 (.53)	ab 1.69 (.21)	*** d 3.44 (.38)
Control	a 3.15 (.36)	a 3.54 (.57)	a 1.48 (.22)	ab 1.92 (.29)
Sugar	ab 3.69 (.53)	a 3.34 (.46)	ab 1.70 (.23)	ab 1.86 (.22)
Shade	a 3.16 (.16)	a 2.96 (.52)	a 1.36 (.16)	a 1.59 (.25)

Table 5. Percent nitrogen and phosphorus in tissues from the November harvest plants.
Each value is the mean (+- s.e.) of 10 replicates. Comparisons of means using
HSD done only when one-way ANOVA F was significant.

Treatments	% Nitrogen			% Phosphorus		
	Leaves	Stems	Roots	Leaves	Stems	Roots
Nitrogen	1.64 (.20)	0.50 (.05)	0.98 (.14)	0.16 (.02)	0.09 (.01)	0.10 (.01)
Nutrients	1.32 (.11)	0.54 (.09)	1.02 (.14)	0.14 (.01)	0.08 (.01)	0.11 (.01)
Shade plus Nutrients	1.45 (.18)	0.69 (.10)	1.05 (.14)	0.15 (.01)	0.09 (.01)	0.13 (.01)
Sugar plus Nutrients	0.99 (.13)	0.41 (.05)	0.72 (.09)	0.16 (.02)	0.08 (.01)	0.11 (.01)
Control	0.51 (.05)	0.22 (.02)	0.43 (.12)	0.17 (.02)	0.08 (.01)	0.07 (.01)
Sugar	0.34 (.03)	0.24 (.04)	0.32 (.03)	0.18 (.01)	0.06 (.01)	0.08 (.01)
Shade	0.36 (.03)	0.23 (.04)	0.34 (.04)	0.16 (.01)	0.07 (.01)	0.08 (.01)
HSD	.465	.201	.432		.028	.024
ANOVA	.0001	.0001	.0001	-	.032	.0001

Table 6. Per cent starch and sugar (sucrose and glucose) in tissues from the November harvest plants. Each value is the mean (+- s.e.) of 10 replicates. Comparisons of means using HSD done only when ANOVA F is significant.

Treatment	% Starch			% Sugar		
	Leaves	Stems	Roots	Leaves	Stems	Roots
Nitrogen	2.00(1.17)	0.70 (.32)	1.24 (.30)	2.14 (.28)	1.25 (.17)	2.23 (.25)
Nutrients	1.85 (.50)	0.31 (.08)	1.26 (.23)	1.96 (.22)	1.29 (.15)	2.01 (.19)
Shade plus Nutrients	0.40 (.19)	0.38 (.14)	0.98 (.16)	1.99 (.21)	1.40 (.18)	2.16 (.20)
Sugar plus Nutrients	2.13 (.69)	0.63 (.22)	1.97 (.22)	2.18 (.14)	1.45 (.15)	2.33 (.17)
Control	5.38 (.98)	2.15 (.29)	4.31 (.51)	3.18 (.24)	1.25 (.10)	2.46 (.19)
Sugar	7.45 (.84)	2.70 (.22)	4.20 (.40)	2.73 (.18)	1.31 (.13)	2.69 (.21)
Shade	5.59(1.34)	1.97 (.25)	3.79 (.44)	3.14 (.34)	1.34 (.34)	2.88 (.29)
HSD	3.71	.96	1.34	.89		.73
ANOVA	.0001	.0001	.0001	.0001	--	.01
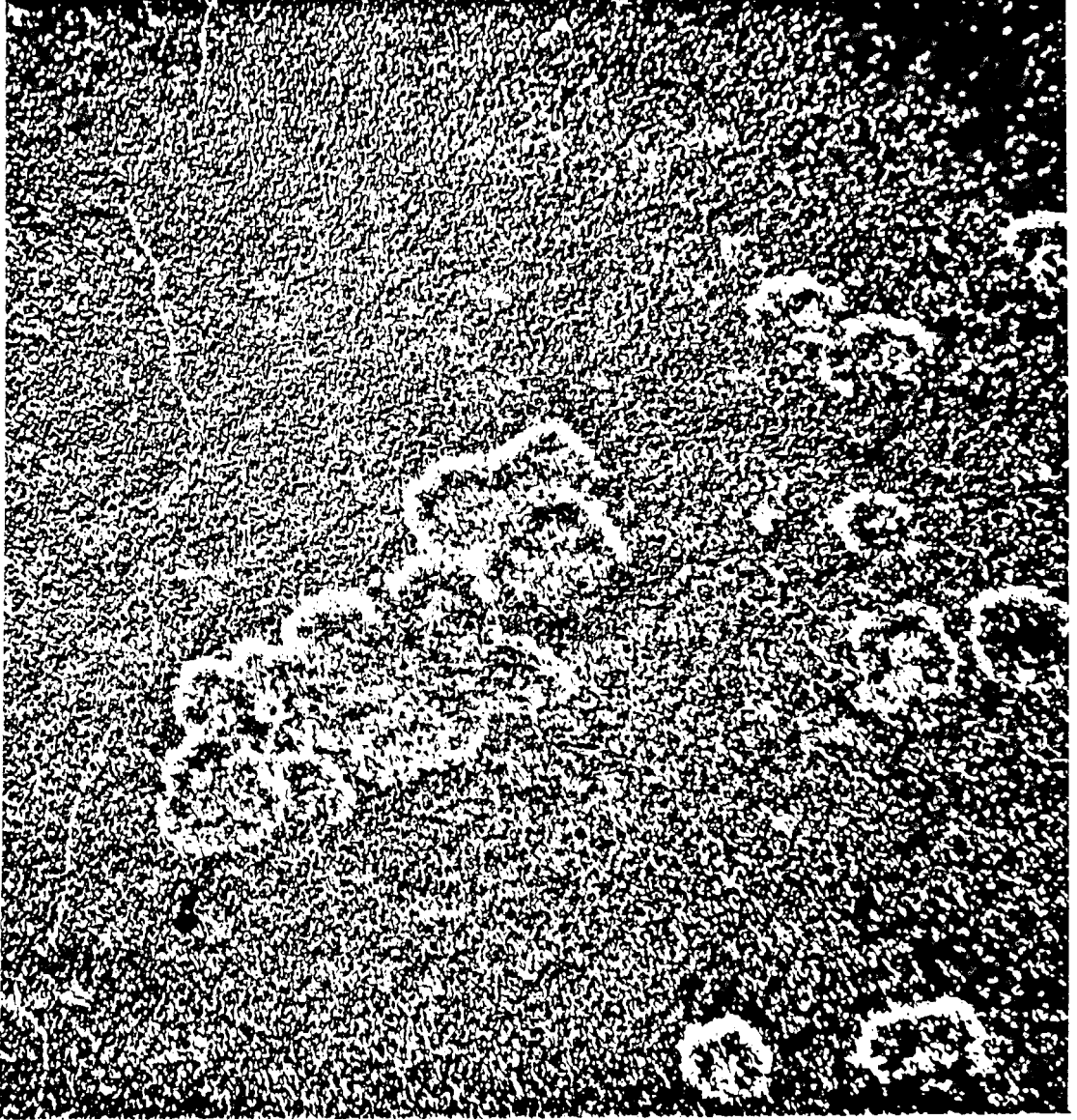
Figure 1.   Aerial photograph of dieback waves in mountain
            hemlock forests near Waldo Lake, OR.
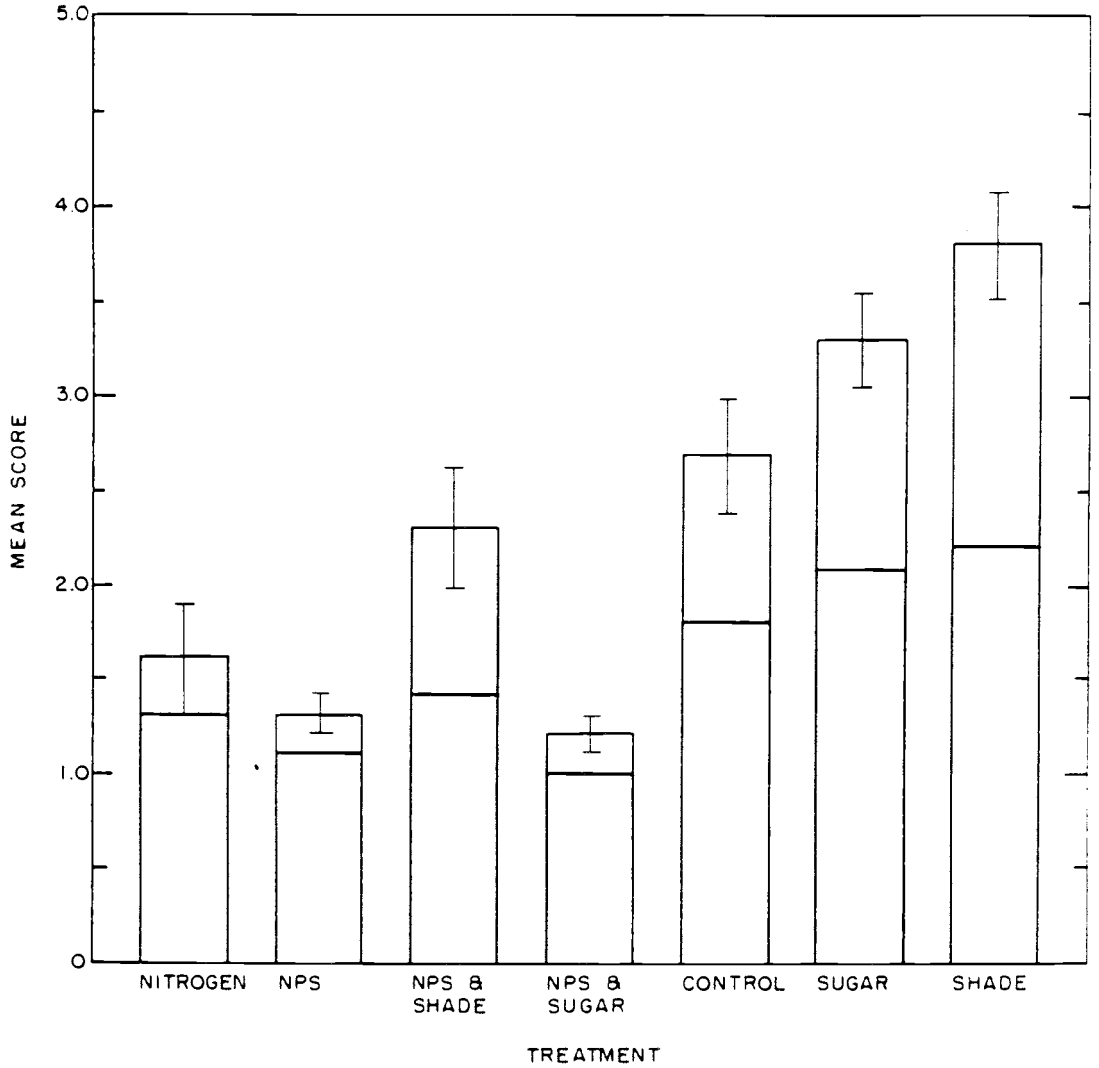
Figure 2. Foliage damage scores for January harvest plants.
Upper line is the mean score (+-s.e.) of 10
Phellinus-inoculated trees. Lower line is the
mean score of 10 wounded-controls. Lower scores
indicate little damage; high scores indicate
severe damage.
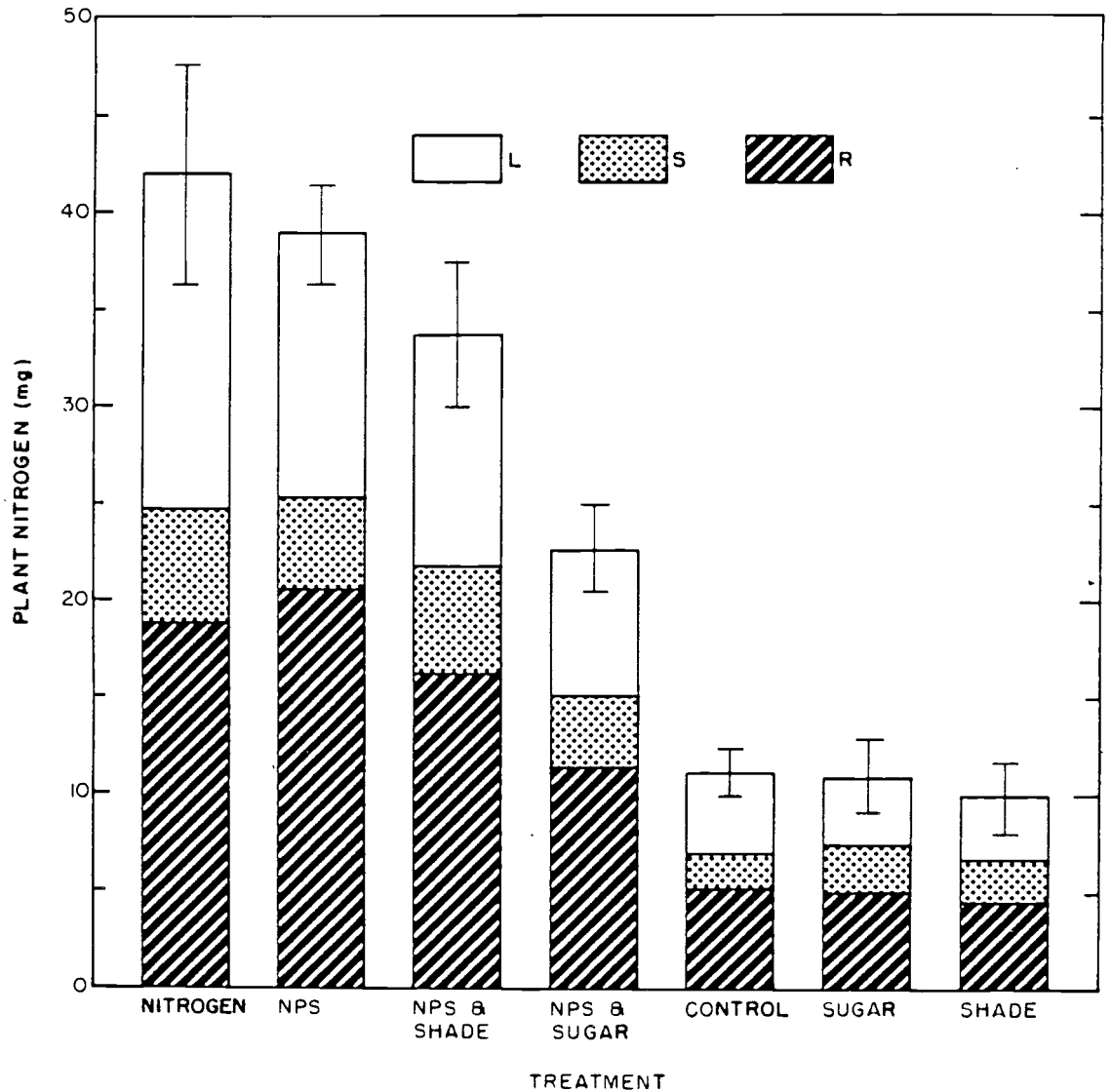
Figure 3.

Total plant nitrogen (mg/plant), divided into leaves (L),
stems (S), and roots (R). Upper lines are total plant
nitrogen means (+-s.e.) of 10 replicates.
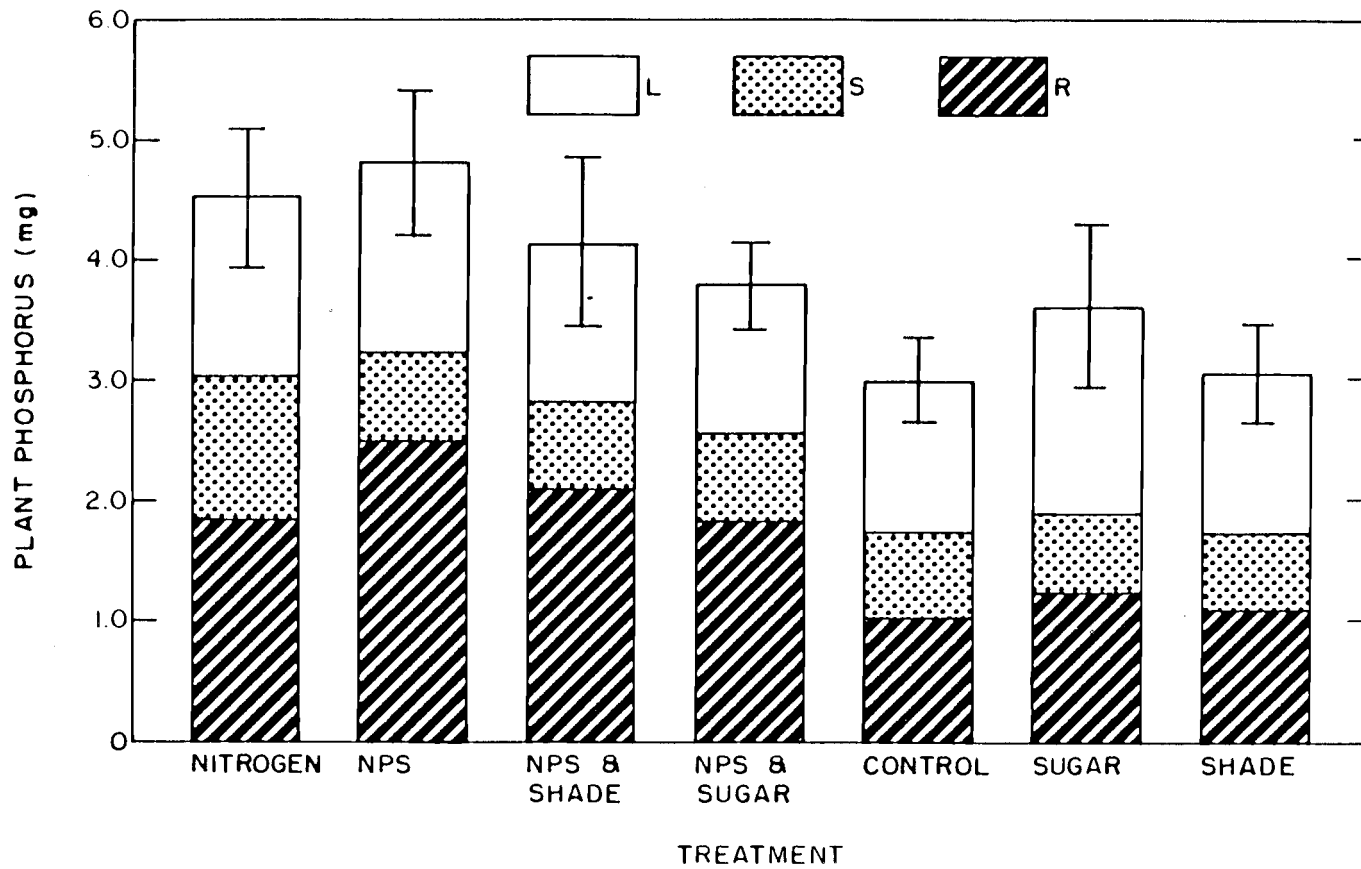
Figure 4. Total plant phosphorus (mg/plant), divided into leaves (L), stems (S), and roots (R). Upper line indicates total plant means (+-s.e.) of 10 replicates.
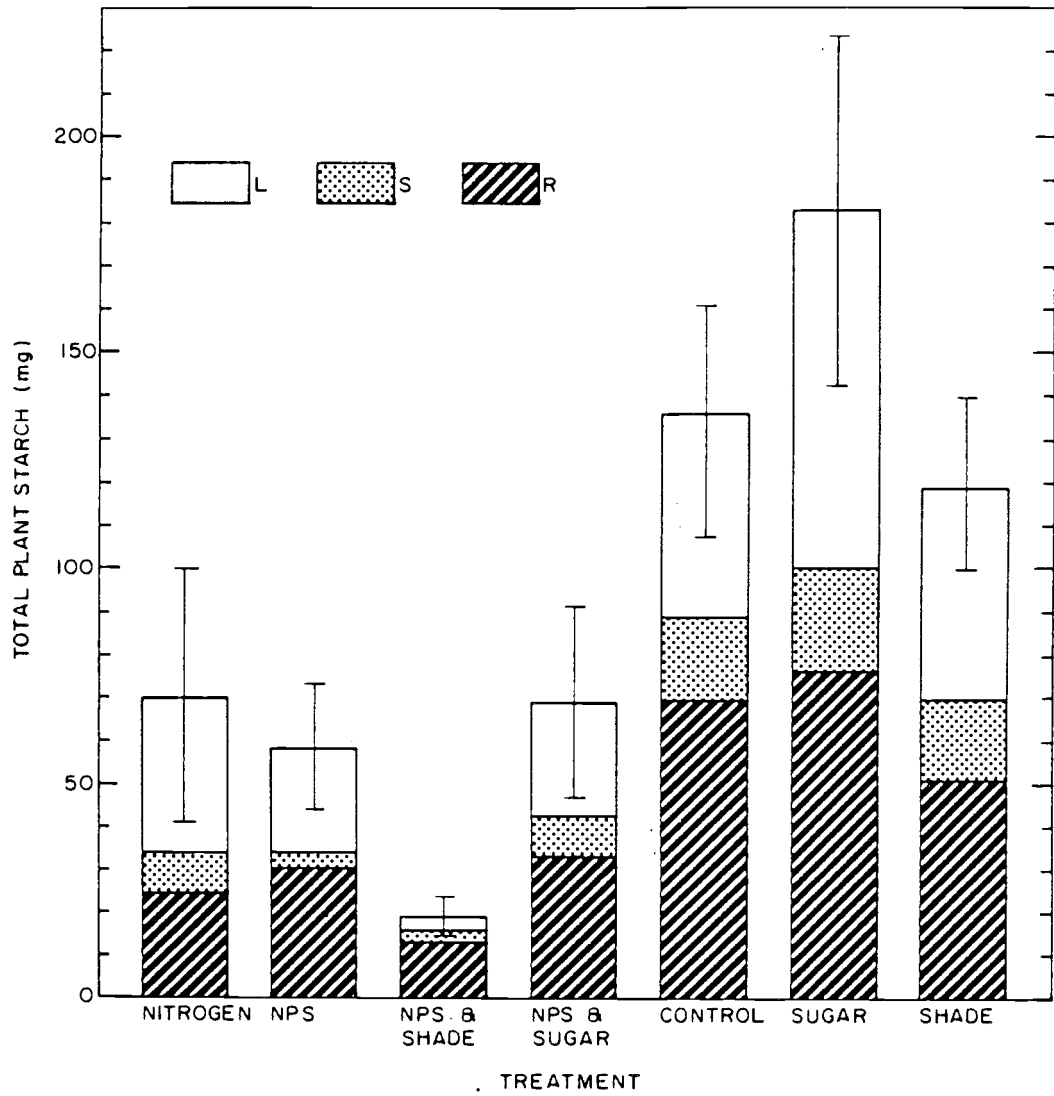
Figure 5. Total plant starch (mg/plant), divided into
leaves (L), stems (S), and roots (R). Upper line
indicates total plant starch means (+-s.e.) of 10
replicates.

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APPENDICES

APPENDIX 1.

NATURAL DISTURBANCE AND NITROGEN MINERALIZATION:

WAVE FORM DIEBACK OF MOUNTAIN HEMLOCK

IN THE OREGON CASCADES

by

Pamela Matson

and

Richard Boone

NATURAL DISTURBANCE AND NITROGEN MINERALIZATION:

WAVE-FORM DIEBACK OF MOUNTAIN HEMLOCK

IN THE OREGON CASCADES

ABSTRACT

A pathogen-induced disturbance at least doubled nitrogen
mineralization rates in both the mineral soil and O2 horizon
of a mountain hemlock forest. As the regenerating stands
develop, rates decline again to the very low pre-disturbance
levels. These changes in nitrogen availability may in turn
influence tree resistance to the pathogen, suggesting that
in this system the pattern of nitrogen availability is both
a consequence and a cause of natural disturbance.

INTRODUCTION

Many studies have reported increased losses of nitrogen
and other elements from forest ecosystems following
clearcutting. It has been suggested that these losses are
caused by increased rates of nitrogen mineralization and
nitrification as well as by reduced plant uptake of nitrogen
after cutting (Stone et al. 1978, Vitousek and Melillo 1979,
Bormann and Likens 1979), but relatively few studies have
actually examined rates of nitrogen turnover in clearcut
forests directly. Matson and Vitousek (1981) and Gordon and
Van Cleve (submitted) used in situ incubations to
demonstrate increased rates of net nitrogen mineralization
within three years after clearcutting. Glavac and Koenies
(1978) reported similar increases in a European site.
Increased nitrogen mineralization could be due to changes in
microclimate, substrate quality, or both; Matson and
Vitousek (1981) used a combination of laboratory and field
incubations to show that microclimate was more important in
controlling changes in a one year old clearcut while
substrate quality was more important in a four year old site
in southern Indiana.

Changes in nitrogen mineralization and availability
after disturbance could influence the productivity and
species composition of regrowing vegetation. Many early
successional species appear to be adapted to high nutrient

availability (Bazzaz 1979, Grime 1979), and the germination
of some species is enhanced by high nitrate concentrations
(Bazzaz 1979). These adaptations suggest that natural
disturbance must have led to elevated nutrient availability
as well. Swank et al. (1981) found that the defoliation of
hardwood stands by the fall cankerworm increased both
mineral nitrogen pools in surface soil and nitrate losses
from the stands. Schindler et al. (1980) found increased
nitrogen losses from windstorm-damaged watersheds. However,
the effects of natural disturbance on nutrient cycling
processes have been studied intensively only in relation to
fire (Raison 1979, Woodmansee and Wallach 1981).

Changes in nutrient availability caused by natural
disturbance have been difficult to study due to the
unpredictability of disturbance in space, time, and
intensity. However, the wave-form diebacks of certain
coniferous forests in the northeastern (Sprugel 1976) and
northwestern (McCauley and Cook 1980) United States offer
promising areas for such studies, because overstory
mortality is predictable. We examined patterns of nitrogen
availability following dieback in several mountain hemlock
stands in the Oregon Cascades.

STUDY SITE

In the subalpine zone of the Oregon Cascades,
relatively pure stands of mountain hemlock (Tsuga
mertensiana (Bong.)Carr.) die in distinct waves after their

roots become infected by laminated root rot (Phellinus (Poria) weirii (Murr.)Gilbertson). The dieback occurs in a radial pattern as root infection and subsequent tree death spread outward from a central infection point. Changes in species composition and importance (McCauley and Cook 1980) and soil carbon levels (Boone 1982) have been examined in detail in several of these dieback areas.

Our study site was located in the Oakridge Ranger District of the Willamette National Forest, Oregon, at 1770 m elevation about 2 km northeast of Waldo Lake: it is in the coolest of western Oregon's forested zones, and is relatively wet (1600-2800 mm annually) with most precipitation falling during the winter months (Franklin and Dyrness 1973). Snowpack in this zone often remains from November until early June.

The vegetation of the study area includes relatively pure mature stands of mountain hemlock, with occasional lodgepole pine (Pinus contorta var latifolia Engelm.), western white pine (P. monticola Dougl.), Pacific silver fir (Abies amabilis (Dougl.)Forbes), and subalpine fir (A. lasiocarpa (Hook.)Nutt.), and an understory of grouse huckleberry (Vaccinium scoparium Leiberg). The regenerating stands have relatively fewer mountain hemlock, with lodgepole pine assuming increased importance.

The soil is a sandy, well-drained Entic cryorthod in the Winopee series. The parent material is volcanic pumice and ash deposited by the explosive Mount Mazama eruption ca

6600 years ago, and the forest floor is a relatively well defined mor. More detailed site characterization is found in Boone (1982).

METHODS

1981 Sampling and Analysis

In July 1981 we collected mineral soil and forest floor samples from two random transects in each of three distinct dieback areas. On each transect, three points in the old-growth and seven points in the regeneration area were established at selected distances from the dieback front (Boone 1982). Sampling points were selected randomly within five meters to one side of each point. Mineral soil was collected from exposed walls of soil pits at 0-15 cm and 15-30 cm depths. Samples for bulk density measurements were taken from the middle 7.5 cm of each 15 cm layer with a 7.5 cm diameter core. Both O1 and O2 material were collected using a 20 x 40 cm template.

Soil and forest floor material collected for bulk density, horizon mass, and total nitrogen (N) estimates were dried at 70 C for 24 hours. Bulk densities were calculated as dry weight of soil from a known volume. Masses of the forest floor horizons were estimated on the basis of dry weight per known area. Total N was determined for one or two subsamples for the O1, O2, and 0-15 cm samples using a micro-kjeldahl technique followed by distillation and titration.

Per cent carbon and potential N availability were estimated using air-dried forest floor samples and mineral soil samples which had been passed through a 2 mm sieve. Per cent carbon was analyzed on ground soil and forest floor samples using a LECO 12 Carbon Analyzer (Boone 1982). Nitrogen availability was estimated using an anaerobic incubation procedure. Three 10 g subsamples of each soil were placed in 50 ml deionized water, gently shaken, incubated for seven days at 40 C, and then extracted in 1 N KCl. Three 10 g subsamples were extracted without incubation to provide initial ammonium concentrations. Three 3 g subsamples of the forest floor horizons were treated in the same way.

Extracts were analyzed for ammonium using a Technicon Autoanalyzer II (Technicon Instruments Corp. 1977). Nitrate is not produced under waterlogged conditions, so nitrate concentrations were not measured. Initial values of ammonium were subtracted from seven-day values to yield production estimates.

1982 Sampling and Analysis

In early July 1982, just after snowmelt, the O2 and O-' 15 cm soil horizons were collected near the 1981 sampling points and used for _in situ_ estimates of potential N mineralization. Mineral soil was collected with a soil corer 6 cm in diameter, removed intact, and placed in polyethylene bags before being replaced in the corer holes

and covered with forest floor (Ellenberg 1977). Adjacent to
these soil samples, O1 was removed and intact O2 material
was collected, placed in polyethylene bags, and buried
beneath the O1. Additional soil and O2 samples were
collected at each point, stored at 0 C for 48 hours,
then extracted in 100 ml 2N KCl to represent initial
nitrogen pools.

After 10 weeks (the end of the growing season), the
soil and forest floor buried bags were collected, stored at
0 C for three days, and then two subsamples of each were
extracted as described above. Ammonium and nitrate in
initial and 10-week extracts were measured using the
Autoanalyzer (Technicon Instrument Corp. 1977, 1973).
Samples from the initial extraction were contaminated with
fertilizer during handling, so only final 10-week values are
reported for the in situ incubations.

Statistical Analysis

Sample points along the transects were grouped into
four classes on the basis of location and temperature,
moisture, and vegetative characteristics measured by Boone
(1982). The four groups are as follows: Points 1,2,3=Old-
growth; 4,5=bare zone; 6,7,8=young regrowth; 9,10=old
regrowth. The major site characteristics of each are listed
in Table 7.

Treatment means were analyzed using analysis of
variance (ANOVA) for a randomized block design with

subsampling. The three dieback areas were considered block replicates, with the two transects within each providing subsamples. The four groups defined above were considered treatments. All comparisons of treatment means followed Steel and Torrie (1980) and used the MSE from the ANOVA for the lsd tests.

RESULTS AND DISCUSSION

With the exception of the O1 horizon, all forest floor and mineral soil horizons from both the 1981 and 1982 collections show a similar trend (Figures 6,7,8). Mineral N production and final N values increase in the bare zone and early regrowth areas, and then decline again as the trees become older and biomass accumulates.

For the 1981 O2 incubation, the ANOVA F-tests indicate significant differences among treatment means. Individual comparisons show that there is a significant decrease in N mineralization from the bare zone to the older regrowth ($p < .05$, Figure 6). The F value for the treatment means from the 1982 O2 _in situ_ incubation is not significant, but the trend is nearly identical to the 1981 results (Figure 6).

We observed very low levels of nitrification (.03-6.1 ug/g) in several of the _in situ_ O2 incubations. With one exception, these samples are all from the bare zone and young regrowth areas.

The increases in N mineralization in the O2 after dieback correspond to the increased temperature in both the

O2 and mineral soil which were observed in 1981 (Table 7).
However, both laboratory and in situ incubations show the
same trend, indicating that field temperature conditions
like those observed in 1981 are not solely responsible for
the observed mineralization rates. Rather, substrate
quality (in terms of its ability to release mineral N under
constant conditions) also contributes to the differences
observed.

Nitrogen availability in the O1 layer shows an opposite
trend, with a sharp decline in N mineralization in the young
regrowth (Figure 6). Although the ANOVA F test is not
significant, a t-test between the young regrowth and the
older regrowth means is significant (p<.001). Nitrogen
concentrations in the O1 decrease dramatically in this area
(Table 8), apparently because woody material becomes a
relatively more important component in the O1. The high C:N
ratio of this substrate reduces the potential for N
mineralization.

Analysis of variance for anaerobic mineralization
values in the 0-15 cm mineral soil indicates significant
differences between means (p<.05). The old-growth and the
older regrowth areas have nearly identical negative
production values; nitrogen is immobilized during
incubation. Bare zone and young regrowth mineralization
values are substantially greater (Figure 7). The 1982 in
situ mineralization trend is also similar, and the ANOVA F
value is significant (p<.01), although individual

comparisons reveal a significant difference between final N values of only the old-growth and young regrowth (p<.05, Figure 7).

These trends, as well as the trend from a preliminary aerobic incubation for mineral soil in 1980 (P. Matson, unpublished data), correspond to variations in soil temperature. Because both in situ incubations and incubations under controlled conditions yield the same results, the altered microclimate once again cannot be considered the sole control of mineralization rates. Conceivably, altered environmental conditions in the field could improve substrate quality by increasing the rate of decomposition,thereby decreasing the C:N ratio or reducing the proportion of recalcitrant organic matter. Alternatively, the organic material added to the mineral soil as fine roots could be either more readily decomposable or in greater quantity.

The general pattern of mineralization is similar in the mineral soil and the O2. However, the rate at which they reach the maximum mineralization is different. In situ mineralization rates in the O2 peak 5 m from the dieback wave front (Figure 8). On the basis of tree age, Boone (1982) has estimated that this is approximately 10 years after the dieback front has passed. Maximum mineralization rates for the 0-15 cm mineral soil horizon occus several meters further from the wave front (16 to 20 years after the front has passed), perhaps because of the more recalcitrant

organic material in the mineral soil.

Forest floor horizon weight in the undisturbed old-growth forest are greater than in the bare zone and regrowth zones (Table 8). Nitrogen mineralization on an aerial basis is nevertheless still greater in the areas behind the wave front because of the higher mineralization rates there (Table 9). Although the forest floor horizon weights are far less than those of the surface soil, forest floor in this high elevation site represents a much more important ecosystem component than it does in many lower elevation Pacific northwest sites. Forest floor accumulation at lower elevations are often less than 20 T/ha (Vitousek et al. 1982), while we found over 75 T/ha in our mature mountain hemlock forest, and Turner and Singer (1976) found 180 T/ha at a similar high elevation Abies amabilis site. At the Waldo Lake site, forest floor contributes twice as much mineralizable N as the mineral soil (Table 9).

Overall, the Phellinus-induced disturbance causes a doubling of N mineralization rates. Because the death of the overstory also decreases N uptake in the short term, the proportional increase in N availability is even greater. Moreover, the inorganic N released is nearly all in the form of the relatively immobile ammonium cation, and so is unlikely to be lost by leaching.

The increased N availability after dieback disturbance probably increases productivity in the regenerating stands. Geist (1977) showed that forests growing on Mazama ash-

derived soils are generally limited by nitrogen, even though
N availability in his sites (measured with anaerobic
incubations) was nearly always higher than in our site.
Perhaps more importantly, the increased nitrogen
availability after disturbance can influence mountain
hemlock resistance to reinfection by Phellinus. Matson and
Waring (submitted) demonstrated that under controlled
conditions, N nutrition substantially influences the ability
of mountain hemlock seedlings to survive Phellinus
inoculation. The mortality of old-growth trees at the wave
front could be influenced by low N availability; the higher
availability in the regrowth could explain why trees are not
killed despite the presence of Phellinus in dead roots and
stumps. The fact that dieback frequently begins again after
88 years (McCauley and Cook 1980) (which is approximately 40
m from the wave-fronts at the Waldo Lake site), where
we have shown that nitrogen availability is again very low,
supports this suggestion.

Table 7.   Characteristics of the four treatment areas, from
           Boone (1982). Measurements were taken in July.

Treatment	Sampling Point [*]	Mean Age [**]	Temperature C at 6 cm	% Moisture Soil O1
1 Old-growth	1,2,3	213	24.3	20.5 13.4
2 Bare Zone	4,5	15	30.5	27.5 7.8
3 Young Regrowth	6,7,8	32	31.5	18.9 8.2
4 Old Regrowth	9.10	75	23.5	17.9 12.3

   *   see Figure 9
  **   All tree species

Table 8. Forest Floor and mineral soil nitrogen and carbon content (%) and horizon weights (T/ha) for each treatment. Values for treatments 1 and 3 are means (+- s.e.) of 9 (3 sampling points in each of 3 blocks). For treatments 2 and 4, values are means (+- s.e.) Of 6 (2 sampling points in each of 3 blocks).

| | Forest Floor | | | | | | Mineral Soil | | |
| | O1 | | | O2 | | | 0-15 cm | | |
Treatment	% C	% N	Horizon Wt	% C	% N	Horizon Wt	% C	% N	Horizon Wt
1 Old-growth	46.5(1.9)	.85(.06)	12.5(1.24)	24.2(2.28)	.53(.05)	65.5(5.39)	2.34(.17)	.08(.003)	988.(17.4)
2 Bare Zone	47.1(.98)	.90(.06)	12.2(0.53)	25.5(2.02)	.56(.04)	46.8(3.88)	2.60(.18)	.09(.002)	956.(23.9)
3 Young Regrowth	45.2(1.8)	.64(.04)	12.0(1.22)	20.8(1.66)	.43(.04)	54.6(5.62)	2.77(.17)	.09(.004)	994.(19.8)
4 Old Regrowth	48.5(.99)	.84(.03)	11.1(1.00)	25.9(4.49)	.45(.06)	49.9(2.71)	2.69(.15)	.10(.003)	961.(28.4)

Table 9. N mineralization (g NH4-N/ha) after 10 week <u>in</u> <u>situ</u> incubation. Values are final N concentrations x horizon weights. Each value is the mean (+- s.e.) of 9 (for treatments 1,3) or 6 (for treatments 2,4).

Treatment	O2	O-15 Soil	Total
1 Old-Growth	2100.(363.)	421.(86.4)	2520.(397.)
2 Bare Zone	4260.(946.)	1150.(139.)	5410.(835.)
3 Young Regrowth	2970.(424.)	1500.(343.)	4470.(646.)
4 Old Regrowth	1760.(597.)	826.(158.)	2590.(610.)
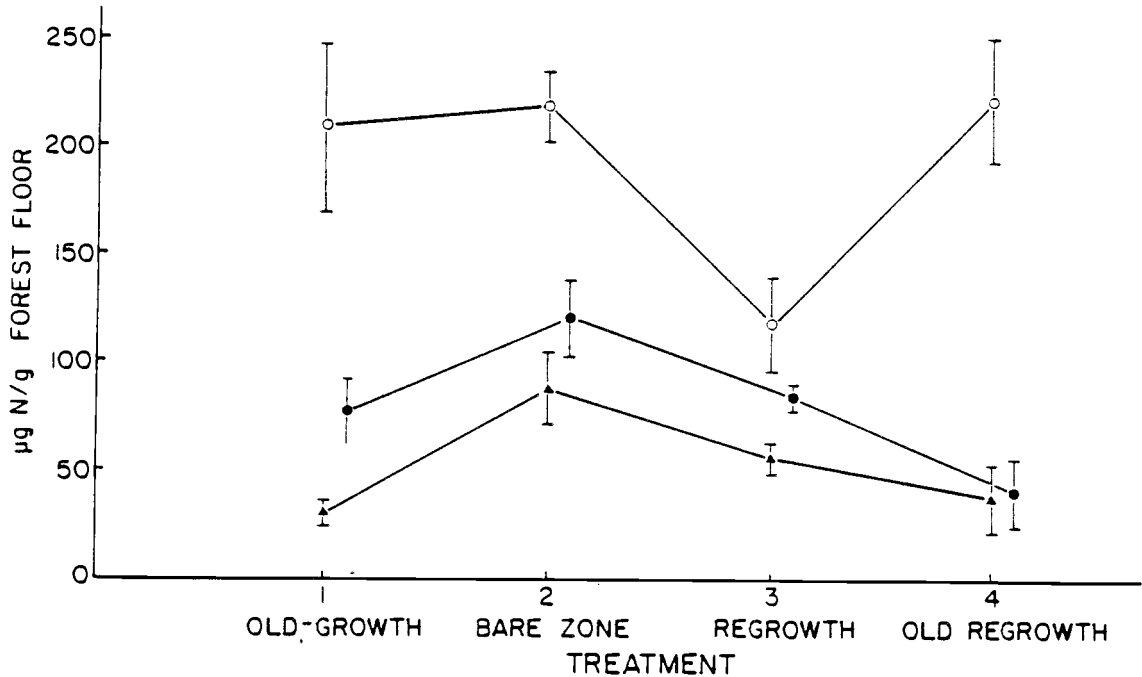
Figure 6.   Potential N mineralization (ug NH4-N/g dry wt)
            for forest floor collected in 1981 (open circles
            represent O1 horizon and closed circles represent
            O2) and final mineral N values (ug NH4-N/g dry
            wt) for the 1982 in situ incubations (triangles).
            Each value is the mean (+-s.e.) of 9 (3 sampling
            points in each of 3 blocks) for treatments 1 and
            3; for treatments 2 and 4, each value is the
            mean of 6 (2 sampling points in each of 3
            blocks).

Figure 7. Potential N mineralization (1981 anaerobic incubations, open circles represent the 15-30 cm soil horizon, and closed circles represent 0-15 cm) and final N values (1982 *in situ* incubations, represented by triangles) (ug NH4-N/g dry wt) for mineral soil. Each value is the mean (+- s.e.) of 9 or 6 points as in Figure 6.
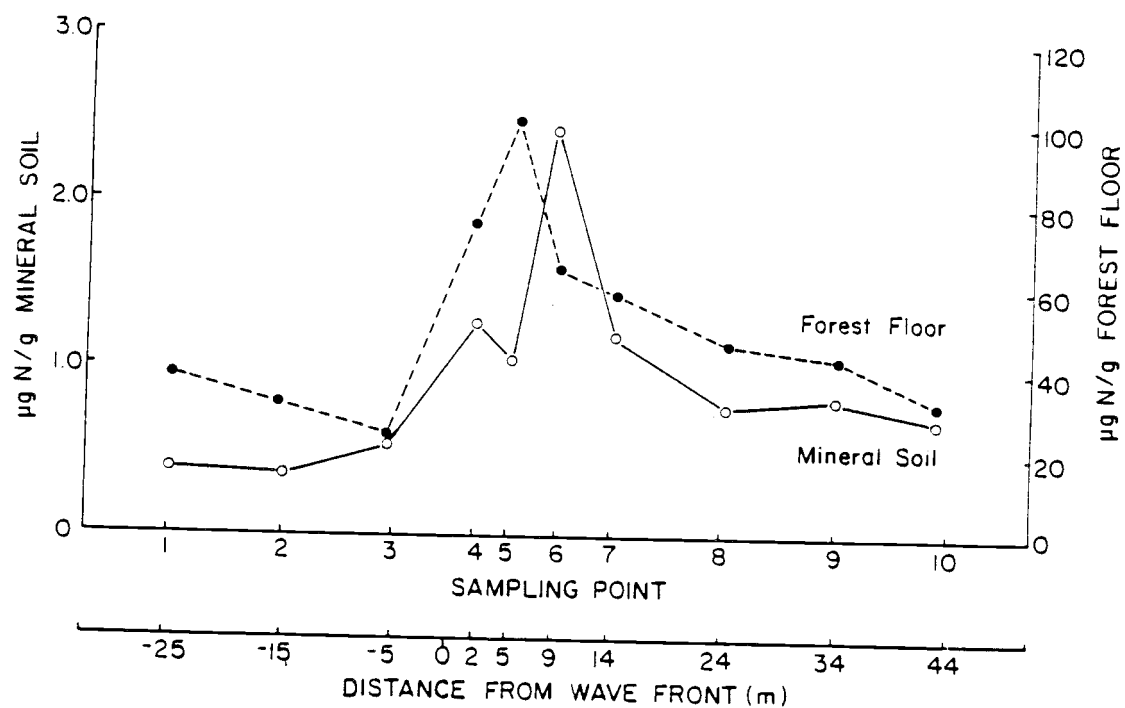
Figure 8.   Final mineral N values (ug NH4-N/g) after 10
weeks in situ incubation for mineral soil and
forest floor (02 only).   Each value is the mean
of three block replicates, each with two
subsamples (transects).

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APPENDIX 2. ADDITIONAL TREATMENT EFFECTS

FROM THE GROWTH-ROOM STUDY

A variety of additional information was collected during or after the growth-room study at the Duke Phytotron. Although this information is not essential or appropriate for the manuscript thesis, it is in itself useful and interesting, and is thus provided here.

Foliar Fertilization Treatment: Description and Effects

A foliar fertilization treatment was designed to alter plant nutrient status without directly affecting the soil pH, microbial population, or even the pathogenic fungus itself. Therefore, using foliar fertilization to improve plant nutrient status would allow a very clean answer to the question "does plant nutrient status influence resistance to Phellinus?"

Foliar fertilization in this experiment was not successful: Tree nutrient contents were not significantly different from those of the nutrient-stressed treatments (shade, sugar, control). Likewise, starch and sugar contents were similar to the nutrient-stressed plants (Table 10). In fact, this treatment apparently provided an even greater stress than did nutrient or light limitation: Mean scores of foliage damage for both the wounded-control and the Phellinus-infected trees were higher than all other treatment means, and the leaf weight/stem weight ratios were

significantly less (Table 10). Interestingly, this treatment showed the same relationship between the inoculation treatments--Phellinus infected plants had a significantly higher mean score than the wounded-controls. However, given that the stress is undefined, and not controlled, it is not appropriate for publication.

I believe that foliar fertilization probably caused a salt stress. Although the nutrient solution was relatively dilute (110. ppm NH4Cl, 4.6 ppm KH2PO4, 12.5 ppm K2SO4, .1% calgon as a surfactant, with a pH near 6), the foliage was apparently damaged.

Table 10. Foliar fertilization effects on foliage damage score and nutrient and carbohydrate contents.

Variable	Leaves	Stems	Roots	Total
Starch %	3.21(.67)	1.56(.31)	4.60(.60)	
Sugar %	3.29(.20)	1.25(.11)	2.51(.19)	
Starch mg	24.3(5.2)	14.5(3.25)	74.5(13.2)	113.(17.)
Sugar mg	25.1(4.6)	11.5(1.74)	38.0(4.87)	74.(10.)
Nitrogen %	.399(.044)	.213(.025)	.296(.038)	
Phosphorus %	.200(.013)	.096(.012)	.082(.004)	
Nitrogen mg	3.11(.006)	2.03(.004)	4.78(.010)	9.93(2.0)
Phosphorus mg	1.48(.002)	.86(.001)	1.24(.020)	3.58(.45)

	Phellinus-Inoculated	Wounded-Control
Score	4.0 (.45)	2.9 (.43)

Table 11. Mean ratios of leaf weight (not including brown
           leaves) to stem weight for January hearvest
           plants. Asterisks indicate significant
           differences (p<.05). This ratio is meant to
           relativize the amount of leaves lost per plant
           over the 2 month infection period.

Treatment	Inoculation		
	Wounded Control		Phellinus Inoc.
Nitrogen	.847 (.12)		.749 (.08)
Nutrient	.891 (.13)		.889 (.09)
Shade plus Nutrient	.788 (.13)		.669 (.09)
Sugar plus Nutrient	.967 (.12)		.847 (.06)
Control	.931 (.07)	*	.676 (.12)
Sugar	.999 (.16)	*	.673 (.07)
Shade	.743 (.09)		.601 (.08)

Table 12. Treatment effects on root characteristics. Each
           value is the mean (+- s.e.) of 10 replicates.

Treatment	Root length/g	Specific Root Area cm2/g	Root Area cm2	Root tips / cm	% ART *	% My **
Nitrogen	442.(66.1)	29.4(2.21)	63.8(9.45)	3.08(.24)	10	30
Nutrient	503.(60.4)	30.6(3.27)	75.0(14.7)	2.95(.13)	100	10
Shade plus Nutrient	501.(93.8)	35.4(4.64)	61.9(11.8)	2.75(.16)	100	0
Sugar plus Nutrient	496.(72.2)	29.4(2.86)	50.6(8.19)	2.56(.18)	90	30
Control	961.(131.)	16.6(1.53)	22.4(5.15)	2.82(.33)	10	30
Sugar	971.(178.)	17.1(2.29)	28.3(4.66)	2.57(.08)	0	60
Shade	869.(192.)	17.9(3.20)	23.9(5.67)	2.75(.22)	20	20
Foliar	776.(151.)	16.5(1.95)	28.6(5.40)	2.53(.22)	10	30

*   Per cent having >50 % active root tips
** Percent with "mycorrhizae" present. These were actually
   simply unusual root characteristics seen microscopically.
   Staining and thin-sections of a subset of these did not
   show presence of mycorrhiza.

The ANOVA's for root length/g, SRA and RA were highly
significant, with the nutrient stressed plants having longer
but thinner roots.

Table 13. Individual amino acids for root tissues for four
           treatments. Values are means of two replicates.
           Each amino acid is represented as percent of
           total amino acid N.

Fraction	Control	Shade	Nutrient	Shade plus Nutrient
% Total N	.33	.29	1.00	1.07
% Amino Acid N	.31	.24	.78	1.00
Arginine N	12.	11.5	25.	35.5
Glutamic acid N	7.	7.	7.	7.
Phenylalanine N	2.1	2.5	1.7	1.4
Tryosine N	1.5	1.5	1.3	1.2
Proline N	4.	4.	3.5	2.5
Serine N	5.1	5.5	4.2	3.4
Alanine N	6.1	6.5	5.1	4.1
Valine N	4.1	4.6	3.6	2.9
Methionine N	.7	.8	.7	.7
Histidine N	5.3	6.2	5.5	3.5
Lysine N	8.0	9.0	8.4	6.3
Leusine N	4.5	6.6	4.6	3.8
Isoleusine N	2.9	3.3	2.5	2.0
Glycine N	7.2	7.0	5.5	4.5
Aspartic acid N	7.0	7.3	6.4	4.9
Threonine N	4.1	2.6	3.6	2.9
1/2 Cystine N	1.8	.2	0.	.2
Ammonium N	14.5	15.4	12.4	15.3

Table 14. Extractable nitrogen in growth-room soil. Values
are ug NH4-N/ g dry weight soil. Soil extracts
were done one day after treatment applications.

Treatment	November	January
Nitrogen	34.05	17.27 (4.52)
Nutrient	15.06	5.64 (1.21)
Shade plus Nutrient	13.79	6.50 (1.97)
Sugar plus Nutrient	1.95	2.30 (.23)
Control	.03	.21 (.06)
Sugar	.01	.06 (.06)
Shade	.01	.13 (.05)

Before the experiment was begun, extractable N was
approximately 1.00 ug/g in this soil, and anaerobic
production over 7 days was 3.25 ug/g. Without plants,
additions of 10 mg N/kg soil increased extractable N to 14.8
ug/g.

Table 15. Individual monoterpenes measured in non-wounded,
           composited root and foliage tissues. Each value
           is the mean of two analytical replicates. Units
           are % fresh weight.

Fraction	Treatment		
	Control	Nutrient	Shade plus Nutrient
Foliage			
-pinene	10.297	10.350	13.16
-pinene	1.996	2.067	2.40
-phellandrine	1.848	1.816	2.208
-phellandrine	6.650	6.563	7.337
limonene	1.820		1.751
-terpineol	4.380	4.433	5.873
Bornyl acetate	1.509	1.771	
v terpinene			.601
Roots			
-pinene	1.552	1.279	1.446
-3-carene	.994		.753

Gas Exchange Response to Light

To ensure that the shading treatment was reducing light enough to reduce photosynthetic rate, I measured change in CO2 flux with light intensity change using Infrared gas analysis (IRGA).

The growth room intensity was rated at 600 uE/m2/sec, but at canopy level it was 400 uE/m2/sec. Shading reduced that to 240 uE/m2/sec, and so protentially reduced photosynthetic rate to about 60 % of maximum.

Figure 9. Change in carbon dioxide flux with light intensity.
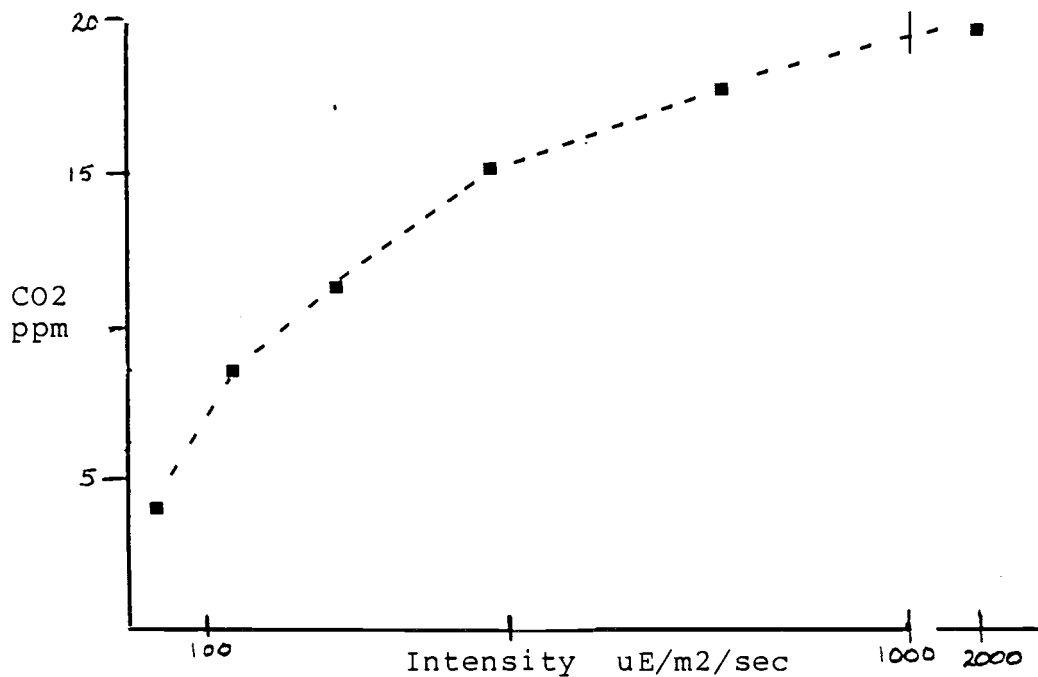
Statistical Tests for Comparisons of Means

A. Comparisons of means using MSE for split-plot design.

   1. Significance tests for comparing means of Factor B in the same level of Factor A.

$$\bar{Y}_1 - \bar{Y}_2 \bigg/ \sqrt{\left(\frac{2\ MSE_b}{r}\right)}$$

   2. Significance tests for comparing means of Factor A in one level of Factor B.

$$\bar{Y}_1 - \bar{Y}_2 \bigg/ \sqrt{\frac{2\left((b-1)MSE_b + MSE_a\right)}{rb}}$$

$$t' = \frac{(b-1)\ E_b t_b + E_a t_a}{(b-1)E_b + E_a}$$

B. Comparisons of means using LSD. Used for planned comparisons, with MSE from one-way ANOVA.

$$LSD = t_\alpha S_{\bar{Y}_1 - \bar{Y}_2} = t_\alpha \sqrt{\frac{2MSE}{r}}$$

$$\left|\bar{Y}_1 - \bar{Y}_2\right| \geq LSD$$

C. Comparisons of means using Tukey's HSD (honestly significnat difference. Used for all possible pair-wise comparisons.

$$HSD = Q_\alpha S_{\bar{Y}_1 - \bar{Y}_2} = Q_\alpha \sqrt{\frac{MSE}{r}}$$

$$\left|\bar{Y}_1 - \bar{Y}_2\right| \geq HSD$$

* Steel and Torrie 1980

APPENDIX 3.   WALDO LAKE FIELD TREATMENT EFFECTS:

NITROGEN MINERALIZATION AND FOLIAR NUTRIENTS

The Waldo Lake field experiment was begun in June 1981.
It consists of a wave front manipulation, where 5 x 5 m
plots are treated twice annually with nutrients or carbon
(sugar) to alter nutrient availability and tree nutrient
status, and individual tree treatments in both the old-
growth and regrowth areas, where 3 m tall trees in openings
are similarly treated after having their roots infected with
Phellinus in June 1981. Ultimately, we will measure tree
vigor and advance of the pathogen in these treatment areas.
The following two tables contain preliminary data indicating
response to the treatments in terms of nitrogen availability
and foliar nitrogen, phosphorus, and starch content.

For treatment rationale see Methods section in thesis.
Sugar additions are at the rate of 1000 kg sucrose/ha, and
nitrogen additions at the rate of 50 kg N/ha.

Table 16. Potential N mineralization (ug NH4-N / g dry
           weight of mineral soil (0-15 cm) or forest floor
           (O2) for the Waldo Lake field experiments. Each
           value is the mean (+-s.e.) of 4 block replicates,
           and is production (7 day values - initial values)
           from anaerobic incubations (see Appendix 1 for
           details of the method).

Treatments	June 1981 Mineral Soil	July 1982 Mineral Soil	Forest Floor
Wave-Front Plots			
Control	-1.50 (1.76)	1.53 (.76)	114.0 (20.8)
Nitrogen	-5.51 (1.20)	3.48 (2.02)	126.5 (28.7)
Sugar	-1.94 (1.05)	1.18 (0.56)	85.1 (20.2)
Nutrient	-0.03 (3.21)	1.08 (1.79)	98.9 (11.4)
Regrowth Tree Plots			
Control	3.57 (1.28)	9.93 (3.44)	112.7 (25.2)
Nitrogen	2.04 (3.39)	16.20 (3.39)	169.9 (33.9)
Sugar	1.43 (1.67)	1.08 (0.67)	44.5 (20.8)
Nutrient	0.05 (2.50)	6.28 (2.96)	65.1 (26.1)
Foliar	8.71 (2.71)	10.98 (7.31)	136.3 (60.1)
Old-Growth Tree Plots			
Control	1.12 (2.62)	3.54 (2.45)	74.6 (59.6)
Nitrogen	0.22 (2.14)	0.48 (0.53)	134.4 (57.4)
Sugar	-3.32 (0.58)	0.23 (0.17)	68.5 (13.8)
Nutrient	-1.92 (2.55)	3.76 (3.98)	105.4 (22.7)
Foliar	-3.34 (2.85)	7.24 (4.16)	160.9 (27.2)

Table 17. Total nitrogen, phosphorus, and starch (%) in
foliage collected from Waldo Lake experimental
plots. For procedures, see Methods section in
thesis.

Treatments	% N		% P	% Starch	
	July 82	Sept 82	Sept 82	July 82	Sept 82
Wave-Front Plots					
Control	.56(.05)	.92(.08)	.205(.030)		1.11(.33)
Nitrogen	.53(.03)	.77(.03)	.174(.004)		2.98(.44)
Sugar	.48(.08)	1.09(.12)	.205(.020)		1.00(.52)
Nutrient	.52(.03)	.72(.08)	.161(.009)		1.84(.51)
Regrowth Tree Plots					
Control	.64(.13)	.72(.04)	.145(.005)	11.2	.84(.22)
Nitrogen	.64(.07)	.96(.06)	.183(.013)	10.9	.66(.12)
Sugar	.68(.07)	.65(.18)	.143(.020)		1.66(.83)
Nutrient	.68(.06)	.75(.12)	.161(.021)		.83(.15)
Foliar	.78(.11)	.91(.15)	.161(.026)		.42(.08)
Old-Growth Tree Plots					
Control	.47(.07)	.79(.08)	.155(.02)	12.3	.99(.26)
Nitrogen	.60(.03)	.91(.08)	.137(.019)	12.5	.65(.17)
Sugar	.65(.05)	.85(.14)	.194(.022)		.97(.21)
Nutrient	.64(.07)	1.01(.05)	.228(.024)		.65(.33)
Foliar	.62(.07)	.79(.14)	.172(.036)		.66(.24)

Notes for Further Work

Most assuredly, the work of pathologists and forest managers alike would profit from an understanding of the actual pathway of resistance that particular species use against Phellinus. This, of course, would ultimately require biochemical-level research. However, a simple study using ^{14}C could indicate if storage carbon is involved in the defense, and an examination of the presence, intensity, or composition of a "hypersensitive response" at the infection site allow insight into the mechanisms of response.

On an ecosystem level, from the point of view of forest managers, some simple measure of tree vigor and susceptibility would allow management decisions to be made. We will test some possible indices in the field. Perhaps a measurement of growth efficiency will be sufficient. The composition and quantity of easilty measured reserves may also provide an index. Possibly, the rate of use of those reserves after budbreak would give a good estimate of tree vigor.