
Thinning and Nitrogen Fertilization in a Grand Fir Stand Infested with Western Spruce Budworm.

Part IV: An Ecosystem Management Perspective

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ABSTRACT. A stand of grand fir, *Abies grandis* (Dougl.) Lindl., was thinned and (or) fertilized with 350 kg/ha of nitrogen during an outbreak of the western spruce budworm, *Choristoneura occidentalis* Freeman. With thinning, the leaf area index was reduced by >30%. Tree growth efficiency, measured as wood production per unit of leaf area, increased by 60% within 2 years. Thinning combined with fertilization improved growth efficiency by 140%. Fertilization without thinning brought a much delayed response in growth, awaiting some beneficial effects of defoliation.

Fertilization provided tree roots in the upper soil horizons access to nitrogen during the spring, increasing the concentration of nitrogen in emerging foliage from 1 to 1.5% of dry weight and free amino acids levels 4-fold. Foliage enriched in amino acids increased shoot growth 3-fold, more than compensating for any nutritional benefits to insect larvae.

From an ecosystem perspective, managers should recognize that allowing pine forests to be replaced with fir through fire protection and selective logging has increased the nitrogen demand beyond that readily supplied in the ponderosa pine/true fir type. Fertilizing with one application of nitrogen at the time of an insect outbreak may reduce mortality and associated fire hazard through a period of up to 5 years. FOR. SCI. 38(2): 275-286.

ADDITIONAL KEY WORDS. Integrated pest management, nitrogen cycling, environmental change, tree vigor, leaf-area index.

IN COOPERATION WITH COLLEAGUES at the USDA Forestry and Range Sciences Laboratory in La Grande, OR, we initiated an experiment on a forest of grand fir (*Abies grandis* [Dougl.] Lindl.) to investigate the effects of thinning and fertilization on forest productivity of a stand severely infested by western spruce budworm. The extent of the western United States now covered by fir forests susceptible to native defoliating insects has grown so that continuing outbreaks of defoliating insects appear likely. The spraying of pesticides to protect forests through to harvest is an expensive and ecologically questionable option (Torgersen et al. in review). Thus, for practical as well as scientific reasons we asked the question: can the addition of nitrogen fertilizer (with or without thinning) during an insect outbreak more than compensate for the loss of foliage sustained?

The answer to this question underlies an integrated project involving assessment of insect population dynamics (Mason et al. 1992), consumption of foliage and long-term tree growth responses (Wickman et al. 1992), interactions with pathogens (Filip et al. 1992), and changes in the availability of water, nutrients, and light affecting host-tree physiology (this paper).

The region of study, described in Part I of this series, like much of the mountainous western United States, was once dominated by open stands of ponderosa pine (*Pinus ponderosa* Doug. ex Laws.). With the advent of fire protection at the turn of this century, a dense understory of grand fir established under the pine (Franklin and Dyrness 1973, Filip and Goheen 1984). The extensive forests of fir, including some Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco), periodically suffer severe defoliation from native insects. Defoliation, if sufficiently severe, causes death of some shoots, reduces stem growth, and in extreme cases results in tree mortality. The long-term goal of management on public and private land is to convert back to pine forests, but in the interim there is a need to minimize mortality in the larger size classes of fir to reduce fire hazards and maintain commercial and esthetic values.

To view management in an ecosystem perspective we must consider a number of linked interactions: (1) how nitrogen fertilization and thinning affect the availability of critical resources required for tree growth, (2) how trees respond in growth and in biochemical composition, (3) the implications of changes in foliar quality and quantity on insect diet, (4) changes in insect performance, and perhaps also in the performance of pathogens, which together complete the cycle by modifying the availability of critical resources to the trees.

To provide a synthesis we draw not only on other sectors of the project, but also on understanding gained from previous research. We first report new data on how soil resources and the light environment were affected by treatments, then characterize early tree responses in growth and foliar chemistry. Insect responses are next linked to the biochemistry of emerging foliage. In the discussion section we consider longer term growth responses and management implications from an ecosystem perspective.

MATERIALS AND METHODS

EXPERIMENTAL DESIGN AND TREATMENTS

Four replicate study areas of approximately 2.6 ha each were randomly selected at the experimental site (Mason et al. 1992). Four treatments were tested in each area—fertilization, thinning, fertilization and thinning, and untreated controls. In each area, half was fertilized with 350 kg/ha of urea nitrogen. Half of the fertilized area and half of the unfertilized area were thinned to maintain approximately 5.5 m spacing between trees. This spacing would have reduced the total basal area by about 50%. However, due to operational policies of the USDA Forest Service, grand fir trees larger than 12.7 cm and any remaining pine above 17.8 cm diameter could not be removed at the time of experiment, resulting in an overall reduction in basal area of about 30%. In addition, no untreated buffers were present between plots. To overcome these limitations, we sampled only dominant or co-dominant grand fir trees that met the original spacing requirements and were well away from plot boundaries.

The data were analyzed using analysis of variance for a split-plot design with F tests set at a probability level of $P < 0.05$. These tests examined the main and interactive effects of thinning and fertilization (Steel and Torrie 1980). Specific comparisons of treatment means were made using Tukey's procedure (Steel and Torrie 1980). When treatment effects were interactive, mean comparisons were performed using the least square means procedure (SAS Institute, Inc. 1985). Correlation analyses were used to relate foliar chemistry to the pupae weights of male and female spruce budworms reported by Mason et al. (1992).

ASSESSMENT OF ENVIRONMENTAL RESOURCES

Light penetration through the canopy can be calculated as a function of stand leaf-area, assuming a light extinction coefficient of 0.5, and applying the Beer-Lambert law (Pierce and Running 1988). To estimate stand leaf-area we used linear relationships with sapwood cross-sectional area. Sapwood area was derived from first estimating total basal area with a prism (BAF of 0.75 m²/ha) while standing at the base of each sampled tree. These data were adjusted according to measurements taken on grand fir and pine at the study sites that indicated the sapwood area averaged respectively, 60% and 80% of the total basal area. A square meter of ponderosa pine sapwood basal area was assumed to support 2500 m² of projected leaf area, whereas a square meter of grand fir sapwood supports 4800 m² of leaf area (Waring et al. 1982).

Soil nitrogen was evaluated in two ways, extractable and mineralizable fractions. Composite samples of mineral soils (0–15 cm) were collected in June of 1985 from all subplots. These were stored at 4°C for 2 days, sieved to retain the <2 mm fraction, and then air dried for a week. The <2 mm fraction was subsampled to determine by extraction with 1 mol KCl the initial concentration of NH₄⁺ and NO₃⁻ for each treatment and the control. Other subsamples were incubated for 48 hr to estimate available N by the anaerobic method (Waring and Bremner 1964, as modified by McNabb et al. 1986).

To obtain an indirect, but easily interpretable measure of available soil moisture, twigs from five trees in each of the four treatments were collected at predawn hours in early September, 1986, following 2 months without measurable precipitation. Immediately, after collection the twigs were sealed in a pressurized chamber and xylem water potentials determined (Scholander et al. 1965).

TREE PHYSIOLOGICAL RESPONSES

Five grand fir trees were selected on each of the 16 treatment plots. Collection of foliage from these trees was made for biochemical analysis. These trees were also cored to estimate growth and sapwood area. Samples of emerging foliage weighing 5–10 g fresh weight were collected on June 23 and 24, 1986, from the midcrown of each sample tree. The samples were placed in plastic bags and stored on dry ice during transport to the laboratory. They were stored at -40°C until prepared for biochemical analysis.

Soluble sugars were extracted in 80% ethanol, with insoluble PVPP added as a phenolic binder (Sanderson and Perera 1966, Harborne 1984). Total free amino acids and total sugars were quantified colorimetrically (Moore and Stein 1954, Yemm and Willis 1954).

Starch, holocellulose (cellulose and acid-labile hemicellulose), and Klason lignin (true lignin and cutin) were determined by sequential digestion of the pellet remaining after the 80% ethanol extraction. Starch was extracted in 35% perchloric acid as described in McCready et al. (1950), and quantified colorimetrically (Viles and Silverman 1949). A modified version of the standard fiber analysis method (Goering and Van Soest 1970), was used to measure holocellulose. Klason lignin was determined by weight loss of the sample after ashing in a muffle furnace at 500°C for 5 hr (Swain 1979).

Tannin-precipitating capacity of the foliage was measured using the bovine serum albumin technique of Martin and Martin (1982) as modified by Robbins et al. (1987). Finally, the concentration of total nitrogen was determined on a separate 0.5 to 1.0 g sample of emerging foliage by standard micro-Kjeldahl techniques.

Tree growth efficiency, defined as stemwood production per unit of leaf area, was estimated from correlation with sapwood basal area. In the case of grand fir, a square centimeter of sapwood cross-sectional area supports 0.48 m² of projected leaf area (Waring et al. 1982). Sapwood was identified on cores by its translucence or with bromocresol green stain (Kutscha and Sachs 1962). Where defoliation occurs, leaf area could be overestimated. We therefore assessed the index only once, 2 years following treatment when defoliation was still relatively modest.

Radial growth was measured microscopically to 0.1 mm from single cores taken from each tree at the end of the growing season in 1986. An allometric relationship between diameter and stemwood biomass served to calculate wood production (Gholz et al. 1979).

RESULTS

CHANGES IN ENVIRONMENTAL RESOURCES

Thinning reduced stand basal area, as measured by prism counts, from an average of 22.5 m²/ha to 15.3 m²/ha. This was equivalent to a reduction in leaf-area index (LAI) from about 8.0 to 5.5 (Table 1). The significance of this reduction in terms of illumination to the lower canopy and the effects on photosynthesis associated with changes in N status will be discussed in the next section.

Drought stress, as estimated from predawn readings of twig water potentials in September, averaged -0.75 MPa across all treatments. This value is not indicative of drought and suggests that less than three quarters of the water available in the rooting zone was used before autumn rains commenced (Waring and Cleary 1967, Sucoff 1972). Thinning opened the canopy sufficiently to allow grass to become well established so water from the upper soil horizon was quickly utilized in all treatments as shown by Margolis and Waring (1986b).

Fertilization, as expected, increased the extractable and mineralizable fraction of nitrogen in the surface 15 cm of soil by some orders of magnitude over unfertilized treatments (Table 1). Significant nitrification occurred in the thinned and fertilized plots, presumably because thinning reduced the total stand uptake of NH₄⁺. The extractable and mineralizable ammonium fraction in the soil also doubled in the thinned and fertilized treatment compared to the fertilized treatment alone.

TABLE 1.

Important tree, soil, and insect responses measured within the first 2 years following treatments. Mean values with different superscript letters are significant at the 5% level.

Variable	Control	Thinned	Fertilized	Thinned + fertilized
<i>Structural and environmental variables</i>				
LAI	7.7 ^a	5.9 ^b	8.3 ^a	4.9 ^b
Growth efficiency ¹	23 ^a	37 ^b	19 ^a	54 ^c
H ₂ O pot., MPa	-0.72 ^a	-0.75 ^a	-0.74 ^a	-0.75 ^a
Extract. NH ₄ , ppm	1 ^a	2 ^a	62 ^b	133 ^b
Extract. NO ₃ , ppm	0.1 ^a	0.6 ^a	7 ^b	51 ^c
Mineral. NH ₄ , ppm	19 ^a	23 ^a	81 ^b	180 ^c
<i>Foliar chemistry²</i>				
Total N, % dwt	1.1 ^a	1.0 ^a	1.6 ^b	1.4 ^b
Free amino acids ³	0.027 ^a	0.024 ^a	0.102 ^b	0.099 ^b
Precip. tannin ⁴	0.22 ^a	0.23 ^a	0.25 ^a	0.23 ^a
Sugars, mg/g dwt	36 ^a	39 ^a	39 ^a	48 ^a
Starch, mg/g dwt	95 ^a	89 ^a	61 ^a	76 ^a
Lignin, mg/g dwt	238 ^a	299 ^a	248 ^a	251 ^a
Cellulose, mg/g	171 ^a	151 ^a	140 ^a	152 ^a
<i>Wt. of pupae, mg⁵</i>				
Female	97 ^a	102 ^a	118 ^a	113 ^b
Male	75 ^a	72 ^a	80 ^b	82 ^b

* Thinning was completed by September 1984; fertilizer was applied in October 1984. Emerging foliage was sampled for biochemical analyses in June 1986. Tree growth efficiency was calculated from cores extracted in September 1986. Predawn water potentials also were measured in September 1986.

¹ g wood/m²/yr.

² Data from Savage (1987).

³ mmol leucine eq./g dwt.

⁴ mg BSA protein/mg leaf extract.

⁵ Data from Mason et al. (1992).

CHANGES IN TREE PHYSIOLOGY

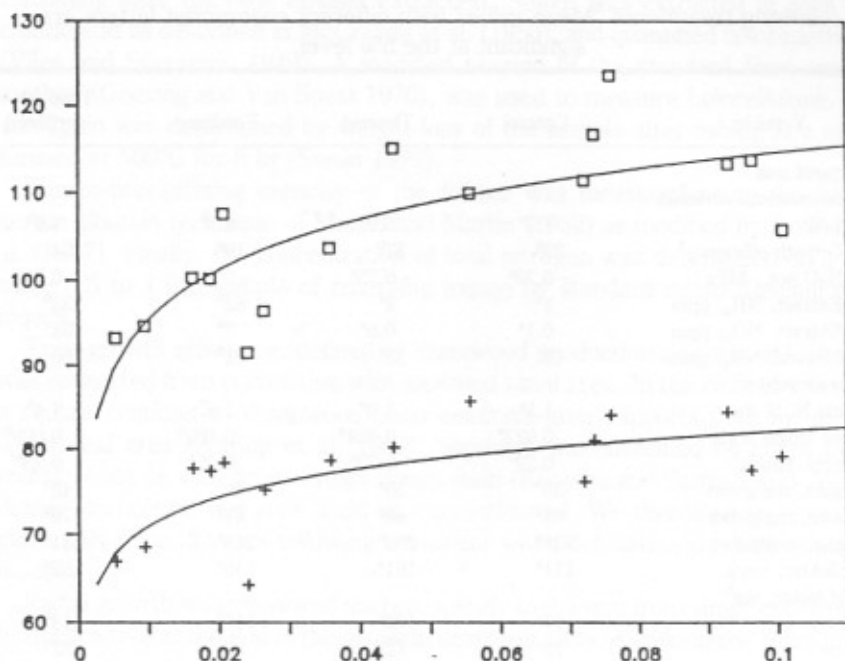
Growth efficiency of surviving trees improved by nearly twofold following thinning from a very low value of around 20 g of wood produced/m² leaf area in unthinned conditions to an average of 37 g/m²/yr (Table 1). Fertilization and thinning together increased growth efficiency still more to 54 g/m²/yr. Initially, fertilization did not improve tree growth efficiency on unthinned plots.

Physiological changes were also noted in foliar biochemistry within 2 years after the application of fertilizer. Fertilization significantly increased the total N and free amino acids (FAA) in emerging foliage (Table 1). Fertilization did not affect the concentration of other measured chemical constituents in foliage, nor did thinning.

EFFECTS OF FOLIAR BIOCHEMISTRY ON PUPAE WEIGHT

While fertilization increased levels of both total nitrogen and free amino acids in the emerging foliage, only FAA levels were correlated with budworm pupal weights (Figure 1). The logarithmic form of the FAA-pupal weight relationship

Pupal Dry Weight (mg)



Free Amino Acid Levels in Foliage

(expressed as mmol leucine eq./g dry weight)

FIGURE 1. Mean male (+) and female (□) pupal weights collected for each of the 16 subplots showed a logarithmic response to increased amino acid levels (x-axis). Female pupal wt. = $8.40 \ln \text{FAA} + 76.1$, $r^2 = 0.62$; Male pupal wt. = $4.84 \ln \text{FAA} + 59.9$, $r^2 = 0.49$. Free amino acid values above 0.04 mmol/g were from fertilized plots (Savage 1987).

suggests that budworm development is limited only when FAA levels fall below 0.04 mmole leucine eq./g dry weight. Such limitations would be characteristic in foliage from unfertilized plots (Table 1).

DISCUSSION

TREE RESPONSES TO CHANGES IN RESOURCE AVAILABILITY

The correlation between foliar N levels and photosynthetic capacity in evergreen plants is not as strong as with deciduous plants (Field and Mooney 1983). Increasing the availability of nitrogen to grand fir is likely to result in some enhancement of photosynthetic capacity (Field and Mooney 1983). However, field experiments with Douglas-fir (Brix 1981) and Scots pine (Linder and Rook 1984) demonstrated that a maximum gain of about a 20% in photosynthetic performance of new foliage is possible, and the performance of older foliage may not change.

Changes in photosynthetic capacity are therefore unlikely to explain the increase in growth efficiency observed, even in the thinned plots. The upper bounds of carbon uptake by vegetation is primarily set by the amount of visible light absorbed and CO₂ levels (Waring and Schlesinger 1985). Assuming random distribution of foliage and a light extinction coefficient of 0.5 (Pierce and Running 1988), the unthinned forests absorbed 98% of all radiation while the thinned forests absorbed 94%.

A more likely explanation for increased growth is in how photosynthate was allocated (Waring 1987). Field experiments have previously demonstrated that autumn applications of nitrogen fertilizer significantly increase the number of primordia in the overwintering buds of Douglas-fir seedlings (Margolis and Waring 1986a). In fact, the size of the mobile nitrogen pool (i.e., FAA) relative to needle biomass is recognized in growth simulation models as determining the production rate of new needles (Fagerstrom and Lohm 1977). Campagna and Margolis (1989) demonstrated that the ratio of FAA to mobile carbohydrates in the foliage of spruce seedlings measured throughout the growing season predicted the relative allocation between shoots and roots ($r^2 > 0.9$).

Root growth is essential for plants to capture scarce resources such as water and nutrients. The relative energy expenditure for water, however, is modest compared to that for nutrients. Because water is extracted progressively from the surface horizons downward by all vegetation (Lange et al. 1976), new root growth must occur at lower depths with the absence of summer precipitation. Although water uptake did not limit photosynthesis or transpiration on the experimental site during the summer (predawn potentials remained above -0.75 MPa), the source of water was from lower soil horizons where nitrogen was not available. In the unfertilized treatments, soil nitrogen levels were exceedingly low, even in the uppermost fertile horizon (extractable NO₃ and NH₄ < 2 ppm). In contrast, fertilizing at 350 kg N/ha exceeded what plant roots could take up, even with a full canopy, as indicated by the elevated levels of nitrate (7 ppm) observed in the upper 15 cm of soil.

INSECT DIET AND INSECT PERFORMANCE

It is important to emphasize that biochemical analyses were restricted to emerging foliage because spruce budworm feeds preferentially on this foliage. In such leaves, free amino acids (FAA) provide a highly digestible source of nitrogen and carbohydrates to budworm larvae. The response of herbivores to increased dietary nitrogen has been well documented in both deciduous and coniferous ecosystems (Mattson 1980, Cates et al. 1987), but less attention has been given to the relative importance of FAA, protein, and nitrogen-containing secondary products as sources of dietary nitrogen. The importance of FAA over other forms of nitrogen has been corroborated from studies by Heron (1965) on eastern spruce budworm (*Choristoneura fumiferana*) and by McNeill and Southwood (1978) on whiteflies (*Aleurotrachelus jelinekii*) and aphids (*Brevicoryne brassicae* and *Myzus persicae*).

Proteins may be a less desirable dietary form of nitrogen because they react chemically with tannins to form indigestible complexes. Tannin levels, however, were also consistently low in all treatments as previously found by Redak and Cates (1984). Spruce budworm normally do not feed on older foliage which has

high tannin concentrations, and trees respond to defoliation by further increasing tannin levels (Walters and Stafford 1984).

The relatively low and comparable levels of carbohydrates and lignin reported in emerging foliage reflect leaf immaturity. Expanding foliage is dependent on imports of carbohydrates from older foliage or from reserves in the twig. Because growth is in progress, concentrations of sugars and starch should be expected to be fairly low. Lignification, being the last biochemical step in cell wall formation, has barely started in expanding foliage, so low concentrations of lignin are also recorded.

INSECT EFFECTS ON TREES

The amount of starch accumulated in the twigs of grand fir allows prediction of twig and bud survival following partial or complete defoliation by insects in eastern Oregon (Webb 1981). Increasing the light available to suppressed trees can enhance starch accumulation (Cranswick 1979, cited in Waring and Schlesinger 1985). Although we did not measure starch accumulation in twigs, we expect it occurred following fertilization because more buds survived on fertilized than on unfertilized trees (Wickman et al. 1992).

During the peak year of recorded defoliation in 1987, fertilized trees produced shoots weighing more than 150 mg while unfertilized trees produced shoots weighing 50 mg (Figure 3, Wickman et al. 1992). In addition, proportionally less of the shoots of fertilized trees were consumed (74% vs. 99%). Because of these two factors, fertilized trees produced shoots with a net average weight of 37 mg at the end of the growing season; unfertilized trees had essentially no net shoot production in 1987. The advantage of producing more shoots and having a lower proportion consumed on fertilized trees is cumulative and helps account for the more than a twofold increase in radial growth over the last 3–5 years of the experiment (Figure 5, Wickman et al. 1992).

The index, tree growth efficiency, has served previously in assessing the resistance of conifers to variable intensities of attack by bark beetles (Larsson et al. 1985, Mitchell et al. 1985, Waring and Pitman 1985, Christiansen et al. 1987). The underlying principle is that wood growth has low priority for photosynthate compared to foliage production, twig starch reserves, and root production. Trees with high production of wood per unit of leaf area can shunt energy away from wood growth to meet the needs for repair or defense. The corollary follows that trees of low efficiency have less energy to expend on these functions.

In general, tree growth efficiency requires about 2 years following treatment to respond. In the case of fertilization without thinning, the response was delayed an additional year, as seen in the stem growth data reported by Wickman et al. (1992). This seems reasonable because insect defoliation opened the canopy more slowly than thinning.

FUTURE IMPLICATIONS OF PRESENT FOREST POLICIES

Fire protection has permitted grand fir to reproduce under a canopy of pine. This situation has resulted in about a doubling of total leaf area in the stand from 4 to 8 (Gholz 1982, Oren et al. 1987), which has increased the total demand for nitrogen proportionally. Because the fir canopy only absorbs about 4% more light

than the pine, photosynthesis is not much enhanced (Pierce and Running 1988). With twice the demand for nitrogen, proportional allocation to fine-root production would necessarily increase at the expense of wood production and twig starch content.

As a result of the replacement of pine forests with dense fir over much of the interior western part of the United States, most unthinned stands on similar sites contain trees exhibiting lower than average vigor (Waring 1983). Older stands of pine also fall into low vigor categories unless carefully managed (Waring and Pitman 1985). The situation is clearly reversible as evidenced by the increase in radial growth observed on fertilized trees in this experiment even before foliage levels had fully recovered.

Although surface soils may dry, water is not the major factor limiting growth in much of the region where pine and true fir are mixed. The rapid removal of water from the surface soils in the first month of the growing season does limit the time period when tree roots can access the higher nitrogen levels available in surface layers. We calculated that 5 cm of water could be stored in the upper 30 cm of soil and that this amount would be completely utilized by mid-July (these calculations were made using an ecosystem simulation model, Running 1984).

Fertilization with nitrogen improves the availability of a critically limiting resource during the time period when water is available in the surface horizons. In the arid climate typifying the region, much of the added nitrogen remains available in the system, as evidenced by a sustained or increasing level of growth for up to 5 years following application (Wickman et al. 1992) and by direct bioassay of the soils (Dr. Art Tiedeman, La Grande, OR, personal communication).

MANAGEMENT IMPLICATIONS

The results of this study suggest that nitrogen fertilization, even without thinning, may offer a viable alternative to the present policy of temporarily reducing insect populations through the expensive and repetitive application of pesticides or bio-cides. Carefully timed fertilization with nitrogen, and possibly other nutrients (Geist 1977), could significantly improve the ability of grand fir forests to withstand moderately large outbreaks of insect defoliators. Thinning, unless well planned, may perpetuate the reestablishment of grand fir and by itself does not maintain stand growth at comparable levels to what was obtained through fertilization alone or in combination.

A threat of insect populations building up on fertilized trees does not seem likely. Insect populations returned to endemic levels regardless of treatment during 1989 as a result of increasing parasitism on pupae and eggs (Mason et al. 1992). Larger scale experiments by the USDA Forest Service are now underway near La Grande, OR, to test the general application of these research findings.

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