Modifying Lodgepole Pine Stands to Change Susceptibility to Mountain Pine Beetle Attack

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Abstract. The premise that mature lodgepole pine forests are susceptible to mountain pine beetle attack when physiologically stressed was supported experimentally by manipulating the canopy density and availability of nitrogen in a 120-yr-old forest exposed to a high population of beetles. Where canopy density was reduced, either by us or by the insects, surviving trees significantly increased their resistance to attack over a 3-yr period. Increased resistance was reflected by changes in wood production per unit of leaf area (tree growth efficiency). Improved nitrogen nutrition hastened tree recovery but did not prevent attacks by beetles until growth efficiencies exceeded 100 g of wood production per square metre of foliage. Growth efficiency, as here defined, is an index of vigor that may reflect the relative ability of susceptible trees to produce defensive compounds following attack.

Key words: bark beetles; canopy density; epidemics; forest management; lodgepole pine; mountain pine beetle; nitrogen availability; physiological stress; susceptibility; tree growth efficiency; vigor.

INTRODUCTION

Epidemics of mountain pine beetles (*Dendroctonus ponderosae* Hopkins) periodically sweep across the western forests of lodgepole pine (*Pinus contorta* Dougl.), killing most of the larger diameter trees (Wellner 1978). Outbreaks are accelerated when it is the larger trees that are successfully attacked, because they have thicker inner bark for the larvae to feed upon and offer a larger suface area to support broods of beetles (Amman 1972, Amman and Pace 1976, Berryman 1976, Klein et al. 1978).

We envisioned bark beetles (Scolytidae) as having a similar influence as defoliating insects, which are known to improve the environment of surviving trees following an epidemic attack (Mattson and Addy 1975, Wickman 1978, Piene 1980). Ecosystem responses following bark beetle epidemics may be less rapid, however, because surviving trees may be old and unable to respond and because beetle-killed trees do not immediately drop their foliage.

Upon successfully attacking a pine tree, the female beetle burrows a characteristic gallery between the bark and wood, where she lays her eggs. Her burrowing introduces into the conducting sapwood inoculum from various fungi, which she carries in a mycangial pouch. The fungi spread across the sapwood and eventually can halt all water transport through the stem. Soon after trees are killed, the smaller diameter roots are incorporated into the soil. Any reduction in the canopy will permit more solar radiation and precipitation to penetrate to the ground, stimulating decomposition, mineralization, and proliferation of ground flora. The degree of stimulation might be less than that associated with complete defoliation (Piene 1980, Sollins et al. 1981), but the stimulation itself might be more per-

sistent and cause an increase in growth rates of surviving trees.

An increase in a tree's growth rate tends to decrease its susceptibility to attack. This may occur because of an increased ability to allocate scarce resources for defense. In dense, slow-growing forests characteristic of the subalpine zone (Franklin and Dyrness 1973), the amount of photosynthesis is limited. As trees grow they require more carbohydrates for maintenance and may have proportionally fewer to allocate to allelochemics (defensive chemicals).

We designed a field experiment to evaluate how changes in nutrition, light, and moisture might interact to increase the growth rates of trees and reduce their susceptibility to beetle attack. Our ability to assess changes in a tree's susceptibility to bark beetle attack was enhanced by having epidemic populations of beetles in the experimental area, synthetic pheromones with which to attract beetles to the plots, and precise indices for assessing insect-attack density and changes in tree growth efficiency (Waring and Pitman 1983).

METHODS

Study site

The study site is on the eastern slope of the Cascade Mountains in west-central Oregon near Craine Prairie reservoir (43°27'N, 121°41'W), ≈80 km southwest of Bend. The climate is subalpine, with winter temperatures < −10°C and summer temperatures rarely > 30°. Annual precipitation averages 500 mm with <10% falling during the summer. Snowfall averages 300 cm annually. The growing season generally starts in late June and ends in early September. The site is almost flat, with deep sandy soils derived from Mazama pumice.

The understory vegetation is normally sparse, consisting of a few species of grasses, small shrubs, and a

few herbs. The vegetation has been classified as a *Pinus contorta/Purshia tridentata–Ribes cereum* community by Franklin and Dyrness (1973). The overstory trees were 120-yr-old lodgepole pine averaging 20 m in height and 15 cm in diameter at breast height.

Experimental design

A total of 16 quarter-hectare plots were laid out, with 25-m buffer strips on all sides of each plot. All trees >10 cm in diameter within a central circular 200-m² subplot of each quarter-hectare plot were marked with numbered tags. In the fall of 1978, one of four treatments was randomly applied to each quarter-hectare plot: (1) fertilization with urea, providing nitrogen at 420 kg/ha, (2) additions of sugar (454 kg/ha) and fresh lodgepole-pine sawdust (2000 kg/ha), (3) fertilization with urea as in treatment 1, along with removal of most of the smaller diameter trees, leaving ≈20% of the original canopy, or (4) untreated controls.

In the summer of 1979, five vials of pheromone attractants were put in each plot. The synthetic pheromone "ponderlure," consisting of 40% alpha-pinene and 60% *trans*-verbenol (Pitman 1971), escaped slowly through a pinhole in each vial at a rate dependent on the air temperature. Whenever two trees in the same plot and separated by >6 m had each been attacked by more than five beetles, all pheromone vials in that plot were removed.

The experiment was in the vicinity of an epidemic population of mountain pine beetles, and thus we were confident that many of the beetles would be attracted to the plots. In fact, the population of beetles was so high that it limited the area available for our experiment and forced us to delete a treatment involving canopy reduction alone. Fortunately, this experimental treatment had previously been conducted on a number of 40–80 yr old stands of lodgepole pine across eastern Oregon (Mitchell et al. 1983; see Discussion).

Nitrogen stress

The choice of nitrogen as a fertilizer was based on soil analyses of the site that indicated extremely low levels of mineralizable nitrogen. The carbohydrates incorporated in sugar and sawdust were added to increase microbial activity and further reduce, if possible, the availability of nitrogen (Turner 1977, Bååth et al. 1978, Johnson and Edwards 1979).

At various periods (8 mo to 3 yr after initiation of treatments in the fall of 1978), we collected soils from the 0–15 cm depth from all plots; all plots were sampled each year, although not at the same time. Initially, three separate soil samples were taken from each plot; later a single composite sample was made for each plot (each treatment included four plots). Mineralizable nitrogen was determined under anaerobic conditions after incubation of 20 g soil (fresh mass) with 20 mL of water for 7 d at 40° (Waring and Bremner 1964).

On each plot, foliage was sampled from three trees unattacked by beetles; a shotgun was used to sever branches from the midcrown of each selected tree. Twig foliage was separated into new (i.e., current-year) foliage, older foliage, and that ready to fall as litter. Each foliage sample was dried and ground through a 425-μm mesh screen in a Wiley mill in preparation for micro-Kjeldahl analysis of nitrogen. A subsample of the fresh (i.e., new and older) foliage was taken and its projected surface area determined with a LI-COR model LI-3000 leaf-area meter. After the subsample was dried, the foliage was weighed and the specific leaf mass calculated, permitting nitrogen data to be expressed as grams per square metre of foliage (Smith et al. 1981).

Samples of small-diameter roots were collected from the 0–10 cm depth on each plot in June 1980, taken to the laboratory, washed, then dried at 70° for 24 h before being ground and analyzed for nitrogen. In August 1980, triplicate samples of inner bark were taken with a number 6 cork borer (area 2 cm²) from three unattacked trees on each plot. Samples were dried and prepared for nitrogen analyses with procedures similar to those described for foliage.

Moisture stress

We wanted to determine whether the soil water supply was increased by reduction in the canopy, so we sampled soils in September 1980 following more than a month without precipitation. Three samples were collected from the 15–20 cm depth on each plot. These samples were combined, stored in airtight cans, and returned to the laboratory, where moisture contents were determined gravimetrically.

To determine whether trees experienced any difference in water stress, we collected twigs in September 1980 from the midcrown position of one dominant tree on each plot. Earlier sampling would have been less likely to distinguish differences (Waring and Cleary 1967). Samples were collected with the aid of a shotgun at noon and a few hours before dawn. We used a pressure chamber to assess water stress (Scholander et al. 1965). Predawn values indicate whether soil water supply is near exhaustion (Hinckley et al. 1978, Waring et al. 1980a). Noon values taken on clear days indicate whether water uptake is restricted because of poor rooting distribution, low wood permeability, or disease.

As an additional measure of root efficiency we measured changes in the relative water content of the conducting sapwood on 25 tagged trees from each of the four treatments. Normally, the sapwood loses water during the day as uptake by roots lags behind transpiration (Waring et al. 1980b). We contrasted values of relative water content observed in October 1978, following initiation of the experiment, with those in June 1979, before any trees were attacked by beetles. A sapwood sample was taken in the early morning with an increment borer. The outer 2 cm of core was precisely trimmed and stored in an airtight glass vial. Relative

water contents were calculated (Waring and Running 1978, Waring et al. 1980b).

Changes in canopy and wood production efficiency

Leaf area index was estimated from a regression derived from eight trees, indicating that for every square centimetre of sapwood cross-sectional area, lodgepole pine supports 0.15 square metres of foliage ($r^2 = 0.98$; Waring et al. 1982). To estimate growth efficiency (i.e., the increment in stem biomass per square metre of foliage), we used an equation allometric with diameter (Gholz et al. 1979):

$$\text{ln(Biomass, in kilograms)} = 2.4287 \text{ ln(Tree Diameter, in centimetres)} - 2.9849. \quad (1)$$

Diameter growth and sapwood thickness were estimated from wood cores extracted with an increment borer from opposite sides of all tagged living trees within each of the circular subplots in fall 1979, 1980, and 1981. Sapwood was identified either by its relative translucence, due to a moisture content higher than that of the heartwood, or, in the summer, when water content in wood is low, with the aid of a bromocreosol-green ethanol solution, which differentially stains the two kinds of wood (Kutscha and Sachs 1962). To assess the change in canopy resulting from thinning or beetle-induced mortality, we calculated the living sapwood area (in square centimetres) remaining on each of the 200-m² subplots, then multiplied sapwood area by 0.15 to convert to square metres of leaf area. We assumed that the regression of leaf area with sapwood was unaffected by treatments.

Because a large number of tagged trees were eventually killed or at least attacked, it became increasingly more difficult to compare average stand growth efficiencies. Data presented are from 12 trees in each treatment (3 from each of four circular subplots) that remained unattacked throughout the entire experiment.

We measured mass both of old foliage and of current year's foliage on branches collected for nitrogen analysis in August 1980. We then calculated new foliage dry mass per current year's shoot, and new foliage as a percentage of total foliage. We also measured shoot length for the current year (1980) and the previous year to compare relative shoot length.

Susceptibility of trees to beetle attack

As a measure of beetle flight activity, we made a weekly count, from June through mid-September in 1979, of the number of mountain pine beetles caught on sticky traps placed with pheromone attractants at the center of each circular plot. In September 1979 we inspected all trees in each plot and recorded which had been attacked. In September 1979, 1980, and 1981, we estimated the number of beetles attacking each tree growing within the 200-m² circular subplots by in-

specting a band 30 cm wide that was centered on the tree at the conventional height for measuring diameter, 1.37 m above the ground. Pitch-tube formation and either sawdust or oleoresin exudation marked sites of beetle entrance. The number of attacks was expressed per square metre of bark surface.

Mortality of trees was assessed the following spring (1981) from observation of browning foliage and blue-stained sapwood associated with fungi introduced by the beetles. Occasionally, only a fraction of the entire conducting sapwood was stained, which meant that a tree might continue to live with a portion of its sapwood inoperative. Such trees were considered fractionally dead, depending upon the area of sapwood stained.

Since we had estimates of the growth efficiency for each attacked tree in the central 200-m² subplots, we were able to test a relationship (established from a previous survey outside the experimental area) that predicted the number of attacks required to kill trees of known growth efficiency (Waring and Pitman 1980). These predictions were compared with observed mortality the following spring.

To evaluate responses to the experimental treatments we performed one-way analysis of variance upon the data. If an F value indicated significant differences among treatments, we calculated least significant difference (LSD) at $\alpha = .05$ and compared means among treatments (Fisher protected analysis; Steel and Torrie 1980:176). In appropriate cases we compared variation within one treatment from one year to the next with a two-tailed t test (Steel and Torrie 1980).

RESULTS

Nitrogen

Application of nitrogen caused a 10-fold increase in mineralizable soil nitrogen the following spring. Both the plots receiving carbohydrate additions and the control plots were initially low in mineralizable nitrogen, but in the latter there was a significant increase from 1980 to 1981. In contrast, mineralizable nitrogen content in the fertilized treatments (with and without thinning; Table 1) decreased significantly over the experimental period, but was still twice that of the unfertilized treatments in fall 1981, 3 yr after fertilization.

In the tree canopy the nitrogen status of the 1st-yr age-class of foliage increased significantly by the first spring (1979) following fertilization. Fertilizing with thinning increased nitrogen content of older foliage as well. A year later, nitrogen levels had decreased significantly ($P < .05$) but still remained higher than in the unfertilized treatments.

Fresh litter, inner bark, and small-diameter roots also increased significantly in nitrogen following fertilization. As the oldest needles died and were about to be shed, a large proportion of nitrogen was translocated: 54–60% in the fertilized treatments and 47–48% in the unfertilized.

TABLE 1. Response of lodgepole pine (*Pinus contorta*) ecosystem to each of four treatments applied fall 1978.

Responses	Treatment†				Samples per treat-ment	F‡	LSD.05‡
	Fer-tilized and thinned	Fer-tilized	Control	Sugar and sawdust			
Nitrogen							
Soil (mg/kg)							
1979	40.7^a ⎤	48.8^a ⎤	4.4^b ⎤	3.8^b	12	13.07**	18.2
1980	16.2^a	10.5^a	3.5^a	5.3^a	4	3.2	
1981	12.6^a ⎦	12.0^a ⎦	6.7^b ⎦	5.1^b	4	4.28*	5.5
Plant foliage 1979 (g/m²)							
1st yr	6.7^a	6.8^a	5.1^b	5.2^b	12	4.51**	1.6
2nd yr	7.3^a	5.7^b	4.8^b	5.4^b	12	4.31**	1.5
3rd yr	7.3^a	4.8^b	4.2^b	4.4^b	12	3.99**	1.9
Plant foliage 1980 (g/m²)							
1st yr	3.5^a	4.1^b	2.5^c	2.4^c	12	30.6**	0.3
Older	4.4^a	4.6^a	3.0^b	2.9^b	12	38.8**	0.4
Fresh litter	2.0^a	2.1^a	1.6^b	1.4^b	12	4.68**	0.4
Inner bark 1980 (%)	0.37^a	0.33^a	0.20^b	0.23^b	12	12.16**	0.06
Small roots 1980 (%)	0.72^a	0.79^a	0.55^b	0.53^b	4	5.95**	0.15
Carbon							
Stand leaf area index (m²/m²) 1978	1.03^a	4.5^b	4.68^b	4.95^b	4	8.40**	2.02
Twig foliage mass (g) 1980	28.9^a	23.0^{ab}	17.9^b	17.7^b	12	4.97**	6.98
% new foliage 1980	31.2^a	27.6^a	16.6^b	17.6^b	12	12.20**	5.86
Comparative shoot length 1980/1979	1.52^a	1.46^{ab}	1.28^b	1.02^c	12	10.34**	0.20
Growth efficiency§ (g·m⁻²·yr⁻¹)							
1979	77.0^a ⎤⎤	66.9^a ⎤	51.0^a ⎤	76.0^a	12	1.60	
1980	95.0^a ⎦⎥	83.8^a ⎥	59.0^a ⎥	80.8^a	12	2.59	
1981	120.0^a ⎦	108.0^a ⎦	73.0^a ⎦	88.3^a	12	1.77	
Moisture							
Soil moisture (%) September 1980	9.1^a	9.2^a	8.4^a	9.9^a	4	0.50	
Predawn tree water potential (−MPa) September 1980	0.30^a	0.30^a	0.30^a	0.31^a	4	0.10	
Noon tree water potential (−MPa) September 1980	1.55^a	1.54^a	1.52^a	1.63^a	4	0.92	
Sapwood relative water content (%) October 1978	79.5^a	81.9^a	85.1^a	85.9^a	25	2.08	
Sapwood relative water content (%) June 1979	53.1^a	53.1^a	54.2^a	59.5^a	25	0.87	

† Fertilization and thinning: urea-N applied at 420 kg/ha and the canopy thinned 80%; fertilization alone: urea-N applied at 420 kg/ha; control: no treatment applied; sugar and sawdust: sugar applied at 454 kg/ha and fresh sawdust applied at 2000 kg/ha. Each treatment covered four quarter-hectare plots.

‡ F value for one-way analysis of variance, with significance indicated at * $P < .05$ or ** $P < .01$. LSD column shows the least significant difference at the .05 level; common superscript letters within a row indicate that the difference between treatments is not significant. Brackets indicate pairs of years for which differences within a treatment were significant ($P < .05$).

§ Stem biomass increment per unit foliage area per year.

Carbon

Initial thinning (fertilized-and-thinned treatment) removed ≈80% of the canopy, thereby reducing the Leaf Area Index (leaf area/ground area) to 1 m²/1 m² (10,000 m²/ha). Fertilization together with thinning had a dramatic impact on foliage production, the proportion of current to total foliage, and shoot length (Table 1). Within 2 yr following thinning and the ap-plication of fertilizer in 1978, foliage on midcrown twigs had increased by as much as 63%, including al-most a doubling in the amount of current foliage and an increase of about a third in the foliage remaining in older age-classes. Fertilizing alone significantly in-creased the proportion of current to total foliage. Other attributes were similar to the fertilized-and-thinned treatment. These responses are similar to those re-

ported in fertilizer experiments with Douglas-fir (Turner 1977). Shoot elongation improved in 1980 over the value observed the previous year in all but the sugar-and-sawdust treatment. The fertilization-and-thinning treatment exceeded the control by nearly 20% (P = .05).

One of the most important changes noted was in tree growth efficiency. Over a 3-yr period, the same 12 unattacked trees in each treatment showed progressive improvement; in all but the sugar-and-sawdust treatment the changes were significant (P = .05). Because of the large variation among trees, there were no apparent differences among treatments in a given year. Nevertheless, by the 3rd yr, in each of the fertilized treatments wood production averaged >100 g/m² of foliage. This indicates greatly reduced susceptibility to beetle attack (see Beetle Attack and Tree Growth Efficiency below).

Moisture

Monitoring of moisture in trees and soil indicated no differences attributable to treatments. In the site's coarse pumice sands, some available water was still present in the surface 15 cm during September. Removing 80% of the tree canopy allowed native grasses to grow more rapidly, so that the root zone was quickly reoccupied. In spite of the dry summer, moisture never approached exhaustion in the root zone, as indicated by the modest predawn stress values (−0.30 MPa) recorded in late September. Noon values were normal, averaging −1.55 MPa for healthy trees growing in this bright, desiccating environment (Waring and Cleary 1967, Running 1976).

Sapwood water reserves, which are an indicator of how well the root system meets transpiration demands, showed no differences among treatments. In October, when transpiration was much reduced, sapwood was within 15–20% of saturation. In June, under high evaporative demand, reserves were reduced another 25–30% below values observed in the fall. A few trees, usually <10 cm in diameter and thus not susceptible to beetle attack, showed sapwood water contents <40%. These trees were suspected of harboring root rot and had long ago lost their competitive position in the forest.

We conclude that water is readily available to most trees throughout a normal growing season and that drought stress is generally uncommon in Oregon's subalpine forests (McNeil and Zobel 1980), even along the California border (Waring 1969, Waring et al. 1978).

Beetle attack and tree growth efficiency

The effect of bark beetles upon growth efficiency interacted with environmental changes induced through tree mortality from beetle attack. Surviving trees on the fertilized-and-thinned plots significantly increased in growth (= stem biomass increment per unit foliage area per year) from 1979 to 1980 (Table 1). The fer-

TABLE 2. Reductions in lodgepole-pine stocking attributed to bark beetle attack in plots subjected to one of four treatments.†

Treatment	Distribution of mortality losses over 3 years			Cumulative percent loss over 3 years (1979–1981)
	1979	1980	1981	
	Mortality‡ (%)			
Fertilized and thinned	73.5ᵃᵇ	18.7	7.7ᵃ	20.2
Fertilized	87.5ᵃ	12.0	0.5ᵃ	29.9
Sugar and sawdust	29.0ᵇ	47.0	24.5ᵇ	28.5
Control	73.7ᵃᵇ	15.0	11.2ᵇ	24.5
F§	3.4*	2.2	4.6*	0.4
LSD.₀₅‡	50.0		16.7	

† Treatments defined in Table 1; each treatment was applied to four quarter-hectare plots.

‡ Within the same year, different superscript letters indicate significant differences between treatment means ($P \leq .05$, least significant difference [LSD] test).

§ Asterisks identify significant ($P \leq .05$) F values from a one-way analysis of variance among treatments within a year.

tilized treatment and the control also improved in growth efficiency or tree vigor, but to a lesser extent; significant improvements in vigor were not noted until 1981. Treating with sugar and sawdust prevented trees from making a significant improvement in vigor even after 3 yr.

Over the 3-yr period, beetles reduced the live canopy on all plots an average of 16.0% ± 4.3% (SE). Although initial tree stocking levels were highly variable among plots, reductions were comparable for all treatments, with cumulative losses of 25.8% ± 3.2% (Table 2). The annual distribution of mortality, however, differed significantly among treatments. Plots receiving carbohydrate additions suffered sustained mortality throughout the experiment. In contrast, both fertilized treatments experienced proportionally heavier mortality during the 1st yr of attack and very little by the 3rd yr. We noted a correspondence between significant reduction in mortality and the cases where vigor indices first exceeded 100 g of wood production per square metre of foliage (compare data in Tables 1 and 2).

To further evaluate this relationship, we compared the survival of 100 trees attacked by various numbers of bark beetles in 1979. We found good agreement between tree growth efficiency and the number of bark beetles required to kill lodgepole pine trees (Fig. 1). Trees of low growth efficiency (≤70 g·m⁻²·yr⁻¹ were most likely to be heavily attacked. Those trees with growth efficiency values of <20 g wood production per square metre of foliage per year actually produced no exudation of pitch upon attack (see Raffa and Berryman 1982). At the other extreme, few trees with growth efficiencies >100 g·m⁻²·yr⁻¹ were attacked; of the few attacked, even fewer were killed, even at attack den-
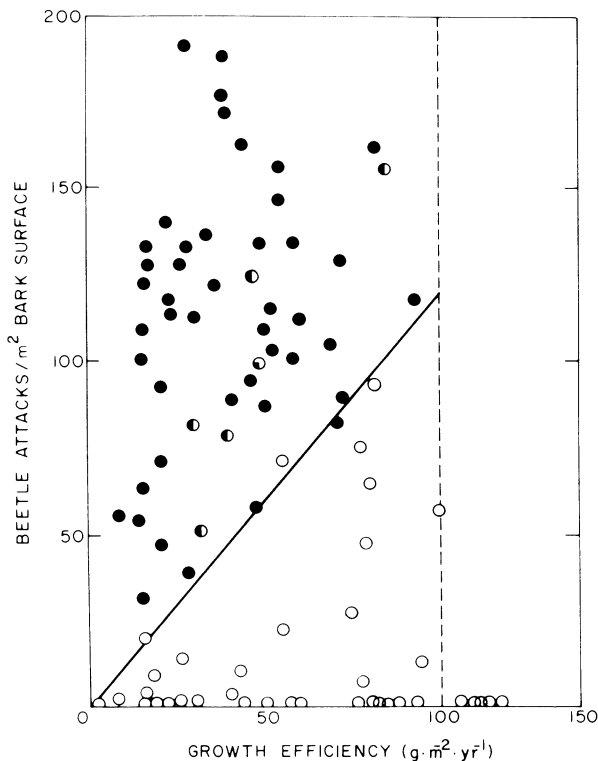
FIG. 1. Growth efficiency (stem biomass increment per unit foliage area per year; *x* axis), the density of attack by mountain pine beetle (*y* axis), and the degree of morbidity as estimated by stained sapwood (represented by the blackened portions of the circles) on lodgepole pine attacked in 1979 on all 16 treatment plots. The solid line indicates the division between trees that survived beetle attack with no permanent sapwood damage (open circles) and trees that sustained permanent sapwood damage (partially or completely filled circles; the degree of damage is indicated by the extent to which a circle is filled). The dotted line indicates the threshold of tree growth efficiency above which beetle attacks are unlikely to cause mortality. (Beetle attacks are also unlikely to exceed 200 attacks/m² bark surface.) After Waring and Pitman 1983.

sities for individual trees of 100 beetles/m² of bark surface. Out of nearly 100 trees attacked during 1979, the tree mortality line (Fig. 1) derived from an earlier survey (Waring and Pitman 1980) correctly predicted blue-stain injury in all but 5% of the cases.

DISCUSSION

The experiment demonstrated that a 120-yr-old lodgepole pine forest can respond to fertilization and thinning. Mortality induced by bark beetles alone reduced stand leaf area and was associated with an increase in vigor of surviving trees. Because little change in nitrogen status was observed in the control and sugar-and-sawdust treatments, we conclude that the major impact of beetles is the reduction they cause in canopy, which in turn increases the available light and improves photosynthesis. Separate studies where thinning 40–80 yr old lodgepole pine preceded beetle at-

tacks by at least 3 yr showed that stand tree resistance improved dramatically, reducing attacks and subsequent mortality (Mitchell et al. 1983). Similar findings have also been reported for thinned stands of ponderosa pine (*Pinus ponderosa* Law S.) (Larsson et al. 1983).

The rapid improvement in resistance noted in surviving trees in both fertilized treatments suggests that, if more widely used, such ameliorations might reduce the duration of mountain pine beetle epidemics. Even in the normal situation, represented by the control plots, initial mortality stimulated surviving trees, so that after ≈3 yr they too were predicted to be relatively safe from attack. It is probably no accident, therefore, that epidemic populations in a particular area usually start to subside 3–5 yr after the initial outbreak, and rarely persist for >9 yr (Cole and Amman 1980).

Carbohydrate stress

One of our basic premises is that any environmental stress eventually may lead to a scarcity of carbohydrates within trees. Even with a favorable climate and soils, densely stocked forests might experience carbohydrate stress associated with competition among trees for the available light (Waring et al. 1981). As forests grow in stature, the biomass of respiring tissue increases. Since the canopy can only increase to a certain level, its photosynthetic capacity is constrained, while demands for carbohydrates continue to increase. Eventually, the forest must use more of its stored reserves, increasing its susceptibility to insects and diseases (Schoeneweiss 1975, Webb 1981).

Exactly how carbohydrates are rationed by stressed plants is an active field of investigation. Certainly the proportions of carbohydrates allocated to roots, shoots, and protective chemicals can be expected to change as stress increases (McLaughlin et al. 1982). From observations of stressed plants, we know that buds are likely to be preserved at the expense of older foliage. At the other extreme, diameter growth in the lower bole is constrained or temporarily stopped when trees are subjected to extreme stress (Waring 1983).

In Fig. 2, we present a simplified diagram that illustrates probable priorities for carbohydrate allocation within a lodgepole pine tree. We have assigned a low priority to chemical barriers, after storage reserves and diameter growth. This ranking matches observations that some starch reserves (≈ 1.5% by mass) are still present in the sapwood of susceptible lodgepole pine trees and in the twigs of other species attacked by defoliating insects (Webb 1981). At the same time, susceptible trees usually produce rather small growth rings in their stems.

The rationing process is a relative one. Larger trees have more foliage and produce more carbohydrates than smaller trees; usually they also grow more wood. We provided a common index of carbohydrate stress by comparing wood production, which is one of the last priorities for carbohydrates, with the amount of

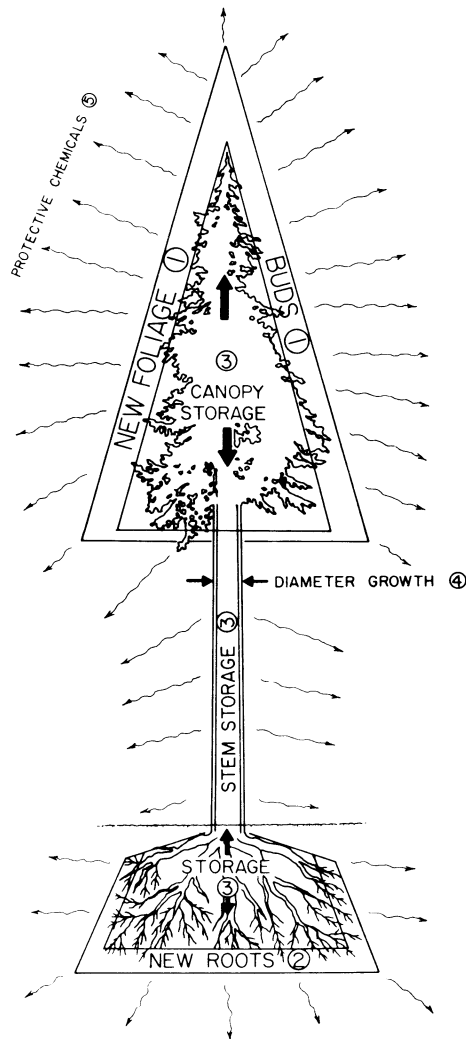POSTULATED CARBON ALLOCATION HIERARCHY

FIG. 2. Probable carbohydrate-allocation priorities in lodgepole pine. Under stressed conditions trees modify the allocation of carbohydrates so that new foliage and roots are relatively favored over the production of protective chemicals or stem growth. Priorities are numbered from 1 (highest) to 5 (lowest).

photosynthetic tissue. This ratio is an index of tree growth efficiency and is similar to the net assimilation rate (Briggs et al. 1920), which includes production of all dry matter. We express foliage in units of surface area rather than mass to avoid problems related to changes in carbohydrate storage within the foliage (Smith et al. 1981).

In a recent study, Waring et al. (1981) demonstrated that tree growth efficiency increased almost linearly as the amount of canopy was reduced in a coastal Douglas-fir forest. Mitchell et al. (1983) and Larsson et al. (1983) reported similar relationships with lodgepole and ponderosa pine forests. We might expect, then, that removing 80% of the lodgepole pine canopy should

significantly increase the photosynthetic efficiency of remaining trees and, presumably, their resistance to insect attack. Fertilization alone might reduce the proportion of carbohydrates allocated to small roots (Linder and Axelsson 1982), but carbohydrate storage reserves may be exhausted in the process of converting inorganic nitrogen to amino acids (Pate 1980, Matson and Waring 1984). Exhaustion of carbohydrates reduces the production of defensive compounds (Bryant et al. 1983).

MANAGEMENT IMPLICATIONS

The old forests of lodgepole pine proved to be extremely responsive to subtle changes in their environment. The effects of treatments and subsequent beetle-induced mortality quickly permeated the entire system. Even the stimulating effects of fertilization were rapidly dissipated, so that concentrations in the soil, plant, and litter were expected to return nearly to their original levels $\approx$ 3–4 yr after fertilization.

As a result of this research, management practices are being developed to maintain lodgepole pine forests at a resistant state to even epidemic populations of mountain pine beetles (Pitman et al. 1982b). These practices are designed to permit the growing of large-diameter trees that are more valuable and provide good genetic stock. The key feature of the practice in its present state is the precise control of spacing among selected surviving trees.

Concerns about the future stem in part from a recognition that fire protection policies that are not coordinated with intensive forestry have created a situation in which many of the pine-dominated forests in eastern Oregon and Washington have growth efficiencies no greater than $\approx$ 80 g wood production per square metre of foliage per year (Schroeder et al. 1982). It is not known whether the risk rating system for pine can be applied directly to other species of conifers, but research on epidemic outbreaks of native defoliators such as spruce budworms (*Choristoneura* spp.) and Douglas-fir tussock moth (*Orgyia pseudotsugata* McD.) should consider such comparisons and employ experimental thinnings. European pine sawfly (*Neodiprion sertifer* Geoffr.) studies in Sweden reported by Pitman et al. (1982a) support the contention that native defoliating insects might well select trees of low resistance and with low amounts of foliar allelochemics (Perry and Pitman 1983).

CONCLUSIONS

The major influence of bark beetles in lodgepole pine forests appears related to canopy reduction, which improves the penetration of solar radiation and causes greater photosynthetic efficiency in surviving trees. From this study and related ones we know the risk of beetle epidemics can be greatly reduced by periodic thinning.

By fertilizing with nitrogen or, by analogy, rapid can-

opy defoliation, improvement in nitrogen status can be expected throughout the system. Normally, both managed and natural forests experience alternating periods of stimulation and stress. The diagnostic approach followed in this study provides insights that could allow forests to be managed without experiencing stress sufficient to foster an insect outbreak.

The experimental approach that was followed identified the relative importance of various environmental factors and clarified basic relationships difficult or impossible to recognize through observation of natural forests alone. For these reasons, we strongly endorse an experimental approach for the analysis of how environmental interactions affect various ecosystem processes.

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