Physiological stress in lodgepole pine as a precursor for mountain pine beetle attack

By R. H. Waring and G. B. Pitman

Abstract

The premise that mature lodgepole pine forests are susceptible to mountain pine beetle attack when physiologically stressed was evaluated by manipulating the canopy density and availability of nitrogen in a 120-year-old forest exposed to a high population of beetles. Where canopy density was reduced and nitrogen nutrition improved, trees significantly increased their resistance to attack. Changes in tree vigor were quantified by estimating increases in wood production per unit of leaf area. These changes were determined from cores and are therefore practical for assessing mortality risk from beetle attacks and for developing protective strategies for management.

1 Introduction

Outbreaks of mountain pine beetle (Dendroctonus ponderosae Hopkins) in lodgepole pine (Pinus contorta Dougl.) are common in large tracts of trees more than 60 years old or 25 cm in diameter (Cole and Amman 1969; Amman 1978; Wellner 1978). Although stress has been postulated as a cause of susceptibility to insect attack (Sáfranyik et al. 1975; Berryman 1976, 1982), the preference of beetles for larger, faster growing trees has been difficult to explain. Large trees usually have thick inner bark, which provides a critical food source and greater surface area for beetle colonization and multiplication (Amman 1972; Amman and Page 1976; Klein et al. 1978; Cole and Amman 1983).

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rate dependent upon the air temperature. When two widely separated trees in a block were attacked by more than five beetles, all pheromone vials in that block were removed.

Diameter growth and sapwood thickness were estimated from wood cores extracted with an increment borer from opposite sides of all tagged trees within each circular plot in fall 1979, 1980, 1981, and 1982. Sapwood was identified by its translucence (due to higher moisture content) relative to heartwood, or with the aid of bromoresol-green dissolved in ethanol, which differentially stains the two kinds of wood. Because many tagged trees were eventually killed or attacked, changes in growth efficiency became increasingly difficult to compare. However, we were able to follow changes in the growth efficiency of at least a dozen trees for each treatment (4 per plot) which remained unattacked throughout most of the experiment. These samples provided a differential measure of treatment effects.

In fall 1979 and 1980 we surveyed beetle attacks on all trees within the circular plots. Either sawdust, oleoresin exudation, or pitch-tube formation marked the site of each attack, so counts were accurate. On each attacked tree, we inspected a band 30 cm wide centered at the conventional height for measuring diameter, 1.37 m above ground. Attacks were expressed as number per square meter of bark surface to allow comparison of trees of different diameters. Tree mortality was assessed the following spring from browning foliage or the presence of blue-stained sapwood associated with fungi introduced by the beetles. Occasionally, not all conducting sapwood was stained, and a tree continued to live with only a portion of its sapwood inoperative. Such trees were considered fractionally dead, depending upon how many of the four cores extracted at equal intervals were stained. It should be noted that microflora, such as blue-stain fungi, are the principal agents of mortality and that bark beetles are their carriers (Mathre 1964).

3 Results and discussion

Two years after initiation of the experiment, between 5% and 10% of the canopy had been killed by bark beetles. Although the percentage did not differ significantly among treatments, the time of mortality did. After the first year, no additional mortality was recorded in fertilized and thinned plots, and in those fertilized alone mortality was nearly zero—only two trees being killed.

Initially, E (= index of radial growth efficiency) of all trees averaged only 70 g of wood production per square meter of foliage. By 1980, however, wood production of all surviving trees on the fertilized and thinned plots increased an average 60% (112 g wood m⁻² foliage yr⁻¹). Unthinned plots showed smaller increases during 1979, ranging from 17% to 29% (average 25%). Differences in growth response between thinned and unthinned plots were again significant (P < 0.05).

To clarify whether increases in E were associated with climate or with canopy reduction from insect-caused mortality, we compared E of a dozen unattacked trees from each treatment over the 3 years of the study (table). E improved significantly each year for the trees from the fertilized and thinned plots. Fertilized and control plots improved similarly after 2 years, but in absolute terms, they lagged behind those fertilized and thinned. Plots stressed with carbohydrates showed no significant increase in E during the study.

We attempted to predict tree mortality from a previously observed relationship that the number of beetle attacks required to kill a tree was directly related to E (Waring and Pitman 1980). Data points from nearly 100 attacked trees recorded in 1979 across all treatments strongly supports the initial correlation (figure). Prediction of death or survival of attacked trees was more than 95% correct. In some cases, death was partial. With detailed knowledge of the attack pattern and the corresponding E of each side of a tree, the degree of blue-stain infection could often be predicted. At E above 100 g wood m⁻² foliage yr⁻¹, beetle attacks were not fatal, and attacking beetles were overcome by excuding oleoresin.

In a related paper, we report that production of terpenoids increases and
Growth efficiency (wood production per unit leaf area) under various treatments (n = 12)

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<tbody>
<tr>
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<td>95.0</td>
<td>120.0</td>
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<td>59.0</td>
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<td>65.6</td>
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<td>80.8</td>
<td>88.3</td>
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<td>1.60</td>
<td>2.59</td>
<td>1.77</td>
<td>5.09*</td>
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Means connected by brackets are significantly different (paired t-test) at P<0.05. F values are for one-way analysis of variance.

*Significantly different at P<0.01.

Qualitative and quantitative changes in their chemistry occur quickly when the competing canopy is reduced sufficiently (PITMAN, WARING, and SÖDERBERG, manuscript in prep.). These changes appear to be associated with increased resistance to bark beetle attack and the observed changes in E, although they are not linearly related nor in perfect synchrony.

These findings, and the results from a survey of beetle attacks on thinned and unthinned stands (MITCHELL et al. 1982), suggest that mountain pine beetle damage could be controlled or significantly reduced by growing trees more widely spaced (PITMAN et al. 1982). Growth efficiency provides an accurate index of susceptibility of lodgepole or ponderosa pine trees (LARSSON et al. 1983) and forests to mountain pine beetle attack. Because lodgepole pine forests in North America are unmanaged, grow in harsh environments, and have been protected from fire for the last half century or more, a wide region exists in which the forests now have reached critically low E values and are susceptible to mountain pine beetle attack (SCHROEDER et al. 1982).

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Growth efficiency (x-axis), the density of beetle attack (y-axis), and the degree of mortality (blackened portion of circles) on lodgepole pine attacked in 1979 on all treatment plots. The solid line indicates the attack level predicted (WARING and PITMAN 1980) to kill lodgepole pine of specified E (= index of radial growth efficiency). The dotted line indicates the threshold above which beetle attacks are unlikely to cause mortality.

Zusammenfassung

Physiologischer Streß in Pinus contorta als Befallsauslöser für den Kiefernborkenkäfer Dendroctonus ponderosae


References


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