Physiological Differences Between Lodgepole Pines Resistant and Susceptible to the Mountain Pine Beetle1 and Associated Microorganisms2

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ABSTRACT

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Lodgepole pines, Pinus contorta Douglas var. latifolia Engelm., were assayed for traits associated with resistance to the mountain pine beetle, Dendroctonus ponderosae Hopkins (Coleoptera: Scolytidae). There was no relationship between resistance and the daily rate of resin flow, rate of resin crystallization, monoterpene content, monoterpene composition, or current growth rate. The major difference between trees which survived or died during exposure to naturally occurring high beetle populations was the extent of their active response to fungal invasion. Resistant trees responded to artificial inoculation with fungi vectored by D. ponderosae by forming greater quantities of resin than did susceptible trees. This wound response is general in nature, quantitatively variable, metabolically active, rapid, and localized. It appears to form the major line of defense to D. ponderosae and its associated fungi, and to be related to the general vigor of the tree. The wound response was greatest in those trees which had a periodic growth ratio greater than unity.

Unlike most phytophagous insects, the successful reproduction of bark beetles (Coleoptera: Scolytidae) is contingent on host mortality (Thalenhorst 1958, Berryman 1972, Wood 1972). Their ability to colonize living hosts is augmented by their mutualistic relationship with microbial phytopathogens (Craighead 1928, Mathre 1964). In addition, their ability to utilize pheromones derived from host compounds enables them to overcome tree defenses through rapid, highly concentrated attack (Thalenhorst 1958, Miller and Keen 1960, Vité et al. 1972, Safranyik et al. 1975, Berryman 1976, Raffa 1981).

Several physiological properties of trees have been investigated in relation to bark beetle attack. The early literature contains numerous references to the “pitching out” of beetles by a copious flow of resin (e.g., Cullham 1955), and consequently the relationship between oleoresin exudation pressure (OEP) and susceptibility has received considerable attention. Vité and Wood (1961) reported a strong correlation between low OEP in Pinus ponderosa Lawson and Dendroctonus brevicomis LeConte attack. Later studies, however, failed to support these findings (Wood 1962, Stark 1965).

Hodges et al. (1979) compared the physical properties of oleoresin from two relatively resistant species, Pinus palustris Miller and Pinus elliotii Engelm., and two relatively susceptible species, Pinus taeda L. and Pinus echinata Miller, to D. frontalis. They observed that P. elliotii resin had a very slow rate of crystallization and P. palustris had a high resin yield and high flow rate relative to the more susceptible species.

Studies on the monoterpene composition of xylem resin have demonstrated high variation, both within stands and between geographic regions (Hanover 1966). Hanover and Furniss (1966) found no consistent differences in monoterpene composition between Pseudotsuga menziesii var. glauca (Beissn.) Franco which had resisted attack by Dendroctonus pseudotsugae Hopkins and unattacked trees. Smith (1966) examined the resin of dead and surviving ponderosa pines, found a lower combined concentration of limonene plus myrcene in the former group, and also observed that D. brevicomis was less likely to enter stumps of trees which had a high limonene and total-resin content (Smith 1975). Stan­geon (1979) found higher concentrations of limonene in ponderosa pines from geographic areas which had historically been the sites of D. brevicomis outbreaks. Hodges et al. (1979) found no relationship between the monoterpene or resin acid composition of four southern pine species and their resistance to Dendroctonus frontalis Zimmerman.

In addition to their constitutive resin system, all conifers demonstrate a secondary, or hypersensitive, response to attack (Reid et al. 1967, Berryman 1969, 1972). This defense mechanism involves a series of metabolic processes by which the tree isolates the insect and fungi within a lesion of dead cells. The tree responds to invasion by local autolysis of parenchyma cells, the formation of traumatic resin ducts, and the production of secondary resin which contains increased concentrations of monoterpenes and phenolics (Reid et al. 1967, Berryman 1969, 1972, Shrimpton 1973, Russell and Berryman 1976, Wong and Berryman 1977, Wright et al. 1979). After cellular necrosis and the secretion of secondary resin, the phloem is no longer suitable for larval or fungal development. The induction of this response is not well understood, but it can be initiated by artificial inoculation with the beetles'
symbiotic fungi (Reid et al. 1967). The hypersensitive reaction does not occur in trees that are successfully colonized (Reid et al. 1967, Berryman 1969, 1972). This does not represent an inability to respond, however, but rather the exhaustion of the tree’s defensive abilities because of the high concentration of beetles involved in the successful attack (Raffa 1981).

The purpose of the present experiment is to examine the differences between trees resistant and susceptible to bark beetle attack. Previous studies on host resistance have involved comparisons of dead and living trees (Callaham 1955, Smith 1966, Reid et al. 1967, Berryman and Ashraf 1970), different geographic areas (Hansner and Furnes 1966, Sturgeon 1979), resistant and susceptible species (Hodges et al. 1979), or artificial circumstances (Smith 1975, Raffa 1981). To eliminate as many extraneous factors as possible, all test trees were living lodgepole pines, located in the same region and exposed to natural conditions. A series of assays on trees exposed to high intensities of beetle pressure was conducted. Under such conditions, it may be assumed that only the unusually resistant trees survived beetle infestation.

The purpose of the present study is to expand our knowledge of chemical changes which occur in the host during its active response to attack. Shrimpton (1973) compared the monoterpenic content of resinous sapwood on trees 5 weeks after they had successfully resisted natural attack with the nonresinous sapwood of killed trees and unattacked trees. In this investigation, we concentrated on changes in host chemistry which occur during the first week of response under controlled conditions.

The test system for this study consisted of the mountain pine beetle, *D. ponderosae*, its symbiotic fungi, *Europhium clavigerum* Robinson, and their primary host in the study area, lodgepole pine, *Pinus contorta* Douglast larotiafEngelmann.

### Materials and Methods

#### Sample Collection and Field Assays

Field experiments were conducted in the Umatilla National Forest in northeastern Oregon (Morrow and Umatilla Counties). This area is the site of a mountain pine beetle outbreak of several years duration during which over 2 × 10⁷ lodgepole pines were killed. Trees selected for study were at elevations ranging from 1,100 to 1,200 m. The flight period within this region is concentrated in late July and early August.

Test trees, each of which was at least 50 years old and 18 cm in diameter, were selected from two stands. One stand, located 17 km east of Ukiah, had been subjected to severe mountain pine beetle pressure during 1976 and 1977. Over 90% of the lodgepole pines of suitable age and size had been killed during this period, and consequently, the surviving individuals were considered to be highly resistant. Thirteen of these trees, each of which had pitch tubes demonstrating successfully resisted attacks, were assayed in this region. The second stand was located ca. 15 km west of Ukiah, and was situated at the leading edge of the outbreak. Fifty-seven unattacked trees were chosen from this area to provide approximately equal sample sizes of trees with large crowns and a periodic growth ratio greater than 1.0 and those with more narrow crowns and periodic growth ratio of less than 1.0 (Mahoney 1978). No diseased or mechanically injured trees were included in the sample.

A series of assays were performed on each tree in mid-July 1978, and their condition was examined in October 1978. Each tree was assayed as follows.

1. **Radial increment cores** were taken from each tree. The current growth rate was determined by measuring the total radial increment over the last 5 years, and the periodic growth ratio was obtained by dividing this figure by the growth of the previous 5 years (Mahoney 1978). Growth data from the plot east of Ukiah were not analyzed in this manner because of possible growth responses after the drastic “thinning” by the beetles.

2. **The rate of oleoresin exudation flow** was sampled for each tree, using a modification of Mason’s (1969) technique. A 1.1-cm (O.D.) cork borer was driven to the cambium at a slightly upward angle on the northern exposure of each tree at 1.2 m above ground. The borer was removed, and a 1.2-cm (O.D.), 50-ml, threaded vial was screwed into the hole. The quantity of resin present after 24 h was recorded. This procedure was performed on an additional seven trees in 1978 and 32 trees in 1979. The rate of crystallization was assigned on a four-point scale ranging from purely viscous (1) to completely crystallized (4).

3. **A section of phloem tissue (4 by 1.3 cm)** was removed from the northern aspect of each tree at a height of 1.2 m. The tissue was inserted into a capped vial and placed immediately into a portable thermocontaining dry ice. The samples were kept frozen until analysis.

4. **Adjacent to the site of phloem removal**, each tree was administered three inoculations with E. clavigerum by using the method described by Wong and Berryman (1977). The fungus was obtained from culture no. Colo. 453, U.S. Department of Agriculture (USDA) Forest Service Rocky Mountain Forest and Range Experiment Station, Ft. Collins, Colo., and was originally isolated from a *P. contorta* killed by *D. ponderosae*. One inoculation site was sampled 3 days after inoculation, and the remaining two sites were sampled after an additional 4 days. Upon sampling, the length of the lesion formed at the sapwood was recorded, and the phloem area containing the lesion was then excised and frozen as described above. Any flow of liquid resin which occurred immediately upon cutting the bark (i.e., where the resin content exceeded the absorbency of
the tissue was also collected.

Sample Analysis

For each tree the noninoculated phloem tissue and the tissue from one randomly selected 7-day inoculation were analyzed by gas-liquid chromatography. The tissue was finely chopped and then extracted in 6 ml of pentane with anhydrous CaCl₂ at room temperature for 18 h. P-cymene was used as an internal standard (Hodges and Lorio 1975) because this monoterpenes is absent or negligible in P. contorta (Smith 1964, Lotan and Joyce 1970, Shumilton 1973). Samples were evaporated as described by Burbott and Loomis (1967).

A 1-µl amount of extract was injected into a Perkin Elmer Sigma 3 chromatograph equipped with a flame ionization detector. The column consisted of a methyl silicone capillary tube (30 m by 0.25 mm) (Supelco, SP-2100). The helium flow rate was 0.61 cm³/min. The injector and detector temperatures were both 250°C. The temperature program began at 45°C, remained isothermal for 6 min., rose at 1°/min to 74°C, and then rose at 3°/min to 110°C. Data were recorded by means of an electronic digital integrator. Qualitative analysis was accomplished by comparison with the retention times of known standards and in each case verified by mass spectrometry. The latter procedure was performed by the Air Pollution Research Group, Department of Chemical Engineering, at Washington State University. Upon completion of analysis, each phloem sample was oven-dried and weighed.

Results

During 1978, 59% of all test trees in the stand west of Ukiah were killed by D. ponderosae. Of the test trees which survived the 1978 season, all but two survived during 1979 as well. Because the test trees were chosen to include equal numbers of thick-crowned and thin-crowned trees, with the former usually occurring in particularly good sites, total stand mortality was actually much higher. Only 10% of the trees greater than 18 cm DBH survived this 2-year period (David Tupper, personal communication). None of the 13 test trees in the eastern stand were killed during this period.

There was no significant difference in the current growth rate of trees which survived (7.39 ± 1.54 mm) or died (6.32 ± 1.27 mm) during this study. Resistant trees, however, had a periodic growth rate of 1.01 ± 0.13, whereas susceptible trees had a ratio of only 0.78 ± 0.08 (t = 3.07, p < 0.01). Similar results were obtained by Mahoney (1978).

The rate of oleoresin exudation flow (OEF) from punctured tissues did not differ between resistant and susceptible trees. In 1978, resistant trees had an average OEF of 8.5 ± 2.6 ml/day, and susceptible trees averaged 8.1 ± 4.1 ml/day (nonsignificant). In 1979, these values were 5.8 ± 3.3 and 5.4 ± 5.4 ml/day, respectively (nonsignificant). There was no relationship between the rate of resin crystallization and tree mortality.

The percent composition of the monoterpenes present in constitutive phloem is shown for surviving and killed trees in Table 1. There are no qualitative differences between these two groups. In addition, there are no significant differences in the proportions of any of the major (>1%) monoterpenes found in the uninjured phloem tissue of resistant and susceptible trees. Likewise, resistant and susceptible trees are nearly identical in their rank-order of monoterpen content. Of the 13 monoterpenes found to be present in lodgepole pine phloem, only three showed any differences, and each of these was below 1% total monoterpen content in either group. Such low levels of abundance are subject to high experimental error, so little importance can be attributed to these differences.

The monoterpene composition of P. contorta in northeastern Oregon is generally similar to that reported elsewhere (e.g., Smith 1964, Anderson et al. 1969, Lotan and Joyce 1970, Shumilton 1973). The β-phellandrene content is somewhat higher and the Δ3-carene content lower than that found in other regions. These differences probably reflect the ecologically isolated nature of the Blue Mountains and the poor dispersal ability of P. contorta seeds.

The percent composition for each of the monoterpenes found in the reaction resin of surviving and killed trees is shown in the right column of Table 1. There are no qualitative differences between these two groups, there are few significant differences in the relative proportions of the major monoterpenes, and their rank-order is in nearly total agreement. The reaction resin of resistant trees was somewhat higher in limonene, γ-terpinene, and terpinolene than that of susceptible trees, but each of these is a minor constituent.

The monoterpene composition of constitutive phloem and reaction resin showed no qualitative differences, but compositional changes did occur. There were significant increases in the percentages of α-pinene and limonene in the reaction zone, whereas Δ3-carene and sabine decreased (Table 2). Of these, only Δ3-carene and α-pinene are major constituents of the uninjured tissue.

The total monoterpen content of constitutive phloem was similar for resistant and susceptible trees (Table 3). The resistant trees, however, responded much more extensively to artificial inoculation than did susceptible trees. In most cases, removing the reaction tissue from resistant trees released a vigorous flow of resin from the wound site, whereas this response was much less pronounced or absent in living, susceptible individuals. The total monoterpen content of the reaction zones of trees which survived the beetle flight season was 6.8 times that found in the reaction zones of trees which were killed 1 to 3 weeks after sampling (Table 3). This difference persists even if the trees in the stand east of Ukiah are removed from the sample. The monoterpene content of reaction resin in surviving trees in the western stand was 88.99 mg/g (dry weight), and the same level of significance is maintained. The two
trees which died in 1979 ranked 23rd and 33rd among the 35 trees in their secretion of resin after artificial inoculation. All 70 trees responded to artificial inoculation by forming necrotic lesions and successfully confining the pathogen. During the first 3 days, the average length of lesion formation was 7.0 mm/day. During the remaining 4 days, the average vertical expansion was 2.4 mm/day. There were no differences in vertical lesion length between killed and surviving trees.

**Discussion**

The major difference between resistant and susceptible lodgepole pines is that the former respond more extensively after invasion of their phloem tissue by the pathogen *E. clavigerum*. Resistant trees secrete much greater quantities of terpenes around the inoculation site than trees which were later killed by *D. ponderosae*. Based on our results, the secondary wound response appears to be the most important defense mechanism of *P. contorta* to the *D. ponderosae-E. clavigerum* complex. The following six aspects of this response appear to be particularly relevant.

**Table 1.** Monoterpene content (% composition) of lodgepole pines resistant and susceptible to mountain pine beetle attack; statistical tests refer to differences between surviving and killed trees

<table>
<thead>
<tr>
<th>Monoterpene</th>
<th>Constitutive phloem resin</th>
<th>Wound reaction resin</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Resistant</td>
<td>Susceptible</td>
</tr>
<tr>
<td>α-Thujene</td>
<td>0.07</td>
<td>0.15</td>
</tr>
<tr>
<td>α-Pinene</td>
<td>2.58</td>
<td>3.36</td>
</tr>
<tr>
<td>Camphene</td>
<td>0.38</td>
<td>0.61</td>
</tr>
<tr>
<td>Sabinene</td>
<td>0.27</td>
<td>0.36</td>
</tr>
<tr>
<td>β-Pinene</td>
<td>7.42</td>
<td>8.84</td>
</tr>
<tr>
<td>Myrcene</td>
<td>1.34</td>
<td>2.07</td>
</tr>
<tr>
<td>α-3-Carene</td>
<td>6.44</td>
<td>5.08</td>
</tr>
<tr>
<td>Limonene</td>
<td>0.40</td>
<td>0.94*</td>
</tr>
<tr>
<td>β-Phellandrene</td>
<td>80.78</td>
<td>75.44</td>
</tr>
<tr>
<td>γ-Terpinene</td>
<td>0.29</td>
<td>0.42</td>
</tr>
<tr>
<td>Terpinolene</td>
<td>1.59</td>
<td>1.72</td>
</tr>
<tr>
<td>cis-ocimine</td>
<td>0.09</td>
<td>0.25**</td>
</tr>
<tr>
<td>trans-ocimine</td>
<td>0.36</td>
<td>0.81***</td>
</tr>
</tbody>
</table>

* See footnote to Table 1.

(1) It is a highly generalized response, there being a net increase in the abundance of all monoterpenes. This indicates that the attack site and the surrounding region are undergoing de novo synthesis of monoterpenes, receiving transported monoterpenes from adjacent tissues, or both, rather than undergoing chemical interconversions among constitutive products alone. Increased production of all monoterpenes suggests that the enzymes activated by the presence of *E. clavigerum* are those which catalyze pathways leading directly to the monoterpene precursors, rather than a particular enzyme or group of enzymes responsible for the production of a specific phytotoxicin.

(2) The response is quantitative rather than qualitative. Every tree was capable of initiating a defensive response and each fungal inoculation was successfully confined by its potential host. All but three of the susceptible trees and all but one of the resistant trees showed an increase in the concentration of monoterpenes after inoculation.

(3) The response is energy demanding (Wright et al. 1979). In pines, monoterpene synthesis occurs in the epithelial cells surrounding the resin ducts (Mirov 1945, Hanover 1966) and involves the utilization of translocated photosynthate in the form of stored sugars (Gerry and Hall 1935). Biosynthesis occurs via the mevalonic acid (MVA)-geranyl pyrophosphate pathway (Banthorpe et al. 1972), and three molecules of ATP are required for each

**Table 2.** Comparison of the monoterpene content (percent composition) of lodgepole pine resin from uninjured phloem and reaction lesions resulting from fungal inoculation

<table>
<thead>
<tr>
<th>Monoterpene</th>
<th>Constitutive phloem resin</th>
<th>Reaction resin</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Weight (%)</td>
<td>Weight (%)</td>
</tr>
<tr>
<td>α-Thujene</td>
<td>0.11</td>
<td>0.19</td>
</tr>
<tr>
<td>α-Pinene</td>
<td>2.92</td>
<td>4.97</td>
</tr>
<tr>
<td>Camphene</td>
<td>0.40</td>
<td>0.58</td>
</tr>
<tr>
<td>Sabinene</td>
<td>0.31**</td>
<td>0.10</td>
</tr>
<tr>
<td>β-Pinene</td>
<td>8.06</td>
<td>7.23</td>
</tr>
<tr>
<td>Myrcene</td>
<td>1.66</td>
<td>1.00</td>
</tr>
<tr>
<td>α-3-Carene</td>
<td>4.72***</td>
<td>2.49</td>
</tr>
<tr>
<td>Limonene</td>
<td>0.64</td>
<td>1.25*</td>
</tr>
<tr>
<td>β-Phellandrene</td>
<td>78.44</td>
<td>75.44</td>
</tr>
<tr>
<td>γ-Terpinene</td>
<td>0.31</td>
<td>0.42</td>
</tr>
<tr>
<td>Terpinolene</td>
<td>1.59</td>
<td>1.72</td>
</tr>
<tr>
<td>cis-ocimine</td>
<td>0.09</td>
<td>0.25**</td>
</tr>
<tr>
<td>trans-ocimine</td>
<td>0.36</td>
<td>0.81***</td>
</tr>
</tbody>
</table>

*See footnote to Table 1.

**Table 3.** Total monoterpene abundance (mg/g, dry weight) in the constitutive and actively responding phloem tissue of lodgepole pines resistant and susceptible to mountain pine beetle; Samples include flow of liquid resin when the bark was severed

<table>
<thead>
<tr>
<th>Class</th>
<th>Uninjured phloem tissue</th>
<th>Wound reaction tissue</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Class</td>
<td>Weight</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(mg/g)</td>
</tr>
<tr>
<td>Resistant</td>
<td>36</td>
<td>1.27</td>
</tr>
<tr>
<td>Susceptible</td>
<td>28</td>
<td>1.12</td>
</tr>
</tbody>
</table>

*See footnote to Table 1.
MVA utilized. Glycolysis provides both the energy and acetyl Co-A for these reactions (Croteau et al. 1972). Increasing the supply of sucrose available to Mentha piperita L. resulted in increased terpene production, indicating that the biosynthetic sites are normally energy deficient (Croteau et al. 1972). The major feature determining the extent of the wound response may be the quantity of stored energy available for the rapid synthesis of, and conversion to, compounds which render the tissue unfavorable to D. ponderosae or E. clavigerum development.

(4) The response is related to the overall vigor of the host. The induced production of monoterpenes was most extensive in trees with a periodic growth ratio equal to or greater than one. This indicates that trees which have not yet attained physiological maturity, and are growing under favorable conditions, are more resistant than trees with a declining growth rate due to age or environmental stress (Safranyik et al. 1975, Mahoney 1978). Accordingly, mortality due to bark beetle attack is less indicative of a genetic predisposition to attack, as in certain other plant-insect systems, than of the selective predation by beetles on the weakened members of the population.

(5) The response is rapid. The fastest rates of necrotic lesion formation occurred within the first 3 days after inoculation, and resinosis was usually apparent by this time. Furthermore, detailed studies of hypersensitivity in other plant-pathogen interactions have usually detected significant expression of the response within a few minutes to several hours after inoculation (e.g., Tani et al. 1975, Hadwiger and Adams 1978).

(6) The response is localized. No lesion formation or resinosis occurred away from the inoculation site. In addition, lesion development proceeds only as long as the pathogen continues to make progress (Wong and Berryman 1977, Raffa 1981). Consequently, this mechanism represents a highly conservative system, and energetic investment in defense is dictated by spatial and temporal needs rather than any "allocation" extending over the lifespan of the tree.

There were some qualitative differences in the chemical responses of resistant and susceptible trees to inoculation. Among resistant trees, the reaction resin contained a higher percentage of a-pinene than did the uninjured phloem resin (t = 2.73, P < 0.01) (Table 1). This alteration did not occur among susceptible trees. The concentration of limonene quadrupled in resistant trees following inoculation (t = 3.02, P < 0.01), while remaining unchanged in susceptible trees (Table 1). The latter result is biologically interesting, because limonene is the most toxic (Smith 1965, Coyne and Lott 1976) and repellent (Smith 1975, Bordasch and Berryman 1977) monoterpane to bark beetles; but again, caution must be exercised in interpreting results from compounds which occur at such low levels.

Several aspects of this system contribute to the high variation in the total quantity of resin shown in Table 3: First, high between-tree differences exist in the quantitative monoterpane content of the constitutive resin system. In addition to genetic differences, ecological factors such as light and temperature contribute to the quantitative variation of monoterpenes (Burbott and Loomis 1967). Second, monoterpane synthesis during the interaction between P. contorta and E. clavigerum is subject to higher variation than the constitutive resin. Phytoalexin synthesis in response to inoculation is generally characterized by very high between-plant differences. Third, the colonization behavior of bark beetles is likely to obscure some of the differences between resistant and susceptible trees. During the latter stages of colonization, there is generally a "switching" from the initial focus of attack to adjacent trees by the aggregated beetles (Gara and Coster 1968). Consequently, trees of high resistance are likely to be killed by very rapid attack if they happen to be near trees undergoing successful colonization. Finally, differences between locally co-evolved host-pathogen complexes from various areas may influence the response.

The quantity of defensive chemicals secreted in response to fungal inoculation represents the potential, but not necessarily the realized, ability of the host to inhibit successful pathogen development. That is, the antibiotic effect of the conifer is not a static component. Rather, the tree's ability to actively mobilize toxins is diminished as a function of the rapidly increasing attack density during aggregation (Raffa 1981). Consequently, the expressed response is determined by the interaction of two rates, the defensive metabolism of the host and the arrival rate of the beetles. The preformed resin system may be involved in altering these dynamics. Berryman (1972) proposed that the passive flow of preformed resin from severed ducts may mechanically delay the beetle, thus allowing the tree more time to respond actively. This is supported by the observation that beetles which are engaged in shovelling a copious flow of resin from their entrance sites are unlikely to elicit attraction (Raffa 1981). That is, trees which are entered by beetles and are not near other trees undergoing successful colonization are less likely to become the foci of aggregation if they exhibit high rates of resin flow. The potential role of the resin canal system in delaying or impeding attraction can be negated, however, by the "switching" effect of aggregated beetles from neighboring trees (Raffa 1981). In the present study, surviving trees had higher, but statistically insignificant, OEF rates than killed trees in both 1978 and 1979.

Of critical importance to our understanding of bark beetle population behavior is a more clearly defined concept of host availability. Based on these results, future investigations should concentrate on the influence of biotic, climatic, and edaphic factors on both the extent and intensity of dynamic wound responses and the initiation and rate of bark beetle
aggregation.

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