INTERACTING SELECTIVE PRESSURES IN CONIFER–BARK BEETLE SYSTEMS: A BASIS FOR RECIPROCAL ADAPTATIONS?

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Classical models of plant-insect coevolution have emphasized that related species of insects frequently exploit closely related groups of plants (Ehrlich and Raven 1964; Benson et al. 1976). Implicit in this concept is a series of adaptations and counteradaptations by both the host and the parasite. Such models, although descriptive of broad patterns in evolutionary time, do not address the ecological factors affecting individual fitness nor the genetic capacity for change. The purpose of this report is to concentrate on one aspect of coevolution, the phenotypic traits affecting plant and insect fitness, in one type of interaction. This is an essential first step before the heritability of the relevant features can be quantified.

Bark beetles (Coleoptera: Scolytidae), particularly species that colonize the stems of living trees, provide a useful model system for evaluating the extent to which reciprocal selective pressures may prevail in host-parasite interactions (Sturgeon 1979; Mitton and Sturgeon 1982a,b). Several aspects of their biology allow direct evaluation of how various traits affect plant and insect success.

1. Bark beetles are a major cause of conifer mortality in North America; S. Wood (1982, p. 3) estimated that they are responsible for 54% of the natural deaths of all mature trees. For many species, reproduction is contingent on the death of the tree (Berryman 1972; D. Wood 1972; Safranyik et al. 1975; Raffa and Berryman 1980, 1983a). Failure to kill all or part of the tree usually results in failure to reproduce caused by gallery abandonment, adult mortality, or brood intoxicification (Miller and Keen 1960; Berryman and Ashraf 1970; Amman 1975; Raffa and Berryman 1980, 1982a). Some species occasionally kill just the upper portion of the trunk, but these trees are often killed by subsequent attacks and/or secondary agents.

2. A number of the compounds present in the tissue of their normal hosts are toxic to bark beetle adults and their brood (Smith 1965; Reid and Gates 1970; Coyne and Lott 1976; Raffa and Berryman 1983b).

3. Within a particular geographical region, phloem-feeding scolytids that attack

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living trees are usually found in one or two major host species. Conversely, each host species is usually attacked by one or two particularly important lethal scolytids in a given region. This close association between host and insect is especially evident in the forests of the Pacific Northwest, where our research was conducted (Sturgeon and Mitton 1982; S. Wood 1982).

4. Individual trees within a species vary enormously in their suitability as potential hosts (Miller and Keen 1960; Rudinsky 1962; Wright et al. 1984). Colonizing beetles must locate and detect not only the proper species, but also the more susceptible individuals within the host population.

5. Much of the mortality expressed in scolytid life tables is host-related, particularly in location and colonization (Berryman 1968, 1973, 1982a; Coulson 1979; Wright et al. 1984). Host availability and suitability are usually considered the major factors affecting beetle population behavior (Reid 1963; Berryman 1973, 1976, 1978a, 1982a; Cole 1981; Amman 1984).

Our studies have concentrated on the physiological, behavioral, and ecological aspects of conifer–bark beetle interactions. In particular, we have examined two beetle-fungus-conifer systems in northeastern Oregon, northern Idaho, and northwestern Montana: the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, and its symbiotic fungi, *Ceratocystis clavigera* (Robinson-Jeffrey and Davidson) Upadhyay and *C. montia* (Rumb.) Hunt, infesting lodgepole pine, *Pinus contorta* var. *latifolia* Engelmann; and the fir engraver, *Scolytus ventralis* LeConte, and its symbiotic fungus, *Trichosporium symbioticum* Wright, infesting grand fir, *Abies grandis* (Douglas) Lindley. The fir engraver is found entirely within true firs, of which grand fir was the only representative in these stands. Of all trees killed by the mountain pine beetle, 95% are lodgepole pines, 4% are ponderosa pines, and 1% are from other species (McGregor 1985). Information from related conifer-bark beetle systems is included where applicable. Our objectives are to identify the insect and host traits that determine the outcome of individual beetle-fungus-conifer interactions, to determine how these conifer and beetle traits affect their respective reproductive success, and to describe how these traits interact to affect ecological coexistence and allow for evolutionary change.

### CONIFER AND BEETLE TRAITS ASSOCIATED WITH HOST RESISTANCE AND COLONIZATION SUCCESS

#### Life History and Population Dynamics

The life history of bark beetles consists of three rather distinct phases: migration, colonization, and development. Adult beetles emerge from dead brood trees, undertake a dispersal flight, and locate new hosts. The colonization phase, during which the beetles bore into the bark of selected trees, is characterized by rapid aggregation (D. Wood 1982). Because pheromones released by the excavating beetles are attractive to both sexes, successfully attacked trees are usually colonized by large numbers of beetles (Rudinsky 1962; Berryman 1972; D. Wood 1972; Raffa and Berryman 1983a). As beetles bore through the phloem, they transmit phytopathogenic fungi, which disrupt translocation and assist in killing
the tree (Mathre 1964; Horntvedt et al. 1983). If the tree cannot resist attack, beetle development proceeds. Mating, oviposition, and brood development occur within the phloem or outer bark. The newly eclosed adult beetles emerge through the outer bark and again disperse, completing the cycle.

Bark beetle populations often remain at low densities for long periods of time, during which they colonize only highly stressed trees (Rudinsky 1962; Cobb et al. 1968, 1974; Stark et al. 1968; Wright et al. 1979, 1984; Coulson et al. 1983). Droughts, windstorms, and other environmental disturbances, however, can suddenly increase the availability of weakened hosts, causing beetle populations to rise dramatically. Following the exhaustion of this breeding material, some species may then invade healthy trees. When this occurs, the beetle population expands rapidly and declines only after most of the host population has been exploited (Miller and Keen 1960; Rudinsky 1962). Other scolytid species are unable to overcome the resistance of vigorous hosts and usually remain restricted to decadent or unhealthy trees (Craighead et al. 1931; Rudinsky 1962; Atkins 1966; Berryman 1973, 1979, 1982b). In these species, population increases are directly related to the number of low-vigor trees and may not be strongly affected by beetle population density. Their host populations experience chronic low-level mortality that varies with environmental conditions.

Physiological Mechanisms of Conifer Resistance to Bark Beetles

Several features of conifer physiology can potentially interfere with bark beetle colonization and development. First, the cortical tissue of conifers contains several classes of terpenoid compounds, stored in resin canals or glands. One prominent class of terpenes, the monoterpenes, is toxic to a broad range of insects, including bark beetle adults, eggs, and larvae (Smith 1963; Berryman and Ashraf 1970; Reid and Gates 1970; Coyne and Lott 1976; Raffa and Berryman 1983b). Resin flow from these canals does not necessarily kill the adults of some Dendroctonus species, however, because they are able to tolerate the moderate levels of monoterpenes normally present in their hosts (Smith 1963). During entry, beetles remove resin from the entrance site, and the cortical monoterpenes dissipate into the atmosphere. Oviposition does not usually commence until the gallery is drained of resin, after which the eggs hatch and larval development can proceed normally.

In addition to excreting resins in situ, conifers also initiate a secondary induced defensive reaction following attack. In this case, wounded phloem and xylem parenchyma cells induce necrosis in neighboring cells, and a lesion develops around the beetle-fungus inclusion. Within this lesion, monoterpenes, sesquiterpenes, and phenolics accumulate in concentrations much higher than those occurring in uninfected tissue (Shrimpton and Watson 1971; Shrimpton 1973a; Wright et al. 1979; Raffa and Berryman 1982b,c, 1983b; Hain et al. 1983). These compounds are detrimental to beetle adults, brood, and symbiotic fungi at the concentrations produced. When this reaction is successful, the parasites are confined or repelled (Reid et al. 1967; Berryman 1969; Wong and Berryman 1977; Shrimpton 1978).

The various monoterpenes differ in their effects on beetles, and the more toxic compounds experience the greatest percentage increase during the induced re-
**TABLE 1**

<table>
<thead>
<tr>
<th>Host Species</th>
<th>Inoculating Organism</th>
<th>Defensive Property</th>
<th>Monoterpene</th>
<th>Level of Activity</th>
<th>% Increase During Response</th>
</tr>
</thead>
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<td><em>Pinus taeda</em></td>
<td>Ceratocystis minor (also Dendroc- tonus frontalis adults)</td>
<td>Toxicity to Limonene</td>
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<td>1&lt;sup&gt;b&lt;/sup&gt;</td>
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<td></td>
<td></td>
<td>α-pinene</td>
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<td>Camphene</td>
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<tr>
<td><em>Abies grandis</em></td>
<td>Trichosporium symbioticum</td>
<td>Repellency to Scolytus ventralis adults</td>
<td>Limonene</td>
<td>1&lt;sup&gt;c&lt;/sup&gt;</td>
<td>1&lt;sup&gt;d&lt;/sup&gt;</td>
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<td>Tricyclene</td>
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<td><em>T. symbioticum</em></td>
<td>Toxicity to <em>S. ventralis</em> adults</td>
<td>α-pinene</td>
<td>1&lt;sup&gt;e&lt;/sup&gt;</td>
<td>5&lt;sup&gt;d&lt;/sup&gt;</td>
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<td><em>A. grandis</em></td>
<td><em>T. symbioticum</em></td>
<td>Inhibition of <em>T. symbioticum</em> (white mycelium)</td>
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<td>Camphene</td>
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<td><em>T. symbioticum</em></td>
<td>Inhibition of <em>T. symbioticum</em> (brown mycelium)</td>
<td>Limonene</td>
<td>1&lt;sup&gt;e&lt;/sup&gt;</td>
<td>1&lt;sup&gt;d&lt;/sup&gt;</td>
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<td>Camphene</td>
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<td></td>
<td>Myrcene</td>
<td>5</td>
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<td><em>P. contorta</em></td>
<td><em>C. clavigera</em> (Europhium clavigerum)</td>
<td>Ovicidal to <em>D. ponderosae</em></td>
<td>Limonene</td>
<td>1&lt;sup&gt;f&lt;/sup&gt;</td>
<td>1&lt;sup&gt;a&lt;/sup&gt;</td>
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<td></td>
<td>α-pinene</td>
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</table>

* Sources.—a, Coyne and Lott 1976; b, Hain et al. 1983; c, Bordasch and Berryman 1977; d, Raffa and Berryman 1982c; e, Raffa et al. 1985 (LT90 at 83 ppm); f, Raffa and Berryman 1983b; g, Raffa and Berryman 1982b.

In table 1 we have compiled all the available data about compounds for which both biological activity and the rate of increase during induced responses are known. The monoterpene are ranked according to their level of activity and their relative rate of increase following controlled inoculation. These two ranking parameters are closely correlated, although the number of compounds involved per test is usually too small for statistical analysis. When the data from these tests are pooled and analyzed by Spearman’s coefficient-of-rank
test (Steel and Torrie 1960), the trend is highly significant \( p = 0.81, t = 7.57, P < 0.001 \). Selection on the host plants appears to have favored those biochemical alterations, at least in the monoterpenic fraction, that most adversely affect the insect herbivores. The available data with whole-resin extracts support this view. Shrimpton and Whitney (1968) found that sapwood from reaction tissue inhibited the growth of _Ceratocystis montia_ and _C. clavigera_ when incorporated into potato dextrose agar, but sapwood from nonreaction tissue did not. Likewise, Bordasch and Berryman (1977) found that reaction resin was more repellent than constitutive resin to fir engravers.

The preformed and dynamic defense systems operate in conjunction, rather than as independent processes (Berryman 1972). Resin flow from severed ducts can physically delay beetle progress, thus allowing the induced response time to proceed. In addition, a copious flow of resin can interfere with beetle chemical communication, thereby limiting the attack to a density well below the threshold of resistance (Berryman 1972; Raffa and Berryman 1980, 1983a). For example, although trees beyond the pheromone range of other trees being attacked have all the monoterpenic precursors required for pheromone synthesis (Raffa and Berryman 1982b, 1983a), only about half of the attacks on them by “pioneer” mountain pine beetles result in aggregation. The means by which resin flow prevents attacks from becoming attractive, however, is not clear.

Even though the relationship between host properties and survival under natural conditions is quite complex, the following generalizations can be made for the systems we have studied.

1. **Monoterpene concentration.**—Total constitutive (preformed) monoterpenic concentration in the phloem is not correlated with host survival, but the extent of total induced monoterpenic accumulation following invasion is a major factor in resistance (Wright et al. 1979; Raffa and Berryman 1982b,c).

2. **Monoterpene composition.**—The relative proportions of constitutive monoterpenes are not related to host survival. Following controlled inoculation, however, resistant trees undergo more-extensive changes in these proportions, particularly among the most toxic and most repellent monoterpenes (Raffa and Berryman 1982b,c).

3. **Oleoresin flow.**—The rate of resin flow from ducts is related to the survival of lodgepole pines, if only trees attacked by “pioneer” beetles are considered. If all trees are included, there is no statistical difference in resin flow between successfully and unsuccessfully attacked trees (Raffa and Berryman 1982b, 1983a).

4. **Chance.**—Trees adjacent to successfully attacked trees are more likely to become the foci of aggregation (Gara and Coster 1968), because an initial beetle “threshold of aggregation” may be needed to generate optimal chemical communication and beetles are already concentrated near the killed trees (Burnell 1977; Raffa and Berryman 1983a).

**Adaptations of Bark Beetles to Host Defense**

Bark beetles can reproduce in living trees despite host defenses by avoiding strong resistant responses and attacking only trees in a weakened condition, or by
overwhelming relatively resistant trees through mass attack. Within the family Scolytidae there exists a gradation along this continuum. “Secondary” or non-aggressive scolytids attack weakened trees, whereas “primary” or aggressive species can attack healthy trees (Rudinsky 1962).

The advantage of colonizing weak trees is that they do not exhibit extensive wound responses, and the environment is more readily made suitable for brood production (Shrimpton 1973b; Wright et al. 1979; Raffa and Berryman 1982b). Among the factors that weaken host-tree resistance are disease, mistletoe infection, age, wounding, defoliation, drought, and crowding (Rudinsky 1962; Safaranyik et al. 1975; Berryman 1976; Wright et al. 1979, 1984; Raffa and Berryman 1982b, c).

Certain costs, however, are incurred by orienting solely to weakened trees. First, such trees are relatively rare, and migratory losses can be extremely high during the search for suitable hosts (Atkins 1966). For example, Wright et al. (1984) found that mortality during dispersal and host finding was much higher among the relatively nonaggressive fir engraver than among the moderately aggressive Douglas-fir beetle. Second, weak trees of some species may have thin or poor-quality phloem; for example, phloem thickness and moisture in lodgepole pines are directly correlated with tree growth or vigor (Amman 1972; Berryman 1976; Mahoney 1978; Raffa and Berryman 1982a; Haack et al. 1984). In these cases the trees most suitable for brood production (i.e., those with thick phloem) may be the most healthy and resistant trees in the stand. Finally, severely weakened trees can be colonized by other less-aggressive beetle species, giving rise to intense interspecific competition (Stark and Borden 1965; Berryman 1973). Thus, the relatively aggressive mountain pine beetle is subjected to less interspecific competition during outbreaks (Cole 1981; Amman 1984) than is the fir engraver (Stark and Borden 1965; Berryman 1973). When aggressive species do attack severely weakened trees, they show poor competitive ability against secondary beetles (Berryman 1973; S. Wood 1982).

The ability of bark beetles to conduct mass attack is made possible by the oxidation of host terpenes to aggregation pheromones (Renwick and Vité 1970; Hughes 1973; D. Wood 1982). The extent to which conifer defensive responses progress is inversely related to the density of attacking beetles and to the phytopathogenicity of the fungi that they transmit for two reasons: (1) the capacity of the tree to contain beetle broods and fungi is limited (fig. 1); and (2) mass beetle attack can transform the potentially toxic environment into a favorable substrate. Thus, the absence of a host response under natural conditions does not mean that the tree is incapable of reacting, but rather that its potential to resist is overcome. This effect can be simulated under controlled conditions by inoculating trees with fungi vectored by the beetle and measuring monoterpene accumulation. The intensity of the induced response declines with increasing inoculum density (fig. 1). Moreover, the inoculum dose at which the defensive response for an individual tree becomes ineffective is directly related to the maximum potential response of that particular tree, varying widely within a population (Wright et al. 1979; Raffa and Berryman 1982b, c). The dose-response curves in figure 1 can be viewed as characterizing individual trees within a stand, or as average representatives of different stands, or as the average for a particular tree species.
EFFECT OF ATTACK DENSITY ON BROOD LOSS

\[ y = 26.3e^{-0.0015 \times x^{1.6}} \]
\[ r^2 = 0.99 \]

A

EFFECT OF MULTIPLE INOCULATIONS ON HOST RESPONSE

\[ y = 59.2e^{-0.00076 \times x^{1.58}} \]
\[ r^2 = 0.96 \]

\[ y = 41.6e^{-0.000139 \times x^{2.47}} \]
\[ r^2 = 0.97 \]

\[ y = 31.1e^{-0.000029 \times x^{2.42}} \]
\[ r^2 = 0.92 \]

B

Fig. 1.—Relationship between the defensive response of lodgepole pines and beetle attack density. A, The effect of the host in limiting brood production by mountain pine beetles. Left axis, Difference in brood production per female between beetles colonizing dead logs and living trees. Right axis, Percent brood loss to resinosis (data from Raffa and Berryman 1983a). (Figure redrawn from Raffa and Berryman 1983a, fig. 12. © 1983 by The Ecological Society of America.) B, Monoterpene accumulation (expressed in digitizer units) in response to controlled inoculation with *Ceratocystis clavigera*. Trees are grouped according to whether their response to single inoculation is high, average, or low (data from Raffa and Berryman 1983b).
As with avoidance behavior, there are certain reproductive costs of aggregation. At any attack density, the addition of more beetles decreases the food and space available per individual. Moreover, the first beetles to enter relatively resistant trees incur the risk of failing to elicit aggregation.

In summary, both aspects of colonization behavior, allelochemical avoidance and cooperative behavior, have relative advantages and disadvantages. Our hypothesis is that the pattern and extent of defense physiology in the host species, and its ability to resist and/or tolerate the beetle-fungal complex, determine the optimal beetle behavior.

EFFECTS OF HOST-MEDIATED SELECTIVE PRESSURES ON BARK BEETLE BEHAVIOR

We have examined and compared two very different host-parasite systems. The mountain pine beetle, clearly an ‘‘aggressive’’ species, undergoes extensive population eruptions during which lodgepole pine mortality often exceeds 90% (Amman and Baker 1972; Orr and Brown 1978). The fir engraver, however, colonizes only grand firs that are severely weakened by external environmental stresses (Struble 1957; Berryman 1973). Population increases of fir engravers are more localized and of shorter duration than those of mountain pine beetles, and they rarely kill more than 10% of their hosts in any given location. Both species, however, are the most important sources of insect-caused mortality in their respective hosts (Furniss and Carolin 1977).

Comparison of Defense Responses Encountered by Fir Engravers and Mountain Pine Beetles

The resistance mechanisms of grand fir and lodgepole pine differ in several ways. Pines have a highly developed primary resin system that beetles encounter as they first enter the tree. Firs, however, have limited primary defenses. Although they possess resin pockets and ducts in the cortex, these are avoided by attacking beetles (Ferrell 1983). A second difference is in their hypersensitive wound response. Both species are capable of dynamic defensive reactions in response to beetle attack, but lodgepole pine conversions are less extensive. Changes in monoterpene composition are significant only among the minor components, and only one compound, limonene, increases from trace amounts (<1%) to minor abundance (table 2). In both constitutive (uninjured) and reaction tissue of lodgepole pine, β-phellandrene and β-pinene make up almost 90% of the monoterpene fraction. In grand fir, however, the reaction tissue bears less resemblance to the environment originally selected by the beetle. Seven compounds that are present only as traces in constitutive phloem tissue are present in significant amounts (>1%) in the reaction tissue and form a total of over 17% of the monoterpene fraction (table 2). Whereas the constitutive monoterpene fraction contains over 90% α-pinene and β-pinene, this proportion in reaction tissue comprises six compounds. In addition, limonene, the most toxic and repellent of the monoterpenes (Bordasch and Berryman 1977), increased by 474% in grand fir as compared to 95% in lodgepole pine (Raffa and Berryman 1982b,c). Thus, fir
TABLE 2

COMPOSITIONAL CHANGES IN THE MONOTERPENE FRACTION OF TWO CONIFERS FOLLOWING INOCULATION WITH FUNGI

<table>
<thead>
<tr>
<th>Constitutive Phloem Tissue</th>
<th>% Composition</th>
<th>Reaction Phloem Tissue</th>
<th>% Composition</th>
</tr>
</thead>
<tbody>
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<td>Phloem Tissue</td>
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<td>A. <em>Pinus contorta</em></td>
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<td>2.9</td>
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<tr>
<td></td>
<td></td>
<td>Terpinolene</td>
<td>2.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Camphene</td>
<td>2.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Unknown no. 5</td>
<td>1.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Limonene</td>
<td>1.3</td>
</tr>
</tbody>
</table>

Note.—*Pinus contorta* was inoculated with *Ceratocystis clavigera* and *Abies grandis* with *Trichosporium symbioticum*. Monoterpenes representing less than 1% of the total are not shown.

Engavers are confronted with a more diverse chemical environment in resistant hosts than are mountain pine beetles.

Previous authors (Mattson et al. 1982; Schultz 1983) have argued that plants undergoing the greatest chemical changes are least suitable for phytophagous insects, an idea supported by our within-species comparisons of resistant and susceptible pines and firs (Raffa and Berryman 1982b). If a plant can change its composition rapidly, it is highly probable that some chemicals at some time will exceed the tolerance limit of the insect. Because the host environment, at least in terms of monoterpene content, is much less predictable for fir engravers, one would expect the evolution of detoxification mechanisms to be retarded.

The more diverse environment confronting fir engravers also includes differences between trees. Lodgepole pine normally grows in relatively pure (single-species), even-aged stands (Staheln 1943; Crossley 1956; Loope and Gruell 1973; Romme 1982). Trees also tend to be closely related, with lower isozyme variation than in most other conifers (Knowles 1980) and mean genetic distance within populations only one-tenth that normally found in higher plants (Wheeler et al. 1983). Grand fir, however, grows in mixed-species, mixed-age stands (Staheln 1943) that are genetically diverse (Hamrick et al. 1979).

A third difference in the defensive chemistry of these two tree species is their relative inhibitory effect on beetle-vectored fungi. Defensive chemicals from both tree species inhibit fungal growth, but grand fir resin inhibits *Trichosporium*...
**TABLE 3**

**INHIBITION OF FUNGAL GROWTH BY HOST RESIN**

<table>
<thead>
<tr>
<th>Fungus</th>
<th>Vector</th>
<th>Tree</th>
<th>Dose (ppm)</th>
<th>Growth Delay*</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ceratocystis</em></td>
<td>Mountain pine beetle</td>
<td>Lodgepole pine</td>
<td>1000</td>
<td>1.6&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td><em>C. clavigera</em></td>
<td>Mountain pine beetle</td>
<td>Lodgepole pine</td>
<td>500</td>
<td>1.3&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td><em>Trichosporium</em></td>
<td>Fir engraver</td>
<td>Grand fir</td>
<td>50</td>
<td>2.5&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>* Growth delay is the ratio of the period required for 90% growth on a PDA plate with and without host resin. Growth period calculated by probit analysis.</sup>

<sup>a Data from Shrimpton and Whitney 1968.</sup>

<sup>b Data from Raffa et al. 1985.</sup>

*symbioticum* more effectively, and at lower doses, than lodgepole pine resin inhibits *Ceratocystis clavigera* or *C. montia* (table 3). Thus, grand fir appears to be more efficient in containing the organisms that actually kill the plant, the phytopathogenic fungi.

Finally, lodgepole pine and grand fir can be viewed as having different functions along the general dose-response curve. High densities of attacking mountain pine beetles can completely eliminate the host resistance effect in most trees (fig. 1). Cole (1981) and Amman (1984) calculated that only around 1% of the brood are killed by resinosis in successfully attacked lodgepole pines. High-density attacks on grand fir are rather rare, but when they do occur, the plant resistance effect is still manifested, and both the tree and beetles often die. For example, Berryman and Ashraf (1970) observed that fir engraver broods died from resinosis in about 15% of beetle-killed firs. Wright et al. (1979) reported that the average attack density on trees in which fir engravers reproduced was 53.9 female beetles per square meter, but a single tree attacked by 378 female beetles per square meter completely intoxified the brood. This tree had responded to artificial inoculation by producing 35 times as much monoterpene as the other killed trees, and so was quite different from the typically selected host. By comparison, the highest attack density at which Reid (1963) observed any defensive effect by lodgepole pine was 108 attacks per square meter. Even so, 86% of the beetle gallery length remained free of resin in this tree.

**Relationship between Beetle Colonization Behavior and the Host’s Defense Mechanisms**

The defensive response of lodgepole pine is both qualitatively predictable (tables 2 and 3) and, at times, quantitatively moderate (Safranyik et al. 1975). Under these conditions, mountain pine beetles entering relatively healthy trees have a competitive advantage over conspecifics that select only a more limited range of severely weakened trees. Fir engravers, however, are confronted with a highly unpredictable environment within the host, and resistance is always very strong in healthy trees. Under these conditions, cooperative behavior is only
adaptive to the extent that slightly resistant trees can be included in the host range. Several features of the biology of the fir engraver and the mountain pine beetle appear to reflect this divergence in host-mediated selection pressures. These include responses to host chemicals, physiological tolerance of host toxins, and mechanisms that limit overcrowding.

Bordasch and Berryman (1977) found that all of the monoterpenes present in grand fir were repellent to fir engraver adults. Mountain pine beetles, on the other hand, are not strongly repelled by any host compounds. Instead, they arrest in response to the monoterpene \( \alpha \)-pinene (Renwick and Vité 1970) and feed equally on extracts from resistant and susceptible trees (Raffa and Berryman 1982a). The result of these different sensory responses is that the fir engraver avoids all but the most weakened hosts (Berryman and Ashraf 1970), whereas the mountain pine beetle enters trees having a much broader physiological range. When fir engravers are caged against healthy trees, for example, they will not initiate extended attacks and eventually die on the bark surface (Struble 1957; Berryman and Ashraf 1970; Scott and Berryman 1971; Raffa 1981). Caged mountain pine beetles, on the other hand, readily enter living lodgepole pines and often continue gallery excavation in trees that subsequently entomb and kill them (Raffa and Berryman 1980, 1982a,b, 1983a).

Berryman (1974) compiled data for fir engraver and mountain pine beetle attacks on living trees, and described a general form for the relationship between brood emergence and attack density. In both cases, reproductive success, expressed in terms of brood emergence per female, initially increased with attack density, reached a maximum, and then declined (fig. 2). The rising part of the curve is mainly caused by a diminishing ability of the host to intoxicate the brood, and the descending section is mainly caused by crowding. In the case of grand fir, optimal brood productivity occurred at about 44 engraver attacks per square meter, whereas lodgepole pines could still reduce mountain pine beetle reproductive success by about 50% at this attack density. Complete elimination of the host effect was not achieved in the average lodgepole pine until attack density reached about 87 attacks per square meter. This does not imply that grand fir is less resistant than lodgepole pine because killed trees are not a random sample of the host population. Rather, they represent members of the host subpopulation that elicit entry and continued excavation behavior. For example, we sampled the resistance capacity of lodgepole pines and grand firs by inoculating them with beetle-vectored fungi under controlled conditions before the beetle flight period. In our studies, the average defensive response of trees subsequently killed by mountain pine beetles was 30% that of the average member of the host population (Raffa and Berryman 1982a), but the average response of subsequently killed firs was only 6.8% of that of the average grand fir (Raffa and Berryman 1983a). Thus, fir engravers experience a cooperative effect, but it extends over a narrower range of attack densities and acts on a smaller proportion of the host population than the effect among mountain pine beetles.

This difference in cooperative behavior between the two species may also be expressed in their developmental cycles. Both beetles are primarily univoltine with relatively short-lived adult stages. However, emergence and flight occur over
a much shorter period in mountain pine beetle populations, with over 96% of the beetles flying within a 3-wk period in midsummer (Reid 1962). Fir engravers, on the other hand, fly throughout the summer months with 95% of the flight extending over an 8-wk period (Struble 1957; Ashraf and Berryman 1969). In the absence of strong cooperative behavior, there is presumably no advantage to synchronous flight. Instead, fir engravers are adapted to an opportunistic existence, responding to trees throughout the growing season as they become stricken by wind, lightning, root disease, etc.

Besides differences in behavior, *Dendroctonus* are also physiologically more tolerant of host resins that are *Scolytus*. We exposed fir engraver adults to monoterpene vapors using the same method that Smith (1965) used with the western pine beetle, *Dendroctonus brevicomis* LeConte (table 4). In each case, mortality was higher in *Scolytus*, despite the shorter observation period. The high quantities of preformed monoterpenes in pines may have contributed to this tolerance by *Dendroctonus*. The invasion of the living pine, but not the living fir, necessitates adaptation to high monoterpene levels, even in weakened trees (Raffa and Berryman 1982b). This is particularly true during the pre-aggregation phase of host entry, which can last several days (Raffa and Berryman 1980, 1983a). Selection may also favor increased tolerance when the chemicals in the reaction tissue are qualitatively similar to the preformed resins, as in lodgepole pine. The more variable response of grand fir offers less chance for physiological resistance to develop.
TABLE 4

TOXICITY OF MONOTERPENES TO *Scolytus* AND *Dendroctonus* ADULTS

<table>
<thead>
<tr>
<th>MONOTERPENE</th>
<th>Scolytusa</th>
<th>Dendroctonusb</th>
</tr>
</thead>
<tbody>
<tr>
<td>83 ppm</td>
<td>33 ppm</td>
<td>53 ppm</td>
</tr>
<tr>
<td>a-pinene</td>
<td>100</td>
<td>93</td>
</tr>
<tr>
<td>l3-pinene</td>
<td>100</td>
<td>93</td>
</tr>
<tr>
<td>-3-carene</td>
<td>93</td>
<td>56</td>
</tr>
<tr>
<td>Limonene</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>Myrcene</td>
<td>100</td>
<td>94</td>
</tr>
</tbody>
</table>

**NOTE.**—Mortality at 1 day for *Scolytus* and 4 days for *Dendroctonus*.

a Data from Raffa et al. 1985.
b Data from Smith 1965.

Although cooperative behavior enables mountain pine beetles to include healthy trees as a food source, mass attack can also limit the availability of nutrients for individual insects (Cole 1962, 1974; Berryman and Pienaar 1973; Berryman et al. 1985). The mountain pine beetle has developed more-complex mechanisms for minimizing the effects of overcrowding than has the fir engraver. First, mountain pine beetles limit the number of colonizers to the density required to kill and physiologically condition the tree. As host resistance is depleted, attractive pheromone emission decreases (Raffa and Berryman 1980, 1983a) and anti-aggregation pheromones may be produced (Rudinsky 1968). No such mechanism appears to regulate fir engraver colonization, which usually extends over 2 to 4 wk (Struble 1957; Ashraf and Berryman 1969). The frequency of fir engraver attacks is best described by functions indicating a continual decline in pheromones rather than a shutoff system (Berryman 1968; Berryman and Pienaar 1973).

Second, the number of mountain pine beetle eggs deposited by each female can be regulated according to attack density so that fewer offspring compete for the limited food resource and more larvae survive to pupation (Cole 1962; Raffa 1981). This inverse relationship between attack density and oviposition per female has also been observed in the southern pine beetle, *Dendroctonus frontalis* Zimmerman (Coulson et al. 1976; Fargo et al. 1978). The females that have not laid their full egg complement reemerge to attack new trees (Reid 1958a,b). This behavior has a selective advantage in species that cooperatively overwhelm host defenses, since each reemerging female increases the chance that an adjacent tree is turned into a breeding site. The number of fir engraver eggs deposited by each female, however, is independent of attack density (Berryman and Pienaar 1973). In this species, the cost of dense aggregation is directly transferred to brood survival. A species that relies on a very scarce and temporary resource (weakened or dead hosts) and that cannot greatly increase host availability by aggregated attack probably maximizes individual reproductive fitness by depositing the full egg complement in a stricken tree, even if this leads to increased competition and brood mortality.
are required to kill the host than can be supported by the available substrate (Cole and Amman 1969). Their "threshold of resistance," as estimated by monoterpane production per controlled inoculation, is lower than that of mature trees, but their thin phloem is less capable of supporting brood (Amman 1969, 1972, 1978; Safranyik et al. 1975). Such trees represent a poor habitat for the colonizing beetles because the average individual fails to replace itself (Cole 1962, 1974; Berryman 1974, 1978a,b; Coulson 1979). Thus, beetles that avoid such trees are at a selective advantage, and the trees are, in a sense, "resistant." Some pines do not fit this pattern, in that they are young and have thick phloem, but these very vigorous trees also have the most pronounced defensive responses (Shrimpton 1973b).

Except under postepidemic conditions, healthy young lodgepole pines are rarely killed by mountain pine beetles (Amman 1978). Likewise, most young grand firs are not suitable for colonization because of their moderate defensive capacity relative to their thin phloem. Severe stresses such as overstory competition or defoliation can alter this relationship, however, allowing some young firs to be killed by fir engravers.

Although healthy mature pines and firs constitute an increased food supply, their resistance capacity is high enough to make them an unfavorable resource (Safranyik et al. 1975; Shrimpton 1978; Raffa and Berryman 1982c). During this phase, cones are produced for several decades, and the tree remains a relatively unfavorable resource for colonization; that is, a successful attack requires more beetles than can be supported by the substrate. Once trees begin to decline physiologically, their resistance is reduced. Because old trees provide a substantial food source requiring relatively few beetles for a successful attack, beetle productivity in them is high, and orientation to such trees is adaptive. This orientation is mediated by physical (Rasmussen 1974), chemical (Cole et al. 1981), and visual (Shepherd 1966) cues associated with age. The result is successful host reproduction before beetle colonization and, consequently, stable coexistence.

The extent to which mortality at a particular age affects host reproductive fitness may also depend on the successional status of the tree. These effects are likely to differ for lodgepole pine and grand fir.

Lodgepole pine is predominantly, at least in the areas of our studies, an early-successional species. Following fires, it germinates from serotinous cones (Clements 1910; Crossley 1956; Lotan 1975) and grows rapidly to reproductive maturity (Crossley 1956; Tackle 1964). It is eventually replaced by more shade-tolerant climax species (except in very localized areas of low-quality soil and severe frost) such as Abies and Picea (Pfister and Daubenmire 1975; Romme 1982). In the event of fire, however, lodgepole pine can become reestablished.

Recent authors (Amman 1977; Peterman 1978; Geizler et al. 1980; Berryman 1982a; Stark 1982) have pointed out that severe outbreaks of mountain pine beetle can alter stand succession, thus preventing the local extinction of lodgepole pine. Beetle-killed stands may provide an abundant fuel source, which increases the likelihood, intensity, and extent of fires (Brown 1975; Romme 1982). A large fuel source is critical because restricted and low-intensity fires are not sufficient to eliminate Picea and Abies from the understory (Loope and Gruell 1973; Despain 1983). Following intense fires, understory Picea and Abies are killed, and any
CONIFER–BARK BEETLE ADAPTATIONS

In summary, the adaptive value of cooperative behavior is largely determined by the host’s defense system. Given the low likelihood of exhausting the defense system of healthy grand firs by mass attack, orientation away from token stimuli associated with resistance is adaptive for fir engravers. Because there is an appreciable likelihood of overcoming lodgepole pines by mass attack, orientation to healthy trees can be adaptive. Because of the trees’ primary canal system, beetles attacking unhealthy pines require some tolerance of host resin, a trait that may have served as an evolutionary pre-adaptation. Other beetle adaptations that appear to result from and/or contribute to cooperative behavior include synchronous flight (probably less so in multivoltine species), efficiency of egg deposition, and effective regulation of attack density. All these features may contribute to eruptive beetle outbreaks.

EFFECTS OF BARK BEETLES ON HOST REPRODUCTIVE SUCCESS

Despite the high rates of tree mortality sometimes caused by bark beetles, it is difficult to assess their importance as selective agents on host populations. We have identified certain host traits associated with tree survival, but little is known about the heritability of these characteristics. Some factors, such as monoterpane composition, are under strong genetic control (White 1983), but others, such as resin synthesis and flow rates, may simply be associated with external environmental conditions. Furthermore, all plants are subject to a wide variety of selective pressures, and defense allocation needs to be viewed within this context. Finally, the effectiveness of host physiological properties is relative to beetle population density. Therefore, simple models of adaptation and counteradaptation cannot fully explain selective pressures on trees, and quantitative factors must be considered at all levels of the interaction. To consider the effect of bark beetles on plant reproduction, a variety of demographic and ecological factors must be considered.

Consequences of Host Mortality

The effect of tree mortality on reproductive success depends on the age and ecological status of the individual. In many cases, cones may accumulate for several decades before successful attack, and the killed tree may be able to replace itself. For example, lodgepole pine starts producing viable seeds in dense stands (as in our studies) at 15–20 yr (Fowells 1965). At any given time, there are about 36,000 seeds per mature tree. Grand fir produces some seed at about 20 yr, and production increases with age. At any given time, there are about 3400 seeds per tree (Fowells 1965). Any loss of fitness from beetle attack must be considered in relation to already established seedlings and losses caused by the premature mortality of the parents.

Lodgepole pine and grand fir show the highest capacity for defense while they are of intermediate age, with lower responses before maturity and during over-maturity (Safranyik et al. 1975; Raffa and Berryman 1982c). However, young trees are not necessarily a favorable resource for beetle development. Typically, the defensive capacity of healthy young lodgepole pines is such that more beetles
overstory survivors from these species are unable to compete with reseeding by lodgepole pine (Staheln 1943). Within this feedback system, then, mountain pine beetles may contribute to the competitive fitness of their host.

We compiled physiological and ecological data from the literature in order to consider the age-specific effect of widespread *Dendroctonus ponderosae* outbreaks on *Pinus contorta* reproduction. The interspecific consequences of stand disturbance by fire are shown in table 5A, column 2. Depending on the time of the fire, *Larix, Populus, Pinus, Pseudotsuga, Picea,* or *Tsuga* will predominate. Before a stand is 20 yr old, lodgepole pine cone development is not extensive; thus, disturbances result in pure *Larix* or *Populus* stands and subsequently in climax *Picea-Abies* forests (Staheln 1943). However, fires occurring when a stand is 60 to 100 yr old yield pure lodgepole pine stands. Later fires yield mixed stands. If a major fire does not incinerate the stand before it is 150 yr old, lodgepole pines are usually eliminated and succession proceeds along a *Larix-Pseudotsuga* to *Picea-Tsuga* pathway (Habeck and Mutch 1973; Cattelino et al. 1979). The timing of fires also affects intraspecific competition among germinating seedlings. Peterman (1978) found that the number of lodgepole pine saplings produced per parent was optimal in stands that were incinerated at 80 to 90 yr of age. In younger stands, reproduction decreased because of reduced cone crops, whereas in older stands seeds became so abundant that intense competition resulted in a lower average offspring fitness (table 5A, column 3). These seedlings are largely the progeny of the incinerated trees in the stand because serotinous cones are not destroyed by fire and seeds can remain viable for several decades after tree death (Staheln 1943; Lotan 1975). In both analyses, then, lodgepole pine reproductive success is optimized when fires occur 80 to 100 yr after stand establishment.
The relationship between lodgepole pine defensive responses and age was described by Safranyik et al. (1975). Their data, expressed as the percentage of trees that can respond to fungal inoculation, are shown in table 5A, column 4. Defensive capacity remains high until trees are about 60 yr old, then declines rapidly. Less than a third of the trees over 100 yr old are capable of resisting attacks. If the decline in defensive responses is synchronous through even-aged lodgepole pine stands, outbreaks should occur every 80 to 100 yr, increasing the probability of lodgepole pine reestablishment and persistence.

Alternative relationships between lodgepole pine resistance and age would not promote host reestablishment. If the trees’ resistance persisted until they were 110 yr old, for example, the outbreak-fire phase of the cycle would be complete at about 115–120 yr (depending on the rate of beetle reproduction and fuel accumulation), and lodgepole pines would have a lower chance of becoming reestablished. If resistance declined before age 50, lodgepole pines would have to compete with the other early-successional species.

A widespread outbreak of fir engravers, on the other hand, could not promote grand fir reproductive success. The progeny of the killed trees would be outcompeted by those of the fast-growing, high seed-producing, early-successional species. Grand fir produces fewer seeds than most conifers and has the lowest rate of germination of any of its associates (Fowells 1965). It is shade-tolerant and cannot become established in open conditions when subjected to competition. Because a continual production of seeds over many years provides the greatest chance of success, the adaptive value of investment in both defense and reproduction persists throughout maturity. Large-scale disturbances would also be deleterious to the fir engraver, because several hundred years could pass before mature trees were again locally available.

The relationship between grand fir resistance and age is shown in table 5B. The decline in resistance occurs later and is less pronounced than in lodgepole pine. There is no sudden increase in the frequency of susceptible individuals, although monoterpenes accumulation per inoculation does decline with age (Raffa and Berryman 1982c). Except for very old trees, all but the most severely stressed grand firs are able to resist attack (Berryman 1969; Wright et al. 1979; Raffa and Berryman 1982c).

The data in table 5 do not prove that differences in allocation to resistance in lodgepole pine are age-related, nor that selective pressures exerted by the beetle are causal. Concurrent with the decline in resistance, lodgepole pines show reduced radial growth and other signs of decline (Shrimpton 1978). The data do, however, allow us to propose how mountain pine beetles reinforce the lodgepole pine–fire cycle in mechanistic individual-tree terms. First, after late-successional species are established in the understory, lodgepole pines capable of resisting bark beetle attack are no more likely to reproduce than are susceptible trees, because neither group can establish seedlings in the shade. Second, the likelihood and extent of fires is increased by the accumulation of dead trees (Heinselman 1981). Trees that survive an infestation and beetle-killed trees are both incinerated. In evolutionary time, trees that had invested primarily in reproduction by 100 yr of age were probably the most successful. Thus, the synchronous age-dependent decline in the resistance of lodgepole pine stands need not rely on group selection.
The view that host defensive and reproductive processes compete for the tree's available resources (Mooney et al. 1983) is supported by the high energy cost of monoterpenes production (Wright et al. 1979; Miller and Berryman 1985; Christiansen and Ericsson 1986), the energetically conservative nature of induced defensive responses (Berryman 1972; Wong and Berryman 1977; Raffa and Berryman 1983a), and the allocation of resin both to the stems, where it increases resistance to mountain pine beetles, and to serotinous cones, where it functions as a sealant (Clements 1910; Fowells 1965). Lorio and Hodges (1985) provided some evidence that the growth of southern pines is at the expense of defensive capability. These presumed trade-offs refer to within-tree processes. They do not necessarily predict an inverse relationship of defensive capability and seed production between trees, because photosynthetic capability and resistance are directly related (Mahoney 1978; Wright et al. 1979; Raffa and Berryman 1982a,b; Mitchell et al. 1983; Waring and Pitman 1983). The most vigorous trees may simply produce the most seeds, grow the fastest, and synthesize the highest levels of defensive chemicals.

**Effects of Physical Factors and Plant Community Structure on Selective Pressures Exerted by Bark Beetles**

Not all factors affecting beetle epidemiology are related to the physiology of host defense, but they need to be included when considering selective pressures. Like age and successional status, the physical environment and plant community structure can modify the impact beetles have on tree reproductive fitness.

Physical conditions affect beetle population densities both directly and indirectly. Low temperatures, for example, slow beetle development, limit the period of flight and oviposition (Safranyik et al. 1975), and cause high brood mortality (Amman 1977). Because host susceptibility is related to beetle population density, a given level of resistance probably confers different levels of protection throughout the host range. Likewise, acute stress factors that make trees susceptible to attack, such as water deficit, lightning, root pathogens, defoliators, and nutritional imbalance, vary in their frequency and occurrence throughout the host range. Schenk et al. (1976) found that the highest mortality from attack by *Scolytus ventralis* occurred in stands with understory compositions that reflect continually low soil moisture.

The lodgepole pine–mountain pine beetle system illustrates how biotic and abiotic factors may interact in different sites. Short intervals between fires and high mortality from mountain pine beetle attack commonly occur together (table 6, columns 2, 6). Although this correlation and the available data on cone serotiny and host resistance (table 6, columns 3, 4) are consistent with the hypothesis that increased susceptibility may be a fire-promoting trait in the sense of Mutch (1970), they are hardly definitive. For example, dry conditions directly increase the chance of fire regardless of their effect on beetle outbreaks. Conversely, where lodgepole pine occurs as a semi-climax species (Pfister and Daubenmire 1975), populations may simply be held low by cool temperatures (table 6, column 5).

Plant community structure is a major factor, other than host defense, affecting the behavior of beetle populations and, consequently, the selective pressure they may exert. Whether trees become susceptible to colonization in small groups each
TABLE 6

<table>
<thead>
<tr>
<th>Site Condition</th>
<th>Interval between Fires</th>
<th>Frequency of Cone Serotiny</th>
<th>Host Resistance</th>
<th>MPB Survival</th>
<th>Host Mortality from MPB</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>High</td>
<td>long</td>
<td>low</td>
<td>?</td>
<td>low</td>
<td>low</td>
</tr>
<tr>
<td>Low</td>
<td>short&lt;sup&gt;a&lt;/sup&gt;</td>
<td>high&lt;sup&gt;b&lt;/sup&gt;</td>
<td>?</td>
<td>high&lt;sup&gt;c,d&lt;/sup&gt;</td>
<td>high&lt;sup&gt;c,d&lt;/sup&gt;</td>
</tr>
<tr>
<td>Moisture</td>
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<td></td>
<td></td>
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<td>High</td>
<td>long</td>
<td>?</td>
<td>high</td>
<td>?</td>
<td>low</td>
</tr>
<tr>
<td>Low</td>
<td>short&lt;sup&gt;c&lt;/sup&gt;</td>
<td>?</td>
<td>low&lt;sup&gt;f&lt;/sup&gt;</td>
<td>?</td>
<td>high&lt;sup&gt;d,g&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

Sources: —<sup>a</sup> Arno 1980; <sup>b</sup> Lotan 1975; <sup>c</sup> Amman 1977; <sup>d</sup> Safranyik et al. 1975; <sup>e</sup> Romme 1982; <sup>f</sup> Shrimpton 1978; <sup>g</sup> Powell 1969.

Year or in very large groups all at once depends on the demography and genetic uniformity of the host population. As even-aged stands mature, the food supply for bark beetles increases, and populations may become large enough to overcome the defenses of most trees. In the case of mixed-age stands, individual trees decline as they age past maturity, producing a small but steady supply of susceptible hosts (Amman 1977; Coulson and Stark 1982). Likewise, environmental stress will affect a large proportion of the population if the trees are closely related, but responses are more variable where relatedness is low. Thus, all other things being equal, large-scale epidemics are much more likely in lodgepole pine stands (where seral) than in grand fir stands.

Both population patterns tend to be self-perpetuating. Outbreaks contribute further to the genetic and demographic uniformity of the stand, thereby reinforcing the endemic-epidemic cycle. Conversely, replacement of individual weakened trees promotes genetic and demographic diversity, further limiting beetle replacement rates.

Plant community structure also affects the role of chance in host survival. For example, firs often grow in multiple-canopied stands, and trees that are stressed by shading may be killed by fir engravers (Struble 1957). This diversity of light regimens is less pronounced in the even-aged post-fire stands of lodgepole pine (Crossley 1956; Fowells 1965). A large component of chance in lodgepole pine survival, however, is introduced by the "switching" behavior of mountain pine beetles. Proximity to another tree that succumbs to mass attack can greatly increase the likelihood of mortality (table 7). Because switching behavior is not observed in fir engraver populations, proximity to a killed tree does not reduce the chances of host survival, except in the sense that similar stress factors may be present. For example, firs infected by *Fomes annosus* (Fries) Cooke usually occur in groups (Partridge and Miller 1972; Cobb et al. 1974).

**INTERACTING SELECTIVE PRESSURES IN CONIFER—BARK BEETLE SYSTEMS**

The available data suggest that certain beetle and host traits exert varying degrees of reciprocal selection: individual trees vary in their defensive capacity,
and under natural conditions this capacity is directly related to survival; conversely, certain beetle behavioral traits directly exhaust host defenses or result in their avoidance. Furthermore, beetle reproductive success is decreased when these behaviors are artificially interrupted. However, the adaptive value of these traits needs to be considered relative to age, ecological status, and environmental conditions.

Rather than supporting the idea of strict deterministic pathways or single biochemical causes of coevolution, we feel that multiple feedback processes operating among groups of key traits best explain conifer–bark beetle interactions (fig. 3). According to this view, several plant or insect properties can collectively or separately contribute to or be subjected to the selective pressures shown in column 1 of the figure. Different patterns of coexistence can be favored among different conifer–bark beetle systems depending on the various trade-offs involved in colonization behaviors and host energy allocation. Consequently, eruptive population behavior may or may not emerge as a property of the system.

Several features of this model can be applied to coevolutionary theory in general. First, reciprocal selective pressures need not imply equivalent levels of intensity. The reproductive success of bark beetles is clearly related to selection, colonization, and utilization of host trees. But any effects of the beetle on conifer reproductive success depend on the condition of the host before the attack. For example, species that colonize dead and dying trees are attracted to fermentation products associated with general wood decay (Graham 1968; Moeck 1970) and show host-related patterns of adaptive radiation (S. Wood 1982), but they place no selective pressure on the host. This relationship changes if living trees are colonized. Because trees that cannot resist attack before achieving their reproductive potential are at a disadvantage, there is probably some directional selection. Likewise, these beetles must orient to particular physiological states of their hosts, not just host species. This requires more-specialized responses after landing (Rudinsky 1962; D. Wood 1972, 1982; Hynum and Berryman 1980; Raffa and Berryman 1980; Moeck et al. 1981).

Second, reciprocal selective pressures can be manifested directly and indirectly (or not at all, depending on the genetic control of the various traits involved). For example, features such as density-dependent oviposition and rapid pheromone-shutoff systems are more advantageous to individuals of species that colonize living hosts. Features such as synchronous flight may be favored by selective

### TABLE 7

<table>
<thead>
<tr>
<th>Distance from Nearest Mass-Attacked Tree</th>
<th>% Attacked</th>
<th>% of Attacked Trees That Died</th>
</tr>
</thead>
<tbody>
<tr>
<td>Within 6 m</td>
<td>100</td>
<td>90</td>
</tr>
<tr>
<td>Beyond 6 m</td>
<td>54.8</td>
<td>47.1</td>
</tr>
</tbody>
</table>

Note.—Data from Raffa and Berryman 1983a.
<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>MOUNTAIN PINE BEETLE/LODGEPOLE PINE</th>
<th>FIR ENGRAVER/GRAND FIR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Host Successional Status</td>
<td>Early</td>
<td>Late</td>
</tr>
<tr>
<td>Host Demography</td>
<td>High</td>
<td>Low</td>
</tr>
<tr>
<td>Host Defensive Response</td>
<td>Even-aged</td>
<td>Mixed-age</td>
</tr>
<tr>
<td>Host Defensive Chemicals</td>
<td>Low Biochemical Diversity</td>
<td>High Biochemical Diversity</td>
</tr>
<tr>
<td>Quantitative Host Responses vs Age</td>
<td>Moderate Fungal Inhibition</td>
<td>Strong Fungal Inhibition</td>
</tr>
<tr>
<td></td>
<td>Rapid Decline After Maturity</td>
<td>Gradual Decline</td>
</tr>
<tr>
<td></td>
<td>Extends from Moderate to</td>
<td>Extends from Low to Moderate</td>
</tr>
<tr>
<td></td>
<td>High Densities</td>
<td>Densities</td>
</tr>
<tr>
<td></td>
<td>Weak to Moderate</td>
<td>Weak</td>
</tr>
<tr>
<td></td>
<td>Moderate</td>
<td>Low</td>
</tr>
<tr>
<td>Mutualistic Effect of Aggregation</td>
<td>Mostly No Effect, Some Attractive, Limonene Repellent</td>
<td>All Repellent</td>
</tr>
<tr>
<td>Physiological Condition of Preferred Trees</td>
<td>Short</td>
<td>Long</td>
</tr>
<tr>
<td></td>
<td>Inversely Related to Attack Density</td>
<td>Not Related to Attack Density</td>
</tr>
<tr>
<td></td>
<td>Eruptive: extensive, spreading, self-driven</td>
<td>Gradient: local, non-spreading not self-driven</td>
</tr>
<tr>
<td></td>
<td>Increased</td>
<td>Constant</td>
</tr>
<tr>
<td>Host Species Range During Outbreaks</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Fig. 3.**—A summary of characteristics of two conifer–bark beetle systems. Plant and insect features that exert selective pressures on corresponding traits are indicated by the direction of the arrows in column 1. Specific examples are shown for the mountain pine beetle–lodgepole pine system and the fir engraver–grand fir system.

Pressures associated with cooperative attack, but they could also have arisen independently (from some aspect of diapause physiology, for example) and then, instead, facilitated the evolution of cooperative attack. Likewise, our results suggest that beetle communication systems are closely linked to their host-acceptance behaviors. There appears to be a continuum from beetles with moderately mutualistic communication systems that avoid all host monoterpenes, to species with more-cooperative behavior that are repelled only by high concentrations or active metabolic responses. To date, repellency from low concentrations of monoterpenes has been demonstrated only for such “nonaggressive” species as *Scolytus ventralis* (Bordasch and Berryman 1977), *Trypodendrum lineatum* (Olivier) (Moeck 1970), and *Hylurgops glabatus* (Zetterstedt) (Vasechko 1978). The need to overcome host resistance probably stabilizes bark beetle communication systems. For example, many of the fir engravers responding to pheromones reduce the reproductive success of the pioneer beetles (fig. 2), a relationship that seems unlikely to persist in evolutionary time (Alcock 1981). However, the beneficial effect of the early responders precludes selection against the emission of pheromones.

Third, selective pressures external to the plant–insect interaction can be critical. For example, the consequence of mortality on host fitness depends on intraspecific and interspecific plant competition. The conditions under which progeny
can most successfully compete may select for a particular pattern in defense. Likewise, beetle features such as density-dependent oviposition rates and reemergence cannot be entirely explained by the feedback processes shown in figure 3. Mating biology (Alcock 1981; Kirkendall 1983), weather (Coulsion 1979), and other factors are also involved. The physiology and genetics of microbial symbionts are perhaps the least understood components of the system. Their role extends from nutrient breakdown in the saprophagous species to pheromone synthesis and toxin production in the primary species (Brand et al. 1975, 1976; Hemingway et al. 1977). The development of such metabolic pathways by these microorganisms could have selected for subsequent beetle behaviors and host defensive responses (Whitney 1982).

Finally, the characteristics shown in the figure are not fixed traits but instead comprise a range of phenotypes among individuals in the population. This distribution need not remain static. One example may be the relative advantage of attacking healthy trees. Because aggressive species rely on the arrival of subsequent recruits to overcome resistance, individuals that orient away from healthy trees may be favored when population levels are low, but they may be less competitive when population levels are high. Differences in the type of host tree selected could explain why Amman (1984) observed resistant responses to mountain pine beetle attacks during outbreaks but not during periods of low density. Fir engraver behavior, however, seems to be more fixed. Wright et al. (1984) found that fir engraver populations increased in grand fir stands defoliated by Douglas-fir tussock moth larvae, but cases of attack abandonment increased sharply as the surviving trees returned to normal vigor. This difference could also explain why some aggressive species, such as the mountain pine beetle, broaden their normal host-species range during outbreaks, but less aggressive beetles such as the fir engraver and the spruce beetle, Dendroctonus rufipennis Kirby (Hard 1985), remain limited to a fixed host-species range (S. Wood 1982). This view presumes that the range of host cues eliciting entry behaviors is at least partially under genetic control and varies among individuals, an idea that has not yet been tested.

**SUMMARY**

Conifer-bark beetle interactions provide a useful model system for evaluating potentially reciprocal selective pressures between plants and insects. The phloem-feeding bark beetles that infest living conifer stems are a major source of host mortality, and their successful reproduction is usually contingent on the death of the tree. Trees respond to invasion by producing a series of localized secretions and biochemical alterations that can contain the insect and associated microorganisms. We describe the relative advantages and disadvantages of two beetle reproductive strategies: overwhelming trees with a synchronized mass attack; and selecting weakened trees that cannot offer strong resistance.

Differences in the defensive physiology of grand fir, Abies grandis (Douglas) Lindley, and lodgepole pine, Pinus contorta var. latifolia Engelmann, may be partially responsible for differences in the behavior of the fir engraver beetle,
Scolytus ventralis LeConte, and the mountain pine beetle, Dendroctonus ponderosae Hopkins, respectively. Both tree species react to controlled inoculation with fungal symbionts of the beetle by producing monoterpenes and other defensive chemicals that may or may not be present in uninjured tissue. Grand fir, however, undergoes a more extensive series of biochemical conversions than does lodgepole pine. The relative extent of these responses appears to have resulted in different optimal behaviors by the two bark beetle species. Because they are not strongly repelled by host monoterpenes, mountain pine beetles enter trees that can be made suitable only by the arrival of additional colonizers. Fir engravers are repelled by cues associated with strong defensive capacity and orient solely to weakened trees. Their aggregation behavior is somewhat cooperative, but it also includes elements of social parasitism.

Even though colonization by bark beetles usually leads to tree death, the effect on host fitness varies with age and ecological status. Because of factors affecting both resistance and substrate suitability, most trees are able to produce cones for several decades before attack. Where lodgepole pine is seral, there is probably little selection for resistance once late-successional species have grown into the understory. We examine the theory that a synchronous decline in resistance capacity among old trees in even-aged stands increases the likelihood of beetle epidemics and subsequent fires, thereby favoring reestablishment of lodgepole pine. Later-successional species, like grand fir, are apparently not favored by beetle outbreaks, and all age groups sampled seem physiologically capable of defending themselves against attack.

We discuss the interactions between beetle and conifer traits and whether these can affect reproductive rates. We propose a model in which several feedback processes operating among groups of traits, rather than strictly deterministic pathways or single biochemical causes, structure the plant-insect interaction. Finally, we discuss the general implications to coevolutionary theory.

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