

INDUCED DEFENSIVE REACTIONS IN CONIFER-BARK BEETLE SYSTEMS

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1 INTRODUCTION

Bark beetles (Coleoptera:Scolytidae) have been the object of intense study for several decades, primarily because of the severe economic problems that they pose. However, they also possess a variety of traits that make them extremely useful organisms for studying coevolution between plants and insects (Mitton and Sturgeon 1982, Raffa and Berryman 1987). Among the most important of these are beetle associations with symbiotic fungi, the ability to metabolically convert host allelochemicals into aggregation and antiaggregation pheromones, and kairomonal relationships with natural enemies and competitors (Waters et al. 1985). Bark beetles can impose strong selective pressures on host populations by killing large numbers of mature healthy trees. Induced defenses play a major role in tree survival, but counteradaptations by beetles can interfere with normal functioning of the tree's physiological responses. Interactions between tree metabolic processes and beetle behavior are shaped by environmental and genetic factors. The outcome of each colonization attempt is usually discrete: Either the cohort of attacking beetles kills the tree and reproduces successfully, or the tree resists attack and remains an unsuitable breeding substrate.

2 LIFE HISTORY AND BIOLOGY OF BARK BEETLES

Bark beetle development occurs entirely within the subcortical region of trees. Different species vary in the substrate they typically colonize. Species colonizing relatively healthy trees are called primary species because they are the first organisms to invade otherwise uninfested tissue, or aggressive species because they kill individuals capable of mounting some resistance (Rudinsky 1962). These terms can be used interchangeably, although there are some exceptions in which primary beetles are not particularly aggressive. Conversely, species that attack previously infested hosts or weakened trees are called secondary or nonaggressive species, respectively. Many other species are saprophytic, colonizing only dead trees or dead tree parts. All points along this continuum are represented among the Scolytidae.

Here I will concentrate on primary species that colonize main stems. The rate and extent of active defensive responses in these systems often determine whether the host lives or dies, and whether beetles successfully reproduce or are repelled. The principle genera in this group, *Dendroctonus*, *Ips*, and *Scolytus*, are primarily associated with conifers (Wood 1982).

The subcortical substrate can usually support only one generation of bark beetles. As a resource it is exhausted by the high beetle densities that typically kill the tree, and by numerous secondary insects and microorganisms that follow. Therefore, each adult must locate a new tree suitable for oviposition (Wood 1972).

As beetles bore into selected trees, they oxidize and/or synergize host

monoterpenes into aggregation pheromones that elicit landing by conspecifics of both genders (Renwick and Vite 1970, Borden 1984). These conversions are performed both by the beetles themselves, and by specialized bacteria and fungi present in the gut (Brand et al. 1975, 1976, Borden et al. 1986). Beetles also transport a species specific flora of phytopathogenic fungi that disrupt host translocation and assist in killing the tree (Mathre 1964, Whitney 1982). Mating, gallery construction, and oviposition occur in the phloem. Depending on host responses, beetle attacks may be discontinued before these activities are completed, lethally confined by induced reactions, or successful in killing the host. If the tree can be converted into a passive substrate by aggregating adults, eggs hatch and developing larvae feed on host phloem and bark. Nutrient uptake is facilitated by additional fungal, yeast, and bacterial symbionts. Pupation occurs in the bark through which emerging adults drill exit holes and resume dispersal. Recontamination of callow adults with microbial symbionts is an elaborate process, involving spinning and biting by the last-instar larvae, development of specialized fungal-containing structures termed mycangiae during pupation, and sometimes transport of phloem-limited phytopathogenic fungi by phoretic mites. Bearing fungal spores on specialized sporothecae, these mites attach to emerging beetles (Moser 1985). Because of these symbiotic relationships, the invading agent must be considered a complex of interacting organisms.

3 ROLE OF INDUCED REACTIONS IN CONIFER RESISTANCE

Conifer genera vary in the relative degree to which constitutive versus induced defensive properties confer resistance against bark beetle attack. Members of the genus *Pinus* contain an elaborate system of resin canals throughout the stem (Bannan 1936). Once beetles bore through the outer bark, they sever these canals and resin flows into the wound, thereby impeding their progress (Keen 1938). Duct resin contains monoterpenes that are toxic to a wide variety of insects and microorganisms (Brattsten 1983). These chemicals are also toxic to bark beetles, but apparently not at concentrations actually encountered in the constitutive resin of healthy hosts (Smith 1963, 1965). Once mass attack has commenced, beetles may shovel resin for several days or weeks before finally ovipositing safely (Raffa and Berryman 1983a).

Attempts to correlate aspects of either the constitutive or induced resin defenses of pines with survival during outbreaks have yielded mixed results. For example, physical properties of constitutive resin agree with interspecific rankings in susceptibility to the southern pine beetle, *Dendroctonus frontalis* (Hodges et al. 1979). Conversely, the likelihood of lodgepole pines, *Pinus contorta* var *latifolia*, surviving a severe mountain pine beetle, *D. ponderosae*, outbreak is better correlated with chemical aspects of the induced response than with any constitutive factor (Raffa and Berryman

1982a). Other studies have shown constitutive and/or induced properties to affect the likelihood of host survival; most evidence suggests that both are important (Vite and Wood 1961, Mason 1966, Mahoney 1978, Stark 1965, Hain et al. 1983, Gambliel et al. 1985, Hodges et al. 1985, Paine et al. 1985). The two systems probably function in an integrated fashion that minimizes the chances of beetle colonization success (Berryman 1972, Raffa and Berryman 1983a).

Other members of the Pinaceae have less pronounced resin systems (Bannan 1936). For example, *Abies*, *Tsuga*, and *Cedrus* species do not have a constitutive network of resin canals, but store pockets of resin in subcortical glands. Beetles avoid these glands when entering the tree (Ferrell 1983) and thus can tolerate the host environment. These tree species rely almost exclusively on induced reactions for defense (Berryman 1972, Wong and Berryman 1977, Russell and Berryman 1976, Wright et al. 1979, 1984, Raffa and Berryman 1982b). Some genera, such as *Picea*, and *Larix*, have intermediate constitutive resin systems, with lower duct densities, shorter duct lengths, and lower proportions of functional resin secretory cells within ducts than that which occurs in pines (Bannan 1936).

4 INDUCED CONIFER RESPONSES TO BARK BEETLE ATTACK

4.1 Histological Changes

Rapid cellular reactions are initiated within the host as soon as beetles enter the living tissue beneath the bark. Endogenous and exogenous elicitors diffuse from the wounded cells, resulting in a zone of killed tissue (Bernard-Dagan 1988, Berryman 1988, Cheniclet et al. 1988). An elliptical necrotic lesion forms in advance of the insect-fungal complex (Reid et al. 1967). The center of the lesion is filled with resin, which floods the beetle galleries (Fig. 1). The beetle-fungal complex may become confined within this reaction zone and cease development; in such cases the attack is contained.

Cells continue to die in advance of the beetle as long as the insect-fungal complex continues to progress, so lesion length varies (Wong and Berryman 1977, Raffa and Berryman 1983a, Lieutier and Berryman 1988). Under controlled-inoculation conditions, lesion expansion is sigmoidal with time. Subsequent wound periderm formation protects the living tissue from the killed cells. A layer of nonsuberized impervious tissue prevents the movement of potentially diffusive materials into healthy plant tissue (Hain et al. 1983, Lieutier and Berryman 1988). The wounded area then heals over as new tissue is laid down during the next several years. These scars remain in the growth rings for the rest of the tree's life (Ferrell 1973).

4.2 Chemical Changes

A major feature of host response to bark beetle-fungal attack is the broad array of chemical groups involved in the defense. Table 1 summarizes con-



Figure 1 Induced response of lodgepole pine to mountain pine beetle attack. Note the necrotic lesion and pronounced resinosis about beetle gallery. The attacking beetle is killed within the reaction tissue, and adjacent tissue remains undamaged.

ifer-scolytid-fungal systems for which such changes have been quantified. Although some chemical moieties have been more intensely studied than others, it is clear that no one group is totally responsible for halting the successful development of the invading organisms.

The most thoroughly studied chemical responses to bark beetle attack occur in the monoterpene fraction. Total monoterpene content within the reaction zone increases by about 100-fold within a few weeks. Monoterpenes accumulate exponentially with time during the early stages of response (Raffa and Berryman 1982b).

In addition to the rapid increase in total monoterpene content, changes in the relative proportions of monoterpenes may also occur (Russell and Berryman 1976, Raffa and Berryman 1982a,b, Ferrell 1988). That is, each monoterpene increases in an absolute sense, but some are synthesized and transported more extensively than others. The degree to which these qual-

TABLE 1 Summary of Chemical Changes Occurring in Conifer Subcortical Tissue Following Natural and/or Simulated Attack by Primary Bark Beetles^a

System			Monoterpenes		Resin Acid Content	Increased and de novo Phenol Accumulation	Sugar Content	References
Host	Beetle	Fungus	Content	Altered Ratios				
Pc	Dp	natr. atk.	4, 3.8	+	1.3	+	0.3, 0.8	1, 2
Pc	Dp	Cc	48.2, 2.6, 27	+	3.0	+	0.8	2-4
Pt	Df	Cm	>500, 94.5	+	58.8		0.26	5-8
Ppa	Df	Cm	533.3	+			0.17	6, 7
Pr	Ip	Ci	+					9, 10
Pr	Dv	Lt	+					11, 12
Pb	Ip	Ci	+					9, 10
Pb	Dv	Lt	+					11, 12
Ag	Sv	Ts	25.6	+		+		13-17
Ag	Sv	natr. atk.	+	+				15
Pa	It	Cp	15					18
Ppi	Tp	V	60 ^b		60 ^b			19

^a Contents of monoterpenes, resin acids, and sugars are expressed as ratios of reaction to constitutive concentrations. Where an increase or decrease was determined but an absolute value is not available, a plus or minus is indicated, respectively. *Note:* Because of different sampling and analytical methods used by different researchers, comparisons of absolute values cannot be made between species. If several values are available for one system, each is included.

^b Includes all terpenes.

Abbreviations. Host: Pc, *Pinus contorta*; Pt, *P. taeda*; Ppa, *P. palustris*; Pr, *P. resinosa*; Pb, *P. banksiana*; Ppi, *P. pinaster*; Ag, *Abies grandis*; Pa, *Picea abies*. Beetle: Dp, *Dendroctonus ponderosae*; Df, *D. frontalis*; Dv, *D. valens*; Ip, *Ips pini*; It, *I. typographus*; Sv, *Scolytus ventralis*; Tp, *Tomicinus piniperda*. Fungi: natr. atk., natural attack; Cc, *Ceratocystis clavigera*; Cm, *C. minor*; Ci, *C. ips*; Cp, *C. polonica*; Lt, *Leptographium terebrantis*; Ts, *Trichosporium symbioticum*; V, *Vetricliadiella* spp.

References. 1, Shrimpton 1973a; 2, Miller et al. 1986; 3, Raffa and Berryman 1982a; Raffa and Berryman 1983b; 4, Shrimpton and Watson 1971; 5, Hain et al. 1983; 6, Cook and Hain 1985; 7, Cook and Hain 1986; 8, Gambliel et al. 1985; 9, Raffa and Smalley, 1988a; 10, Raffa and Smalley 1988c; 11, Raffa and Smalley 1988b; 12, Raffa and Smalley, unpublished data; 13, Russell and Berryman 1976; 14, Wright et al. 1979; 15, Raffa and Berryman 1982b; 16, Wong and Berryman 1977; 17, Ferrell et al. 1988; 18, Christiansen and Horntvedt 1983; 19, Cheniclet et al. 1988.

NOTE: The designation of most *Ceratocystis* and *Trichosporium* associated with Scolytidae has been changed to *Ophiostoma*. The older designations are retained here to facilitate literature review.

itative changes occur varies between tree species. In general, qualitative changes are more pronounced in *Abies* than in *Pinus* (Raffa and Berryman 1987). Interestingly, aggressive colonization behavior has not evolved among scolytids that colonize *Abies*. Such extensive changes in host chemistry during induction may lower the relative advantage to beetles that attack healthy trees (Raffa and Berryman 1987).

A complex of other chemical conversions occurs during induction, most of which are associated with the mevalonic acid or phenylalanine pathways. Resin acids and other oxygenated terpenes, sesquiterpenes, and phenolics undergo both qualitative and quantitative changes (Shrimpton 1973a,b, Wong and Berryman 1977, Raffa and Berryman 1983b, Gambliel et al. 1985).

4.3 Biological Effects

In cases where induced defensive responses are successful, the beetles and their symbiotic fungi are unable to develop. The beetles usually leave the

tree, and the only evidence of their colonization attempt is the necrotic lesions described previously. If beetles are not soon joined by a sufficient number of other beetles to overwhelm the tree's defenses, the galleries become flooded, few eggs hatch, and those larvae that do eclose construct very short mines before dying. The adults are also eventually trapped and killed in a thick mass of resin (Fig. 1).

Chemicals that accumulate during defensive reactions are largely responsible for the failure of beetles and fungi to become established. Extractives from induced but not constitutive lodgepole pine phloem inhibit the growth of *Ceratocystis clavigera* and *C. montia*, the two major fungal symbionts of *D. ponderosae* (Shrimpton 1973a,b). Likewise, resin collected from induced reaction tissue is more repellent to the fir engraver, *Scolytus ventralis*, than resin from constitutive glands (Bordasch and Berryman 1977). Paine et al. (1985) simulated the effects of reaction tissue on *D. frontalis* by inducing responses on living trees, allowing defensive reactions to proceed for 6 weeks, and then forcing beetles to colonize these trees after felling. They found higher adult mortality in induced than control tissue and reproduction was reduced by 56%.

Purified components of reaction tissue have been shown to affect the invading complex in several ways. For example, synthetic monoterpenes

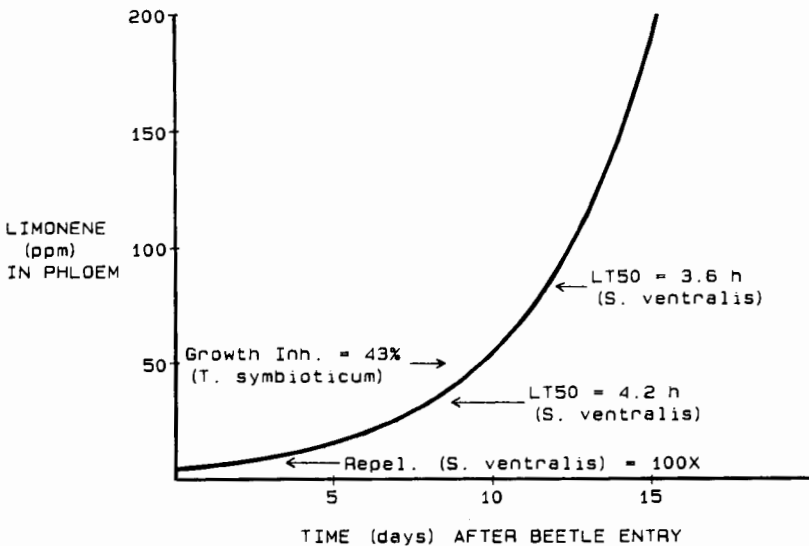


Figure 2 Effect of *Abies grandis* allelochemical transport and synthesis during an induced response to beetle attack on beetle behavior, survival, and symbionts. The accumulation of limonene through time is shown by the solid line fit to data from Raffa and Berryman (1982b). At various concentrations, results of beetle and fungal assays with synthetic limonene are shown (Bordasch and Berryman 1977, Raffa et al. 1985).

are toxic (Smith 1963, 1965, Coyne and Lott 1976, Raffa et al. 1985) and repellent (Bordasch and Berryman 1977) to adult beetles, ovicidal (Raffa and Berryman 1983b), and inhibitory to associated fungi (Cobb et al. 1968, Raffa et al. 1985) at concentrations present in reaction tissue. The significance of chemical changes induced by beetle attack in reducing the suitability of selected tissue is illustrated in Figure 2. The accumulation of limonene in *A. grandis* phloem following a controlled inoculation is shown through time, and a sampling of results from various bioassays are indicated along the curve. For example, an exposure of only 4.2 h to the concentration of limonene that is present 7 days after inoculation killed half of *S. ventralis* adults. All died within 22 h. The concentration of limonene present at this stage is also high enough to greatly reduce the growth of the fir engraver's most virulent symbiotic fungus, *Trichosporium symbioticum*. A single attack is

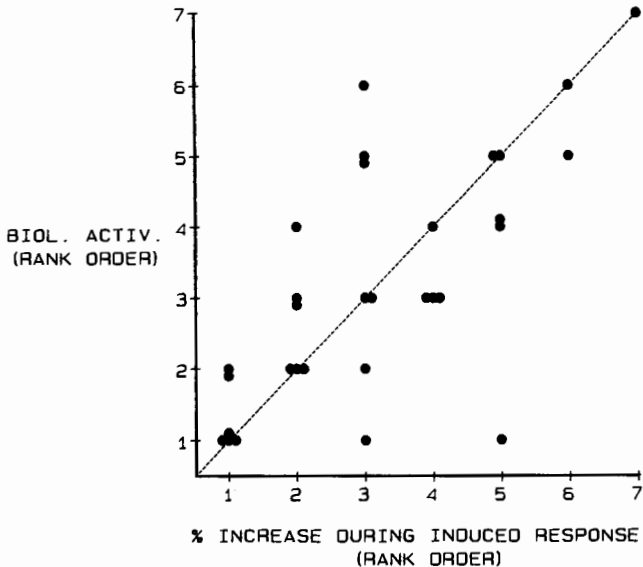


Figure 3 Disproportionate increase of monoterpenes most deleterious to bark beetles during conifer subcortical induced responses. For all systems where both compositional changes during induction and biological effects of synthetic materials are known, the relative increases are ranked along the abscissa and the relative biological activities are ranked along the ordinate. The dashed line indicates the hypothetical perfect correspondence: Spearman's coefficient of rank = 0.82, $t = 7.57$, $p < .001$. Chemical data are from *Pinus taeda* (Hain et al. 1983), *Abies grandis* (Raffa and Berryman 1982b), and *P. contorta* (Raffa and Berryman 1982b). Biological data include toxicity to *Dendroctonus frontalis* (Coyne and Lott 1976) and *Scolytus ventralis* (Bordasch and Berryman 1977), ovicidal effects against *D. ponderosae* (Raffa and Berryman 1983b), and fungistatic effects against *Trichosporium symbioticum* (Raffa et al. 1985).

unlikely to persist even this long, however, because the concentration of limonene in the phloem 3 days after attack is sufficient to repel most adults. Although Figure 2 shows the effects of only one monoterpene for simplicity, the total defensive profile of the tree is further augmented by corresponding increases in seven additional major monoterpenes, phenolics, and possible synergistic interactions. In summary, the invasion of the *S. ventralis*-*T. symbioticum* complex causes changes in a healthy host that eventually render the substrate intolerable to bark beetles.

This relationship between defensive efficacy and conformational changes during induction applies to several compounds and several conifer-scolytid systems. Raffa and Berryman (1987) summarized all of the published data where both proportionate changes in host monoterpenes during induction and biological effects of the purified compounds were known. In general, those monoterpenes most deleterious to beetles and their symbionts undergo the largest proportionate increases during induced reactions (Fig. 3). This conclusion is strengthened by the large number of independent studies from which these data were generated, and the variety of conifer-scolytid systems and biological modes of action represented. Interestingly, Blanche et al. (1985) found that the monoterpene content of lightning-struck trees differs from constitutive tissue in a pattern almost exactly opposite of that produced during induced reactions. Their results are ecologically important because lightning-struck trees are highly susceptible to bark beetle attack (Coulson et al. 1983).

Very few bioassays have been conducted with purified oxygenated or higher terpenes, phenolics, and combinations. Such studies are needed before we can fully characterize the effects of induced chemical conversions, because these groups are known to possess insecticidal and fungistatic properties.

5 ELICITATION OF INDUCED RESPONSES

5.1 Biotic and Purified Elicitors

The question of what actually initiates host defensive responses has been addressed by a progression of studies from observations with intact beetle-fungal complexes to purified biochemical probes. Reid et al. (1967) reported necrotic lesions and resinosis associated with naturally resisted mountain pine beetle attacks. Similar observations have been made with every host-beetle system examined to date. Subsequent studies demonstrated that inoculation with fungi vectored by bark beetles can induce responses that are morphologically and chemically similar to naturally occurring defensive reactions (Shrimpton 1973a,b, 1978, Raffa and Berryman 1982b, Hain et al. 1983, Cook and Hain 1985, Miller et al. 1986). The similarities between host responses to controlled fungal inoculations and natural attack are illustrated for two systems in Table 2.

TABLE 2 Comparison of Host Responses to Naturally Resisted Beetle Attacks and Simulated Attack by Inoculation with Fungal Symbiont^a

System	Parameter	Natural Attack	Fungal Inoculation	Constitutive
Ag-Sv-Ts ^b	% Tricyclene	0.54	0.38	1.4
	% α -Pinene	46.39	33.85	48.1
	% Camphene	0	2.26	1.2
	% β -Pinene	30.46	24.35	42.1
	% Myrcene	14.71	14.54	4.5
	% Sabinene	0	8.72	2.2
	% δ -3-Carene	2.83	2.86	0.3
	% Limonene	2.33	1.32	0.23
	% β -Phellandrene	0.59	3.28	0.01
	% Terpinolene	0.98	2.61	0.17
Pc-Dp-Cc ^c	Monoterpenes (mg/g)	9.2	7.4	2.4
	Soluble sugars (mg/g)	53.9	58.9	67.8
	Starch (mg/g)	15.2	15.5	12.5

^a Abbreviations as in Table 1. No comparisons between columns 3 and 4 are significant at $p < .05$.

^b Raffa and Berryman 1982.

^c Miller et al. 1986.

Comparisons between fungal-inoculated and aseptically injured tissue show that simple physical damage to host cells causes little monoterpene accumulation and no proportionate changes in chemical constituents (Table 3). Therefore, the induced reaction is not a mere wound response. Likewise, inoculations with killed fungi yield less pronounced host responses than with living inoculum (Stephen and Paine 1985, Gamliel et al. 1985, Raffa and Smalley 1988a,b). Depending on the fungus and tree involved, these reactions may be equivalent to aseptic-wound reactions, or intermediate between mechanical wounds and living inoculum. Thus, fungal cell wall constituents are not sufficient to induce a full reaction, and products associated with active fungal metabolism are probably also involved.

A beetle-vectored fungus can induce different levels of reaction in different host species. Conversely, a host species can react differently to various fungal associates of the major bark beetle species that colonize it. It is difficult to generalize at this time, but certain trends are apparent. First, trees respond more extensively to fungal symbionts of those bark beetle species that normally colonize them (Lieutier and Berryman 1988). For example, grand fir, *Abies grandis*, responds actively to fungal symbionts of the fir engraver, but not to symbionts of the mountain pine beetle. Mountain pine beetle symbionts induce active responses in lodgepole pine, but not in the nonhosts *Thuja plicata*, *Larix occidentalis*, and *Pseudotsuga menziesii*. Lieutier and Berryman (1988) proposed that constitutive chemicals or other forms of incompatibility prevent fungal establishment in nonhosts. A second

TABLE 3 Comparisons of Conifer Responses to Aseptic Wounds and Fungi Vectored by Bark Beetles^a

System	Monoterpenes						References
	Content		Altered Ratios Mech. ^b	Resin Acid Content		Lesion Formation Mech/Inoc	
	Mech/Const	Mech/Inoc ^b		Mech/Const ^b	Mech/Inoc ^b		
Pc-Dp-Cc	2	0.16					1
Pt-Df-Cm	1.7	0.017, 0.002		1.72	0.0098	0.18, 0.29	2-4
Pr-Ip-Ci	>1	<1	—			0.27	5, 6
Pr-Dv-Lt	>1	<1	—			0.35	6, 7
Pb-Ip-Ci	>1	<1	—			0.52	5, 6
Pb-Dv-Lt	>1	<1	—			0.65	6, 7
Ppa-Dp-Cm						0.56	8
Ag-Sv-Ts	1.42	0.28	—			0.22	9
Ppi-Tp-V		0.08			0.08		10

^a Contents of monoterpenes and resin acids are expressed as ratios of mechanical to inoculum treatment concentrations. *Note:* Because of different sampling methodologies, time intervals, and analytical methods, cross-comparisons are not intended.

^b Negative signs indicate no difference between monoterpene ratios present in constitutive and mechanically wounded tissue.

Abbreviations. As in Table 1. Ppo, *Pinus ponderosa*; Db, *Dendroctonus brevicornis*; Mech, mechanical wound; Const, constitutive tissue; Inoc, inoculation.

References. 1, Miller et al. 1986; 2, Gambiel et al. 1985; 3, Paine et al. 1985; 4, Hain et al. 1983; 5, Raffa and Smalley 1988a; 6, Raffa and Smalley, unpublished data; 7, Raffa and Smalley 1988b; 8, Paine 1984; 9, Raffa and Berryman 1982b; 10, Cheniclet et al. 1988.

trend is that mycangial fungi induce less extensive responses than external symbionts (Paine and Stephen 1987a).

Although fungi alone have been used to induce responses similar to fungal-beetle complexes, I am not aware of any studies using aseptic beetles. Whether beetles alone can induce these responses is academic, however, as all beetles in nature are contaminated.

A number of chemicals have been identified that can elicit responses the same as or very similar to the defensive reactions described previously. Shrimpton (1978) found that cellulolytic enzymes such as proteinases, pectinases, and cellulases cause hypersensitive lesions in lodgepole pine. Phytopathogenic fungi produce such materials during cellular invasion, and presumably resistant hosts respond to their presence by initiating a series of biochemical events that culminate in successful defense.

Miller et al. (1986) found that chitosan, a common fungal cell wall fragment, and proteinase inhibiting inducing factor (PIIF), a pectic fragment released by tomato leaves during wounding that elicits systemic induced reactions (Green and Ryan 1972), induce monoterpene accumulation, soluble sugar reduction, elevated starch titres, and lesion formation in lodgepole pine. Moreover, the changes induced by inoculation with living mountain pine beetles, their symbiont *C. clavigera*, and PIIF were qualitatively identical and quantitatively very similar. Chitosan treatments yielded higher monoterpene accumulation than the other inocula. These results suggest that components of fungal cell walls are at least partially involved in the process of induction, and that diffusion of molecules released at the invasion site initiates cellular reactions in advance of the pathogen.

Not all products of fungi vectored by bark beetles elicit defensive reactions. For example, Hemingway et al. (1977) isolated three isocoumarins from *Ceratocystis minor* that are toxic to loblolly pine, *Pinus taeda*. These materials cause abnormal transpiration, membrane disruption, reduced waterflow, and reduced oleoresin flow, which render trees more favorable to southern pine beetle brood (Hodges et al. 1985). None of the morphological or chemical changes associated with induced defenses have been reported in response to these fungal metabolites.

5.2 Sequential Stages of Induction

Induced responses to bark beetle–fungal invasion can be metabolically costly, involving 90 molecules of ATP for each molecule of monoterpene synthesized (Croteau et al. 1972, Wright et al. 1979). Carbohydrates probably provide the substrate for terpene biosynthesis during induction; a 30% decrease in soluble sugars and a 15% decrease in reducing sugars correspond with this response (Miller and Berryman 1985). Reduced sugar content has been observed within 24–36 h of fungal inoculation. Berryman et al. (1988) proposed that two phases of elicitation are involved that together provide a flexible conservation of energy. First, plant cell wall fragments (such as PIIF) released during beetle feeding activate a controlled metabolic response to mechanical wounding. Neighboring cells undergo multiplication of ribosomes, dictyosomes, and mitochondria, development of endoplasmic reticula, decreased lipid content, starch accumulation, and increased number and size of plastids (Cheniclet et al. 1988). This is followed by enlargement of the leucoplasts and differentiation of new secondary resin ducts. Thereafter, fungal products such as chitosan may stimulate hyperactivity of the parenchyma cells, which then produce large quantities of defensive chemicals causing cell wall ruptures (Cheniclet et al. 1988, Lieutier and Berryman 1988). Water-soluble enzymes such as prenyl transferase are activated. Endoelicitors diffuse from cells destroyed during hyperactivity and activate cells in advance of the invading complex (Berryman 1988, Cheniclet et al. 1988, Lieutier and Berryman 1988). Ethylene appears to contribute to this process by acting as a wound hormone (Raffa and Berryman 1982c, Popp et al. 1988). Thus, elicitor release continues until the beetle–fungal complex is contained.

6 BEETLE COUNTERADAPTATIONS TO INDUCED DEFENSES

A variety of mechanisms may allow insects and microorganisms to reproduce despite the presence of potential plant defensive traits (Rhoades 1985). For example, some insects are able to tolerate, sequester, or excrete host defensive chemicals. Others can avoid noxious chemicals through temporal asynchrony with allelochemical abundance (Feeny 1970) or specialization

on plant parts low in allelochemicals (Jones 1972). All of these processes occur to varying degrees among bark beetles, but the most significant adaptation is direct interference with the tree's ability to intoxicate the brood.

6.1 Exhaustion of Host Defenses

Bark beetles overcome conifer resistance by mass attack and mechanical disruption of the vascular system (Thalenhorst 1958, Rudinsky 1962, Raffa and Berryman 1983a,b, Cook and Hain 1986). Each beetle cuts across resin ducts, causing the flow of oleoresins to drain out of the entrance tunnel. Beetles physically carry resin away from their galleries until resin flow ceases. This behavior is analogous to the trenching and vein-cutting actions that have been described among certain folivores (Carroll and Hoffman 1980, Dussourd and Eisner 1987), but on a more massive scale. Because host allelochemicals are converted by bark beetles into aggregation pheromones, recruits continue to arrive as long as the tree's defenses are viable.

Once a tree's defensive capacity is physically depleted, its previous ability to respond is never manifested. This can be demonstrated in three ways. First, if trees are artificially screened from further arrivals during natural mass attack, there is a direct relationship between the chances of a tree being killed and the density of entered beetles at the time of caging. This relationship is not linear, but instead reveals a rather clearly defined *threshold of resistance* (Thalenhorst 1958), above which trees are killed and below which attacks are contained (Table 4A). Although beetles enter an environment that is or will become lethal to them, it can be converted into a suitable breeding substrate by the combined effects of the original colonizers and a critical number of subsequent recruits.

Second, each phytochemical response depletes the tree's ability to resist further attacks (Horntvedt et al. 1983, Raffa and Berryman 1983b, Christiansen and Ericsson 1986). Multiple-inoculation experiments generate classic dose-response curves, and eventually the concentrations of allelochemicals fall within the beetles' tolerance limit (Table 4B). Moreover, a tree's response to a single inoculation is related to its inflection point along this curve, suggesting that each tree is characterized by a unique threshold of resistance.

Third, there is a marked decline in both the constitutive and induced defensive properties of a tree during mass attack, even though aggregation lasts only a few days. Unattacked trees do not show equivalent declines during the same period. Thus, beetles entering a tree during the later phase of mass attack encounter an environment with lower resin flow and lesion formation rates than those encountered by earlier arrivals (Table 4C).

6.2 Tolerance and Avoidance of Host Toxins

Primary bark beetles can survive the concentrations of allelochemicals present in the constitutive tissue of most trees. However, the continual syn-

TABLE 4 Evidence for Direct Exhaustion of *Pinus contorta* Defenses by *Dendroctonus ponderosae*/*Ceratocystis clavigera* Mass Attack

A. Interruption of Natural Mass Attack with Screen Cages (Raffa and Berryman 1983a)			
Attack Density (females/m ²)	Tree Condition (number of trees/category)		
	Living		Killed
	Lightly Damaged	Strip- or Patch-Killed	
Below 40	6	3	0
Above 40	0	2	21

B. Monoterpene Accumulation Following Artificial Inoculation (Raffa and Berryman 1983b)			
Inoculation/m ²	Monoterpene Accumulation (digitizer units)		
	All Trees	Trees with Low Response to Single Inoculation	Trees with High Response to Single Inoculation
		3.3	42.1
6.2	30.3	25.9	40.6
13.2	46.2	40.4	54.8
25.6	48.0	39.0	86.6
52.8	29.6	18.2	39.1
105.6	11.0	7.3	16.6

C. Comparison of Pre- and Postattack Measures of Host Resistance (Raffa and Berryman 1983a)			
Resistance Parameter	Preattack	Postattack	
Constitutive: Oleoresin flow (mL/day)	1.10	0.39	
Indeed: Necrotic lesion formation (cm)			
3 days postinoculation	24.56	12.33	
7 days postinoculation	24.5	15.06	

thesis and transport of a broad array of chemicals to the attack site results in higher concentrations than beetles and their progeny can endure. Because trees continue to produce resin as long as they and the beetles remain alive, there is little opportunity for the evolution of beetle tolerance. To be genetically transferred, tolerance would have to be conferred by a gene or genes against high concentrations of all chemical groups simultaneously, and among all life stages of an individual. Total reliance on tolerance does not appear to be common in conifer-scolytid systems.

Likewise, subcortical reactions make avoidance of host allelochemicals in space or time difficult to achieve, at least in the manner achieved by

folivores (e.g., Feeny 1970). For example, fir engravers bore between preformed resin pockets (Ferrell 1983), but tissue disruption during induced reactions soaks the entire gallery with secondary resin. There is circumstantial evidence, however, that some bark beetles may attack trees during predictable periods of relative host susceptibility. Trees show seasonal variation in both their preformed (Lorio 1986) and induced (Paine 1984) reactions, but the ecological significance of this variation is still unclear; there are differences in the extent of the response, not in the frequency of its occurrence. Mountain pine beetles commonly initiate attacks during the late afternoon when diurnal tree water deficits peak. Similarly, beetles are seasonally active only during mid summer, also a period of maximum water stress. However, these relationships have not been thoroughly studied and there are other plausible explanations of beetle activity rhythms, as well as exceptions to the patterns.

A common means by which plant pathogens avoid defensive reactions is suppression of host recognition mechanisms (Albersheim and Valent 1974, Sequeira 1980), but this option also is not available to bark beetle-fungal complexes. Shredding live tissue with sclerotized mandibles and legs seems too crude a method of attack to disguise. Moreover, all beetles are covered with an array of microbe species, some of which are simply random contaminants. The likelihood of all components of this flora simultaneously evolving sophisticated nonrecognition properties is remote.

Although primary bark beetles have little opportunity to avoid induced defenses once they have entered healthy trees, they can greatly increase their chances of success by orienting solely to weakened hosts. Beetles undergo a sequence of visual, tactile, olfactory, and gustatory responses that govern host acceptance and discriminate against healthy trees (Elkinton et al. 1981, Hynum and Berryman 1980, Moeck et al. 1981, Raffa and Berryman 1980, 1982c, Raffa 1988). There are also some disadvantages to this behavior, however; stressed trees are normally rather rare, such breeding substrates are usually of lower quality and quantity, and interspecific competition for such limited resources can be severe. The relative advantage of avoiding healthy trees depends on the physiological allocation to defense that typifies most members of a particular host species. This, in turn, depends on the host's general life history parameters (Raffa and Berryman 1987).

Certain bark beetle species that breed just above the soil line seem to provide exceptions to the above generalizations. *Dendroctonus micans*, *D. valens*, and *D. terebrans* can reproduce in living trees without killing them. These species do not engage in mass attack. Rather, the brood feed together, mediated by larval aggregation pheromones (Gregoire et al. 1982). It is not entirely clear how these species tolerate and/or avoid host responses, especially considering the consistent association of *D. valens* and *D. terebrans* with *Leptographium terebrantis* (Barras and Perry 1971), which induces strong defensive responses (Raffa and Smalley 1988b). Maternal care, in the

form of extensive and sophisticated gallery architecture that facilitates resin canal drainage, probably contributes to brood survival.

6.3 Integration of Colonization Strategies

The relative importance of avoiding resistant trees, tolerating and/or avoiding resistant responses within trees, and overwhelming the defenses of healthy trees varies among different bark beetle species. The importance of concerted mass attack is related to the preattack vigor of selected trees. This parameter can be estimated by plotting the beetle replacement rate (brood/parent) achieved against the attack density of the parental generation. This curve is typically an inverted parabola with the rising portion attributable to the beetle's cooperative effect and the falling portion due to intraspecific competition (Berryman 1974, Raffa and Berryman 1983a, 1987). Aggressive species such as *D. ponderosae* achieve their maximum replacement rates at higher attack densities than do less aggressive species such as *D. rufipennis*, *S. ventralis*, or *D. pseudotsugae* (Table 5, column 1). Yet, when *D. ponderosae* colonize dead trees, the curve closely resembles that of less aggressive species.

The degree to which avoidance of healthy trees (Table 5, column 2) is critical for reproduction can be estimated by caging beetles onto trees. For example, *D. ponderosae* show higher entry rates and more frequent cases of fatal persistence than *S. ventralis*. Life table data can also reflect these differences, since losses during adult dispersal are presumably related to an

TABLE 5 Proposed Mechanisms by Which Primary Bark Beetles in the Genera *Dendroctonus*, *Ips*, and *Scolytus* Contend with Host Defenses^a

Species	Exhaust Host Defenses	Avoid Host Defenses by Selecting Weakened Trees	Tolerate Host Defenses
<i>D. frontalis</i>	H	M	M
<i>D. brevicomis</i>	H	M	M
<i>D. ponderosae</i>	H	M	M
<i>I. typographus</i>	MH?	MH	M?
<i>D. rufipennis</i>	MH?	MH	M?
<i>D. pseudotsugae</i>	M	H	M?
<i>I. pini</i>	M?	H	L?
<i>S. ventralis</i>	ML?	H	L
<i>I. grandicollis</i>	L?	H	L?
<i>D. terebrans</i>	L	M	H
<i>D. valens</i>	L	M	H
<i>D. micans</i>	L	M	H

^a The terms low (L), moderate (M), and high (H) beetle reliance on a particular strategy are intended to depict points along a continuum, not absolute categories.

inability to locate a suitable host. In general, less aggressive species experience higher relative losses during dispersal, and more aggressive species experience higher mortality due to resinosis (Raffa and Berryman 1987).

Estimates of tolerance are based on published laboratory studies with purified chemicals and field observations (Table 5, column 3). Species that can colonize trees without killing them and those colonizing pines with developed constitutive resin duct systems generally exhibit the greatest tolerance. Based on available data, it appears that most bark beetles fall into one of several clearly defined groups, although each species relies on a variety of adaptations to some extent (Table 5).

6.4 Conflicting Rate Reactions: Accumulation versus Depletion of Allelochemicals

The ability of bark beetles and/or their microbial symbionts to convert host compounds into aggregation pheromones and thereby attract conspecifics as long as host resistance persists may seem to render all trees susceptible. Yet under most conditions most trees are not attacked (Hodges et al. 1985). This is not because beetles fail to locate trees. Flight-trap data show that in some systems almost all (if not all) trees in a stand are located by bark beetles each growing season (Raffa and Berryman 1980). When beetles are caged onto trees, only a minority bore in, and many of these subsequently exit (Raffa and Berryman 1982c, 1983b). Beetles orient away from many trees of the preferred host species, despite the beetle population's apparent ability to kill any tree if enough join in the attack.

A complex system of host defense that integrates constitutive and induced mechanisms appears to explain why healthy trees can survive periods of moderate beetle abundance (Berryman 1972). A rapid flow of resin at the attack site may interfere with beetle communication, thereby reducing the interactions among beetles that exhaust host defense. Although monoterpenes from host resin are readily converted to oxidized attractants in the laboratory (Hughes 1973), a beetle tunneling in a pitch tube does not necessarily attract other beetles, even when populations are high. Only about half of the natural attacks that are initiated by single mountain pine beetles elicit aggregation (Raffa and Berryman 1983a). Likewise, when beetles are caged onto lodgepole pines, only a third of the beetles that enter are joined by conspecifics. These observations cannot be attributed to an absence of pheromone precursors in the host or the unavailability of recruits, because phytochemical analyses, concurrent aggregation on neighboring trees, and trapping data discount these possibilities. Although some of these beetles may simply be poor pheromone producers, there appears to be a host role as well. If only attacks that begin in true pioneer fashion are considered, trees on which natural entries do not elicit mass attack have constitutive resin flow rates that are nearly 6 times as high as those on which natural entries lead to mass attack (Raffa and Berryman 1983a).

Several mechanisms involving pheromone biosynthesis, volatile emission, and/or chemoreception could contribute to this interference (Raffa and Berryman 1983a). However, the simplest theory is that volatiles produced by beetles in resinous galleries cannot permeate the tree's gummy secretions, at least in a form that elicits beetle landing. Following initial beetle entry, induced responses begin, and the survival time of the insect is limited (Fig. 2). If additional colonizers do not arrive quickly, secondary resins augment the primary resin flow, and the colonization sequence is interrupted.

Attacks that begin through switching (Gara and Coster 1968, Geizler et al. 1980) from trees in the terminal phase of attack onto healthier neighbors are more likely to attract flying beetles than attacks initiated by solitary beetles (Raffa and Berryman 1983a). In the same stands described above, 90% of the lodgepole pines on which attacks were started by switching underwent mass attack. Likewise, if all trees are included in the analysis, there is no difference in constitutive resin flow rates between naturally entered trees that were or were not subsequently mass attacked. These results suggest that the tree's potential ability to limit pheromone emission is depleted by the simultaneous initiation of several attacks. The interactions between the rate of beetle arrival, determined by the number of entered beetles, local density of flying beetles, and constitutive resin content, and the intensity of the induced host response, determined by tree age, vigor, and heredity, largely determine the outcome of colonization attempts.

The above considerations refer to outbreaks in which there are sufficient beetles to respond to volatile attractants, a condition that may not be fulfilled when populations are low. However, even the most aggressive beetle species exist for decades in stands without undergoing an outbreak; beetles must survive and reproduce during lengthy periods when conspecifics are rare. Because the outcome of colonization attempts is strongly influenced by beetle population density, there may be behavioral differences between outbreak and nonoutbreak populations. That is, selection may favor relatively discriminating host entry behavior when the arrival of many additional recruits is unlikely, but favor more indiscriminant behavior at high beetle densities (Raffa and Berryman 1983a, 1987, Raffa 1988). This may partially explain repeated observations of foresters who have long described beetles as being more aggressive in their attacks during outbreaks (Keen 1938).

6.5 Reproduction Costs of Mass Attack

The ability of beetles to overcome relatively resistant trees incurs the cost of distributing the host among a large number of colonizers. Although each beetle increases the likelihood of successful colonization, it also decreases the available substrate per individual (Rudinsky 1969). This may provide an explanation as to why some trees are consistently avoided; there is little advantage to colonizing trees that require more beetles to overcome tree defenses than the tree can support in reproduction.

Selecting optimal hosts can be paradoxical, however, because trees that provide the most substrate are usually the most resistant (Raffa 1988). For example, very young trees often have less pronounced induced reactions than healthy mature trees (Safranyik et al. 1975, Raffa and Berryman 1982b), but they also tend to have thinner phloem, bark, and stem diameters, and can therefore support fewer larvae (Amman 1969, 1972, Cole 1962). Conversely, healthy mature trees provide a good food base, but resistance capacity is highest during this stage of development. Older trees that are beginning to decline and mature trees that are suddenly stressed have both sufficient phloem for development and a relatively low threshold of resistance. This trade-off between a tree's threshold for attack and its carrying capacity may have favored bark beetle behaviors that facilitate orientation to old or highly stressed trees (Raffa and Berryman 1987). Tree mortality patterns appear to reflect such beetle preferences (Keen 1938, Rudinsky 1962, Struble 1957, Amman and Cole 1983). While in flight, mountain pine beetles prefer broad objects over narrow dark vertical objects, a trait that is likely to lead them to old trees (Shepherd 1966). Likewise, they are repelled by heavy resin flow during gallery initiation, and beetles orient away from trees with very high thresholds of resistance (Raffa and Berryman 1983b). Moreover, the most toxic allelochemicals to scolytids are generally the most repellent as well (Smith 1975, Bordasch and Berryman 1977, Raffa et al. 1985).

Although cooperative behavior incurs intraspecific competition, beetles can reduce this effect by preventing further entries once selected trees have been overcome and/or reducing oviposition to a fraction of the potential egg complement before reemerging to attack new hosts. These behaviors are governed by a complex integration of chemical, acoustic, and visual cues (Renwick and Vite 1970, Rudinsky 1969, 1973, Coulson et al. 1976).

7 FACTORS AFFECTING THE EXTENT OF INDUCED RESPONSES

7.1 Host Stress

Conifers show considerable intraspecific variation in their extent and rate of response to simulated and natural bark beetle-fungal attack. Induced responses are decreased by disease, mechanical damage, intraspecific competition, water deficit, natural and artificial defoliation, and poor site condition (Wright et al. 1979, 1984, Raffa and Berryman 1982b, Waring and Pitman 1983, Paine et al. 1985, Miller et al. 1986). These physiological relationships are ecologically significant because bark beetle outbreaks are correlated with each of the above factors (Keen 1938, Rudinsky 1962). They also support the view that almost any biotic or abiotic stress will lower tree resistance (Waring and Pitman 1983). For example, lodgepole pines with high growth rates have stronger resistant responses to controlled inoculations (Shrimpton 1973a,b) and are more likely to survive natural mountain

pine beetle outbreaks than trees with slow growth rates (Mahoney 1978, Raffa and Berryman 1983).

7.2 Effects of Prior Exposure, Inoculum Load, and Site of Attack

Most of the available evidence suggests that conifer responses to subcortical invasion are short term and localized (Miller 1984, Paine et al. 1985). In this regard they seem to differ substantially from many induced responses to defoliators. However, Cook and Hain (1988) observed elevated and altered monoterpene composition in previously attacked and inoculated trees. Within a tree's capacity to respond, inoculum load does not affect the magnitude of host responses (Paine and Stephen 1985).

Experiments examining within-tree variation along different heights of trees have yielded mixed results. Reid and Shrimpton (1971) observed more resinous responses along the basal 20 ft than in the upper stem of lodgepole pines, but Paine et al. (1985) found no height-related variation in loblolly pines. No significant variation due to aspect was observed in *P. resinosa* or *P. banksiana* inoculated with *Ceratocystis ips*, *C. nigrocarpa*, or *L. terebrantis* (Raffa and Smalley 1988a,b).

7.3 Seasonal and Age Related Variation

Pronounced seasonal differences occur in the induced subcortical responses of conifers. However, the pattern of change for each host or fungal species is unique (Paine 1984, Raffa and Smalley 1988c).

Age-specific patterns (Section 6.5) in induced defensive capacity may allow for substantial host reproduction prior to attack and have important implications to conifer-bark beetle coexistence. In many systems trees produce cones for several decades before their resistance to bark beetles declines. In other systems mortality to bark beetles of aging trees may even be adaptive. If the host is a pioneer species likely to be replaced by understory successors, reduced resistance to bark beetles, bark beetle outbreak, fuel accumulation in the form of thousands of hectares of dead trees, intense large-scale fire, and rapid seed germination from long-lived serotinous cones provide the most likely route of insuring successful conifer reproduction (Amman 1977, Peterman 1978, Raffa and Berryman 1987).

7.4 Genetic and Environmental Components of Constitutive and Induced Defenses

Unfortunately, the degree to which variation in conifer defenses is under genetic vs environmental control is unknown. Available data suggest that the proportion of genetic and environmental regulation of various components of the constitutive and induced defense systems varies considerably (Table 6). For example, an extensive literature on chemotaxonomy, tree

TABLE 6 Proposed Relative Genetic and Environmental Contributions to Various Constitutive and Induced Parameters of Conifer Resistance to Bark Beetles

Parameter	Source of Variation		References
	Genetic	Environmental	
CONSTITUTIVE			
Monoterpene composition	High	Low	1-4
Resin acids	High	Low	5, 6
Total oleoresin content	Moderate	Moderate	7-10
Viscosity	High	Low	9, 11
Rate of crystallization	High	Low	12
Oleoresin exudation flow and pressure	Low	High	8, 13, 14
INDUCED			
Elicitation (occurrence)	High?	Low	15-19
Extent and rate of response	Moderate?	High	17-23

References. 1, Hanover 1966; 2, Hanover 1975; 3, Zavarin et al. 1969; 4, Tobolski and Hanover 1971; 5, Zinkel 1977; 6, Hanover 1966; 7, Mergen 1953; 8, Rudinsky 1966; 9, Mergen et al. 1955; 10, Squillace and Gansel 1974; 11, McReynolds and Lane 1971; 12, Buijtenen and von Santamour 1972; 13, Lorio and Hodges 1968; 14, Vite 1961; 15, Raffa and Smalley 1988a; 16, Raffa and Smalley 1986b; 17, Wright et al. 1979; 18, Wright et al. 1984; 19, Raffa and Berryman 1982a; 20, Raffa and Berryman 1982b; 21, Paine et al. 1985, Miller et al. 1986; 22, Paine and Stephen 1987b; 23, Shrimpton and Watson 1971.

breeding, and naval stores production indicates strong genetic control of the chemical and physical properties of constitutive conifer resin. Nevertheless, constitutive resin composition can be altered by stressful site conditions or severe trauma such as a lightning strike (Blanche et al. 1985). Other aspects of the constitutive defense system are largely determined by environmental conditions. Resin flow rate, for example, is strongly influenced by edaphic, climatic, biotic, and anthropogenic factors (Waters et al. 1985).

There is little intraspecific variation in the qualitative elicitation of induced responses, as all (or almost all) members of the host population respond to their normal beetle-vectored pathogens (Raffa and Berryman 1982a,b, 1983a,b, Paine 1984, Paine and Stephen 1987a,b, Lieutier and Berryman 1988, Raffa and Smalley 1988a-c). Quantitative aspects of the response vary enormously, however, and these are strongly influenced by environmental factors (see section 7.1). There is some circumstantial evidence for a genetic component to these parameters as well. Raffa and Berryman (1982a) assayed surviving lodgepole pines in a stand where mortality exceeded 99%. Although there were no microsite, canopy structure, age, or size differences between the few trees that survived and those that were killed, the former group had higher monoterpene accumulation rates during induced responses to controlled inoculations than other trees in the population.

Whitham (1983) has proposed that a combination of both genetic and environmental control of host defensive traits may partially explain why long-lived trees can remain resistant against insects with short generation times and high potential for evolutionary change. This appears to be the case in conifer-scolytid systems. Selection may have favored beetle orientation to a particular physiological condition, rather than to a particular genetic condition. As a consequence, stable coexistence is common in such a potentially stable system.

8 ROLE OF HOST RESISTANCE IN THE POPULATION DYNAMICS AND MANAGEMENT OF BARK BEETLES

8.1 Population Dynamics

Bark beetle populations are governed by host availability, which is determined by the interface of tree resistance levels with beetle density on an areawide basis (Rudinsky 1962, Berryman 1974, 1976, 1979, 1979, Coulson et al. 1983). During endemic periods, beetle populations rise and fall with the availability and size of stressed trees that are susceptible to resist attack. Each successful attack depletes the limited pool of susceptible trees, and there are rarely sufficient beetles to kill healthy trees during dispersal offset reproductive gains, and populations can reach a stable equilibrium density. If an areawide stress such as drought weakens many of the trees, however, the population can rise above equilibrium density, beyond which enough beetles are present to overcome vigorous tree defenses through mass attack. Each reproductive increment exhausts a range of susceptible trees, generating a positive feedback cycle. If the predisposing stress is alleviated, the population can continue to increase exponentially. Nearly all suitably sized trees within the host species range are eventually killed. With their resource exhausted, beetle populations crash. Such outbreaks have major effects on forest composition and structure (Borden 1971, Amman and Baker 1972, Amman 1977, Geiszler et al. 1977, Raffa and Berryman 1987).

At low population densities of beetles, mortality due to resinosis and tree defenses might be expected to be great. However, because the loss of trees from well-defended trees is adaptive and occurs frequently, beetle populations typically reveal low numbers of beetles killed by resinosis, and the losses during their search for acceptable hosts (Berryman 1973, 1979, 1981, Wright et al. 1984).

The effects of induced plant responses on the population dynamics of bark beetles can be quite different from what typifies folivores. In high folivore populations often result in decreased host suitability, and subsequent population decline, high scolytid densities are only marginally influenced by induced defenses. Conversely, low folivore densities

likely to induce long-term responses and so their progeny are unaffected; at low scolytid densities, host defenses play a major role in population behavior. The rapid, lethal responses exhibited by both the herbivore and the plant have apparently led to more eruptive cycles in conifer-bark beetle systems as compared to less dynamic folivore-host interactions.

8.2 Management Considerations

The use of induced host resistance in the management of insect pests has much potential, but also poses several difficult problems. Of foremost importance is the trade-off between defensive capacity and desirable agronomic traits. Plants must allocate limited resources to growth, reproduction, maintenance and defense (Bazzaz et al. 1987); resistance can be correlated with reduced growth rate. There may also be disparities between crop defensive capabilities and palatability to humans, cropping convenience, or resistance to other biotic and abiotic agents (Raffa 1987).

Fortunately, these problems are largely alleviated in bark beetle management. First, the crop is not for human consumption, so noxious defensive chemicals are of less concern. Second, the correlation between defensive capacity (both constitutive and induced) and general plant vigor (see section 7.1) provides much flexibility in terms of cultural manipulation. There is a high degree of compatibility between enhancing host resistance to bark beetles and overall forest management objectives. For example, thinning a stand increases both growth rate and resistance by reducing crowding (Mitchell et al. 1983). Likewise, trees begin to lose resistance about the same time their growth rate slows (Shrimpton 1978, Paine and Stephen 1987b), an optimal time for harvest. Maintenance of high host vigor through stand management practices is the most effective means of preventing bark beetle outbreaks (Rudinsky 1962, Waters et al. 1985).

There are, however, several complicating factors that can reduce the compatibility of resistance enhancement with general forest management. Fluctuations in the value of wood products can make adherence to prescribed rotation and thinning regimens difficult. When these practices are not cost-effective in terms of the immediate return on the removed wood, their pest management value must offset operational costs. Also, cultural practices that disfavor one insect or pathogen may favor another. Thinning young stands, for example, can favor certain root-dwelling insects and fungi. Once established, these organisms can increase susceptibility to bark beetles. A greater understanding of tree physiology, stand dynamics, and forest economics is needed to resolve these issues.

The natural pattern of intertree variation in defensive capability also lends a cautionary note to some proposed methods of enhancing resistance. Specifically, the insertion of foreign genes that encode for an exotic form of resistance may strongly favor insect biotype evolution in this system. The availability of a small pool of weakened trees due to such inevitable events

as lightning, wind, and drought is a major factor in competition among individual beetles and consequently the genetic makeup of the beetle population (Raffa 1987, 1988). Forest managers should determine and provide conditions under which those beetles that primarily orient to weakened trees outcompete less discriminating conspecifics. Conferring a resistant factor to all members of the host population, including stressed trees, could place intense selective pressures on bark beetles to overcome the resistance factor. A large pool of accumulated stressed trees would suddenly become available, and eruptive population cycles could result. There is no certainty that under these conditions the current compatibility between host vigor and host resistance would be preserved, or that currently available methods of utilizing host resistance would remain effective. This caution does not necessarily apply to all plant-herbivore systems to equivalent degrees, but stresses the unique features of bark beetle-conifer associations.

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REFERENCES

- Albersheim, P., and S. S. Valent. 1974. Host-pathogen interactions. VII. Plant pathogens secrete proteins which inhibit enzymes of the host capable of attacking the pathogen. *Plant Physiol.* 53:684-687.
- Amman, G. D. 1969. Mountain pine beetle emergence in relation to the depth of lodgepole pine bark. *USDA Forest Service Research Note INT-96.*
- Amman, G. D. 1972. Mountain pine beetle brood production in relation to thickness of lodgepole pine phloem. *J. Econ. Entomol.* 65:138-140.
- Amman, G. D. 1977. In W. J. Mattson (ed.), *Arthropods in Forest Ecosystems.* New York: Springer, pp. 3-18.
- Amman, G. D., and B. H. Baker. 1972. Mountain pine beetle influence on lodgepole pine stand structure. *J. For.* 70:204-209.
- Amman, G. D., and W. F. Cole. 1983. Mountain pine beetle dynamics in lodgepole pine forests. II. Population dynamics. *USDA Forest Service General Technical Report INT-145.*
- Bannan, M. W. 1936. Vertical resin ducts in the secondary wood of the Abietineae. *New Phytol.* 35:11-46.
- Barras, S. J., and T. Perry. 1971. *Leptographium terebrantis* sp. nov. associated with *Dendroctonus terebrans* in loblolly pine. *Mycopathol. Mycol. Appl.* 43:1-10.

- Bazzaz, F. A., N. R. Chiariello, P. D. Coley, and L. F. Pitelka. 1987. Allocating resources to reproduction and defense. *BioScience* 37:58-67.
- Bernard-Dagan, C. 1988. Seasonal variations in energy sources and biosynthesis of terpenes in Maritime Pine. In W. J. Mattson, J. Levieux, and C. Bernard-Dagan (eds.), *Mechanisms of Woody Plant Defenses against Insects*. New York: Springer, pp. 93-116.
- Berryman, A. A. 1972. Resistance of conifers to invasion by bark beetle-fungal associations. *BioScience* 22:598-602.
- Berryman, A. A. 1973. Population dynamics of the fir engraver *Scolytus ventralis* (Coleoptera: Scolytidae). I. Analysis of population behavior and survival from 1964 to 1971. *Can. Entomol.* 105:1465-1488.
- Berryman, A. A. 1974. Dynamics of bark beetle populations: toward a general productivity model. *Environ. Entomol.* 3:579-585.
- Berryman, A. A. 1976. Theoretical explanation of mountain pine beetle dynamics in lodgepole pine forests. *Environ. Entomol.* 5:1225-1233.
- Berryman, A. A. 1979. Dynamics of bark beetle populations: analysis of dispersal and redistribution. *Mitt. Schweiz. Entomol. Ges.* 52:227-234.
- Berryman, A. A. 1988. Towards a unified theory of plant defense. In W. J. Mattson, J. Levieux, and C. Bernard-Dagan (eds.), *Mechanisms of Woody Plant Defenses against Insects*. New York: Springer, pp. 39-56.
- Blanche, C. A., J. D. Hodges, and T. E. Nebeker. 1985. Changes in bark beetle susceptibility indicators in a lightning-struck loblolly pine. *Can. J. Forest Res.* 15:397-399.
- Bordash, R. P., and A. A. Berryman. 1977. Host resistance to the fir engraver beetle, *Scolytus ventralis* (Coleoptera: Scolytidae). 2. Repellency of *Abies grandis* resins and some monoterpenes. *Can. Entomol.* 109:95-100.
- Borden, J. H. 1971. Changing philosophy in forest-insect management. *Bull. Entomol. Soc. Am.* 17:268-273.
- Borden, J. H. 1984. Semiochemical-mediated aggregation and dispersion in the Coleoptera. In T. Lewis (ed.), *Insect Communication*. London: Academic, pp. 123-149.
- Borden, J. H., D. W. A. Hunt, D. R. Miller, and K. N. Slessor. 1986. An uncertain outcome of response by individual beetles to variable stimuli. In T. L. Payne, M. C. Birch, and C. E. J. Kennedy (eds.), *Mechanisms in Insect Olfaction*. Oxford: Clarendon, pp. 98-109.
- Brand, J. M., J. W. Bracke, A. J. Markovetz, D. L. Wood, and L. E. Browne. 1975. Production of verbenol pheromone by a bacterium isolated from bark beetles. *Nature* 254:137.
- Brand, J. M., J. W. Bracke, L. N. Britton, A. J. Markovetz, and J. S. Barras. 1976. Bark beetle pheromones: production of verbenone by a mycangial fungus of *Dendroctonus frontalis*. *J. Chem. Ecol.* 2:195-199.
- Brattsten, L. B. 1983. Cytochrome P-450 involvement in the interactions between plant terpenes and insect herbivores. In P. A. Hedin (ed.), *Plant Resistance to Insects*. Washington, D.C.: American Chemical Society, pp. 173-198.
- Buijtenen, J. P., and F. Van Santamour. 1972. Resin crystallization related to weevil resistance in white pine (*Pinus strobus*). *Can. Entomol.* 104:215-218.

- Carroll, C. R., and C. A. Hoffman. 1980. Chemical feeding deterrent mobilized in response to insect herbivory and counter adaptation by *Epilachna tredecimnotata*. *Science* 209:414-416.
- Cheniclet, C., C. Bernard-Dagan, and G. Pauly. 1988. Terpene biosynthesis under pathological conditions. In W. J. Mattson, J. Levieux, and C. Bernard-Dagan (eds.), *Mechanisms of Woody Plant Defenses against Insects*. New York: Springer, pp. 117-130.
- Christiansen, E., and A. Ericsson. 1986. Starch reserves in *Picea abies* in relation to defense reaction against a bark beetle transmitted blue-stain fungus, *Ceratocystis polinica*. *Can. J. Forest Res.* 16:78-83.
- Christiansen, E., and R. Horntvedt. 1983. Combined *Ips Ceratocystis* attack on Norway spruce and defensive mechanisms of the trees. *Z. Angew. Entomol.* 96:110-118.
- Cobb, F. W., K. Krstic, E. Zavarin, and H. W. Barber, Jr. 1968. Inhibitory effects of volatile oleoresin components on *Fomes annosus* and four *Ceratocystis* species. *Phytopathology* 58:1327-1335.
- Cole, W. E. 1962. The effects of intraspecific competition within mountain pine beetle broods under lab conditions. *USDA Forest Service Research Note* 97.
- Cole, W. E. 1981. Some risks and causes of mortality in mountain pine beetle populations: a long-term analysis. *Res. Popul. Ecol.* 23:116-144.
- Cook, S. P., and F. P. Hain. 1985. Qualitative examination of the hypersensitive response of loblolly pine, *Pinus taeda* L., inoculated with two fungal associates of the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera:Scolytidae). *Environ. Entomol.* 14:396-400.
- Cook, S. P., and F. P. Hain. 1986. Defensive mechanisms of loblolly and shortleaf pine against attack by southern pine beetle, *Dendroctonus frontalis* Zimmermann, and its fungal associate, *Ceratocystis minor* (Hedgecock) Hunt. *J. Chem. Ecol.* 12:1397-1406.
- Cook, S. P., and F. P. Hain. 1988. Wound response of loblolly and shortleaf pine attacked or reattacked by *Dendroctonus frontalis* Zimmermann (Coleoptera:Scolytidae) or its fungal associate, *Ceratocystis minor* (Hedgecock) Hunt. *Can. J. Forest Res.* 18:33-37.
- Coulson, R. N. 1979. Population dynamics of bark beetles. *Annu. Rev. Entomol.* 24:417-447.
- Coulson, R. N., M. Mayyasi, J. L. Foltz, F. P. Hain, and W. C. Martin. 1976. Resource utilization by the southern pine beetle, *Dendroctonus frontalis* (Coleoptera:Scolytidae). *Can. Entomol.* 108:353-362.
- Coulson, R. N., P. B. Hennier, R. O. Flamm, E. J. Rykiel, L. C. Hu, and T. L. Payne. 1983. The role of lightning in the epidemiology of the southern pine beetle. *Z. Angew. Entomol.* 96:182-193.
- Coyne, J. F., and L. H. Lott. 1976. Toxicity of substances in pine oleoresin to southern pine beetle. *J. Ga. Entomol. Soc.* 11:301-305.
- Croteau, R., A. J. Burbott, and W. D. Loomis. 1972. Apparent energy deficiency in mono- and sesqui-terpene biosynthesis in peppermint. *Phytochemistry* 11:2937-2948.
- Dussourd, E. E., and T. Eisner. 1987. Vein-cutting behavior: insect counterplay to the latex defense of plants. *Science* 237:898-901.

- Elkinton, J. S., D. L. Wood, and L. E. Brown. 1981. Feeding and boring behavior of the bark beetle, *Ips paraconfusus*, in extracts of ponderosa pine phloem. *J. Chem. Ecol.* 7:209-220.
- Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by Winter Moth caterpillars. *Ecology* 51:565-581.
- Ferrell, G. T. 1973. Weather logging, and tree growth associated with fir engraver attack scars in white fir. *USDA Forest Service Research Paper PSW-92*. 11 pp.
- Ferrell, G. T. 1983. Host resistance to the fir engraver, *Scolytus ventralis* (Coleoptera: Scolytidae): frequency of attacks contacting cortical resin blisters and canals of *Abies concolor*. *Can. Entomol.* 115:1421-1428.
- Ferrell, G. T. 1988. Wound-induced oleoresins of *Abies concolor*: is it part of host resistance to the fir-engraver, *Scolytus ventralis*? In W. J. Mattson, J. Levieux, and C. Bernard-Dagan (eds.), *Mechanisms of Woody Plant Defenses against Insects*. New York: Springer, pp. 305-312.
- Gambliel, H. A., R. D. Cates, M. Caffey-Moquin, and T. D. Paine. 1985. Variation in the chemistry of loblolly pine in relation to infection by the blue-stain fungus. In S. J. Branham and R. C. Thatcher (eds.), *Integrated Pest Management Research Symposium: The Proceedings*, pp. 177-185. USDA FS Gen. Tech. Rept. SO-56. Asheville, NC.
- Gara, R. I., and J. E. Coster. 1968. Studies on the attack behavior of the southern pine beetle. III. Sequence of tree infestation within stands. *Contrib. Boyce Thompson Inst.* 24:69-79.
- Geiszler, D. R., R. I. Gara, C. H. Driver, V. F. Gallucci, and R. E. Martin. 1980. Fire, fungi, and beetle influences on a lodgepole pine ecosystem of south-central Oregon. *Oecologia* 46:239-243.
- Green, T. R., and C. A. Ryan. 1972. Wound-induced proteinase inhibitor in plant leaves: a possible defense against insects. *Science* 175:776-777.
- Gregoire, J. C., J. C. Braekman, and A. Tondeur. 1982. Chemical communication between larvae of *Dendroctonus micans* Kug. (Coleoptera:Scolytidae). *Les Colloques de L'INRA*. 7. Les Mediateurs chimiques:16-20.
- Hain, F. P., W. D. Mawby, S. P. Cook, and F. H. Arthur. 1983. Host conifer reaction to stem invasion. *Z. Angew. Entomol.* 96:247-256.
- Hanover, J. A. 1975. Physiology of tree resistance to insects. *Annu. Rev. Entomol.* 20:75-95.
- Hanover, J. W. 1966. Genetics of terpenes. 1. Gene control of monoterpenes levels in *Pinus monticola* Dougl. *Heredity* 21:73-84.
- Hemingway, R. W., G. W. McGraw, and S. J. Barras. 1977. Polyphenols in *Ceratocystis minor*-infected *Pinus taeda*: fungal metabolites, phloem and xylem phenols. *J. Agric. Food Chem.* 25:717-720.
- Hodges, J. D., W. W. Elam, W. F. Watson, and T. E. Nebeker. 1979. Oleoresin characteristics and susceptibility for four southern pines to southern pine beetle attacks. *Can. Entomol.* 11:889-896.
- Hodges, J. D., T. E. Nebeker, J. D. DeAngelis, and C. A. Blanche. 1985. Host/beetle interactions: influence of associated microorganisms, tree disturbance, and host vigor. In S. J. Branham and R. C. Thatcher (eds.), *Integrated Pest Management Research Symposium: The Proceedings*, pp. 161-168. USDA FS Gen. Tech. Rept. SO-56. Asheville, NC.

- Hornthvedt, R., E. Christiansen, H. Solheim, and S. Wang. 1983. Artificial inoculation with *Ips typographus*-associated blue stain fungi can kill healthy Norway spruce trees. *Meddelelser Norsk Inst. Skogforskning* 38:1-20.
- Hughes, P. R. 1973. *Dendroctonus*: production of pheromones and related compounds in response to host monoterpenes. *Z. Angew. Entomol.* 73:294-312.
- Hynum, B. J., and A. A. Berryman. 1980. *Dendroctonus ponderosae* (Coleoptera:Scolytidae): pre-aggregation landing and gallery-initiation on lodgepole pine. *Can. Entomol.* 112:185-191.
- Jones, D. A. 1972. Cyanogenic glycosides and their function. In J. B. Harborne (ed.), *Phytochemical Ecology*. New York: Academic, pp. 103-124.
- Keen, F. P. 1938. Insect enemies of western forests. *USDA Misc. Pub. No. 273*.
- Lieutier, F., and A. A. Berryman. 1988. Elicitation and defensive reactions in conifers. In W. J. Mattson, J. Levieux, and C. Bernard-Dagan (eds.), *Mechanisms of Woody Plant Defenses against Insects*. New York; Springer, pp. 313-320.
- Lorio, P. L., Jr. 1986. Growth-differentiation balance: a basis for understanding southern pine beetle-tree interactions. *For. Ecol. Manag.* 14:259-273.
- Lorio, P. L., Jr. and J. D. Hodges. 1968. Microsite effects on oleoresin exudation pressure of large loblolly pines. *Ecol.* 49:1207-1210.
- Mahoney, R. L. 1978. Lodgepole pine/mountain pine beetle risk classification methods and their applications. In A. A. Berryman, G. D. Amman, R. W. Stark, and D. L. Kibbee (eds.), *Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests*. Moscow: University of Idaho, pp. 106-113.
- Mason, R. R. 1966. Dynamics of *Ips* populations after summer thinning in a loblolly pine plantation: with special reference to host tree resistance. Ph.D. dissertation, University of Michigan.
- Mathre, D. E. 1964. Pathenogenicity of *Ceratocystis ips* and *Ceratocystis minor* to *Pinus ponderosa*. *Contrib. Boyce Thompson Inst.* 22:363-388.
- McReynolds, R. D., and J. M. Lane. 1971. Adapting the bubble-time method for measuring viscosity of slash pine oleoresin. *USDA Forest Service Research Note* 147.
- Mergen, F. 1953. Gum yields in longleaf pine are inherited. *USDA Forest Service SE Forest Experiment Station Research Notes* 29.
- Mergen, F., P. E. Hoekstra, and R. M. Echols. 1955. Genetic control of oleoresin yield and viscosity in slash pine. *For. Sci.* 1:19-30.
- Miller, R. A. 1984. Physiological responses of lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelmann) to bark beetle attack (*Dendroctonus ponderosae* Hopkins) and artificial stress. Ph.D. Dissertation, Washington State University, Pullman.
- Miller, R. A., A. A. Berryman, and C. A. Ryan. 1986. Biotic elicitors of defense reactions in lodgepole pine. *Phytochemistry* 25:611-612.
- Miller, R. H., and A. A. Berryman. 1985. In L. Safranyik (ed.). *The Role of the Host in the Population Dynamics of Forest Insects*. Victoria, BC: Candian Forest Service and USDA Forest Service, pp. 13-23.
- Miller, R. H., H. S. Whitney, and A. A. Berryman. 1986. Effects of induced translocation stress and bark beetle attack (*Dendroctonus ponderosae*) on heat pulse

- velocity and the dynamic wound response of lodgepole pine (*Pinus contorta* var. *latifolia*). *Can. J. Bot.* 64:2669-2674.
- Mitchell, R. G., R. H. Waring, and G. B. Pitman. 1983. Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. *For. Sci.* 209:204-211.
- Mitton, J. B., and K. B. Sturgeon. 1982. Biotic interactions and evolutionary changes. In J. B. Mitton and K. B. Sturgeon (eds.), *Bark Beetles in North American Forests: A System for the Study of Evolutionary Biology*. Austin: University of Texas Press, pp. 3-20.
- Moeck, H. A., D. L. Wood, and K. Q. Lindahl, Jr. 1981. Host selection behavior of bark beetles (Coleoptera:Scolytidae) attacking *Pinus ponderosa* with special emphasis on the western pine beetle, *Dendroctonus brevicomis*. *J. Chem. Ecol.* 7:49-83.
- Moser, J. C. 1985. Use of sporothecae by phoretic *Tarsonemus* mites to transport ascospores of coniferous bluestain fungi. *Trans. Br. Mycol. Soc.* 84:750-753.
- Paine, T. D. 1984. Seasonal response of ponderosa pine to inoculation of the mycangial fungi from the western pine beetle. *Can. J. Bot.* 62:551-555.
- Paine, T. D., and F. M. Stephen. 1985. Fungi associated with the southern pine beetle: avoidance of the induced response in pine hosts. *Oecologia* 74:377-379.
- Paine, T. D., and F. M. Stephen. 1987a. Fungi associated with the southern pine beetle: avoidance of induced defense response in loblolly pine. *Oecologia* 74:337-379.
- Paine, T. D., and F. M. Stephen. 1987b. Influence of tree stress and site quality on the induced defensive system of loblolly pine. *Can. J. Forest Res.* 17:569-571.
- Paine, T. D., F. M. Stephen, and R. G. Cates. 1985. Induced defenses against *Dendroctonus frontalis* and associated fungi: variation in loblolly pine resistance. In S. J. Branham and R. C. Thatcher (eds.), *Integrated Pest Management Research Symposium: The Proceedings*, pp. 169-176. USDA FS Gen. Tech. Rept. SO-56. Asheville, NC.
- Peterman, R. M. 1978. The ecological role of the mountain pine beetle in lodgepole pine forests. In A. A. Berryman, G. D. Amman, R. W. Stark, and D. L. Kibbee (eds.), *Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests*. Moscow: College of Forest Resources, University of Idaho, pp. 16-26.
- Popp, M. P., J. J. Johnson, and R. C. Wilkinson. 1988. Ethylene's role in the response of slash pine to beetle vectored fungi. *Entomological Society of America National Meeting, Dec. 4-8, Louisville, KY*.
- Raffa, K. F. 1987. Devising pest management tactics-based on plant defense mechanisms: theoretical and practical considerations. In S. Ahmad and L. B. Brattsten (eds.), *Molecular Mechanisms in Insect-Plant Interactions*. New York: Plenum, pp. 303-329.
- Raffa, K. F. 1988. Host orientation behavior of *Dendroctonus ponderosae*: integration of token stimuli and host defenses. In W. J. Mattson (ed.), *Mechanisms of Woody Plant Resistance to Insects and Pathogens*. New York: Springer, pp. 369-390.
- Raffa, K. F., and A. A. Berryman. 1980. Flight responses and host selection by bark

- beetles. In A. A. Berryman and L. Safranyik (eds.), *Proceedings of the Second IUFRO Conference on Dispersal of Forest Insects: Evaluation, Theory, and Management Implications*. Pullman: Conference Office, Cooperative Extension Service, Washington State University, pp. 213-233.
- Raffa, K. F., and A. A. Berryman. 1982a. Physiological differences between lodgepole pines resistant and susceptible to the mountain pine beetle and associated microorganisms. *Environ. Entomol.* 11:486-492.
- Raffa, K. F., and A. A. Berryman. 1982b. Accumulation of monoterpenes and associated volatiles following fungal inoculation of grand fir with a fungus transmitted by the fir engraver *Scolytus ventralis* (Coleoptera:Scolytidae). *Can. Entomol.* 114:797-810.
- Raffa, K. F., and A. A. Berryman. 1982c. Gustatory cues in the orientation of *Dendroctonus ponderosae* (Coleoptera:Scolytidae) to host trees. *Can. Entomol.* 114:97-104.
- Raffa, K. F., and A. A. Berryman. 1983a. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera:Scolytidae). *Ecol. Monogr.* 53:27-49.
- Raffa, K. F., and A. A. Berryman. 1983b. Physiological aspects of lodgepole pine wound responses to a fungal symbiont of the mountain pine beetle. *Can. Entomol.* 115:723-734.
- Raffa, K. F., and A. A. Berryman. 1987. Interacting selective pressures in conifer-bark beetle systems: a basis for reciprocal adaptations? *Am. Natur.* 129:234-262.
- Raffa, K. F., and E. B. Smalley. 1988a. Response of Red and Jack pines to inoculation with microbial associates of the pine engraver, *Ips pini*. *Can. J. Forest Res.* 18:581-586.
- Raffa, K. F., and E. B. Smalley. 1988b. Host resistance to invasion by lower stem root infesting insects of pine: response to controlled inoculations with the fungal associate *Leptographium terebrantis*. *Can. J. Forest Res.* 18:675-681.
- Raffa, K. F., and E. B. Smalley. 1988c. Seasonal and longterm responses of host trees to microbial associates of the pine engraver, *Ips pini*. *Can. J. Forest Res.* 18:1624-1634.
- Raffa, K. R., A. A. Berryman, J. Simasko, W. Teal, and B. L. Wong. 1985. Effects of grand fir monoterpenes on the fir engraver beetle (Coleoptera; Scolytidae) and its symbiotic fungi. *Environ. Entomol.* 14:552-556.
- Reid, R. W., and D. M. Shrimpton. 1971. Resistance response of lodgepole pine to inoculation with *Europhium clavigerum* in different months and at different heights on stem. *Can. J. Bot.* 49:349-351.
- Reid, R. W., H. S. Whitney, and J. A. Watson. 1967. Reactions of lodgepole pine to attack by *Dendroctonus ponderosae* Hopkins and blue stain fungi. *Can. J. Bot.* 45:1115-1126.
- Renwick, J. A. A., and J. P. Vite. 1970. Systems of chemical communication in *Dendroctonus*. *Contrib. Boyce Thompson Inst.* 24:283-292.
- Rhoades, D. F. 1985. Offensive-defensive interactions between herbivores and plants: their relevance in herbivore population dynamics and ecological theory. *Am. Natur.* 125:205-238.
- Rudinsky, J. A. 1962. Ecology of Scolytidae. *Annu. Rev. Entomol.* 7:327-348.

- Rudinsky, J. A. 1966. Host selection and invasion by the Douglas fir beetle, *Dendroctonus pseudotsugae* Hopkins, in coastal Douglas-fir forests. *Can. Entomol.* 98:98-111.
- Rudinsky, J. A. 1969. Masking of the aggregation pheromone in *Dendroctonus pseudotsugae* Hopk. *Science* 166:884-885.
- Rudinsky, J. A. 1973. Multiple functions of the Douglas-fir beetle pheromone 3-methyl-2-cyclohexen-1-one. *Environ. Entomol.* 2:579-585.
- Russell, C. E., and A. A. Berryman. 1976. Host resistance to the fir engraver beetle. I. Monoterpene composition of *Abies grandis* pitch blisters and fungus-infected wounds. *Can. J. Bot.* 54:14-18.
- Safranyik, L., D. M. Shrimpton, and H. S. Whitney. 1975. An interpretation of the interaction between lodgepole pine, the mountain pine beetle and its associated blue stain fungi in western Canada. In D. M. Baumgartner (ed.), *Management of Lodgepole Pine Ecosystems*. Pullman: Washington State University Cooperative Extension Service, pp. 406-428.
- Sequeira, L. 1980. Defenses triggered by the invader: recognition and compatibility phenomena. In J. G. Horsfall and E. B. Cowling (eds.), *Plant Disease: An Advanced Treatise*. New York: Academic, pp. 179-200.
- Shepherd, R. F. 1966. Factors influencing the orientation and rates of activity of *Dendroctonus ponderosae* (Coleoptera:Scolytidae). *Can. Entomol.* 98:507-518.
- Shrimpton, D. M. 1973a. Extractives associated with the wound response of lodgepole pine attacked by the mountain pine beetle and associated microorganisms. *Can. J. Bot.* 51:527-534.
- Shrimpton, D. M. 1973b. Age- and size-related response of lodgepole pine to inoculation with *Europhium clavigerum*. *Can. J. Bot.* 51:1155-1160.
- Shrimpton, D. M. 1978. Resistance of lodgepole pine to mountain pine beetle infestation. In A. A. Berryman, G. D. Amman, R. W. Stark, and D. L. Kibbee (eds.), *Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests*. Moscow: College of Forest Resources, University of Idaho, pp. 64-76.
- Shrimpton, D. M., and J. A. Watson. 1971. Response of lodgepole pine seedlings to inoculation with *Europhium clavigerum*, a blue stain fungus. *Can. J. Bot.* 49:373-375.
- Smith, R. H. 1963. Toxicity of pine resin vapors to three species of *Dendroctonus* bark beetles. *J. Econ. Entomol.* 56:823-831.
- Smith, R. H. 1965. Effects of monoterpene vapors on the western pine beetle. *J. Econ. Entomol.* 58:509-510.
- Smith, R. H. 1975. Formula for describing effect of insect and host tree factors on resistance to western pine beetle attack. *J. Econ. Entomol.* 68:841-844.
- Squillace, A. E., and C. R. Gansel. 1974. Juvenile: mature correlations in slash pine. *Forest Sci.* 20:225-229.
- Stark, R. W. 1965. Recent trends in forest entomology. *Annu. Rev. Entomol.* 10:303-324.
- Stephen, F. M., and T. D. Paine. 1985. Seasonal patterns of host tree resistance to fungal associates of the southern pine beetle. *Z. Angew. Entomol.* 99:113-122.

- Struble, G. R. 1957. The fir engraver, a serious enemy of western true firs. *USDA Prod. Res. Rep. No. 11*.
- Thalenhorst, W. 1958. Grundzuge der populations-dynamik des grossen Fichtenborkenkafers *Ips typographus* L. *Schriftenreihe der Forstlichen Fakultar der Universitat Gottingen. No. 21*.
- Tobolski, J. J., and J. W. Hanover. 1971. Genetic variation in the monoterpenes of Scotch pine. *Forest Sci.* 17:293-299.
- Vite, J. P. 1961. The influence of water supply on oleoresin exudation pressure and resistance to bark beetle attack in *Pinus ponderosa*. *Contrib. Boyce Thompson Inst. Plant Prot.* 21:37-66.
- Vite, J. P., and D. L. Wood. 1961. A study on the applicability of the measurement of oleoresin exudation pressure in determining susceptibility of second-growth ponderosa pine to bark beetle infestation. *Contrib. Boyce Thompson Inst.* 21:67-78.
- Waring, R. H., and G. B. Pitman. 1983. Physiological stress in lodgepole pine as a precursor to mountain pine beetle attack. *Z. Angew. Entomol.* 96:265-270.
- Waters, W. E., R. W. Stark, and D. L. Wood. 1985. *Integrated Pest Management in Pine Bark Beetle Ecosystems*. New York: Wiley.
- Whitham, T. G. 1983. Host manipulation of parasites: within-plant variation as a defense against rapidly evolving pests. In R. F. Denno and M. S. McClure (eds.), *Variable Plants and Herbivores in Natural and Managed Systems*. New York: Academic, pp. 15-39.
- Whitney, J. H. 1982. Relationships between bark beetles and symbiotic organisms. In J. B. Mitton and K. B. Sturgeon (eds.), *Bark Beetles in North American Forests: A System for the Study of Evolutionary Biology*. Austin: University of Texas Press, pp. 183-211.
- Wong, B. L., and A. A. Berryman. 1977. Host resistance to the fir engraver beetle. 3. Lesion development and containment of infection by resistant *Abies grandis* inoculated with *Trichosporium symbioticum*. *Can. J. Bot.* 55:2358-2365.
- Wood, D. L. 1972. Selection and colonization of ponderosa pine by bark beetles. In H. F. van Emden (ed.), *R.E.S. Symposium No. 6, Insect/Plant Relationships*. Oxford: Blackwell, pp. 101-107.
- Wood, D. L. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera:Scolytidae), a taxonomic monograph. *The Great Basin Nat. Mem.* 6, Provo, UT: Brigham Young University.
- Wright, L. E., A. A. Berryman, and S. Gurusiddaiah. 1979. Host resistance to the fir engraver beetle, *Scolytus ventralis* (Coleoptera: Scolytidae). 4. Effect of defoliation on wound monoterpenes and inner bark carbohydrate concentrations. *Can. Entomol.* 111:1255-1261.
- Wright, L. E., A. A. Berryman, and B. E. Wickman. 1984. Abundance of the fir engraver, *Scolytus ventralis*, and the Douglas-fir beetle, *Dendroctonus pseudotsugae*, following tree defoliation by the Douglas-fir tussock moth, *Orgyia pseudotsugata*. *Can. Entomol.* 116:293-305.
- Zavarin, E., W. B. Critchfield, and K. Snazberk. 1969. Turpentine composition of *Pinus banksiana* hybrids and hybrid derivatives. *Can. J. Bot.* 47:1444-1453.
- Zinkel, D. R. 1977. Pine resin acids as chemiotaxonomic indicators. In *TAPPI Conference Papers*. Forest Biology Wood Chemistry Conference, Madison, WI, pp. 53-56.