XYLEM RESIN IN THE RESISTANCE OF THE PINACEAE TO BARK BEETLES

Richard H. Smith

Xylem resin—a supersaturation of resin acids in terpenes—appears to play a paradoxical role in the relation of the Pinaceae to tree-killing bark beetles. It has been suggested as the agent responsible for the susceptibility of this coniferous family to beetle attacks. And, at the same time, it has been linked with the ability of the Pinaceae to resist bark beetles. The hosts of tree-killing bark beetles are nearly all Pinaceae—*Pinus* (pine), *Abies* (fir), *Pseudotsuga* (Douglas-fir), *Picea* (spruce), *Tsuga* (hemlock), and *Larix* (larch). Significantly, among conifers, xylem resin is most common and abundant in these Pinaceae. Bark beetles are found on other families of conifers, but they are usually considered of minor importance.

Much experimental work has been done since the early reports of an apparent association of resin with resistance. Nearly all studies have dealt with attacking adult beetles; virtually no research has been directed at effects of resin on immature forms. Most work has been with *Pinus* and *Dendroctonus*, with lesser attention to spruce, fir, Douglas-fir, and the other genera of bark beetles.

This report summarizes the early findings, updates them with results of more recent reports and, in some cases, reinterprets these previous reports. This review deals only with bark beetles that attack living trees and with xylem resin, although in a few instances, it concerns resin-related chemicals as well.

This review follows the approach of Painter (1951), who proposed that plant resistance to insects depends on one or more

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Xylem resin of Pinaceae is closely linked with their resistance and susceptibility to tree-killing bark beetles. This review of the literature on attacking adults suggests that all three resistance mechanisms proposed by Painter—preference, antibiosis, and tolerance—are active in this relationship: preference by attraction, repellency, and synergism; antibiosis by both chemical and physical properties; tolerance by healing and secondary resinosis.

Oxford: 453–145.7X19.92 Scolytidae: 174.7 Pinaceae: U547.914.
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sides of a triangle—insect preference, antibiosis, and tree tolerance—and attempts to show the action of resin through these three mechanisms. Preference refers to the selection or avoidance of the plant by the insect. Painter defined antibiosis as "the tendency to prevent, injure, or destroy (insect) life." In this discussion, the physical and chemical manifestations of resin will be considered separately. Tree tolerance, with reference to Pinaceae and bark beetles, is an active response of the tree to attack; and a brood of beetles successfully develops without killing an exteriorly noticeable part of the tree.

Stark's review (1965) was oriented somewhat along Painter's lines, but he omitted preference, and he treated antibiosis from a different viewpoint by using the classical entomological classification of stomach, contact, and fumigant toxicity. In discussing the nature of resistance, Callaham (1966) followed Painter's triangle. He proposed that the host specificity of pine bark beetles is primarily attributable to interspecific resin variation, and he rests his case largely on antibiosis.

The term allelochemics (Wittaker and Feeny 1971) may be applied to much of the interaction of resin and beetles described herein. It is another example of the importance of secondary plant substances in insect-host relationships.

Commercially, the resin acids are called rosin; the terpenes, turpentine. Resin may also include small amounts of related alcohols and aldehydes. The terpenes are volatile hydrocarbons and are usually considered the active portion of resin in relation to bark beetle reaction.

Three main groups of terpenes are: (a) the monoterpenes, by far the most abundant in the xylem resin of most Pinaceae, which are a 10-carbon molecule and are quite volatile; (b) the sesquiterpenes, which are a 15-carbon molecule and considerably less volatile than the monoterpenes; and (c) the diterpenes, which are a 20-carbon molecule and even less volatile than the sesquiterpenes. Each of the 18 different monoterpenes has the same molecular weight and elemental composition, but different bonding or molecular configuration or both.

EFFECT OF RESIN ON BEETLE PREFERENCE

Studies to show that resin attracts or repels adult beetles have not been conclusive. Even different experiments with the same beetle and tree species have not yielded similar results. This discrepancy is not unexpected, since behavior studies are complex and difficult to interpret.

For a long time it has been known that both red *(D. valens* Lec.*)* and black *(D. terebrans* [Oliv.]*)* turpentine beetles are attracted to resin—even to fresh paint thinned with turpentine. The attractiveness of freshly cut logs to some bark beetles, notably the spruce beetle *(D. rufipennis* Kirby*)* and Douglas-fir beetle *(D. pseudotsugae* Hopk.*)*, has been attributed to resin volatiles. Johnson (1966) found lightning-struck ponderosa pines were readily attacked by the western pine beetle *(D. brevicomis* Lec.*)*. This phenomenon, which has been observed for other species of *Dendroctonus* and for several species of *Ips*, could be caused by reduced tree vigor. Since these attacks are often made immediately after the lightning strike, however, the tree's attractiveness could have been increased by the sudden release of the volatile portion of resin or their chemical derivatives, at the time of the damage to the tree.

Mirov[1] noted that in the laboratory the volatile components of ponderosa pine *(P. ponderosa* Laws. resin both attracted and repelled western pine beetle. Gordon[2] was the first to show differences in the response of this beetle to terpenelike compounds in laboratory olfactometers. The difficulty of interpreting these older results may be attributed to the use of gross and impure materials. Using an improved and reliable field olfactometer and pure materials, Bedard, *et al.* (1969) found western pine beetle to be generally unresponsive to the monoterpene components of ponderosa pine resin.

McMullen and Atkins (1962) found the Douglas-fir beetle attracted to the odors of freshly cut Douglas-fir *(Pseudotsuga menziesii* [Mirb.] Franco*)*. No specific component was identified. However, since freshly cut logs were much more attractive than older logs, McMullen and Atkins were apparently observing response to resin vapors. This observation was supported by Heikkenen and Hrutfiord (1965), who found that α-pinene attracted Douglas-fir beetle and β-pinene repelled it. They theorized that the α- to β-pinene ratio in Douglas-fir caused it to be attractive or repellent. Working with the same beetle and tree species, Rudinsky (1966a) reported a general ranking of attractiveness as follows: camphene > gross resin > α-pinene > limonene > four other terpenes or ter-

[1]Mirov, N. T. *A preliminary study of attraction with the western pine beetle, Dendroctonus brevicomis Lec.* 1928. (Unpubl. rep. on file Pacific Southwest Forest and Range Exp. Stn., Berkeley, Calif.)

[2]Gordon, A. *Tree injection in white fir and ecological studies of insects attacking ponderosa pine.* 1932. (Unpubl. rep. on file Pacific Southwest Forest and Range Exp. Stn., Berkeley, Calif.)

penoid compounds, including β-pinene. He concluded (1966b) that "oleoresin appears to have a dual function for the Douglas-fir beetle: as an attractant orienting the beetles in flight and as a repellent. Resinosis is the most important factor in the defense mechanism of the tree."

Perttunen (1957) found that different concentrations of α-pinene changed the behavior of *Hylastes ater* and *Hylurgops palliatus.* Chararas and Deschamps (1962) speculated that resin and its volatile components of Scots pine *(P. sylvestris* L.*),* Norway spruce *(Picea abies* L.*),* and Douglas-fir were associated with host selection by *Ips typographus* L. and *I. sexdentatus* Boern. They based their case on earlier work by Chararas on bark beetle response to terpenes and on studies of the terpene composition of resin of the three coniferous species. Kangas, *et al.* (1967) found the gross extract of Scots pine phloem to be attractive to *Blastophagus piniperda* L.; they then identified the most active component as α-terpineol, an alcohol derivative of a number of monoterpenes.

Data on the synergistic action of terpenes on insect-produced pheromones continue to grow. In the early period of bark beetle attraction work, the most attractive condition was found to be feeding beetles plus the tree. The most recent work narrows the tree's contribution to individual monoterpenes from resin. Bedard, *et al.* (1969) found that myrcene, a naturally occurring terpene of pines, synergizes brevicomin, a pheromone produced by the western pine beetle; myrcene by itself was not attractive. Other studies (Pitman and Vité 1969; Vité and Pitman 1968) imply somewhat similar synergistic relationships of host terpenes and the pheromones of the mountain pine *(D. ponderosae* Hopk.*),* southern pine *(D. frontalis* Zimm.*),* and Douglas-fir beetles. Stark (1968) touches upon the possible synergistic action of host terpenes.

These advances in pheromones research and others by Pitman (1966) and Wood, *et al.* (1968) offer a new explanation about terpenes and preference. The stereochemical theory of olfaction (Amoore 1963) holds that the shape of a molecule rather than its elemental composition is responsible for the reaction of an animal to an odor. This could explain the attractiveness of natural terpenes and terpenoid compounds, since some of the terpenes are related to pheromones or are similar to them in molecular structure (Silverstein, *et al.* 1967).

The evidence for attraction or repellency has not been adequately resolved, but it is apparent that resin, particularly the terpenes, is closely aligned with host selection or avoidance. Possibly the host specificity of bark beetles is determined by the presence in resin of one or more terpenes which do or do not synergize the insect-produced pheromone. Likewise, these findings suggest new pathways in breeding for tree resistance by seeking to eliminate a natural compound which is a strong synergist to insect-produced attractants. As an example, ponderosa pines without myrcene have been found.

ANTIBIOSIS BY RESIN TO ADULT BEETLES

Antibiosis, with reference to bark beetle attack, has both physical and chemical aspects, and interaction between the two will be considered.

Physical Antibiotic Action

Some of the earliest observations on the adverse effect of resin on bark beetles suggest attribution to physical impediment; witness the term "pitch-out" and "drown-out," used to describe unsuccessful attack. At least four measures of resin flow have been devised: duration of flow, oleoresin exudation pressure (o.e.p.), oleoresin exudation flow (o.e.f.), and quantity of flow. Duration of flow is the time in days during which measurable amounts of resin flow from a standard wound; o.e.p. is pounds of pressure per square inch immediately after wounding; o.e.f is cubic millimeters per minute immediately after wounding: quantity of flow is cubic centimeters of resin exuding over the first 24-hour period per foot of circumference from a full cross-sectional cut.

The quantity of flow as it affects beetle success was considered by Mirov[3] when he measured the volume of resin flow of ponderosa pines in four areas in northeastern California. He found generally that stands with the highest average flow had less current activity by western pine beetle than stands having the lowest rate of flow.

Callaham[4] found the duration of resin flow shorter from high-risk ponderosa pines (those most likely to be attacked and killed by bark beetles) than from low-risk trees; the predominant beetle in his study was the western pine beetle, with a much smaller incidence of Jeffrey pine beetle *(D. jeffreyi*

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[3]Mirov, N. T. *A study of western yellow pine (Pinus ponderosa) as the host tree of Dendroctonus brevicomis.* 1928. (Unpubl. rep. on file Pacific SW. Forest and Range Exp. Stn., Berkeley, Calif.)

[4]Callaham, Robert Z. *Oleoresin production in the resistance of ponderosa pine to bark beetles.* 1955. (Unpubl. rep. on file Pacific Southwest Forest and Range Exp. Stn., Berkeley, Calif.)

Hopk.), on Jeffrey pine (*P. jeffreyi* Grev. & Balf.). Callaham speculated that the quick subsidence of the flow of resin allowed the beetle to proceed unhampered with feeding and ovipositing. On the other hand, the prolonged flow from more resistant trees either exhausted, repelled, or trapped the beetle and prevented oviposition.

After one season of research on o.e.p., Vité and Wood (1961) suggested that ponderosa pines having high pressure survived bark beetle attack (primarily mountain pine beetle, with some western pine beetle) considerably more frequently than did those having low pressure. A second season of beetle attack and pressure measurements produced results of the same kind but with less difference. The stand was second-growth ponderosa pine at about 6,500 feet elevation in the central Sierra Nevada, the upper elevational limit for ponderosa pine in this area. Stark (1965) reported a similar study in which the western pine beetle was predominant, and mountain pine bettle occurred in much smaller numbers. This time little or no differential in survival was noted between trees with high and low pressure. Wood (1962), working with the California five-spined engraver (*I. confusus* Lec.) and ponderosa pine, found that trees with low and high pressure survived attack equally well. However, he did find that successful attacks became established quickest in cut logs in which the pressure dropped to zero or near zero.

Mason (1966,[5] 1969) used the term "o.e.f." to express the initial rate of resin flow on an amount/time basis. His results suggest that the incidence of successful attack by *I. avulsus* Eichh. was greatest in loblolly pine (*P. taeda* L.) with lower o.e.f.; *I. grandicollis* Eichh., on the other hand, resembled *I. confusus* in being unable to tolerate any flow of resin. He also obtained data which suggest fairly strong gene control of o.e.f. However, there was evidence that stand and tree condition also influenced the initial rate of resin flow.

Casual observations of several pine species have attributed unsuccessful attacks of both the red and black turpentine beetle to quantity of resin flow.

Tests in which western pine beetle were forced to attack ponderosa pines were the first to show experimentally the effect of resin quantity on beetle success (Smith 1969). When the flow of resin for a 24-hour period was changed in different portions of the same tree, the success of beetle attack increased as resin flow decreased. The number of beetles also was an important factor in determining the success of beetle attack.

Viscosity and rate of crystallization of resin are characteristics which could act as physical impediments, as Stark (1968) suggests, but experimental evidence has not been produced.

A recent study of smog-damaged ponderosa pine in the southern California mountains sought to associate a number of resin characteristics with bark beetle susceptibility (Stark, *et al.* 1968). Trees visually classified as heavily damaged by smog had, in general, lower resin pressure, lower rate of resin flow, lower total volume of flow, and higher rate of crystallization. In another part of this study, the highest percent of trees attacked by western pine beetle and mountain pine beetle was found in the heavy smog damage category. Putting the two parts of the studies together, Stark, *et al.* (1968) concluded that smog affects resin characteristics which then reduce the trees' resistance to bark beetles. It should be pointed out that the two sets of trees were not the same and that the bark beetle attacks in the second set of trees could have caused changes in the characteristics of the foliage, which are used in classifying smog damage.

Chemical Antibiotic Action

Mirov (1961) postulated that resin chemistry could be the reason for the host specificity of western pine beetle and Jeffrey pine beetle. Callaham (1966) expanded and formalized Mirov's ideas and suggested that host specificity depends on the beetle's ability to tolerate the resin of hosts and inability to tolerate the resin of nonhosts. He specifically indicated that differential toxicity is most likely in the turpentine constituents of resin.

Gordon[6] was the first to show the terpenes and terpenelike compounds to be differentially toxic to adult western pine beetles. Smith (1963) found that resin vapors of nonhost pines were significantly more toxic than host resin vapors to the western pine, mountain pine, and Jeffrey pine beetle. Resin vapors of hybrids between host and nonhost were usually intermediate in effect, and the differences were not always significant; however, in laboratory feeding tests, these hybrid resin vapors caused a significant reduction in the feeding of adult beetles (Smith 1966a). Forced attacks under field conditions on both altered and unaltered pines generally substan-

[5]Mason, Richard R. *Dynamics of Ips populations after summer thinning in a loblolly pine plantation: with special reference to host tree resistance.* 1966. (Unpubl. Ph.D. thesis on file at Univ. Mich., Ann Arbor, Mich.)

[6]Gordon, A. *op. cit.*

tiated the laboratory results. Hybrids between host and nonhost pines were unsuitable hosts (Smith 1966b; Callaham and Miller[7]), and other tests showed that western pine beetle could attack and oviposit in cut logs of the same species and hybrids when there was no flow of resin, thus again associating resin flow with resistance.

A series of laboratory and field tests showed that the individual monoterpene components of ponderosa pine were differentially toxic to the western pine beetle (Smith 1965, 1966b, 1966c, 1969); this pine species is the primary host of the beetle. Other studies indicated a large variation among trees in a stand and among geographic regions in the monoterpene composition of ponderosa pine xylem resin. Only very slight differences in terpene composition were found within individual trees over 30 years of age (Smith 1964, 1968).

Chemical-Physical Interaction

Smith (1966) attempted to treat the interaction of chemical and physical impediment by forcing attacks of western pine beetle on ponderosa pines with different monoterpene composition. The trees were altered to change the amount of resin which flowed during different 24-hour periods. The effects of resin quality and resin quantity could then be assessed by regulating the number of attacking beetles. The results indicate that as resin flow decreases beetle success increases. But, at comparable resin flow, the degree of beetle success was markedly affected by the quality of the resin as measured by its monoterpene composition. The ranking of the monoterpene components for their effectiveness against beetle success was limonene $>$ 3-carene $>$ β-pinene = standard; a standard tree is one without a high concentration of any of these three terpenes. This ranking is similar to that obtained from laboratory tests of the toxic effect of individual monoterpene vapors on adult beetles (Smith 1965). Thus, the favorable effect of quality may be negated by poor quantity, as evidenced by the previously cited observation that beetles can be forced to attack and oviposit on non-resin-producing logs of nonhost species. Likewise, poor quality may be offset by good quantity.

[7]Callaham, Robert Z., and John M. Miller. *Studies of the resistance of pine hybrids to bark-beetle attacks, season of 1951.* 1952. (Unpubl. rep. on file Pacific Southwest Forest and Range Exp. Stn., Berkeley, Calif.)

TREE TOLERANCE TO BEETLE ATTACK

The concept of tree tolerance is somewhat paradoxical, since bark beetles must kill all or part of a tree in order for a successful brood to develop. However, tolerance may be understood as present in those instances in which successful brood development causes no external evidence of killing or causes an active response by the tree, such as the production of different tissue or chemicals. With bark beetles, tolerance is a relative term, depending on the population density. Nevertheless, there are at least three fairly well documented cases which might be classified as tolerance.

In an early study of the fir engraver *(Scolytus ventralis* Lec.*)* on white fir *(Abies concolor* [Gord. & Glend.] Lindl.*)*, Struble (1957) noted that there is often successful brood development without external evidence of injury, although a patch of dead phloem remained beneath the bark. Struble also noted that a great many attacks are not successful in producing a brood. Work by Berryman (1969, 1970) with this insect on *A. grandis* (Dougl.) shows this tree response to be a type of tolerance. Callus tissue develops to heal the wound and a secondary resin system is formed to produce a copious flow of resin which is far greater than that normally encountered. Reid, *et al.* (1967) found a somewhat similar condition with lodgepole pine *(P. contorta* Dougl. var. *latifolia* Engelm.*)* in response to attack by the mountain pine beetle. Callus tissue formation has been observed in species of conifers with attacks of the red and black turpentine beetle. But some uncertainty exists in these investigations about the terms "resinosis," "secondary resin," and "traumatic resin."

IMPROVING RESIN CHARACTERISTICS

Once a property of pine resin has been firmly associated with relative resistance, attempts to augment it should be considered. Merker (1967) found that irrigation and application of fertilizers increased the resistance of pine to bark beetles. He attributed this increased vigor to improved water balance. The better water balance would, in time, directly increase the production of resin. Conventional silvicultural practices, such as thinning to regulate growing stock, may indirectly improve the resin production characteristics of trees which adversely affect bark beetle attack.

Lyon[8] suggested the possibility of introducing a chemical into the tree to increase the toxic or repel-

[8]Lyon, Robert L. Personal communication, May 1971.

lent action of the natural components of resin. The chemical could be introduced physically, or genetically, if a genetic basis could be found.

The level of the resin property might be increased through tree selection or breeding. Selection could be for both phenotypes and genotypes. Certain properties of resin—quality, synthesis, and o.e.f—have been shown to be under strong genetic control. It is not difficult to envision the advantages of a breeding program, once the target properties have been determined.

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