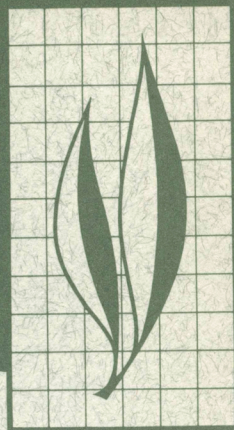


HILGARDIA

A JOURNAL OF AGRICULTURAL SCIENCE PUBLISHED BY
THE CALIFORNIA AGRICULTURAL EXPERIMENT STATION



Volume 39, Number 6 • May, 1968

Photochemical Oxidant Injury and Bark Beetle (Coleoptera: Scolytidae) Infestation of Ponderosa Pine

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**R. W. Stark, P. R. Miller, F. W. Cobb, Jr., D. L. Wood,
and J. R. Parmeter, Jr.**

II. Effect of Injury upon Physical Properties of Oleoresin, Moisture Content, and Phloem Thickness

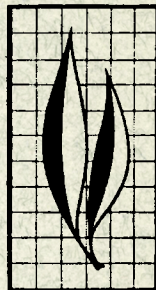
F. W. Cobb, Jr., D. L. Wood, R. W. Stark, and P. R. Miller

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IV. Theory on the Relationships between Oxidant Injury and Bark Beetle Infestation

F. W. Cobb, Jr., D. L. Wood, R. W. Stark, and J. R. Parmeter, Jr.



Certain aspects of insect-disease relationships, especially those concerning transmission of pathogens, have been studied extensively and their significance has been well established. However, the role of diseases as factors predisposing coniferous trees to bark beetle infestation has received only minor attention. There has been little effort to determine the extent of the association between disease and bark beetle infestation, the significance of predisposing diseases in the ecology of the beetles, or the effects of disease upon the host that may increase susceptibility to beetle attack.

The series of papers in this issue presents the results of studies to determine (a) the degree of association between photochemical atmospheric pollution injury to ponderosa pine and infestation by bark beetles (paper I), and (b) the changes in the physiology of diseased trees which might influence host susceptibility to bark beetles (papers II and III). The results show that oxidant injury does, in fact, predispose ponderosa pine to beetle infestation, and that the injury leads to physiological changes in the host which may be related to increased bark beetle susceptibility. The significance of these results in relation to the present knowledge on bark beetle ecology and host susceptibility is discussed in paper IV.

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IV. Theory on the Relationships between Oxidant Injury and Bark Beetle Infestation¹

INTRODUCTION

CERTAIN RELATIONSHIPS between insects and tree-invading fungi have long been recognized (Schmidberger, 1837; Hartig, 1878) and provide well-established ecological concepts. Ambrosia beetles serve as vectors for various fungi and feed upon them (Batra, 1963; Franke-Grossmann, 1963; Graham, 1967), apparently in some cases using them as the sole source of nutrition. Other insects feed upon sporophores and mycelia of plant pathogenic fungi (Paviour-Smith, 1960; Lawrence, 1965) or upon diseased tissue such as galls caused by rust fungi. Various insects serve as vectors for plant pathogens (Leach, 1940; Carter, 1962; Stillwell, 1966), and others have a major role in spermatization of heterothallic fungi, including the rusts (Craigie, 1931). Some insects can also be important in pollination of dioecious higher plant parasites such as mistletoes (Hawsworth, 1961). Through their activities, insects may create wounds that can serve as infection courts for aerial (Craighead, 1916; McLarty, 1933; Graham and Harrison, 1954) or subterranean (Thomas and Wright, 1961) pathogens, and there may be synergistic relationships between insect and pathogen.

The above examples relate to the effects of insects in the epiphytology of

plant pathogens. The influences of disease on the population dynamics of insects are less obvious and less clearly established. Evidence suggests that blue-stain fungi associated with bark beetles might alter the environment of the tree to favor the beetles (Craighead, 1925; Nelson and Beal, 1929; Leach, 1940; Mathre, 1964a). These fungi have often been thought to be instrumental in causing the rapid death of infested trees (Nelson, 1934; Craighead and St. George, 1940; Thatcher, 1960), and inoculations have shown that they are capable of causing death of the host in the absence of beetles (Craighead, 1928; Bramble and Holst, 1940; Mathre, 1964a, 1964b).

The possible relationship of diseases as predisposing factors for bark beetles has been suggested by a number of researchers. Rudinsky (1962a) associated the occurrence of heart rot caused by *Fomes pini* (Thor) Lloyd with increased susceptibility to these insects. Ehrlich (1939), Hetrick (1949), and Thomas and Wright (1961) observed *Armillaria mellea* (Vahl.) Quel. infecting the roots of various conifers prior to beetle attack. Franke-Grossmann (1948, 1954), Jorgensen and Petersen (1951), Bega, *et al.* (1966), Wagener and Cave (1946), and Gohrn, *et al.* (1954) have associated root infection by

¹ Submitted for publication June 15, 1967.

Fomes annosus (Fr.) Cke. with bark-beetle infestation. Wagener and Mielke (1961) noted the association of beetle outbreaks with occurrence of *Verticilladiella wagenerii* Kendrick. Both Lorio (1966) and Hartigan (1964) have associated beetle attacks with root disease caused by *Phytophthora cinnamomi* Rands. Struble (1957) and Miller and Keen (1960) have observed an increased incidence of beetle attacks on trees with dwarf mistletoe. The latter also noted the occurrence of beetle infestation in forest stands severely infected by *Elytroderma deformans* (Weir) Darker, a needle pathogen. However, many of these reports have been based on observations alone. Studies to determine the effects of disease on the host that may help to elucidate the mechanisms of resistance are also lacking.

Recently we studied the relationship between disease caused by photochemical atmospheric pollution and the occurrence of bark beetle (Scolytidae) in-

festations (paper I), and the effects of this disease on host physiology (papers II and III). The effects of photochemical air pollution (chlorotic decline) on ponderosa pine (*Pinus ponderosa* Laws.) described in the three previous papers may be transmitted through the host to the beetle in various ways. This paper describes the importance of these effects in terms of bark beetle epidemiology.

The behavior of bark beetles culminating in an "infested" tree is for convenience considered in three phases. The first is the *dispersal* phase, which begins with emergence from brood trees and ends with initial boring activity in the selected host. The second is termed the *concentration* phase, in which successful penetration through the outer bark into the phloem tissue occurs. This activity results in the production of an attractant and subsequent mass attack. The third phase, *establishment*, includes the construction of egg galleries, oviposition, and development of the brood from egg to emerging adult.

RELATIONSHIP OF ATMOSPHERIC POLLUTION INJURY TO THE DISPERSAL PHASE

Trees in an advanced state of chlorotic decline are attacked more frequently by both the western pine beetle and the mountain pine beetle than are healthy trees. The latter, *D. ponderosae*, showed a greater "preference" for diseased trees than did *D. brevicornis* (see paper I in this issue). The question arises as to whether these trees are "selected" by the beetles and, if so, does perception occur at a distance from or in contact with the host. Our study indicates that selection of diseased trees does occur (paper I). However, the lack of external evidence of attack on healthy trees may result from inhibition of boring activity by some unknown host factor such as a repellent or the absence of a phagostimulant.

An attack stimulus might be per-

ceived at various distances and probably involves at least vision and chemoreception. Thorsteinson (1960), reviewing insect host selection, attaches little significance to host shape or color except at "close range" on the grounds that they are too variable and lack identifiable uniqueness which could explain the discriminating capability of insects.

However, recent studies indicate that vision could play an important role in host selection. Some emerging bark beetles are photopositive within certain temperature limits (Rudinsky and Vité, 1956; Graham, 1959; Perttunen, 1959; Rudinsky, 1962b; Atkins, 1966; Tsao, 1966). Shepherd (1966) has shown that the mountain pine beetle is photopositive at most prevailing temperatures (<35–37°C) and shows a positive re-

sponse to black objects on a white arena or white objects on a black arena. This suggests that a flying beetle may respond to any strong color contrast, e.g., the chlorotic foliage of advanced-disease trees against a background of darker green. He further found that *D. ponderosae* responded positively to vertical stripes rather than to a mosaic, suggesting that the beetle is responding in its search for a host to the "vertical striping" of tree trunks against the background of underbrush or filtered light. Other authors have shown the importance of "striping" or vertical images in host selection by other scolytids (Chapman and Kinghorn, 1958; Henson, 1962; Vité and Gara, 1962; Gara, *et al.*, 1965).

Beetles may also be responding to a characteristic wave length of the electromagnetic spectrum. Kimmins (1966) showed that *Ips confusus* (LeC.) adults react positively to the regions between ultraviolet (3600Å) and deep-red (7000Å). Ultraviolet radiation is generally much more attractive than other wave lengths. Other authors have shown that many insects respond to infrared (Callahan, 1966; Evans, 1966). Measurable differences in infrared emissivity may exist between trees under stress and healthy trees (Weber, 1965; Heller, *et al.*, 1966). Therefore, it is possible that insects respond to these differences. Although the spectrum of ponderosa pine injured by atmospheric pollution has not been determined, such differences undoubtedly exist.

Long-range reception of olfactory stimuli by bark beetles has not been proven. Most researchers seem to agree that reception is "relatively short-range" (Thorsteinson, 1960). Selection by bark beetles of hosts in various physiological states is well established. Trees under stress from drought (Craighead, 1925; St. George, 1930; Hall, 1958) or injured by fire (Furniss, 1965), lightning (Johnson, 1966), wind (Jacobs, 1936; Bedard, 1950; Massey and Wy-

gant, 1954), defoliation (Wallace, 1944; Wickman, 1963) or in other "subnormal" physiological conditions (Anderson, 1944; Lejeune, *et al.*, 1961; Rudinsky, 1962b; Goeden and Norris, 1964) are more subject to attack by insects. This may be due to the formation of specific attractants (Person, 1931; Adlung, 1958), creation of visual stimuli as discussed above, or by providing susceptible material which is found by some random process (Vité and Wood, 1961; Wood, 1963). Considerable evidence now exists that bark beetles respond to odors of cut host material during dispersal (Vité and Gara, 1962; McMullen and Atkins, 1962; Chapman, 1963; Atkins, 1966; Rudinsky, 1966b). The possibility that bark beetles are responding to specific odors produced by trees injured by atmospheric pollution must be considered.

There were no apparent changes in relative amounts of the major xylem monoterpenes in trees injured by air pollution (paper III). However, other undetected changes which may influence host attractiveness to bark beetles could be associated with disease. Bark beetle species are attracted or repelled by whole oleoresin or its various components (Perttunen, 1957; Vité and Gara, 1962; Chararas, 1962; Kangas, *et al.*, 1965; Heikkinen and Hrutfiord, 1965; Rudinsky, 1966b). The terpenes presently thought to be involved in host or primary attraction are α - and β -pinene, limonene, camphene, geraniol and α -terpineol. The Douglas fir beetle, *D. pseudotsugae* Hopkins, is attracted most by α -pinene, limonene and camphene; less by β -pinene, geraniol and α -terpineol (Rudinsky, 1966b). Perttunen (1957) showed that species of *Hylurgops* and *Hylastes* also respond to α -pinene and Kangas, *et al.* (1965) have shown that α -terpineol is attractive to *Blastophagus piniperda* L.

Respiratory fermentation products not directly related to the oleoresin sys-

tem may also play a role in attraction (Person, 1931). Reduction of phloem carbohydrates in pollution-injured trees (see paper III) may affect their quantity and quality.

Heikkinen and Hrutford (1965) suggest that the quantity and character of vapors emanating from Douglas fir vary with the condition of the tree and may be associated with the water regime. During transpiration in healthy

trees, a mixture of needle oils repellent to the Douglas fir beetle may be emitted whereas during subnormal transpiration caused by drought, defoliation, etc., more attractive concentrations may be produced because of an increase in temperature, absorption and/or a decrease in photosynthetic activity. Air pollution injury to ponderosa pine may have the same effect.

RELATIONSHIP OF DISEASE TO THE CONCENTRATION PHASE

The concentration phase of bark beetle attack is better understood than dispersal. Feeding activity associated with the establishment of initial galleries produces a pheromone which concentrates the population on host material. This phenomenon has been established for *Ips pini* (Say) (Anderson, 1948), *I. confusus* (Wood and Vité, 1961), *Dendroctonus brevicomis* and *D. ponderosae* (Vité and Wood, 1961; Vité and Gara, 1962), *D. pseudotsugae* (McMullen and Atkins, 1962; Rudinsky, 1963), and *Trypodendron lineatum* (Oliv.) (Rudinsky and Daterman, 1964; Chapman, 1966) among others.

The stimuli which induce boring activity may be olfactory, tactile, gustatory, or may involve the absence of an inhibitor or repellent. It is difficult to assess how air pollution injury may affect this process, but the reduction in yield of oleoresin observed in this study could be important. Certain monoterpenes reportedly repel the Douglas fir beetle (Heikkinen and Hrutford, 1965; Rudinsky, 1966b) at close range in the laboratory. If this occurs in nature, a change in its relative concentration may lessen its repellent action. Such repellency for other *Dendroctonus* is not known. The quantity and composition of attractant precursors or stimulants present in phloem (Wood, et al., 1966) may also be influenced by disease.

Oleoresin in living trees is a major obstacle to successful establishment of bark beetle galleries (Schwerdtfeger, 1955; Miller and Keen, 1960; Chararas, 1962; Rudinsky, 1962a; Stark, 1965). Resistance may manifest itself through oleoresin exudation pressure, rate and quantity of flow, propensity to crystallize, chemical composition, and possibly other characteristics which may, individually or together, affect the boring beetle.

Oleoresin exudation pressure (OEP) has been considered to be a decisive factor in the success or failure of the attacking pioneer beetles of some species (Vité, 1961; Vité and Wood, 1961; Rudinsky, 1966b). Our observations indicate that high OEP has little effect on the establishment of *D. valens*, a moderate effect on *D. brevicomis*, and a marked effect on *D. ponderosae*. These studies (paper I) reveal that 86 per cent and 59 per cent of the trees killed by the mountain pine beetle and the western pine beetle respectively were in the advanced-diseased group. Advanced- and intermediate-diseased trees were shown to have consistently lower OEP than healthy trees (see paper II). A similar effect was noted in Douglas fir infected with *Fomes pini* (Rudinsky, 1962a).

There is also evidence that OEP affects infection by blue-stain fungi

thought to be important in bark beetle establishment. Mathre (1964b) showed that large ponderosa pines with OEP of 35 psi or less were susceptible to both *Ceratocystis minor* and *C. ips*, while large trees with OEP greater than 35 psi were resistant. Small diameter trees were susceptible regardless of OEP. However, the exact role of OEP as a resistance mechanism is still not clear. In a second-growth ponderosa pine stand, *D. brevicomis* infested the trees at the same rate in high- and low-pressure classes (Stark, 1965).

Rate of oleoresin flow and yield may be important in host resistance. Our study (paper II) has shown that severe air pollution injury reduces the rate and quantity of flow. This may also be related to the higher mortality rate caused by the mountain pine beetle in the advanced-disease class. We have also observed that mountain pine beetle appears to infest ponderosa pine of low resin yield in westside Sierra stands. Struble (1965) observed the same phenomenon in second-growth sugar pine. However, in the dense, second-growth ponderosa pine stands of the eastside Sierra, and in sugar pine generally, resin flow does not appear to impede this insect's success (Smith, R. H., personal communication).

Although the western pine beetle can overcome trees of high resin yield (Stark, 1965), trees of lower yield may be more easily killed. This was indicated by our results showing that mortality caused by *D. brevicomis* was significantly higher in advanced-diseased trees (paper I).

The rate of resin crystallization was increased in advanced-diseased trees (paper II). While there is no evidence that crystallization rate is a resistance factor to bark beetles, we believe that rapid crystallization of oleoresin would enhance successful establishment. Bor-

ing activity in the entrance tunnel and introduction of boring dust, fungal spores, etc., could initiate crystallization, facilitating removal of oleoresin from the gallery. The Douglas fir beetle cannot survive in liquid resin (Rudinsky, 1966b) while *D. valens* can. Dead adults of *D. brevicomis* and *D. ponderosae* have been observed in pitch tubes and galleries flooded with resin. Thus, the increased propensity to crystallize, associated with air pollution injury, could favor establishment.

Once a beetle has successfully established an initial entrance tunnel in its host, the secondary or sex attractant becomes the dominant stimulus in subsequent attack behavior. Not only is the initially attacked tree "filled in," but surrounding trees in all physiological states may be attacked. The sex attractant produced by bark beetles is so potent it may induce attack and infestation in nonhosts (Johnson, 1966; Miller and Keen, 1960) as well as apparently healthy host trees (Vité and Wood, 1961; Stark, 1965). If changes occur in monoterpene constituents in trees damaged by air pollution, the potency of the secondary attractant may be altered. Recent studies (Silverstein, *et al.*, 1968) indicate that such hydrocarbons may be involved.

The effects of air pollution injury in reducing sapwood and phloem moisture content indicate a water "disturbance" which in turn could affect the properties of oleoresin. Because feeding appears to be necessary before the secondary attractants are produced, changes in the nutritional qualities of the phloem could affect its potency (Pitman, 1966). We have shown that reductions in phloem carbohydrates (paper III) and phloem thickness (paper II) are associated with air pollution injury and could therefore influence the concentration phase.

RELATIONSHIP OF DISEASE TO THE ESTABLISHMENT PHASE

The effects of photochemical air pollution on the properties of oleoresin affecting initial penetration may also be operative during the establishment phase. Reduction in exudation pressure, flow rate, yield and the increase in crystallization of oleoresin may affect the amount of toxic vapors to which the beetle is exposed.

Reid (1963) found that "resinosis," the formation of secondary oleoresin in callous tissue, adjacent to the parent gallery, reduced egg eclosion. Rudinsky (1966a) suggests that resinosis in Douglas fir is greater and occurs sooner in trees with a high oleoresin exudation pressure than in trees of intermediate (and presumably low) pressure. Vité and Wood (1961) observed that in trees with an OEP greater than 1.5 atmospheres egg deposition and development were delayed. No observations were made on production of secondary oleoresin in our studies, but reduction in oleoresin yield and flow rate associated with photochemical air pollution injury may influence the degree of resinosis in the tree.

The recent discovery that growth of some species of blue-stain fungi is adversely affected by monoterpene vapors (Cobb, et al., 1967) may also be significant, especially in relation to the decreased resin flow in severely diseased trees and to the possible effects of disease on monoterpene constituents of xylem resin.

By providing a more favorable environment for the establishment of blue-stain fungi, reduction in phloem and sapwood moisture associated with photochemical air pollution (paper II) may enhance gallery construction. Various authors have indicated that drying of the sapwood and phloem may occur through beetle activity in the absence of

blue stain (Hetrick, 1949; Callaham, 1955; Rudinsky, 1962b). However, considerable evidence exists to support the hypothesis that blue-stain fungi facilitate beetle invasion by disturbing water conduction (Caird, 1935; Shepherd and Watson, 1959; Reid, 1961). Reid (1961) showed that *D. ponderosae* is unable to establish broods in trees which maintain a high moisture content. Mathre (1964b) showed that moisture content of the sapwood inoculated with *Ceratomyces* spp. was greatly reduced while uninoculated wounds in control trees did not dry appreciably. He also showed that a reduced sapwood moisture content may be related to increased susceptibility to the fungi. By comparing colonization in limbed and unlimbed severed trees, he demonstrated the apparent effect of moisture on *C. minor* and *C. ips*. Thirty-five days after inoculation, the sapwood of an unlimbed, severed tree was completely "blue-stained" and dry, but infection in a limbed tree was not extensive and the sapwood was still wet. Münch (1907) believed that blue-stain fungi are most pathogenic when water content of wood is below normal, and Bier (1964) has shown that relatively small reductions in phloem moisture content are associated with increased susceptibility of trees to other pathogenic fungi.

However, air pollution injury might adversely affect successful brood establishment by severely reducing moisture content. Reid (1962) found that when inner bark and sapwood moisture content in lodgepole pine dropped below 105 per cent and 60 per cent oven dry weight respectively, oviposition of the mountain pine beetle ceased and the beetles often reemerged. Miller and Keen (1960) report that infested ponderosa pine maintains a moisture con-

tent of 200–300 per cent and drying reduces brood success of the western pine beetle.

The effect of reductions in phloem thickness and carbohydrates associated with disease on success of beetle establishment is unknown. It may be deleterious to both the western pine beetle and the mountain pine beetle, since these insects establish their galleries primarily in the phloem-cambial region, scoring the sapwood only slightly. The effect on the mountain pine beetle should be greater because both the parent and the larvae develop within phloem whereas only parents and the early instar larvae of the western pine beetle utilize this tissue.

Limited observations on gallery formation and brood production in advanced-diseased trees and healthy trees showed some indication that both gal-

lery length and total brood production were less in advanced-diseased trees. Thus, while advanced-diseased trees seem to provide a more attractive host, they may be physiologically less suitable for successful beetle development.

Air pollution injury increases the susceptibility of ponderosa pines to both attack and infestation by the western pine beetle and mountain pine beetle. This injury facilitates establishment of the beetle on the host but may actually reduce the suitability of such trees as breeding material. Therefore, advanced-disease trees may act as "trap trees" in the sense that they absorb the resident beetle population and may actually prevent further build-up. In spite of the great abundance of advanced-disease trees in the area of the studies, there has been no noticeable increase in bark beetle infestations.

SUMMARY

The foregoing discussion presents our views that a reduction of oleoresin exudation pressure, quantity, rate of flow, and an increase in the propensity of oleoresin to crystallize, and a reduction in phloem and sapwood moisture content enhance successful establishment of the western pine beetle and mountain pine beetle in ponderosa pine injured by photochemical atmospheric pollution. Hypotheses are presented which relate these results (papers II and III) to host susceptibility.

ACKNOWLEDGEMENTS

The authors acknowledge the assistance of the U. S. Forest Service and the California Division of Forestry in locating study areas, and of the U. S. Forest Service for use of land in various phases of these studies. The authors are also indebted to H. Barber, J. Bergot, B. Flick, J. Lanier, W. Morgan, W. Platt, M. Srago, and B. Uhrenholdt for technical assistance. These studies were supported by National Science Foundation Grant GB-5970 and United States Public Health Service Grant AP-409-03, with supplemental support from the T. B. Walker and Surdna Foundations and the California Division of Forestry.

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