-8-

Host Response to Bark Beetle and Pathogen Colonization

T. E. NEBEKER[1], J. D. HODGES[2] and
C. A. BLANCHE [3]
[1]Department of [1]Entomology and[2]Forestry,
Mississippi State University, MS, USA
[3]Department of Plant and Soil Sciences,
Southern University and A & M College, Baton
Rouge, LA, USA

8.1 INTRODUCTION

Bark beetles must identify suitable hosts to colonize. Colonization then requires overcoming the resistance mechanisms of the host tree in order to successfully utilize the resource, but this can be accomplished only by recruitment of a critical minimum number of beetles (Wood, *1972;* Hodges *et al., 1979, 1985;* Chapter *6).* The mechanism by which the host attempts to resist the invasion of bark beetles and their associated fungi has two recognized components: (1) the preformed or constitutive (primary) resin system and *(2)* the induced hypersensitive response. The oleoresin system in pines traditionally has been considered the primary defense against attack by bark beetles *(Vité, 1961;* Rudinsky, *1966;* Reid *et al., 1967;* Smith, *1975;* Hodges *et al., 1979).* This chapter evaluates these two components in relation to the colonization process and its effect on the survival or death of the host tree.

8.2 RESPONSE TO INITIAL COLONIZATION

Host selection has been attributed to the efforts of the first beetles to arrive. Colonization of the potential host begins with the biting process that is stimulated by chemical and physical cues (Chapter *6).* This process is not particularly well understood. The cues used in host finding may also be stimuli for host selection and colonization. Thomas *et al. (1981)* assayed for biting responses of *Dendroctonus frontalis* to bark extracts of different polarities. The greatest number of biting responses was elicited when outer bark extracts were tested. By contrast, *Ips paraconfusus* distinguished a host, *Pinus ponderosa,* from a nonhost, *Abies concolor,* only after beetles had bored through the outer bark into the phloem (Elkinton and Wood, 1980). Tunneling by *D. frontalis* was influenced by diethyl ether and methanol extracts of inner and outer bark of *Pinus taeda* (White, 1981). White (1981) viewed these responses as indicative of responses to gustatory stimulants and deterrents. Considerable variation was observed and attributed to the variability in the hosts.

Raffa and Berryman (1982a), investigating the gustatory cues in the orientation of *D. ponderosae* to host trees, found that both benzene and methanol-water extracts increased feeding activity. Non-polar host compounds exhibited greater incitant (initiation of feeding) properties, while polar compounds were more powerful stimulants for the continuation of feeding.

Cues other than chemical signals also may be important in initiating the colonization process. Mattson and Haack (1987) hypothesized that some bark- and wood-boring species might utilize (orient toward) drought-induced acoustic signals during host selection and colonization. Such ultrasonic emissions produced as a result of water columns breaking in the xylem of stressed trees

may serve as short-range stimuli to trigger the biting response and initiate the boring process. They may also act synergistically with other cues, such as bark texture (Elkinton and Wood, 1980) to enhance the behavioral response.

Once the adults have cut through the outer bark and into the inner bark and cambial tissue, resin ducts are severed and resin flow usually begins. At this point the adults spend time removing the resin from the entrance hole as it flows. The adults must cope with both the preformed and induced defense systems in order to colonize.

8.2.1 Preformed defensive system

Many coniferous species have a well defined resin duct system, while others do not (Chapter 5). The preformed resin system is most highly developed in coniferous species that are capable of mobilizing large quantifies of oleoresin to pitch out large numbers of attacking beetles (Christiansen *et al.,* 1987). In *P. taeda,* which has a well-formed resin duct system, formation of the radial resin ducts and their associated secretory cells is influenced by the age and growth rate of the annual ring in which the ducts are formed (DeAngelis *et al.,* 1986; Chapter 5). These radial resin ducts and associated epithelial cells serve two functions in the defense of the tree: (1) synthesis of new resin, and (2) delivery of resin to attack sites. Resin flow is the most important characteristic of this system for colonizing bark beetles and is partially under genetic control (Hodges *et al.,* 1977, 1979; Nebeker and Hodges, 1983; Nebeker *et al.,* 1988). Chapters 5 and 6 provide information on resin production and contribution to tree defense. This section will focus on the effects of disturbance and successful bark beetle and pathogen colonization on resin flow and chemistry.

Varying amounts of resin may be stored in this system and available upon demand to resist attack by bark beetles. The amount and rate of delivery of preformed resin, in *P. taeda,* are determined by (1) volume of the resin-producing system, (2) size of the resin pool at the time of attack, (3) physiological state of the system at time of attack, and (4) resin viscosity (DeAngelis *et al.,* 1986).

Resin flow can be stimulated or blocked by disturbance. Blanche *et al.* (1985a) reported that no oleoresin exudation could be detected in a lightning-struck *P. taeda* for at least 3 days following the strike. Eleven days after strike the flow was about 10% of that before the strike. Twenty-one days after the strike the flow had increased to about 2.3 times pre-strike levels. Resin flow from the unstruck control tree remained at about the same level during the period of observation.

Resin flow also is altered in root pruned and basally wounded trees. Blanche *et al.* (1985b) reported that root pruning on two sides of *P. taeda* significantly reduced total resin flow 2 weeks after treatment. Normal flow was restored 7 months later. On the other hand, basal wounding stimulated resin flow for 10 months. Apparently, basal wounding stimulates the accumulation of resin precursors, resulting in an increase in available resin.

If the tree is successfully attacked, resin flow drops off rapidly (Christiansen et al., 1987; Hodges *et al.*, 1989). Hodges et al. (1989) noted that the decrease in flow begins below and well above the attack zone and takes place within the first 2 days after initial attack. However, resin flow is evident at a reduced level up to 6 days after initial attack in the upper section of the infested *P. taeda* bole.

Resin chemistry also plays a role in the ability of a tree to resist attack by bark beetles and associated fungi. Toxicity tests of substances in pine oleoresin demonstrated that several monoterpenes are toxic to *D. frontalis (Coyne* and Lott, 1976). Those found to be toxic were limonene, *alpha*-pinene, *beta*-pinene, myrcene and *delta*-3-carene. Smith (1966) found the same monoterpenes to be toxic to other *Dendroctonus* spp. but in a slightly different order. Popp *et al.* (1991) reported that *Ophiostoma minus* and *0. ips* stimulated resin flow in *P. elliottii* and *P. taeda.* It appears that monoterpenes have antibiotic and repellent properties (Callaham, 1966; Bordasch and Berryman, 1977).

Trees struck by lightning exhibit dramatic changes in levels of specific monoterpenes (Blanche *et al.*, 1985a). Three weeks after being struck by lightning, the *alpha*-pinene level in *P. taeda* had increased 71%. Myrcene and camphene followed the same pattern of increase, with myrcene increasing more than three-fold. However, *beta*-pinene levels declined significantly, 37 times lower than before the strike. Limonene and beta-phellandrene also declined, but in an attenuated manner.

In light of current knowledge, the observation that lightning-struck trees almost invariably serve as focal points of bark beetle infestations (Coulson *et al.*, 1983, 1985) may be the result of one or all of the following conditions (Blanche *et al.*, 1983, 1985a):

(1) Fermentation of the phloem, either by anaerobic cellular respiration or by microorganisms, could result from wounding of *P. ponderosa* by lightning. Volatile odors from fermented phloem attract newly emerged beetle adults (Johnson, 1966).

(2) Certain host volatiles are released from the exposed wood and phloem of lightning-struck pines. Some of these volatiles are attractive to *Ips* spp. (Anderson and Anderson, 1968).

(3) The sudden release of ozone following a lightning strike attracts beetles (Howe *et al.*, 1971).

(4) Microorganisms invading a lightning wound produce chemicals attractive to bark beetles (Howe *et al.*, 1971).

(5) *D. terebrans* may respond to an attractant(s), produced as a result of the strike, and in turn produce a secondary attractant responsible for attack by *D. frontalis* (Hodges and Pickard, 1971).

(6) The ejection and deposition of the debris shower from the struck tree on neighboring trees cause a short-term oleoresin release that enhances the probability of discovery and attack by pioneer beetles (Taylor, 1974).

(7) Trees become more susceptible after lightning strike owing to the absence of, or reduction in, xylem resin flow immediately after a tree is struck by lightning (Blanche *et al*., 1985a).

(8) Increased attractiveness results from quantitative changes in the volatile monoterpene fractions after the tree is struck by lightning (Blanche *et al*., 1985a).

(9) Trees become more suitable after lightning strike, due to carbohydrate alteration and reduction in the relative water content of the bark (Hodges and Pickard, 1971).

From this we can see that there are a number of ways in which a tree can become more attractive or suitable when struck by lightning. Blanche *et al.* (1983) discussed the merits of each hypothesis and reviewed the supporting literature. Given the general evolutionary success of the bark beetles, they appear capable of responding to these chemical changes and may even detoxify defensive compounds, if they occur in abundance, in order to utilize resources such as lightning struck trees.

8.2.2 Induced defensive system

The second line of defense against attacks by bark beetles and associated fungi is known as the induced defense system (induced response). By its very nature, this induced response must have an instantaneous source of stored reserves to be effective in containing invasion. This system has been referred to as secondary resinosis (Reid *et al.,* 1967), dynamic reaction zone (Shain, 1967), hypersensitive response (Berryman, 1972), and wound response (Shrimpton, 1978). Basically, this response consists of: (a) localized autolysis of parenchyma cells accompanied by rapid cellular dessication, (b) tissue necrosis (lesion formation with accumulation of toxic or allellochemic compounds), (c) secondary resinosis by adjacent secretory and parenchyma cells, and (d) formation of wound periderm to physically isolate the lesion from the mainstream of metabolism and transport (see Chapter 6).

The process works by chemically and physically containing and nutritionally depriving the invading organisms. Because this process of defense involves rapid and intense mobilization and utilization of storage reserves, particularly carbohydrates and other precursors of defensive chemicals, this constitutes a substantial drain of energy that otherwise could be channelled to growth and reproduction. For instance, a 30% decrease in soluble sugars and a 15% decrease in reducing sugars in the reaction zone of *Ophiostoma clavigerwn*-inoculated *P. contorta* have been reported (Miller and Berryman, 1985). Declines of 36%, 80%, and 300% in amino nitrogen, carbohydrates, and triglyceride fatty acids, respectively, have been observed during a 5-week incubation period in *P. taeda* inoculated with *0. minus* (Richmond *et al*., 1970). Barras and Hodges (1969) reported a drastic reduction in reducing sugars, but starch remained unchanged, in the inner bark of *P. taeda* treated with *D. frontal*is-microorganism complex and two beetle-associated fungi.

Conifers that lack well developed resin duct systems, i.e. species in the genera *Abies, Tsuga, Cedrus, and Pseudolarix* (Cates and Alexander, 1982), rely primarily on this induced defense strategy to contain invasion, whereas those with a well developed resin duct system, such as *Pinus*, defend themselves against invading organisms primarily through the preformed or constitutive defense system. However, pines also possess the ability to defend themselves through the induced defense system. The occurrence of hypersensitive response in *P. taeda* has been documented (Shain, 1967; Hain *et al.,* 1983; Paine *et al.,* 198S). Whether this induced defense system is effective in preventing successful host colonization by bark beetles has not been demonstrated unequivocally. There are observations of dead beetles within a fully formed hypersensitive lesion (Berryman, 1969; Christiansen and Horntvedt, 1983; Stephen and Paine, 1985), but it is not known if this was a result of resinosis or other factors.

The induced response is considered to be a more universal defensive system than the preformed defense system (Cates and Alexander, 1982). We suggest, however, that it probably has a minor role in the defense of *Pinus* spp. against bark beetle-fungus invasion in the southern US, largely due to the rapid mass attack behavior of *D. frontalis. This* certainly merits further investigation.

At present there are no hard data comparing the efficacies of these two defense systems with respect to bark beetle-microorganism invasion. However, Russell and Berryman (1976) reported that the induced system of *Abies grandis*, a conifer that lacks a well developed resin duct system, was more effective than the preformed resin system in preventing infection by *Trichosporium symbioticum*, a fungal associate of *Scolytus ventralis*. Also, Christiansen *et al*. (1987) concluded from the literature that the impregnation of the necrotic area with resinous and phenolic compounds prevents beetle gallery construction and fungal proliferation (Reid *et al*., 1967; Berryman, 1969; Richmond *et al*., 1970; Shrimpton, 1973). In *Picea* the first response is the quick death of phloem tissue in an elliptical area adjacent to the egg gallery and secretion of resin (Safranyik, 1988). The dead tissue eventually is

sealed off by wound periderm and sloughed. Within 3-6 weeks, traumatic resin ducts form on the xylem side of the cambium adjacent to the wound and completely surround the dead tissue, which becomes resin soaked (Safranyik, 1988).

Hypersensitive responses induced by bark beetle-associated-fungi have been reported to vary with season (Paine, 1984; Stephen and Paine, 1985; Cook *et al.,* 1986; Raffa and Smalley, 1988), tree species (Cook and Hain, 1987; Raffa and Smalley, 1988), general vigor of the tree (Raffa and Berryman, 1982b; Paine and Stephen, 1987a,b), and time of inoculation (Cook and Hain, 1987; Owen *et al.,* 1987; Raffa and Smalley, 1988). Larger lesions are formed from February to October than during the remainder of **the year in** *Pinus taeda* and *P. echinata, with* the largest lesions forming in August or September in *P. taeda* and September in *P. echinata* (Stephen and Paine, 1985; Cook *et al.,* 1986). The period during which larger lesions are formed coincides with the growing period for both species. This implies that the induced hypersensitive response depends on the physiological status or activity of the host, which in turn is influenced largely by temperature. Lesion size is also positively correlated with temperature (Cook *et al.,* 1986). Interestingly enough, the time of peak lesion formation (Stephen and Paine, 1985; Cook *et al.,* 1986) coincides with the peak of resin flow (September) in *P. taeda* under generally mild soil water deficit (Lorio *et al.,* 1990). This suggests that these two defense systems respond in accordance with the growth and differentiation principles as discussed in Chapter 5 and Lorio *et al.* (1990). These two defense systems may act in concert, rather than one after the other, in containing invasion.

Qualitative and quantitative variations in the chemistry of this response have been reported (Shain, 1967; Hadwiger and Schwochan, 1969; Kosuge, 1969; Shain and Hillis, 1971; Russell and Berryman, 1976; Hemingway *et al.,* 1977; Shrimpton, 1978; Ryan, 1979; Cates and Alexander, 1982; Raffa and Berryman, 1983; Gambliel *et al.,* 1985; Paine *et al.,* 1987). Comparing monoterpenes of induced lesion and sapwood resin from *P. taeda* inoculated with *0. minus,* Paine *et al.* (1987) showed significant differences in the quantitative and qualitative composition of these two defensive systems. The lesion resin is qualitatively richer in monoterpenes than is the sapwood resin. Two unknown monoterpenes were detected in the lesion but not in the sapwood resin. Quantitative characterization of the secondary chemistry of this induced response in *P. taeda* revealed considerable variation among individual trees (Gambliel *et al.,* 1985) which suggests an influence of individual tree vigor in the effectiveness of the induced system for infection containment. Although Gambliel *et al.* (1985) found similar monoterpenes, resin acids, and condensed tannins in both sterile and fungal inoculations, the latter caused greater than 40-fold increase in the accumulation of monoterpenes and a 20-fold increase in resin acids over those found in the sterile inoculations. Levels of condensed tannins, a reflection of proteincomplexing capacity, decreased slightly relative to the controls. Gambliel *et al.* (1985) suggested that condensed tannins do not play a defensive role against *0. minus.* In fact, Hemingway *et al.* (1977) found that the condensed tannins, catechin, and flavonols were degraded by *0. minus.* The stilbenes pinosylvin, pinosylvin monomethyl ether, and resveratrol also were found to decline in *P. taeda* phloem and xylem inoculated with *0. minus,* during the later stages of incubation, suggesting the detoxification of these compounds by *0. minus.* Also isolated from *0. minus*-inoculated *P. taeda* phloem in significant quantity was 4-allyl anisole, a phenylpropanoid previously unreported in *P. taeda* (Gambliel *et al.,* 1985). Interestingly, this compound recently has been demonstrated to be highly inhibitory to the three symbiotic fungi associated with *D. frontalis* (Bridges, 1987). Whether this compound is a newly evolved chemical, as a result of selection pressure, or a pre-existing compound missed in previous investigations, is an interesting but challenging question worth investigating.

Although our understanding of the chemistry of this induced defense system in pines, as discussed above, is limited, it appears that many of the phenolic (polyphenolic) compounds isolated and identified from the hypersensitive lesion of *P. taeda* play very little or no role in host defense against the fungi associated with *D. frontalis.* Effects of individual compounds or groups of compounds from the hypersensitive lesions of specific hosts on known specific invading organisms should be assessed experimentally. This would improve understanding of the defensive strategies of conifers against the invasion by bark beetle-fungal associations and ultimately produce a clearer picture of the host-bark beetle-microorganism interactions.

8.3 TREE DECLINE

8.3.1 Decline process

After bark beetles have successfully overcome the tree's preformed and induced defensive system by mass attack, colonization begins. This involves two major events: (1) introduction of associated microorganisms into the phloem and xylem tissues and (2) the physical construction of the egg gallery.

Tree-killing bark beetle species introduce a number of fungal organisms. The amount of fungal inoculum introduced into the xylem generally is accepted to be important with respect to eventual death of the tree (Wood, 1972, 1982; Hodges *et al.,* 1985). The fungi penetrate and kill live tissue surrounding bark beetle galleries and enhance host colonization by the beetles (Safranyik 1988).

Successful attack by most bark beetles usually results in the death of the tree. Anderson (1960) suggested several mechanisms by which the associated fungi could cause rapid host death. These include: (1) toxin production, (2) mycelial plugging of the tracheids, (3) release of gas bubbles into the tracheids, and (4) production of particles that block the pit openings by causing tori aspiration. Shepard and Watson (1959) suggested that *Ophiostoma* spp. reduce stored food in the paranchyma cells and restrict water conduction by destroying the ray parenchyma cells that partially control water movement.

There are, however, strip attacks in which the beetles successfully kill vertical strips of phloem, but the tree survives (Miller and Keen, 1960). When resinosis is extensive, the invading beetles are pitched out or heavy brood mortality results; *Ophiostoma* becomes entombed in the resinous tissue, and the tree survives. However, in successful *D. rufipennis* attacks on fully or strip-attacked trees, windfall, and logs, neither resin-producing tissues nor wound periderm is produced to any significant extent (Safranyik, 1988).

We put forth a hypothesis (Hodges *et al.,* 1985) that has served as a basis for investigating the role of the microorganisms in the death of the tree in the southeastern US. The success of beetle attack, and thus the death of the tree, is directly related to the complete circumferential introduction of fungal inoculum into the living tree. The subsequent production of toxic substances by the pathogen in turn alters physiological processes (e.g. water relations) in the tree, and makes the tree far more susceptible to subsequent attacks. Relative resistance is, therefore, a function of the ease with which inoculum can be introduced and successfully established.

An important consequence of beetle attack is the disruption of normal plant water relations that eventually leads to severe water stress (DeAngelis *et al.,* 1986). Secondary symptoms often attributed to water stress include: (1) rapid drop in turgor pressure throughout living cells of the bole, as evidenced by reduction in oleoresin exudation pressure shortly after successful beetle invasion; (2) blockage or aspiration of tracheids and concomitant reduction in the volume of water transported to the crown (Basham, 1970); and (3) drying of the outer bole tissues as water is withheld from below and within (Nelson, 1934; Basham, 1970). Cause and effect relationships have not been elucidated clearly. Symptoms may result from blockage of xylem tracheids by fungal hyphae, by toxic fungal metabolites, or by aspiration of individual tracheids when tracheid walls are penetrated by growing hyphae (DeAngelis *et al.,* 1986). Any or all of the above may occur after fungal inoculation, but none has been proven responsible for tree death, nor has the possible involvement of other mechanisms been eliminated (Hodges *et al.,* 1989).

Accumulating evidence suggests the involvement of toxic fungal metabolites in overcoming tree resistance and causing the death of the tree. Hemingway *et al.* (1977) and McGraw and Hemingway (1977) isolated three phenolic acids from liquid cultures of *0. minus* and from infected tissues of *P. taeda.* The compounds isolated were 6,8-dihydroxy-3-hydroxymethyl isocoumarin (Compound I), 6,8-dihydroxy-3-methyl isocournarin (Compound II) and 3,6,8-trihydroxy-2-tetralone (Compound III). Compound I was in greatest abundance followed by II. Compound III was isolated only from the liquid culture and not from infected *P. taeda* tissue. DeAngelis *et al.* (1986) verified the production of Compounds I and II and demonstrated that purified extracts from liquid cultures greatly increased the rate of water loss from seedlings when applied to cut stems.

Concerning the effects of these compounds on various physiological processes, Hodges *et al.* (1989) found that at least one of the phenolic compounds (Compound I) appears to increase transpiration rates in *P. taeda.* Apparently, this occurs as a result of decreased stomatal control of water loss in infected trees. Of special interest is the slowness with which moisture stress develops even though transpiration has increased. This suggested that water transport in the stem is not markedly affected, at least in the early stages of beetle attack. Large reserves of water in the bole could ameliorate the effects of increased transpiration. Parmeter *et al.* (1989, 1992) reported limited occlusion of sapwood by *0. minus* and *Leptographium terebrantis* in 17-32 cm DBH (diameter at breast height) *P. ponderosa;* water moved readily through uncolonized sapwood. The rate of sapwood occlusion was considered inadequate *per se* to account for moisture stress in colonized trees. Even though moisture stress does not develop rapidly, the increased water loss over time is likely to be a major factor in desiccation of the foliage and eventual death of the tree.

The mechanism(s) responsible for the decrease in oleoresin flow and pressure in trees attacked by bark beetles has not been identified. However, Blanche *et al.* (1983) concluded that moisture stress does not increase rapidly in infested trees as a result of excessive water loss, introduction of air bubbles, or blockage of the transport system, as suggested by Anderson (1960). Thus, the decrease in resin flow is not the result of a rapid increase in moisture stress. This factor may contribute later to the death of the tree but is not responsible for the initial decrease in resistance. One possible explanation for the rapid decrease in flow is a decrease in turgor pressure of the epithelial cells surrounding the resin ducts. This could result from toxic effects of compounds produced by *0. minus* or other fungi (Hodges *et al.,* 1989).

Mechanical wounding, to simulate beetle attacks, causes a rapid decrease in resin flow. Thus, reduced resin flow may result simply from rapid draining of the oleoresin reservoir through the hundreds of wounds caused by attacking beetles. This does not rule out the effects of associated fungi on tree water relations and the eventual death of the tree (DeAngelis *et al.,* 1986).

8.3.2 Visual symptoms

Boring dust and pitch tubes are usually the first signs of bark beetle attack. The initial boring dust is the color of the bark. This dust accumulates on the upper surfaces of the understory and in spider webs at or near the base of the tree. The initial resin flow is clear, but turns pink as boring dust becomes mixed with it. The resin then begins to turn white as it reacts with the air and hardens. The size of the pitch tube is proportional to the size of the attacking beetle and amount of resin available to defend against invasion at that point in time. Although the amount of available resin depends on a number of factors, pitch tubes may not be formed during drought periods, and may be larger than normal during periods of excess moisture.

Foliar color changes occur as a result of bark beetle/fungal colonization and subsequent death of the tree. The foliage gradually changes from green to light brown ("fader") to red ("red top"), and finally falls to the ground. The rate of color change varies with

season of the year, geographic location, and tree-species (Coulson and Witter, 1984). An interesting observation is that the foliage of the host tree always exhibits a deep red color when killed by *D. frontalis* but not by other agents (personal observation).

The point at which tree death has occurred has been debated for a long time. We suggest that a tree is dead when it no longer can recover sufficiently for resin flow to resume. For example, when a tree is struck by lightning the resin flow ceases but resumes after a period of time if the tree is not colonized by bark beetles or killed by the strike (Blanche *et al.,* 1985a).

8.3.3 Fungal growth and wood staining

Fares *et al.* (1980a) described basic tree anatomy and general fungal growth patterns. The hyphae of *0. minus* are initiated from spores deposited by beetles in their egg galleries in the phloem-cambiurn tissues. The hyphae enter the wood primarily through the wood rays. Thus, their initial growth is radially inward. Fares *et al.* (1980b) estimated fungal growth rate at 2.5 mm day^{-1} under favorable conditions, using data presented by Lagerberg *et al.* (1927). Paine and Stephen (1987a) observed that *0. minus* associated with *D.frontalis* grew 20 mm in the phloem within 48 hours of inoculation. At 15-30'C the rates of spread were 10-15 mrn week^{-1} and 50 mm week^{-1} in the radial and longitudinal directions, respectively, in artificially inoculated samples of *P. sylvestris* wood (Hennington and Lundstrom, 1974). Eventually, the three-dimensional pattern of *0. minus* spread varies 1:2:7 to 1:4:15 in the tangential, radial, and longitudinal directions, respectively (Fares *et al.,* 1980a). Goldhammer *et al.* (1989) investigated the radial growth rate and chlamydospore production of *0. minus, 0. minus* var. *barrasii* and SJB 122 on three different media. They concluded, as have others (Parmeter *et al.,* 1992), that growth rate depends on tree condition or nutritional status.

Parmeter *et al.* (1989) measured growth of single and paired isolates of *0. minus* and *0. nigrocarpum* from *D. brevicomis,* and *0. ips* and *Letographium terebrantis* from *D. valens* inoculated into small (10-25 cm DBH) *P. ponderosa.* Rates of spread in the radial direction varied from 2 mm week^{-1} for *0. nigricarpum* to 6 mm week^{-1} for *L. terebrantis* and in the longitudinal direction from 0.3 mm week^{-1} for *0. nigricarpum* to 20 mm week^{-1} for *L. tere*brantis. Radial penetration of *L. terebrantis* alone was significantly greater than penetration when this pathogen was coinoculated with *0. ips*.

A generally observed phenomenon in bark beetle-colonized trees is the blue coloration of the sapwood. This staining has been attributed to *Ophiostoma* introduced by the bark beetles during the colonization process. This sapwood discoloration is believed to be a result of chelation of iron by iron chelating agents called siderophores. Metabolites formed by *0. clavigerum*, *0. ips*, and *0. huntii* in still culture include 2,3-dihydroxybenzoic acid, a known iron-chelating agent (Ayer *et al*., 19.86). Ayer et al. (1986) were able to induce blue staining in *P. taeda* sapwood shavings using a methanol solution of 2,3-dihydroxybenzoic acid. In our tests of cell membrane impairment by metabolites produced by *Ophiostoma*, we also observed blue staining of *P. taeda* callus when treated with aqueous solution of the same compound (Blanche, Nebeker, and Hodges, unpublished data).

Ophiostoma minus in still cultures forms a different iron-chelating agent identified as ceratenolone (Ayer *et al*., 1987). Although 2,3-dihydroxybenzoic acid and ceratenolone are capable of forming ferric complexes, these were not detected in the blue-stained wood of diseased *P. taeda* (Ayer and Migaj, 1989). Thus, the iron chelates of these compounds may not be responsible for the blue coloration, although the iron chelates could have been lost in the extraction and partitioning process or, alternatively, other iron chelating agents may remain to be identified.

The role of staining in host colonization is not entirely clear but early investigations demonstrated that stained portions of the sapwood were generally drier than unstained portions, and that water conduction was impaired in stained portions (Nelson, 1934; Caird, 1935; Bramble and Holst, 1940; Mathre, 1964). Hence, the implication of the blue-staining fungi in the rapid death of the host has attracted considerable research attention. However, observations of pines successfully colonized by bark beetles without *Ophiostoma* (Hetrick, 1949; Whitney and Cobb, 1972; Bridges *et al.*, 1985) challenged the importance of the fungi in host mortality. In fact, we have observed *P. taeda*, attacked by *D. frontalis* that remained alive despite extensive blue staining of the sapwood (Blanche and Nebeker, unpublished data). Based on their studies on the relationship between *Ophiostoma* and bark beetle activity, Bridges *et al.* (1985) suggested that the absence of blue stain in *D.frontalis*-infested trees can be an indicator of *D. frontalis* outbreaks (see Chapter 7). In light of these observations, efforts to elucidate the roles of other bark beetle-associated microorganisms (non-staining) in the death of the host must be intensified to gain a full understanding of the cause of host mortality.

8.4 CONCLUSIONS

The preformed and induced systems have been assumed to be responsible for host resistance to successful beetle attack. The induced system may be particularly important to tree survival, by preventing growth or spread of the pathogenic fungi associated with the beetles. However, the importance of these systems in preventing death of the tree cannot be evaluated adequately until we know the exact role of the fungi in the death of the tree.

The preformed (constitutive) oleoresin system of pines is considered to be the primary defense against bark beetle attack. This assumption appears justified, but has not been demonstrated conclusively, largely because oleoresin flow in individual trees cannot be manipulated without seriously altering other processes in the tree. Also, the decrease in oleoresin flow after beetle attack has been assumed to result from moisture stress, but our recent work indicates other factors. We suggest that the rapid reduction in oleoresin

flow following bark beetle attack results from mass wounding and a depletion of the oleoresin reservoir in the tree, not from moisture stress. We further suggest that the fungi, or compounds produced by the associated fungi, are not responsible for the initial decrease in oleoresin flow but do have an effect on tree water relations and are likely to be involved in the eventual death of the tree.

When bark beetles attack a tree, death of the tree occurs as a result of progressive events initiated by both the beetle and its associated fungi. Steps in the decline process involve suppression of initial tree resistance, inoculation of fungi in beetle galleries, production of fungal metabolites, alterations of host physiological functions by the metabolites, and subsequent death of the tree.

REFERENCES

Anderson, R.F. (1960). "Forest and Shade Tree Entomology" John Wiley and Sons, New York, 428 pp.

Anderson, N.H. and Anderson, D.B. (1968). *Ips* bark beetle attacks and brood development on a lightning-struck pine in relation to its physiological decline. *Florida Entomol.* **51 (l),**23-30.

Ayer, W.A. and Migaj, B.S. (1989). Acids from blue-stain diseased lodgepole pine. *Can. J. Bot.* **67**,1426-1428.

Ayer, W.A., Browne, L.M., Feng, M.C., Orszanska, H. and Saeedi-Ghomi, H. (1986). The chemistry of the blue-stain fungi. I. Some metabolites of *Ceratocystis* species associated with mountain pine beetle infected lodgepole pine. *Can. J. Chem.* **64**, 904-909.

Ayer, W.A., Attah-Poku, S.K., Browne, L.M. and Orszanska, H. (1987). The chemistry of the bluestain fungi. III. Some metabolites of *Ceratocystis minor* (Hedgc.) Hunt. *Can. J. Chem.* **65**, 765-769.

Barras, S.J. and Hodges, J.D. (1969). Carbohydrates of inner bark of *Pinus taeda* as affected by *Dendroctonus frontalis* and associated microorganisms. *Can. Entomol.* **101***, 489-493.

Basham, H.G. (1970). Wilt of loblolly pine inoculated with blue-stain fungi of the genus *Ceratocystis. Phytopathology* **60**, 750-754.

Berryman, A.A. (1969). Response of *Abies qrandis* to attack by *Scolytus ventralis* (Coleoptera: Scolytidae). *Can. Entomol.* **101***, 1033-1041.

Berryman, A.A. (1972). Resistance of conifers to invasion by bark beetle-fungus association. *BioScience* **22,** 598-602.

Blanche, C.A., Hodges, J.D., Nebeker, T.E. and Moehring, D.M. (1983). Southern pine beetle: the host dimension. Mississippi Agric. For. Exp. Stn. Bull. 917, 29 pp.

Blanche, C.A., Hodges, J.D. and Nebeker, T.E. (1985a). Changes in bark beetle susceptibility indicators in a lightning-struck loblolly pine. *Can. J. For. Res.* **15**, 397-399.

Blanche, C.A., Nebeker, T.E., Hodges, J.D., Karr, B.L. and Schmitt, J.J. (1985b). Effect of thinning damage on bark beetle susceptibility indicators in loblolly pine. *In* "Proc. 3rd Biennial Southern Silvicultural Res. Conf." (E. Shoulders, ed). pp. 471-479. USDA Forest Serv. Gen. Tech. Rep. SO-54. USDA Forest Serv., Southern Forest Exp. Stn., New Orleans, LA.

Bordasch, R.P. and Berryman, A.A. (1977). Host resistance to the fir engraver beetle, *Scolytus ventralis* (Coleoptera: Scolytidae) 2. Repellency of *Abies qrandis* resins and some monoterpenes. *Can. Entomol.* **109,** 95-100.

Bramble, W.C. and Holst, E.C. (1940). Fungi associated with *Dendroctonus* in killing shortleaf pines and their effect on conduction. *Phytopathology* **30***, 881-899.

Bridges, J.R. (1987). Effects of terpenoid compounds on growth of symbiotic fungi associated with the southern pine beetle. *Phytopathology* **77**, 83-85.

Bridges, J.R., Netteleton, W.A. and Conner, M.D. (1985). Southern pine beetle (Coleoptera: Scolytidae) infestations without the blue-stain fungus, *Ceratocystis minus. J. Econ. Entomol*. **78**, 325-327.

Caird, R.W. (1935). Physiology of pines infected with bark beetles. *Bot. Gaz.* **96**, 709-733.

Callaham, RX (1966). Nature of resistance of pines to bark beetles. *In* "Breeding Pest-resistant Trees" (H.D. Gerhold, R.E. McDermott, E.J. Schreiner and J.A. Winieski, eds), pp. 197-206. Pergamon Press, Oxford.

Cates, R.G. and Alexander, H. (1982). Host resistance and susceptibility. *In:* "Bark Beetles in North American Conifers: Ecology and Evolution." (J.B. Mitton and K.B. Sturgeon, eds), pp. 212-263. University of Texas Press, Austin, TX.

Christiansen, E. and Horntvedt, R. (1983). Combined *Ips/Ceratocystis* attack on Norway spruce, and defensive mechanisms of the trees. *Z. Ang. Entomol.* **96**, 110-118.

Christiansen, E., Waring, R.H. and Berryman, A.A. (1987). Resistance of conifers to bark beetle attack: searching for general relationships. *For. Ecol. Manage.* **22**, 89-106.

Cook, S.P. and Hain, F.P. (1987). Four parameters of the wound response of loblolly and slash pines to inoculation with the blue-staining fungus associated with the southern pine beetle. *Can. J. Bot.* **65**, 2403-2409.

Cook, S.P., Hain, F.P. and Nappen, P.B. (1986). Seasonality of the hypersensitive response by loblolly and shortleaf pine to inoculation with fungal associates of the southern pine beetle (Coleoptera: Scolytidae). *J. Entomol. Sci.* **21(3),** 283-285.

Coulson, R.N. and Witter, J.A. (1984). "Forest Entomology: Ecology and Management?" John Wiley & Sons, Inc., New York. 669 pp.

Coulson, R.N., Hennier, P.B., Flamm, R.O., Rykiel, E.J., Hu, L.C. and Payne, T.L. (1983). The role of lightning in the epidemiology of the southern pine beetle. *Z. Ang. Entomol.* **96**, 182-193.

Coulson, R.N., Saunders, M.C., Payne, T.L., Flamm, R.O., Wagner, T.L., Hennier, P.B. and Rykiel, E.J. (1985). A conceptual model of the role of lightning in the epidemiology of the southern pine beetle. *In* "The Role of the Host in Population Dynamics of Forest Insects" (L. Safranyik, ed.), pp. 136-146. Canadian Forestry Serv., Pacific Forestry Centre, Victoria, BC.

Coyne, J.F. and Lott, L.H. (1976). Toxicity of substances in pine oleoresin to southern pine beetles. *J. Ga. Entomol. Soc.* **11(4)**, 297-301.

DeAngelis, J.D., Nebeker, T.E. and Hodges, J.D. (1986). Influence of tree age and growth rate on the radial resin duct system in loblolly pine *(Pinus taeda). Can. J. Bot.* **64,** 1046-1049.

Elkinton, J.S. and Wood, D.L. (1980). Feeding and boring behavior of the bark beetle *Ips paraconfusus* (Coleoptera: Scolytidae) on the bark of a host and non-host tree species. *Can. Entomol.* **112**, 797-809.

Fares, Y., Goeschl, J.D. and Sharpe, P.J.H. (1980a). Dynamics of bark beetle-fungus symbiosis: I. pine tree anatomy and fungus growth pattern. *In* "Modeling Southern Pine Beetle Populations" (F.M. Stephen, J.L. Searcy and G.D. Hertel, eds), pp. 54-60. USDA Forest Serv. Tech. Bull. No. 1630. USDA Forest Serv., Washington, DC.

Fares, Y., Magnuson, C.E., Doraiswamy, P.C. and Sharpe, P.J.H. (1980b). Dynamics of bark beetle-fungus symbiosis: II. pine tree drying model. *In* "Modeling Southern Pine Beetle Populations" (F.M. Stephen, J.L. Searcy and G.D. Hertel, eds), pp. 61-74. USDA Forest Serv. Tech. Bull. No. 1630. USDA Forest Serv., Washington, DC.

Gambliel, H.A., Cates, R.G., Caffey-Maquin, M.K. and Paine, T.D. (1985). Variation in the chemistry of loblolly pine in relation to infection by the blue-stain fungus. *In* "Integrated Pest Management Research Symposium: The Proceedings" (S.J. Branham and R.C. Thatcher, eds), pp. 177-184. USDA Forest Serv. Gen. Tech. Rep. SO-56. USDA Forest Serv., Southern Forest Exp. Stn., New Orleans, LA.

Goldhammer, D.S., Stephen, F.M. and Paine, T.D. (1989). Average radial growth and chlamyhdospore production of *Ceratocvstis minus, Ceratocystis minus* var. *barrasii* and SJB 122 in culture. *Can. J. Bot.* **67**, 3498-3505.

Hadwiger, L. and Schwochan, M. (1969). Host resistance responses - an induction hypothesis. *Phytopathology* **7,** 13-22.

Hain, F.P., Mawby, W.D., Cook, S.P. and Arthur, F.H. (1983). Host conifer reaction to stem invasion. *Z. Ang. Entomol.* **96,** 247-256.

Hemingway, R.W., McGraw, G.W. and Barras, S. (1977). Polyphenols in *Ceratocystis minus* infected *Pinus taeda:* fungal metabolites, phloem and xylem phenols. *Agric. Food Chem.* **25,** 717-722.

Hermington, B. and Lundstrom, H. (1974). "The Growth of Insect-borne Blue-stain, and Effects caused by Immersion of the Wood; Some Laboratory Tests" Rapporter, Institutionen for Virkeslara No. R 92, 20 pp.

Hetrick, L.A. (1949). Some overlooked relationships of southern pine beetle. *J. Econ. Entomol.* **42**, 466-469.

Hodges, J.D. and Pickard, L.S. (1971). Lightning in the ecology of the southern pine beetle, *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Can. Entomol.* **103***,* 44-5 1.

Hodges, J.D., Elam, W.W. and Watson, W.F. (1977). Physical properties of the oleoresin system of the four major southern pines. *Can. J. For. Res.* **7**, 520-525.

Hodges, J.D., Elam, W.W., Watson, W.F. and Nebeker, T.E. (1979). Oleoresin characteristics and susceptibility of four southern pines to southern pine beetle (Coleoptera: Scolytidae) attacks. *Can. Entomol.* **111***,* 889-896.

Hodges, J.D., Nebeker, T.E., DeAngelis, J.D., Karr, B.L. and Blanche, C.A. (1985). Host resistance and mortality: a hypothesis based on the southern pine beetle-microorganism-host interactions. *Bull. Entomol. Soc. Am***. 31(l),** 31-35.

Hodges, J.D., Nebeker, T.E., Blanche, C.A., Honea, C.R., Fisher, T.H. and Schultz, T.P. (1989). Southern pine beetle-microorganisms-host interactions: influence of compounds produced by *Ceratocystis minor. In* "Proceedings 5th Silvicultural Research Conference" (J.H. Miller, ed.). pp. 567-572. USDA Forest Serv. Gen. Tech. Rep. SO-74. USDA Forest Serv., Southern Forest Exp. Stn., New Orleans, LA.

Howe, V.K., Oberle, A.D., Keeth, T.G. and Gordon, W.J. (1971). The role of microorganisms in the attractiveness of lightning-struck pines to southern pine beetles. Western Illinois University Bull. Vol. L, No. 3. (Series in Biological Sciences 9), 44 pp.

Johnson, P.C. (1966). Attractiveness of lightning-struck ponderosa pine trees to *Dendroctonus brevicomis* (Coleoptera: Scolytidae). *Ann. Entomol. Soc. Am.* **59***,* 615.

Kosuge, T. (1969). The role of phenolics in host response to infection. *Annu. Rev. Phytopathol.* **7***,* 195-222.

Lagerberg, T., Lundberg, G. and Melin, E. (1927). Biological and practical researches into blueing in pine and spruce. Sveska Skogsvardsfor. *Tidsk Haft* **II***,* 145-272.

Lorio, P.L., Jr., Sommers, R.A., Blanche, C.A., Hodges, J.D. and Nebeker, T.E. (1990). Modeling pine resistance to bark beetles based on growth and differentiation balance principles. *In* "Forest Growth: Process Modeling of Responses to Environmental Stress" (R.K. Dixon, R.S. Meldahl, G.A. Ruark, and W.G. Warren, eds), pp. 402-409. Timber Press, Portland, OR.

Mathre, D.E. (1964). Effect of *Ceratocystis ips* and *C*. *minus* on the free sugar pool in ponderosa pine sapwood. *Contrib. Boyce Thompson Inst.* **22**, 509-512.

Mattson, W.J., and Haack, R.A. (1987). The role of drought in outbreaks of plant-eating insects. *BioScience* **37***,* 110-118.

McGraw, G.W. and Hemingway, R.W. (1977). 6,8-Dihydroxy-3hydroxymethyl isocournarin, and other phenolic metabolites of *Ceratocystis minus. Phytochemistry* **16***,* 1315-1316.

Miller, J.M. and Keen, F.P. (1960). Biology and Control of the Western Pine Beetle, USDA Forest Serv. Misc. Publ. 800, USDA Forest Serv., Washington, DC, 381 pp.

Miller, R.H. and Berryman, A.A. (1985). Energetics of conifer defense against bark beetles and associated fungi. *In* "The Role of the Host in the Population Dynamics of Forest Insects." (L. Safranyik ed.), pp. 13-23. Canadian Forestry Serv., Pacific Forestry Centre, Victoria, BC.

Nebeker, T.E. and Hodges, J.D. (1983). Influence of forestry practices on host-susceptibiliry to bark beetles. *Z. Ang. Entomol.* **96***,* 194-208.

Nebeker, T.E., Hodges, J.D., Honea, C.R. and Blanche, C.A. (1988). Preformed defensive system in loblolly pine: variability and impact on management practices. *In* "Integrated Control of Scolytid Bark Beetles" (T.L. Payne and H. Saarenmaa, eds), pp. 147-162. Virginia Polytechnic Institute Press, Blacksburg, VA.

Nelson, R.M. (1934). Effect of blue-stain fungi on southern pine attacked by bark beetles. *Phytopathology* **7***,* 327-353.

Owen, D.R., Lindahl, K.Q., Jr., Wood, D.L. and Parmeter, J.R., Jr. (1987). Pathogenicity of fungi isolated from *Dendroctonus valens, D. brevicomis,* and *D. ponderosae* to ponderosa pine seedlings. *Phytopathology* **77***,* 631-636.

Paine, T.D., Stephen, F.M. and Cates, R.G. (1985). Induced defenses against *Dendroctonus frontalis* and associated fungi: variation in loblolly pine resistance. *In* "Integrated Pest Management Research Symposium: the Proceedings" (Branham, S.J. and R.C. Thatcher, eds), pp. 169-176. USDA Forest Service Gen. Tech. Rep. SO-56. USDA Forest Serv. Southern Forest Exp. Sm., New Orleans, LA.

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 Stephen, F. M. (1987a). Fungi associated with southern pine beetle: avoidance of induced defense response in loblolly pine. *0ecologia* **74**, 377-379.

Paine, T.D. and Stephen, F.M. (1987b). The relationship of tree height and crown class to the induced plant defenses of loblolly pine. *Can. J. Bot.* **65**, 2090-2092.

Paine, T.D., Blanche, C.A., Nebeker, T.E. and Stephen, F.M. (1987). Composition of loblolly pine resin defenses: comparison of monoterpenes from induced lesion and sapwood resin. *Can. J. For. Res.* **17**, 1202-1206.

Parmeter, J.R., Jr., Slaughter, G.W., Chen, M.-M., Wood, D.L. and Stubbs, H.A. (1989). Single and mixed inoculations of ponderosa pine with fungal associates of *Dendroctonus spp. Phytopathology* **79**, 768-772.

Parmeter, J.R., Jr., Slaughter, G.W., Chen, M.-M. and Wood, D.L. (1992). Rate and depth of sapwood occlusion following inoculation of pines with bluestain fungi. *Forest Sci.* **38,** 34-44.

Popp, M.P., Johnson, J.D. and Massey, T.L. (1991). Stimulation of resin flow in slash and loblolly pine by bark beetle vectored fungi. *Can. J. For. Res.* **21**, 1124-1126.

Raffa, K.F. and Berryman, A.A. (1982a). Gustatory cues in the orientation of *Dendroctonus ponderosae* (Coleoptera: Scolytidae) to host trees. *Can. Entomol.* **114**, 97-104.

Raffa, K.F. and Berryman, A.A. (1982b). Physiological differences between lodgepole pines resistant and suceptible to the mountain pine beetle and associated microorganisms. *Environ. Entomol.* **11**, 486-492.

Raffa, K.F. and Berryman, A.A. (1983). Physiological aspects of lodgepole pine wound responses to a fungal symbiont of the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae). *Can. Entomol.* **115**, 724-734.

Raffa, K.F. and Smalley, E.B. (1988). Seasonal and long-term responses of host trees to microbial associates of the pine engraver, *Ips pini. Can. J. For. Res.* **18**, 1624-1634.

Reid, R.W., Whitney, H.S. and Watson, J.A. (1967). Reactions of lodgepole pine to attack by *Dendroctonus ponderosae* Hopkins and blue-stain fungi. *Can. J. Bot.* **45**, 1115-1126.

Richmond, J.A., Mills, C. and Clark, E.W. (1970). Chemical changes in loblolly pine, *Pinus taeda* L., inner bark caused by blue-stain fungus, *Ceratocystis minus* (Hedg.) Hunt. *J. Elisha Mitchell Sci. Soc.* **86**, 171

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.

Russell, C.E. and Berryman, A.A. (1976). Host resistance to the fir engraver beetle. I. Monterpene composition of *Abies grandis* pitch blisters and fungus-infected wounds. *Can. J. Bot.* **54**, 14-18.

Ryan, C.A. (1979). Proteinase inhibitors. *In* "Herbivores: Their Interaction With Secondary Plant Metabolites" (G. Rosenthal and D. Janzen, eds), pp. 599-618. Academic Press, New York.

Safranyik, L. (1988). The population biology of the spruce beetle in western Canada and implications for management. *In* "Integrated Control of Scolytid Bark Beetles" (T.L. Payne and H. Saarenmaa, eds), pp. 3-23. Virginia Polytechnic Institute Press, Blacksburg, VA.

Shain, L. (1967). Resistance of sapwood in stems of loblolly pine to infection by *Fomes annosus. Phytopathology* **57**, 1034-1045.

Shain, L. and Hillis, W.E. (1971). Phenolic extractives in Norway spruce and their effects on *Fomes annosus. Phytopathology* **61**, 841-845.

Shepherd, R.F. and Watson, J.A. (1959). Blue-stain fungi associated with the mountain pine beetle. Canadian Dept. Agric. For. Biol. Div. Prog. Rep. **15(3),** pp. 2-3.

Shrimpton, D.M. (1973). 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. (1978). Resistance of lodgepole pine to mountain pine beetle infestations. *In* "Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests - a Symposium." (A.A. Berryman, G.D. Amman, R.W. Stark and D.L. Kibbee, eds), pp. 6476. College of Forest Resources, Univ. of Idaho, Moscow.

Smith, R. H. (1966). Resin quality as a factor in the resistance of pines to bark beetles. *In* "Breeding Pest-resistant Trees" (Gerhold, H.D., R.E. McDermott, E.J. Schreiner and J.A. Winieski, eds), pp. 189-196. Pergamon Press, Oxford.

Smith, R.H. (1975). Formula for describing effect of insect and host tree factors on resistance to westem pine beetle attack. *J. Econ. Entomol.* **68**, 841-844.

Stephen, F.M. and Paine, T.D. (1985). Seasonal patterns of host tree resistance to fungal associates of the southern pine beetle. *Z. Ang. Entomol.* **99***,* 113 -122.

Taylor, A.R. (1974). Ecological aspects of lightning in forests. Ann. Proc. Tall Timbers Fire Ecol. Conf. No. 13. Tallahassee, FL, pp. 455-496.

Thomas, H.A., Richmond, J.A. and Bradley, E.L. (1981). Bioassay of pine bark extracts as biting stimulants for the southern pine beetle. USDA Forest Serv. Res. Note SE-302. USDA Forest Serv. Southeastern Forest Exp. Stn. Asheville, NC, 5 pp.

Vité, 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.* **21,** 37-66.

White, J.D. (1981). A bioassay for tunneling responses of southern pine beetle to host extractives. J. *Ga. Entomol. Soc.* **16(4),**484-492.

Whitney, H.S. and Cobb, F.W., Jr. (1972). Non-staining fungi associated with the bark beetle *Dendroctonus brevicomis* (Coleoptera: Scolytidae) on *Pinus ponderosa. Can.* J. *Bot.* **50***,* 1943-1945.

Wood, D.L. (1972). Selection and colonization of ponderosa pine by bark beetles. *In* "Insect/Plant Relationships" (H.F. van Emden, ed.), pp. 101-117. Blackwell Scientific Publications, Oxford.

Wood, D.L. (1982). The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark-beetles. *Annu. Rev. Entomol.* **27***,* 411-446.