

INTERACTIONS AMONG SCOLYTID BARK BEETLES, THEIR ASSOCIATED FUNGI, AND LIVE HOST CONIFERS

T. D. Paine

Department of Entomology, University of California, Riverside, California 92521

K. F. Raffa

Department of Entomology, University of Wisconsin, Madison, Wisconsin 53706

T. C. Harrington

Department of Plant Pathology, Iowa State University, Ames, Iowa 50011

KEY WORDS: plant-insect interactions, insect-fungal interactions, *Dendroctonus*, *Ophiostoma*, host plant resistance

ABSTRACT

Scolytid bark beetles that colonize living conifers are frequently associated with specific fungi that are carried in specialized structures or on the body surface. These fungi are introduced into the tree during the attack process. The continuing association suggests that there is mutual benefit to the fitness of both beetles and fungi. The fungal species may benefit from the association with the beetles by transport to new host trees. Beetle species may benefit from the association with fungi by feeding on the fungi, or by the fungi contributing to the death of the host trees through mycelial penetration of host tissue, toxin release, interactions with preformed and induced conifer defenses, or the combined action of both beetles and fungi during colonization. Extensive research has been directed towards characterizing the interactions of beetle-fungal complexes with live host conifers and determining the ecological advantages for maintaining the associations. However, differences among systems and how species interact under different population and environmental conditions make it difficult to generalize about the importance of the separate biological components in successful host colonization.

INTRODUCTION

Bark Beetle Life History Strategies

Bark beetles of the family Scolytidae are among the most economically important forest insects. Although distributed across a wide range of host trees (121), primary and secondary bark beetles that feed on subcortical tissue of conifers are particularly interesting because of (a) their use of aggregation pheromones, which ensures mass colonization of host trees (253) and (b) their interactions with associated fungi. Three general scolytid life history strategies have been investigated in relation to their association with fungi: primary, secondary, and saprophytic.

Primary bark beetles in the genus *Dendroctonus* (e.g. *D. frontalis*, *D. vitei*, *D. mexicanus*, *D. adjunctus*, *D. brevicornis*, *D. ponderosae*, and *D. jeffreyi*) or *Ips* (e.g. *I. typographus*) that are near obligate parasites (197) attack healthy living trees, and kill them as a result of mass colonization (70, 253). Eggs are laid along the margins of parental galleries, and developing larvae mine into the inner bark tissue and complete their development in pupal cells constructed at the end of the larval feeding gallery. When beetle populations are at low density, primary bark beetles colonize trees of low vigor. However, when populations are at high densities, the insects can rapidly colonize and kill healthy and vigorous trees (19, 184, 193, 210, 213).

There are a few species of near obligate parasite bark beetles (e.g. species of the genus *Dendroctonus*: *D. micans* in Europe or *D. terebrans* and *D. valens* in North America) that rarely kill their host trees. These nonaggregating species colonize the base of trees that are often weakened by injury or root diseases (121, 231). The larvae of these turpentine beetles are gregarious and feed in large feeding chambers in the inner bark. Trees are rarely killed outright by the turpentine beetles, but they can predispose the trees to subsequent invasion by other bark beetles or to reinvasion by subsequent generations (93, 123).

Secondary bark beetles (e.g. *Ips pini*, *Scolytus ventralis*, *Dendroctonus rufipennis*, *Dendroctonus pseudotsugae*, *Dendroctonus simplex*, or *Tomicus piniperda*) are facultative parasites (197) capable of colonizing weakened, stressed, and recently killed trees (123, 125). Gallery construction and larval development is similar in both primary and secondary bark beetles. At low population levels, the beetles often colonize trees attacked by primary bark beetles or those heavily stressed from disease or drought. They may also use fallen trees, logging residue, or storm damaged stems. High beetle populations resulting from favorable environmental or management conditions can colonize and kill healthy trees. However, outbreaks are generally less expansive or persistent compared to those of the more aggressive primary bark beetles.

The third general life history pattern, that of herbivore/saprophyte (197), is the most common and contains the greatest number of species (254). Scolytid species in this ecological grouping colonize dead hosts. Although their life histories may be fascinating (121), interactions with living trees are minimal and not the subject of additional consideration in this review.

Distinctions Among Bark Beetle/Fungal Associations

The association of conifer-infesting bark beetles and fungi is complex (92, 101, 246). There are several general patterns, but associated fungi may be broadly divided into those carried within or outside mycangia. It is important to distinguish among the fungal species and how they are carried by the insect because this may provide insight into the nature of their relationship.

Mycangia are cuticular structures that function to carry fungal spores and mycelia (84). *Dendroctonus approximatus*, *D. frontalis*, *D. brevicomis*, and *D. adjunctus* have invaginated cuticular structures lined with secretory cells at the anterior edge of the prothorax (11–13, 96–98, 248). Among the species with thoracic mycangia, *D. frontalis* and *D. brevicomis* are best understood (12, 42, 97, 98, 102, 174, 248). Females of *D. frontalis* and *D. brevicomis* carry closely related species of unnamed basidiomycetes that are closely related to *Entomocorticium dendroctoni* (Hsia & Harrington, unpublished observations). *Ceratocystiopsis ranaculosus*, a nonstaining ascomycete, is common in the mycangium of *D. frontalis* (105), and a related *Ceratocystiopsis* species is common in the mycangium of *D. brevicomis* (102). *Ophiostoma minus*, a bluestaining ascomycete, and *Ophiostoma nigracarpum*, a nonstaining fungus, have been isolated from the external body surface of both beetles (105, 151, 209, 248).

Staining ascomycetes *Ophiostoma montium* and *Ophiostoma clavigerum* have been isolated from the maxillary mycangia on both sexes of *D. ponderosae* (249), and a staining fungus apparently closely related to *O. clavigerum* has been isolated from the maxillary mycangia of *D. jeffreyi* (176). Isolations of related basidiomycetes have been made from pupal chambers of both beetles but not from the mycangia (247). Yeasts are also commonly isolated from mycangia (248, 249). Staining *Ophiostoma ips* and *O. minus* have been isolated from the body and gallery systems of *D. ponderosae* (151).

Dryocoetes confusus has a mandibular mycangium (81) and is associated with the staining fungus *Ophiostoma dryocoetidis* (159). However, other scolytid species carry fungal spores of bluestaining species in uncovered cuticular pits on the head, prosternum, or elytra [e.g. *Scolytus ventralis* associated with *Trichosporium symbioticum* (146); *Ips sexdentatus* with *Ophiostoma brunneo-ciliatum* (130); *I. typographus* with *Ceratocystis polonica*, *Ophiostoma bicolor*, and *Ophiostoma penicillatum* (86); *D. pseudotsugae* with *Ophiostoma*

pseudotsugae (131) and *Leptographium abietinum* (100); and *D. rufipennis* with *L. abietinum* (225)]. Similarly, fungi isolated from the external surface (151) and from phoretic mites (38, 39, 130, 160–62) are frequently staining fungi.

Another fungal genus superficially similar to *Ophiostoma* is *Ceratocystis*, a group containing plant pathogens commonly associated with insect vectors but rarely associated with bark beetles (99, 101, 120). Like some *Ophiostoma* species, many *Ceratocystis* species stain sapwood and have been referred to as bluestain fungi. Associations of scolytids and *Ceratocystis* species include *C. polonica* with *I. typographus* and *C. laricicola* with *Ips cembrae* (104).

BEETLE-ASSOCIATED FUNGI AND TREE MORTALITY

The interactions among bark beetles and associated fungi in relation to host conifers have been the subject of intense study since last reviewed (92, 229). The conclusion repeated in the literature that pathogenic bluestain fungi are primarily responsible (i.e. 119) or required (246) for mortality of trees attacked by bark beetles followed a logical thread, beginning with the observations that sapwood of beetle-killed trees is stained, beetles are capable of vectoring or dispersing staining fungi, beetles are rarely found in the absence of staining fungi, and staining fungi can kill artificially inoculated trees in the absence of the beetles. A more comprehensive paradigm suggests that although the mechanisms are not fully understood (165), a tree is killed as a result of simultaneous actions and interactions of both components rather than successive actions of vector and pathogen (18). The relationship between beetles and bluestaining fungi has been described as symbiotic or mutualistic (246).

Von Schrenk (241) reported the close association between beetle-killed trees and bluestain fungi, but it was Craighead (74) and Nelson & Beal (170) who suggested that the bluestain fungi must be responsible for tree mortality because trees died too quickly to be killed solely by the girdling action of the insect. Subsequent studies clearly indicated that colonizing beetles were transmitting fungi (128, 151, 207, 209). Fungal penetration into the sapwood was associated with drying of the tissue and disruption of water conduction (14, 47, 186, 226) through aspiration of tracheid tori (169) or vascular plugging with resin (31). Isocoumarin toxins produced by the fungus may also affect water relations in the tree (77, 107, 113, 153, 172). Inoculation of the bluestain fungi has demonstrated that the fungi may be capable of killing trees if the inoculation pattern is around the tree (14, 151, 171, 234) or above a threshold density of inoculum (50, 51, 56, 57, 116, 227). However, in evaluating the significance of such pathogenicity, it is important to distinguish between the early phase of overcoming host defense (initial phloem colonization) and subsequent mortality of the host (sapwood colonization).

Host Resistance to Beetle/Fungal Invasion

Diverse bark beetle species have highly effective aggregation pheromones and close associations with pathogenic bluestain fungi, but the annual probability of the beetle-caused death of any particular tree is relatively low. Obviously, trees have effective defenses against successful beetle colonization. Berryman (18) identified preformed and induced components of conifer resistance. The preformed oleoresin and resin duct systems constitute the initial defenses encountered by attacking beetles, and the invasion process induces both cellular and biochemical changes in the host tissues that can isolate and intoxicate invading organisms. Although distinguishing between components has been a useful convention for framing research hypotheses, these constituents are best recognized as integrated elements linked to the health and vigor of the host tree and not independent characteristics of resistance (48, 165, 193). Matson & Hain (152) proposed that the relative importance of preformed and induced components of resistance would be expected to vary depending on the geographic range of the host and the number of annual generations of the colonizing insect.

The ability of the host tree to resist colonization is a function of the vigor of the tree, site and stand conditions, and the size of the beetle population (19, 184, 193, 213, 233). Through studies of beetle colonization and inoculation of fungi, it has been clearly demonstrated that host resistance has a threshold (expressed in attacks per unit bark surface) that is related to host condition (55, 58, 164, 193). The threshold concept of host resistance has been crucial to understanding how the tree responds to environmental and biotic stress (20, 23, 24, 58, 195). The colonization behavior of the beetles can be linked directly to the resistance of the tree: If beetle attack density is below the resistance threshold of the tree and the tree defenses have not been depleted, the insects will continue to produce aggregation pheromones, but aggregation is terminated once host resistance has been exhausted (20, 25, 26, 193, 197, 205).

Primary or Preformed Resistance

For conifers with well-developed resin ducts, the preformed resin system is the component of resistance first encountered by invading organisms. The flow of resin, composed of monoterpenes, sesquiterpenes, and resin acids, functions in wound cleansing by flushing wounded tissue with the initial liquid flow and then sealing the tissue through resin crystalization (18, 167, 168). Species of *Pinus* have well developed resin duct systems, but other genera of conifers (e.g. *Abies*, *Tsuga*, or *Cedrus*) do not have preformed resin ducts (7, 18, 89). Some bark beetle species, however, are not adversely affected by the preformed resin. For example, monoterpene resin toxicity is apparently not important in resistance of *Picea abies* to *D. micans* (141), but lignin stone cells in the outer

bark may be important as an alternative preformed factor conferring resistance against this beetle (243).

Primary resin biosynthesis is an energy-demanding process (119) that occurs in secretory cells lining the resin ducts of pines. Xylem resin is produced by young cells just after differentiation from meristem, and ability to secrete resin is lost as cells age (16, 89). Vertical resin ducts are produced in xylem at higher densities in latewood than earlywood, and the amount of resin flow has been correlated with the density of vertical ducts (28, 148). Horizontal or radial resin ducts connect vertical ducts in the same radial plane and are found at the same density and the same spatial pattern in both phloem and xylem tissues (28, 78, 148). Radial ducts occur in vertical bands, probably aligned with the vertical ducts, and although the pattern remains the same throughout the life of the tree, radial resin duct density decreases with tree age and diameter growth (78). The radial ducts are, however, discontinuous at the cambium (217). Consequently, the amount of resin in the phloem ducts is very low in some species, and reported rapid increases in phloem resin content upon wounding may be primarily a function of opening a link between phloem and xylem radial resin ducts (87). By definition, this cellular change connecting phloem and xylem resin ducts is an induced response and demonstrates the continuity between the preformed and induced defenses. Similarly, monoterpene resins are also rapidly induced *de novo* in injured inner bark tissues (132, 133, 135, 230) and may increase resin flow from wounds in the bark (189).

Two major factors associated with the preformed resin system are associated with resistance to beetles and fungi: (a) the chemical composition of the resin and (b) the physical properties of resin pressure, resin flow, and resin crystallization. The monoterpenes and the diterpene resin acids have antibacterial (109) and antifungal actions (37, 59, 176, 196). These compounds may have different effects, whether incorporated in the growth media or presented to the fungi as saturated vapors (59, 176), but nonpolar resin components may be primarily inhibitory to fungal growth by protecting resin-impregnated substrates from extracellular enzymes of the fungi (255). However, some resin components may actually stimulate fungal growth (176). Also, components of preformed resins can be toxic or repellent to colonizing beetles (73, 196, 202, 221), although beetles are generally more tolerant of host resins than nonhost resins (220). It has been suggested that evolution of bark beetle pheromone communication was an outcome of detoxification of the host resin system (21, 237).

Physical characteristics of the resin system have been identified as important components of host resistance to bark beetles (112). Low oleoresin pressure, derived from the transpiration stream of the tree, has been associated with susceptibility to bark beetles (48, 211, 240). High resin flow rate, a function of

both resin pressure and the reservoir of resin in the ducts, has been recognized as characteristic of resistant trees (3, 122, 166). The flow of resin can force beetles from the tree or physically stop emission of pheromones from the entrance hole (193). However, as much as 70–80% of the available resin may flow from a wound in the first eight hours (166). Thus, mass colonization by large numbers of beetles can drain the resin reservoir. Colonizing beetles will continue to produce aggregation pheromones as long as the resin system of the host remains active, but aggregation is terminated when the preformed resin is exhausted and a threshold attack density reached (150, 193).

Although the constitutive resin system is under genetic control, environmental factors and host condition can influence both physical properties and the chemical constituents of the resin (95, 166, 250). Root diseases (122, 167, 168), physical injury (29), and lightning strikes (27, 71, 114) may adversely affect resin composition and flow characteristics. Alternatively, improving growing conditions through thinning, site selection, and other management practices can increase the resistance characteristics of the preformed resin system (45, 95, 158, 175, 190).

The seasonal or ontogenetic variation in volume of resin flow seems to be critical to understanding the initial interactions between insect and host. Maximum resin flow has been associated with late spring and summer months (115, 236) or with periods of moderate moisture deficit (149, 150). Lorio has hypothesized that photosynthate produced by the foliage is allocated primarily to shoot growth when there is adequate moisture for cell expansion and to cell differentiation (including production of resin ducts and resin synthesis) when moisture is limited (148). For example, periods of *D. frontalis* peak activity (January, May, and October) coincide with periods of reduced moisture stress and reduced tree defenses; lightning struck trees may serve as reproductive refuges for beetle populations during mid-summer, when trees are under the highest moisture stress and have the greatest resin flow (70, 147).

Induced Resistance

The induced component of resistance of conifers is elicited following invasion or infection of host inner bark tissues (18, 204, 215). Induction involves cellular and biochemical changes at the affected site, including cellular necrosis, initiation of new impermeable cell layers, and synthesis of new phenolic and monoterpene constituents (163, 204, 217, 218) that precede fungal growth and tend to confine fungal colonization to a discrete area (94, 252). Trees that successfully resist colonization produce a resinous induced response, but successfully colonized trees may not (4, 17, 204). In addition to confining fungal growth, induced physical and chemical changes in host tissue have a significant detrimental effect on the reproductive fitness of colonizing beetles (22, 181, 193, 204).

Although the induced response has been described as nonspecific (163), infection by different species of fungi produce different intensities of response. Trees respond with greater intensity and longer lesions to the most pathogenic fungi (62, 140, 177, 182, 200). The intensity of the response is apparently caused, in part, by the rate of fungal growth in the host (142, 208). However, the pattern of response development is similar to different fungi: an initial lag in visual and chemical changes, followed by a rapid increase in lesion size and a termination in lesion expansion (49, 76, 177).

The mechanism of induction or elicitation of the response is not well understood. A response can be produced following treatment of host tissues with chitosan (a fungal cell wall fragment) or with a proteinase inhibitor inducing factor (PIIF) (135, 156). However, subsequent studies have indicated that intensity of the response may depend on an elicitor from the tree that is produced internally, in response to either the fungi or fungal metabolites (49, 143). Continued diffusion of elicitor from a site of continued wounding by beetle tunnelling or from fungal growth extends the reaction zone until the fungal growth or the beetle activity is slowed (140). Variation in fungal growth, elicitor production, and diffusion through host inner bark may be responsible for the tremendous amount of intra-tree and inter-tree variation in the size of induced responses to a standardized inoculation (139, 183). In addition, diffusion of an elicitor and the finite capacity of a tree to respond could explain why increased levels of inoculum above a threshold do not result in an increase in induced lesion size (178).

Induction also initiates a series of chemical changes in host tissue, including changes in phenolic and phenylpropanoid chemistry. Gambliel et al (87) reported the appearance of the phenylpropanoid 4-allyl-anisole and decreases in condensed tannins in induced *Pinus taeda* tissue compared to normal inner bark tissue. Concentration of phenolic constituents of induced *Pinus sylvestris* inner bark vary significantly from normal tissue (145). Inoculation of *P. abies* with *C. polonica* results in an initial increase in phenolic concentration, a subsequent conversion to condensed tannins, followed by a decline in protein binding capacity (43, 44).

It is unclear how the changes in phenolic chemistry affect fungal growth or beetle fitness (203); however, the effects cannot be separated from simultaneous changes in monoterpene chemistry. Significant quantitative changes in concentrations of individual monoterpenes are induced in pines (66, 79, 87, 136, 137, 175, 194), and qualitative changes are reported in firs (190, 212). Minor monoterpene constituents in preformed resins can increase in concentration following induction, such that induced resins are more toxic or repellent than preformed resins to colonizing beetles (30, 190, 191, 197, 244). Induced resins may inhibit growth of beetle-associated fungi in bioassays, but they do not

appear to be fungicidal (196, 219, 222, 252). Also, the concentration of resins in the lesions is an important factor in resistance (83, 192). Fungal growth in resin-impregnated tissues may be reduced because readily available nutrients (especially starch) are converted to less easily metabolized resin components, and also because the nonpolar components of the resin may protect the phloem and sapwood from the extracellular enzymes of fungi (238, 252, 255).

As with the preformed system, prolonged colonization can exhaust the ability of the host to respond. Once an attack threshold is achieved, the tree can be overcome (51, 134, 197). The threshold of resistance is a function of tree vigor; stress reduces the ability of a tree to respond and lowers the threshold number of beetles required to overcome the resistance (18, 51, 157, 193, 210, 213, 228). Vigorous trees are thought to rapidly inhibit fungal growth within small visible lesions (134). Note, however, that the chemical changes in the tissue are critical to the resistance (192, 194), and although size may be a useful index, without supporting chemical analyses, lesion size should be used with caution (187). Trees with very low vigor may also produce small lesions that do not delimit the fungus if the tree's capacity to respond is very low (179, 180). Although moderate stress may result in an increased ability of the tree to limit fungal growth (75), more significant reductions in vigor from competition (179, 190), site quality (180), root disease (122), pruning (126, 256), and age (127, 213, 216) may affect the allocation of energy and the capacity of the tree to produce an induced response.

Different tree species may allocate relatively more energy to the preformed resin system and less to the induced response (63, 64, 244). The amount of energy available for the induced response may be critical. Induction results in decreases in sugar and starch concentrations in inner bark (55, 154, 215), but the capacity of the tree to respond may depend less on starch reserves in the inner bark (53, 58) and more on translocation of photosynthate from the foliage (52, 54, 80, 155).

As with the preformed component of resistance, the process of induction may be affected by the balance in allocation of photosynthate between growth and differentiation (138, 147). Trees inoculated with bark beetle fungal associates tend to respond either less intensely (65, 67, 144, 198, 203, 235) or more slowly (173, 232) in the months when carbohydrate is shunted to growth processes, in comparison to months when limited moisture restricts growth (147). Both the preformed and the induced components of resistance are linked through the source-sink relations of the host. The relation of resource allocation within the host and expression of components of resistance is critical to the concept of changing resistance thresholds and to the behavior of the beetles in host selection and colonization.

MULTIPLE INTERACTIONS AMONG BEETLES AND FUNGI

Extensive studies over the last 30 years in diverse North American and European conifer–bark beetle systems have demonstrated that the mechanisms of host resistance to invasion are highly effective. However, the question of whether they are specific adaptations to resist invasion by bark beetles and associated fungi or are general nonspecific responses to injury and invasion by pathogens remains unresolved (140, 163). The inference that fungi associated with bark beetles contribute to insect fitness through their pathogenic interactions with the host tree is well established in the literature. In fact, artificial inoculation trials have demonstrated that bluestain fungi can cause tree mortality. However, despite potential methodological problems with the inoculation techniques or inoculation densities, death following inoculation occurs several weeks to several months after treatment (14, 31, 56, 57, 116, 151, 169, 228). This time between infection/invasion and tree death is significantly longer than typically observed with natural attacks by beetle–fungal complexes. Recent studies have brought into question the inference that fungi are primarily responsible for mortality of trees colonized by beetles (110, 165, 185, 231) and suggest that tree mortality is a consequence of the combined dynamic interactions of the beetles and fungi with the responding host tree.

There are three key complex areas of bark beetle/fungal/host tree relations that require more detailed information for more integrative and flexible interpretations of these relationships. These areas include characterization of the multiplicity of potential interactions among organisms, description of the dynamic rate of interactions at the biochemical level, and examination of a broader taxonomic range of associated microorganisms. Each system should be examined independently because there may be important features that prevent broad generalizations.

Range of Potential Interactions Among Organisms

Mycangial fungi benefit from associations with beetle vectors by transferral between trees. The evolution of mycangia strongly suggests that the beetles also benefit from the association. Most of the mycangial fungi are, at best, only weakly pathogenic in their host trees (101, 102, 208, 251). Those studies that indicated there might have been an effect on host vigor (172) used fungi that were initially identified as mycangial (248), but these have been subsequently reevaluated (105). Although it appears that the mycangial fungi may not be solely responsible for tree mortality, their potential role in reducing tree resistance during colonization with their beetle vector cannot be discounted. However, there may be other ways the beetles benefit from the association.

Many species of wood-boring beetles closely related to bark beetles feed on ambrosia fungi carried between host trees by the insects (15). The *D. frontalis* and *D. brevicomis* larval instars that feed most intensively are found in chambers in the nutritionally impoverished outer bark of their host trees. However, the larvae appear to be feeding primarily on mycangial fungi with an ambrosial growth form in contact with the beetles (13, 90, 97, 98). The fungi or other associates may also alter the nutritional quality of the host tissue (10, 35, 111). Whether through direct consumption of fungi or feeding on fungal-modified host tissue, *D. frontalis* developing in the presence of mycangial fungi are larger and more fecund than those that develop in the absence of the fungi (9, 36, 68, 91).

The nutritional relationships between beetles with maxillary mycangia or external pit mycangia and their associated fungi are less well studied. There are indications, however, that there may be similarities. *Entomocorticium dendroctoni*, associated with *D. ponderosae*, appears to improve food quality and adult reproductive fitness (247), although it is not clear if this basidiomycete is a mycangial fungus. Late larval instars of *D. ponderosae* feed in tissue not colonized by the mycangial fungus, but contact between beetles and fungi is reestablished in pupal chambers (245), and newly eclosed adults feed extensively on fungi in the pupal chambers.

The mycangial fungi may improve beetle fitness by limiting growth of other species of fungi. The bluestain fungus, *O. minus*, assumed to benefit beetles through its pathogenicity to the tree, may be detrimental to *D. frontalis* and other bark beetle larvae (8, 206, 257). Ovipositing beetles avoid stained areas and beetle reproduction is lower when the bluestain fungus is present (85, 91). However, growth of the mycangial fungi may inhibit growth of the bluestain fungi (8, 41, 248; see 208 for opposing argument).

The mycangial fungi, bacteria, and yeasts associated with the mycangia may also contribute to the bark beetle chemical communication system (25, 33, 34, 46, 129). Microorganisms associated with *D. ponderosae* and *D. frontalis* have been shown to be capable of converting verbenols to verbenone (32, 117, 118). The reported increase in production of trans-verbenol by axenic *D. ponderosae* may have been a function of decreased oxidation of the verbenol to verbenone that would have occurred if associated microorganisms had been present (61). However, there also is increasing evidence that natural enemies may be using odors produced by the microorganisms to locate their insect hosts [Dahlsten & Berisford, unpublished results (231)].

The interactions between beetles and fungi clearly are multifaceted and complex, and interactions may be both positive and negative, depending on the stage in the life history of the insect. The net effect on beetle fitness will depend on

the precolonization vigor of the host and the composition of the fungal flora associated with the insect.

Pathogenicity of Staining Fungi and Interactions with Beetle Vectors

Hetrick (108) first observed trees killed by *D. frontalis* that lacked any sapwood staining. The report was initially discounted, but active *D. frontalis* and *D. brevicornis* infestations have since been observed with little or no bluestain (40, 248). These infestations have higher infestation densities, and Bridges et al (40) suggested that the bluestain fungi were not necessary for tree mortality or beetle development under these conditions. However, the presence of other nonstaining fungi that could contribute to tree mortality cannot be ruled out because fungal isolations were generally conducted using selective media (e.g. 40). Although the bluestain fungi were not required for successful tree colonization, this may represent one extreme of a broad range of conditions where the combined actions of beetles and fungi are more successful in reducing tree resistance than would be expected for beetles without fungi.

Studies of other *Dendroctonus* systems have indicated that sapwood colonization by staining fungi may not be critical for tree mortality. Parmeter et al (185) suggested that sapwood occlusion could not account for the crown symptoms following bark beetle attack. Hobson et al (110) demonstrated that fungal penetration of the sapwood followed sapwood occlusion, and they concluded that there was no mutualism between beetles and staining fungi. Others have noted that the speed of mortality of bark beetle-attacked pines is too rapid to be accounted for by extensive fungal colonization of sapwood (231). Monoterpenes or other compounds released by the tree following injury, rather than fungal compounds, could cause aspiration of bordered pits and tracheid cavitation, resulting in disruption of transpiration (72, 124). Harrington (102) suggested that sapwood drying could be induced by death of phloem tissue. Using a technique that mimics the physical penetration of the outer bark by the beetles, Nebeker et al (165) have shown that the resin flow can be rapidly reduced as the oleoresin reservoir is drained, but flow will resume after several days. Continued tunnelling action by the beetles and local invasion of the phloem by fungi could enhance the draining of host defenses.

Harrington (102) argued that the frequency of association between beetles and fungi does not necessarily imply a mutualism, and evolution of pathogenicity may have been driven as much by competition with other fungi as by mutualism with bark beetles. Weakly pathogenic fungi are often associated with the most aggressive beetles (101, 102). Alternatively, *Leptographium terebrantis*, a highly pathogenic fungus (based on seedling inoculation and dye conduction

studies), is associated with the turpentine beetles *D. terebrans* and *D. valens* (102, 103, 171, 186), two species that rarely kill trees and are highly tolerant of host resins (82, 231). However, the fungus has not been demonstrated to kill mature trees (123, 199).

Tomicus piniperda is a relatively weakly aggressive bark beetle that appears to be incapable of sustaining successful populations when colonizing vigorous trees (125). This species is associated with a more pathogenic fungus, *Lep-tographium wingfieldii*, than the moderately aggressive *I. sexdentatus*, which is associated with a less pathogenic fungus, *O. brunneo-ciliatum* (143). The relationship between staining fungi and *T. piniperda* may be fortuitous (188), and staining fungi are not required for reproductive success of either *T. piniperda* or *I. sexdentatus* (60, 188).

I. typographus is associated with three species of bluestain fungi, but the fungal populations are not consistently isolated. It has been argued that the most pathogenic species, *C. polonica*, is more common when the beetles are at epidemic population levels and are colonizing living trees, but this fungus is replaced by the less pathogenic species *O. bicolor* when the beetle population is at endemic levels and is colonizing dead or dying trees (223). However, it is difficult to determine if changes in fungal populations contribute to the ability of the beetle to colonize different hosts (dead or vigorous) or whether the different host conditions are selective forces favoring different fungal populations (see 222).

The fact that plant pathogenic *Ceratocystis* species are rarely associated with bark beetles (120), yet the primarily saprophytic *Ophiostoma* species are common associates (102), is worth noting. Highly pathogenic *Ceratocystis* species associated with *I. typographus* (104), *I. cembrae* (201), and *D. rufipennis* (225) are all closely related to *Ceratocystis coerulescens*, a good sapwood colonizer of wounds in living spruce, and the attributes that allow for the bark beetle associations are apparently derived characters (104). While these three *Ceratocystis* species are pathogenic to the host, it is clear that the associated bark beetle is not obligatorily dependent on the fungus; often only a small percentage of the beetle population carries the *Ceratocystis* species (201, 225, 239). Following beetle attack, the *Ceratocystis* species, if present, are the first to invade the sapwood, which evidently shows their greater pathogenicity when compared to the *Ophiostoma* species (201, 224, 225). Although only a small percentage of the attacking adult beetles carry the *Ceratocystis* species, their pathogenic nature allows them to spread sufficiently and sporulate in at least a few of the pupal chambers for spore acquisition by the next generation of adults. Less pathogenic fungi may be carried by a higher percentage of emerging beetles if the fungi are more saprophytically competitive and can sporulate in pupal chambers along with other fungi.

Tree Colonization and Dynamic Rate of Interactions

The process of tree colonization by bark beetles can be divided into dispersal and selection, concentration, and establishment (253). Production of aggregation pheromones during the concentration phase continues as long as the trees are resisting beetle colonization (21, 24, 150, 193, 195, 205). The establishment phase begins when the host resistance stops (20) and death of the tree is assured (253); only then will beetles produce galleries and initiate oviposition (20, 70, 253). Thus, beetle gallery construction and oviposition can be used as a bioassay to indicate when tree mortality has occurred. It is also critical to distinguish between the overcoming of the host defense system (phloem colonization) and the development of foliar symptoms (fading related to sapwood occlusion).

With these criteria for tree mortality, the temporal relationship between fungal penetration (potential pathogenicity), host condition, and beetle success in several systems can be closely examined. Raffa & Berryman (193) determined that peak attack by *D. ponderosae* on *Pinus contorta* occurred during the second to third day after attack was initiated; the attack was usually terminated in just over 5 days, when the tree was overcome. However, Solheim (226) examined *P. contorta* colonized by *D. ponderosae* and determined that sapwood was occluded to a depth of only 20 mm and fungi were isolated at a depth of 15 mm, 14 days after the trees had been attacked. The staining fungi introduced by beetles are initially confined to the ray parenchyma cells (204) with only 5–18% of tracheids colonized by hyphae until at least 8–10 weeks after beetle attack (6). Water stress was not observed in attacked trees until 8 weeks after beetle attack (5). Thus, it appears that if the beetle bioassay for tree mortality is an accurate reflection of irreversible stress, trees are overcome very quickly, and well in advance of fungal growth in sapwood or changes in tree moisture status.

Similarly, *I. typographus* colonizes *P. abies* in a pheromone mediated mass attack that can be 90% complete within 4 days (2). Once oviposition is initiated, 50% may be complete in 2–4 days (1), suggesting that tree mortality can occur within 6 days following attack. However, fungi were isolated from beetle-attacked trees at a depth of only 18 mm in the sapwood at 4–5 weeks after attack (223), when beetle progeny were in larval and pupal stages (224).

Caird (47) followed the moisture relations of *Pinus echinata* following *D. frontalis* attack and reported that as adults were laying eggs, the first sapwood ring was nonconducting, and only 1% of tracheid tori were aspirated 4 days after attack. Using data determined from artificial inoculations of *P. taeda*, *O. minus* was isolated 15 mm into sapwood at 26 days (208); yet beetles can complete development from egg to adult in the same amount of time (106, 242). The most rapid penetration of bluestain observed was approximately 15% of sapwood bluestained by 7 days after beetle attack (31). However, beetle colonization is

completed in 4–7 days (69, 88, 214) and oleoresin pressure is depleted in only 2 or 3 days (113).

The critical question of whether fungi introduced by colonizing bark beetles are important in killing host trees must be addressed during the early phases of the interaction. There has been a tremendous amount of research examining the potential pathogenicity of beetle-vectored fungi in artificial inoculations, and there does not appear to be a universally accepted indicator of death. Trees may be irreversibly stressed (i.e. a tree cannot recover and survive) but will remain green and continue to transpire for many weeks (150). This has led to a significant amount of confusion about the critical interactions and host response to invasion or infection. However, it is apparent that the fungi alone are not responsible for tree death and that it is the dynamic interactions of tunnelling insects, inoculated fungi, and a responding tree of a specific state of vigor that determines attack success. The fungi must facilitate tree mortality through the interactions with beetles and trees in ways that are not signaled by sapwood staining or occlusion.

AREAS OF FUTURE INVESTIGATION

There has been a great deal of research focused on the invasion of conifer sapwood by bluestain fungi because of the assumption that disruption of the transpiration stream is the cause of tree mortality. However, mechanical damage to inner bark caused by colonizing beetles may be important both in depleting/disrupting the capability of the tree to resist colonization and in initiating changes in host tissue that disrupt water conduction (18, 72, 124, 165). More likely, infection by associated fungi at each beetle entry point and subsequent death of the phloem and inner bark (246), combined with the mechanical actions of the beetles, may reduce the components of resistance, irreversibly stress the trees, and permit successful oviposition. Invasion of sapwood by the bluestain fungi may be a characteristic sign of beetle attack but not a requisite event. Thus, it is critical to develop detailed studies of the dynamic biochemical and cellular changes that occur at localized sites in the inner bark during the initial phases of the invasion/inoculation process, including the production of translocatable toxins.

The accumulated contributions of many local interactions between both beetles and fungi with the tree are required to induce the rapid changes in the host that are essential for reproductive success of beetles. These local and cumulative changes must be better characterized. Results of studies in this area will provide a firmer foundation for the concept of the fungi as facilitators or expeditors of beetle colonization success through localized interactions with the beetles in exhausting tree resistance rather than as tree killers.

It may not be possible to develop an encompassing hypothesis of bark beetle/fungus/host tree interactions because of the differences among species associations. Also, it is critical to distinguish among the following: (a) primary bark beetles that normally kill their hosts, (b) bark beetles that colonize dead or dying trees at normal low-population densities but colonize living trees when populations increase to very high levels, and (c) beetles that do not normally kill their host trees. The questions that stem from the differences in host selection and colonization behavior are very different, and the ecological relationships may vary depending on beetle population size.

Staining fungi may be important for successful colonization of vigorous trees when beetle populations are at low levels and the attack rate is low. Inoculation of a pathogenic fungus may help exhaust the capacity of a tree to respond defensively or may kill local areas of inner bark tissue and increase the probability that beetle attack will exceed the mortality threshold. However, this is potentially a precarious ecological balance because exhausting the host defenses through inoculation of the pathogenic fungus also means initiation of the induced response that is detrimental to beetle fitness. If induction proceeds, that is if the host tissue is not killed and a reaction is produced, then beetles in the reaction zone have a low probability of survival. The ecological interactions of beetles with staining fungi facilitating attack success, potential subsequent detrimental effects on progeny, and the interactions with other fungal associates must be further explored. Obviously, the benefits to the participants in each beetle/fungus association could change as population levels, tree vigor state, or attack rates change. Other possible benefits of maintaining fungal symbionts (e.g. larval nutritional ecology and biological control of other fungi) may be critical to the association. In addition, it is possible that the associations are results of fungal exploitation of the insect rather than the reverse case (102).

Many questions remain unresolved. The research in the area of conifer resistance to invasion by beetles and associated fungi has greatly increased the understanding of induced resistance in plants. Similarly, the research on tree vigor, resistance, and beetle colonization behavior has expanded our understanding of chemical communication and population dynamics of insects. However, research needs to continue on the contributions of a broader taxonomic range of associated fungi on bark beetle fitness, the potential benefits of the association to the fungi, the differences among beetle/fungus associations in the colonization of trees in different vigor states, and the interactions and responses of the tree to the initial stages of invasion and/or infection. An understanding of the interactions at the cellular and tissue levels seems particularly important to an understanding of how trees are killed, how normal defense physiology functions, and how its expression can be limited.

Whitney suggested that tree death from bark beetles is unique compared to mortality from other causes and results from the summation of fungus-caused tissue mortality and mechanical damage around beetle attack sites (246). However, the research to support this assumption has been minimal, and it seems important to understand the dynamics of the initial interspecific interactions following wounding or infection. Fungi may be critical to the death of the host in some systems and under some conditions, but the critical tests to determine the range of these conditions have not been conducted. Resolution of these issues lies in future research.

ACKNOWLEDGMENTS

We thank K Gilbert and C Hanlon for collecting references and sending them to TDP in Queensland, Australia. We also thank G Gordh and the Department of Entomology at the University of Queensland for providing space and computer support that greatly facilitated efforts to write this manuscript.

Visit the Annual Reviews home page at
<http://www.annurev.org>.

Literature Cited

1. Anderbrant O. 1990. Gallery construction and oviposition of the bark beetle *Ips typographus* (Coleoptera: Scolytidae) at different breeding densities. *Ecol. Entomol.* 15:1–8
2. Anderbrant O, Schlyter F, Lofqvist J. 1988. Dynamics of tree attack in the bark beetle *Ips typographus* under semi-epidemic conditions. In *Integrated Control of Scolytid Bark Beetles*, ed. TL Payne, H Saarenmaa, pp. 35–51. Blacksburg: Virg. Polytech. Inst. State Univ.
3. Anderson NH, Anderson DB. 1968. *Ips* bark beetle attacks and brood development in a lightning-struck pine in relation to its physiological decline. *Fla. Entomol.* 51:23–30
4. Ashraf M, Berryman AA. 1969. Biology of *Scolytus ventralis* (Coleoptera: Scolytidae) attacking *Abies grandis* in northern Idaho. *Melandria* 2:1–23
5. Ballard RG, Walsh MA, Cole WE. 1982. Blue-stain fungi in xylem of lodgepole pine: a light-microscopy study on extent of hyphal distribution. *Can. J. Bot.* 60:2334–41
6. Ballard RG, Walsh MA, Cole WE. 1984. The penetration and growth of blue-stain fungi in the sapwood of lodgepole pine attacked by mountain pine beetle. *Can. J. Bot.* 62:1724–29
7. Bannan MW. 1936. Vertical resin ducts in the secondary wood of the Abietineae. *New Phytol.* 35:11–46.
8. Barras SJ. 1970. Antagonism between *Dendroctonus frontalis* and the fungus *Ceratocystis minor*. *Ann. Entomol. Soc. Am.* 63:1187–90
9. Barras SJ. 1973. Reduction in progeny and development in the southern pine beetle following removal of symbiotic fungi. *Can. Entomol.* 105:1295–99
10. Barras SJ, Hodges JD. 1969. Carbohydrates in inner bark of *Pinus taeda* as affected by *Dendroctonus frontalis* and associated microorganisms. *Can. Entomol.* 101:489–93
11. Barras SJ, Perry T. 1971. Gland cells and fungi associated with prothoracic mycangium of *Dendroctonus adjunctus* (Coleoptera: Scolytidae). *Ann. Entomol. Soc. Am.* 64:123–126
12. Barras SJ, Perry T. 1972. Fungal symbionts in the prothoracic mycangium of *Dendroctonus frontalis* (Coleoptera:

- Scolytidae). *Z. Ang. Entomol.* 71:95–104
13. Barras SJ, Taylor JJ. 1973. Varietal *Ceratocystis minor* identified from mycangium of *Dendroctonus frontalis*. *Mycopath. Mycol. Appl.* 50:295–305
 14. Basham HG. 1970. Wilt of loblolly pine inoculated with blue-stain fungi of the genus *Ceratocystis*. *Phytopathology* 60:750–54
 15. Beaver RD. 1989. Insect-fungus relationships in the bark and ambrosia beetles. In *Insect-Fungus Interactions*, ed. N Wilding, NM Collins, PM Hammond, JF Webber, pp. 121–43. London: Academic
 16. Bernard-Dagan C. 1988. Seasonal variation in energy sources and biosynthesis of terpenes in maritime pine. In *Mechanisms of Woody Plant Defenses Against Insects: Search for Patterns*, ed. WJ Mattson, J Leveux, C Bernard-Dagan, pp. 93–116. New York: Springer-Verlag
 17. Berryman AA. 1969. Response of *Abies grandis* to attack by *Scolytus ventralis* (Coleoptera: Scolytidae). *Can. Entomol.* 101:1033–41
 18. Berryman AA. 1972. Resistance of conifers to invasion by bark beetle fungus associations. *BioScience* 22:598–602
 19. Berryman AA. 1976. Theoretical explanation of mountain pine beetle dynamics in lodgepole pine forests. *Environ. Entomol.* 5:1225–33
 20. Berryman AA. 1982. Population dynamics of bark beetles. In *Bark Beetles in North American Conifers*, ed. JB Mitton, KB Sturgeon, pp. 264–314. Austin: Univ. Texas
 21. Berryman AA. 1989. Adaptive pathways in scolytid-fungus associations. In *Insect-Fungus Interactions*, ed. N Wilding, NM Collins, PM Hammond, JF Webber, pp. 145–59. London: Academic
 22. Berryman AA, Ashraf M. 1970. Effects of *Abies grandis* resin on the attack behavior and brood survival of *Scolytus ventralis* (Coleoptera: Scolytidae). *Can. Entomol.* 102:1229–36
 23. Berryman AA, Dennis B, Raffa KF, Stenseth NC. 1985. Evolution of optimal group attack, with particular reference to bark beetles (Coleoptera: Scolytidae). *Ecology* 66:898–903
 24. Berryman AA, Raffa KF, Millstein JA, Stenseth NC. 1989. Interaction dynamics of bark beetle aggregation and conifer defense rates. *Oikos* 56:256–63
 25. Birgersson G, Bergstrom G. 1989. Volatiles released from individual spruce bark beetle entrance holes. Quantitative variation during the first week of attack. *J. Chem. Ecol.* 15:2465–83
 26. Birgersson G, Schlyter F, Bergstrom G, Lofqvist J. 1988. Individual variation in aggregation pheromone content of the bark beetle, *Ips typographus*. *J. Chem. Ecol.* 9:1737–61
 27. Blanche CA, Hodges JD, Nebeker TE. 1985. Changes in bark beetle susceptibility indicators in a lightning-struck loblolly pine. *Can. J. For. Res.* 15:397–99
 28. Blanche CA, Lorio PL Jr, Sommers RA, Hodges JD, Nebeker TE. 1992. Seasonal cambial growth and development of loblolly pine: xylem formation, inner bark chemistry, resin ducts, and resin flow. *For. Ecol. Man.* 49:151–65
 29. Blanche CA, Nebeker TE, Hodges JD, Karr BL, Schmitt JJ. 1985. Effect of thinning damage on bark beetle susceptibility indicators in loblolly pine. In *Proc. Third Biennial Southern Silvicult. Res. Conf.*, ed. E Shoulders, pp. 471–79. USDA For. Serv. Gen. Tech. Rep. SO-54. New Orleans: USDA For. Serv. South. For. Exp. Stn.
 30. Bordsch RP, Berryman AA. 1977. Host resistance to the fir engraver beetle, *Scolytus ventralis* (Coleoptera Scolytidae). 2. Repellency of *Abies grandis* resins and some monoterpenes. *Can. Entomol.* 109:95–100
 31. Bramble WC, Holst EC. 1940. Fungi associated with *Dendroctonus frontalis* in killing shortleaf pines and their effect on conduction. *Phytopathology* 30:881–99
 32. Brand JM, Bracke JW, Britton LN, Markovetz AJ, Barras SJ. 1976. Bark beetle pheromones: production of verbenone by a mycangial fungus of *Dendroctonus frontalis*. *J. Chem. Ecol.* 2:195–99.
 33. Brand JM, Bracke JW, Markovetz AJ, Wood DL, Browne LE. 1975. Production of verbenol pheromone by a bacterium isolated from a bark beetle. *Nature* 254:136–37
 34. Brand JM, Schultz J, Barras SJ, Edson LJ, Payne TL, Hedden RL. 1977. Bark beetle pheromones: enhancement of *Dendroctonus frontalis* (Coleoptera: Scolytidae) aggregation pheromone by yeast metabolites in laboratory bioassays. *J. Chem. Ecol.* 3:657–66
 35. Bridges JR. 1981. Nitrogen-fixing bacteria associated with bark beetles. *Microb. Ecol.* 7:131–37
 36. Bridges JR. 1983. Mycangial fungi of *Dendroctonus frontalis* (Coleoptera: Scolytidae) and their relationship to beetle population trends. *Environ. Entomol.*

- 12:858–61
37. Bridges JR. 1987. Effects of terpenoid compounds on growth of symbiotic fungi associated with the southern pine beetle. *Phytopathology* 77:83–85
 38. Bridges JR, Moser JC. 1983. Role of two phoretic mites in transmission of blue-stain fungus, *Ceratocystis minor*. *Ecol. Entomol.* 8:9–12
 39. Bridges JR, Moser JC. 1986. Relationship of phoretic mites (Acari: Tarsonemidae) to the bluestaining fungus, *Ceratocystis minor*, in trees infested by southern pine beetle (Coleoptera: Scolytidae). *Environ. Entomol.* 15:951–53
 40. Bridges JR, Nettleton WA, Conner MD. 1985. Southern pine beetle (Coleoptera: Scolytidae) infestations without the blue-stain fungus, *Ceratocystis minor*. *J. Econ. Entomol.* 78:325–27
 41. Bridges JR, Perry TJ. 1985. Effects of mycangial fungi on gallery construction and distribution of blue-stain in southern pine beetle infested pine bolts. *J. Entomol. Sci.* 20:271–75
 42. Bridges JR, Perry TJ. 1987. *Ceratocystis ranunculosis* sp. nov. associated with the southern pine beetle. *Mycologia* 79:630–33
 43. Brignolas F, Lacroix B, Lieutier F, Sauvard D, Drouet A, et al. 1995. Induced responses in phenolic metabolism in two Norway spruce clones after wounding and inoculations with *Ophiostoma polonicum*, a bark beetle-associated fungus. *Plant Physiol.* 109:821–27
 44. Brignolas F, Lieutier F, Sauvard D, Yart A, Drouet A, Claudot A-C. 1995. Changes in soluble phenolic content of Norway spruce (*Picea abies* Karst.) ploem in response to wounding and inoculation with *Ophiostoma polonicum*. *Eur. J. For. Pathol.* 25:253–65
 45. Brown MW, Nebeker TE, Honea CR. 1987. Thinning increases loblolly pine vigor and resistance to bark beetles. *South. J. Appl. For.* 11:28–31
 46. Byers JA, Wood DL. 1981. Antibiotic-induced inhibition of pheromone synthesis in a bark beetle. *Science* 213:763–64
 47. Caird RW. 1935. Physiology of pines infested by bark beetles. *Bot. Gaz.* 96:709–33
 48. Cates RG, Alexander H. 1982. Host resistance and susceptibility. In *Bark Beetles in North American Conifers*, ed. JB Mitton, KB Sturgeon, pp. 212–63. Austin: Univ. Texas
 49. Cheniclet C, Bernard-Dagan C, Pauly G. 1988. Terpene biosynthesis under pathological conditions. In *Mechanisms of Woody Plant Defenses Against Insects: Search for Patterns*, ed. WJ Mattson, J Levieux, C Bernard-Dagan, pp. 117–30. New York: Springer-Verlag
 50. Christiansen E. 1985. *Ceratocystis polonica* inoculated in Norway spruce: blue-staining in relation to inoculum density, resinosis, and tree growth. *Eur. J. For. Pathol.* 15:160–67
 51. Christiansen E. 1985. *Ips/Ceratocystis* infection of Norway spruce: What is a deadly dosage? *Z. Ang. Entomol.* 99:6–11
 52. Christiansen, E. 1992. After-effects of drought did not predispose young *Picea abies* to infection by the bark beetle-transmitted blue-stain fungus *Ophiostoma polonicum*. *Scand. J. For. Pathol.* 7:557–69
 53. Christiansen E, Ericsson A. 1986. Starch reserves in *Picea abies* in relation to defense reaction against a bark beetle-transmitted blue-stain fungus, *Ceratocystis polonica*. *Can. J. For. Res.* 16:78–83
 54. Christiansen E, Fjone G. 1993. Pruning enhances susceptibility of *Picea abies* to infection by the bark beetle-transmitted blue-stain fungus, *Ophiostoma polonicum*. *Scand. J. For. Res.* 8:235–42
 55. Christiansen E, Hornvedt R. 1983. Combined *Ips/Ceratocystis* attack on Norway spruce, and defensive mechanisms of the trees. *Z. Ang. Entomol.* 96:110–18
 56. Christiansen E, Solheim H. 1990. The bark beetle-associated blue-stain fungus *Ophiostoma polonicum* can kill various spruces and Douglas fir. *Eur. J. For. Pathol.* 20:436–46
 57. Christiansen E, Solheim H. 1994. Pathogenicity of five species of *Ophiostoma* fungi to Douglas-fir. *Medd. Nor. Inst. Skogforsk.* 47:1–12
 58. Christiansen E, Waring RH, Berryman AA. 1987. Resistance of conifers to bark beetle attack: searching for general relationships. *For. Ecol. Man.* 22:89–106
 59. Cobb FW Jr, Krstic M, Zavarin E, Barber HW Jr. 1968. Inhibitory effects of volatile oleoresin components on *Fomes annosus* and four *Ceratocystis* species. *Phytopathology* 58:1327–35
 60. Colineau B, Lieutier F. 1994. Production of *Ophiostoma*-free adults of *Ips sexdentatus* Boern. (Coleoptera: Scolytidae) and comparison with naturally contaminated adults. *Can. Entomol.* 126:103–10
 61. Conn JE, Borden JH, Hunt DWA, Holman J, Whitney HS, et al. 1984. Pheromone

- production by axenically reared *Dendroctonus ponderosae* and *Ips paraconfusus* (Coleoptera: Scolytidae). *J. Chem. Ecol.* 2:281-90
62. Cook SP, Hain FP. 1985. Qualitative examination of the hypersensitive response of loblolly pine, *Pinus taeda* L., inoculated with two fungal associates of the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae). *Environ. Entomol.* 14:396-400
 63. Cook SP, Hain FP. 1986. Defensive mechanisms of loblolly and shortleaf pine against attack by the southern pine beetle, *Dendroctonus frontalis* Zimmermann, and its fungal associate, *Ceratocystis minor* (Hedgecock) Hunt. *J. Chem. Ecol.* 12:1397-406
 64. Cook SP, Hain FP. 1987. Susceptibility of trees to southern pine beetle, *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Environ. Entomol.* 16:9-14
 65. Cook SP, Hain FP. 1987. Four parameters of the wound response of loblolly and shortleaf pines to inoculation with the blue-staining fungus associated with the southern pine beetle. *Can. J. Bot.* 65:2403-9
 66. Cook SP, Hain FP. 1988. Wound response of loblolly and shortleaf pine attacked and reattacked by *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae) or its fungal associate, *Ceratocystis minor* (Hedgecock) Hunt. *Can. J. For. Res.* 18:33-37
 67. Cook SP, Hain FP, Nappen PB. 1986. Seasonality of the hypersensitive response of loblolly and shortleaf pine to inoculation with a fungal associate of the southern pine beetle (Coleoptera: Scolytidae). *J. Entomol. Sci.* 21:283-85
 68. Coppedge BR, Stephen FM, Felton GW. 1995. Variation in female southern pine beetle size and lipid content in relation to fungal associates. *Can. Entomol.* 127:145-54
 69. Coster JE, Vite JP. 1972. Effects of feeding and mating on pheromone release in the southern pine beetle. *Ann. Entomol. Soc. Am.* 65:263-66
 70. Coulson RN. 1979. Population dynamics of bark beetles. *Annu. Rev. Entomol.* 24:417-47
 71. Coulson RN, Hennier PB, Flamm RO, Rykiel EJ, Hu LC, Payne TL. 1983. The role of lightning in the epidemiology of the southern pine beetle. *Z. Ang. Entomol.* 96:182-93
 72. Coutts MP. 1977. The formation of dry zones in the sapwood of conifers. II. The role of living cells in the release of water. *Eur. J. For. Pathol.* 7:6-12
 73. Coyne JF, Lott LH. 1976. Toxicity of substances in pine oleoresin to southern pine beetles. *J. Geogr. Entomol. Soc.* 11:301-5
 74. Craighead FC. 1928. Interrelation of tree killing bark beetles (*Dendroctonus*) and blue stain. *J. For.* 26:886-87
 75. Croise L, Lieutier F. 1993. Effects of drought on the induced defense reaction of Scots pine to bark beetle-associated fungi. *Ann. Sci. For.* 50:91-97
 76. Croteau R, Gurkewitz S, Johnson MA, Fisk HJ. 1987. Biochemistry of oleoresins: monoterpene and diterpene biosynthesis in lodgepole pine saplings infected with *Ceratocystis clavigera* or treated with carbohydrate elicitors. *Plant Physiol.* 85:1123-28
 77. DeAngelis JD, Hodges JD, Nebeker TE. 1986. Phenolic metabolites of *Ceratocystis minor* from laboratory cultures and their effects on transpiration in loblolly pine seedlings. *Can. J. Bot.* 64:151-55
 78. DeAngelis JD, Nebeker TE, Hodges JD. 1986. Influence of tree age and growth rate on the radial resin duct system in loblolly pine (*Pinus taeda*). *Can. J. Bot.* 64:1046-49
 79. Delorme L, Lieutier F. 1990. Monoterpene composition of the preformed and induced resins of Scots pine, and their effect on bark beetles and associated fungi. *Eur. J. For. Pathol.* 20:304-16
 80. Dunn JP, Lorio PL Jr. 1992. Effects of bark girdling on carbohydrate supply and resistance of loblolly pine to southern pine beetle (*Dendroctonus frontalis* Zimm.) attack. *For. Ecol. Man.* 50:317-30
 81. Farris SH. 1969. Occurrence of mycangia in the bark beetle *Dryocoetes confusus* (Coleoptera: Scolytidae). *Can. Entomol.* 101:527-32
 82. Fatzinger CW. 1985. Attraction of the black turpentine beetle (Coleoptera: Scolytidae) and other forest Coleoptera to turpentine-baited traps. *Environ. Entomol.* 14:768-75
 83. Ferrell GT, Otrerosina WJ, DeMars CJ Jr. 1993. Assessing the susceptibility of white fir to the fir engraver, *Scolytus ventralis* LeC. (Coleoptera: Scolytidae), using fungal inoculation. *Can. Entomol.* 125:895-901
 84. Francke-Grossmann H. 1967. Ectosymbiosis in wood inhabiting insects. In *Symbiosis*, ed. SM Henry, Vol. 2, pp. 141-205. New York: Academic
 85. Franklin R. 1970. Observations on the

- bluestain-southern pine beetle relationship. *J. Georg. Entomol. Soc.* 5:53-57
86. Furniss MM, Solheim H, Christiansen E. 1990. Transmission of blue-stain fungi by *Ips typographus* (Coleoptera: Scolytidae) in Norway spruce. *Ann. Entomol. Soc. Am.* 83:712-16
 87. Gambliel H, Cates RG, Caffey-Moquin MK, Paine TD. 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*, ed. SJ Branhams, RC Thatcher, pp. 177-84. New Orleans: USDA For. Serv. Gen. Tech. Rep. SO-56 USDA For. Serv. So. For. Exp. Stn.
 88. Gara RI, Coster JE. 1968. Studies on the attack behavior of the southern pine beetle. III. Sequence of tree infestation within stands. *Contrib. Boyce Thompson Inst.* 24:77-86
 89. Gibbs JN. 1968. Resin and the resistance of conifers to *Fomes annosus*. *Ann. Bot.* 32:649-65
 90. Goldhammer DS, Stephen FM, Paine TD. 1989. Average radial growth rate and chlamydospore production of *Ceratocystis minor*, *Ceratocystis minor* var *barrasii*, and SJB 122 in culture. *Can. J. Bot.* 67:3498-505
 91. Goldhammer DS, Stephen FM, Paine TD. 1990. The effect of the fungi *Ceratocystis minor* (Hedgecock) Hunt, *Ceratocystis minor* (Hedgecock) Hunt var *barrasii* Taylor, and SJB 122 on reproduction of the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae). *Can. Entomol.* 122:407-18
 92. Graham K. 1967. Fungal-insect mutualism in trees and timber. *Annu. Rev. Entomol.* 12:105-26
 93. Gregoire JC. 1988. The greater European spruce bark beetle. In *Dynamics of Forest Insect Populations: Patterns, Causes, and Implications*, ed. AA Berryman, pp. 455-78. New York: Plenum
 94. Hain FP, Mawby WD, Cook SP, Arthur FH. 1983. Host conifer reaction to stem invasion. *Z. Ang. Entomol.* 96:247-56
 95. Hanover JW. 1975. Physiology of tree resistance to insects. *Annu. Rev. Entomol.* 20:75-95.
 96. Happ GM, Happ CM, Barras SJ. 1971. Fine structure of the prothoracic mycangium, a chamber for the culture of symbiotic fungi in the southern pine beetle, *Dendroctonus frontalis*. *Tissue Cell* 3:295-308
 97. Happ GM, Happ CM, Barras SJ. 1975. Bark beetle-fungal symbiosis. III. Ultrastructure of conidiogenesis in a *Sporothrix* ectosymbiont of the southern pine beetle. *Can. J. Bot.* 53:2702-11
 98. Happ GM, Happ CM, Barras SJ. 1976. Bark beetle-fungal symbiosis. II. Fine structure of a basidiomycete ectosymbiont of the southern pine beetle. *Can. J. Bot.* 54:1049-62
 99. Harrington TC. 1987. New combinations in *Ophiostoma* of *Ceratocystis* species with *Leptographium* anamorphs. *Mycotaxon* 28:39-43
 100. Harrington TC. 1988. *Leptographium* species, their distribution, hosts, and insect vectors. In *Leptographium Root Diseases on Conifers*, ed. TC Harrington, FW Cobb Jr, pp. 1-39. St. Paul, MN: Am. Phytopathol. Soc.
 101. Harrington TC. 1993. Biology and taxonomy of fungi associated with bark beetles. In *Beetle-Pathogen Interactions in Conifer Forests*, ed. TD Schowalter, GM Filip, pp. 37-58. New York: Academic
 102. Harrington TC. 1993. Diseases of conifers caused by species of *Ophiostoma* and *Leptographium*. In *Ceratocystis and Ophiostoma: Taxonomy, Ecology, and Pathogenicity*, ed. MJ Wingfield, KA Seifert, JF Webber, pp. 161-72. St Paul, MN: Am. Phytopathol. Soc.
 103. Harrington TC, Cobb FW Jr. 1983. Pathogenicity of *Leptographium* and *Verticicladiella* spp. isolated from roots of western North American conifers. *Phytopathology* 73:596-99
 104. Harrington TC, Steimel J, Wingfield MJ, Kile GA. 1996. Isozyme variation and species delimitation in the *Ceratocystis coerulea* complex. *Mycologia* 88:104-13
 105. Harrington TC, Zambino PJ. 1990. *Ceratocystiopsis ranaculosis* not *Ceratocystis minor* var. *barrasii* is the mycelial fungus of the southern pine beetle. *Mycotaxon* 38:103-15
 106. Heddon RL, Billings RF. 1977. Seasonal variation in the fat content and size of the southern pine beetle in east Texas. *Ann. Entomol. Soc. Am.* 70:876-80
 107. Hemingway RW, McGraw GW, Barras SJ. 1977. Polyphenols in *Ceratocystis minor* infected *Pinus taeda*: fungal metabolites, phloem and xylem phenols. *J. Agric. Food Chem.* 25:717-22
 108. Hetrick LA. 1949. Some overlooked relationships of the southern pine beetle. *J. Econ. Entomol.* 42:466-69
 109. Himejima M, Hobson KR, Otsuka T, Wood DL, Kubo I. 1992. Antimicrobial terpenes from oleoresin of ponderosa pine

- Pinus ponderosa*: a defense mechanism against microbial invasion. *J. Chem. Ecol.* 18:1809–18
110. Hobson KR, Parmeter JR Jr, Wood DL. 1994. The role of fungi vectored by *Dendroctonus brevicornis* LeConte (Coleoptera: Scolytidae) in occlusion of ponderosa pine xylem. *Can. Entomol.* 126:277–82
 111. Hodges JD, Barras SJ, Mauldin JK. 1968. Amino acids in inner bark of loblolly pine as affected by the southern pine beetle and associated microorganisms. *Can. J. Bot.* 46:1467–72
 112. Hodges JD, Elam WW, Watson WF, Nebeker TE. 1979. Oleoresin characteristics and susceptibility of four southern pines to southern pine beetle (Coleoptera: Scolytidae) attacks. *Can. Entomol.* 111:889–96
 113. Hodges JD, Nebeker TE, DeAngelis JD, Karr BL, Blanche CA. 1985. Host resistance and mortality: a hypothesis based on the southern pine beetle–microorganism–host interactions. *Bull. Entomol. Soc. Am.* 31:31–35
 114. Hodges JD, Pickard LS. 1971. Lightning in the ecology of the southern pine beetle, *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Can. Entomol.* 103:44–51
 115. Horntvedt R. 1988. Resistance of *Picea abies* to *Ips typographus*: tree response to monthly inoculations with *Ophiostoma polonicum*, a beetle transmitted blue-stain fungus. *Scand. J. For. Res.* 3:107–14
 116. Horntvedt R, Christiansen E, Solheim H, Wang S. 1983. Artificial inoculation with *Ips typographus*-associated blue-stain fungi can kill healthy Norway spruce trees. *Medd. Nor. Inst. Skogforsk.* 38:1–20
 117. Hunt DWA, Borden JH. 1989. Terpene alcohol pheromone production by *Dendroctonus ponderosae* and *Ips paraconfusus* (Coleoptera: Scolytidae) in the absence of readily culturable microorganisms. *J. Chem. Ecol.* 15:1433–63
 118. Hunt DWA, Borden JH. 1990. Conversion of verbenols to verbenone by yeasts isolated from *Dendroctonus ponderosae* (Coleoptera: Scolytidae). *J. Chem. Ecol.* 16:1385–97
 119. Johnson MA, Croteau R. 1987. Biochemistry of conifer resistance to bark beetles and their fungal symbionts. In *ACS Symposium Series No. 325: Ecology and Metabolism of Plant Lipids*, ed. G Fuller, WD Nes, pp. 76–92. Washington, DC: Am. Chem. Soc.
 120. Kile GA. 1993. Plant diseases caused by species of *Ceratocystis sensu stricto* and *Chalara*. In *Ceratocystis and Ophiostoma: Taxonomy, Ecology, and Pathogenicity*, ed. MJ Wingfield, KA Seifert, JF Webber, pp. 173–84. St Paul, MN: Am. Phytopathol. Soc.
 121. Kirkendall LR. 1983. The evolution of mating systems in bark and ambrosia beetles (Coleoptera: Scolytidae). *Zool. J. Linn. Soc.* 77:293–352
 122. Klepzig KD, Kruger EL, Smalley EB, Raffa KF. 1995. Effects of biotic and abiotic stress on induced accumulation of terpenes and phenolics in red pines inoculated with beetle-vectored fungus. *J. Chem. Ecol.* 21:601–26
 123. Klepzig KD, Raffa KF, Smalley EB. 1991. Association of an insect-fungal complex with red pine decline in Wisconsin. *For. Sci.* 37:1119–39
 124. Kuroda K. 1991. Mechanism of cavitation development in the pine wilt disease. *Eur. J. For. Pathol.* 21:82–89
 125. Langstrom B, Hellqvist C. 1993. Induced and spontaneous attacks by pine shoot beetles on young Scots pine trees: tree mortality and beetle performance. *J. Appl. Entomol.* 115:25–36
 126. Langstrom B, Solheim H, Hellqvist C, Gref R. 1993. Effects of pruning young Scots pine on host vigor and susceptibility to *Leptographium wingfieldii* and *Ophiostoma minus*, two blue-stain fungi associated with *Tomicus piniperda*. *Eur. J. For. Pathol.* 23:400–15
 127. Langstrom B, Tenow O, Ericsson A, Hellqvist C, Larsson S. 1990. Effects of shoot pruning on stem growth, needle biomass, and dynamics of carbohydrates and nitrogen in Scots pine as related to season and tree age. *Can. J. For. Res.* 20:514–23
 128. Leach JG, Orr LW, Christensen C. 1934. The interrelationships of bark beetles and blue-stain fungi in felled Norway pine timber. *J. Agric. Res.* 49:315–42
 129. Leufven A, Bergstrom G, Falsen E. 1984. Interconversion of verbenols and verbenone by identified yeasts isolated from the spruce bark beetle, *Ips typographus*. *J. Chem. Ecol.* 10:1349–61
 130. Levieux J, Lieutier F, Moser JC, Perry TJ. 1989. Transportation of phytopathogenic fungi by the bark beetle *Ips typographus* Boerner and associated mites. *J. Appl. Entomol.* 108:1–11
 131. Lewinsohn D, Lewinsohn E, Bertagnolli CL, Patridge AD. 1994. Blue-stain fungi and their transport structures on the Douglas-fir beetle. *Can. J. For. Res.* 24:2275–83
 132. Lewinsohn E, Gijzen M, Croteau R. 1991.

- Defense mechanisms of conifers. *Physiol. Plant Pathol.* 96:44–49
133. Lewinsohn E, Gijzen M, Savage TJ, Croteau R. 1991. Defense mechanisms of conifers. *Physiol. Plant Pathol.* 96:38–43
 134. Lieutier F. 1992. Les réactions de défense des conifères et stratégies d'attaque de quelques Scolytides européens. *Mem. Soc. R. Belge Entomol.* 35:529–39
 135. Lieutier F, Berryman AA. 1988. Preliminary histological investigations on the defense reactions of three pines to *Ceratocystis clavigera* and two chemical elicitors. *Can. J. For. Res.* 18:1243–47
 136. Lieutier F, Berryman AA, Millstein JA. 1991. Preliminary study of the monoterpene response of three pines to *Ophiostoma clavigerum* (Ascomycetes: Ophiostomatales) and two chemical elicitors. *Ann. Soc. For.* 48:377–88
 137. Lieutier F, Cheniclet C, Garcia J. 1989. Comparison of the defense reactions of *Pinus pinaster* and *Pinus sylvestris* to attacks by two bark beetles (Coleoptera: Scolytidae) and their associated fungi. *Environ. Entomol.* 18:228–34
 138. Lieutier F, Ferrell GT. 1988. Relationships between indexes of tree vigour and the induced reaction of Scots pine to a fungus associated with *Ips sexdentatus* Boern. (Coleoptera: Scolytidae). In *Integrated Control of Scolytid Bark Beetles*, ed. TL Payne, H Saarenmaa, pp. 163–78. Blacksburg: Virg. Polytech. Inst. State Univ.
 139. Lieutier F, Garcia J, Romary P, Yart A, Jactel H, Sauvard D. 1993. Inter-tree variability in the induced defense reaction of Scots pine to single inoculations by *Ophiostoma brunneo-ciliatum*, a bark-beetle-associated fungus. *For. Ecol. Man.* 59:257–70
 140. Lieutier F, Garcia J, Yart A, Romary P. 1995. Wound reactions of Scots pine (*Pinus sylvestris* L.) to attacks by *Tomicus piniperda* L. and *Ips sexdentatus* Boern. (Coleoptera: Scolytidae). *J. Appl. Entomol.* 119:591–600
 141. Lieutier F, Vouland G, Pettinetti M, Garcia J, Romary P, Yart A. 1992. Defense reactions of Norway spruce (*Picea abies* Karst.) to artificial insertion of *Dendroctonus micans* Kug. (Col., Scolytidae). *J. Appl. Entomol.* 114:174–86
 142. Lieutier F, Yart A. 1989. Préférence thermique des champignons associés à *Ips sexdentatus* Boern. et *Tomicus piniperda* L. (Coleoptera: Scolytidae). *Ann. Sci. For.* 46:411–15
 143. Lieutier F, Yart A, Garcia J, Ham M-C. 1990. Cinétique de croissance des champignons associés à *Ips sexdentatus* Boern. et à *Tomicus piniperda* L. (Coleoptera: Scolytidae) et des réactions de défense des pins sylvestres (*Pinus sylvestris* L.) inoculés. *Agronomie* 10:243–56
 144. Lieutier F, Yart A, Garcia J, Ham M-C, Morelet M, Levieux J. 1989. Champignons phytopathogènes associés à deux coleoptères scolytidae du pins sylvestre (*Pinus sylvestris* L.) et étude préliminaire de leur agressivité envers l'hôte. *Ann. Sci. For.* 46:201–16
 145. Lieutier F, Yart A, Jay-Allemand C, Delorme L. 1991. Preliminary investigations on phenolics as a response of Scots pine phloem to attacks by bark beetles and associated fungi. *Eur. J. For. Pathol.* 21:354–64
 146. Livingston RL, Berryman AA. 1972. Fungal transport structures in the fir engraver, *Scolytus ventralis* (Coleoptera: Scolytidae). *Can. Entomol.* 104:1793–800
 147. Lorio PL Jr. 1988. Growth and differentiation-balance relationships in pines affect their resistance to bark beetles (Coleoptera: Scolytidae). In *Mechanisms of Woody Plant Defenses Against Insects: Search for Patterns*, ed. WJ Mattson, J Levieux, C Bernard-Dagan, pp. 73–92. New York: Springer-Verlag
 148. Lorio PL Jr. 1993. Environmental stress and whole-tree physiology. In *Beetle-Pathogen Interactions in Conifer Forests*, ed. T Schowalter, G Filip, pp. 82–101. San Diego: Academic
 149. Lorio PL Jr, Sommers RA. 1986. Evidence of competition for photosynthates between growth processes and oleoresin synthesis in *Pinus taeda* L. *Tree Physiol.* 2:301–6
 150. Lorio PL Jr, Stephen FM, Paine TD. 1995. Environment and ontogeny modify loblolly pine response to induced acute water deficits and bark beetle attack. *For. Ecol. Man.* 73:97–110
 151. Mathre DE. 1964. Survey of *Ceratocystis* spp. associated with bark beetles in California. *Contrib. Boyce Thompson Inst.* 22:353–62
 152. Matson PA, Hain FP. 1985. Host conifer defense strategies: a hypothesis. In *The Role of the Host in the Population Dynamics of Forest Insects: Proc. IUFRO Conf.*, ed. L Safranyik, pp. 33–42. Victoria: Can. For. Serv. Pac. For. Res. Cent.
 153. McGraw GW, Hemingway RW. 1977. 6, 8-Dihydroxy-3-hydroxymethyl-isocoumarin and other phenolic metabolites

- of *Ceratocystis minor*. *Phytochemistry* 16:1315–16
154. Miller RH, Berryman AA. 1985. Energetics of conifer defense against bark beetles and associated fungi. In *The Role of the Host in the Population Dynamics of Forest Insects: Proc. IUFRO Conf.*, ed. L Safranyik, pp. 13–23. Victoria: Can. For. Serv. Pac. For. Res. Cent.
 155. Miller RH, Berryman AA. 1986. Carbohydrate allocation and mountain pine beetle attack in girdled lodgepole pine. *Can. J. For. Res.* 16:1036–40
 156. Miller RH, Berryman AA, Ryan CA. 1986. Biotic elicitors of defense reactions in lodgepole pine. *Phytochemistry* 25:611–12
 157. Miller RH, Whitney HS, Berryman AA. 1986. Effects of induced translocation stress and bark beetle attack (*Dendroctonus ponderosae*) on heat pulse velocity and the dynamic wound response of lodgepole pine (*Pinus contorta* var. *latifolia*). *Can. J. Bot.* 64:2669–74
 158. Mitchell RG, Waring RH, Pitman GB. 1983. Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. *For. Sci.* 29:204–11
 159. Molnar AC. 1964. Pathogenic fungi associated with a bark beetle on alpine fir. *Can. J. Bot.* 43:563–70
 160. Moser JC. 1985. Use of sporothecae by phoretic *Tarsonemus* mites to transport ascospores of coniferous bluestain fungi. *Trans. Br. Mycol. Soc.* 84:750–53
 161. Moser JC, Perry TJ, Bridges JR, Yiu H-F. 1995. Ascospore dispersal of *Ceratocystiopsis ranaculosus*, a mycangial fungus of the southern pine beetle. *Mycologia* 87:84–86
 162. Moser JC, Perry TJ, Solheim H. 1989. Ascospores hyperphoretic on mites associated with *Ips typographus*. *Mycol. Res.* 93:513–17
 163. Mullick DB. 1977. The non-specific nature of defense in bark and wood during wounding, insect, and pathogen attack. *Rec. Adv. Phytochem.* 11:359–441
 164. Mulock P, Christiansen E. 1986. The threshold of successful attack by *Ips typographus* on *Picea abies*: a field experiment. *For. Ecol. Man.* 14:125–32
 165. Nebeker TE, Hodges JD, Blanche CA. 1993. Host response to bark beetle and pathogen colonization. In *Beetle-Pathogen Interactions in Conifer Forests*, ed. T Schowalter, G Filip, pp. 157–73. San Diego: Academic
 166. Nebeker TE, Hodges JD, Blanche CA, Honea CR, Tisdale RA. 1992. Variation in the constitutive defense system of loblolly pine in relation to bark beetle attack. *For. Sci.* 38:457–66
 167. Nebeker TE, Schmitz RF, Tisdale RA. 1995. Comparison of oleoresin flow in relation to wound size, growth rate, and disease status of lodgepole pine. *Can. J. Bot.* 73:370–75
 168. Nebeker TE, Schmitz RF, Tisdale RA, Hobson KR. 1995. Chemical and nutritional status of dwarf mistletoe, Armillaria root rot, and comandra blister rust infected trees which may influence tree susceptibility to bark beetle attack. *Can. J. Bot.* 73:360–69
 169. Nelson RM. 1934. Effect of bluestain fungi on southern pines attacked by bark beetles. *Phytopath. Zeit.* 7:327–53
 170. Nelson RM, Beal JA. 1929. Experiments with bluestain fungi in southern pines. *Phytopathology* 19:1101–6
 171. Owen DR, Lindahl KQ Jr, Wood DL, Parmeter JR Jr. 1987. Pathogenicity of fungi isolated from *Dendroctonus valens*, *D. brevicomis*, and *D. ponderosae* to ponderosa pine seedlings. *Phytopathology* 77:631–36
 172. Paine TD. 1984. Influence of the mycangial fungi of the western pine beetle on water conduction through ponderosa pine seedlings. *Can. J. Bot.* 62:556–58
 173. Paine TD. 1984. Seasonal response of ponderosa pine to inoculation of the mycangial fungi from the western pine beetle. *Can. J. Bot.* 62:551–55
 174. Paine TD, Birch MC. 1983. Acquisition and maintenance of mycangial fungi by *Dendroctonus brevicomis* LeConte (Coleoptera: Scolytidae). *Environ. Entomol.* 12:1384–86
 175. Paine TD, Blanche CA, Nebeker TE, Stephen FM. 1987. Composition of loblolly pine resin defenses: comparison of monoterpenes from induced lesion and sapwood resin. *Can. J. For. Res.* 17:1202–6
 176. Paine TD, Hanlon CC. 1994. Influence of oleoresin constituents from *Pinus ponderosa* and *Pinus jeffreyi* on the growth of the mycangial fungi from *Dendroctonus ponderosae* and *Dendroctonus brevicomis*. *J. Chem. Ecol.* 20:2551–63
 177. Paine TD, Stephen FM. 1987. Fungi associated with the southern pine beetle: avoidance of induced defense response in loblolly pine. *Oecologia* 74:377–79
 178. Paine TD, Stephen FM. 1987. Response of loblolly pine to different inoculum doses of *Ceratocystis minor*, a bluestain fungus associated with *Dendro-*

- tonus frontalis*. *Can. J. Bot.* 65:2093–95
179. Paine TD, Stephen FM. 1987. The relationship of tree height and crown class to the induced plant defenses of loblolly pine. *Can. J. Bot.* 65:2090–92
 180. Paine TD, Stephen FM. 1987. Influence of tree stress and site quality on the induced defense system of loblolly pine. *Can. J. For. Res.* 17:569–71
 181. Paine TD, Stephen FM. 1988. Induced defenses of loblolly pine, *Pinus taeda*: potential impact on *Dendroctonus frontalis* within-tree mortality. *Entomol. Exp. Appl.* 46:39–46
 182. Paine TD, Stephen FM, Cates RG. 1988. Phenology of an induced response in loblolly pine following inoculation of fungi associated with the southern pine beetle. *Can. J. For. Res.* 18:1556–62
 183. Paine TD, Stephen FM, Cates RG. 1993. Within and among tree variation in the response of loblolly pine to a fungus associated with *Dendroctonus frontalis* (Coleoptera: Scolytidae) and sterile wounding. *Can. Entomol.* 125:65–71
 184. Paine TD, Stephen FM, Taha HA. 1984. Conceptual model of infestation probability based on bark beetle abundance and host tree susceptibility. *Environ. Entomol.* 13:619–24
 185. Parmeter JR Jr, Slaughter GW, Chen M-M, Wood DL. 1992. Rate and depth of sapwood occlusion following inoculation of pines with bluestain fungi. *For. Sci.* 38:34–44
 186. Parmeter JR Jr, Slaughter GW, Chen M-M, Wood DL, Stubbs HA. 1989. Single and mixed inoculations of ponderosa pine with fungal associates of *Dendroctonus* spp. *Phytopathology* 79:786–72
 187. Peterman RM. 1977. An evaluation of the fungal inoculation method of determining the resistance of lodgepole pine to the mountain pine beetle (Coleoptera: Scolytidae) attacks. *Can. Entomol.* 109:443–48
 188. Piou D, Lieutier F, Yart A. 1989. Observations symptomatologiques et roles possibles d'*Ophiostoma minus* Hedgc. (ascomycete: Ophiostomatales) et de *Tomiscus piniperda* L. (Coleoptera: Scolytidae) dans le déperissement du pin sylvestre en forêt d'Orleans. *Ann. Sci. For.* 46:39–53
 189. Popp MP, Johnson JD, Massey TL. 1991. Stimulation of resin flow in slash and loblolly pine by bark beetle vectored fungi. *Can. J. For. Res.* 21:1124–26
 190. Raffa KF, Berryman AA. 1982. Accumulation of monoterpenes and associated volatiles following inoculation of grand fir with fungi transmitted by the fir engraver, *Scolytus ventralis* (Coleoptera: Scolytidae). *Can. Entomol.* 114:797–810
 191. Raffa KF, Berryman AA. 1982. Gustatory cues in the orientation of *Dendroctonus ponderosae* (Coleoptera: Scolytidae) to host trees. *Can. Entomol.* 114:97–104
 192. Raffa KF, Berryman AA. 1982. Physiological differences between lodgepole pines resistant and susceptible to the mountain pine beetle and associated microorganisms. *Environ. Entomol.* 11:486–92
 193. Raffa KF, Berryman AA. 1983. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). *Ecol. Monogr.* 53:27–49
 194. Raffa KF, Berryman AA. 1983. Physiological aspects of lodgepole pine wound responses to a fungal symbiont of the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae). *Can. Entomol.* 115:723–34
 195. Raffa KF, Berryman AA. 1987. Interacting selective pressures in conifer-bark beetle systems: a basis for reciprocal adaptations? *Am. Nat.* 129:234–62
 196. Raffa KF, Berryman AA, Simasko J, Teal W, Wong BL. 1985. Effects of grand fir monoterpenes on the fir engraver *Scolytus ventralis* (Coleoptera: Scolytidae) and its symbiotic fungus. *Environ. Entomol.* 14:552–56
 197. Raffa KF, Phillips TW, Salom SM. 1993. Strategies and mechanisms of host colonization by bark beetles. In *Beetle-Pathogen Interactions in Conifer Forests*, ed. T Schowalter, G Filip, pp. 102–28. San Diego: Academic
 198. Raffa KF, Smalley EB. 1988. Seasonal and long-term responses of host trees to microbial associates of the pine engraver, *Ips pini*. *Can. J. For. Res.* 18:1624–34
 199. Raffa KF, Smalley EB. 1988. Host resistance to invasion by lower stem and root infesting insects of pine: response to controlled inoculations with the fungal associate *Leptographium terebrantis*. *Can. J. For. Res.* 18:675–81
 200. Raffa KF, Smalley EB. 1995. Interaction of pre-attack and induced monoterpene concentrations in host conifer defense against bark beetle-fungal complexes. *Oecologia* 102:285–95
 201. Redfern DB, Stoakley JT, Steele H, Minter DW. 1987. Dieback and death of larch caused by *Ceratocystis laricicola* sp. nov. following attack by *Ips cembrae*.

- Plant Pathol.* 36:467-80
202. Reid RW, Gates H. 1970. Effect of temperature and resin on hatch of eggs of the mountain pine beetle (*Dendroctonus ponderosae*). *Can. Entomol.* 102:617-22
 203. Reid RW, Shrimpton DM. 1971. Resistant response of lodgepole pine to inoculation with *Europhium clavigerum* in different months and at different heights on stem. *Can. J. Bot.* 49:349-51
 204. Reid RW, Whitney HS, Watson JA. 1967. Reactions of lodgepole pine to attack by *Dendroctonus ponderosae* Hopkins and blue stain fungi. *Can. J. Bot.* 45:1115-26
 205. Renwick JAA, Vite JP. 1970. Systems of chemical communication in *Dendroctonus*. *Contrib. Boyce Thompson Inst.* 24:283-92
 206. Richmond JA, Mills C, Clark EW. 1970. Chemical changes in loblolly pine, *Pinus taeda* L., inner bark caused by bluestain fungus, *Ceratocystis minor* (Hedg.) Hunt. *J. Elisha Mitchell Sci. Soc.* 86:171
 207. Robinson RC. 1962. Blue stain fungi in lodgepole pine (*Pinus contorta* Dougl. var *latifolia* Engelm.) infested by the mountain pine beetle (*Dendroctonus ponderosae* Hopk.). *Can. J. Bot.* 40:609-14
 208. Ross DW, Fenn P, Stephen FM. 1992. Growth of southern pine beetle associated fungi in relation to the induced wound response in loblolly pine. *Can. J. For. Res.* 22:1851-59
 209. Rumbold CT. 1936. Three blue-stain fungi, including two new species, associated with bark beetles. *J. Agric. Res.* 52:419-37
 210. Rudinsky JA. 1962. Ecology of Scolytidae. *Annu. Rev. Entomol.* 7:327-48
 211. Rudinsky JA. 1966. Host selection and invasion by the douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, in coastal douglas-fir forests. *Can. Entomol.* 98:98-111
 212. Russell CE, Berryman AA. 1976. Host resistance to the fir engraver beetle. I. Monoterpene composition of *Abies grandis* pitch blisters and fungus-infected wounds. *Can. J. Bot.* 54:14-18
 213. Safranyik L, Shrimpton DM, Whitney HS. 1975. An interpretation of the interactions between lodgepole pine, the mountain pine beetle and its associated blue stain fungi in western Canada. In *Management of Lodgepole Pine Ecosystems*, ed. D Baumgartner, pp. 406-28. Pullman: Wash. State Univ. Coop. Ext.
 214. Schowalter TD, Pope DN, Coulson RN, Fargo WS. 1981. Patterns of southern pine beetle (*Dendroctonus frontalis* Zimm.) infestation enlargement. *For. Sci.* 27:837-49
 215. Shrimpton DM. 1973. Extractives associated with wound response of lodgepole pine attacked by the mountain pine beetle and associated microorganisms. *Can. J. Bot.* 51:527-34
 216. Shrimpton DM. 1973. Age and size related responses of lodgepole pine to inoculation with *Europhium clavigerum*. *Can. J. Bot.* 51:1155-60
 217. Shrimpton DM. 1978. Resistance of lodgepole pine to mountain pine beetle infestation. In *Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests*, ed. AA Berryman, GD Amman, RW Stark, DL Kibbee, pp. 64-76. Moscow: Univ. Idaho
 218. Shrimpton DM, Watson JA. 1971. Response of lodgepole pine seedlings to inoculation with *Europhium clavigerum*, a blue stain fungus. *Can. J. Bot.* 49:373-75
 219. Shrimpton DM, Whitney HS. 1968. Inhibition of growth of blue stain fungi by wood extractives. *Can. J. Bot.* 46:757-break 61
 220. Smith RH. 1963. Toxicity of pine resin vapors to three species of *Dendroctonus* bark beetles. *J. Econ. Entomol.* 56:827-31
 221. Smith RH. 1966. Resin quality as a factor in the resistance of pines to bark beetles. In *Breeding Pest-Resistant Trees*, ed. HD Gerhold, RE McDermott, EH Schreiner, JA Winioski, pp. 189-96. Oxford: Pergamon
 222. Solheim H. 1991. Oxygen deficiency and spruce resin inhibition of growth of blue stain fungi associated with *Ips typographus*. *Mycol. Res.* 95:1387-92
 223. Solheim H. 1992. The early stages of fungal invasion in Norway spruce infested by the bark beetle *Ips typographus*. *Can. J. Bot.* 70:1-5
 224. Solheim H. 1992. Fungal succession in sapwood of Norway spruce infested by the bark beetle *Ips typographus*. *Eur. J. For. Pathol.* 22:136-48
 225. Solheim H. 1995. A comparison of blue-stain fungi associated with the North American spruce beetle *Dendroctonus rufipennis* and the Eurasian spruce bark beetle *Ips typographus*. *Aktuelt fra Skogforsk* 4:61-67
 226. Solheim H. 1995. Early stages of blue-stain fungus invasion of lodgepole pine sapwood following mountain pine beetle attack. *Can. J. Bot.* 73:70-74
 227. Solheim H, Langstrom B. 1991. Blue-stain fungi associated with *Tomicus*

- piniperda* in Sweden and preliminary observations on their pathogenicity. *Ann. Sci. For.* 48:149–56
228. Solheim H, Langstrom B, Hellqvist C. 1993. Pathogenicity of the blue-stain fungi *Leptographium wingfieldii* and *Ophiostoma minus* to Scots pine: effect of tree pruning and inoculation density. *Can. J. For. Res.* 23:1438–43
 229. Stark RW. 1965. Recent trends in forest entomology. *Annu. Rev. Entomol.* 10:303–24
 230. Steele CL, Lewinsohn E, Croteau R. 1995. Induced oleoresin biosynthesis in grand fir as a defense against bark beetles. *Proc. Natl. Acad. Sci.* 92:4164–68
 231. Stephen FM, Berisford CW, Dahlsten DL, Fenn P, Moser JC. 1993. Invertebrate and microbial associates. In *Beetle-Pathogen Interactions in Conifer Forests*, ed. T Schowalter, G Filip, pp. 129–53. San Diego: Academic
 232. Stephen FM, Paine TD. 1985. Seasonal patterns of host tree resistance to fungal associates of the southern pine beetle. *Z. Ang. Entomol.* 99:113–22
 233. Stephen FM, Paine TD, Lih MP. 1983. Understanding bark beetle/host interactions: a means for improving decision strategies. *Z. Ang. Entomol.* 96:256–65
 234. Strobel GA, Sugawara F. 1986. The pathogenicity of *Ceratocystis montia* to lodgepole pine. *Can. J. Bot.* 64:113–16
 235. Swart WJ, Wingfield MJ. 1991. Seasonal response of *Pinus radiata* in South Africa to artificial inoculation with *Sphaeropsis sapinea*. *Plant Dis.* 75:1031–33
 236. Tisdale RA, Nebeker TE. 1992. Resin flow as a function of height along the bole of loblolly pine. *Can. J. Bot.* 70:2509–11
 237. Vanderwel D. 1994. Factors affecting pheromone production in beetles. *Arch. Insect Biochem. Physiol.* 25:347–62
 238. Verrall AF. 1938. The probable mechanism of the protective action of resin in the fire wounds on red pine. *J. For.* 36:1231–33
 239. Viiri H, von Weissenberg K. 1995. *Ophiostoma* blue-staining fungi associated with *Ips typographus* in Finland. *Aktuelt fra Skogforsk* 4:58–60
 240. Vite JP. 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
 241. VonSchrenk H. 1903. The “bluing” and the “red rot” of the western yellow pine, with special reference to the Black Hills Forest Reserve. *U.S. Bur. Plant Ind. Bull.* #36. 40 pp.
 242. Wagner TL, Gagne JA, Doraiswamy PC, Coulson RN, Brown KW. 1979. Development time and mortality of *Dendroctonus frontalis* in relation to changes in tree moisture and xylem water potential. *Environ. Entomol.* 8:1129–38
 243. Wainhouse D, Cross DJ, Howell RS. 1990. The role of lignin as a defence against the spruce beetle *Dendroctonus micans*: effect on larvae and adults. *Oecologia* 85:257–65
 244. Werner RA, Illman BL. 1994. Response of lutz, sitka, and white spruce to attack by *Dendroctonus rufipennis* (Coleoptera: Scolytidae) and blue stain fungi. *Environ. Entomol.* 23:472–78
 245. Whitney HS. 1971. Association of *Dendroctonus ponderosae* (Coleoptera: Scolytidae) with blue stain fungi and yeasts during brood development in lodgepole pine. *Can. Entomol.* 103:1495–503
 246. Whitney HS. 1982. Relationships between bark beetles and symbiotic organisms. In *Bark Beetles in North American Conifers*, ed. JB Mitton, KB Sturgeon, pp. 183–211. Austin: Univ. Texas
 247. Whitney HS, Bandoni RJ, Oberwinkler F. 1987. *Entomocorticium dendroctoni* gen. et. sp. nov. (Basidiomycotina), a possible nutritional symbiote of the mountain pine beetle in lodgepole pine in British Columbia. *Can. J. Bot.* 65:95–102
 248. Whitney HS, Cobb FW Jr. 1972. Non-staining fungi associated with the bark beetle *Dendroctonus brevicomis* (Coleoptera: Scolytidae) on *Pinus ponderosa*. *Can. J. Bot.* 50:1943–45
 249. Whitney HS, Farris SH. 1970. Maxillary mycangium in the mountain pine beetle. *Science* 167:54–55
 250. Wilkinson RC, Hanover JW, Wright JW, Flake RH. 1971. Genetic variation in the monoterpene composition of white spruce. *For. Sci.* 17:83–90
 251. Wingfield MJ. 1983. Association of *Verticilladiella procera* and *Leptographium terebrantis* with insects in the Lake States. *Can. J. For. Res.* 13:1238–45
 252. Wong BL, Berryman AA. 1977. Host resistance to the fir engraver beetle. 3. Lesion development and containment of infection by resistant *Abies grandis* inoculated with *Trichosporium symbioticum*. *Can. J. Bot.* 55:1358–65
 253. Wood DL. 1982. The role of pheromones, kairomones, and allomones in the host se-

- lection and colonization behavior of bark beetles. *Annu. Rev. Entomol.* 27:411–46
254. Wood SL. 1982. The Bark and Ambrosia Beetles of North and Central America (Coleoptera: Scolytidae), a Taxonomic Monograph. Great Basin Nat. Mem. 6. 1359 pp.
255. Worrall JJ, Harrington TC. 1988. Respirometric testing of decay resistance of discolored root wood. *Phytopathology* 78:676–82
256. Wright LC, Berryman AA, Gurusiddaiah S. 1979. Host resistance to the fir engraver beetle, *Scolytus ventralis* (Coleoptera: Scolytidae): 4. effect of defoliation on wound monoterpene and inner bark carbohydrate concentrations. *Can. Entomol.* 111:1255–62
257. Yearian WC, Gouger RJ, Wilkinson RC. 1972. Effects of the bluestain fungus, *Ceratocystis ips*, on development of *Ips* bark beetles in pine bolts. *Ann. Entomol. Soc. Am.* 65:481–87



CONTENTS

J. S. KENNEDY (1912–1993): A Clear Thinker in Behavior's Confused World, <i>John Brady</i>	1
ADAPTATIONS IN SCALE INSECTS, <i>Penny J. Gullan, Michael Kosztarab</i>	23
ECOLOGY AND EVOLUTION OF GALLING THRIPS AND THEIR ALLIES, <i>Bernard J. Crespi, David A. Carmean, and, Thomas W. Chapman</i>	51
DIPTERA AS PARASITOIDS, <i>Donald H. Feener Jr, Brian V. Brown</i>	73
WILD HOSTS OF PENTATOMIDS: Ecological Significance and Role in Their Pest Status on Crops, <i>Antônio R. Panizzi</i>	99
BEHAVIORAL MANIPULATION METHODS FOR INSECT PEST-MANAGEMENT, <i>S. P. Foster and, M. O. Harris</i>	123
VISUAL ACUITY IN INSECTS, <i>Michael F. Land</i>	147
INTERACTIONS AMONG SCOLYTID BARK BEETLES, THEIR ASSOCIATED FUNGI, AND LIVE HOST CONIFERS, <i>T. D. Paine, K. F. Raffa, T. C. Harrington</i>	179
PHYSIOLOGY AND ECOLOGY OF DISPERSAL POLYMORPHISM IN INSECTS, <i>Anthony J. Zera, Robert F. Denno</i>	207
EVOLUTION OF ARTHROPOD SILKS, <i>Catherine L. Craig</i>	231
INSECTS AS TEACHING TOOLS IN PRIMARY AND SECONDARY EDUCATION, <i>Robert W. Matthews, Lynda R. Flage, and, Janice R. Matthews</i>	269
LIFE-STYLES OF PHYTOSEIID MITES AND THEIR ROLES IN BIOLOGICAL CONTROL, <i>J. A. McMurtry, B. A. Croft</i>	291
PHOTOPERIODIC TIME MEASUREMENT AND RELATED PHYSIOLOGICAL MECHANISMS IN INSECTS AND MITES, <i>Makio Takeda, Steven D. Skopik</i>	323
SYSTEMATICS OF MOSQUITO DISEASE VECTORS (DIPTERA, CULICIDAE): Impact of Molecular Biology and Cladistic Analysis, <i>Leonard E. Munstermann, Jan E. Conn</i>	351
HOST PLANT INFLUENCES ON SEX PHEROMONE BEHAVIOR OF PHYTOPHAGOUS INSECTS, <i>Peter J. Landolt, Thomas W. Phillips</i>	371
MIGRATORY ECOLOGY OF THE BLACK CUTWORM, <i>William B. Showers</i>	393
PHYLOGENY OF TRICHOPTERA, <i>J. C. Morse</i>	427
THE BIOLOGY, ECOLOGY, AND MANAGEMENT OF THE CAT FLEA, <i>Michael K. Rust, Michael W. Dryden</i>	451

BEHAVIOR AND ECOLOGICAL GENETICS OF WIND-BORNE MIGRATION BY INSECTS, <i>A. G. Gatehouse</i>	475
BIONOMICS OF THE FACE FLY, <i>MUSCA AUTUMNALIS</i> , <i>Elliot S. Krafsur, Roger D. Moon</i>	503
PERITROPHIC MATRIX STRUCTURE AND FUNCTION, <i>M. J. Lehane</i>	525
GENETIC DISSECTION OF SEXUAL BEHAVIOR IN <i>DROSOPHILA MELANOGASTER</i> , <i>Daisuke Yamamoto, Jean-Marc Jallon, Akira Komatsu</i>	551
BIOLOGY OF <i>WOLBACHIA</i> , <i>John H. Werren</i>	587
BIOLOGICAL MEDIATORS OF INSECT IMMUNITY, <i>Jeremy P. Gillespie and, Michael R. Kanost, Tina Trenczek</i>	611