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

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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.

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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. brevicomis, 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* (Hsiau & 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 brunneociliatum* (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 crystalization. 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. brevicomis* 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, *Leptographium 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 expediters 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/fungal 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.

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