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Synopsis

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12.1 SYNTHESIS OF CURRENT KNOWLEDGE

Our understanding of bark beetle–pathogen interactions and their consequences in conifer forests clearly has increased dramatically over the past two decades. Research in this area has contributed to and benefitted from emerging views of species interactions and forest pest management.We are recognizing the need to view forests as ecosystems with natural checks and balances, rather than as collections of independent species, if long-term forest management goals are to be achieved. Forest managers must address potential cumulative effects of management practices on bark beetles and pathogens over long time periods, even under shortened rotation periods. Furthermore, forest health must be sustainable in the long term if forest resources are to remain available to future generations. Forest resources, such as timber and wildlife, must be effectively balanced. Pest management should avoid contributing to pesticide resistance, outbreaks of non-target pests, and environmental degradation.

Management of bark beetle–pathogen complexes has improved over the past two decades as a result of two new concepts: the importance of species interactions in controlling pest epidemiologies, and integrated pest management (IPM) methodology. Interactions among bark beetles, pathogenic fungi and conifers are a major concern to forest managers in North America. Loss of timber volume to bark beetles and root pathogens has been estimated at 0.9–1.1 billion m^3 $year^{-1}$ in western North America (Chapter 9). Consequently, suppression of these mortality agents has been a priority. However, these organisms together with fire have been instrumental (through natural thinning, nutrient cycling and selection for pest and fire tolerance) in maintaining the structure and productivity of these forests (Chapter 1).

We have made progress in identifying important mortality agents (Chapters 2 and 3). New systematics techniques, such as cytogenetics and enzyme electrophoresis, have permitted discrimination among pathogenic and non-pathogenic species and varieties. Morphological characteristics, such as bark beetle mycangia and sticky conidia, that facilitate interaction between bark beetles and fungi have been identified.

Abiotic and biotic factors often predispose conifers to attack by mortality agents (Chapter 4). Water stress is a major predisposing factor. Both drought and soil saturation can disrupt plant physiological processes and increase susceptibility to insects and pathogens. Soil com-

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paction, nutrient imbalances, lightning strike, windthrow, atmospheric pollution, and road building also have been shown to predispose conifers to attack by insects and pathogens. Although wildfire traditionally has been viewed as a disturbance, creating damaged trees susceptible to bark beetles and pathogens, fire suppression in western North America has resulted in dense forests predisposed to bark beetles and pathogens.

Stress is not inevitably bad for trees and good for the invading organisms. Tree physiological processes mediate the relationship between environmental conditions and pest epidemiology (Chapter 5). Even healthy trees undergo physiological changes during seasonal and ontogenetic growth and development that increase susceptibility to invading organisms. The timing, intensity and duration of stress, as well as the proximity and size of bark beetle or pathogen populations, determine the risk of attack by these organisms (Chapters 5 and 6). Biotic factors often exacerbate plant stress and increase susceptibility to less virulent organisms. Root pathogens increase tree susceptibility, and often attractiveness, to bark beetles. On the other hand, relatively innocuous stem rusts, mistletoes, defoliators and some bark beetles and fungi can increase tree susceptibility to tree-killing organisms (Chapter 4).

Over the past 20 years we have learned much about the mechanisms of tree defense against bark beetles and pathogenic fungi. Conifer defense mechanisms include both a preformed resin system and/or an induced wound response (Chapters 5 and 8). Oleoresin exudation pressure and flow rate have been correlated with conifer susceptibility to attack by bark beetles, especially for *Pinus* in the western and southern US. Trees with low OEP or flow rate tend to be more susceptible to attack by bark beetles. The induced wound response includes localized autolysis of parenchyma cells, tissue necrosis, secondary resinosis by adjacent secretory and parenchyma cells, and formation of wood periderm to physically isolate the lesion. These two defense mechanisms function to limit the number of organisms that can successfully penetrate the bark and to isolate or kill those that do reach the subcortical habitat. However, these defenses constitute a substantial drain of energy that could otherwise be channeled into growth and reproduction. Consequently, defensive capability often is reduced during periods of physiological stress.

Stand factors can affect susceptibility. Conifers with large crowns produce more photosynthate and are more capable of defense. Dense stands are characterized by reduced light, temperature, leaf area, growth rate, and distance between trees. All of these factors can facilitate host discovery and colonization by bark beetles and pathogenic fungi (Chapters 5 and 6).

Host colonization by bark beetles consists of four phases: dispersal, host selection, concentration, and establishment (Chapter 6). Bark beetles often can travel many kilometers, depending on physiological and environmental conditions, but most travel much shorter distances. Long-distance dispersal by some individuals facilitates outbreeding.

Bark beetles can be divided into two functional groups on the basis of host selection and concentration mechanisms. Secondary, or non-aggressive, bark beetles, such as *Dendroctonus valens* and *Scolytus ventralis*, are attracted to weakened trees by host chemical cues. Aggregation is not required to overcome defenses of such trees. These beetles typically are restricted to scattered susceptible hosts but have relatively stable populations. The primary, or aggressive, bark beetles, such as *D. frontalis* and *D. ponderosae*, use primarily visual cues to locate tree boles. Once on the bark, beetles respond to feeding, pressure and/or tactile stimuli and either initiate boring or resume flight. At large population levels, pheromones in combination with host tree volatiles attract large numbers of beetles, resulting in mass attack and exhaustion of tree defenses. These species are capable of attacking and killing more resistant trees in forest stands. However, populations of these species are unstable because of the dependence on large populations to attack living trees (Chapter 6).

Colonization begins with boring activity initiated by chemical and/or physical stimuli. Drought-induced acoustic signals also may trigger the tunneling response. Penetration of the bark provides entry to pathogenic *Ophiostoma* spp. and *Leptographium* spp. that may accelerate tree decline and death, perhaps through toxin production, mycelial plugging of tracheids, gas release into tracheids, and/or blockage of pit openings. The establishment phase begins when tree defenses are exhausted and beetle oviposition becomes possible.

At least 100 species of microorganisms associated with bark beetles have been discovered, and more likely await discovery. Dissemination is the primary benefit fungi receive from this association. Mycangia are specialized structures that provide nutrients to mutualistic microorganisms, but mycangia are not necessary for vectoring of many fungi. *Ophiostoma* and other pathogenic fungi are transported externally on dispersing beetles or on phoretic mites. Microorganisms can be both beneficial and detrimental to the bark beetles. Some bark beetles may feed on associated fungi, but most larvae mine in advance of fungal penetration. The suitability of the subcortical environment as a food base is enhanced by some microorganisms, such as yeasts and nitrogen-fixing bacteria. Nitrogen-fixing bacteria may improve the nutritional status of the phloem for bark beetles. Some bacteria and fungi convert host tree terpenes into beetle aggregation pheromones, thereby facilitating mass attack and successful colonization.

In addition to the microorganisms, bark beetles vector or provide entry for a large number of associated invertebrates, including mites, nematodes, microorganisms and protozoans (Chapter 7). Many of the microorganisms and invertebrates carried by bark beetles into their galleries are mutualists that increase the nutritional suitability of the subcortical resources or prey on bark beetle parasites and predators. A large number of predators and competitors are attracted by bark beetle pheromones or by volatiles emanating from the dying tree. These associates interact with each other and with the bark beetles and microorganisms within the gallery system. Even indirect interactions, such as nematophagous mites feeding on bark beetle parasites, or saprophagous mites feeding on or carrying host spores, can influence bark beetle and pathogen epidemiologies.

Under natural conditions, bark beetles and pathogenic fungi do not threaten the long-term productivity of the forest (Chapter 9). These organisms, together with fire, function as natural thinning agents and accelerate nutrient cycling from decomposing trees, contributing to forest diversity, health and long-term productivity and stability. Humans and their activities have become part of this ecosystem. Bark beetles and pathogenic fungi become viewed as destructive agents warranting suppression when we introduce the concept of economic value to timber resources. Although the ultimate effect of bark beetle and pathogen attack is usually tree mortality, our response to this mortality depends on forest management objectives. For example, mortality in stands managed for timber production could be detrimental to management goals to the extent that the number of high yield crop trees is reduced or altered harvest or salvage scheduling is required. On the other hand, this mortality might contribute to timber management goals if the pattern of natural thinning and increased light and soil fertility enhance long-term productivity and resistance of surviving trees. Mortality in stands managed for wildlife or biodiversity could contribute to these objectives if it increased stand diversity and wildlife habitat, or it could be detrimental if it threatened habitat for endangered species.

Development of complex mathematical simulation models has improved our ability to predict and evaluate the effects of bark beetle and pathogen outbreaks (Chapter 10). These models also can indicate priorities for future research. A model developed for western North America has been used to simulate effects of root diseases and associated bark beetles.

Currently, the model incorporates effects of combinations of three root diseases and four bark beetle functional groups. Continued testing and refinement of this model will improve its use for forest management decisions.

Tree mortality due to bark beetles and pathogenic fungi should be rare events in forests managed to facilitate natural interactions and balances among species. Prevention of outbreaks through forest management practices that mimic natural processes is a key to reducing losses without disrupting natural processes in integrated ecosystems (Chapter 11). This goal can be achieved through management of tree species composition, density, age or size distribution (stand structure), and disturbance-related factors such as tree injury and stump density.

12.2 RECOMMENDATIONS FOR FUTURE RESEARCH

Despite our advanced understanding of species interactions in forests, this synthesis has demonstrated the limits of our knowledge. Major questions remain to direct future research on interactions between bark beetles and pathogenic fungi in conifer forests.

Failure to meet forest management objectives often indicates inaccurate identification of target species. Funding for bark beetle and fungal systematics typically corresponds to concern during outbreaks. While much has been learned through the use of modern morphological techniques, both bark beetles and pathogenic fungi continue to challenge those who wish to distinguish species or ecologically significant varieties (biotypes). Among bark beetles, morphologically indistinguishable populations (cryptic and sibling species) respond differently to host factors and management strategies. Perhaps new chemosystematic techniques, such as cuticular hydrocarbons or DNA analysis, or behavioral chemicals (semiochemicals), will distinguish incipient species (Chapter 2). Similarly, fungal systematists still contend with questions of hyphal interfertility and life history relationships between sexual and asexual stages among the Deuteromycotina, Ascomycotina and Basidiomycotina. The difficulty in distinguishing pathogenic and non-pathogenic species of *Armillaria* and *Leptographium* is an obvious example (Chapter 3). Again, new techniques in cytogenetics and molecular systematics are certain to reveal new information about the relationships among insects and fungi.

We need more information on factors predisposing conifer forests to outbreaks of bark beetles and pathogenic fungi. For example, what degree of stress is necessary to increase tree susceptibility to mortality agents? What combinations of stress, resource concentration, and incipient populations of bark beetles and pathogenic fungi are sufficient to trigger outbreaks? What are the likely consequences of global climate change for trees, insects, and fungi? How will forest management practices stabilize forests or exacerbate effects of climate change? Because forests respond to changing conditions over long time periods, often with significant lag time because of mediating interactions (Franklin *et al.*, 1989; Perry and Borchers, 1990), research on effects of predisposing factors must cover sufficiently long time periods. This will require agency commitments to longer term research support than currently available. At the same time, critical scientific methods for evaluating effects of specific factors must be balanced against the need for information on interactive effects among multiple predisposing factors. Assessing interactions among many factors will require use of multivariate analytical techniques, as well as multiple analysis of variance (ANOVA) techniques.

Our current understanding of interactions among the invertebrates and microorganisms in this system inspire awe at their complexity. Apparently innocuous interactions, such as between bark beetles and nematophagous mites, or between fungi and the saprophagous mites phoretic on bark beetles, influence the reproductive and developmental success of the beetles. The tarsonemid mites phoretic on bark beetles only recently were found to be the principle vectors of the pathogenic *Ophiostoma minus* (Bridges and Moser, 1986). Because funding for work on these interactions traditionally has been limited to outbreak periods, we still know little about changes in interactions that trigger the shift from endemic to epidemic populations. Further intricacies in interactions critical to regulating bark beetle and pathogen epidemiologies likely await discovery.

The physical and biochemical defenses of conifers still are imperfectly understood. The roles of oleoresin production and flow rate, terpene composition, lesion development, and resource partitioning patterns underlying these tree defenses require clarification. Evaluation of the relative importances of the oleoresin system and the induced response to wounding will improve our understanding of tree defense physiology. The mechanisms by which fungal growth or metabolites interfere with tree defensive mechanisms and lead to tree death also require further investigation.

We have only begun to appreciate the variety of effects of these interactions on forest ecosystems. Bark beetles and pathogenic fungi regularly cause extensive tree mortality and loss of forest resources (Filip and Goheen, 1982, 1984; Leuschner and Berck, 1985). However, bark beetle and pathogen roles in thinning and decomposition processes contribute to soil structure and fertility, and to long-term forest productivity and biodiversity (Franklin *et al.*, 1989; Schowalter *et al.*, 1992). Research has addressed non-destructive effects only during the past decade. Experimental evaluation of the importance of insects, pathogens and fire to long-term forest health lags far behind advancing concepts on potential roles. Few entomologists or pathologists have been integrated in long-term multidisciplinary research on nutrient cycling and forest health. Experimental studies on these long-term effects will require funding over longer periods.

We have seen considerable advance in computer technology and modeling software. However, even the most complex simulation models and decision-support systems still rely on untested assumptions, especially regarding the roles of tree physiological processes and stand structure and composition. Knowledge about these roles will form the links between environmental conditions and tree susceptibility to bark beetles and pathogenic fungi. In addition, models have yet to incorporate effects of bark beetles and fungi on soil fertility and biodiversity into evaluations of "pest" epidemiology and treatment efficacy. Furthermore, model structure and data requirements necessarily represent a compromise between scientific validity and management utility. Data requirements for model initialization often cannot be collected conveniently by forestry personnel. Few models have been evaluated for the costs, in terms of accuracy and reliability of predictions, of using inadequate data to initiate model simulations (Schowalter *et al.*, 1982).

Finally, we have recognized that our forest management practices, especially fire suppression and tree species selection, have created forests susceptible to bark beetles and pathogenic fungi over broad geographic areas and that this susceptibility is likely exacerbated by problems of atmospheric pollution and global climate change. Nevertheless, few critical experiments have demonstrated the effects of particular management practices on bark beetle and pathogen responses. For example, is the reduced tree mortality to bark beetles following thinning due to increased resource availability for remaining trees, to increased distance between hosts, and/or to changes in ambient temperature and moisture? How will bark beetles and pathogens respond to reintroduction of periodic fire? Similarly, few critical experiments have evaluated the long-term or region-wide consequences of pest activity or suppression tactics (Honnold and Wood, 1990)

A large proportion of the pest control measures in current use have not been evaluated for efficacy, in terms of resource protection, through appropriate controlled comparisons among replicated treatments (Waters and Stark, 1980; Wood *et al.*, 1985; Honnold and Wood, 1990). Typically, an infested (or treated) stand is compared to an uninfested (or untreated) stand. Inadequate replication and non-random assignment of treatments among study plots preclude convincing statistical evaluation. Random assignment of treatments often is especially difficult where insect and disease-caused damage dictates the type of treatment employed (e.g. plots containing numerous root disease centers cannot receive commercial thinning treatment).

Data necessary to evaluate effects of pest activity and pest suppression must be obtained experimentally, with adequate replication and random assignment of treatments among experimental plots. Application of results will require that replicate plots be distributed across large areas rather than contained within individual stands. For example, Schowalter and Turchin (1993) evaluated the effects of stand density and composition on initiation of *Dendroctonus frontalis* infestations by introducing a standard number of brood beetles (two infested trees) into replicate treatment plots (Fig. 12.1) distributed over 100 000 ha in each of 2 years. Replication and equal exposure to bark beetle populations among plots were ensured using this method.

Rigorous scientific testing of hypotheses using experimental methods will require greater collaboration between researchers (including entomologists, pathologists and forest ecologists) and forest managers. Such scientific evaluation of management practices is absolutely necessary to justify pest management decisions, especially in sensitive areas or areas set aside to protect ecosystem integrity, such as designated wilderness (Honnold and Wood, 1990). In fact, areas set aside as preserves will become increasingly important as natural laboratories for evaluation of natural interactions as demands for resources from managed forests increase (Schowalter, 1988; Filip, 1990; Honnold and Wood, 1990; Wickman, 1990).

The traditional emphasis in North American forestry has been on timber values. Increasing concern over sustainable forest health, preservation of biodiversity, protection of long-term site productivity, and the fate of future forests subject to changing atmospheric quality and global climate already is altering our management objectives and approaches. Our research efforts must be directed toward a better understanding of the roles played by bark beetles, pathogenic fungi, environmental factors, and their interactions, in meeting these objectives. Perhaps by incorporating or mimicking these natural roles into our forest management, we can accomplish our management objectives more efficiently.

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Fig. 12.1. Experimental design for testing effects of stand treatments on bark beetle infestation development. Trees containing mature beetles ready to emerge were cut into 1.3 m sections and distributed evenly among replicate treatment plots. These methods ensured that treatments were equally exposed to beetle populations, rather than allowing naturally distributed beetles to discover some treatment plots and not others.

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