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Bark Beetle–Pathogen–Conifer Interactions: an Overview

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1.1 INTRODUCTION

In North America, as in other parts of the world, forest management historically has been equated with timber management. A narrow focus on maximizing productivity of commercially valuable tree species precluded recognition of the importance of associated species or their interactions for sustained forest productivity and stability. Any factor (biotic or abiotic) which interfered with the goal of maximum timber yields was considered a "pest" to be vigorously suppressed (Stark and Waters, 1985). Only recently have interactions among the various forest species, including "pests," become recognized both as indicators of forest health and as contributors to long-term forest health. Accumulating scientific evidence now supports a view of forests as integrated ecosystems in which species interactions respond to changes in forest condition and maintain nutrient cycling and soil fertility critical to forest productivity and stability. This view, supported by increasing insect and pathogen problems in stressed managed forests and increasing public demand for non-timber amenities, together with recent legislation requiring environmental impact assessment and protection of endangered species, is revolutionizing forestry and, consequently, our approach to forest protection.

1.2 THE ECOSYSTEM VIEW OF FORESTS

1.2.1 The importance of interactions

The complexity of forest systems and the need to manage forests for productivity and water yield over long time periods led to development of an ecosystem perspective during the

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1950s and 1960s. Forested watersheds were ideal ecosystems with relatively distinct boundaries. Various instruments were used to measure amounts of materials added to the ecosystem (input) through bedrock weathering, precipitation, atmospheric filtering and biomass accumulation and lost from the ecosystem (output) through evapotranspiration, leaching, streamflow and harvest (see Bormann and Likens, 1979; Edmonds, 1982; Swank and Crossley, 1987; Perry *et al.*, 1989). Eventually, as part of the International Biological Program (IBP) and Long Term Ecological Research (LTER) Program, studies of species diversity led to consideration of the consequences of mutualistic, competitive and predatory interactions among species within integrated communities (Edmonds, 1982). The emerging view of forests as ecosystems with internal mechanisms for maintaining productivity and stability, in the face of constant change in environmental conditions, is changing our approach to managing forest resources and the organisms often viewed as "pests."

Natural forests are typically composed of more than one tree species or age class, many other plant and animal species, and various structures such as snags (dead standing trees) and decomposing logs. These components function in various ways to maintain nutrient cycles (critical to soil fertility) and long-term forest productivity and stability (Franklin *et al.*, 1989) and influence regional and global climate. Forests reduce solar heating of the soil surface and contribute to cloud formation, moderating regional climates, and regulate fluxes of atmospheric oxygen and carbon dioxide. Plants and autotrophic bacteria capture water, carbon dioxide and nutrients from the atmosphere and soil and incorporate these resources into biomass. Herbivores consume plants and plant parts, influencing nutrient requirements by vegetation and controlling the flow of energy and nutrients to the forest floor. Saprophagous invertebrates, bacteria and fungi release nutrients from biomass and control soil fertility. Mycorrhizal fungi infuse soil and decomposing litter and provide nutrients to host trees in return for necessary photosynthates. The activities and interactions of these components prevent bottlenecks in nutrient supply that could limit forest productivity and reduce stability to environmental fluctuations (Mattson and Addy, 1975; Tilman, 1982, 1988; Seastedt, 1984; Schowalter *et al.*, 1986).

Selective consumption of particular plants and plant parts by herbivores and pathogens not only maintains nutrient cycling but also provides for continuous turnover and rejuvenation of vegetative material. Such turnover is necessary to prevent stagnation and reduced photosynthetic efficiency and to facilitate adaptation to environmental change. Replacement of stressed plants by plants more tolerant of prevailing conditions could enhance long-term productivity and the stability of forest function.

1.2.2 Importance of non-commercial components

The functions of many forest components remain unknown. However, experience has shown that inconspicuous or unappreciated components often are critical to maintenance of forest health and long-term productivity. Temple (1977) noted that the age (300–400 years) of the last 13 surviving *Sideroxylon sessiliflorum* (=*Calvaria major*), a tree that once covered the South Pacific island of Mauritanius, coincided with the extermination of the dodo bird in 1680. When *S. sessiliflorum* seeds were force-fed to turkeys (approximately the size of a dodo), the seed coats were sufficiently abraided during passage through the bird's gut to permit germination, thereby indicating the dodo's contribution to reproduction of *S. sessiliflorum*. A major tree species was nearly lost because of the extermination of its unappreciated, but necessary, associate.

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Other components of natural forests also have been found to promote long-term productivity and stability. Loss or suppression of these components can disrupt necessary interactions and ecological processes. Bark beetles and pathogens interact with many of these components to enhance forest health, as in the examples below.

1.2.2.1 Non-commercial plants

Non-commercial trees and shrubs often have been regarded as "weeds," competing with crop trees for limiting resources. However, many of these tree and shrub species also contribute to soil fertility (often through association with nitrogen-fixing bacteria), soil retention on steep slopes, moisture retention through soil shading, and interruption of fire, insect and pathogen transmission (Binkley *et al.*, 1982; Perry, 1988; Borchers and Perry, 1990). For example, interspersed hardwoods or other non-hosts disrupt *Dendroctonus frontalis* infestations in southern pine forests (Schowalter and Turchin, 1993) and *Leptographium wageneri* infection in northwestern conifer forests (Hansen *et al.*, 1988; Chapter 11). Disruption of infestations by non-host vegetation may be due to the physical interruption of dispersal from host to host or to confusing of attractive host compounds by non-attractive or repellent non-host compounds in the forest aerosol (Visser, 1986; Hansen *et al.*, 1988). Although competition may slow growth of crop trees in the short term, these compensatory effects of plant associates may contribute to the survival and growth of crop trees over the longer period of forest development.

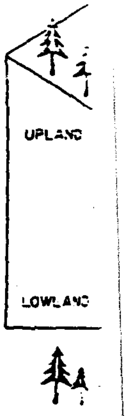
1.2.2.2 Dead trees and decomposing logs

Dead trees and decomposing logs have been viewed as wasted biomass, fire hazards, sources of destructive insects and pathogenic fungi, or impediments to reforestation efforts. Consequently, these structures have been zealously removed or destroyed. Recent research has demonstrated that dead trees and decomposing logs provide habitat for insectivorous birds and vectors of mycorrhizal fungi; stabilize soils, especially on steep slopes; contribute to soil development and fertility; and store water during dry periods (Harmon *et al.*, 1986; Carpenter *et al.*, 1988; Edmonds and Eglitis, 1989; Zhong and Schowalter, 1989; Schowalter *et al.*, 1992). Roots and mycorrhizae infuse logs and transport nutrients into growing tissues. Models indicate that forest health and productivity are enhanced by decomposing logs and may decline if these structures are removed (Harmon *et al.*, 1986). Healthy forests are more resistant to pest outbreaks than are forests stressed by resource limitation (Mattson and Haack, 1987; Chapters 4 and 5). Consequently, retention of woody residues has become a management priority in many North American forests. Bark beetles and wood-boring insects initiate and stimulate this process of nutrient turnover by channelizing wood and introducing nitrogen-fixing bacteria and saprophytic fungi necessary for nutrient turnover (Bridges, 1981; Edmonds and Eglitis, 1989; Schowalter *et al.*, 1992).

1.2.2.3 Fire

Fire historically has been suppressed at any cost, leading to changes in tree species composition or density, imbalances in nutrient availability for tree growth, and predisposition of stressed forests to insect and pathogen outbreaks. *Pinus* forests, in particular, depend on frequent fires to mineralize nutrients and remove competing fire-intolerant vegetation. Frequent fires maintain open, park-like forests that are resistant to crown fires and pest spread (Wright and Heinselman, 1973; Schowalter *et al.*, 1981a; Perry, 1988). Fire suppression can contribute to development of dense conifer forests stressed by competition for resources, susceptible to spread of bark beetles, root pathogens, and dwarf mistletoe and, inevitably, vulnerable to catastrophic crown fire (Fig.1.1). Fire suppression in the southern US contributes to eventual replacement of pines by shade-tolerant hardwoods, in large part through pine mortality to *D. frontalis* (Fig. 1.2). Fire suppression, together with selective harvest of *Pinus* and *Larix*, in western North America has favored forest succession to mixed *Pseudotsuga* and *Abies* forests

Fig. 1.1. Effects of wildfire in mixed-conifer forest in Yellowstone National Park, Wyoming. Note distribution and reduced density of surviving trees.



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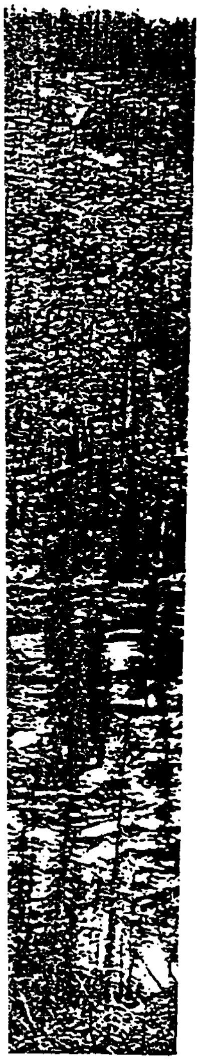

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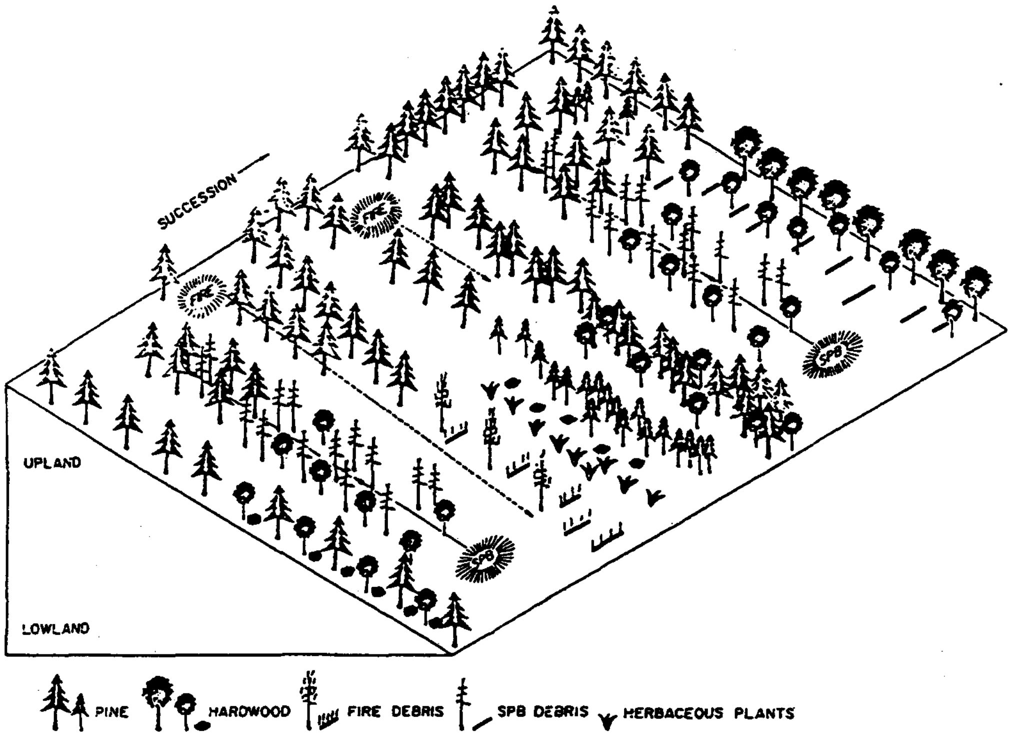

Fig. 1.2. Diagrammatic representation of the coniferous forest (upland and lowland) in the southeastern US, illustrating interaction between *Dendroctonus frontalis* (SPB) and fire. Successional transformations resulting from fire and *D. frontalis* extend from left to right; dotted arrows indicate direction of movement. Fire, a regular feature of the generally dry, well-drained uplands, invades generally moist, poorly drained lowlands where drought or *D. frontalis* create favorable conditions. *D. frontalis* depends upon fire for regeneration of pine stands. The hardwood climax forest (far right lowland) results from freedom from fire and can be reduced by fire (from Schowalter *et al.* (1981a), copyright Entomological Society of America).

now subject to widespread mortality to a variety of insects, including *Choristoneura occidentalis* and *Orgyia pseudotsugata*, and pathogens, including *Armillaria* (Hadfield, 1988). In the absence of fire or other disturbances that maintain particular tree species composition, insects and pathogens selectively remove fire-tolerant tree species stressed by increased competition and decreased nutrient turnover and often accelerate succession to a forest of shade-tolerant species (Geiszler *et al.*, 1980; Schowalter *et al.*, 1981a). Although politically controversial, periodic fire is necessary to preserve the health and composition of many natural forests. Fire now is used in many forested regions as a management tool to reduce fuel accumulation and enhance forest productivity, especially in the southern US, and to reduce susceptibility to insects and pathogens (Wade and Ward, 1976; Miller, 1979).

1.2.2.4 Insects and Pathogens

Insects and pathogens also are integral components of forest ecosystems. These organisms contribute to forest health and long-term productivity in several ways.

First, insects and fungi select particular host species on the basis of their biochemical suitability and attractiveness (Rosenthal and Janzen, 1979; Cates and Alexander, 1982;

Wood, 1982; Coley *et al.*, 1985). Insect and pathogen outbreaks are not random events, but reflect conditions that promote population growth and spread, e.g. conditions that increase abundance of hosts with limited defensive capabilities or that stress trees and weaken their chemical defenses (Rosenthal and Janzen, 1979; Cates and Alexander, 1982; Kareiva, 1983; Coley *et al.*, 1985; Waring and Schlesinger, 1985; Schowalter *et al.*, 1986; Mattson and Haack, 1987; Chapters 4 and 5). Such selection tailors tree density and species composition to site conditions. For example, *D. frontalis* selectively removes pines and favors hardwoods on wetter sites in the southern US (Fig. 1.2). Increased plant diversity resulting from mortality to abundant hosts increases the ability of the forest to maintain canopy conditions and forest functions under a wider range of environmental conditions and reduces the likelihood of future population outbreaks.

Second, nutrient turnover from foliage and wood increases nutrient availability for more efficient plants and plant tissues (Mattson and Addy, 1975). Schowalter *et al.* (1991) found that 20% defoliation in young *Pseudotsuga menziesii* doubled the amount of precipitation and litter reaching the forest floor and increased nitrogen, potassium, and calcium turnover 20–30%, compared to non-defoliated trees. These nutrients became available for new foliage production. Forest productivity can be enhanced for decades following defoliator outbreaks (Wickman, 1980; Alfaro and MacDonald, 1988), provided that defoliation does not trigger bark beetle or pathogen outbreaks (Berryman and Wright, 1978). Similarly, mining by bark beetles and wood-boring insects rapidly fragments the nutrient-rich phloem and provides entry and food resources for nitrogen-fixing bacteria and saprophytic microorganisms that mineralize and release bound nutrients for uptake by roots and mycorrhizae (Carpenter *et al.*, 1988; Edmonds and Eglitis, 1989; Zhong and Schowalter, 1989; Schowalter *et al.*, 1992).

Finally, tree deformation, mortality and canopy opening create habitat and food resources for other species with roles equally critical to forest productivity and stability (Franklin *et al.*, 1989). For example, *Tsuga* and other trees germinate best on the nutrient-rich substrates provided by decaying logs. Many cavity-nesting birds and other important predators of forest insects depend on habitats in snags and heart-rotted trees.

Recognition of the importance of species interactions to the productivity and stability of forest ecosystems has emerged only over the past two decades (cf. Mattson and Addy, 1975; Edmonds, 1982; Franklin *et al.*, 1989). Progress has been limited by the difficulties of organizing and supporting the multidisciplinary research necessary to evaluate the effects of interactions, and by scientific methodologies that focus on effects of single, or a few, factors rather than on interactions among many factors. Nevertheless, our appreciation for the complex effects of these organisms on forest productivity and stability is fundamental to our approach to managing forest insects and pathogens.

Although tree-injuring outbreaks may continue to be undesirable from a timber management perspective, their occurrence may provide clues to problems of forest health that require remedy. Suppression of pests without regard for the factors triggering outbreaks may be counterproductive.

1.3 ADVANCES IN FOREST PEST MANAGEMENT

1.3.1 The management context

Our approach to managing forest resources and pests is determined by our perception of forests as integrated ecosystems or loosely organized species assemblages. A traditional view of forests as collections of independent species justified removal of non-commercial

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species from the forest and led to a forestry in which crop species were managed as tree farms. Declining forest health and pest problems resulting from this approach, and the emergence of the ecosystem perspective, encourage a broader management approach that addresses critical ecological processes, including nutrient cycling and species interactions, and their consequences for forest health.

Management of forest resources presents a number of problems distinct from those of agricultural systems. First, forests are managed over long time periods (decades to centuries), allowing for cumulative effects of various factors affecting resource values. Second, management often must balance competing demands for forest resources, such as timber and fiber, watersheds, recreation, rangeland and fish and wildlife (Leuschner and Berck, 1985). This balance applies especially in the USA and other countries where multiple use of forest resources is mandated by federal legislation. Identification of the management goals for particular forest tracts is a prerequisite for effective management of multiple resources, hence for management of pests.

Management of North American forests has become controversial as vast areas of undisturbed forests have been replaced rapidly by cities, farms and younger, managed forests over the past century, with serious consequences for pest activity. At a time when little forested land in North America remains in its natural condition, subject to natural disturbances, accumulating evidence indicates that current management practices are promoting insect and pathogen outbreaks (Fig. 1.3; Franklin *et al.*, 1989; Chapter 11). Fire suppression results in dense, unhealthy stands of conifers with retarded nutrient cycling and

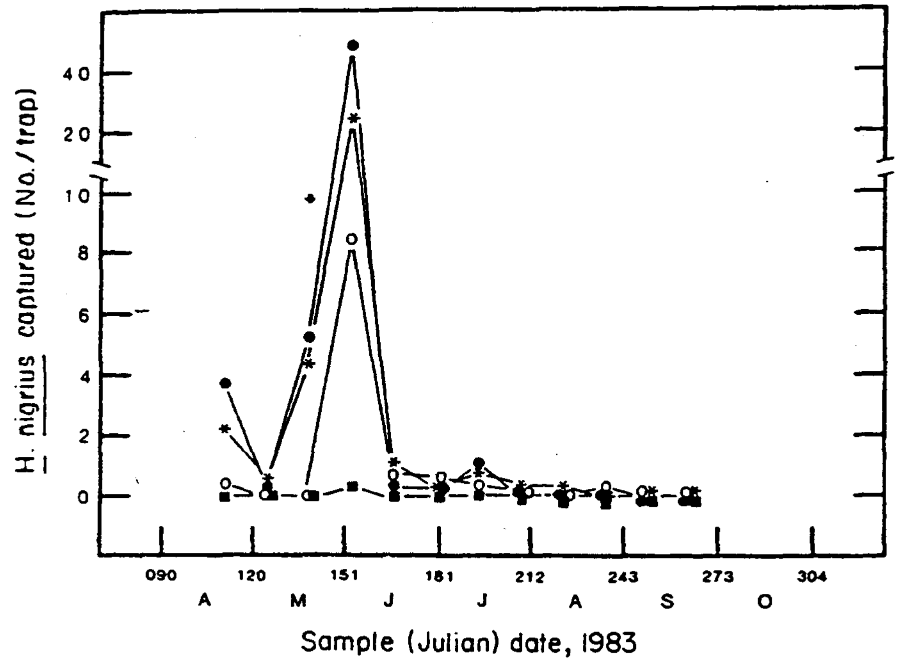

Fig. 1.3. Mean number of *Hylastes nigrinus* caught per trap on sticky traps during 1983 in precommercially thinned and unthinned 2-ha plots in two 12-year-old plantation of Douglas-fir (n = 8 plots per treatment). Stars designate plots thinned in September 1982; closed circles, plots thinned in January 1983; open circles, plots thinned in May 1983; closed squares, unthinned (control). The arrow indicates the time of thinning in May. Elevated populations of *H. nigrinus* increase the probability of introducing black-stain root disease fungus, *Leptographicus wageneri* (from Witcosky *et al.* 1986, copyright National Research Council of Canada).

little resistance to potential pests, especially where fire naturally occurred frequently. Young, rapidly growing monocultures favored by forest managers soon become vulnerable to pests because of selective breeding for rapid growth at the expense of resistance to pests, inadequate nutrient supply by impoverished soils, exposure to extreme environmental conditions prior to canopy development, and elimination of natural barriers (present in diverse stands and landscapes) to pest spread (Franklin et al., 1989). Air pollution and climate change exacerbate forest susceptibility to pests (Cobb *et al.*, 1968; Smith, 1981; Franklin *et al.*, 1992).

The responsiveness of forest insects and pathogens to changes in forest conditions is ominous in view of the regional scale of forest conversion to managed forests, increased atmospheric pollution, and potential global climate change (Graham *et al.*, 1990; Gear and Huntley, 1991). Forest researchers and managers must adopt a broader view of forest ecosystems and the importance of species interactions if our current activities are to provide the diversity and flexibility necessary for continued productivity in future forests.

1.3.2 Emerging views

Major advances have occurred over the past decade in our approach to managing forest pests (Waters and Stark, 1980; Coulson and Stark, 1982; Waters *et al.*, 1985). The traditional approach focused on suppression of individual pest species as plant injury was detected. Chemical pesticides were the favored control option because of their low cost and apparent effectiveness. Reliance on pesticides resulted in pesticide resistance (due to inherent ability of pests to detoxify plant defenses) and environmental degradation (due to disruption of community structure and function). During the 1970s two emerging views began to change the way in which forests and forest "pests" are managed.

1.3.2.1 Recognition of species interactions

Species interactions have a key role in promoting or mitigating destructive population trends. The ability of most healthy trees to resist colonization by insects and pathogens by means of physical barriers, chemical toxins and feeding deterrents has become a major focus of research (Rosenthal and Janzen, 1979; Cates and Alexander, 1982; Harborne, 1982; Coley *et al.*, 1985; Bazzaz *et al.*, 1987; Chapters 5 and 8). However, chemical defense is subject to resource availability and plant metabolic priorities (Tuomi *et al.*, 1984; Haukioja *et al.*, 1985; Lorio *et al.*, 1990; Chapter 5). Community diversity also dictates the ease by which herbivores can identify and reach acceptable hosts (Kareiva, 1983; Rausher, 1983; Hunter and Aarssen, 1988) and the combination of predators and parasites available to prevent herbivore population growth (Dahlsten, 1982).

Furthermore, tree injury or death no longer can be attributed simply to attack by the most conspicuous species. Rather, multiple-species pest complexes, interacting with soil and climatic factors that impair tree resistance, drive a process of gradual decline and replacement of susceptible trees and stands (Berryman and Wright, 1978; Goheen and Filip, 1980; Filip and Goheen, 1982; Whitney, 1982; Schowalter, 1985; Chapters 4 and 9). Populations of adapted insects and pathogens can grow on dense populations of relatively healthy plants. Such species and environmental factors that stress a tree predispose it to other species that depend on stressed hosts. For example, defoliators, especially when aided by moisture limitation, can predispose conifers to bark beetles (Berryman and Wright, 1978, Chapter 4). Associated species can have profound effects on the success of tree-killing species

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(Dahlsten, 1982; Chapter 7). For example, tarsonemid mites phoretic on *D. frontalis* are responsible for the transmission of pathogenic *Ophiostoma minus* into pines attacked by the bark beetle (Bridges and Moser, 1986; Chapter 7).

1.3.2.2 Integrated pest management

Emergence of the ecosystem and multiple-pest concepts resulted in integrated pest management (IPM), or integrated forest protection (IFP), methodology (e.g. Coulson and Stark, 1982; Stark and Walters, 1985). This methodology addresses the need to manage pest species within the framework of an integrated ecosystem. Assessment of various impacts of pests on other species and on key ecosystem processes is particularly important within the context of multiple-use forest management. IPM is based on four premises: (1) pest management must contribute to the resource management goals; (2) pest management must be consistent with ecological principles; (3) the target of pest management is maintenance of pest populations below economic thresholds; and (4) pest management is accomplished through a combination of treatment strategies. These premises are intended to maintain a resource focus, with pest management applied only as necessary to prevent unacceptable losses of resource values to the target pest(s), and to protect key ecological processes and species interactions that limit further damage by target or non-target pests.

Studies of interactions within integrated forest communities have increased our understanding of the contributions of these interactions to processes fundamental to long-term forest productivity and stability. At the same time, these studies provide the practical information necessary to improve our management of forest resources and forest pests. Multidisciplinary research on bark beetles and pathogens in conifer forests over the past 15 years has been both contributor to and beneficiary of concepts of forest ecosystems, multiple-species interactions, and IPM.

1.4 BARK BEETLES, PATHOGENS AND CONIFERS

1.4.1 Nature of interactions

Bark beetles and pathogenic fungi have been recognized as major interacting factors affecting the productivity and ecological succession of conifer forests. Traditionally, these organisms have been viewed as enemies by forest managers. The ability of bark beetles and fungal pathogens to kill or deform conifers over extensive areas is beyond dispute (Coulson and Stark, 1982; Filip and Goheen, 1982, 1984; Waters *et al.*, 1985; Hansen *et al.*, 1988; Chapter 9). Considerable effort and expense have been directed toward suppression, usually of individual species as tree injury or mortality became apparent.

With the emergence of new perspectives outlined above, these organisms have been recognized as integral components of forest ecosystems. Rather than threatening forests, these "pests" have contributed largely to the forest structure and productivity appreciated by early settlers and forest managers. Bark beetles and fungal pathogens, interacting with fire, have been instrumental in maintaining healthy conifer forests through natural thinning, nutrient cycling, and selection for site-adapted trees (Schowalter *et al.*, 1981a; Chapter 9).

Conifers display a variety of adaptations to prevent or tolerate injury by fire, pathogens or bark beetles under normal conditions. These adaptations include fire-resistant bark or meristems, and chemical defenses such as terpenes and phenols (Fig. 1.4). In fact, destructive wild-

Fig. 1.4. *Dendroctonus ponderosae* removing pitch from entrance bored into *Pinus contorta*. Oleoresin flow is a major physical and chemical barrier to bark beetle or pathogen invasion of conifers with a primary oleoresin system. Oleoresin flow depends on tree condition.

fires typically occur where fuels have accumulated as a result of extensive tree mortality in dense stands (Perry, 1988). Bark beetles and pathogenic fungi normally are restricted in occurrence to scattered weakened or dead trees which have impaired chemical and physical defenses. By removing these trees gradually, bark beetles and pathogens reduce tree crowding and prevent massive fuel accumulation. Populations of insects or pathogens remain inocuous as long as suitably injured or weakened trees are scattered across forest landscapes. Tree-killing epidemics occur when populations reach critical thresholds in stands that are composed predominantly of host trees (Kareiva, 1983; Rausher, 1983) and/or stressed by storm damage, drought, air pollution, overstocking, prior defoliation, mistletoe, fungal infection, etc. (Berryman and Wright, 1978; Mattson and Haack, 1987; Schowalter *et al.*, 1981b; Chapters 4, 5 and 11). Under such conditions, sheer numbers of beetles or fungal propagules assure that widely distributed resources are colonized and increase the likelihood that resistant hosts, as well as more susceptible hosts, will succumb to mass attacks (Schowalter, 1985).

Outbreaks of bark beetles and pathogens usually are associated because bark beetles transport fungal spores into attacked trees, and pathogens create newly stressed hosts attractive to bark beetles (Whitney, 1982; Chapters 6, 8 and 9). The association of bark beetles and fungal pathogens with dead and dying conifers has, over evolutionary time, led to interdependence, characterized by life history synchronization (Dowding, 1984), nutritional enhancement of wood by fungi and other microorganisms (Bridges, 1981; Whitney et al., 1987; Chapter 7), fungal adaptation for transport by beetles (Dowding, 1984; Beaver, 1988; Chapter 3), specialized structures (mycangia) for transporting fungal propagules (Whitney, 1982; Chapter 2), and beetle orientation to diseased trees (Cobb *et al.*, 1968, 1974; Witcosky *et al.*, 1987; Chapters 4 and 9). The interaction between bark beetles and pathogenic fungi,

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acting in concert to exploit suitable resources, requires that they be managed as a unit. Management of one without regard for the other will be ineffective in protecting forest resources.

Interactions among trees and their associated organisms create unlimited opportunities for collaboration among entomologists, pathologists, ecologists, tree physiologists, chemists and forest managers for the purpose of understanding and managing these interactions. Clearly, appreciation of the nature of interactions among the beetles, pathogens and conifer hosts will contribute to better management of conifer ecosystems. While these interactions are the focus of this book, interactions with other components of forest ecosystems, such as fire, mistletoes, defoliators, etc., also will be considered as these affect forest productivity and management goals.

1.4.2 Scope of this book

The interactions highlighted in this work involve bark beetles of the family Scolytidae (and some weevils, family Curculionidae), root pathogenic fungi belonging to several taxa, and their conifer hosts, primarily in the family Pinaceae. Conifer forests dominate large portions of North America, including the boreal region that spans the continent between 45° and 68° north latitude, the coastal plain forests from the mid-Atlantic states south and west across the Gulf of Mexico (Fig. 1.5), and the western montane forests (Fig. 1.6). These forests range in structure and complexity from young single-species plantations to the complex temperate rainforests of the Pacific Northwest, the most massive conifer forests in the world with tree diameters often exceeding 2 m and heights exceeding 70 m. Bark beetles and pathogenic fungi occur throughout these regions, accounting for extensive tree growth loss and mortality (Leuschner and Berck, 1985; Chapter 9). Global warming and drying are expected to increase the incidence and severity of tree mortality to these organisms (Franklin *et al.*, 1992; Chapter 4).

The considerable ecological and economic effects of these interacting organisms has warranted a concerted effort over the past 15 years to improve our understanding and management of these interactions. The resulting work is among the best examples of successful collaboration between scientists and managers on interactions among trees and associated organisms. This book represents a synthesis of information derived from this effort and is organized around four major problem areas fundamental to understanding and managing interactions among bark beetles, pathogenic fungi, and conifers.

1.4.2.1 Systematics

First, the systematics of the taxa involved must be understood. Pest species must be distinguishable from closely related non-pests. Such distinction is necessary for proper ascription of tree injury or death, and for assessment of future injury potential and feasibility of management options. New techniques for distinguishing species or biotypes are being evaluated. This topic is addressed in Chapters 2 and 3.

1.4.2.2 Factors influencing interactions

Second, while insects and pathogen propagules may land randomly on suitable and unsuitable plants, neither insects nor pathogens colonize trees at random. Rather, insects and pathogens most often colonize trees that are susceptible as a result of impaired defensive

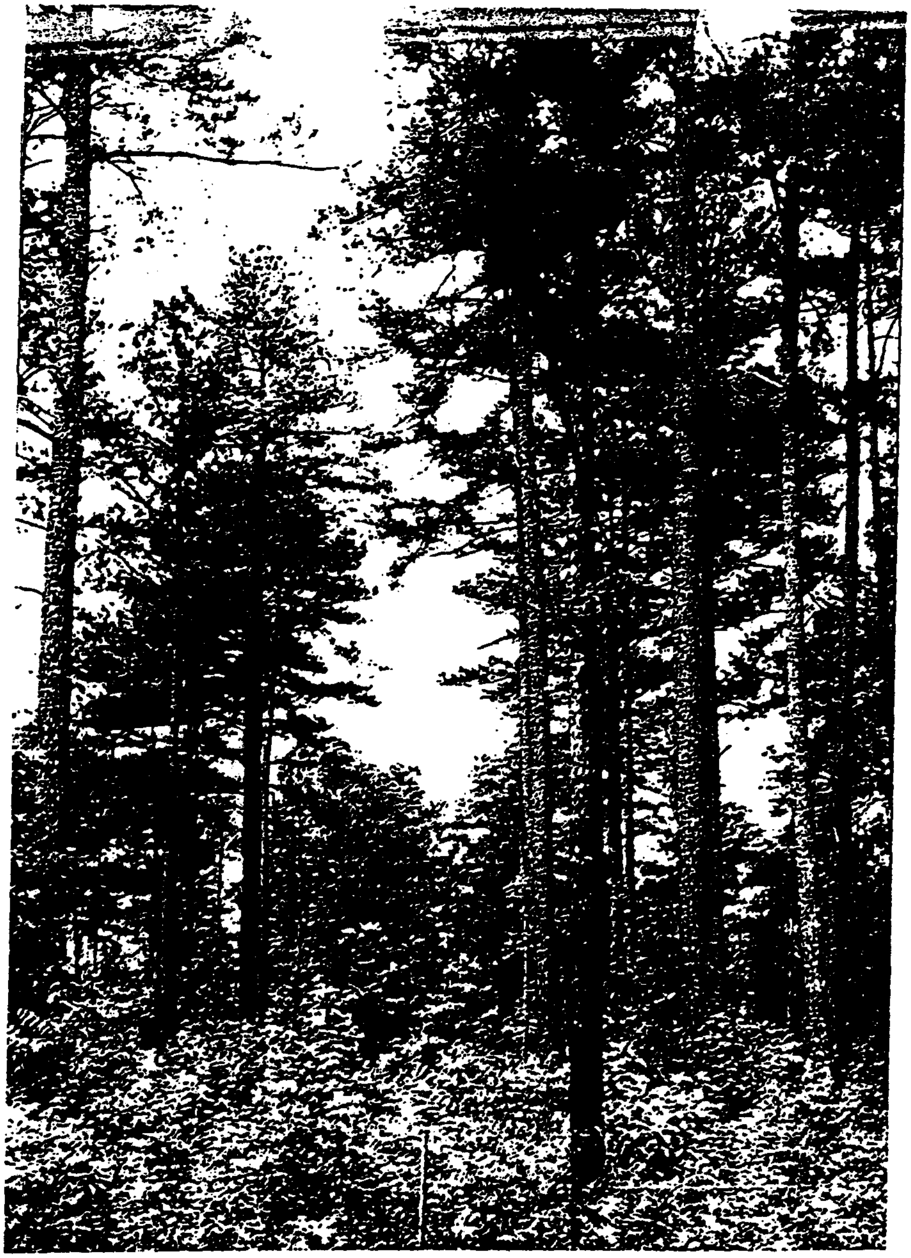

Fig. 1.5. Coastal plain *Pinus* forest in the southern US (Louisiana).

capabilities or of rapid growth at the expense of defenses (Coley *et al.*, 1985; Lorio *et al.*, 1990). However, in diverse forests, limited life span or dispersal capability often prevents discovery of suitable hosts (Kareiva, 1983; Rausher, 1983). Therefore, factors influencing host susceptibility, host distribution across forest landscapes, and host apparency (perception by dispersing beetles) largely determine bark beetle and pathogen epidemiologies. Furthermore, bark beetles and pathogens show complex interactions that often facilitate each other's population growth and spread, but which under some circumstances may be antagonistic. Associated species that may or may not achieve pest status also are involved in

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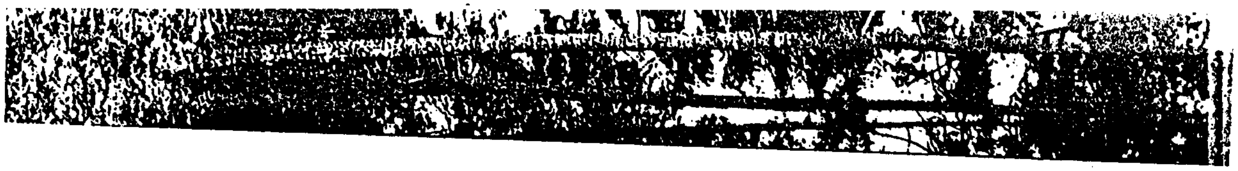

Fig. 1.6. Montane coniferous forest in the western US (Oregon).

the epidemiologies of the pests (Dahlsten, 1982). Various invertebrates compete with the bark beetles or feed on fungi. Microorganisms influence the nutritional quality of the wood resource for beetles and pathogens and/or compete with pathogenic fungi. These factors are discussed in Chapters 4–7.

1.4.2.3 Effects of interactions

Effects of bark beetle–pathogen interactions are the topics of Chapters 8 and 9. Effects on trees begin with cellular disruption and blockage of water transport by pathogens and proceed through tree death. Effects on stands are variable, depending on stand age and condition and the severity of tree suppression or mortality. Stands can be thinned, or subjected to waves of mortality that can require unscheduled salvage and replanting. Both stands and landscapes become more diverse, in terms of both species composition and age structure, thereby tending to provide natural barriers to continued pest activity.

1.4.2.4 Management of interactions

Finally, we must be concerned with managing forest resources effectively and efficiently. Models have become powerful tools for predicting future pest activity as well as assessing the need for and efficacy of suppression strategies. Models, however, represent state-of-the-art information availability and are necessarily based on assumptions with regard to parameters with insufficient data. Management strategies are available to manage pests pursuant to established resource management goals. However, given that current pest problems often reflect past management strategies, we must assess carefully the scientific basis for management decisions and anticipate responses of non-pests within the forest community. Models are the subject of Chapter 10; management options are addressed in Chapter 11.

Interactions among bark beetles, pathogens and conifers are sufficiently complex and well known to warrant their emphasis in this book. However, our approach to studying and managing these relationships is applicable to other interactions or ecosystem types. Therefore, our synthesis may serve as a model for understanding and managing other pest complexes.

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