Integrating the Ecological Roles of Phytophagous Insects, Plant Pathogens, and Mycorrhizae in Managed Forests

Timothy Schowalter, Everett Hansen, Randy Molina, and Yanli Zhang

Insects, fungi, other arthropods, and bacteria often are overlooked, both in catalogs of forest dwellers and in discussions of forest ecosystem function. Though small, these organisms are numerous and diverse. In most forests, they comprise the greatest portion of biological diversity and even a surprising portion of the biomass, especially belowground. They impact many ecosystem functions, sometimes controlling them, and their populations can fluctuate dramatically, responding quickly to changes in resource availability and environment. Some are considered pests when they interfere with management objectives, usually by killing or damaging valuable trees, and others are valued for their essential contribution to survival and growth of planted trees.

Much has been written about the economic losses caused by tree-killing insects and plant pathogenic fungi in forests. Similarly, the benefits of mycorrhizal fungi to tree growth are well documented. In this chapter, we aim to broaden the traditional view of forest pests and symbionts in order to consider them as part of functioning ecosystems, and thus to pro-

vide a better basis for predicting their responses to changes in forest management and other disturbances. To reach this goal, we provide a very brief review of insect and fungus biology as background to a discussion of the contributions of insects and fungi, especially herbivores, pathogens, and mycorrhizae, to ecosystem function. From this base, we discuss the responses of phytophagous insects, tree pathogens, and mycorrhizal fungi to changes in forest conditions as a basis for integrating these organisms into the "new" practices of ecosystem-based forest management. One of the keys to successful forestry is understanding and accepting the species and site specificity of the knowledge base. Our examples come largely from the forests of the western United States with which we are most familiar. Different organisms in different environments will respond differently, but we hope to establish underlying principles to allow predictions in new situations.

Insect and Fungus Biology

Fungi and insects are important in forest ecosystems in terms of numbers of species and ecological and economic impact. A given site will harbor thousands of species of insects and fungi, many undescribed, compared to a few dozen species of plants and vertebrates. Insects and fungi have diversified through evolution to fill a broad array of often very narrow niches in forest ecosystems.

The Fungi compose a separate kingdom of organisms, very different from plants, animals, and bacteria. The insects are the most numerous and diverse of the groups in the animal kingdom (Wilson 1992). Both groups are heterotrophic—that is, they gain their energy for growth and reproduction indirectly from carbohydrates manufactured first by plants through photosynthesis. Many species are detritivores or saprotrophs, feeding on dead organic matter. These are essential to ecosystem function for their roles in nutrient cycling. Another large group of species are predaceous or parasitic and represent important mechanisms for regulating prey or host populations. Our focus, however, is on a relatively small subset of species that have evolved nutritional strategies based on feeding on living plants, especially the

trees that dominate forests. These phytophagous insects and pathogenic fungi, together with the mutualistic mycorrhizal fungi, have evolved with the trees and other organisms of the forests and are normal components of all forests. The diversity of nutritional strategies among these species utilizing living trees for energy is great. Some canker fungi and bark beetles, for example, are only successful on weakened or dying trees or parts of trees and may spend much of their life on dead material, but other species, such as rust fungi and some aphids, prefer vigorously growing plants and die when their host plant dies. Many live on leaves and needles, but because trees have many leaves, their impact on whole tree growth is insignificant, except in years when populations are very large. Others kill trees, singly or in large groups, and can alter the structure and composition of the entire forest.

The reproductive potential of insects and fungi is immense. Some species produce hundreds or thousands, even millions, of offspring each generation, and generation times may be as short as two weeks. They often possess effective means of dispersal as well, carried through the air on their own wings or on air currents. New genotypes, produced through mutation or recombination, appear frequently and spread widely. Beneficial changes to the insect or fungus may be favored through natural selection. Asexual reproduction is found in both groups, and the fungi have haploid genomes. Both life cycle adaptations favor rapid selection and increase of favorable mutations, such as pathogenicity to new host genotypes. These reproductive advantages of the insects and fungi are countered in the ecosystem by the continuing evolution of host defenses and by limitations imposed by the environment.

The success of both insects and fungi is dependent on access to suitable hosts and a favorable environment. The interplay between tree resistance and environmental limitations serves to limit the frequency and extent of damage from insects and fungi. Trees have evolved a diverse array of mechanisms of defense against attack. Most tree species are resistant to attack by most insects and fungi. Susceptibility is the special case, and phytophagous insects and pathogenic fungi have evolved the necessary specialized behaviors and physiology to bypass host resistance.

Most, perhaps all, plant-feeding insect and fungus species show strong host preferences; many are host specific. Even a broad host-ranging species, such as the laminated root rot fungus found on most western conifers, spreads much more rapidly on Douglas-fir than on western hemlock and does not attack angiosperms at all (Thies 1984). The mountain pine beetle kills all western pines, but allozyme and morphometric analyses of beetles indicate that sympatric populations from lodgepole pine are distinct from populations from limber pines, with populations from ponderosa pine intermediate (Sturgeon and Mitton 1986).

Insects and fungi often are protected from adverse environments by their host trees, but during critical times of reproduction and dispersal they are exposed and vulnerable. Environmental and host conditions normally limit the opportunities for rapid population growth to particular microsites or especially favorable years.

Mycorrhiza translates literally as "fungus-root" and defines the common association of specialized soil fungi with the fine roots of nearly all forest plants. Mycorrhizal associations represent one of the more widespread forms of mutualistic symbioses in terrestrial ecosystems. Indeed, these plant–fungus associations have coevolved over the millennia such that each partner depends on the other for survival. The mycorrhizal fungus basically serves as an extension of the plant root system, exploring soil far beyond the roots' reach and transporting water and nutrients to the roots. The uptake of phosphorus and nitrogen is an especially critical function of mycorrhizal fungi, which can release bound forms of these nutrients otherwise unavailable to the roots. In return, the plant is the primary energy source for the fungus, providing simple sugars and vitamins produced through photosynthesis and transported to the roots and then the fungus.

Although mycorrhizal fungi compose a functional group, individual species differ strongly in their biology, ecology, and host range. Three primary classes of mycorrhizae occur in forest ecosystems: ectomycorrhizae, vesicular-arbuscular mycorrhizae, and ericoid mycorrhizae. Ectomycorrhiza is pervasive in temperate coniferous forests because tree species in the Pinaceae, Betulaceae, and Fagaceae families form this type. Fungi are primarily basidiomycetes and ascomycetes (mushroom, truffle, and cup fungi); many of the diverse mushroom species seen on the forest floor during autumn are the reproductive structures of ectomycorrhizal fungi. Some ectomycorrhizal fungi have broad host ranges, while others are restricted to certain tree genera (Molina et al. 1992). Vesicular-arbuscular mycorrhiza is the most common type worldwide. and many trees and understory plants form this type. Vesicular-arbuscular mycorrhizal fungi are zygomycetes and reproduce primarily as large soil-born spores. Ericoid mycorrhiza is restricted to the Ericales order and is widespread in forest ecosystems because many ericaceous species are dominant understory components. Ericoid mycorrhizal fungi are mostly ascomycetes that form small cuplike reproductive sporocarps. This diversity in fungal life histories and host associations among mycorrhizal fungi leads to a variety of functional interdependencies between forest plants and fungi in space and time (Harley and Smith 1983).

Functional Roles

Until relatively recently, forest insects and fungi, to the extent that they were noticed by forest managers and researchers at all, were regarded largely as pests, interfering with commodity production or experimental design. Beginning in the mid-1970s, this view began to change. A rapidly developing ecosystem concept of forests was fueled by multidisciplinary studies of functioning forest communities initiated by programs such as the International Biological Program (IBP). These programs raised awareness of the integration of biotic and abiotic ecosystem components and the coupled ecological processes underlying ecosystem stability and productivity (e.g., Bormann and Likens 1979, Edmonds 1982, Swank and Crossley 1987).

Mattson and Addy (1975) first challenged the narrow view of phytophagous insects and pathogens as pests by suggesting that these organisms could actually increase primary productivity through pruning, thinning, and stimulating nutrient cycling. Wickman (1980) and Alfaro and Shepard (1991) subsequently showed that trees often compensate over long time

periods for short-term growth losses during defolia-tor outbreaks. A number of authors have presented an integrated view of insects and pathogen roles within forest ecosystems (Castello et al. 1995; Hansen 1977; Schowalter 1985, 1994; Van der Kamp 1991).

Much has been written from an economic perspective on the losses caused by insects and pathogenic fungi in the forest and on the benefits of mycorrhizal fungi to tree seedling success (Castellano 1994, Castellano and Molina 1989), and these impacts will not be reviewed again here. The impacts of these organisms on ecosystem structure and function have received much less attention. They kill big trees and in the process change the character of the forest, and they kill small, young, and weak trees, maintaining the fitness of the ecosystem. They are important in nutrient capture and cycling, and many of the insects are pollinators. Species of both insects and fungi are predators and parasites on other insects, fungi, and small organisms, helping to regulate populations in the forest.

Determinants of Forest Structure, Composition, and Succession

Insects and pathogens affect forests most dramatically by killing trees. They are agents of disturbance with pattern and periodicity different from physical disturbances such as fire and wind. In some ecosystems, they are the most important disturbance agents, particularly in the long intervals between stand-replacing events such as fire or harvest, and they thus determine the character of the forest (Dickman and Cook 1989). The range of effects is illustrated with observations from the Douglas-fir forest ecosystem, where extensive tracts of wild forest are still available for observation.

The Douglas-fir forests of western North America are largely in the western hemlock zone of Franklin and Dyrness (1984). They are maintained in the seral stage by periodic stand-replacing wildfire or, in recent decades, by clearcut forest harvest. The late-successional western hemlock regenerates in the shade of the seral Douglas-fir, but extensive late-successional forests, with hemlock replacing itself in a dynamic equilibrium, are seldom encountered. Instead,

hemlock trees remain in the understory until mortality begins to create light gaps in the fir overstory. Pathogens, particularly root and stem decay fungi and the associated Douglas-fir beetle, are the principal gap formers in these forests and the agents that drive succession between wildfires.

The two decay fungi that cause brown cubical butt rot and red ring rot in tree boles are responsible for much of the single-tree mortality of Douglas-fir in old forests. Butt rotted trees typically snap near the base in wind storms and may destroy or damage adjacent trees as they fall. Butt rot–caused mortality is often ascribed to wind, but in most storms few sound trees are toppled. In one study, windthrow resulting from a winter storm on Mary's Peak in the Oregon Coast Range was almost exclusively related to root rot or to exposure along recent clearcut margins (Hansen unpublished data). Red ring rot kills trees as they stand or weakens them sufficiently to make them susceptible to attack by the Douglas-fir beetle. It is often difficult to assign cause of death to standing dead trees, since both decay indicators and signs of beetle attack may be far above ground. Death of single trees gradually reduces the dominant overstory, but canopy openings may fill with the expanding crowns of surrounding trees before understory trees can reach the upper levels.

Larger gaps in the Douglas-fir canopy are frequently caused by the laminated root rot fungus. This pathogen spreads slowly from tree to tree across root contacts. It takes decades to kill large trees, and they either fall from root decay or die standing, mortality often hastened by the Douglas-fir beetle. A large portion of the Douglas-fir beetle mortality in the Northwest is intimately associated with root rot (Goheen and Hansen 1993). The result is slowly expanding openings that develop through the life of the stand and may reach several acres in size (Figure 11.1). In the Douglas-fir forest, fir is most susceptible, hemlock is tolerant of infection, cedars are resistant, and hardwoods are immune. If hemlock or cedar seed sources are available in the adjacent stand, root rot openings fill with these species, and succession is advanced toward the late-successional condition. If seed sources are too distant, gaps fill with hardwood brush and trees and succession is reversed to earlier seral stages (Holah et al. 1993). Regional surveys suggest that
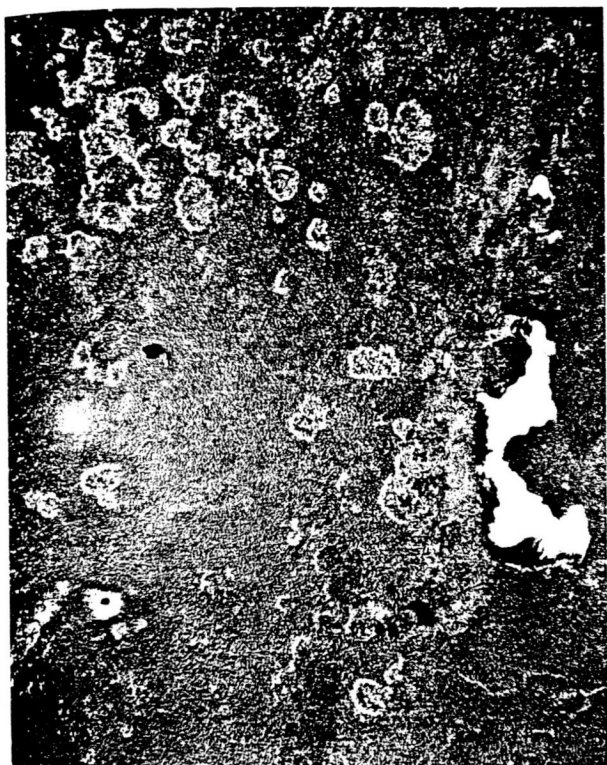
Figure 11.1 Patchiness in forest structure resulting from multi-tree gaps formed by Douglas-fir mortality because of laminated root rot near Waldo Lake, Oregon.

about 5 percent of the land area is affected by laminated root rot, with individual stands having 30 percent or more of their area affected (Figure 11.1).

Death of dominant trees from pathogens also affects forest structure and diversity. As dying trees are replaced with smaller individuals, two- and three-level canopies, characteristic of the old-growth forest condition, are created. Dead trees, as standing snags or as down logs, are ecosystems in themselves, providing food and shelter for a succession of microorganisms, insects and other arthropods, animals and plants (Harmon et al. 1986, Schowalter et al. 1992). Gaps created in the canopy allow light to reach the forest floor, creating growth opportunities for a different suite of herbaceous and shrubby plants and the animals that feed on them. If hemlock colonizes the gap, the long-term consequence may be a reduction in local diversity of herbaceous and shrub species beneath the dense shade of the developing hemlock canopy (Holah et al. 1993). Temperature and moisture relations are changed in the gaps, sometimes greatly increasing rates of nutrient release and cycling from killed trees and litter (Waring et al. 1987).

While pathogens and insects change the character of stands, they usually do so slowly, across the decades. Some bark beetles can change entire stands within a few years. The mountain pine beetle, western pine beetle, and southern pine beetle, for example, often act like a slow-moving fire through sufficiently dense pine stands, killing all host pines of particular size classes or physiological condition in a matter of months and either accelerating successional transition toward nonhost species or fueling stand-replacing fire that facilitates regeneration of pines (e.g., Amman et al. 1988, Schowalter and Turchin 1993, Schowalter et al. 1981a).

Mycorrhizae can be primary regulators in the successional interactions between plants and influence community development (Allen 1991). Successional outcomes, especially following disturbance, are often affected by the presence or abundance of mycorrhizal fungus propagules. For example, the lack of mycorrhizal fungus propagules was a primary cause of afforestation failures around the world, particularly in establishing pine plantations where pines had not occurred previously (Mikola 1973). Many exotic plantations were established successfully only after mycorrhizal fungi were purposely, or accidentally, introduced. Mine spoils and other reclamation sites often need inoculation with mycorrhizal fungi to reestablish plants because the sites are devoid of fungus propagules. Likewise, severely disturbed forest sites can experience low mycorrhizal inoculum potential that impedes forest recovery and development (Perry et al. 1987). Hence, it is essential that anthropogenic disturbances of forest ecosystems fall within the threshold tolerances of mycorrhizal fungi so that adequate viable inoculum remains on site.

Successional patterns will also be influenced by the degree of host dependence on mycorrhizal functions. Plants range from obligate, to facultative, to lacking dependence on mycorrhizal fungi for survival and growth. Janos (1980) and Allen and Allen (1990) present an interactive model of successional outcomes

as determined by relative plant dependence on mycorrhizae and environmental conditions. Plants less dependent on mycorrhizal fungi often invade disturbed habitats quickly, while obligately mycorrhizal plants invade more slowly, especially if fungal inoculum is low. Allen (1991) notes examples that fit this model in several ecosystems. The microhabitat scale of microbial interactions in soil, however, often hides the successional dynamics influenced by mycorrhizae, such that they are overlooked by plant ecologists. For example, ectomycorrhizae of forest trees are often abundant in buried wood (Harvey et al. 1991), and many ectomycorrhizal fungi specialize in this soil habitat. Because many plant species, such as western hemlock and several ericaceous plants, often use logs and coarse woody debris as primary colonization sites (i.e., nurse logs), the presence of active, ecologically adapted mycorrhizal fungi in those substrates directly affects plant survival and final community composition. Similarly, live legacies such as the scattered trees and shrubs that survive disturbance (or purposely retained living trees) maintain active mycorrhizal fungi on their roots, thereby directly benefiting the next generation of trees and other forest plants (Molina et al. 1992). Hence, fungus and plant community dynamics are intricately linked through mycorrhizal connections in space and time.

Maintaining Fitness and Productivity

The stem decay and laminated root rot fungi attack and parasitize trees with little regard for tree vigor. If anything, the larger, more rapidly growing trees are more likely to be infected. Opportunistic pathogens, including most canker fungi, some root-rotting organisms, and wound decay fungi, on the other hand, successfully attack only weakened or injured trees. They are usually found on understory, suppressed trees or trees wounded or weakened by some other agent such as lightning or severe drought. The bark beetles preferentially attack trees weakened by drought, competitive stresses, or pathogens. By removing weaker individuals from the stand, these organisms reduce competition for limiting resources and help maintain fitness of the entire population.

Canker fungi and opportunistic bark beetles are often particularly active at the edges of a tree

species's range. The mountains and valleys of southwest Oregon enjoy hot, dry summer conditions. Douglas-fir dominates the forest at mid and upper elevations, where winter rainfall is higher. The drier valleys are grassland-savanna, grading into ponderosa pine woodland. In many years, Douglas-fir can establish and grow at lower elevations, but in periodic drought cycles, the encroaching fir is killed by various canker fungi, Douglas-fir beetle, and flathead borers.

The absolute requirement for mycorrhizal functioning, especially at seedling establishment, characterizes the profound influence of mycorrhizae on plant fitness. Such is true not only for well-studied woody trees and shrubs, but for the smallest of forest plants. The notoriously tiny seeds of orchids, for example, require mycorrhizal colonization from the earliest stage of germination to begin their life cycle (Harley and Smith 1983). Chlorophyll-lacking plants in the Ericaceae family likewise depend completely on the mycorrhizal fungi that they share with neighboring overstory trees to obtain carbon (Furman and Trappe 1971); when the trees (the original sources of photosynthate) are removed, these achlorophyllous plants do not survive. After plant establishment, the many functional benefits of mycorrhizae continue to affect plant fitness directly and indirectly. Some mycorrhizal fungi produce antibiotics that protect fine roots from pathogens (Goldfarb et al. 1989, Marx 1973, Pfleger and Linderman 1994). The enhanced uptake of nutrients and water via mycorrhizae improves plant vigor and natural defenses against insects and pathogens.

The functional diversity of mycorrhizal fungi also contributes to plant fitness. Most plants form mycorrhizae simultaneously with several fungal species, and mycorrhizal fungi differ in their seasonal activity as well as in their dominance in different seres of community development (Deacon and Fleming 1992). Some mycorrhizal fungi are host-specific and provide unique benefits or exclusive access to a particular resource to their co-adapted host (Molina et al. 1992). Perry et al. (1989) found that competitive interactions between Douglas-fir and ponderosa pine seedlings were influenced by the presence of mycorrhizal fungi host-specific to either of the conifer hosts. Such diversity in mycorrhizal associa-

tions and function allows mycorrhizal fungi to partition use of the soil resource in space and time, thereby maximizing plant fitness over the life of the stand.

Phytophagous insects and plant pathogens also contribute to forest productivity over the long-term through defoliation and pruning. By killing foliage and twigs, they reduce plant competition for water and nutrients by reducing water use, increasing water penetration through the canopy, and stimulating nutrient turnover. Schowalter et al. (1991) reported that 20 percent defoliation of young Douglas-fir doubled the amount of precipitation and litter reaching the forest floor and increased nitrogen, potassium, and calcium input to the litter by 25 to 30 percent. Defoliator outbreaks associated with drought conditions (Mattson and Haack 1987) could improve forest conditions by reducing water use and increasing water supply to the forest floor. Parks (1993) found that defoliation of drought-stressed grand fir seedlings reduced susceptibility to Armillaria root rot by improving the internal moisture status of the seedlings. Trees often compensate for short-term growth losses during defoliation events by increasing productivity for decades following defoliator outbreaks (Alfaro and Shepard 1991, Trumble et al. 1993, Wickman 1980).

Mycorrhizal fungi make their contribution to productivity directly by enhancing nutrient and water uptake and plant fitness, as noted above. However, their effects on total ecosystem productivity go beyond enhancing accumulation of plant biomass. Mycorrhizae and mycorrhizal fungi also are major sinks for photosynthate in forest ecosystems. Fogel and Hunt (1983) estimated that fungi accounted for 28 percent of the total organic matter throughput in a Douglas-fir forest; Vogt et al. (1982) estimated that mycorrhizal fungi consume 15 percent of the net primary productivity in Pacific silver fir forests. These data indicate the range in carbon cost for reciprocal plant benefits in mycorrhizal mutualisms. Productivity cannot be measured simply as carbon allocation to various forest components. Use of carbon (energy to fuel organisms) must also be considered within the soil to understand the broad effects of fungi on forest productivity. Organic molecules from live and dead hyphae feed the microbial food web in forest

soils. Some are exuded from fungal hyphae and, together with fungal mycelium, bind soil particles, producing the microaggregates critical to soil porosity, hence to aeration and moisture retention (Amaranthus et al. 1989, Perry et al. 1987). Fungi also use their stored energy to develop reproductive structures such as mushrooms and truffles. Although the amount of carbon spent on reproductive structures is small compared to total net primary production, the sporocarps are essential to fungal life cycles and are significant dietary components for many animals. Finally, the recent large-scale commercial harvest of wild edible forest mushrooms in the Pacific Northwest (nearly 4 million pounds were collected in Oregon, Washington, and Idaho in 1992, contributing $41 million to the regional economy [Schlosser and Blatner 1995]) exemplifies the value of this fungal portion of forest productivity to the public.

Nutrient Capture and Recycling

Nutrient capture and recycling are essential to the long-term stability and health of ecosystems. When nutrient inputs no longer balance nutrient loss (such as following disturbance or climate change), nutrients become limiting and vegetation changes, initially as increased mortality of the most-sensitive species, followed by reduced stature of dominant vegetation.

Nitrogen is often limiting in forest ecosystems because of high demands for protein and nucleotide synthesis by living tissues coupled with losses from denitrification (under anaerobic conditions, such as from soil compaction and flooding) and volatilization during fires. The rate of nitrogen-fixation by some bacteria, blue-green algae, and lichens often is substantial, but depends on conditions. For example, free-living nitrogen-fixing bacteria require suitable habitats, such as decomposing logs (Schowalter et al. 1992, Silvester et al. 1982). Nitrogen fixation rates in more-decayed wood are substantially higher than rates in less-decayed wood or soil. Symbiotic nitrogen fixation depends on host plant productivity. In this case, nitrogen-fixing bacteria provide nitrogen to the host plant and receive photosynthates in return. Symbiotic hosts, such as alder and ceanothus, typically are fast-growing plants with the high resource

requirements that characterize earlier successional ecosystems and frequently are viewed as competitors with the more valuable tree species. Suppression of the symbiotic hosts through management or eventual overtopping by later successional trees reduces photosynthate allocation to root nodules and suppresses nitrogen fixation. Canopy lichens may fix substantial amounts of nitrogen, but are limited in occurrence to canopies of old-growth trees. Forest management practices have only begun to address the importance of nitrogen-fixing organisms to forest productivity and the sensitivity of these organisms to silvicultural manipulations.

Mycorrhizal fungi play a critical role in nutrient acquisition and plant nutrition. These symbiotic fungi acquire nutrients from decomposing litter and soil pools and exchange nutrients for photosynthates from their host plants, thereby facilitating nutrient and water uptake by their host plants and minimizing nutrient loss from the ecosystem. Carbon and nutrients also can be exchanged among plants via mycorrhizal connections. Such linkages influence interplant interactions and successional patterns in forest development (Molina et al. 1992, Amaranthus and Perry 1994).

The direct allocation of photosynthate from plant to mycorrhizal fungi sets mycorrhizal fungi apart in ecosystem function from soil saprobes that cycle carbon from organic matter. Host photosynthate not only fuels the physiological activity of the symbiotic fungi, but contributes directly to the soil processes and functions performed by mycorrhizal fungi. The large biomass of mycorrhizal fungi stores significant quantities of nutrients in the soil. Some ectomycorrhizal fungi form dense, perennial mats that occupy up to 28 percent of the forest floor (Cromack et al. 1979). Numbers of microbes and microarthropods are greater in these physiologically active fungal mats than in immediately surrounding soil (Cromack et al. 1988). The mycelium of mycorrhizal fungi also exudes organic molecules that not only support rhizosphere microbes, but also bind soil particles.

Mycorrhizal fungi also compose a key functional group in forest food webs. Approximately 80 percent of soil microarthropods are fungivores. Ectomycorrhizal fungal sporocarps (mushrooms and truffles) are major food sources for many forest animals, es-

pecially small mammals. Because small mammals are the primary prey for predators such as the endangered northern spotted owl, understanding these functions is vital to integrated conservation efforts.

Detritivores and saprophytes have a widely recognized role in nutrient cycling (Seastedt 1984). These organisms are instrumental in the decomposition and mineralization of organic matter. Larger invertebrates fragment ingested litter and infuse it with saprophytic fungi and bacteria, increasing decomposition rate. Wood-boring insects (including many bark beetles) penetrate bark and inoculate wood with symbiotic saprophytic fungi and bacteria that enhance nutritional quality of wood. Bark penetration also facilitates colonization by a diverse community of detritivores, saprophytic fungi, and bacteria, including nitrogen-fixing bacteria. The activities of these organisms increase wood porosity and water-holding capacity and nutrient availability, making logs "hot spots" of limited resources (Harmon et al. 1986, Schowalter et al. 1992).

Litter organic compounds are decomposed by action of extracellular enzymes secreted by saprophytic fungi and bacteria. The nutrients released become available for uptake by the saprophytes, but also by mycorrhizal fungi and tree roots infusing the litter.

Mycorrhizal fungi are typically viewed as being limited in saprophytic capabilities. Recent research, however, has shown that several species are able to decompose organic substrates, particular organic nitrogen (Read 1992). Mycorrhizal fungi of ericaceous plants, for example, produce proteases that allow them to mobilize protein-nitrogen. Because ericaceous plants such as salal, rhododendron, and huckleberry are widespread dominant understory forest plants and often colonize woody substrates, their mycorrhizal associates directly benefit not only their hosts, but contribute to nitrogen cycling in many forest ecosystems.

Pollination

Pollination is the transport of pollen to the ovary. For most trees, pollination is accomplished by air currents. However, some important forest components require insect pollinators, which transport pollen more efficiently than wind. Whereas wind transport

is largely random, many insects orient toward specific flowers and thereby target pollen to conspecific flowers where fertilization is more likely. Given insect capacity for long-distance flight, outcrossing is more efficient with insect pollinators. Trees such as maples and dogwoods, as well as many shrubs, including ceanothus and huckleberry, and understory herbs, including many rare or endangered forest floor plants, require insect pollinators for adequate seed development.

Pollinators represent a number of insect groups, including butterflies and moths; flies, bees, wasps, and ants; and beetles. Most of these insects pollinate only as adults, when they can fly. Immature stages may be defoliators (butterflies and moths), wood borers (some beetles), fungivores (many flies), or predators (beetles, wasps, and flies). Whereas pollination is recognized as a beneficial role, these other roles often seem to conflict with forest management objectives, requiring that we address tradeoffs between the roles represented by different life stages of the same organism.

Biological Control

Much of the diversity of invertebrates and microorganisms in forest ecosystems is represented by predators and parasites (Parsons et al. 1991, Schowalter 1995a), including predaceous insects; arachnids (spiders, mites, centipedes, etc.); nematodes; entomopathogenic, mycopathogenic, or endophytic fungi; bacteria; and viruses. While the importance of many predators and parasites has been recognized and their populations have been augmented for purposes of pest suppression, other groups remain relatively unknown. Examples include endophytic fungi, whose mutualistic association with host foliage and production of mycotoxins may limit feeding by herbivorous insects (Carroll 1988, McCutcheon and Carroll 1993). Mycorrhizal or other saprophagous fungi also may inhibit root infection by pathogenic fungi (Goldfarb et al. 1989, Marx 1973, Pfleger and Linderman 1994).

Biological control research has often focused on predator or parasite species that specifically target pest species, thereby maximizing suppression efficiency. However, specialist species must track their host population in time and space, limiting their ability to respond quickly to incipient pest outbreaks. Abundances of generalist predators and parasites, on the other hand, may be relatively more stable, making these species more responsive to increased prey populations. The diversity of predaceous and parasitic organisms is important in the regulation of prey populations because different species attack different life stages of their prey, thereby limiting prey escape in time or space.

Legacy of Past Practices

Forest management practices, even decisions to do nothing, affect the forest environment in many ways. The responses of various invertebrate and microbial species in the community can be quite different, depending on species tolerances or adaptations to particular conditions. Some species will be favored by a particular silvicultural practice and become "pests," whereas others may decline or disappear as conditions change, leaving healthier forests or eliminating important ecological functions, depending on the roles of the organisms involved.

Predicting the response of insects, fungi, and other microorganisms to changed forest practices is an uncertain art, but comparison with natural disturbance regimes and successional pathways in the environment in which the forest evolved may be useful. Contrasting the conditions in east-side and west-side forests in Oregon and Washington illustrates the point.

A forest health crisis has been declared in many forests of interior western North America as the combined effects of past management practices, bark beetles and defoliating insects, pathogens, drought, and catastrophic wildfire threaten to change the forests more rapidly and more completely than previously recorded. Managed coastal forests have also been changed dramatically in recent decades, but epidemics of insects and fungi are few, and any regional health crisis remains a future concern, not a present reality.

Typically, wild forests west of the Cascade Mountains are relatively even-aged and dominated by Douglas-fir. The intervals of stand-replacing wildfire

range from 100 to 300 or more years (Agee 1993). The light-demanding Douglas-fir is often the first tree species to colonize the fire-disturbed sites, and its rapid growth, large stature, and long life span allow it to maintain dominance for centuries. Clearcutting, often followed by slash burning, is the preferred harvest method in most west-side forests, and sites are planted with Douglas-fir. The disturbance pattern and successional trajectory roughly mimic the wild forest, but on an accelerated timeline. Insects and fungi of the Douglas-fir forest evolved in an environment of periodic catastrophic disturbance and Douglas-fir dominance, and they generally play the same roles in today's managed forests. There are exceptions, and they are instructive.

Several studies show that mycorrhizal fungi and the organisms important in nutrient cycling are more abundant and diverse in old forests than in recent clearcuts or young plantations (e.g., Amaranthus et al. 1994, Perry et al. 1987). This comparison of the ends of the successional spectrum is interesting, but these organisms are adapted to an environment that includes periodic stand-replacing wildfire. More relevant to possible changes in forest health would be a comparison of early successional microbial and insect populations following wildfire and following clearcutting. Removal during harvest of the large woody material (valuable logs), so important to mycorrhizal fungi and free-living nitrogen fixers alike, is cause for concern. Although effects of wood removal were mitigated somewhat by utilization practices through the 1950s that removed only the most perfect logs from the site, unmerchantable timber often was yarded or piled and burned, leaving many regenerated stands with insufficient woody residues. In recent years changes to the forest practices acts of the states have mandated leaving specified numbers of logs following harvest.

Reduction in the average age of managed west-side forests has led to decreases in populations of species that are more abundant in or even dependent on large trees or their residues or old-growth conditions and to increases in populations of organisms that thrive in or are dependent on young forests. Many decay fungi are much less common in young managed forests than in forests with bigger older trees. The fungus that causes red ring rot, for example, was often recorded in more than 50 percent of

the trees in early surveys of mature Douglas-fir stands (Boyce and Wagg 1953), but in stands less than 100 years old, incidence seldom exceeds 4 percent. Old western hemlock, the potential climax species in much of the west side, generally has much more decay than comparable Douglas-fir because it is thin-barked and more easily wounded by animals and falling trees and because the heartwood is much less resistant to decomposition than is Douglas-fir wood.

The fungus that causes black stain root disease is one of very few pathogenic fungi that have increased measurably in young managed west-side forests. This fungus moves from tree to tree by direct growth across adjacent root systems or is carried by root-feeding bark beetles. Young plantations, with regularly spaced susceptible trees, are ideal for spread of the pathogen, especially in stands where pre-commercial thinning has created stumps (breeding opportunities) for the insect vectors and removed non-host trees. The disease is most common on sites where the soil was compacted by tractors used to harvest the previous stand (Hansen et al. 1988).

Populations of some herbivorous insects are higher in young Douglas-fir plantations than in adjacent mature forests (Figure 11.2) (Schowalter 1995a). In west-side forests, however, this has not led to any increase in damaging outbreaks of defoliators. Several needle diseases have caused local epidemics in plantations, and they serve as warning of the importance of using appropriate tree species and genotypes in reforestation. Pine needle cast fungus damages east-side ponderosa pine seed sources planted west of the Cascades in several locales in the southern Oregon Cascades (Harvey 1976), and Swiss needle cast fungus damages off-site Douglas-fir planted on spruce and hemlock sites near Tillamook on the Oregon coast.

Forests east of the Cascade Mountains grow in generally much drier environments than on the west side and are more variable in tree composition, depending largely on local precipitation. On many sites on the drier end of the spectrum, ponderosa pine is seral and Douglas-fir and the true firs are typical of mid to late-successional forests. The historic fire pattern was typically frequent (10- to 20-year interval) with light underburns that often killed young trees, especially Douglas-fir and grand fir, and kept overall
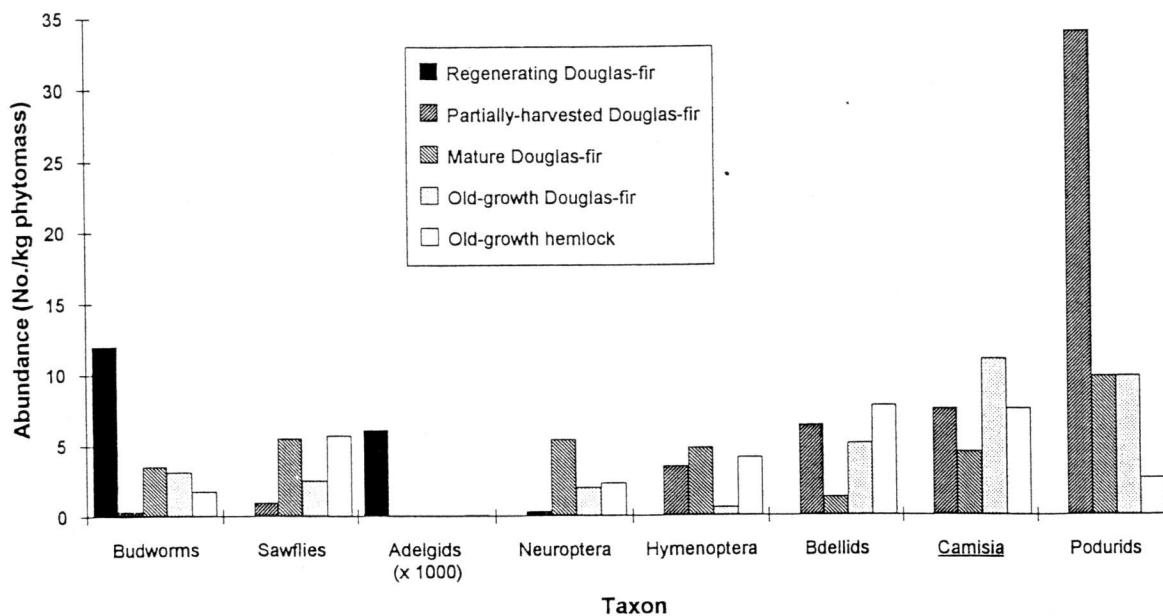
Figure 11.2 Eight canopy arthropod taxa showing significant differences in abundance in forests of contrasting age or harvest practices in western Oregon. Budworms and sawflies are defoliators; adelgids are sap-sucking herbivores; Neuroptera, Hymenoptera, and bdellids (mites) are predators, and *Camisia* (an oribatid mite) and podurids are detritivores. Data represent six replicates of each treatment intermixed in a 15,000-hectare area on and around the H. J. Andrews Experimental Forest (from Schowalter 1995a, and based on a figure from Schowalter 1995b).

stocking levels low. Forests were patchy, with mixed age classes, and often dominated by pine.

Forest management has brought dramatic changes to many sites. Harvest traditionally was by selective cutting, with the goal of maintaining an all-age forest, mimicking the natural fire disturbance regime. Economics and fire-control practices conspired against this outcome, however. Large ponderosa pine and other valuable species were selectively removed, shifting the species mix to the firs. Fire control accelerated this trend, and the result is thousands of acres of very densely stocked stands highly susceptible to insect and pathogen epidemics. Dead wood on the forest floor was consumed in the frequent ground fires of earlier times, but has now accumulated to dangerous levels. The next fire will be a stand-replacing event.

Some phytophagous insects and root pathogens have increased in response to these changes. The Douglas-fir tussock moth and spruce budworm prefer fir species for food, and the frequency and extent of epidemic outbreaks has increased, favored by prolonged drought. Drought conditions have been exacerbated by the overstocked stands, increasing competition for what water is available. The selective harvest created stumps, interspersed among the living trees, and Armillaria and annosus root rot fungi have taken advantage of the new food sources to increase their activity. Again, the firs are more susceptible than the pines. Several species of bark beetle have also responded with increased populations, resulting in increased mortality. Trees weakened by drought, competition, and root rot are especially vulnerable. The killed trees add to the fuel loads and the danger of catastrophic fire.

Conditions That Cause Problems

Changes in forest environments, composition, or structure, beyond the range of conditions that guided development of the ecosystem in question, may lead

to changes in populations of both beneficial and potentially damaging insects and fungi. Major changes induced by silviculture include altered species or genotypic composition, fire suppression and overstocking, creation or elimination of food sources, and forest fragmentation.

Introduced Organisms

Perhaps the greatest threat that insects or fungi pose to forests comes from introduced organisms. Native trees have evolved with native pathogens and insects and coexist with them under a broad range of conditions. They may have no resistance to introduced pests, however. Most accidental introductions undoubtedly fail, because no suitable host is available or because environmental conditions do not allow increase. A few, however, have succeeded and are among the most damaging and dangerous agents threatening our forests. In the West, familiar examples include the larch casebearer, Port Orford cedar root rot fungus, and white pine blister rust. There is no practical way to predict which foreign organisms will be damaging in a particular environment; most are unknown or innocuous in their native forests. Effective quarantines, with constant vigilance at ports of entry and in the forest, and determination to respond quickly to early reports of introductions are necessary.

Monocultures

The limited genetic diversity within monocultures of commercially valuable trees, especially when coupled with intensive breeding programs or genetic engineering to increase growth rates, provides a concentrated resource for adapted herbivores and pathogens (Kareiva 1983, Schowalter and Turchin 1993). This resource inevitably will become more vulnerable to herbivores and pathogens as populations grow through time, especially during adverse conditions that stress plants or limit defensive capability. Localized outbreaks occur where isolated stands become vulnerable. These scattered outbreaks can be restricted in a diverse landscape that provides barriers to herbivore population spread (Figure 11.3). Regionwide outbreaks may occur where a sufficient propor-
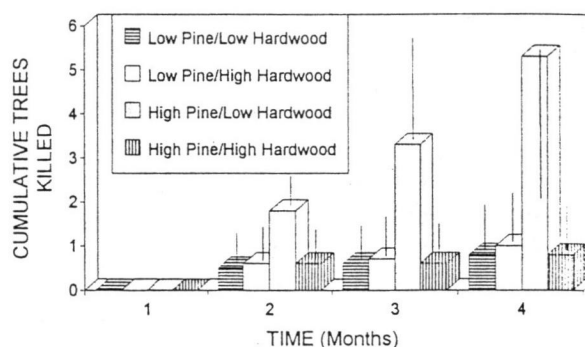

Figure 11.3 Southern pine beetle infestation development in southern pine stands with contrasting basal areas of pine hosts and hardwoods. Low pine = 11–14 m^2/ha basal area; high pine = 23–29 m^2/ha; low hardwood = 0–4 m^2/ha; high hardwood = 9–14 m^2/ha. All infestations were initialized with two infested trees introduced into otherwise uninfested stands. Infested material was placed around a central tree baited with attractant to ensure attack. Data combine four replicated treatment blocks each from the Homochitto National Forest in Mississippi in 1989 and the Kisatchie National Forest in Louisiana in 1990 (from Schowalter and Turchin 1993).

tion of the landscape is occupied by suitable hosts (Schowalter and Turchin 1993). Large populations can expand into otherwise resistant stands and affect resistance of sparsely distributed hosts.

In some ecosystems, seral conifers, such as Douglas-fir, lodgepole pine, ponderosa pine, and the southern pines, develop naturally as extensive single-species stands, especially following stand-replacing fire. It is important to note that these natural populations of a single species are genetically very diverse and adapted to local conditions, including insect and pathogen populations. In the absence of thinning (through disturbance or management), these trees become vulnerable to competitive stress and eventual insect and pathogen outbreaks that accelerate (1) the succession to late-successional species or (2) fuel accumulation and the return of fire (e.g., Hagle and Schmitz 1993).

Silvicultural practices that favor development of one vegetation type over another (e.g., planting monocultures of tree species and eliminating com-

peting vegetation) can also have consequences for the soil microbial community and for ecosystem resilience. After plant community disturbance, the succession of vegetation and soil microbes are interrelated. When natural successional processes are eliminated, the biotic and functional diversity of soil microbes may likewise be altered. For example, many species of hardwoods, such as madrone, manzanita, chinkapin, tan oak, and oaks, quickly reoccupy disturbed sites in forest ecosystems in southwestern Oregon. These pioneering hardwoods form mycorrhizae with many of the same fungal species as the climax conifer species (Molina and Trappe 1982, Molina et al. 1992). Suppression of these hardwoods to promote conifer regeneration thus eliminates a refuge for the diverse array of mycorrhizal fungi and rhizosphere microbes critical to conifer productivity. Recolonizaton must then come from dispersal, via airborne spores or animals, from adjacent stands.

Planting exotic tree species or nonadapted genotypes (off-site planting) or otherwise altering the natural species composition can lead to increased losses. For example, foliage diseases seldom create serious problems in the forest, except where trees are planted off-site in environments that favor fungus infection—for example, pine needle cast suppression of east-side ponderosa pine planted on the west side of the Cascades (Harvey 1976).

Fire Control, Overcrowding, and Thinning

Most forests of the West suffer from too many trees. Fire suppression has had dramatic effects on forest conditions, especially in ecosystems adapted to frequent burning. Fire is a primary mechanism for thinning and reducing competition and also for mineralizing accumulated litter and preventing bottlenecks in nutrient supply. Canopy closure and altered tree species composition as a result of fire suppression have led to serious declines in forest health and consequent insect and pathogen epidemics in forests of the interior West and elsewhere (e.g., Hagle and Schmitz 1993). In stands where fire suppression has lead to an increase in Douglas-fir and true firs in the understory of pine stands, both pines and firs are at increased risk to insects and pathogens. The firs are more susceptible to several root rots and defoliating

insects than are the pines, and the increased competition for moisture with the firs places the large overstory pines at greater risk from bark beetles due to moisture stress. Similarly, the replacement over large portions of the southern United States of fire-tolerant longleaf pine savannas with dense commercial plantations of less tolerant loblolly pine, a species more susceptible to the southern pine beetle and fusiform rust, has contributed to recent widespread outbreaks of these organisms (Schowalter and Turchin 1993, Schowalter et al. 1981a).

Crowding leads to intense competition for limited light, water, and nutrients and to pest outbreaks. Thinning is the usual means of preventing overcrowding. Thinning is an effective way to manage some insects and pathogens sensitive to tree spacing or tree competitive stress. The southern pine beetle and the mountain pine beetle can be controlled by spacing trees at least 6 m (20 ft.) apart, the effective limit to pheromone communication (Larsson et al. 1983, Lorio 1980, Mitchell et al. 1983, Sartwell and Stevens 1975, Schowalter and Turchin 1993, Schowalter et al. 1981b). Some defoliators also are sensitive to tree spacing. Host-switching by gypsy moth larvae can be reduced by increased spacing between hosts (Lance 1983).

However, thinning or partial harvest systems that leave stumps or slash among crop trees may promote insects and pathogens that colonize stumps or woody debris and allow them to spread to surrounding trees. Stumps, created by cutting down a living tree, have no close counterpart in the natural forest. They represent a new infection pathway and a large and suddenly available food source for some insects and pathogens. Black stain root disease is vectored from tree to tree by several bark beetles and weevils that are attracted to and breed in fresh stump roots. These beetles introduce the fungus into healthy roots during feeding prior to breeding in fresh stump roots or the roots of diseased trees. Witcosky et al. (1986) reported that thinning at any time increased colonization of Douglas-fir stumps and crop trees by three species of root-colonizing beetles in western Oregon, but that beetle populations increased most in stands thinned during fall and winter. The stumps remained suitable at the time of beetle dispersal in spring, whereas stands thinned during spring and

summer were less attractive due to drying of stumps and loss of volatiles by the time of the next insect dispersal.

Armillaria root rot fungus attacks and kills several species of conifers, especially when they are growing adjacent to previously infected stumps. If the fungus is present, it quickly colonizes the stump and root system, and with the extra energy it derives from decomposition, hyphal rhizomorphs are able to spread to, colonize, and kill surrounding trees. Annosus root rot fungus relies primarily on spore spread instead of vegetative growth to colonize new trees. Fresh stumps represent a new infection opportunity for the fungus. Spores germinate free from competition from saprophytic decay fungi, grow down through the stump and roots, and pass into the roots of surrounding trees. Tree mortality from each of these root diseases increases in thinned or partially harvested stands as compared to unharvested or clearcut situations (Goheen and Hansen 1994, Hagle and Schmitz 1993 and references therein).

Fertilization

Fertilization is practiced to increase growth and to replace nutrient capital removed from the forest as a result of harvest, fire, or soil disturbance. However, while fertilization may be necessary in some cases, the form and balance of nutrients most appropriate to accomplish silvicultural goals remain poorly understood. The form of subsidized nutrients can have significant effects on plant growth and insect-microbial-plant interactions. Addition of selected nutrients can create relative shortages of other nutrients, limiting realized tree growth.

Fertilization can profoundly affect soil microbial populations. Nitrogen fertilization, for example, typically reduces ectomycorrhizal development and sporocarp formation, and also alters the composition of fungal species (Menge and Grand 1977, 1978). For these reasons, high nitrogen input from pollution is considered partly responsible for ectomycorrhizal fungus decline in European forests (Arnolds 1991, Schafer and Schoeneberger 1994). Fertilization effects may be short-lived, but nonetheless should be considered within the overall objectives of forest management.

Effects of forest fertilization on herbivory are poorly understood and apparently contradictory, perhaps because few studies have included examination of plant allocation of subsidized nutrients (see references in Schowalter et al. 1986). Tuomi et al. (1984) suggested that plants reallocate carbon and nutrients in response to nutrient limitations. If nutrients such as nitrogen are limiting, carbon cannot be used for growth and may be diverted to the production of plant defenses (Haukioja et al. 1985). If other nutrients necessary for plant growth are limiting, nitrogen cannot be used for growth and may increase the nutritional suitability of the plant for herbivores or be used with excess carbon in production of additional defenses (Mattson 1980, Waring 1987).

Examples of changed insect and pathogen behavior in fertilized stands include increased losses to pitch canker in southern pines (Dwinell et al. 1985), increased incidence of fusiform rust in fertilized southern pine stands (Powers et al. 1993), and increases in spruce budworm populations and defoliation (but also net increases in tree growth) (Mason et al. 1992, Wickman et al. 1992). In commercial coastal Douglas-fir forests, operational fertilization has not led to any alarming changes in insect or fungus activity. High levels of nitrogen fertilizer were applied experimentally to a Douglas-fir plantation to test the hypothesis that increased nitrogen availability would lead to increased populations of soil microorganisms antagonistic to laminated root rot fungus (Nelson 1989). There was no effect on the root rot, but black bears showed a strong preference for the fertilized trees, resulting in a dramatic increase in wounding and tree mortality.

Fragmentation

Forest fragmentation can have serious consequences for many species. Fragmentation increases the proportion of stands subject to edge effects such as wind, drying, and temperature extremes. These conditions are unsuitable for organisms that require the moderate temperatures and humidities provided by extensive, intact forests. Soil and litter organisms and canopy lichens are especially vulnerable to warming and drying (Amaranthus and Perry 1994, Perry et al. 1987, Seastedt 1984, Schowalter and Sabin 1991).

Schowalter (1995a) found that arboreal predators and detritivores also are sensitive to canopy opening and virtually disappear from exposed sites (Figure 11.2). Sunscald and wind breakage damage trees directly and also create infection courts for wound decay fungi.

What Changes Are Necessary?

Fungi and insects are integral parts of forest ecosystems. By acquiring and releasing nutrients, promoting growth, and killing trees, they help to shape the forest. Humans are also part of forest ecosystems and have altered forest structure and controlled fire as means for maximizing production of certain forest commodities. However, some anthropogenic changes have induced undesirable changes in species associated with forest ecosystems, causing destructive outbreaks of some and reduced populations and impaired ecosystem functions for others. Successful ecosystem management will recognize and manage the needs and effects of all forest components—insect, fungus, and human—to assure sustainable productivity of the whole ecosystem.

Populations of phytophagous insects, fungal pathogens, and humans can increase to levels that threaten ecosystem processes and values. A forest without insects and fungi probably couldn't exist and would certainly look and function very differently from its wild counterpart. These organisms must be maintained and managed with as much attention as any other forest component. The key is to prevent problems, because available direct remedies for crisis situations are usually at least as disruptive to the ecosystem as, for example, an insect outbreak or a temporary loss of mycorrhizal inoculum.

A real need is to recognize thresholds. Populations of insects and fungi are sensitive to normal variation in the local environment, and they change through the course of stand development. We need to differentiate the normal fluctuations from trends that are leading toward damaging outbreaks or disappearances. Dangerous population levels, high or low, must be defined according to the specific management objectives for particular stands.

A better understanding of insect, pathogen, and mycorrhizal population responses to environmental changes is needed. We know that some populations track some environmental conditions closely, quickly, and dramatically, making these organisms potentially useful indicators of subtle changes in environmental factors. However, we do not yet know if observed high populations of defoliating insects in young plantations or decreased numbers and changed species of decomposing fungi in recent clearcuts are well within the range of normal successional changes or indicate long-term changes in resource availability or microclimate. The challenge, then, is to understand relationships between natural ecosystem processes and populations of insects and microorganisms in order to evaluate the use of these organisms as bioindicators or to anticipate future undesirable trends in populations.

We will never have complete understanding in a timely way, so certain conservative principles of management are needed. We do not know all the functional roles of the various species nor how future environmental changes will affect their populations and ability to continue critical ecosystem functions. Actions that mimic natural disturbances and successional changes are less likely to have unforeseen consequences, but the rate of disturbance and forest fragmentation may exceed the ability of some populations to adjust or to detect and colonize suitable habitats. New silvicultural approaches should be tried on a small scale and in diverse environments. Ecosystem management must be adapted locally to site-specific conditions. Regular monitoring of populations and ecological conditions is important.

Changing forest management practices to meet objectives of sustainable resource production requires an integrated ecosystem framework for managing forests that incorporates the various roles of insects, pathogens, mycorrhizae, and other species, especially the functional importance of interactions among various species. We will need to accept trade-offs among species with differing responses to changes in forest conditions. For example, partial harvests will reduce stand susceptibility to most bark beetles and provide refuges for many species, including mycorrhizal fungi, but will likely increase the incidence of stump-colonizing beetles that vector black stain root disease. However, we can maximize pro-

tection of biodiversity and ecosystem function while at the same time minimizing risk of pest epidemics by maintaining a greater variety of options (e.g., diversity of forest types and ages, clearcuts, partial cuts, etc.) across landscapes, rather than applying a fa-

vored silvicultural system uniformly. This will ensure availability of refuges and stable populations for most species and limit the ability of potential pests to spread unimpeded across the landscape.

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Edited by Kathryn A. Kohm and Jerry F. Franklin

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