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Historical and Current Roles of Insects and Pathogens in Eastern Oregon and Washington Forested Landscapes

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ABSTRACT

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This paper examines by climax conifer series, historical and current roles of many important pathogens and insects of interior Northwest coniferous forests, and their unique responses to changing successional conditions resulting from management.

Insects and pathogens of the subalpine fir and mountain hemlock series historically reduced inter-tree competition for site resources, and generated most of the coarse woody debris between fires. Severity of growth and mortality effects was proportional to the abundance of susceptible seral species such as Douglas-fir, grand fir, and lodgepole pine within and adjacent to subalpine fir and mountain hemlock forests. Laminated root rot, a mortality factor, influenced successional status, fire intensity, and fire behavior. Insect and disease disturbances in present day western hemlock and western redcedar climax forests are much the same as those occurring historically, but increased scale of fire disturbance resulting from fire exclusion, has increased the scale of insect and pathogen disturbances associated with changing successional conditions.

Spectacular differences are apparent when comparing historical and current roles of pathogens and insects of the Douglas-fir and grand fir series. Before the advent of fire control on public lands, late successional and climax forest stands were relatively scarce in comparison with current distribution. A century of fire protection has produced a steady shift away from parklike ponderosa pine and western larch forests toward denser late-successional fir forests. Harvesting of high-value seral overstories accelerated conversion to insect- and pathogen-susceptible late-successional forests. Douglas-fir and grand (white) fir are highly susceptible to root pathogens, bark beetles, defoliators, and dwarf mistletoe. Excluding fire from grand fir and Douglas-fir forests has perhaps been the single greatest detriment to diversity of eastside forests, and a primary factor in current susceptibility to major pathogens and insects.

Low intensity fires, once common to historical ponderosa pine climax forests, maintained low fuel loads, minimized fuel ladders, and spaced trees struggling to survive under severe moisture-limited growing conditions. The western pine beetle and mountain beetle thinned densely stocked areas missed by fire, and killed trees injured by wind and weather, or weakened by root disease, dwarf mistletoe, Pandora moth, or advanced age. With fire control, overstocked conditions became widespread and bark beetles assumed the role of underburning to the elimination of trees in excess of site potential. Regeneration of historical lodgepole pine forests was predicated on mountain pine beetle outbreaks and subsequent stand replacing fire events. Today, with fire control, mountain pine beetle outbreaks affect larger areas, for longer periods, often with greater intensity than historical outbreaks.

Specific solution to elevated insect and disease disturbance in current forests is complicated by great variety in environmental and vegetal conditions where rehabilitation might be needed, and change in biological and physical potentials as a direct result of management. Still, much can be done. Stocking can be reduced where long-term carrying capacity is exceeded. The shift toward late-successional, fire intolerant, pathogen- and insect-susceptible forests can be reversed by developing a seral-dominated forest matrix. Management activities can promote landscape structure, composition, and pattern, consistent with historical disturbance regimes and land potentials.

Future research on forest pathogens and insects should address three primary subject areas: insect and pathogen population dynamics in managed and unmanaged forests; ecological roles and effects of native and introduced pathogens and insects; and, effects of natural disturbances and management practices on native insects, pathogens, and their natural enemies.

Keywords: Forest succession, forest health, insects and diseases, pathogens, landscape patterns, disturbance processes, ecosystem processes, fire regimes.

Contents

INTRODUCTION

Every forest ecosystem has its own unique association of native insects and pathogens. When ecosystem a’butes, such as plant species composition, tree density, canopy structure, and patchwork pattern ttri change, so do insect and disease complexes. Each landscape pattern development pathway yields a unique insect and pathogen population response. One trajectory may mean prosperity for one suite of insects and relative obscurity for others. Varying only species composition or density or canopy structure has profound effects on pathogen and insect population responses and associated ecosystem effects.

Eastside Oregon and Washington landscapes have been dramatically altered by forest management activities of this century. The goal of this paper is to contrast historical and current roles and scales of insect and pathogen disturbances. Highlighted will be the relation of insect and pathogen disturbances to site quality, potential vegetation, and fire regimes. Discussion will also focus on interactions among forest insects and pathogens resulting from changes in scale and intensity of their disturbances, and current size and configuration of their habitats.

Bergoffen (1976) has hypothesized that changes in the eastside forest ecosystems stem largely from two historical management activities—effective fire exclusion, beginning with the creation of the Forest Reserves in 1905, and selective timber harvesting that started with the first European settlers, but was greatly accelerated after World War II (Bolsinger and Berger 1975). Grazing, roading, defoliator suppression, mining, and custodial land management also had significant effects (see papers by Agee, Irwin and others, McIntosh and others, Oliver and others, Wissmar and others 1993). Historically, fire was the most influential disturbance to eastside forest landscapes (see Robbins and Wolf 1993, for an excellent historical review of the settlement of the Intermontane Northwest). Before European settlement, many forests of the interior West were visited by frequent, low-intensity fires that resulted in landscapes tolerant of pathogens, insects, and fires. This fire regime was particularly true for low and middle elevation landscapes dominated by ponderosa pine[1] (fig. 1). Wickman (1992) revives accounts of early pioneers traveling the Oregon Trail in the Blue Mountains; they described forests of ponderosa pine, with little brush, abundant grasses and herbs, an open parklike appearance, and the look of forests that frequently underburned. Early foresters were also impressed by the parklike stands, dominated as they were by magnificent, old ponderosa pines and maintained by fire (Langille and others 1903, Lieberg 1899, Munger 1917).

Figure 1. Parklike ponderosa pine stand. Note the elevated crown bases and open growing conditionsboth effects of frequent underburning. [Photo courtesy of Pat Cochran].

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[1] Scientific names for all taxa mentioned are given in appendix A.

Insects and diseases were part of these simplified forests, but as Wickman (1992) pointed out, the extent of their influence was typically smaller, disturbance events of shorter duration, and the severity of effects less than we observe today. In fact, because of their contribution to animal and plant habitat development, biomass and nutrient recycling, and patch and landscape diversity, historical effects of insects and pathogens were mostly beneficial and integral to fire-adapted ecosystems.

Upper elevation forests of the premanagement-era burned less often and more intensely. Patches regenerated by fires covered large areas. Often, entire landscapes were regenerated by the largest fires. Seral species initially invaded burned landscapes, followed by more shade-tolerant species with increasing passage of time (fig. 2). Landscapes that burned every 100 years or more were comprised of a patchwork of stands with mature and overmature seral overstories of western larch, Douglas-fir, lodgepole pine, and occasionally ponderosa pine, with understories of shade-tolerant species of various sizes and ages, depending on more recent fire history. Most of the insect and disease activity we observe today occurred historically within these high-elevation areas. The effect of fire exclusion on the health of high-elevation ecosystems is relatively minor compared with effects on low- and mid-elevation ecosystems; however, high-elevation ecosystems are now highly interconnected with mid-elevation ecosystems that have been substantially modified by fire exclusion and selective harvesting. Insect and pathogen disturbances, once limited by vegetation conditions dictated by fire frequency and intensity, now freely extend to larger areas.

Figure 2. Multi-layered mixed conifer stands are now prevalent where multi-cohort, parklike ponderosa pine stands once dominated. With the exclusion of fire, Douglas-fir and grand (white) fir understories have developed.

Many current eastside landscapes, with fire return intervals now prescribed by management rather than by fuels and environment, are dominated by shade-tolerant tree species, with little of the patchiness and clumpiness that characterized historical landscapes (Lehmkuhl and others 1993). In addition, tree and shrub densities are substantially increased. Trees, shrubs, grasses, and herbs compete for often severely limited water, sunlight, and nutrients. Increased competition for limited site resources, coupled with dramatically increased abundance of shade-tolerant species, has invited large increases in pathogen and insect populations. The recent 7-year drought has accentuated these escalating effects and drawn attention to declining forest health.

With the exception of a few insects and pathogens introduced to this continent in the last centurynotably the larch casebearer (Tunnock and Ryan 1985), the balsam woolly adelgid (Mitchell 1966), and white pine blister rust (Hagle and McDonald 1989), forests east of the Cascades have the same insect and disease associates now that they had 100 years ago. The difference between then and now is the scale of interaction between insects, pathogens, and their hosts, in both space and time (fig. 3). Although large insect outbreaks clearly occurred before the European settlement of the West (Lieberg 1899, Swetnam and Lynch 1989, Wickman and others 1993), the landscape patterns of vegetation ensured that most disturbances were brief and spatially confined. Some insects now appear to operate nearly continuously over entire landscapes.

Figure 3. Outbreak of western spruce budworm (*Choristoneura occidentalis*) in the Blue Mountains of northeastern Oregon. By the time this particular outbreak had subsided, over ten million acres were defoliated. [Photo courtesy of Craig Schmitt].

A staggering array of insects and fungi is found in interior forests of Oregon and Washington. Some species have evolved relations of mutual benefit to themselves and their hosts. Others are opportunistic on injured or stressed trees, shrubs, or herbs. Most act in beneficial processes such as pollination, or water and mineral nutrient imbibition by plants, nutrient cycling, soil development and moisture retention, reduction of large plant residues and detritus, or biological control of other organisms. All species play a role in ecosystem processes; a relatively few species capitalize on changes in vegetation conditions over large areas and provide significant disturbance to landscapes. These latter few are the focus of this paper:

- Western spruce budworm
- Douglas-fir tussock moth
- Douglas-fir beetle
- Pine bark beetle—the western pine beetle, the mountain pine beetle, and the pine engraver
- Fir engraver
- Spruce beetle
- Laminated root rot

- Armillaria root disease
- P- and S-group annosum root diseases
- Dwarf mistletoes of true firs, Douglas-fir, western larch, ponderosa pine, and lodgepole pine
- Indian paint fungus
- White pine blister rust, Comandra rust, and stalactiform rust
- Brown cubical butt rot

Mountainous regions of eastern Oregon and Washington are dominated by coniferous forest cover. Forested provinces of the east side have been classified according to climatic (and occasionally edaphic) climax plant associations (Daubenmire and Daubenmire 1968, Johnson and Clausnitzer 1992, Johnson and Simon 1987, Volland 1985, Williams and Lillybridge 1983, Williams and Smith 1991, Williams and others 1990). Taxonomically related plant associations are aggregated into series named after the dominant climax conifer. In this paper, we have arranged our discussion of changing roles of insects and pathogens from historical to current conditions by forested climax series. We begin with high-elevation series and finish with low-elevation series and a discussion of the unique pathology and entomology of the lodgepole pine series of the pumice plateau of central Oregon.

All forests have been altered to some degree by the last century of resource management and fire protection, but the greatest changes in vegetation, and insect and pathogen response, have occurred in low- and middle-elevation grand fir, Douglas-fir, lodgepole pine, and ponderosa pine climax forests. Because these forests have been influenced most by fire protection and selective timber harvesting, they receive emphasis in our paper.

SUBALPINE FIR AND MOUNTAIN HEMLOCK SERIES

Climax subalpine fir forests are found at the higher elevations in all major ecoregions of eastern Oregon and Washington (Franklin and Dyrness 1973, Omernik and Gallant 1986). They are the primary subalpine forests of the eastern Cascade Range. Most stands are above 4800 feet, but subalpine fir can easily extend farther downslope to 3000 feet in cool valleys, and along avalanche tracks (Franklin and Mitchell 1967). Fires are infrequent in these cool, moist environments. Before the era of fire protection, fire return intervals for subalpine fir in the Washington Cascade Range were typically more than 100 years, often more than 200 years. Drier subalpine forests to the east had somewhat shorter fire intervals, but usually longer than 150 years. Fires in this series, though infrequent, were intense usually resulting in complete stand replacement on 70 to 100 percent of the affected area (Agee 1990).

The mountain hemlock series is a minor subalpine series only occurring in scattered locations near the Cascade Crest, and in two populations in the Eagle Cap Wilderness of the Blue Mountains of northeast Oregon (Agee 1993). Little is known of the fire ecology of mountain hemlock forests. What is known suggests that fire intensities and return intervals are similar to those of other subalpine fir forests.

Historical Forests

Western spruce budworm—The western spruce budworm infrequently visited subalpine fir forests, and probably was not a major factor in mountain hemlock forests. Unless otherwise indicated, most discussion here will center on subalpine fir forests. Defoliation, when it occurred, was rarely damaging. Of the subalpine fir climax sites exposed to budworm defoliation, those occurring at the lowest elevations were most frequently and severely defoliated. In these locations, subalpine fir stands were often adjacent to grand fir, Douglas-fir, and white fir climax sites; some that were regularly underburned and dominated by seral species; others burned less often, creating an uneven patchwork of early-, mid-, and late-successional stands. Fingers of subalpine fir extended into this patchwork, and mixed coniferous stands with grand fir, white fir, or Douglas-fir overstory and understory components adjoined subalpine fir stands.

Continuity of budworm-susceptible stands was greater in this mid-elevation region where fire regimes were historically of moderate rather than high severity. Budworm outbreaks in the lower extremities of the subalpine fir series were probably of short duration and small in extent relative to current-day outbreaks, minimizing defoliation damage to subalpine fir. Today, areas most susceptible to budworm defoliation are the driest sites of the Douglas-fir, grand fir, and white fir series. Historically, many of these sites were frequently underburned at low intensity, maintaining predominantly seral vegetation. Better sites of these series were less susceptible and less frequently defoliated. Perhaps extended droughts predisposed these more mesic and drier sites to defoliation. We surmise that the extent, duration, and severity of defoliation in subalpine fir varied with the amount of defoliation of Douglas-fir, grand fir, and white fir in adjacent stands. Initiation of outbreaks in subalpine fir was unlikely. Outbreaks more likely developed in adjacent Douglas-fir, grand fir, or white fir stands during droughty periods and extended into subalpine fir where environmental conditions for budworm were typically suboptimal, and budworm populations declined.

The western spruce budworm also fed on associated Engelmann spruce. Defoliation of spruce was rarely significant, but subalpine fir, which is quite susceptible and sensitive to budworm feeding particularly in the Cascades of northern Washington (personal observations, R. Mitchell), suffered some growth loss and top-killing, and occasionally tree mortality. As a result, budworm defoliation might have killed single subalpine fir trees or trees in groups, but it is unlikely that mortality was widespread. The effect of localized group killing would have created patches of snags that could be used by birds and carpenter ants, agents whose predation tends to keep budworm populations low under natural fire disturbance regimes (Campbell and others 1983). Defoliation also enhanced mineral cycling from caterpillar frass (larval excrement) (Crossley 1970, 1977; Klock and Wickman 1978) and added diversity to otherwise eventextured landscapes.

Douglas-fir tussock moth-In eastern Oregon and Washington, Douglas-fir tussock moth populations feed readily on subalpine fir (fig. 4) and damage is occasionally significant in modern times, but defoliation seldom results in long-term growth or mortality effects. Whether tussock moth was a significant problem in presettlement times is somewhat problematical because host stands before fire control were not so extensive as now. Although the tussock moth can be destructive, it prefers warm, dry sites of the Douglas-fir, grand fir, and white fir series (Stoszek and Mika 1978, Wellner 1978, Wickman and others 1973).

Figure 4. Outbreak of the Douglas-fir tussock moth (*Orgyia pseudotsugata*) in a high elevation subalpine fir forest. [Photo courtesy of Jed Dewey].

Mountain pine beetle—Lodgepole pine, an important seral species in both subalpine fir and mountain hemlock series, often regenerated in nearly pure stands after stand-replacement fires, if it was present in the former stand. Stand-replacement fires at intervals less than 200 years favored development of lodgepole pine. In subalpine fir forests, fire severity was sometimes great enough to completely eliminate any residue of subalpine fir because entire trees were consumed (Clinton Williams, personal communication). Fire-regenerated lodgepole pine stands were usually overstocked and stressed by excessive intertree competition from an early age. Suppression mortality and snow-breakage rarely reduced stocking sufficiently to relieve stress. After six or seven decades, some stems in these stands would reach a sufficient diameter to support a mountain pine beetle brood. Mountain pine beetle mortality would continue for decades, eliminating the largest stems and trees in small groups by successful mass attack.

Large, synchronous outbreaks seldom developed at the higher elevations typical for these series, presumably because of shorter growing seasons, and poor larval and young adult overwintering. After longer intervals without fire (> 200 years), these stands would eventually break up and be dominated by subalpine fir and other associated shade-tolerant species. Outbreaks have been recorded in high-elevation stands that included whitebark pine (Burke 1990).

Spruce beetle, fir engraver, western balsam bark beetle—The spruce beetle was likely a regular but minor tree killer of Engelmann spruce in the subalpme fir series, and judging from its current pattern (Scott 1991), usually attacked overmature, windthrown trees. Butt rot associated with S-group annosum root disease and tomentosus root disease is extensive in maturing spruce stands. Overmature spruce trees with butt rot collapse under high winds (fig. 5). Spruce beetle populations were presumably maintained in windthrow

Figure 5. Windhrown Engelmann spruce with tomentosus root disease (*Inonotus tomentosus*). Such trees are often colonized by the spruce beetle (*Dendroctonus rufipennis*).

of mature and overmature spruce, and in fire-killed spruce. Other bark beetles providing background mortality in conifer associates of Engelmann spruce were the silver fir beetle, and the fir root beetle. Both are associated with windthrown and diseased Pacific silver fir (Thomas and Wright 1961). In the same stands, the fir engraver and western balsam bark beetle would have also been minor tree killers of subalpine fir, and grand or white fir, although (as now) drought periods would have made mortality more visible.

Annosum root disease—Annosum root disease (S-group) was prevalent in a wide variety of plant communities of the subalpine fir and mountain hemlock series, infecting subalpine fir, grand and white fir, Engelmann spruce, Pacific silver fir, western hemlock, and mountain hemlock. Annosum root disease attacked trees of all ages, causing root and butt rot at maturity and occasionally killing low-vigor trees in overstocked stands. Grand fir and white fir were often killed by this root disease.

Brown cubical butt rot—Another root and butt disease common to the subalpine fir series was brown cubical butt rot; western larch, lodgepole pine, and Douglas-fir were the primary hosts. Intertree transmission of this root disease in infection centers was root to root by growth of infective mycelia through litter. New infection centers were initiated when spores of the pathogen infected recent fire scars of mature Douglas-fir and western larch. Butt defect associated with this disease was responsible for the collapse of many of the oldest (200 years and older) seral overstory trees.

Tomentosus root disease, Indian paint fungus—Tomentosus root disease was common in maturing lodgepole pine stands, especially in the northern Rocky Mountain ecoregion, where it caused tree collapse and windthrow. The Indian paint fungus was also prevalent in both the subalpine fir and mountain hemlock series causing heart rot of true firs, western hemlock, and mountain hemlock (fig 6.). Hosts were infected as suppressed saplings and small poles. Infected understory trees were released with the break-up of the seral overstory. Infections were activated when trees were wounded near the original point of infection. Activated infections in true firs and hemlocks resulted in substantial heartwood defect, an important habitat for cavity-excavating bird species and secondary cavity users.

Figure 6. Mountain hemlock heartwood decayed by the Indian paint fungus (*Echinodontium tinctorium*). Note the rusty-red stringy advanced decay.

Laminated root rot—Laminated root rot was found in all coniferous species of both the mountain hemlock and the subalpine fir series, but was especially prevalent and visible where Douglas-fir, grand (white) fir, or mountain hemlock (highly susceptible hosts) were present in abundance. Douglas-fir was a common seral species in the subalpine fir series, regenerating with western larch, lodgepole pine, and western white pine after stand replacement fires or other major disturbances. Environments favorable to spread of this root disease were those dominated by susceptible hosts; western larch, western white pine, and lodgepole pine discouraged spread of this disease.

Armillaria root disease—Armillaria root disease infected and killed Douglas-fir, which was seral in both series. Because the fungus that causes Armillaria root disease is both an aggressive pathogen and an opportunist, vigorous as well as injured trees, and those stressed by other insects or diseases, overstocking, or drought also succumbed to this root disease (fig. 7). Stressed or injured trees of coniferous species ordinarily tolerant or resistant to infection were often killed by this fungus. In late-successional plant communities of the subalpine fir series, laminated root rot apparently decreased, although only visibility expressed as mortality changed with the declining dominance of Douglas-fir. Laminated root rot continued to spread to other, less-susceptible hosts, causing butt defect. S-group annosum root disease and tomentosus root disease expressed as butt defect increased with increasing abundance of late-successional species.

None of the native insects or diseases were individually significant mortality factors in the historical subalpine fir series. Collectively, they responded to developing instabilities within ecosystems, reduced competition for limited site resources, and between fires, generated most of the woody debris important to subalpine fir ecosystems. That woody debris was doubtless important to a succession of fragmenters and decomposers, and it was essential to the infrequent fires that regenerated these forests. Within the mountain hemlock series, laminated root rot was a significant mortality factor influencing successional status, fire intensity, and fire behavior.

Figure 7. Mortality of subalpine fir caused by Armillaria root disease (*Armillaria ostoyae*) in northeastern Oregon.

Current Forests

The principal effect of fire suppression in subalpine forests is the marked reduction in the number and size of stand-replacement fires. Conflagrations in any one area were infrequent in historical times, but when they did occur, they were large-scale landscape events. Burned areas naturally regenerated over decades, creating large, unfragmented patches with the qualities of deep interior forest. The most common disturbances today are small harvest units that reproduce none of the characteristics of large-scale disturbances. Fires still commonly occur but they are easily suppressed. Accordingly, early- and mid-seral landscapes have been gradually lost (see Lehmkuhl and others 1993).

Western spruce budworm—Defoliators like the western spruce budworm that prefer feeding on Douglas-fir and true fir needles have not dramatically expanded their influence in the subalpine fir series in this century. That may be changing, though. Current outbreaks of the budworm in the Cascades of central Oregon and the Blue Mountains of northeast Oregon suggest that severe outbreaks of long duration can occur in these forests. This pattern is difficult to explain, but it could stem from a gradually expanding food base. Because subalpine fir and balsam fir are genetically similar, experiences in eastern Canada could offer an explanation. Holling (1986) reported that birds kept budworm populations in check in balsam fir in Canada when stands were young. As the balsam fir forests matured, the supply of new needles gradually expanded and so did budworm populations. Outbreaks developed when the number of budworms became so large that the existing bird populations could not keep pace with budworm population growth. A relation such as this, exacerbated. by the current persistent drought, could contribute to the severe outbreaks in central and northeastern Oregon.

Current subalpine forests are more successionally advanced and contain many more true fir stems than did historical forests. As in historical forests, the extent, duration, and severity of defoliation in modern-day subalpine fir forests correspond with defoliation of adjoining Douglas-fir and grand (white) fir forests. If patches of Douglas-fir and grand fir forest are scattered and embedded in a seral-dominated forest matrix, budworm episodes will be short and mostly undamaging. If these areas are large and contiguous, budworm outbreaks can be long and damaging, with increasing tree mortality and topkilling. Adjacent subalpine fir stands will be affected accordingly.

Mountain pine beetle, western balsam bark beetle, spruce beetle, fir engraver—Large-scale mountain pine beetle infestations in lodgepole pine will be more infrequent with continued fire control. Lacking stand-replacement fires to regenerate new stands, lodgepole pine abundance in mixed stands is decreasing throughout the east side. Continued thinning from above by the mountain pine beetle, coupled with the establishment of shade-tolerant understories (fig. 8), is gradually reducing the abundance of lodgepole stands in the high elevations. Mountain pine beetle attacks on western white pine have increased dramatically with the introduction, early in this century, of white pine blister rust. White pine trees, and tree tops declining from stem-girdling infections of the rust, are destroyed by the mountain pine beetle. Western balsam bark beetle and spruce beetle associated with old, diseased subalpine fir and spruce will likely increase because both old trees and disease incidence are increasing. Fir engraver mortality and topkilling will increase because host type has increased, and because heavy stocking reduces tree vigor and capacity to resist attacks. Drought will accentuate fir engraver affects.

Figure 8. Grand fir beneath an overstory of lodgepole pine. [Photo courtesy of Jim Hadfieid].

Larch casebearer, balsam woolly adelgid—The larch casebearer and the balsam woolly adelgid are two destructive insects introduced into the region in the last decade (Denton 1979, Mitchell 1966). Initial parasite introductions apparently subdued casebearer populations (Ryan 1990), but casebearer damage is again visible in many areas of the central Oregon Cascades and in northeastern Washington in the last three years (Hessburg and Flanagan 1992a, 1992b). The balsam woolly adelgid can be severely damaging to true firs in western Oregon and Washington despite the introduction of natural enemies (Mitchell and Wright 1967). Subalpine fir is especially sensitive to attack and is often killed where the host is invading meadows and lava beds (Franklin and Mitchell 1967, Mitchell 1966). East of the Cascades, the woolly adelgid has been found in only a few environments where subalpine fir has crept downslope into what would normally be considered grand fir climax sites (personal observations, R. Mitchell). Unless distribution and damage change unpredictably, the woolly adelgid cannot be considered a serious threat to eastside subalpine fir forests. The few trees that are killed in high-elevation stands function as upright snags for a long time (personal observations, R. Mitchell) and are probably beneficial to wildlife.

Laminated root rot, Armillaria root disease, annosum root disease—The increasing period between fires as a result of fire exclusion, and the gradual decline in the abundance of Douglas-fir have produced an apparent decrease in laminated root rot expressed as mortality. A lack of fire has reduced the visible manifestation of this disease but it has not eliminated the fungus. The disease continues to spread in less-susceptible hosts, causing a butt defect of maturing trees. Armillaria root disease and S-group annosum root disease are increasing in subalpine fir and other true firs because firs are older and more abundant (Filip, in press; Lehmkuhl and others 1993). More root disease also means more bark beetle mortality from the western balsam bark beetle and the fir engraver.

Laminated root rot centers in mountain hemlock may affect the initiation and spread of fire by killing large numbers of trees of various sizes (Dickman and Cook 1989). Dead trees, both standing and down, in turn increase the frequency of wildfires. Increased frequency of crown fires decreases the incidence of visible laminated root rot by converting the forest from hemlock to root disease-resistant lodgepole pine. In these areas, fire has reduced the visible infestation but has not eliminated the fungus. The disease continues to spread in less susceptible hosts, acting as a butt defect of some mature trees.

WESTERN HEMLOCK AND WESTERN REDCEDAR SERIES

The western hemlock and western redcedar series are found east of the Cascade crest in Washington and to a limited extent in northern Oregon (Franklin and Dyrness 1973). Both are well represented in northeastern Washington in the Pend Oreille River basin and elsewhere in the northern Rocky Mountain ecoregion, which has a maritime climate influence. Coniferous tree species found within these series are those common to the grand fir and subalpine fir series, and the mountain hemlock series. Douglas-fir, grand fir, western larch, western white pine, and lodgepole pine are the most abundant seral species.

For eastside conditions, these forests receive relatively high rainfall, and fire return intervals are often more than 100 years (fig. 9). When fires occurred, they were variable in intensity, resulting in either complete stand replacement, a partially killed overstory, or underburning with little overstory mortality (Williams and Smith 1991, Williams and others 1990). For the western hemlock series, severe fires at intervals less than 200 years tended to favor lodgepole pine regeneration when lodgepole pine was in the original stand. Stand-replacing fires at intervals longer than 200 years tended to favor western larch and western white pine. Fires of moderate intensity favored Douglas-fir, larch, and white pine (Williams and Smith 1991). Before the turn of the century, western white pine was abundant in the western hemlock and western redcedar zones, especially in northeastern Washington, a significant contrast with the rest of eastern Oregon and Washington, where presence of western white pine is incidental.

Figure 9. A late-successional western hemlock-western redcedar forest.

Historical Forests

Mountain pine beetle, western spruce budworm, Douglas-fir beetle, fir engraver—Few insect outbreaks have been recorded in either series. Tree killing by the mountain pine beetle was common in mature, overstocked lodgepole pine, especially in trees with diameters large enough to support broods. Large outbreaks that destroyed entire stands were unlikely. Ordinarily, small groups of overstory trees were mass-attacked and killed. The result was a gradual thinning from above and a steady accumulation of snags and flammable fuels. Western spruce budworm populations likely fluctuated in number and size, but serious defoliation in either forest type is doubtful. Analysis of climatic patterns by Kemp and others (1985) indicated that hemlock and redcedar climax forests resided in low and moderate outbreak-frequency areas. The Douglas-fir beetle and fir engraver responded to root-disease-weakened Douglas-fir and true firs, contributing to their demise. Outbreaks of either beetle must have been exceptional and were associated with large-scale fires or windthrow. On balance, we can deduce that insect disturbances were mostly beneficial, providing habitat, variety, and stability to ecosystems under historical fire disturbance regimes.

Laminated root rot—Diseases probably played a greater role in succession and fire history than did insects, though their effects are somewhat inseparable. The root disease ecology of western hemlock and western redcedar climax forests on the eastern slope of the Cascades was very similar to that in western hemlock climax forests of the western slope of the Cascades today. Four root diseases were a primary influence in these forests: laminated root rot, Armillaria root disease, S-group annosum root disease, and brown cubical butt rot. Laminated root rot was especially common in early- and mid-seral stands dominated by Douglas-fir and grand fir, where trees of all ages were killed. Douglas-fir and grand fir, infected when mature or overmature, often developed extensive butt defect before succumbing to root disease. As more shade-tolerant conifers seeded in or released with the gradual break-up of the overstory, they were also infected but with little effect until they reached maturity. Once trees were mature (> 150 years old), butt rot would develop in western hemlock, Pacific silver fir, subalpine fir, noble fir, Shasta red fir, and occasionally western larch and western white pine. Mountain hemlock, when present, was killed by this root disease (fig. 10). As with Douglas-fir and grand fir, mountain hemlock infected when mature or overmature would often develop extensive butt defect before dying.

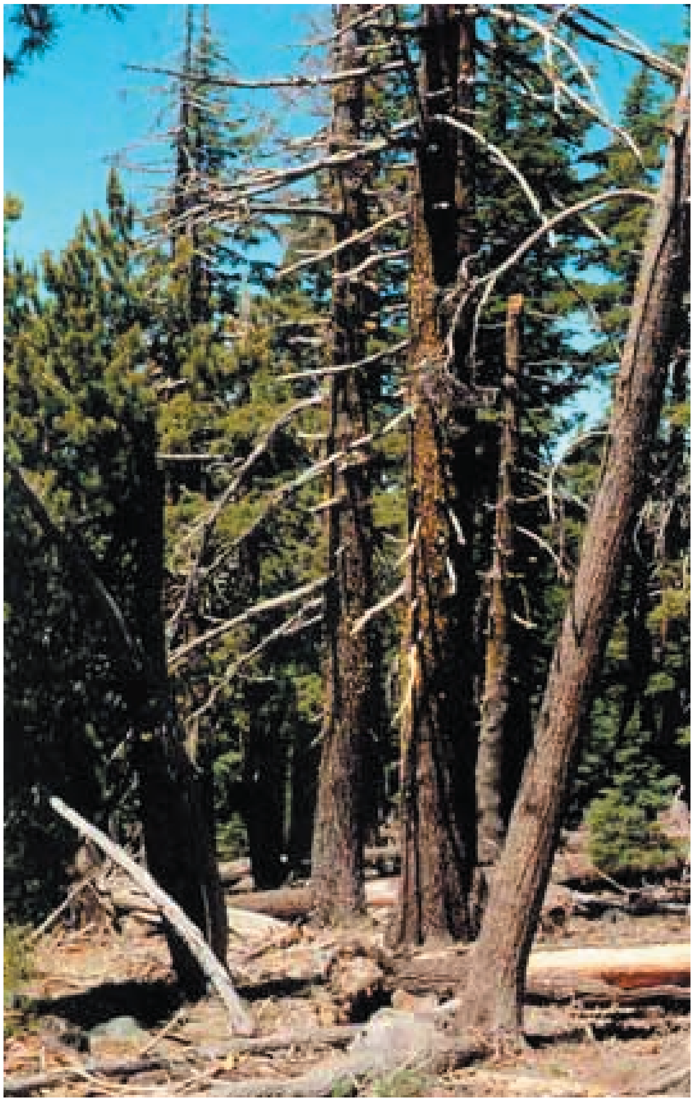

Figure 10. Laminated root rot in high Cascades mountain hemlock. Douglas-fir and grand fir are also killed by the pathogen (*Phellinus weirii*) that causes this root disease. [Photo courtesy of Don Goheen]

Armillaria root disease—The role of Armillaria root disease in western hemlock and redcedar climax forests of the eastern slope of the Cascades was unique, considering its role elsewhere on the east side. Douglas-fir in most drier series was highly susceptible to *Armillaria ostoyae* at all ages (Hadfield and others 1986). Within these series on the eastern slope, juvenile (<40 years old) Douglas-fir were most susceptible; mortality of older, robust trees and stands was relatively uncommon. Armillaria root disease also caused rapid juvenile mortality in almost every other coniferous species in these two series, with the exception of western redcedar (fig. 11). Fire-regenerated landscapes would experience mortality as a thinning effect until stands were dominated by pole-sized trees. Subsequently, Armillaria root disease was a mortality agent of low-vigor trees of developing stands.

In the northern Rocky Mountain ecoregion (Colville National Forest), localized mortality attributable to Armillaria root disease in young and old western redcedar has been observed (personal observation, P. Hessburg). In hemlock and redcedar climax forests of this same ecoregion, Douglas-fir is susceptible and can be killed at any age. Stressed and damaged conifers of all species are also host to this root disease.

Figure 11. Armillaria root disease (*Armillaria ostoyae*) in sapling Douglas-fir. Within the western hemlock and western redcedar zones east or west of the Cascade Crest, seral Douglas-fir and grand fir are most susceptible to this root disease.

Annosum root disease—S-group annosum root disease primarily caused butt defect in western and mountain hemlock, Pacific silver fir, and subalpine fir, although grand fir was killed when infected. Incidence in some mature, late-successional stands might have exceeded 50 percent if current-day stands are any indication. On the west side of the Cascades, Goheen and others (1980) found that, although rates of infection may be high in young hemlock, defect is incidental in wounded or unwounded trees until infected trees reach maturity. We presume that a similar relation exists for infected western hemlock and Pacific silver fir in eastside hemlock and redcedar series forests.

Brown cubical butt—Brown cubical butt rot spreads from host to host much like any root disease, but its influence on succession and fire history is more subtle and has often gone unnoticed. We surmise that a far greater proportion of eastside stands of all climax series are influenced by this root disease than by any other. Because this disease has no visible manifestation in the form of dead trees, it is overlooked, but it is likely the primary source of butt defect in western larch, Douglas-fir, ponderosa pine, and lodgepole pine on the east side. In historical hemlock and redcedar climax forests, Douglas-fir, western larch, and lodgepole pine were the primary hosts, although all other conifers within the series were occasionally infected. In eastern Oregon and Washington, tree mortality was exceptional; extensive butt rotting was the norm. Intertree spread occurred primarily via mycelial extension through duff and litter between host roots in close proximity.

Brown cubical butt rot was especially common in western larch and Douglas-fir, and extensive butt rot was evident in trees 200 years old and older. Fire-scarred survivors of former stands were vulnerable because they had new infection sites for decay pathogens, and were often well advanced in age at the time of fire injury. After fires, scars on surviving trees were infected by spores, thereby initiating new centers of disease. In hemlock and redcedar climax forests, Douglas-fir and western larch collapsed in characteristic barber-chair fashion when defect in the butt compromised vertical stability (fig. 12). Brown cubical butt rot has also been isolated from decayed stems in association with woodpecker cavities in northeastern Oregon (Parks and others 1990).

Figure 12. Trees with severe brown cubical butt rot (*Phaeolus schweinitzii*) often fail at the base when butt decay is advanced, leaving a foreshortened snag or stub. This tree also had butt decay associated with Phellinus weirii which causes laminated root rot.

Dwarf mistletoes—Dwarf mistletoes were not particularly damaging or common to hemlock or redcedar climax forests of the eastern Cascades, although western hemlock dwarf mistletoe does extend to east Cascades western hemlock stands, and can be locally damaging (personal observation, P. Hessburg). Dwarf mistletoes of western larch and lodgepole pine are occasionally associated with stands in these series. We presume their historical association was occasional as well. In western hemlock and western redcedar climax forests of northeastern Washington, dwarf mistletoes played a much greater historical role. Mistletoes of western larch, lodgepole pine, and Douglas-fir were especially damaging when fire return intervals were long. Mistletoe-infected trees surviving prior fires would transmit disease to host conifers in the understory via ballistically discharged seeds. With increasing passage of time between fires, stands would become more layered, more trees would be infected, mistletoe-infected branches would be more severely broomed, and topkilling and tree mortality effects would increase.

Indian paint fungus—In hemlock and redcedar climax forests throughout the east side, the Indian paint fungus was the most widespread stem decay pathogen of living western and mountain hemlock, and grand, noble, subalpine, and Pacific silver fir. Suppressed seedling, sapling, and small poletimber-sized host trees were infected by spores through vascular traces on small, dead, lateral branchlets. Once released from suppression through break-up of the overstory, quiescent infections were later encased in stemwood as trees increased in girth. Wounds, frost cracks, wind shake, and other injuries near the site of original infection stimulated active decay of the heartwood by the pathogen.

Current Forests

Eastside western hemlock and western redcedar climax forests have been logged extensively since World War II. Because of a maritime climate influence, these forests are highly productive. Many regeneration cuts have been made, but 40-acre clearcuts are currently the largest patches allowed on public lands. This size contrasts with the variably-sized openings created by historical fires; some openings were thousands of acres large. Another important difference centers on the disposition of woody debris: historical fires left dead trees of all sizes on each acre. Dead trees functioned as snag habitat for birds and small mammals for many decades. They eventually collapsed, slowly decayed, and were incorporated into the soil in subsequent centuries. Woody residues influenced soil moisture, texture, and fertility, and created an essential environment for microbes, fragmenting arthropods, and detritus feeders. Current management practices produce a scaled-down version of disturbance and woody residue recycling, and the role of large woody residues is diminished or has been all but eliminated. Managed hemlock and redcedar climax forest landscapes are also more fragmented and have more edge (Lehmkuhl and others 1993).

Insect and disease disturbances in current hemlock and redcedar climax forests are very much the same as those of a century ago, with a few major differences in successional status or corresponding insect or pathogen responses. The principal difference between historical and current conditions is the scale of landscape disturbances. Altered scale of fire disturbances has altered scales of pathogen and insect responses to changing successional conditions, but the responses themselves are for the most part the same. Perhaps the greatest change in the role of forest diseases in these ecosystems is associated with the white pine blister rust. Introduced to western North America around 1910, the blister rust is now widespread in five-needle pines throughout the United States, and it has taken a significant toll on western white pine in both western hemlock and western redcedar climax forests (fig. 13). Interacting mountain pine beetle populations have responded to the increase in blister rust, and most stem-cankered trees are ultimately killed by the mountain pine beetle. Once a widely distributed seral species in these series, western white pine is diminished in abundance to such an extent that it occurs in some locations now as an incidental species. Rust-resistant white pine have been identified and resistance factors characterized. In the last decade, genetically improved, rust-resistant white pine stocks have been introduced in single- and some multi-line arrangements.

Figure 13. Western white pine killed by the white pine blister rust fungus, *Cronartium ribicola*, and mass attack by the mountain pine beetle (*Dendroctonus ponderosae*).

DOUGLAS-FIR AND GRAND (WHITE) FIR SERIES

The grand fir series is the most extensive midslope forest east of the Cascade crest. It ranges in elevation from 1800 to 5100 feet in the eastern Washington Cascades, 2500 to 6500 feet in the Ochoco and Blue Mountains, 3000 to 6100 feet in the eastern Oregon Cascades, and 2200 to 4900 feet east of the Kettle Mountains in northeastern Washington. The Douglas-fir series is less extensive, occurring in lower slope positions than grand fir at elevations ranging from 2100 to 5900 feet in the Blue and Ochoco Mountains, 1400 to 5400 feet in the eastern Cascades of Washington, 2200 to 5400 feet in the Okanogan Highlands of northeastern Washington, and 1900 to 6000 feet on the Colville National Forest. Douglas-fir climax forests in the Blue Mountains are fragmented, often confined to dry ridgetops and south- and east-facing slopes.

The most common seral tree species in both series is ponderosa pine, particularly at low and middle elevations. Ponderosa pine is replaced by western larch at higher elevations and on north aspects. Ponderosa pine achieves its optimum growth in the grand fir series (Daubenmire 1961. Other seral species are lodgepole pine and western white pine. Characteristic of both series-almost as distinctive as the overstory stands of ponderosa pine-are scattered large, open, grassy areas on thin soils.

Under historical fire regimes, many grand fir and Douglas-fir climax forest sites were dominated by seral species that arose from infrequent stand-replacement fires and were maintained by frequent underburning (fig. 14). The most commonly regenerated tree species was ponderosa pine, but lodgepole pine was an aggressive pioneer; because of its serotinous cones and tendency to mature sexually at an early age, it often dominated sites when it was present in the burned stand. Western larch was often the dominant seral species in areas interpreted as having historically moderate- or high-severity fire regimes that were characteristic of north slope environments and higher elevations (Agee 1990, Williams and Smith 1991). Underburning fire regimes had little effect on fire-resistant overstory trees like ponderosa pine and western larch, and open, parklike stands were maintained for centuries. Between fires, shade-tolerant species regenerated in the understory but, because of their thin bark and low crowns, few survived frequent underburning.

Figure 14. Underburning in a grand fir zone ponderosa pine stand.

Douglas-fir and grand fir climax forests were characterized by low- and moderate-severity fire regimes (Agee 1993). Low-severity fires (<20 percent of trees killed) maintained parklike stands of seral species. Fires of moderate severity produced a variable landscape patchwork. We would expect that Douglas-fir and grand fir climax forest landscapes were the most diverse of all eastside landscapes under the historical influence of fire. Landscapes created and maintained by moderate-severity fire were constantly changing. Within fire event areas, patches burned by high-intensity fire (20 to 70 percent of the area) were homogenized for a time until unique site characteristics and site potential were manifested, and patterns would then emerge within patches. Similarly, underburned areas would be homogenized for a time, but each successive underburning event would affect different areas of the landscape, and differences according to site climate, species composition, canopy layering, and density would emerge. Excluding fire from Douglas-fir and grand fir climax forests has perhaps been the single greatest detriment to landscape diversity on the eastside.

Historical Forests

Late successional and climax plant communities of the Douglas-fir and grand fir series were relatively scarce before the advent of fire control on public lands. Landscapes that were frequently visited by fire were dominated by seral species. Areas routinely missed by fire (“refugia”) were those that normally burned with difficulty except under extreme fire weather circumstances: riparian areas, moist sites, highelevation sites, headwall sites, sites adjacent to rock outcroppings and scree slopes, and north slopes (Cooper and Pfister 1984). This pattern was true of all ecoregions of the east side except for the area of the Colville National Forest that lies in the northern Rocky Mountains ecoregion (Omernik and Gallant 1986), where moderate- and high-severity fire regimes were more often typical. Refugia were embedded in seral-dominated landscapes, or they were large areas that burned infrequently and had high-severity fire regimes. With the advent of fire suppression, Douglas-fir and grand fir expanded outward from refugia encroaching on new areas, establishing in the shade of seral overstories (Cooper and Pfister 1984). Historical refugia can be located by identifying the oldest patches of Douglas-fir or grand fir, or by dating old stumps if trees have been harvested.

Douglas-fir was also an overstory component of many frequently underburned, ponderosa pine-dominated landscapes. With the exclusion of fire, Douglas-fir readily colonized new areas as parent overstory trees cast their seeds. Historical underburning destroyed most young, fire-intolerant Douglas-fir. With the suppression of natural underburning large areas were rapidly colonized.

Western pine beetle—The western pine beetle would have been one of the most obvious insects associated with regularly burned, presettlement Douglas-fir and grand fir climax forests (Miller and Keen 1960). As documented in pioneer journals and old photographs (Burke 1990; Gruell 1983; Gruell and others 1982; Wickman 1987, 1992), low- and mid-elevation forests were dominated by large, old ponderosa pine; the kind of trees preferred by the western pine beetle (Keen 1943, Miller and Keen 1960, Wickman and Eaton 1962). These trees could magnify beetle populations, particularly when stressed by drought. Many trees were killed by western pine beetle during the great drought of the 1920s and 1930s (Miller and Keen 1960). Most years, the role of the western pine beetle was more benign; beetles killed trees struck by lightning, infected with root diseases, and those too old to resist attack.

Beetle-killed pine became snags that provided roosting and nesting habitat for birds, and when snags eventually fell, they provided temporary habitats for various forest vertebrates, decomposers, and invertebrate fragmenters. No doubt, frequent underburning reduced the abundance and diminished habitat suitability of many large down logs. Beetle-killed pine was a ready source of large and small insect larvae for birds and other insectivores. Woodpeckers snatched late-instar western pine beetles from the outer bark. Shortly after trees died, ambrosia beetles (Coleoptera/Scolytidae and Platypodidae) bored deep into the stem and produced their young. Following the western pine beetle and ambrosia beetles, roundheaded (Coleoptera/Cerambycidae) and flatheaded woodborers (Coleoptera/Buprestidae) mined and channeled stems as saprot claimed the sapwood. Woodborer larval galleries were large, creating ready access for wood decay fungi to the stem interior. In subsequent decades, carpenter ants (Hymenoptera/Formicidae) and termites (Isoptera/Hodotermitidae, Kalotermitidae, and Rhinotermitidae) infested decaying snags and contributed to their ultimate collapse.

Mountain pine beetle—The mountain pine beetle was an important insect of lodgepole pine stands of the Douglas-fir and grand fir series. Some of the first recorded outbreaks were in lodgepole and ponderosa pine (Langille 1903, Lieberg 1899), and the first forest insect control project was funded by Congress in 1910 to suppress an outbreak of the mountain pine beetle in lodgepole and ponderosa pine near Baker, Oregon (Burke 1990). Other early outbreaks have been documented by studying trees strip-attacked by the mountain pine beetle (Mitchell and others 1983a).

Many of the historical outbreaks were obviously severe (Wickman 1990), but the extent and duration of outbreaks were less than we observe today (Mitchell 1988), partly because of greater age diversity that fires created in lodgepole pine forests, the fact that fires would sometimes burn beetle-infested stands, and beetle populations would cycle with developmental stages of stands (Amman 1991, Martin and Mitchell 1980, Mitchell and Martin 1980).

Until regenerated by fire, lodgepole pine stands of the Douglas-fir and grand fir series showed considerable variation in age and structure, reflecting their outbreak and recovery history. In an outbreak, the largest dominant and codominant pine were killed, leaving the lower crown classes to survive. Within a few years, surviving trees responded to improved growing conditions and began expanding their crowns (Mitchell 1987). After 30 or 40 years, tree crowns merged and trees began showing signs of intertree competition. Outbreaks recurred when trees with diameters larger than 9 inches were abundant, and overstocking depressed tree vigor to the point that effective resistance to attack was lost.

Before the 20th century, fires occurred somewhat randomly, ensuring that at any given time, only a small proportion of lodgepole pine stands would be of susceptible size and age. This effect of random distribution of fire regulated both the beetle food supply, and the number of beetles available to attack susceptible trees. The total number of trees killed in a stand depended on stocking within a stand, and beetle populations available to a susceptible stand (Mitchell 1988). Tree vigor also played an important role in susceptibility to beetle attack (Mitchell and others 1983b; Waring and Pitman 1980, 1985), but unmanaged stands rarely contained trees with adequate vigor to resist beetle attack (Mitchell and Preisler 1991).

Stands regenerating after high-intensity fires at upper elevations, particularly on north slopes, frequently began as a mixture of lodgepole pine and western larch. In those instances, outbreaks of the mountain pine beetle often provided a beneficial thinning. Many, nearly pure stands of western larch can be traced to mixed stands where the mountain pine beetle destroyed the lodgepole pine (Mitchell 1988).

Pine engraver beetle—Mountain pine beetles and pine engraver beetles also attacked young, densely stocked ponderosa pine stands (Sartwell 1971, Sartwell and Stevens 1975). Outbreaks were probably small because both species preferred trees in overstocked stands, and frequent underburning tended to keep trees well thinned and free from competition (Weaver 1957, 1967). Nevertheless, pine engraver beetles would have been abundant after light ground fires. They were attracted to scorched trees and assisted in regulating stocking below carrying capacity (Martin and Mitchell 1980, Mitchell 1990a, Mitchell and Martin 1980).

Douglas-fir engraver, fir engraver, Douglas-fir beetle—Engraver beetles—one species in understory Douglas-fir (*Scolytus unispinosus*) and another in grand fir (*S. ventralis*)—played essentially the same role as the pine engravers, removing trees scorched by low-intensity ground fires. In late-successional and climax refugia, engraver and Douglas-fir beetle populations probably increased when stocking was high, during protracted droughts, and when severely diseased trees with dwarf mistletoe or root rot were abundant. Dead trees provided needed snags and down wood. Ultimately, fuels accumulating from trees killed by diseases and insects were predisposing to severe fires, and some refugia were regenerated to seral plant communities.

Western spruce budworm, Douglas-fir tussock moth—Western spruce budworm and Douglas-fir tussock moth outbreaks occurred periodically in mixed coniferous stands of the grand fir and Douglas-fir series, long before the turn of the century (fig. 15). Wickman and others (1993), investigating tree-ring chronologies in the Blue Mountains, detected signatures in growth rings that clearly indicated outbreak episodes dating back to the 1700s. Similar patterns in tree rings from Colorado and New Mexico were found by Swetnam and Lynch (1989). Outbreaks were likely of short duration and small in extent (Anderson and others 1987; Carlson and others 1983, 1985; Fellin and others 1984; Wickman 1992). As noted by several investigators (Gruell 1983, Gruell and others 1982, Mitchell 1990a, Schmidt 1985, Wickman 1978, Williams and others 1980), the food base needed to generate large, prolonged outbreaks of either the western spruce budworm or the Douglas-fir tussock moth was not there. Host species stands were discontinuous, and seral species stands were continuous on most landscapes. This pattern of vegetation localized the extent and duration of outbreaks, mostly by limiting available habitat, but also by reducing dispersal potential between patches of susceptible hosts (Beckwith and Burnell 1982, Mitchell 1979). Historical outbreaks of Douglas-fir tussock moth and western spruce budworm collapsed when shade-tolerant true firs and Douglas-fir were repeatedly defoliated, and starvation became a limiting factor in survival (Carlson and others 1983; Fellin and Dewey 1982; Mason 1974, 1977, 1981a, 1981b; Mason and Thompson 1971; Wickman and others 1973).

Although tree mortality can often be severe after a defoliator outbreak, the damage is often less than appearances would suggest. Wickman (1986) and Wickman and Starr (1990) showed that the thinning effects of defoliation and mortality, along with improved mineral cycling stemming from caterpillar frass, stimulated the growth of grand fir and Douglas-fir long after tussock moth outbreaks were over; growth even exceeded that of nondefoliated stands. Parasites and predators certainly dampen defoliator population growth during outbreaks, but their most important role seems to be in preventing outbreaks and, working with other factors, to increase the speed at which outbreaks collapse (Mason and Luck 1978, Mason and Wickman 1988, Torgersen and Dahlsten 1978, Wickman 1990).

Figure 15. Small-scale outbreak of the Douglas-fir tussock moth (*Orgyia pseudotsugata*) in the Blue Mountains of northeastern Oregon. [Photo courtesy of Craig Schmitt].

Root diseases—Four tree-killing root diseases occurred naturally in grand fir and Douglas-fir climax forests: laminated root rot, Armillaria root disease, and both the P- and S-group annosum root diseases (Byler 1984; Filip 1990; Filip and Goheen 1982, 1984; Hip and Schmitt 1979; Gast and others 1991; Goheen and Filip 1980; Hadfield and others 1986; Hessburg and Flanagan 1992a, 1992b). Root diseases were a subordinate part of most presettlement, mixed-conifer landscapes; root diseases likely provided structural diversity at the patch scale (Cody 1975, Whittacker 1960). Root diseases produced their most visible manifestation in areas infrequently visited by fire, areas where the normal fire regime was of moderate or high severity. Such areas were mixed in composition, with seral overstories and shadetolerant understories. Root diseases were not a threat in such forests; they increased structural diversity, the abundance of coverts (animal habitat focal points: locations in the forest where three or more different patch types converge) (Conlin and Giles 1973, Hunter 1990), and enhanced heterogeneity in size of openings, amount and shape of edge, and size of patches. The result was increased variety in structure in forests that stemmed from moderate- and high-intensity fires (Spies and Franklin 1989).

Laminated root rot—Laminated root rot infected and killed some of the highly susceptible Douglas-fir and grand fir that grew in patches missed by fire. Because the root systems of Douglas-fir and grand fir were usually well rotted, infected trees usually fell over in a jackstraw arrangement (Hadfield and others 1986). Root disease centers provided important coarse- and fine-textured gaps in forest canopies (Spies and Franklin 1989) that enhanced plant species richness (White and Pickett 1985; Whitmore 1988, 1989), and variety of habitats suitable for vertebrates (Maser and others 1979, Thomas and others 1979b). Although snags created by laminated root rot had weakened root systems and did not remain vertical for long, they were probably important as short-term snags and as coarse woody debris on the forest floor, providing habitat for both raptors and their prey, and even for large animals (Bartels and others 1985, Harmon and others 1986, Maser and others 1979, Spies and others 1988, Spies and Cline 1988). Eventually, as coarse woody debris decomposed and was incorporated with the soil, it became important to conifer establishment because of its moisture-holding capacity during summer drought. Coarse woody debris was likewise important in mineral cycling because of its ability to harbor mycorrhizal fungi that were required in the reestablishment of conifer and perennial hardwood vegetation after fire (Harmon and others 1986, Harvey and others 1979, Maser and others 1979).

Armillaria root disease—Armillaria root disease ecology in turn-of-the-century forests was probably very similar to that of laminated root rot. Armillaria root disease probably played a role in forest succession and stand dynamics of many refugia dominated by Douglas-fir or grand fir before European settlement (Byler 1984, Hagle and Goheen 1988, Kile and others 1991). Large centers of mortality were atypical within the forest matrix where frequent underburning maintained seral species. Among seral species, this pathogen functioned as a secondary root pathogen, or as a pathogen of opportunity (Hadfield and others 1986, Kile and others 1991), attacking and overwhelming low-vigor, overmature, weakened or injured trees, as well as those stressed by drought, struck by lightning, scorched by fire, or attacked by other root pathogens (Filip and Goheen 1982, Goheen and Filip 1980). Many of these trees would eventually become high-quality snags used by generations of primary and secondary cavity-nesting birds (Madsen 1985, Thomas and others 1979a).

Refugia dominated by Douglas-fir or grand fir were presumably found in shaded draws, on cooler north slopes, wetter, more productive sites, in riparian areas, and adjacent to rock outcroppings and talus slopes, where fires ordinarily burned with difficulty (Hessburg and Flanagan 1991, 1992a, 1992b; Lehmkuhl and others 1993; Williams and Lillybridge 1983; Williams and Smith 1991). In refugia, where Douglas-fir and grand fir colonized understories, centers of Armillaria root disease may have become quite large, depending on the size of the area, the density of hosts, and fire history. Root disease severity in tolerant and resistant hosts was often magnified in these environments. Extreme disturbance associated with Armillaria root disease may have approached the magnitude of patchy, stand-replacement fires, where a hundred acres or more were visibly affected.

Annosum root diseases—P- and S-group annosum root disease centers were relatively uncommon in presettlement forests. These diseases require freshly cut stumps or wounds for windborne spores to infect and initiate new root-disease centers. Without tree harvesting, annosum root disease existed as a butt rot of trees with stem wounds. In central, southern, and northeastern Oregon, stands with multiple entries (fig. 16) have been shown to have the highest frequency of mortality caused by annosum root disease and associated bark beetles (Schmitt and others 1984, 1991; Filip and others 1992a).

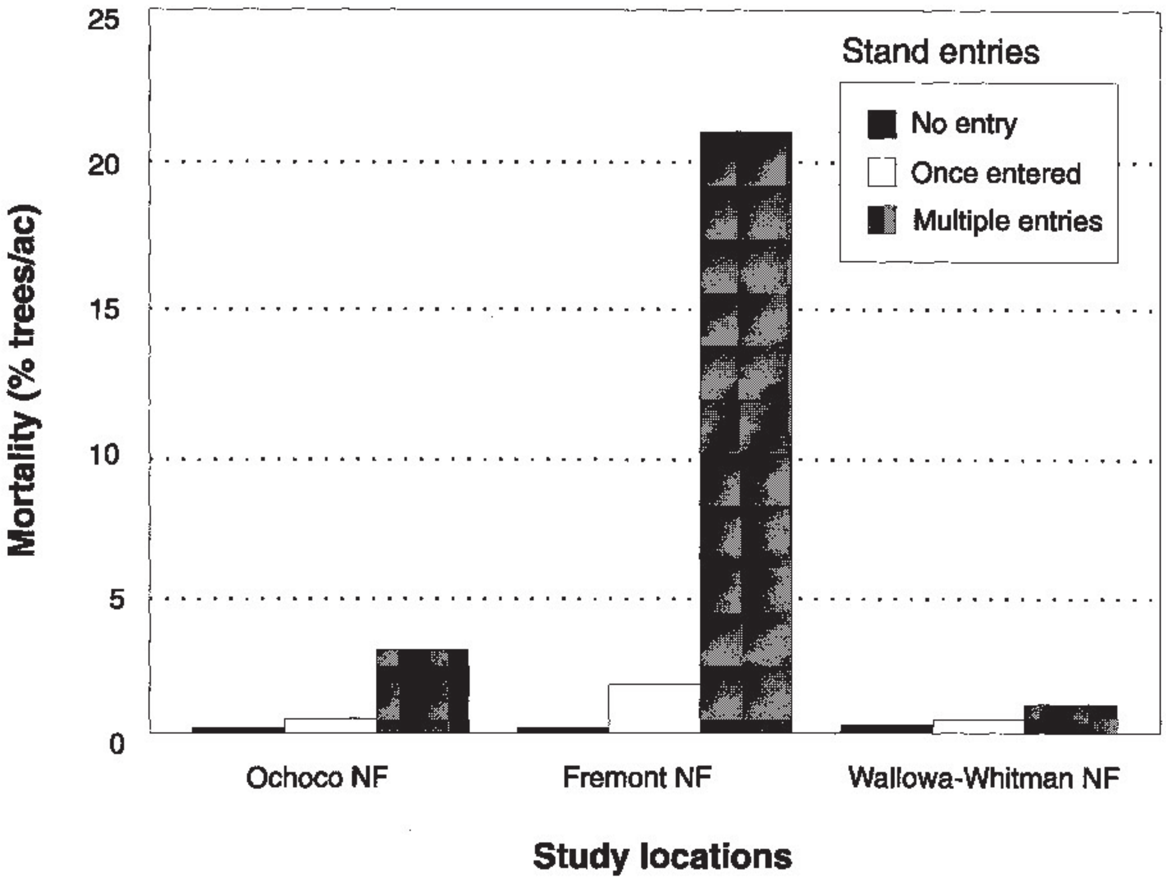

Figure 16. Mortality (trees/acre) of *Abies* spp. caused by *Heterobasidion annosum* in unentered (no harvesting), once entered, and twice or more entered (multiple harvests) stands on three National Forests (Schmitt and others 1984, 1991).

Dwarf mistletoes—Dwarf mistletoes would have occurred in each coniferous species, but none were particularly threatening to their hosts (Alexander and Hawksworth 1975, Parmeter 1978, Tinnin 1981, Wicker and Leaphart 1976). Given fire frequencies in historical forests, and the effects of underburning on tree composition, stocking, and canopy structure, the western larch mistletoe was likely the most prevalent and damaging. Because severe mistletoe infections in ponderosa pine provide an abundance of mistletoe brooms, fine fuels, resinous stems and branches, as well as dead trees and cankers, low-intensity surface fires would tend to torch these trees, destroying severely infected trees and small infection centers (Koonce and Roth 1980, Parmeter 1978, Weaver 1974). No doubt crown fires and patch torching initiated in areas of severe mistletoe infestation.

An often underrated feature of dwarf mistletoes is the wildlife habitat provided by mistletoe brooms (fig. 17). Brooms are used for nesting, roosting, and hiding cover (Allen and Brewer 1986; Baranyay 1968; Bull and Henjum 1990; Bull and others 1989; Buskirk and others 1987; Crawford and others 1986; Farentinos 1972; Forsman 1983; Patton and Vahle 1986; Schellhaas and others, unpublished; Sever and others 1991; Smith 1982; Spencer 1987; Stauffer and Peterson 1986). Dwarf mistletoe in Douglas-fir and was probably more common on northerly aspects and in riparian areas, where the interval between fires was long. Mistletoes of seral species were probably most common on south slopes, where fires maintained seral species, and fires were usually low in intensity. High-intensity fires would eliminate mistletoes over large areas, and mistletoes would slowly re-invade from the perimeter at the rate of 10 to 15 feet a decade (Hawksworth 1958, 1960; Parmeter 1978; Wagener 1965). Birds and squirrels also contributed to reintroduction of mistletoes to large host patches (Hawksworth and others 1987, Nicholls and others 1984, Ostry and others 1983, Punter and

Gilbert 1989, Tinnin and others 1982, Zilka and Tinnin 1976). Mistletoes would persist in residual ponderosa pine and western larch overstory trees by virtue of their resistance to fire, or from irregularities in fuel continuity or arrangement, or fire behavior, and the spread of these mistletoes to newly regenerating patches would be much quicker (Baranyay 1970, Parmeter 1978).

Figure 17. Nest and juvenile owls (lower right) on a natural platform caused by *Arceuthobium laricis* in western larch. [Photo courtesy of Evelyn Bull].

Douglas-fir dwarf mistletoe and western larch dwarf mistletoe were probably common in mid- and lateseral forests before the 20th century. Areas infested with these mistletoes tended to be the more mesic plant associations, where fires appeared with moderate frequency (Agee and Edmonds 1991, Byler 1984, Fellin 1980, Hessburg and Flanagan 1991, Williams and Smith 1991, Williams and Lillybridge 1983, Williams and others 1990.

Mature Douglas-fir, with thick outer bark and crown bases elevated well above the forest floor, were quite resistant to underburning. Young Douglas-fir, conversely, had thin, resinous outer bark and crowns close to the forest floor, two characteristics that increased vulnerability to underburning. When mistletoe brooms occurred on young trees, the likelihood of tree torching was greatly increased (Harrington 1991, Tinnin 1984, Tinnin and Knutson 1980, Wanner and Tinnin 1989). Under the right conditions of wind and weather, fires crowned from mistletoe-infected understories. In addition, mistletoe brooms in Douglas-fir nullified benefits of intertree competition and natural branch pruning by maintaining a flammable link with the forest floor. Mistletoe brooms are water and nutrient sinks nourished by the uninfected portions of trees (Fischer 1983, Hull and Leonard 1964). Mistletoe infections locally elevate cytokinin activity (Paquet 1979, thereby delaying normal senescence (Briede and others 1991.

Under historical fire regimes, Douglas-fir dwarf mistletoe was probably widely distributed but with little intensification; fire maintained open stands of ponderosa pine or mixed sera] stands with Douglas-fir (Arno 1988, Fischer and Bradley 1987, Harrington 1991, Williams and Smith 1991. Douglas-fir dwarf mistletoe was well distributed in scattered, thick-barked overstory trees that had developed on seral dominated landscapes under the influence of frequent low-intensity fire, but further influence was minimal because understory Douglas-fir stocking was minimal. In patches where Douglas-fir was abundant in the understory, Douglas-fir dwarf mistletoe was probably abundant as well.

Western larch dwarf mistletoe was perhaps the most widespread of mistletoes in late seral stands (fig. 18). Of all the dwarf mistletoes, larch mistletoe survived fire in overstory western larch with the greatest constancy (Bolsinger 1978, Hessburg and Flanagan 1992b), perhaps because of larch's exceptional resistance to damage by fire (Kauffman 1991, Lotan and others 1981, Martin and Dell 1978), its resistance or tolerance to both tree-killing and opportunistic root pathogens (Filip and Schmitt 1979, Hadfield and others 1986), and the lack of primary bark beetle associates (Hessburg and Flanagan 1992a, 1992b). Conifers such as Douglas-fir or ponderosa pine with severe mistletoe infections exhibit declining crown vigor and reduced resistance, and are eventually attacked and killed by bark beetles and opportunistic root pathogens like *Armillaria* root disease (Hadfield and others 1986, Morrison and others 1991), and occasionally P-group annosum root disease (personal observation, P. Hessburg).

Larch mistletoe brooms are weak and brittle and frequently break off when still relatively small. Under historical fire regimes, branch litter accumulating under infected hosts caused lethal fire scorching of some infected trees (Alexander and Hawksworth 1975, Tinnin and others 1982, Wicker and Leaphart 1976). According to Tinnin and others (1982), the increased burn potential accentuated the advantage of fire-adapted species such as western larch.

Figure 18. Western larch stand infested with the larch dwarf mistletoe (*Arceuthobium laricis*) in northeastern Oregon.

Severe effects from lodgepole pine dwarf mistletoe were localized because of frequent fire return and the sanitizing effect of fire. Recurring fires eliminated fire-sensitive lodgepole pine and its mistletoe (Martin and Dell 1978, Williams and Lillybridge 1983, Williams and Smith 1991). Stand-replacement fires in lodgepole pine at intervals of less than 150 to 200 years perpetuated nearly pure patches of lodgepole pine or mixed seral stands with a major lodgepole pine component (Lotan and Perry 1983, Williams and Lillybridge 1983, Williams and Smith 1991). Stand-replacement fires in lodgepole pine stemmed from prior mountain pine beetle outbreaks and associated fuel buildup (Amman 1991, Brown 1975, Fellin 1980). Lodgepole pine dwarf mistletoe infested replacement stands from the perimeter, where complete sanitation by fire occurred (Parmeter 1978), and from within (Baranyay 1970) when individual infested trees or islands of trees survived fires and subsequent bark beetle attacks.

Current Forests

The century since the advent of fire protection has seen a steady shift away from historical parklike ponderosa pine and larch stands toward denser late-successional stands. Lacking the low-thinning effect of frequent underburning, many stands were colonized by grand fir and Douglas-fir. Driven by short-term economic goals, the harvesting of high-valued overstories accelerated the conversion to insect- and pathogen-susceptible late-successional forests. In some landscapes, a portion of the original seral overstory remains; in others, the conversion is complete. The harvest supported mills and stabilized populations in many small towns, but the economic success could not be sustained. The stands of large ponderosa pine and western larch began to disappear, and so did other supporting ecosystem components. Wickman and others (1993), in their review of forest inventory reports for the Blue Mountains, showed that the amount of forest land dominated by ponderosa pine declined from 80 percent (all ownerships) in 1936 to about 25 percent in 1992.

Williams and others (1980), comparing the location of Douglas-fir tussock moth outbreaks with 1935 Forest Service timber type maps, showed that 80 percent of the infestations in the worst outbreak areas (east-central Oregon and northeastern Washington) occurred in stands once classified as ponderosa pine type. In the Blue Mountains of northeastern Oregon and southeastern Washington, some 30 to 40 percent of the tussock moth outbreaks were in stands once dominated by ponderosa pine. This relation between rising insect and pathogen populations and the shift toward overstocked late-successional forests is consistent throughout the east side of Oregon and Washington, but low- to mid-elevation climax grand fir and Douglas-fir forests have sustained the most damage.

Western pine beetle—The western pine beetle continues to threaten ponderosa pine in forests east of the Cascades, even though many of the large pure stands of older ponderosa pine, once a dominant signature of eastern forest landscapes, are gone (Scott 1991). In heavily logged areas, the few large ponderosa pine trees that remain in the overstory are often old and decadent, with poor crowns and generally poor vigor. In landscapes still dominated by overstones of ponderosa pine, sanitation salvage entry has often been restricted and veteran trees with poor crowns and poor vigor have accumulated. Such trees attract beetles and generate outbreaks (Salman and Bongberg 1942, Wickman and Eaton 1962). Lacking regular fire, dense understories of shade-tolerant species compound the problem of declining vigor of overstory ponderosa pine by increasing intertree competition for soil moisture and nutrients. Because of the declining vigor of overstory ponderosa pine, both Armillaria root disease and the P-group annosum root disease are more prevalent in pine than before, and both invite attack by the western pine beetle. The recent drought influenced western pine beetle populations by increasing the number of trees available for attack. Dead tree fuels, coupled with dense, live, shade-tolerant understories, have created a dangerous accumulation of fuels for conflagrations, now a serious threat to many eastside forests.

Mountain pine beetle—The mountain pine beetle is probably the most influential bark beetle in current grand fir and Douglas-fir climax forests. It damages overstocked, pole-sized ponderosa and lodgepole pine. On good sites, the beetle is a minor influence on second-growth ponderosa pine (Sartwell 1971). Because ponderosa pine grows best in the grand fir series (Daubenmire 1952) and because the number of pines is reduced there, the mountain pine beetle is a minor problem of ponderosa pine at higher elevations. The beetle has been a major influence in drier forest landscapes downslope, where young stands are often overstocked and stressed (Sartwell and Stevens 1975). Mountain pine beetle infestations can be particularly serious when lodgepole pine is intermixed or when a mature stand of lodgepole pine is nearby (Mitchell 1988). Lodgepole pine can generate substantial populations of the mountain pine beetle, and large beetle populations can overwhelm nearly any tree, particularly when beetles are drawn to stands by low-vigor or lightning-struck trees (Mitchell 1987).

The mountain pine beetle shows a decided preference for lodgepole pine (Mitchell 1988). On good sites, when lodgepole is mixed with ponderosa pine, the only ponderosa pines attacked are those a few feet away from attacked lodgepole pines. Outbreaks of the mountain pine beetle are most severe where pure or nearly pure stands of lodgepole pine are present; the grand fir series has many such stands. Enormous outbreaks have been recorded throughout western North America (McCambridge and others 1979); some of the most severe have been in interior forests of Oregon and Washington (Burke 1990, Mitchell 1988, Scott 1991, Wickman 1990).

Current outbreaks of the mountain pine beetle in lodgepole pine are probably more frequent, more extensive, and more severe than at any time in history (Mitchell 1988). An outbreak in a typical stand will kill 200 to 300 lodgepole pines per acre before it is finished. Oddly enough, most of the trees killed are not very susceptible to beetle attack. Rather, the beetle focuses on 50 to 60 trees larger than 9 inches d.b.h., and other nearby trees are killed somewhat randomly, depending on how close they are to the trees that are the object of attack (Geiszler and Gara 1978; Mitchell and Preisler 1991; Preisler and Mitchell, in press). After 15 to 25 years, many beetle-killed trees are on the ground (Harvey 1986, Mitchell 1990b). Before the era of fire control, those trees would have been the fuel for the next conflagration that regenerated lodgepole pine, and it would have been another 100 years before another outbreak was possible. With fire protection, lodgepole pine stands may suffer two or three outbreaks of the mountain pine beetle before an outbreak is interrupted by fire. Advance lodgepole pine regeneration remaining after an outbreak that is not followed by fire becomes the new stand for the next outbreak. In this sequence, the large trees needed to generate an outbreak are available in about 50 years instead of 100 years (Mitchell 1987). Another consequence of fire protection in lodgepole pine is a reduction in landscape diversity. Outbreaks in modern times simultaneously affect more stands than historically, thus generating larger beetle populations (Mitchell 1988). Beetle outbreaks cycle faster because of advance regeneration, cover larger areas, and—with larger beetle populations—kill more trees. Fuels accumulating from multiple beetle outbreaks generate fires of extreme intensity and large scale.

Pine engraver beetle—The pine engraver beetle is doubtless more abundant and destructive now than in past centuries. This beetle focuses on small and stressed trees (Sartwell 1970), and eastside forests now have more of both than ever before. Damage is most severe on poor, dry sites. The most significant outbreaks today occur in low-elevation ponderosa pine climax forests. More discussion in the next section addresses insects and pathogens of the ponderosa pine series.

Douglas-fir beetle—Since the advent of fire control, the Douglas-fir beetle has become a more frequent influence in Douglas-fir and grand fir climax forests (fig. 19). Douglas-fir is now much more abundant (see fig. 19), and trees weakened by extended outbreaks of the western spruce budworm or Douglas-fir tussock moth are susceptible to attack by the beetle (McGregor and others 1983, Scott 1991, Wright and others 1984). Currently, some of the most serious damage is associated with large trees growing in riparian areas and along ridgetops. Trees in these environments have escaped large fires and consequently are some of the oldest Douglas-fir on the landscape. Douglas-fir in riparian environments are probably sensitive to drought and riparian zone dewatering by irrigation as well. As the Douglas-fir that was regenerated or released in this century ages, the threat of the Douglas-fir beetle will also increase.

Figure 19. Douglas-fir beetle (*Dendroctonus pseudotsugae*) outbreak in the Blue Mountains of northeastern Oregon. Stands were chronically defoliated by the western spruce budworm (*Choristoneura occidentalis*) during a period of prolonged drought, and were attacked by the Douglas-fir beetle when severely vigor-depressed. [Photo courtesy of Craig Schmitt].

Fir engraver—The fir engraver normally attacks low-vigor trees: those weakened by overstocking, root disease, lightning strikes, and drought. Conditions suitable for this beetle certainly occurred in scattered stands before this century, but not to the extent that they do today. From what we know of the historical role of fire, grand fir and white fir, favorite hosts of the fir engraver, have never occurred in such abundance. They are widespread throughout the grand (white) fir series, as are low-vigor growing conditions. The influence of fir engraver from 1987-1992 was great (fig. 20), responding to increasing root disease, dwarf mistletoe, overstocking, persistent drought, and severe defoliation by budworm and tussock moth populations (Wright and others 1984). This drought and its aftereffects will inevitably end, but without management actions to restore widespread seral conditions, the supply of host fir will remain, and root disease and fir engraver influences will persist.

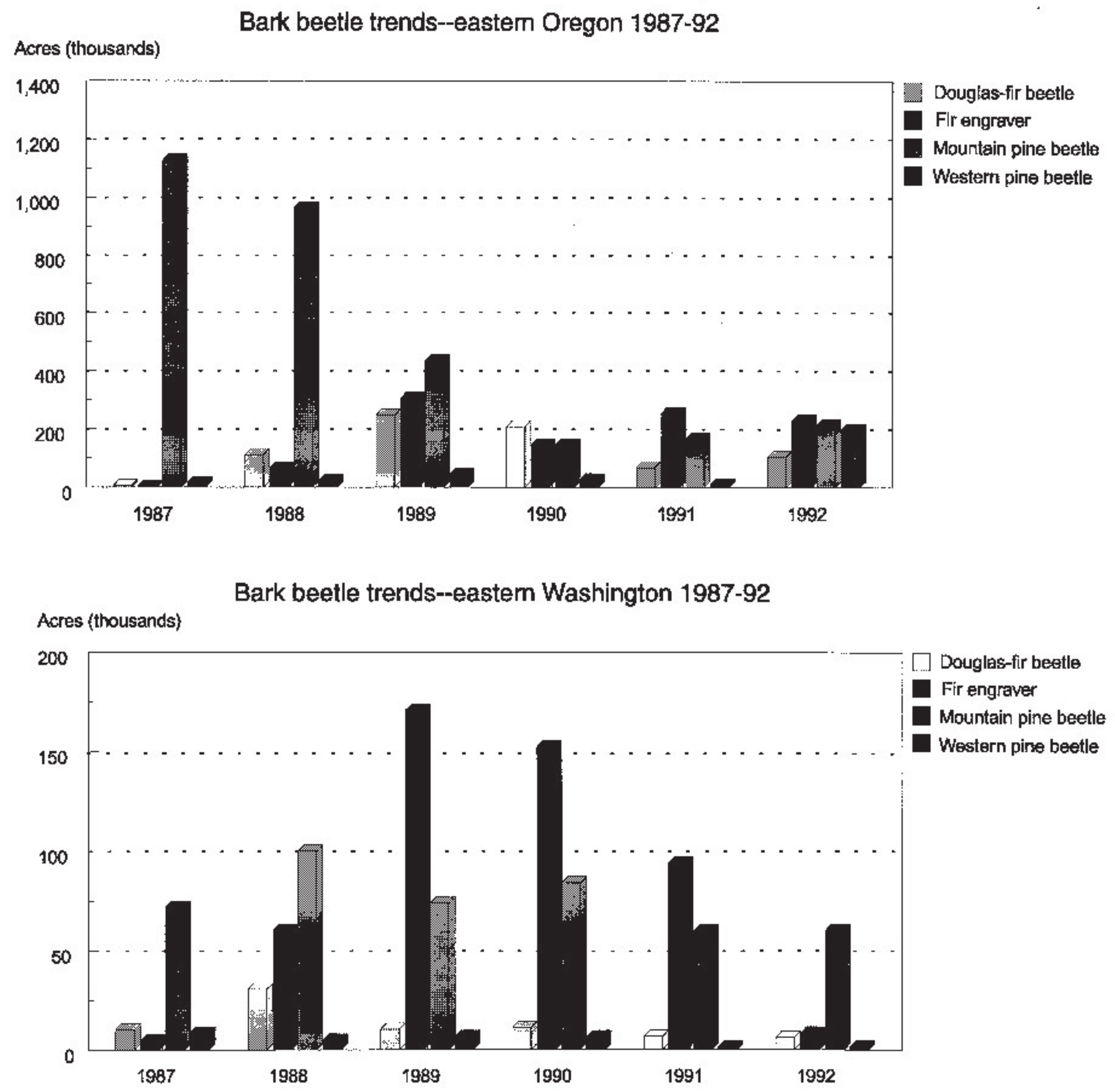

Figure 20. Bark beetle and tree mortality trends in eastern Oregon and Washington for the period 1987-1992.

Western spruce budworm, the Douglas-fir tussock moth—The most dramatic and visually displeasing insect disturbance pattern associated with the increasing shade-tolerance of eastside forests is that caused by the western spruce budworm and the Douglas-fir tussock moth. The ecology and dynamics of both insects have been studied for many years (Brookes and others 1978, 1985, 1987; Mason 1974, 1977, 1981a, 1981b; Mason and Wickman 1988; Wickman 1978; Wickman and others 1992). Spruce budworm larvae feed on new growth and move to old needles (with poor survival) only when the supply of new growth is exhausted. Because old needles can sustain defoliated trees for a time by providing photosynthate for production of new foliage, budworm can survive in a grand fir stand for 5 to 11 years before running out of food. Douglas-fir trees can endure defoliation longer than other trees because they generate new foliage from adventitious buds (Van Sickle 1987).

When susceptible stands were scattered, outbreaks probably collapsed when the local food supply was exhausted. Currently, with an increasing abundance of susceptible stands close to each other, larvae (Beckwith and Burnell 1982) and moths can disperse from stand to stand with minimal loss and with a good chance of finding a new food supply. If the food supply is large and close enough to other host stands, populations can cycle back and forth between stands, chronically defoliating for years. Because most of Oregon and Washington east of the Cascade crest is in a climatic region suitable for western spruce budworm populations (Kemp and others 1985), the problem of chronically long defoliator outbreaks will likely continue for a long time, and outbreak damage severity will likely worsen as susceptible forests are allowed to age.

Like the western spruce budworm, Douglas-fir tussock moth populations respond to widespread changes in forest vegetation composition and vertical structure. Tussock moth larvae also feed on true firs and Douglas-fir, and prefer new needles to old. Late-instar tussock moth larvae, however, readily feed on old needles (fig. 21), and large populations can completely defoliate trees in 1 year and cause mortality in 2 to 3 years (Wickman 1978). Accordingly, damage by tussock moth feeding is often more severe than budworm damage, although severe tussock moth damage tends to be localized, and budworm damage is much more extensive. The western spruce budworm is almost always present in numbers large enough to sample; tussock moth on the other hand, is either found in great numbers or is barely detectable (Mason 1987). We do not know whether the increasing dominance of shade-tolerant species in eastside landscapes will affect the severity or duration of tussock moth outbreaks, but outbreaks will occur in many places where no hosts were growing 100 years ago.

Figure 21. Entire tree crowns are often defoliated by the Douglas-fir tussock moth (*Orgyia pseudotsugata*) because late-instar larvae feed successfully on new and older foliage. [Photo courtesy of Craig Schmitt].

Annosum root disease—In the current fire-restricted condition, all major tree-killing root diseases except P-group annosum (Chase 1989, Otrosina and Cobb 1989) are widespread, following landscape colonization by grand fir and Douglas-fir (Baker 1988, Byler and others 1990, Filip and Goheen 1984, Hagle and Goheen 1988, Hessburg and Flanagan 1992a). Collectively, effects of root diseases on growth and mortality, and their contributions to flammable fuels are ecologically significant. Most surprising is the rate of increase in S-group annosum root disease in grand (white) fir. Grand fir climax forests contain large increases in S-group annosum (fig. 22) because grand fir stumps were infected by spores when stands were logged (Filip and others 1992a, Hadfield and others 1986, Otrosina and Cobb 1989). New centers of annosum root disease mortality are emerging throughout the grand fir climax forest, especially where large grand fir were first harvested. Over the next 15 to 20 years, a large increase is likely in the number of new S-group annosum root disease centers corresponding with the most recent partial-cutting entries in merchantable grand fir (Gast and others 1991; Schrnitt and others 1984, 1991). Infection centers will continue to expand until fire or silvicultural activities create conditions for the reintroduction of seral species.

Pine stumps created after logging were infected by spores of both the P- and S-group annosum diseases. Because S-group isolates are primarily pathogenic on true firs and spruces, the roles these stumps will play in the future incidence of disease is uncertain. Pine stump infection by P-group annosum is often high in Douglas-fir and grand fir climax forests, but mortality in ponderosa pine is uncommon. Without prolonged warming of the climate, we predict that growing conditions for ponderosa pine in these series are adequate to sustain resistance to this root disease. In the event of prolonged global warming, however, Pgroup annosum may become more serious on what are now mesic sites of the Douglas-fir and grand fir series. P-group annosum effects are currently most serious on dry pine sites of the ponderosa pine climax series. Nevertheless, the current drought has depressed the vigor of pines on some drier Douglas-fir and grand fir climax sites, and small P-group annosum centers have been observed (Hessburg and Flanagan 1991, 1992a, 1992b.)

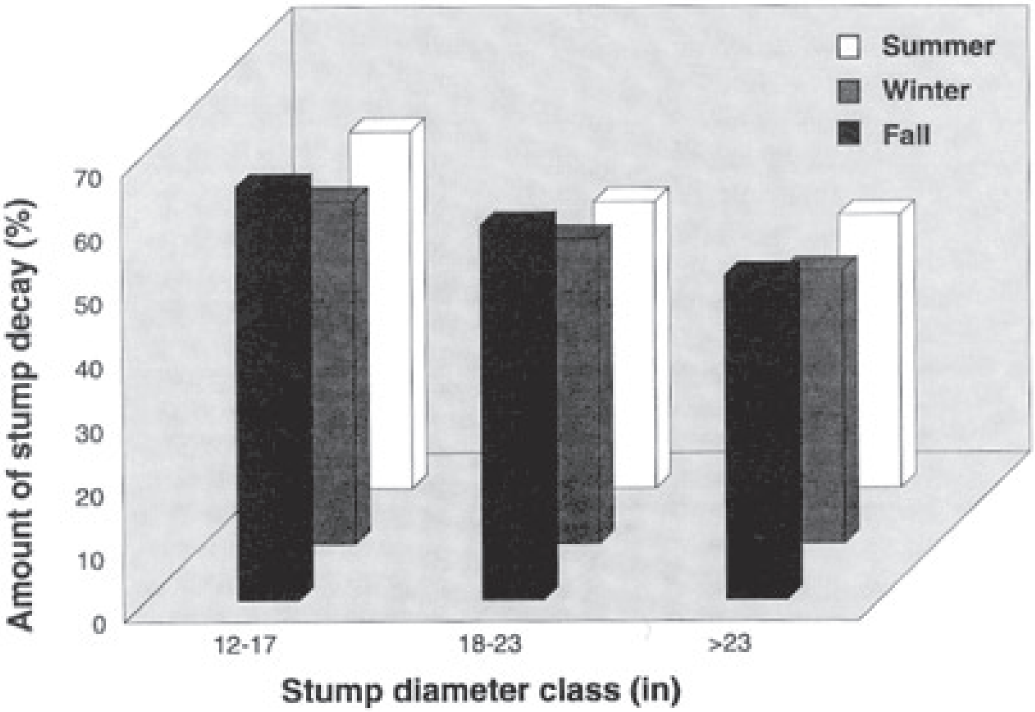

Figure 22. Amount of stump decay caused by *Heterobasidion annosum* in 300 grand fir stumps in northeastern Oregon (Filip and others 1992a).

Armillaria root disease, laminated root rot—Both Armillaria root disease and laminated root rot have expanded their influence from historical infection centers colonizing burgeoning populations of Douglas-fir and grand fir. Both host diseases are now epidemic in many parts of the Douglas-fir and grand fir climax forest. Root pathogen and associated bark beetle populations are building in response to increasing availability of preferred hosts in vertical and horizontal arrangements that are optimal for transmission or dispersal.

Dwarf mistletoes—With the restriction of fire, at least 43 percent of the Douglas-fir east of the Cascades are infected with dwarf mistletoe (Bolsinger 1978; Hessburg and Flanagan 1992a, 1992b). Infections are more widely distributed and more severely damaging than ever before. As the abundance of true firs increased, so did the abundance of dwarf mistletoes in true firs, where 21 percent of true fir stands are infected (Bolsinger 1978). Mortality and growth loss are most severe in central Oregon (fig. 23), where dwarf mistletoe is associated with canker fungi that weaken trees, predisposing them to further attack by fir engravers (Filip 1984).

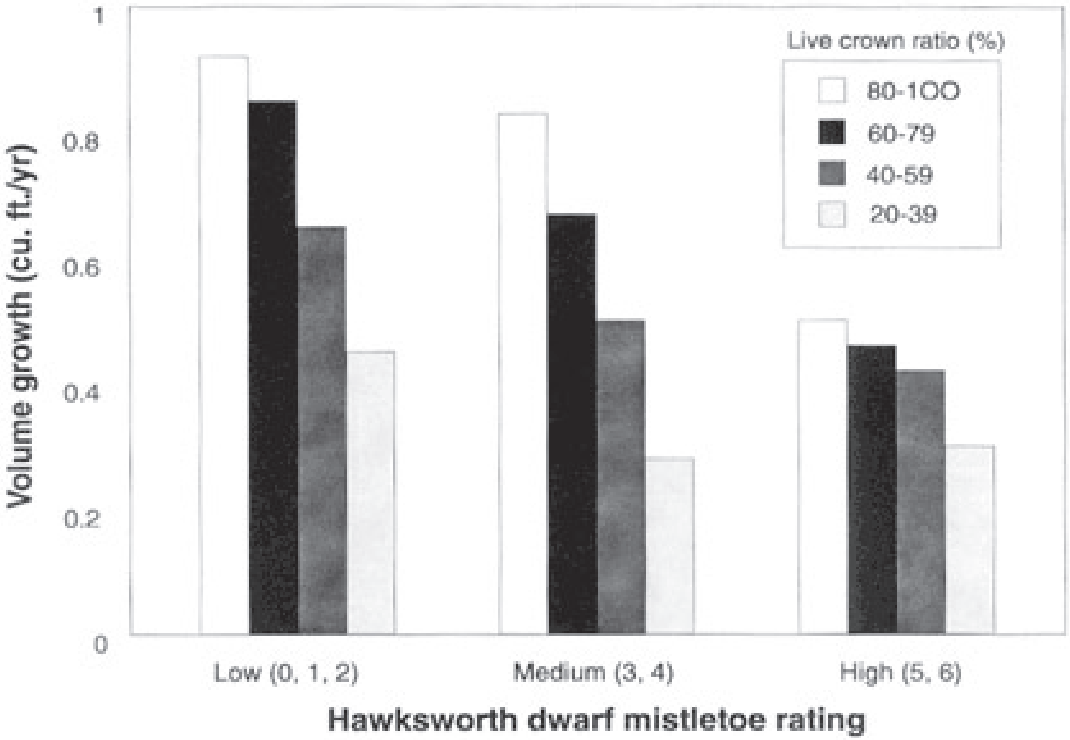

Figure 23. Periodic annual merchantable volume increment (last 25 years) by live crown ratio of grand fir infected by *Arceuthobium abietinum* f. sp. *concoloris* in central Oregon (Filip 1984).

Indian paint fungus—Stem decay of grand fir, especially decay caused by the Indian paint fungus, and butt rot caused by *H. annosum* (Aho and others 1987) are widely distributed throughout mixed conifer landscapes where true firs were not characteristically dominant or abundant. Stem-decay pathogens are essentially pioneering new habitats only recently colonized by their hosts. *Heterobasidion annosum* is competing with *Echinodontium tinctorium* (fig. 24) as the dominant decay agent of grand fir (Filip and others 1992b), perhaps because of increased harvesting of mature and overmature true fir. The Indian paint fungus commonly sporulates on the boles of mature and overmature trees, but *H. annosum* fungus sporulates in the hollows of large stumps.

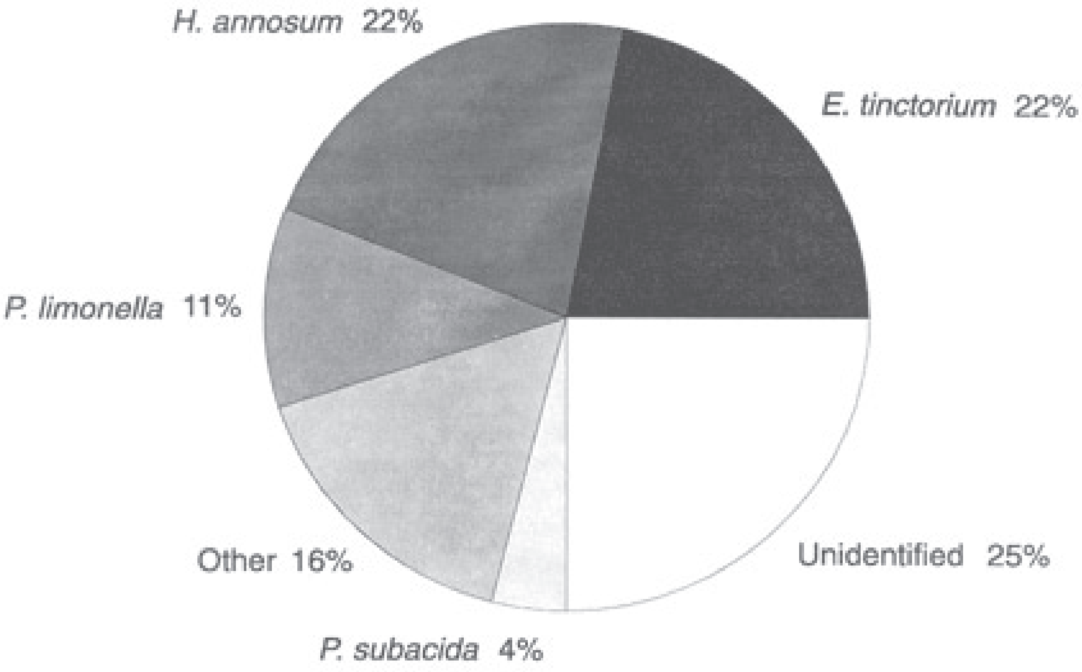

Figure 24. Percentage of total decay volume caused by fungi identified as Hymenomycetes in advanced grand/white fir regeneration in Oregon and Washington (Aho and others 1987).

PONDEROSA PINE SERIES

Ponderosa pine climax forests are distributed throughout eastern Oregon and Washington. They occupy a narrow band running the length of the Cascade Range on the lower slope; spread eastward into the central Oregon pumice plateau; ring large areas of the Blue, Ochoco, and Wallowa Mountains in eastern Oregon and southeastern Washington; and cover extensive areas of the Okanogan Highlands in northeastern Washington (Franklin and Dyrness 1973). The ponderosa pine series occupies the lowest elevations and the hottest, driest environments where ponderosa pine grows in the eastern Oregon and Washington. Above, the ponderosa pine series intergrades with the Douglas-fir, grand fir, and white fir series, depending on the locale. Below, it merges with the sagebrush desert, desert grasslands, and western juniper or Oregon white oak woodlands. The poorest sites for ponderosa pine are at the lower end of this series where ponderosa pine is in tension with other desert species.

Historical Forests

Western pine beetle—This series is well known in historical journals and photographs for its wideopen, multi-cohort ponderosa pine stands (fig. 25). Fire scars on large, old pines reveal that low-intensity ground fires commonly burned at intervals of 15 years or less (Bork 1984, Martin and Dell 1978). In this series, young ponderosa pine or fire-sensitive associates like western juniper or lodgepole pine, invaded recently burned stands, but they seldom survived (Munger 1917). Because of the dominance of large, old ponderosa pine and poor growing conditions, the western pine beetle was probably a greater threat in this series than in either the grand fir or Douglas-fir series. Miller and Keen (1960) noted extensive tree killing by this beetle throughout the ponderosa pine climax forest, especially during the great drought of the 1920s and 1930s.

Mortality caused by the western pine beetle was probably more or less continuous, even in years of adequate soil moisture. In stands dominated by old trees, a few trees each year were always too weak to produce adequate oleoresin exudation pressure to pitch out beetles. In addition, lightning-struck pines were fairly common, inviting attacks by the western pine beetle (Hepting 1971, Martin and Mitchell 1980, Miller and Keen 1960, Mitchell and Martin 1980). In the long run, this mortality was probably important for continued healthy ecosystems for the snag and temporary coarse wood habitat provided (Mitchell and Sartwell 1974).

Figure 25. Low dintensity underburning in a modern-day dry, climax ponderosa pine forest. Historical underburning killed thin-barked, fire-tolerant and intolerant trees. Thick-barked ponderosa pine were killed by means of individual tree and group torching, especially when severely mistletoe infested.

Bark beetle outbreaks probably occurred frequently in the tension zone where forest and desert influences intergraded, and were likely events that correlated with climate flux. In this moisture-limited soil environment, trees were small-diametered and short when young, and the struggle to survive from year to year with only marginal rainfall, invited attacks on the least vigorous by the mountain pine beetle and the pine engraver beetle. These two beetles were also important in areas missed by underburning, where residual tree densities were above long-term carrying capacities.

Pandora moth—Ponderosa pine has many associated defoliating insects, but few were historically significant. The best known defoliator of ponderosa pine is the Pandora moth, an insect with a long history of attacking ponderosa pine throughout the high pumice plateau of Oregon and Yakima River basin of Washington (Furniss and Carolin 1977). It is best known as the largest insect attacking western conifers: caterpillars can be 2 inches long, and moths have wingspans of 2.5 inches. Caterpillars feed exclusively on old needles and have an unusual 2-year life cycle, with defoliation only in alternate years (Schmid and Bennett 1988). Defoliation in the feeding years can be spectacular and some older trees are apparently killed when bark beetles attack defoliated trees (Patterson 1929). Mortality is rare in younger trees (Mitchell 1989) and seems to be confined to trees suffering from severe mistletoe infections and attacks by pine engraver beetles (Wagner and Mathiasen 1985). Defoliation occurs in patches of 5 to 40 acres, and when defoliation has run its course, caterpillar frass on the ground may be up to 1/2 inch deep. This nutrient boost to the soil must be important to soil microbes and nutrient cycling (Crossley 1977).

Other defoliators—Numerous other insects have been recorded as infesting ponderosa pine and even killing a few trees. Examples are the pine butterfly, several sawflies (Hymenoptera/Diprionidae), needle and tip miners (Lepidoptera/Tortricidae), and another budworm, the sugar pine tortrix. Ponderosa pine associations with these insects were not historically important in presettlement forests, nor are they significant problems today (Furniss and Carolin 1977).

Annosum root disease, Armillaria root disease—Before the era of resource management, P-group annosum root disease distribution was scattered. Under the influence of regular underburning, stocking was normally low relative to current conditions, and natural intertree spread was restricted by low tree density. The driest sites of the pine series were most severely damaged. Western juniper and ponderosa pine were both hosts to this variant of annosum root disease. Armillaria root disease was an opportunist of fire-scarred, overmature, stressed, damaged, or weakened ponderosa pine (fig. 26).

Figure 26. Mortality of ponderosa pine caused by *Armillaria ostoyae* in central Oregon (Filip and others 1989).

Comandra rust, Elytroderma needle disease—Comandra rust and Elytroderma needle disease were locally significant in ponderosa pine on occasion but never threatening to entire pine landscapes. Comandra rust topkilled mature and overmature ponderosa pine over many years, providing nesting trees for raptors building stick nests. Topkilled trees typically developed a resin-soaked, case-hardened dead top, ensuring a durable habitat with a long residence time.

Western dwarf mistletoe—Western dwarf mistletoe was most damaging to ponderosa pine on dry sites such as these. Severely infected trees would torch during underburning events. Frequent underburning minimized the accumulation of fuels and the likelihood of stand-replacing events. As a result, dwarf mistletoe was seldom eliminated from pine stands by fire, but frequent underburning sanitized ponderosa pine stands by torching the most infected trees, eliminating infected understories and other ponderosa pine of insufficient bark thickness. Frequent low-intensity fires reduced tree densities, elevated crown bases and simplified canopy structure, slowing mistletoe spread. Simplified canopy structure and reduced stem density reduced the probability of mistletoe seed dispersal to susceptible understory hosts and lateral spread among host trees. On balance, many ponderosa pine stands had a modest amount of mistletoe, but mistletoe severity was continuously reduced under the influence of fire.

Current Forests

Western pine beetle—Intraspecific competition in ponderosa pines for light, water, and nutrients can continue for decades, but the contest has no winners (Barrett 1979). Without underburning fire or a silvicultural thinning to weed out excess trees, a stand of ponderosa pine can stagnate for decades without much detectable growth. Eventually stand vigor declines, and the effects of various stresses, including drought and root disease, accumulate, which invites bark beetle attacks on overstory and understory trees. Site potential is more easily exceeded in the ponderosa pine series than elsewhere. Ponderosa pine sites are poor for tree growth, and even moderate increases in stocking invite beetle attack.

Any large increase in understory pine abundance stresses that cohort of pines, and the overstory trees as well. The western pine beetle is currently responding to these very conditions and to the recent drought, and beetle-killing of the larger trees has increased markedly in the last few years. As elsewhere, the simultaneous increase in P-group annosum root disease distribution is compounding the attractiveness of various stands to beetle attack.

Mountain pine beetle, the pine engraver—One serious problem that is emerging in many dry, central Oregon ponderosa pine stands stems from logging at these lower elevations between 1910 and 1940. Natural regeneration almost always exceeded the carrying capacity of these sites. Trees on naturally regenerated, cutover sites are now large enough for attack by the mountain pine beetle and the pine engraver. The first indications of future problems are visible on some of the poorest sites. Intertree competition is severe and mountain pine beetles-and sometimes, western pine beetles-are beginning to take advantage of the reduced vigor in these trees (Barrett 1979, Larson and others 1983, Sartwell and Stevens 1975). In extreme situations, particularly in years of below-normal spring rainfall, the pine engraver beetle causes mortality in young, overstocked stands (Dolph 1971).

Lacking regular low-intensity fires, lodgepole pine is invading many dry, ponderosa pine climax stands. This invasion presents two problems: first, without fire to remove lodgepole pine, the invading species tends to dominate stands within a few decades (Munger 1914); second, the presence of lodgepole pine invites attack by the mountain pine beetle, increasing the likelihood that ponderosa pine will be killed along with lodgepole pine (Mitchell 1988). In some locations, harvest of the overstory ponderosa pine is aggravating the problem, leaving no natural seed source for regeneration of ponderosa pine.

Annosum root disease, Armillaria root disease—Another serious result of current management practices has been the visible increase in the distribution and severity of the P-group annosum root disease (Goheen 1983, Goheen 1993, Hopkins and others 1988). Marginally commercial ponderosa pine sites have been selectively logged, leaving abundant stumps that have been infected by airborne spores. Two or more decades later, these stumps function as new disease centers. The increase in inoculum is compounded by high tree densities, which increase the probability of successful intertree spread of disease. Under managed conditions, pine sites with productivity ratings less than about 30 ft^3 - $acre^{-1}$ - yr^1 have the highest incidence of this root disease. Disease severity on some sites is now great enough that mortality rates reduce site productivity below the level of 20 ft^3 - $acre^{-1}$ - yr^1 required to be classified as land suitable for timber harvest.

Armillaria root disease has increased in pine-climax stands as a result of overstocking. Filip and others (1989) have shown that thinning such stands can improve tree vigor and reduce mortality (fig. 27).

Western dwarf mistletoe—Western dwarf mistletoe currently infests about 26 percent of ponderosa pine east of the Cascades. We suspect this recent measure of incidence (Bolsinger 1978) is elevated from historical times. Fire had beneficial effects on canopy structure and tree density that discouraged survival and dispersal of this mistletoe (Koonce and Roth 1980).

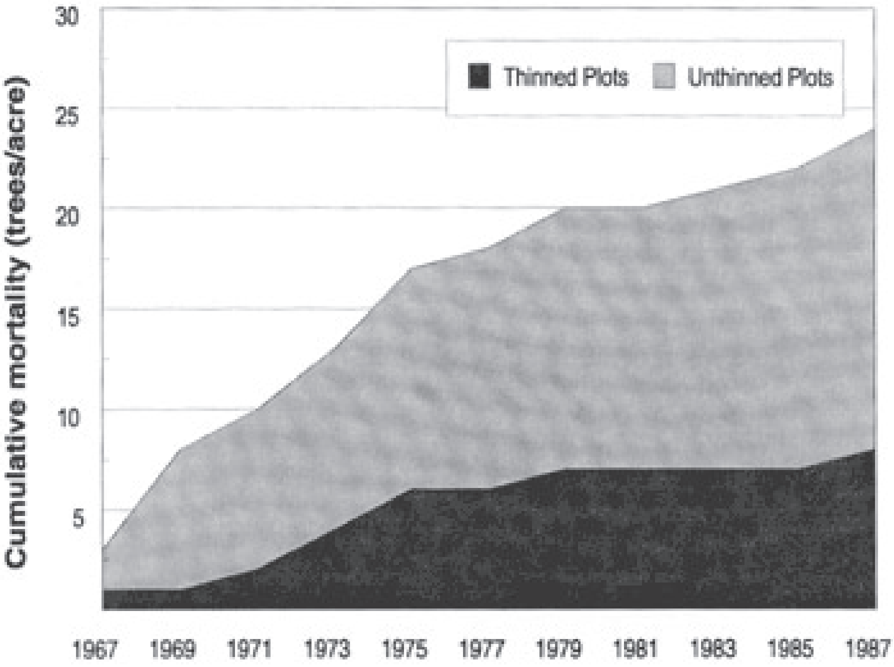

Figure 27. Cumulative mortality of crop trees caused by *Armillaria ostoyae* in precommercially thinned and unthinned plots of ponderosa pine in central Oregon (Filip and others 1989).

LODGEPOLE PINE SERIES

Where it occurs as a climax dominant, lodgepole pine is an edaphic climax species rather than a climatic climax species. Most stands of climax lodgepole pine are found on the high pumice plateau of central Oregon, where in some locales spring temperature regimes at the time of seedling establishment discourage survival of all tree species except lodgepole pine. There, mile after mile of pure lodgepole pine stands (fig. 28) are found on cold air flats, where growing-season temperatures can be 4.5 °C colder than adjacent ponderosa pine-covered slopes (Cochran 1984, Cochran and Berntsen 1973).

Mountain pine beetle—As in the other series, the primary disturbances regulating the ecological character of lodgepole pine landscapes were historical wildfires and mountain pine beetle outbreaks. Stands with 30 to 80, 9-inch-d.b.h. or larger trees were susceptible to beetle attack. Mountain pine beetle outbreaks often killed as many as 250 trees per acre, creating an enormous quantity of flammable fuel (Mitchell 1988). Subsequent fires destroyed remaining stands, allowing regeneration of lodgepole pine. What is unique in central Oregon is that the environment for tree growth is so constraining that each new stand will always be lodgepole pine; no other species can compete successfully. Without fire or aggressive stocking control and regeneration programs, overmature and overstocked lodgepole pine stands will always provide appropriate conditions to initiate and carry a mountain pine beetle outbreak.

Figure 28. Pandemic mountain pine beetle (*Dendroctonus ponderosae*) mortality in lodgepole and ponderosa pine forests of the central Oregon pumice zone.

One variation on the fire and bark beetle cycle is found on the very poorest lodgepole pine sites in central Oregon. Geiszler and others (1984) found a site so poor that it had virtually no understory vegetation. Meager fuels supported only meandering, pencil-like burns that smoldered along downed lodgepole pines killed years earlier by the mountain pine beetle. Pencil burns rarely killed trees, but they did scar tree bases. Scars were entrance points for decay fungi which, years later, predisposed affected trees to beetle attack (Gara and others 1984). Presumably, poor lodgepole sites like these are a kind of refuge for the mountain pine beetle, a place of continuous low activity.

The pattern of mountain pine beetle outbreaks described for the grand fir and Douglas-fir series is essentially the same as that found in the lodgepole pine climax forest, but because lodgepole-dominated landscapes are much more extensive in central Oregon, lack of fire has created a vastly larger area of mature and overmature stands. When an outbreak is initiated in central Oregon, it will produce more beetles, kill more trees, and operate over larger landscapes, generating heavy fuel accumulations over vast, continuous areas. Wildfires in central Oregon's beetle-killed lodgepole pine forests have the potential to be among the most severe fires ever.

Pandora moth, lodgepole needle miner—The pandora moth has been observed defoliating lodgepole pine, usually in association with infestations on ponderosa pine. Another insect of some significance in the lodgepole pine series is the lodgepole needle miner. Outbreaks are uncommon, but they can be very destructive. Mason and Tigner (1972) and Tigner and Mason (1973) showed that vigorous stands on productive sites were most resistant to population buildup. Young trees less than 10 years old also resist infestations. Prolonged outbreaks have occurred in the central and southern Sierra Nevada of California, where the cumulative effects of prolonged needle mining were complete defoliation and widespread tree mortality. In central Oregon, populations are higher on some sites than others, but damage is usually light or moderate.

Western pine shoot borer—Still another insect enemy of lodgepole pine is the western pine shoot borer. A common terminal miner in ponderosa pine in central Oregon and elsewhere, it is occasionally responsible for considerable height-growth loss and stem deformities throughout the range of lodgepole pine (Mitchell and Sower 1991). This insect, like many others, has probably been a regular enemy of lodgepole pine, and the frequency and pattern of damage has probably changed little over the years.

Lodgepole pine dwarf mistletoe—Dwarf mistletoe was often severe in premanagement-era lodgepole pine landscapes. The amount of mistletoe was highly correlated with boom-and-bust fire cycles characteristic of the series. Over long periods without fire (100 to 200 years), mistletoe severity would often be high (fig. 29), depending on the pattern of the last fire event. After fire, mistletoe reinvasion was rapid when islands of live, mistletoe-infected lodgepole pine were scattered throughout the burned area. Slow reinvasion was the pattern when fires were large and intense, resulting in near total stand destruction; then new infections came from diseased trees on distant perimeters, or from chance introductions by birds and small mammals.

Figure 29. Mistletoe in lodgepole pine caused by the lodgepole pine dwarf mistletoe, *Arceuthobium americanum*. With effective fire suppression, lodgepole pine forests developed layered canopies after mountain pine beetle (*Dendroctonus ponderosae*) outbreaks subsided. This facilitated rapid spread of dwarf mistletoe.

On balance, dwarf mistletoe in lodgepole pine is more widely distributed than historically. Lacking nearly a century of cleansing fires, most mistletoe-infected stands of a century ago are still infected. More than 100,000 acres of lodgepole pine in central Oregon, and uncounted thousands of acres elsewhere, have been destroyed by the mountain pine beetle in the last 20 years. Beetle outbreaks killed only the largest trees, encouraging release of residual trees and development of uneven-aged stands. These two features—carry-over of mistletoe infections from a prior generation of trees and development of multiple canopy layers—are optimal for the spread of dwarf mistletoe.

Atropellis canker, western gall rust, stalactiform rust—Atropellis canker, western gall rust, and stalactiform rust are widespread and sometimes locally significant. Atropellis canker and gall rust severity are associated with overstocked lodgepole pine in sites with cool air ponding.

SUMMARY AND CONCLUSIONS

Human activities that contributed to declining health of forests east of the Cascade crest in Oregon and Washington began in the West before the turn of this century with efforts to control wildfires. Early logging of premium quality seral species began before the start of this century, and continued to World War II in some locales. Extensive, economically motivated, selective harvesting of high-value ponderosa pine, western larch, western white pine, sugar pine, and Douglas-fir began after World War II and has continued to some extent to the present day. Fire suppression and control policies favored increasing stand densities and the regeneration of shade-tolerant and fire-intolerant species.

Effective fire exclusion and selective harvesting in all of its forms accelerated forest succession in all major, forested, climax series. The short-term benefits of an effective fire-control policy and selective harvesting apparently justified those management decisions. Clearly, historical management activities have produced unstable ecosystems, excessive disturbance by pathogens and insects, and vegetation conditions that cannot be sustained in the long term. The following is a brief summary of the most important outcomes (see also Lehmkuhl and others 1993):

- Density has significantly increased and vigor has decreased in many lodgepole pine, ponderosa pine, Douglas-fir, and grand fir (white fir) climax forests.
- Extensive areas of the Douglas-fir, grand fir (white fir), and subalpine fir series are dominated by shade-tolerant species.
- Landscapes (rather than patches) are susceptible to defoliator and bark beetle outbreaks in the lodgepola pine, ponderosa pine, Douglas-fir, and grand (white) fir series.
- Landscapes (rather than patches) are susceptible to high-intensity, stand-replacement fires in the lodgepole pine, ponderosa pine, Douglas-fir, and grand (white) fir series.
- The threat of catastrophic fire to subalpine fir, Pacific silver fir, western hemlock, western redcedar, and mountain hemlock series is increased through the increase in fire hazard in nearby lodgepole pine, ponderosa pine, Douglas-fir, and grand (white) fir climax forests.
- The threat of defoliation to subalpine fir, Pacific silver fir, western hemlock, western redcedar, and mountain hemlock series is increased through enhanced continuity of susceptible host types.
- The duration, extent, and severity of defoliator and bark beetle outbreaks have increased with the increased quality, uniformity, and continuity of host types.
- Conditions for nearly optimal spread of root diseases and dwarf mistletoes exist in many parts of the lodgepole pine, ponderosa pine, Douglas-fir, and grand (white) fir climax series.

- Insect and disease growth and mortality effects are increasing fuel loads at an alarming rate.
- Wildlife habitat conditions and populations have developed that are unprecedented, according to historical fire disturbance patterns, and are nonsustainable in the long-term throughout significant areas of the east side.
- The pattern of landscape diversity is anomalous for many forests of the lodgepole pine, ponderosa ipne, Douglas-fir, and grand (white) fir climax series. Landscape diversity of subalpine fir, Pacific silver fir, western hemlock, western redcedar, and mountain hemlock climax forests has been affected but to a lesser degree.

Specific solutions to these problems are complicated by the variety of sites where restoration or rehabilitation is needed, but a few broad goals are obvious:

- Stocking should be reduced on forested acres where long-term carrying capacity is exceeded (fig. 30). This change can be accomplished silviculturally and with the judicious use of fire and other management tools. Many eastside lodgepole pine and ponderosa pine forests are moisture-limited, and site resources are particularly limiting. As long as excess trees and intertree competition depress vigor, effects of bark beetles, root diseases, and dwarf mistletoes will be exaggerated.
- Throughout the Douglas-fir and grand (white) fir series, the shift toward late-successional stands of shade-tolerant species should be reversed, with the goal of restoring a seral-dominated forest matrix. Historical stands and landscapes were more tolerant of fire than current landscapes. Underburning fire, once common and influential to low- and middle-elevation forests, is now unlikely without significant management intervention.
- Management activities should promote restoration of landscape patterns that emulate historical variability. The landscape pattern of species composition, vegetation density, canopy structure and cover, stand (patch) size and shape, and patch adjacency have been significantly altered in this first century of management (Lehmkuhl and others 1993), but the former pattern is recognizable with careful study. The historical picture of the east side is one of regular fire disturbance; fire-adapted species and fire-adapted landscapes were favored. Alternative trajectories for eastside landscapes are certainly possible, but as yet nothing is known about their characteristics or efficacy. With that significant knowledge gap, managing toward vegetation conditions that are known to have been sustained seems appropriate, rather than managing toward conditions that are potentially unsustainable.

Figure 30. A 70-year-old stand of western larch that was commercially thinned in 1970 and 1980 in northeastern Oregon.

Managing for landscapes exactly as they were in presettlement times is probably unwise. The repeated light underburns characteristic of presettlement times, for example, probably reduced the growth potential of ponderosa pine (Cochran and Hopkins 1991, Landsberg and others 1984). Intentional fire-setting by Indians also increased underburning frequently resulting in more fire-tolerant vegetation than might have otherwise occurred (Robbins and Wolf 1993). Until the view of what the future forest should look like is clearer, forest landscapes dominated by seral stands ought to be what managers aim for. Clearly, seral ecosystems are more amenable to management than those approaching climax. Management applications should test alternative landscape constructions on public lands. We offer some specific suggestions for managing vegetation where highly influential insects or pathogens may be threatening:

Pine bark beetles—Pine bark beetles normally attack low-vigor trees, especially those weakened by diseases, drought, or lightning strikes; this role is not their current one. Many pine stands now have more trees per acre than site resources can support. Competition weakens the competitors, and bark beetles have evolved an attack strategy that takes advantage of weakness. Overstocked stands should be thinned (fig. 31), and the ingrowth of shade-tolerant conifers should be discouraged throughout the rotation (or life history) of a patch, unless that understory is vital to a particular habitat and can be sustained in the long term given historical fire regimes. Beetles appear to be discouraged by the physical environment of thinned stands, and improved vigor in residual trees is a deterrent against attacks (Preisler and Mitchell, in press). Lodgepole pine will not tolerate light ground fires, so machine or hand thinning seems to be the solution. Ponderosa pine can be thinned either by prescribed burning or by hand or machine thinning.

Figure 31. A 125-year-old stand of lodgepole pine that was precommercially thinned in 1980 in central Oregon.

Douglas-fir beetle and fir engraver—The best solution for both insects is to reduce the abundance of host trees or, more directly, to manage for seral landscapes. Where late-successional or climax patches are desired as landscape components, and these desires are consistent with historical fire regimes, insect and disease effects will often be considered as benefits.

Douglas-fir tussock moth and western spruce budworm—These defoliators will go where their hosts are plentiful. Landscape patchworks that are seral-dominated but include late-successional and climax habitats will be defoliated. That defoliation will rarely threaten sustainability, however, which is as it should be for low populations. Landscapes dominated by shade-tolerant species will also be defoliated, but this defoliation will threaten sustainability. Stability will ultimately be restored to these landscapes by conflagration. When managers consider landscapes for rehabilitation, particular emphasis should be placed on dry Douglas-fir and grand fir climax sites where defoliation is most severe. On more mesic landscapes, interim solutions may be required. Some grand fir and Douglas-fir forests are within two or three decades of harvest; for them, decisions might be to protect some areas with biological insecticides until they can be harvested and regenerated to seral species. Economic costs of insecticide use should be analyzed against specific resource protection benefits. Other options for managing landscapes susceptible to the western spruce budworm are to thin suscepts (Carlson and others 1985b), or thin and fertilize (Mason and others 1992, Wickman and others 1992). Budworm will attack such landscapes but damage to stands may be reduced (fig. 32).

Figure 32. A precommercially thinned stand of grand fir defoliated by western spruce budworm in northeastern Oregon.

Root Diseases—The pathogens that cause laminated root rot, Armillaria root disease, and S-group annosum are widely distributed throughout the east side, but of concern to management is disease that has developed in areas recently colonized in this century by their hosts. Management activities that restore the dominance of seral species to the Douglas-fir and grand fir climax forests, where that is ecologically appropriate, will effectively manage effects of root diseases. Root diseases will not disappear, but growth and mortality effects, and associated bark beetle effects, will be diminished.

To manage root diseases effectively in a particular area, the geographic distribution of each root pathogen must be determined in its various inoculum structures (stumps, snags, standing dead trees, and live trees with and without symptoms). Root disease inventories are needed, and plant associations or plant association groupings should be characterized for root disease hazard. Host damage characteristics (that is, tree species affected, size and age classes affected) must also be determined in each unique locale because the ecology of root diseases varies by locale. The most ecologically sound management will usually be to favor tree species that are less susceptible (fig. 33) to infection and mortality (Hadfield and others 1986). This strategy can be accomplished silviculturally and with the use of prescribed fire. Stocking control in pure species stands may also decrease damage from some root diseases.

kgawe 33. A mixed plantation of ponderosa pine, western white pine, and western larch. Note the Armillaria root disease mortality in the foreground Douglas-fir.

Stem decays—Thin-barked, nonresinous tree species are more decay-prone than are resinous species, and can be discriminated against during silvicultural operations in mixed-conifer stands. In commercial applications, damage caused by stem decay fungi can be reduced through shortened rotations and with wound prevention (fig. 34). These preventive steps are critical, especially if advance regeneration is already infected and some decay is present. Nondestructive sampling methods for determining the extent of infection and decay by the Indian paint fungus have been developed for white and grand fir (Filip and others 1983) and may be applicable to other coniferous hosts. Wound-prevention guidelines are available and can be applied, both in harvest planning and during woods operations, to prevent wounding and associated stem decay.

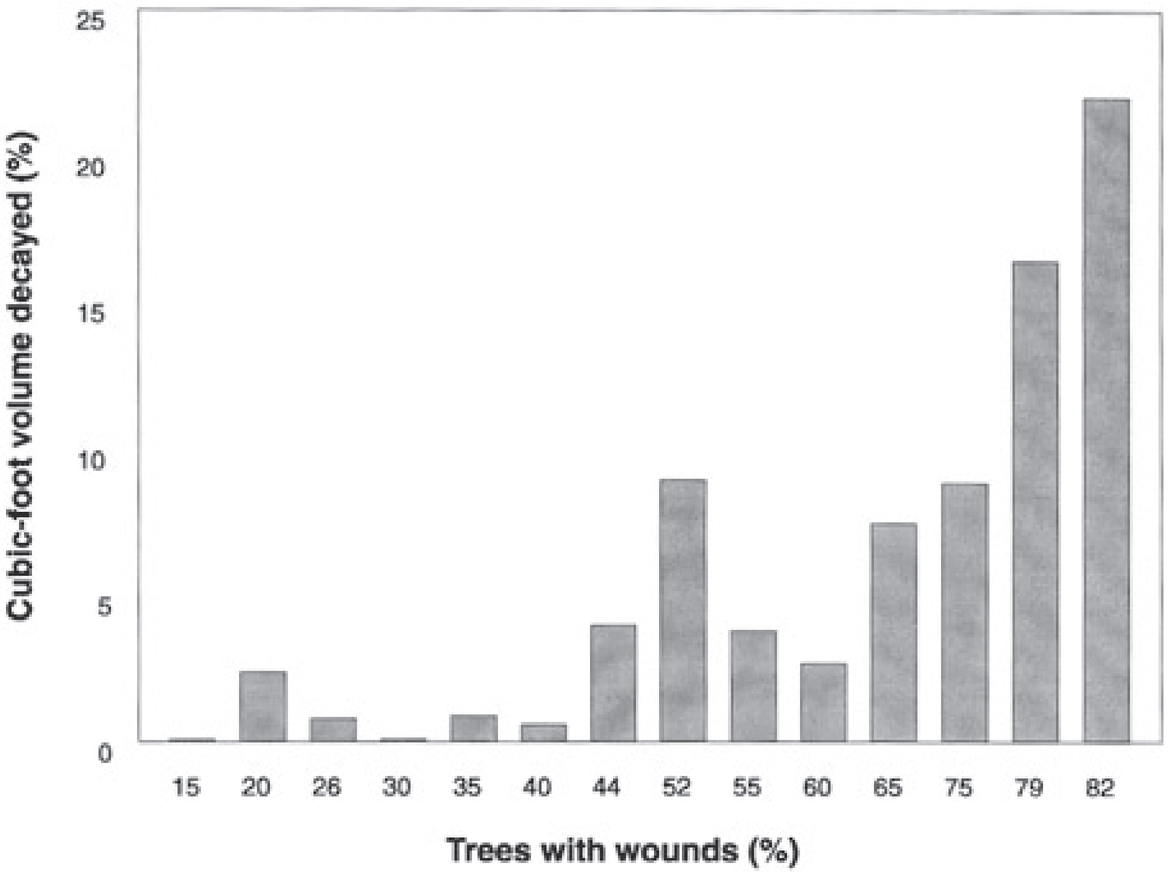

Figure 34. Percentage of cubic-foot volume decayed by percentage of trees with stem wounds in 14 stands of advanced white/grand fir regeneration in Oregon and Washington (Filip and others 1983).

Dwarf mistletoes—Most dwarf mistletoes are highly host specific. Rapid spread of mistletoes is favored by pure stands of host trees and multilayered canopies. Even-aged or single-storied stands can be managed with low and moderate mistletoe infestation. Mistletoe infection can be completely avoided by favoring nonsusceptible species in mixed-conifer stands. Stocking control and removal of the most severely infected trees has also been shown to reduce damage (fig. 35) in several coniferous species (Barrett and Roth 1985, Filip and others 1989, Knutson and Tinnin 1986). That reduction in severity is consistent with sanitizing effects of historical low- and moderate-intensity fires.

Healthy forests must be designed. Managing forested landscapes is a giant experiment with a moving front. Management must sight on the far horizon, and make adjustments as understanding is gained. Careful monitoring of each management experiment is needed to ensure that managers are accountable for management actions, and to learn what works and what does not work. Feedback must result from monitoring, so that management experiments are refined, viable management alternatives are discovered and recorded, and poor methods are discarded. To be successful with this approach, selected management methods should all have the characteristic of conserving options rather than losing them. Giving up options is like giving up capital in the financial world. Management decisions are often needed before all of the relevant information or guidance is available. A resource management model that is adaptive and based on conserving options allows both speculative actions and future adjustments to those actions where they are wrong ornot favored.

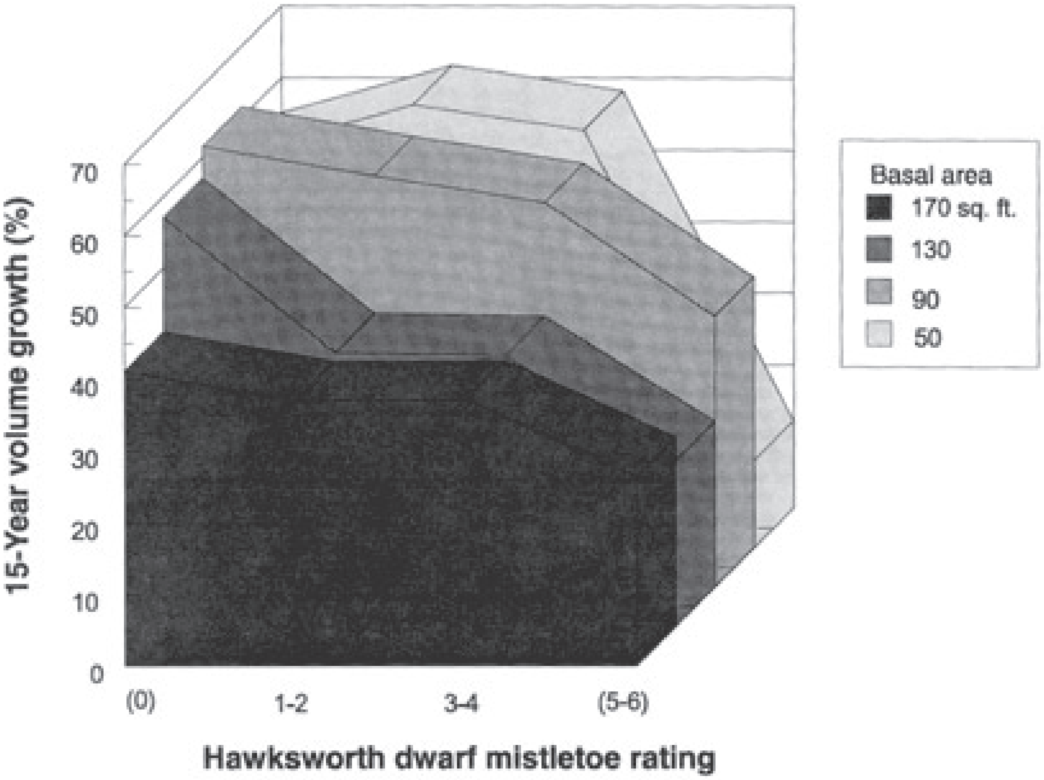

Figure 35. 15-year volume growth of western larch by residual density after thinning (basal area) and dwarf mistletoe severity rating in northeastern Oregon (Filip and others 1989).

FUTURE RESEARCH NEEDS

Future research on forest insects and pathogens in eastern Oregon and Washington should address three primary topics: insect and pathogen population dynamics in unmanaged and managed forests; ecological roles and effects of insects and pathogens; and, effects of natural disturbances and forest management practices on insects and pathogens, and their natural enemies.

Insect and pathogen population dynamics in unmanaged and managed forests—Forest insects and pathogens are important disturbance agents affecting ecosystem health in both favorable and unfavorable ways. The ecology and roles of their natural enemies, and other regulatory processes, are equally important. Critical gaps exist in the knowledge of insect and pathogen population dynamics, regulatory processes and organisms, interactions, roles, and effects. Important research questions are:

- What are the natural population dynamics of insects and pathogens in the major plant associations of eastern Oregon and Washington along various successional trajectories?
- What are the important natural enemies, what are their habitat requirements, and what are their associations and responses to changing environments?
- Can hazard-rating decision support systems be developed for plant associations and successional communities, to predict insect and pathogen responses to natural and management disturbances.

Ecological roles and effects of insects and pathogens—Dwarf mistletoe infection results in substantial economic loss in nearly all coniferous species in eastern Oregon and Washington. On the other hand, mistletoe-infected branches provide nesting and roosting habitat for at least three kinds of owls, and hiding cover for other birds and mammals. Stem decays cause severe economic losses, but decayed trees provide ideal habitats for numerous birds and mammals. Root diseases cause widespread mortality in several coniferous species, and predispose trees to further bark beetle attack. Root diseases and bark beetles ar also a major cause of canopy gaps and are important to forest succession, wildlife habitat, and nutrient cycling. The same comparisons are appropriate for major conifer defoliators. Important research questions are:

- What are the particular roles of root pathogens, bark beetles, and defoliators in forest succession, wildlife habitat development, and nutrient cycling in the major plant associations of eastern Oregon and Washington?
- What are the particular roles of stem decay fungi and dwarf mistletoes in creating and maintaining habitats for birds and mammals?
- Can replacement wildlife habitats be developed using these organisms in areas that are now depauperate as a result of past management practices.

Effects of natural disturbances and forest management practices on insects and pathogens a their natural enemies—Fire, drought, and other severe climatic disturbances have shaped forests of eastern Oregon and Washington for millennia. Knowledge about how these disturbances affect vegetation, inset and pathogen populations and their natural enemies is extremely limited. Important research questions are:

- What effects do fire, drought, and severe weather disturbances have on insect and pathogen population dynamics in the major plant associations of eastern Oregon and Washington along various successional trajectories?
- How do these disturbances affect natural enemies of insects and pathogens?
- In the major plant associations, what are the effects of various vegetation management practices on insect and pathogen populations and their natural enemies?
- Can conventional or new ecosystem management techniques minimize adverse affects, and maintain or enhance beneficial roles of pathogens and insects and their natural enemies (fig. 36)? Are other management techniques, or variants of currents techniques more suitable?

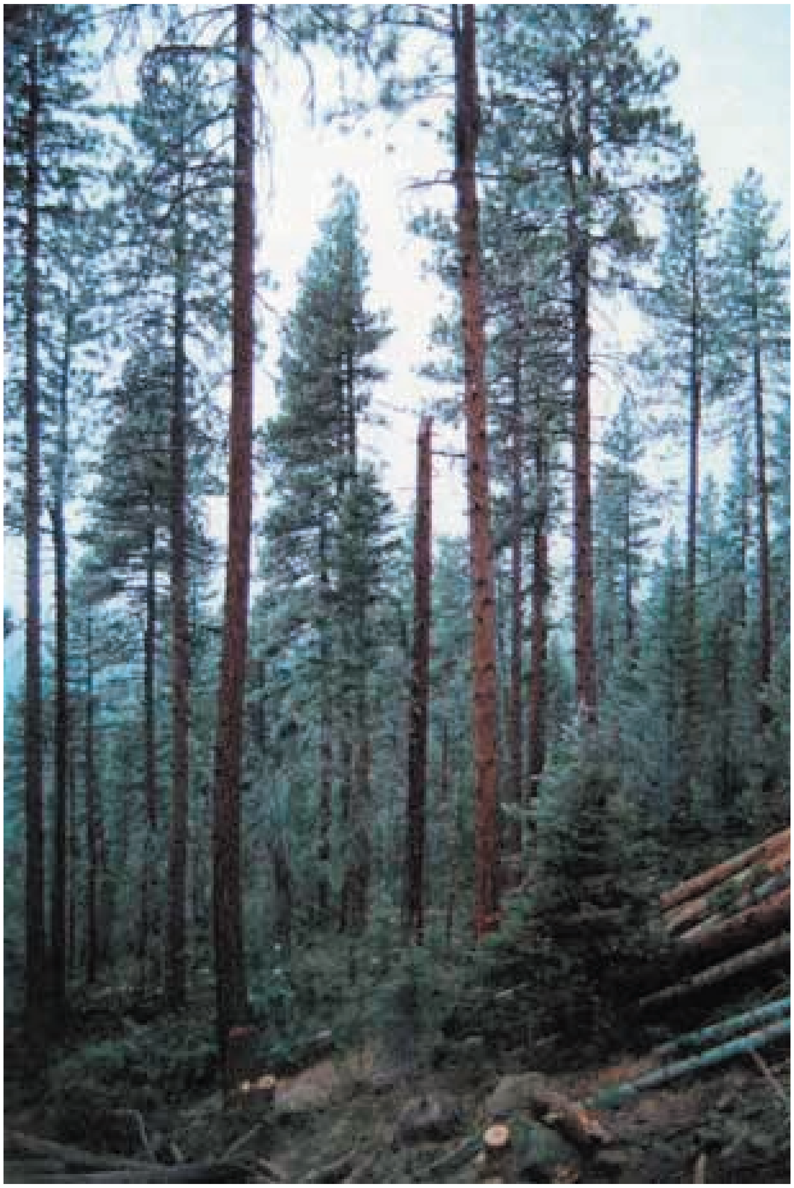

Figure 36 A ponderosa pine stand in northeastern Oregon that was selectively marked and harvested to maintain old-forest attributes through emulation of natural processes of mortality. [Photo courtesy of Steven Fitzgerald].

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Appendix A-List of common and scientific names - TREES

Common Name	**Scientific Name**
Balsam fir	*Abies balsamea* (L.) Mill.
Douglas-fir	*Pseudotsuga menziesii* (Mirb.) Franco
Engelmann spruce	*Picea engelmannii* Parry ex Engelm.
Grand fir	*Abies grandis* (Dougl. ex D. Don) Lindl.
Lodgepole pine	*Pinus contorta* var. *latifolia* Dougl. ex Loud.
Mountain hemlock	*Tsuga mertensiana* (Bong.) Carr.
Noble fir	*Abies procera* Rehd.
Oregon white oak	*Quercus garryana* Dougl. ex Hook.
Pacific silver fir	*Abies amabilis* Dougl. ex Forbes
Ponderosa pine	*Pinus ponderosa* Dougl. ex Laws.
Shasta red fir	*Abies magnifica* A. Murr.
Subalpine fir	*Abies lasiocarpa* (Hook.) Nutt.
Western hemlock	*Tsuga heterophylla* (Raf.) Sarg.
Western juniper	*Juniperus occidentalis* Hook.
Western larch	*Larix occidentalis* Nutt.
Western redcedar	*Thuja plicata* Donn ex D. Don
Western white pine	*Pinus monticola* Dougl. ex D. Don
White fir	*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.

Appendix A (continued)-List of common and scientific names - INSECTS

Common Name	**Scientific Name**
Balsam woolly adelgid	*Adelges piceae* (Ratzeburg)
Douglas-fir beetle	*Dendroctonus pseudotsugae* Hopkins
Douglas-fir engraver beetle	*Scolytus unispinosus* LeConte
Douglas-fir tussock moth	*Orgyia pseudotsugata* (McDunnough)
Fir engraver	*Scolytus ventralis* LeConte
Fir root beetle	*Pseudohylesinus granulatus* (LeConte)
Larch casebearer	*Coleophora laricella* (Hubner)
Lodgepole needle miner	*Coleotechnites milleri* (Busck)
Mountain pine beetle	*Dendroctonus ponderosae* Hopkins
Pandora moth	*Coloradia Pandora* Blake
Pine butterfly	*Neophasia menapia* (Felder and Felder)
Silver fir beetle	*Pseudohylesinus sericeus* (Mannerheim)
Spruce beetle	*Dendroctonus rufipennis* (Kirby)
Sugar pine tortrix	*Choristoneura lambertiana* (Busck)
Western balsam bark beetle	*Dryocoetes confusus* Swaine
Western pine beetle	*Dendroctonus brevicomis* LeConte
Western pine shoot borer	*Eucosma sonoma* Kearfott
Western spruce budworm	*Choristoneura occidentalis* Freeman

Appendix A (continued)-List of common and scientific names - DISEASES

Common Name	**Scientific Name or Causal Agent**
Annosum root disease	*Heterobasidion annosum* (Fr.) Bref.
Armillaria root disease	*Armillaria ostoyae* (Romag.) Herink
Brown cubical butt rot	*Phaeolus schweinitzii* (Fr.) Pat.
Comandra rust	*Cronartium comandrae* Pk.
Douglas-fir dwarf mistletoe	*Arceuthobium douglasii* Engelm.
Elytroderma needle disease	*Elytroderma deformans* (Weir) Darker
Indian paint fungus	*Echinodontium tinctorium* E. & E.
Laminated root rot	*Phellinus weirii* (Murr.) Gilb.
Lodgepole pine dwarf mistletoe	*Arceuthobium americanum* Nutt. ex Engelm.
Stalactiform rust	*Cronartium coleosporoides* Arth. f. *coleosporoides*
Tomentosus root disease	*Inonotus tomentosus* (Fr.) Teng.
True fir dwarf mistletoe	*Arceuthobium abietinum* Engelm. ex Munz f.sp. *concoloris* Hawksworth and Wiens
Western dwarf mistletoe	*Arceuthobium campylopodum* Engelm.
Western hemlock dwarf mistletoe	*Arceuthobium tsugense* (Rosendahl) G.N. Jones
Western larch dwarf mistletoe	*Arceuthobium laricis* (Piper) St. John
White pine blister rust	*Cronartium ribicola* Fisch.

GLOSSARY

Arthropods—Members of the largest phylum in the animal kingdom, including insects, arachnids (spiders, ticks, and mites), myriapods (centipedes, millipedes, and the like), and crustaceans (lobsters, shrimp, crabs, barnacles, and the like).

Brooms or witches-brooms—Abnormally dense clusters of shoots or branches on conifers caused by infection by dwarf mistletoes or rust fungi.

Butt rot—Internal wood decay caused by fungi in the base (butt) of a tree.

Canker—A disease symptom characterized by sharply-limited death of living tissues in the inner bark on branches or trunks of trees.

Climatic climax—A climax condition maintained by climatic factors such as temperature and precipitation regimes, and length of growing season.

Climax—The terminal, theoretically stable, self-perpetuating condition in a series of plant communities that culminates plant succession on any given site.

Climax species or series—The most shade-tolerant tree species predominating on a site at climax, especially in the absence of major disturbance. Sites are often defined in terms of the major forest series they belong to (example: grand fir climax series, which includes plant associations where grand fir is the climax dominant).

Coverts—Animal habitat focal points: locations in the forest where three or more different patch types converge.

Cytokinins—Any of a group of plant growth-regulating substances that regulate cell division.

Decay—The decomposition of wood and the corresponding changes in its physical and chemical properties; usually caused by fungi.

Defoliator—An insect that feeds on tree foliage.

Disease (plant)—Any harmful deviation within a plant that interferes with normal structure, function, or value; often caused by pathogenic fungi and bacteria.

Ecosystem—All of the organisms in any system of interest, and the environments that encompass their interactions.

Edaphic climax—A climax that is the result of unique soil conditions usually differing from those of the surrounding area.

Endemic—Pertaining to insect and pathogen populations that are limited to insignificance of influence by a variety of host, environment, and edaphic factors.

Epidemic or outbreak—Pertaining to pathogen or insect populations that expand to an extreme level, often disturbing processes and interactions within forested stands and landscapes to the point of causing economic or habitat losses.

Frass—Solid excrement from insect larvae such as defoliators; wood fragments made by wood-boring insects (often beetles), usually mixed with excrement.

Fungus, pl. fungi—Any of a vast number of microscopic seedless plants (cryptogams), not including bacteria, that are usually filamentous, lack chlorophyll and vascular tissues, and ordinarily reproduce by spores.

Gallery—A tunnel or pathway, usually in tree bark or wood, in which an insect lives, feeds, and reproduces.

Heartwood—The interior wood in stems of living trees that provides strength and rigidity to stems, has ceased conducting water and nutrients, contains no living cells, and is generally darker than wood to the exterior.

Heart rot—Wood decay that is apparently restricted to heartwood.

Infection—The establishment of a parasite (usually fungal or bacterial) with a host plant.

Infection center—A group of trees (locus) that are infected to various degrees by a particular forest pathogen, usually a root disease pathogen or dwarf mistletoe species.

Insectivores—Organisms that depend on insects as food.

Instars—With insects that undergo metamorphosis, instars indicate the juvenile developmental stages occurring between larval molts that lead to adulthood; they are often numbered, for example, the first instar is the stage between the egg and the first larval molt.

Larva, pl. larvae—A juvenile insect differing in form from the adult; examples are caterpillars, grubs, and maggots.

Mesic—Moderately moist.

Microbe—An microscopic organism such as a bacterium or yeast.

Mycelium, pl. mycelia—The vegetative thallus (body) of a fungus consisting of a mass of microscopic hairlike filaments (fungal hyphae).

Mychorrizal fungi—Specialized fungi that form an association with plant rootlets that is mutually beneficial to the host plant and its fungus. Mycorrhizae assist in host rootlet protection against other invading pathogens, and in water and nutrient uptake.

Oleoresin exudation pressure—The positive pressure associated with oleoresin or pitch within a tree; usually a measure of a tree's ability to resist bark beetle attack.

Parasite—An organism living in or on another living host organism. Parasites obtain their food from their hosts at the expense of the well-being of the host.

Pathogen—An organism such as a fungus, bacterium, or virus that has the capacity to incite disease in another organism (host).

Photosynthate—The carbohydrate products formed within plants through the process of photosynthesis.

P-group annosum—Isolates of the root pathogen, Heterobasidium annosum are divided into two host specialized groups. The S-group principally attacks Spruces, hemlocks, and true firs. The P-group principally attacks Pine species.

Plant association—The distinctive combination of trees, shrubs, grasses, and herbs occurring in the theoretical terminal or climax community of a series of communities.

Root disease center—An infection center in the forest that has infected, dead, and dying trees, where the causative agent is a pathogenic root-infecting fungus. Root diseases typically spread underground by fungal growth from diseased to healthy host roots.

Sanitation-salvage—A type of tree harvesting where individual trees are removed that have been, or are in imminent danger of being killed or damaged by forest pathogens or insects; the method is often used to minimize spread to healthy trees.

Sap rot—Condition of recently killed trees or those with partial stem damage; in which decay is exclusively in the sapwood.

Sapwood—The sapwood is the wood between the inner bark and the heartwood that is responsible for the translocation of water and nutrients to foliage when trees are alive.

Senescence—The plant growth phase that begins at full maturity and ends at death, characterized by declining physiological function.

Seral species—Plant species abundant in early, middle, and late (transitional) successional plant communities of any plant association. Often used to speak of the dominant conifer vegetation that follows major disturbance episodes.

Seral stage—Any of a predictable sequence of transitional plant communities that leads to the terminal or climax community.

Serotinous cones—Conifer cones whose scales are sealed with a droplet of pitch. Cones usually open and release their seeds only when exposed to intense heat.

S-group annosum—Isolates of the root pathogen, Heterobasidium annosum are divided into two host specialized groups. The S-group principally attacks Spruces, hemlocks, and true firs. The P-group principally attacks Pine species.

Spore—A microscopic reproductive propagule of fungi analogous to the seed of green plants.

Sporulate—To produce spores.

Thinning—The planned removal of trees during the development of a forest, used to regulate characteristics of tree growth through adjustments in tree spacing and density.

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This paper examines, by climax conifer series, historical and current roles of many important pathogens and insects of interior Northwest coniferous forests and their unique responses to changing successional conditions resulting from management. Future research on forest pathogens and insects should address three primary subject areas: insect and pathogen population dynamics in managed and unmanaged forests; ecological roles and effects of native and introduced pathogens and insects; and effects of natural disturbances and management practices on native insects, pathogens, and their natural enemies.

Keywords: Forest succession, forest health, insects and diseases, pathogens, landscape patterns, disturbance processes, ecosystem processes, fire regimes.

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