

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.

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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.

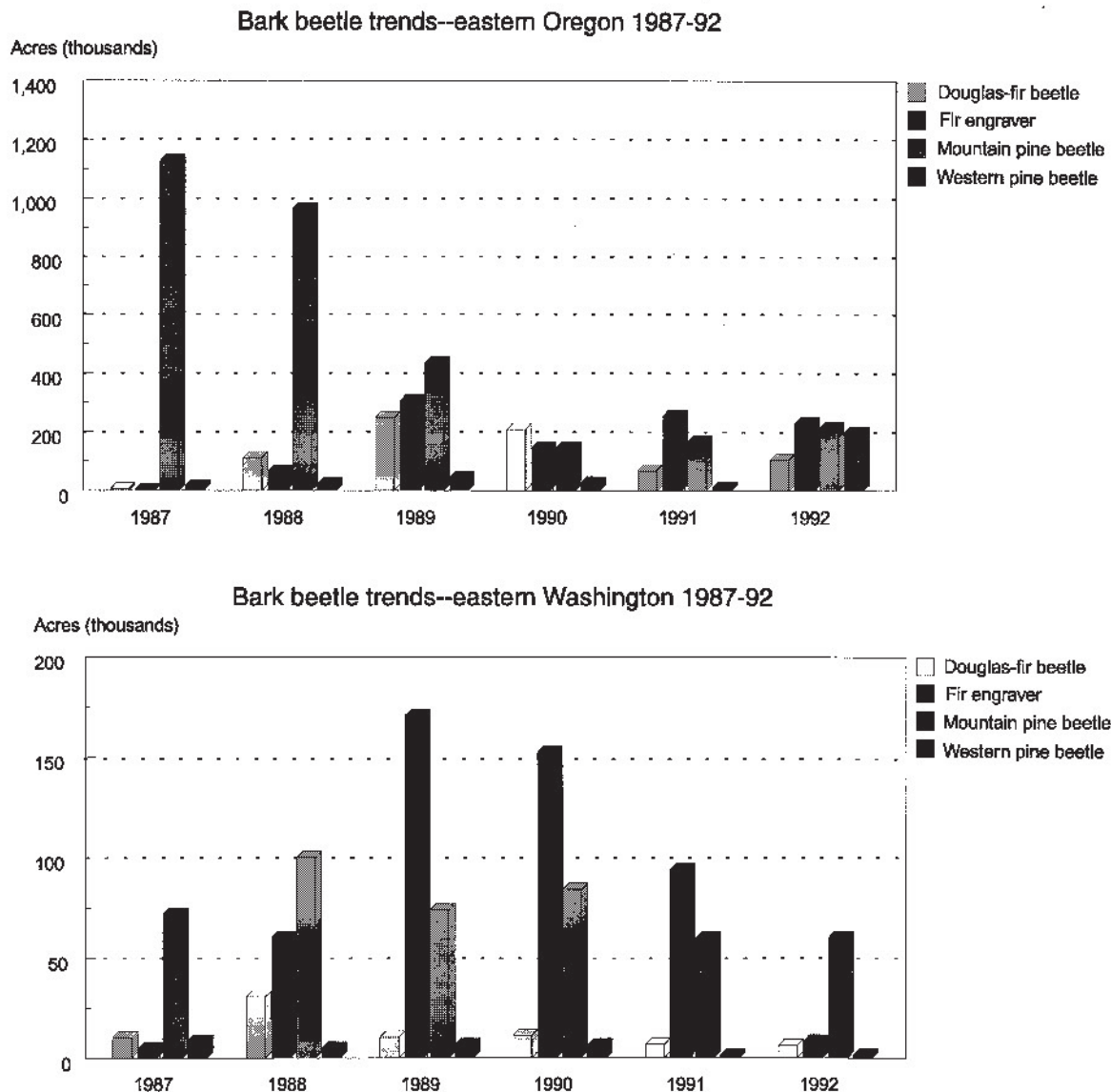


Figure 20. Bark beetle and tree mortality trends in eastern Oregon and Washington for the period 1987-1992.

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; Schnitt 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.)

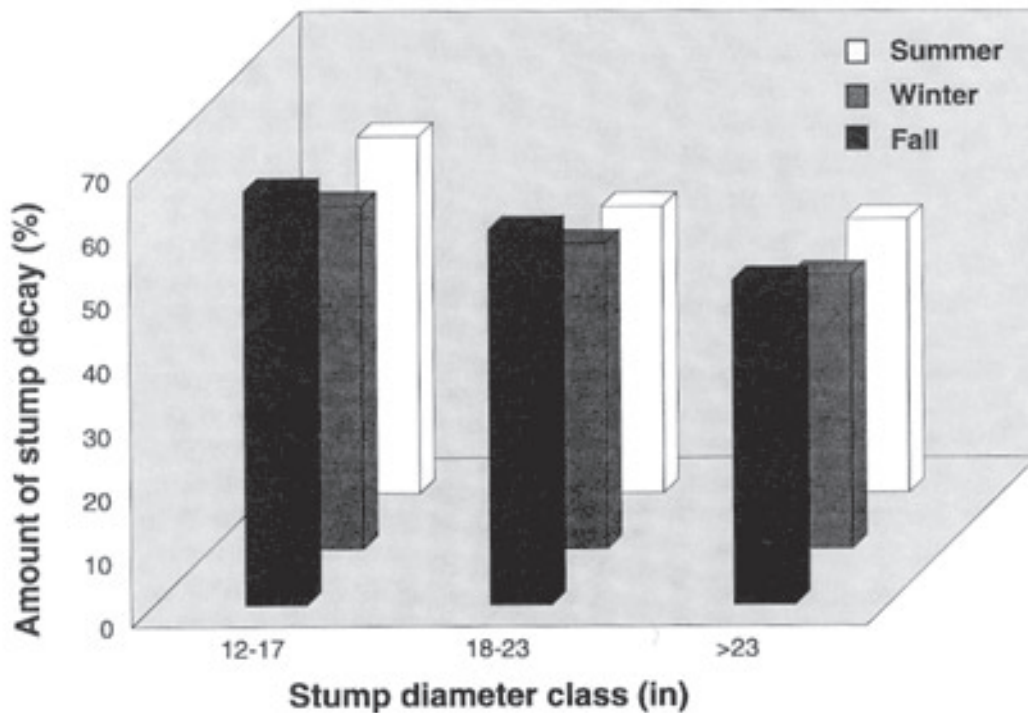


Figure 22. Amount of stump decay caused by *Heterobasidion annosum* in 300 grand fir stumps in northeastern Oregon (Filip and others 1992a).

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).

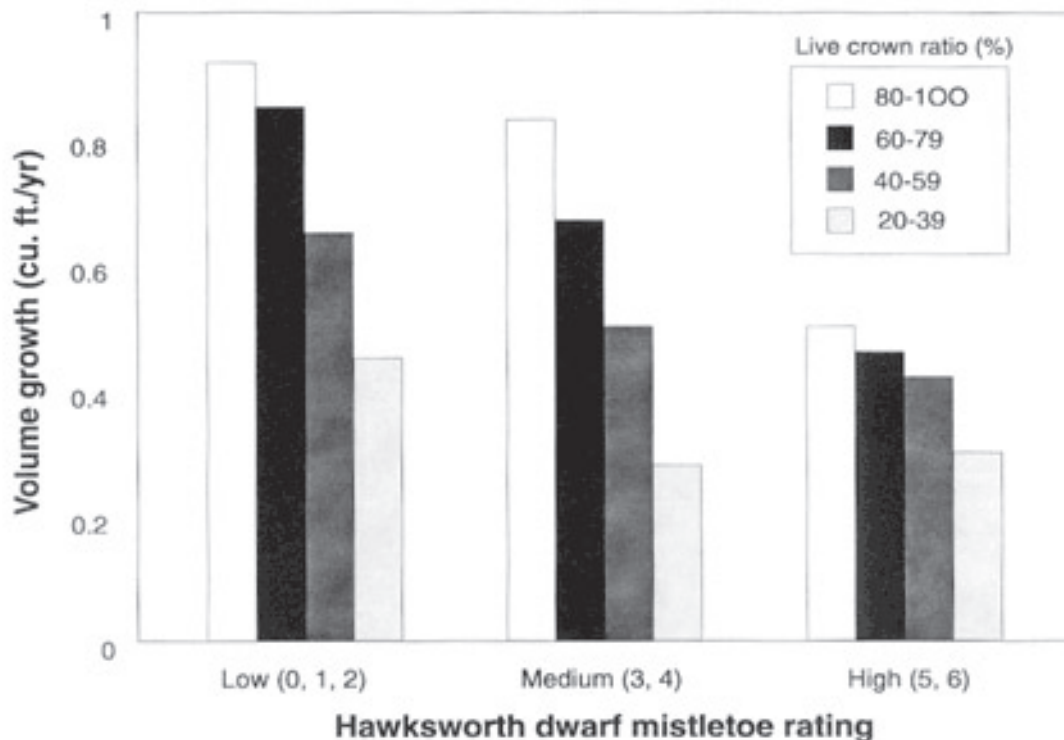


Figure 23. Periodic annual merchantable volume increment (last 25 years) by live crown ratio of grand fir infected by *Arceuthobium abietinum* f. sp. *concoloris* in central Oregon (Filip 1984).

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.

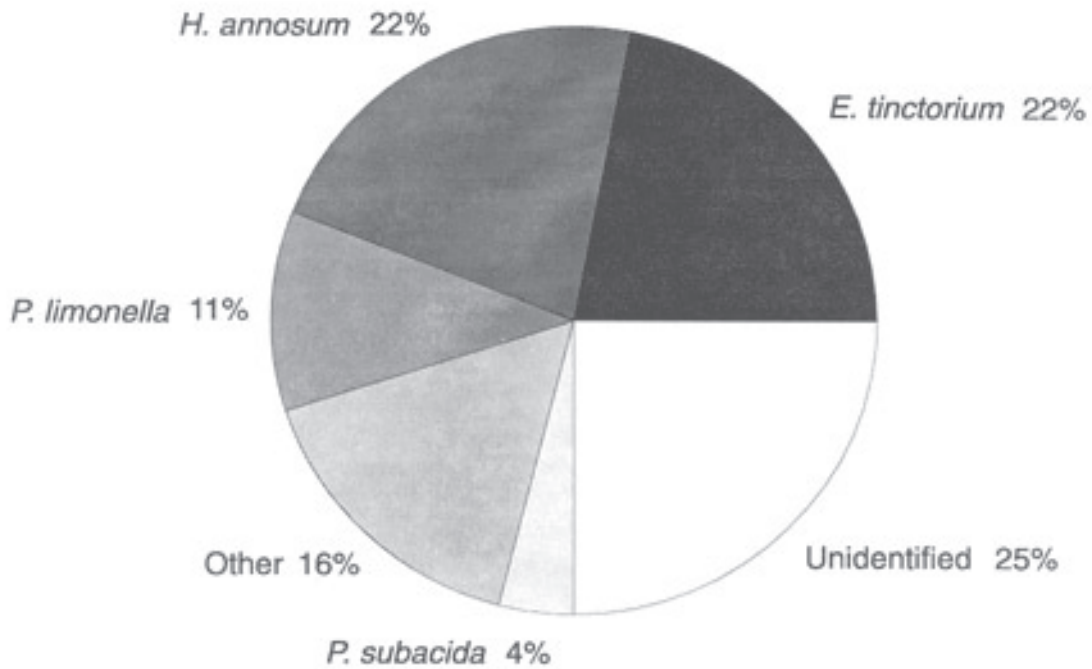


Figure 24. Percentage of total decay volume caused by fungi identified as Hymenomycetes in advanced grand/white fir regeneration in Oregon and Washington (Aho and others 1987).

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 intensity 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 $30 \text{ ft}^3 \cdot \text{acre}^{-1} \cdot \text{yr}^{-1}$ 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 $20 \text{ ft}^3 \cdot \text{acre}^{-1} \cdot \text{yr}^{-1}$ 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).

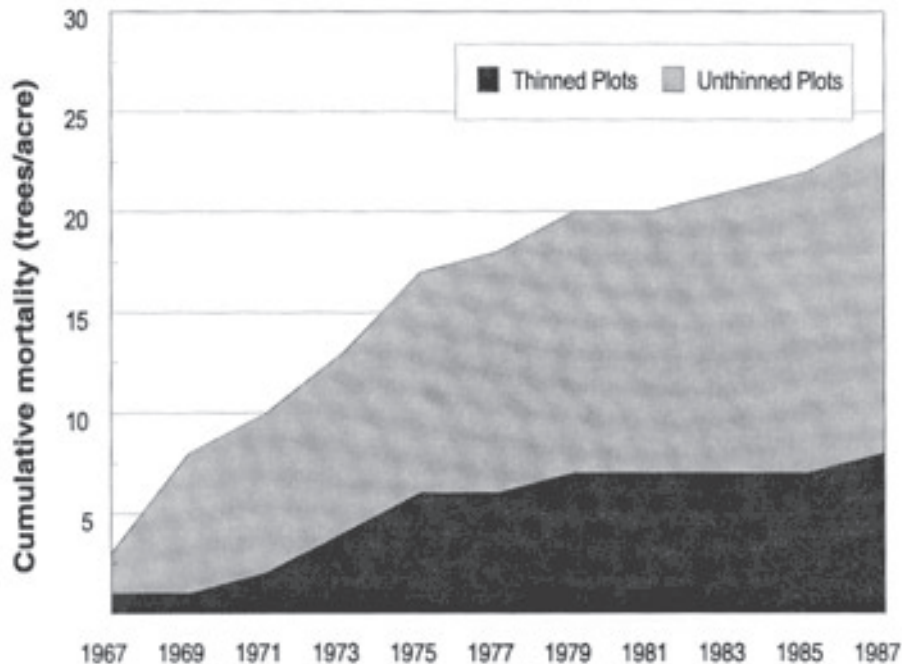


Figure 27. Cumulative mortality of crop trees caused by *Armillaria ostoyae* in precommercially thinned and unthinned plots of ponderosa pine in central Oregon (Filip and others 1989).

LOGEPOLE 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 lodgepole 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 pine, 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 susceptibles (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.



Figure 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.

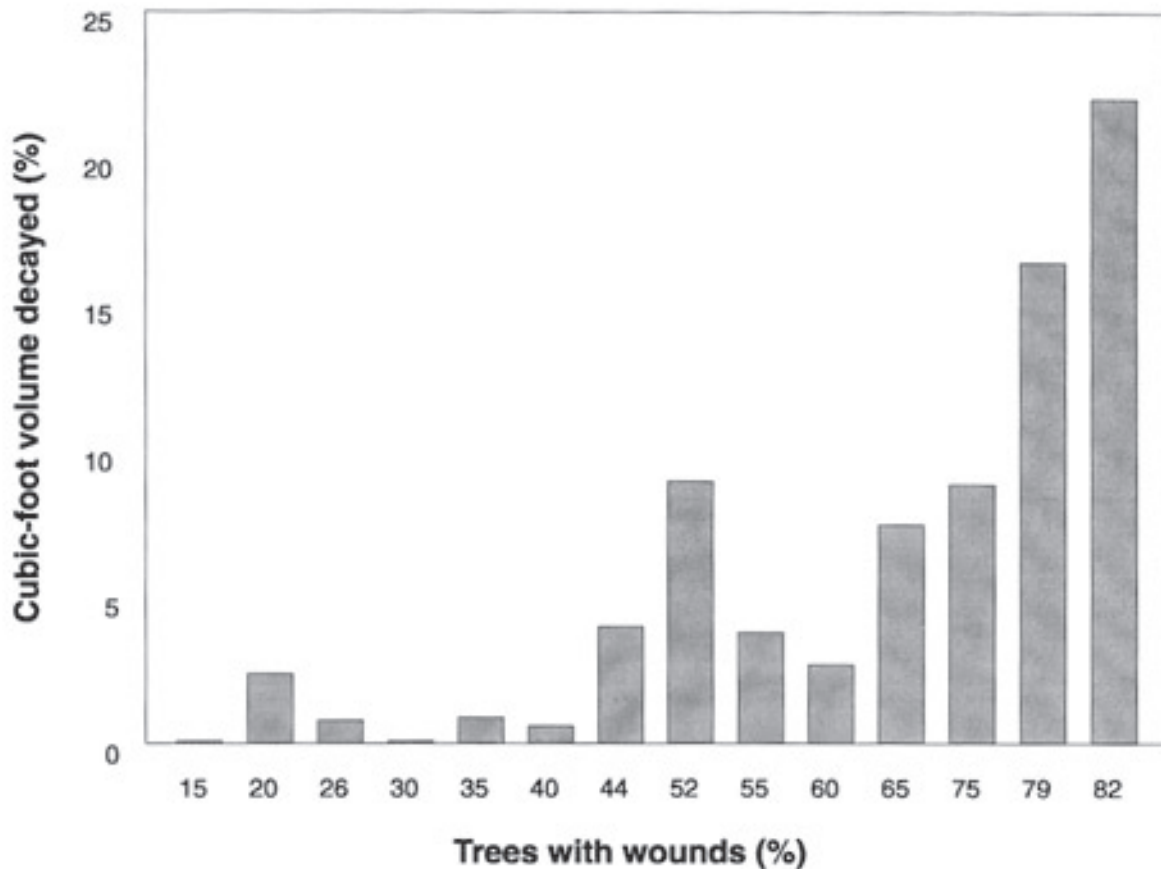


Figure 34. Percentage of cubic-foot volume decayed by percentage of trees with stem wounds in 14 stands of advanced white/grand fir regeneration in Oregon and Washington (Filip and others 1983).

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 or not favored.

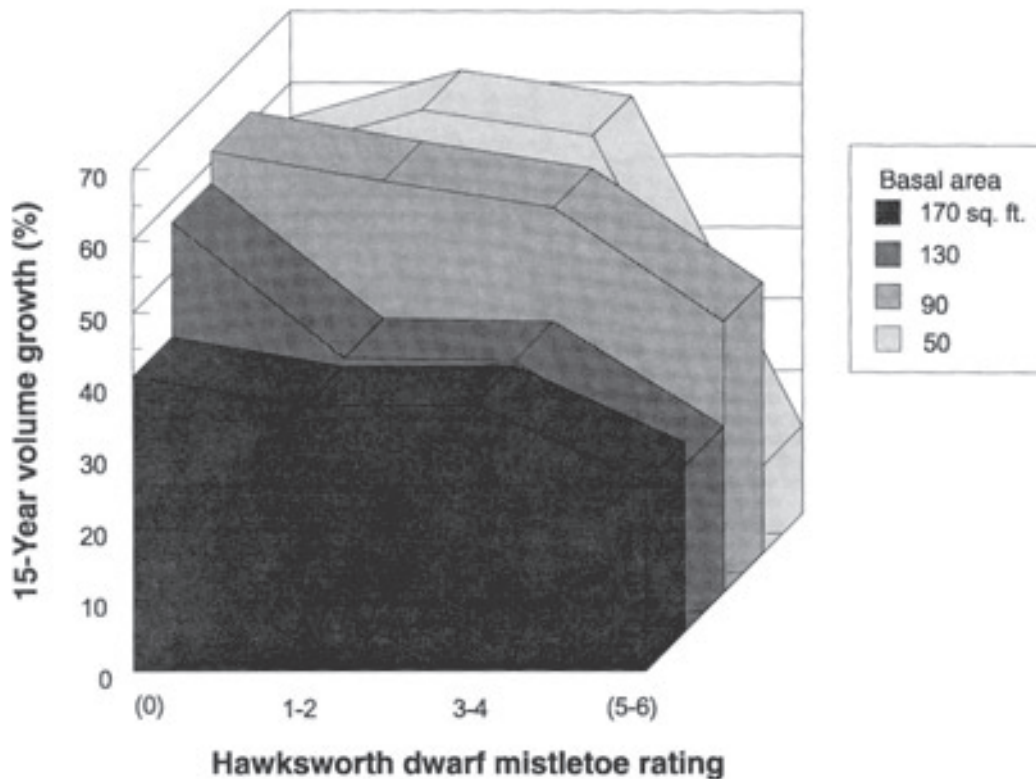


Figure 35. 15-year volume growth of western larch by residual density after thinning (basal area) and dwarf mistletoe severity rating in northeastern Oregon (Filip and others 1989).

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 are 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 and 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, insect 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 effects, and maintain or enhance beneficial roles of pathogens and insects and their natural enemies (fig. 36)? Are other management techniques, or variants of current 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	<i>Abies balsamea</i> (L.) Mill.
Douglas-fir	<i>Pseudotsuga menziesii</i> (Mirb.) Franco
Engelmann spruce	<i>Picea engelmannii</i> Parry ex Engelm.
Grand fir	<i>Abies grandis</i> (Dougl. ex D. Don) Lindl.
Lodgepole pine	<i>Pinus contorta</i> var. <i>latifolia</i> Dougl. ex Loud.
Mountain hemlock	<i>Tsuga mertensiana</i> (Bong.) Carr.
Noble fir	<i>Abies procera</i> Rehd.
Oregon white oak	<i>Quercus garryana</i> Dougl. ex Hook.
Pacific silver fir	<i>Abies amabilis</i> Dougl. ex Forbes
Ponderosa pine	<i>Pinus ponderosa</i> Dougl. ex Laws.
Shasta red fir	<i>Abies magnifica</i> A. Murr.
Subalpine fir	<i>Abies lasiocarpa</i> (Hook.) Nutt.
Western hemlock	<i>Tsuga heterophylla</i> (Raf.) Sarg.
Western juniper	<i>Juniperus occidentalis</i> Hook.
Western larch	<i>Larix occidentalis</i> Nutt.
Western redcedar	<i>Thuja plicata</i> Donn ex D. Don
Western white pine	<i>Pinus monticola</i> Dougl. ex D. Don
White fir	<i>Abies concolor</i> (Gord. & Glend.) Lindl. ex Hildebr.

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

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

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

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

Mycorrhizal 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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