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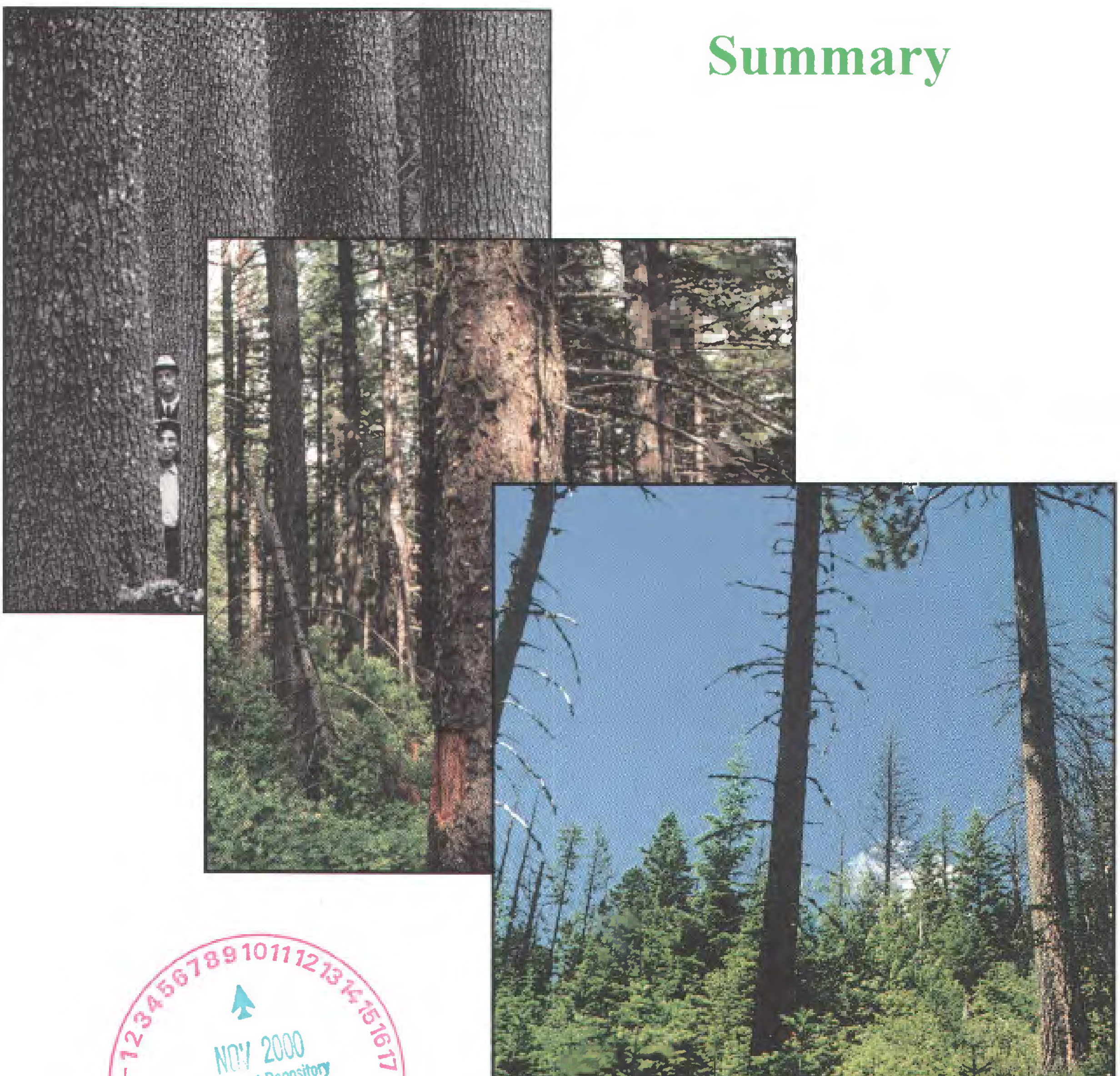
Succession Functions of Pathogens and Insects

Ecoregion Sections M332a and M333d in Northern Idaho and Western Montana

Summary



On the cover:

Pathogen and insect succession functions at work through time.

Mountain pine beetle was an important native insect in mature white pine forests (upper-left photograph). With the introduction of the exotic white pine blister rust fungus, white pines were no longer able to survive in great numbers and their place was filled, in large part, by Douglas-fir and grand fir (middle photograph). These forests, in turn, became hosts to epidemics of bark beetles and root diseases. In the aftermath of these epidemics, some forests have been maintained in conditions of perpetually young trees that die from root disease before reaching maturity (lower-right photograph).

Succession Functions of Forest Pathogens and Insects

Ecosections M332a and M333d in
Northern Idaho and Western Montana.

Summary

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USDA Forest Service
Northern Region

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FOREWORD

This is the summary for two volumes reporting successional effects of pathogens and insects in Northern Region forests. Volume 1 documents analysis methods and Volume 2 presents results from the areas analyzed. The analysis on which all volumes were based was done by plant pathologists and entomologists on the Cooperative Forestry and Forest Health Protection Staff (CFFHP) in the Northern Region of the Forest Service, using methods developed in cooperation with specialists and contractors from the Forest Health Technology Enterprise Team (FHTET). Team members and their areas of responsibility are listed below:

James W. Byler, Plant Pathologist, CFFHP, Coeur d'Alene, Idaho. Administrative leader and co-developer of analysis methods for white pine blister rust.

Susan K. Hagle, Plant Pathologist, CFFHP, Kooskia, Idaho. Project technical leader, technology development co-leader, and also provided the analysis of root disease.

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Sandra J. Kegley, Entomologist, CFFHP, Coeur d'Alene, Idaho. Douglas-fir beetle, mountain pine beetle in western white pine and spruce beetle.

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Jane E. Taylor, Plant Pathologist, CFFHP, Missoula, Montana. Dwarf mistletoes.

Stephen B. Williams, Program Manager, Decision Support Systems, FHTET, Fort Collins, Colorado. Technology development co-leader.

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SUCCESSION FUNCTIONS OF FOREST PATHOGENS AND INSECTS: Ecoregion sections M332a and M333b in Northern Idaho and Western Montana

SUMMARY

By James W. Byler and Susan K. Hagle

ABSTRACT

We analyzed the effects of pathogens and insects on forest succession in the absence of fire or management, addressing a number of related questions:

1. What is the rate of change in such forests?
2. How significant are the roles of pathogens and insects in the forest change?
3. How do pathogens and insects influence forest succession?

Vegetation change was measured using a geographic information system (GIS) analysis method that overlaid 1935-era and 1975-era maps of sample subcompartments on national forest land in two ecoregions in northern Idaho and western Montana. This 40-year period was, coincidentally, the time in which white pine blister rust became epidemic and in which fire suppression policies were implemented. Stand hazard ratings were used to classify stand susceptibility to insects and most pathogens; root disease severity was rated from aerial photographs. We considered an insect or pathogen to be a cause of successional change when the following conditions were met: the insect or disease hazard or severity rating for a cover type/structure stage class was high or moderate; a transition from one class to another was consistent with the expected function of the agent; and the change was not explained by advancing succession in the absence of pathogen or insect influence.

We found high rates of change from pathogens and insects in forests that had no evidence of recent active management or fire. More than 90 percent of the sample stands changed to a different cover type, structure stage, or both during the 40-year period. Insects and pathogens were associated with 75 percent or more of that change. Root pathogens, white pine blister rust, and bark beetles were the cause of most of the observed changes. The most significant pathogen and insect influences on cover type were to accelerate succession of western white pine, ponderosa pine, and lodgepole pine to later successional, more shade-tolerant species. The effects on structure were to reduce stand density or prevent canopy closure. Grand fir, Douglas-fir, and subalpine fir were the predominant cover types at the end of the period, and were highly susceptible to root diseases, bark beetles, fire, and drought. The trend toward mature, dense, climax forest is projected to decrease substantially during the next 40 years, with greater accumulations occurring in low-density mature and younger pole-sized stands that result from root disease- and bark beetle-caused mortality.

Our results underscore the relevance of pathogens and insects to forest planning and forest management. The introduction of white pine blister rust has drastically and perhaps permanently altered succession in this once-significant type. In the absence of fire or management, native pathogens, and insects continue to bring about change in forest composition and structure. This change is different from that produced by fire, as early seral species are usually not regenerated as a result of pathogen or insect activity.

The ecological outcomes of pathogen and insect activities are sometimes desirable and sometimes not desirable. We should consider whether or not their effects create desired conditions for the landscape in deciding whether or not to alter their influence through management. This information on long-term effects of pathogens and insects on succession can be used to address forest health in forest plans, to analyze alternative actions, and to more accurately communicate outcomes of those alternatives to various stakeholders.

We found that pathogens and insects can have large effects on forest succession. The economic impacts of pathogens and insects have been well documented; with this analysis, we have begun to understand and quantify their successional effects.

INTRODUCTION

It is important to understand the kind, degree, and causes of forest vegetation change in the absence of fire or management. Increasingly, the objectives of forest management on federal lands is changing from commodity production to recreation, watershed and biodiversity management. This puts a greater emphasis on the outcomes of pathogen, insect, and fire activity on the composition and structure of vegetation, and less on their effects on commodity outputs. Therefore, we (the Forest Health Protection group of the USDA Forest Service's Northern Region) initiated an analysis to explore forest composition and structure change in the absence of active management or fire, addressing a number of related questions:

1. What is the rate of change in such forests?
2. How significant are the roles of pathogens and insects in the forest change?
3. How do pathogens and insects influence forest succession?

Resource managers should not assume that disease or insect management is needed simply because forest stands are susceptible to insect or disease attack or because an impending outbreak of one of these is likely. The effects of diseases and insects can be positive or negative, depending on human values associated with the change. Only by knowing the outcomes of pathogen or insect activity on forest conditions can informed judgements be made about the need to manage the activity.

In this study, we hypothesized that pathogens and insects were influential and predictable agents of change in most natural forests. By their often selective attack of particular tree species and size classes, they influence which species predominate in a stand at different periods in its development. Most outcomes of pathogen and insect activity are so integral to the pattern of vegetation change that they go unnoticed except for some of the more dramatic insect outbreaks. These agents respond to changes in food and habitat associated with particular vegetative conditions, and in turn, their activities influence the pattern of the vegetative change.

For purposes of this analysis, we have recognized two terms which help us describe effects of pathogens and insects in forest succession. One is *silvical succession*: we use this term to refer to changes in tree species composition and structure that result from the site conditions and the interaction of the trees themselves with little influence from pathogens, insects, fires, or human activities. The second is *pathogen or insect succession function*, defined as the outcome of specific actions of pathogens or insects that alter the course or timing of succession.

We also distinguish between insect or pathogen *risk and hazard indices* and *indices of insect or pathogen-caused successional effect.* Risk and hazard rating systems have been developed for many important insects and diseases in western forests. These systems have been very useful for predicting where outbreaks are likely to occur and the magnitude of the resulting losses in timber volume. The actions of pathogens and insects can also be seen as major influences on the rates and pathways of change in forest cover and structure. In this analysis we used modified hazard ratings to predict both what kinds of stands were susceptible to pathogen and insect activity and what types and rates of successional change were likely to result from that activity.

The objective of this analysis was to identify and characterize important succession functions of forest pathogens and insects in Montana and northern Idaho. These efforts were aimed at 1) describing how pathogens and insects affect spatial and temporal patterns of succession, 2) describing current and historic pathogen and insect regimes (the spatial and temporal patterns of pathogen and insect actions), and 3) predicting future successional trends that reflect the roles of pathogens and insects. General methods and overall results from the study of two ecoregion ecosections, M332a and M333d, classified by Bailey (1994), are summarized in this report. Methods used to assess the succession functions of pathogens and insects for ecosections M332a and M333d are reported in Volume 1 of this report, and detailed results and conclusions are presented in Volume 2.

The analysis consists of four general phases.

1. Measuring 40 years' changes in vegetation in the absence of fire and management.
2. Discovering relationships between pathogen and insect actions and vegetation conditions by rating stand insect hazard or disease severity.
3. Associating actions of pathogens and insects with changes in vegetation (succession functions).
4. Translating results to predict future trends.

METHODS

SAMPLING ECOSECTIONS M332a AND M333d

Our sample of the Northern Region consisted of most National Forest subcompartments selected in the early to mid 1970s to supply the first comprehensive forest planning database. These were stratified by ecosection, subcompartment, and stand. We used 698 of these subcompartments consisting of 5,686 stands and 72,260 hectares.

Harvest activity was identified in 9 percent of the sample stands, which were excluded from further analysis. There were no indications of fire in the sample polygons during the analysis period. Fire exclusion undoubtedly did affect some of the area in the remaining sample base, particularly by allowing stand densities to increase and limiting regeneration opportunities (Atkins et al. 1999). Climatic factors, such as drought or wind, may have also influenced succession, but were not considered in this analysis.

Ecosection M332a, described and mapped by Bailey et al. (1994) as Middle Rocky Mountain Steppe, includes parts of the Nez Perce, Bitterroot, Clearwater, and Lolo National Forests (see Figure 1). Potential natural vegetation based on Kuchler's (1985) national classification system is grand fir and Douglas fir, western spruce-fir, and western ponderosa pine forests.

Ecosection M333d is described as Northern Rocky Mountain Steppe. It includes parts of the Clearwater, Lolo, Idaho Panhandle, Kootenai and Flathead National Forests in Montana and Idaho. Potential natural vegetation includes primarily cedar-hemlock and grand fir forest. This ecosection includes most of the western white pine forest type historically found in the Northern Rocky Mountains within the United States.

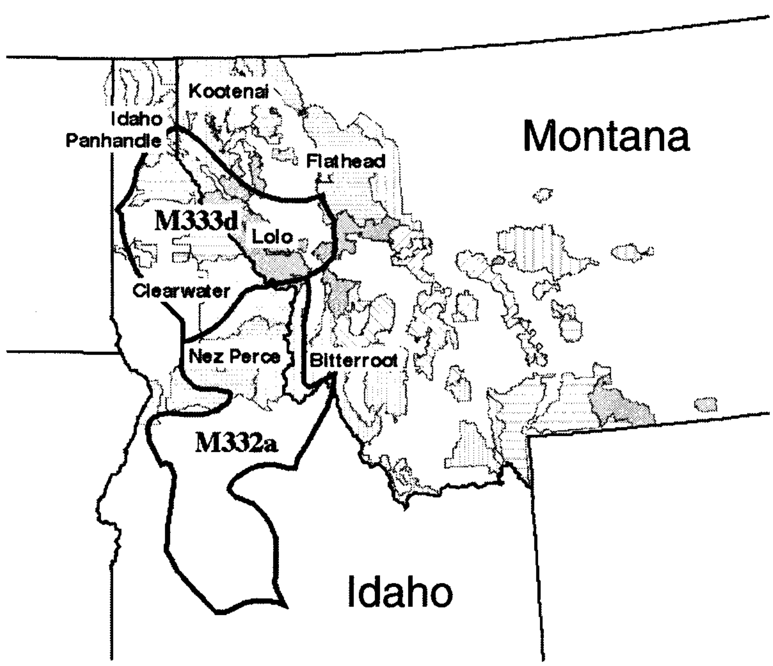


Figure 1: Ecosection boundaries and National Forests in the study area.

MEASURING VEGETATION CHANGE

This study was made possible by the existence of data from surveys conducted in the 1930s (hereafter, the 1935 era) and in the 1970s (hereafter, the 1975 era). Vegetation change was measured using a GIS analysis method that overlaid 1935-era and 1975-era maps of sample subcompartments for which both sets of maps could be found or reconstructed. These maps were used because they were available for a broad sample of the ecoregion sections for both time periods, because stand data were available for the 1975-era maps, and because 40 years seemed to be a reasonable time period to observe successional change. Sixty-three percent of the sampled hectares in M332a and 97 percent of the area in M333d had maps from both eras. The analysis method allowed us to evaluate transitions from one cover type/structure class within a habitat type group to another type and/or class.

Two cover-type classification methods were used, but only one is reported here. Both cover types were named for the tree species that was most abundant in a stand or stand polygon, or that met a designated composition threshold. The definitions used for this report were based on a threshold of the type species, and was developed for the 1935-era survey that was the basis for this analysis. The 1975-era data were classified using this typing method to assure consistency in classification for both time periods. Structure classes were based on the combination of the size and density of trees on the site: structure class 1, seedlings/saplings; structure class 2, poles; structure class 3, mature with closed canopy; and structure class 4, pole to mature with open canopy. The 1935-era data contained information about the cover type, size class, stocking density, age class, and generally, the percent composition of stands by tree species. For the 1975-era sample, stand data were used to classify both cover type and structure class.

ASSESSING STAND HAZARD AND SUCCESSION FUNCTIONS

The following pathogens and insects were selected for the analysis because they were likely to have succession functions across broad areas.

- White pine blister rust of western white pine and whitebark pine, *Cronartium ribicola*
- Root diseases of conifers caused by (primarily) *Armillaria ostoyae*, *Heterobasidion annosum* (s-type), and *Innonotus sulphurascens* (formerly *Phellinus weirii*)
- Douglas-fir beetle, *Dendroctonus pseudotsugae*
- Mountain pine beetle in lodgepole pine, *Dendroctonus ponderosae*
- Mountain pine beetle and western pine beetle in ponderosa pine, *Dendroctonus ponderosae* and *Dendroctonus brevicomis*
- Mountain pine beetle in western white pine, *Dendroctonus ponderosae*
- Dwarf mistletoe in Douglas-fir, *Arceuthobium douglasii,* in lodgepole pine, *Arceuthobium americanum,* and in western larch, *Arceuthobium laricis*
- Stem decay of grand fir, subalpine fir, western hemlock and mountain hemlock, caused by (primarily), *Echinodontium tinctorium*
- Stem decays of various hosts, caused by *Phellinus pini, Phaeolus schweinitzii, Fomitopsis officinalis, and Poria sericeomollis*
- Spruce beetle, *Dendroctonus rufipennis*
- Western spruce budworm, *Choristoneura occidentalis*

Existing stand hazard rating systems were used or made suitable through modification to classify stand susceptibility to insect or pathogen attack. Where these rating systems were unavailable, ratings were developed. The exception was root diseases: root disease severity was rated from aerial photographs using a method developed by Hagle (1992).

An *Action Probability Index* (API) was developed to assign the relative probability that a pathogen or insect will be active in a stand *and* that the actions will likely result in successional changes. For example, consider the actions of needlecast fungi compared to those of mountain pine beetle or western pine beetle. Outbreaks of needlecast fungi turn the needles red, and trees appear to be dying over large areas, but trees recover and the successional effects are negligible. In contrast, low populations of mountain pine beetle and western pine beetle typically kill individual or small groups of ponderosa pine, and are not highly visible, but the cumulative effect of several decades of "endemic" bark beetle activity can greatly reduce the amount of ponderosa pine in the stand, and change pine stands to other cover types.

A *succession influence index* was used to assign the likelihood the agent would cause a particular successional change, such as a transition from mature, closed-canopy ponderosa pine to a young Douglas-fir stage. The distinction between action and function allowed us to narrow the focus of this analysis to only those actions that have corresponding succession functions.

Stands were classified based on their habitat type group, cover type, and structure class. Stands in each class were rated for all agents using the 1975-era data, thus identifying the agents most likely to cause successional change in each class. This information allowed the mapping of stands where pathogen or insect activity was likely and correlation of action indices with stand and site factors. Since detailed stand data were unavailable for the 1935-era sample, pathogen and insect ratings for each habitat type group/cover type/structure class were derived from equivalent 1975-era stand data and assigned to the corresponding 1935-era classes.

Summaries of successional changes that occurred were developed for each class from the map data. In most cases, there were several types of changes within one class: i.e., transitions occurred from one class to several classes. We considered an insect or pathogen to be a cause of the change when the following conditions were met: stand API ratings were high or moderate, the transition was consistent with the expected function of the agent, and the change could not be explained by silvical succession alone. In most cases, no other apparent cause of that change appeared likely.

This approach was essentially testing and interpreting of hazard rating methods according to actual effect. The new index created in integrating by API and the frequency of congruent changes in polygon class was referred to as the succession influence.

The primary hazard/API rating criteria for individual agents are given in Table 1.

Table 1: Primary hazard/API rating criteria for individual pathogens and insects.

Agent	Rating	Primary Criteria			
		1	2	3	4
White pine blister rust	0 - 9	% WWP	Stand Avg. DBH	Hab. Type Group	
Root diseases	0 - 9	[1] Departure from normal tree density attributable to root disease.			
Douglas-fir beetle	L - H	DF DBH	% BA in DF	Total BA	Stand Age
Mountain pine beetle - LPP	L - H	Elev./Lat.	Avg. Age LPP	Avg. DBH LPP	
Mountain pine beetle/western pine beetle - PP	L - H	Stand DBH	Stand Structure	Stand Density	
Mountain pine beetle - WWP	L - H	WWP Avg. DBH	% BA WWP	Total BA	Stand Age
Dwarf mistletoe	0 - 6	% Host BA	Stand Age	TPA Host (>5" DBH)	
Stem decays	Varies by Agent	% Host BA	Stand Age	[2] Stand Structure	[2]% Total BA
Spruce beetle	L - H	Site Factors	Avg. Spruce DBH	Stand BA	% Total Canopy
Spruce budworm	0 - 10	% Host	Stand Structure	Stand TPA	

[1] Rated from color aerial photographs.
[2] *Echinodontium tinctorium* only.

Abbreviations: WWP, western white pine; DBH, diameter at breast height; L - H, low to high; DF, Douglas-fir; BA, basal area; LPP, lodgepole pine; PP, ponderosa pine; TPA, trees per acre.

RESULTS AND DISCUSSION

VEGETATION CHANGES

Over 90 percent of sampled hectares in ecosection M332a and 95 percent of sampled hectares in ecosection M333d changed cover type, structure class, or both during the 40-year period. Specific changes that were caused by pathogens and insects are as follows (net changes from all causes are shown in Figures 15-18).

M332a

Very significant changes in cover type were attributed to pathogens and insects during the 40-year period (Figure 2). The amount of relatively-pure ponderosa pine, lodgepole pine, and western larch declined. The amount of subalpine fir, Douglas-fir, western redcedar and grand fir increased. Thus, the dominant pathogen- and insect-caused trend in cover type was an increase in later-seral species composition. Only a few of the timber stands had volumes that met productivity expectations. Forest structure was also changed by pathogens and insects (Figure 3). The area in pole, mature well-stocked, and nonforest decreased, and the area in seedling/sapling and mature poorly stocked stands increased.

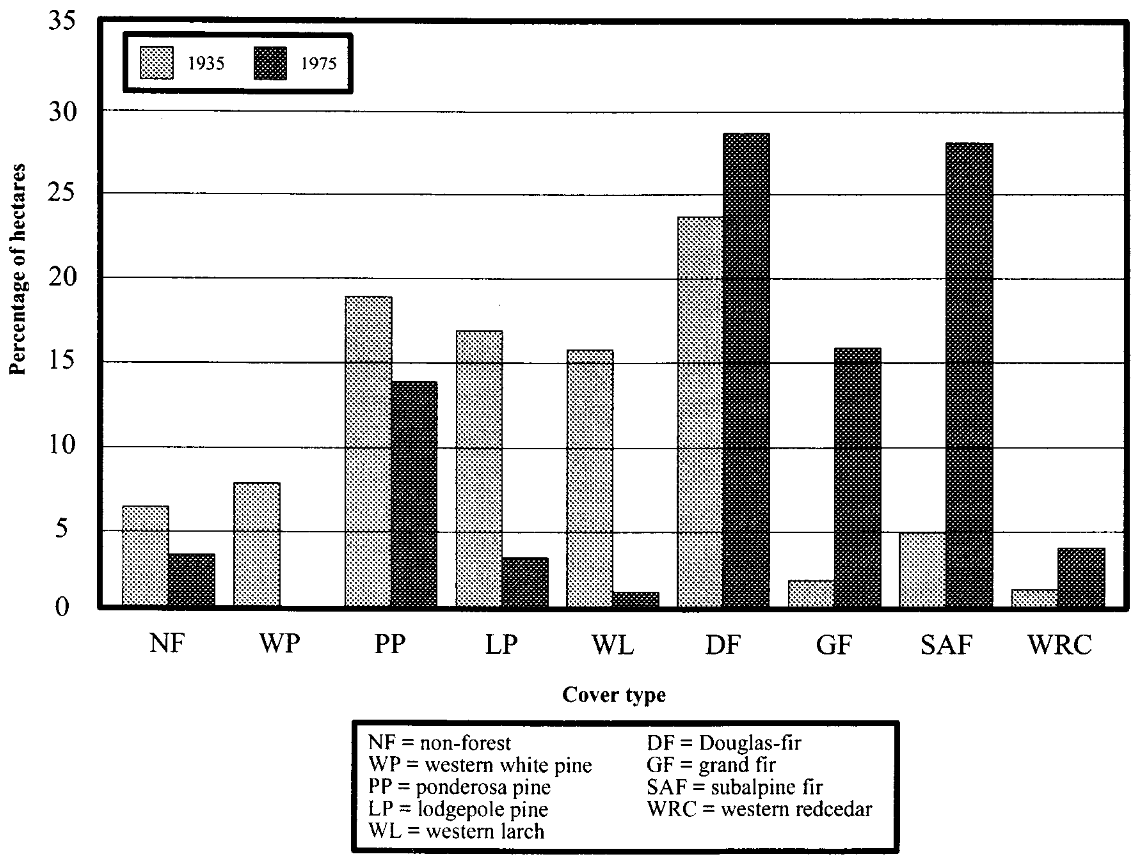


Figure 2: Net changes in cover type at high levels of pathogen and insect influence, 1935 era to 1975 era, ecosection M332a.

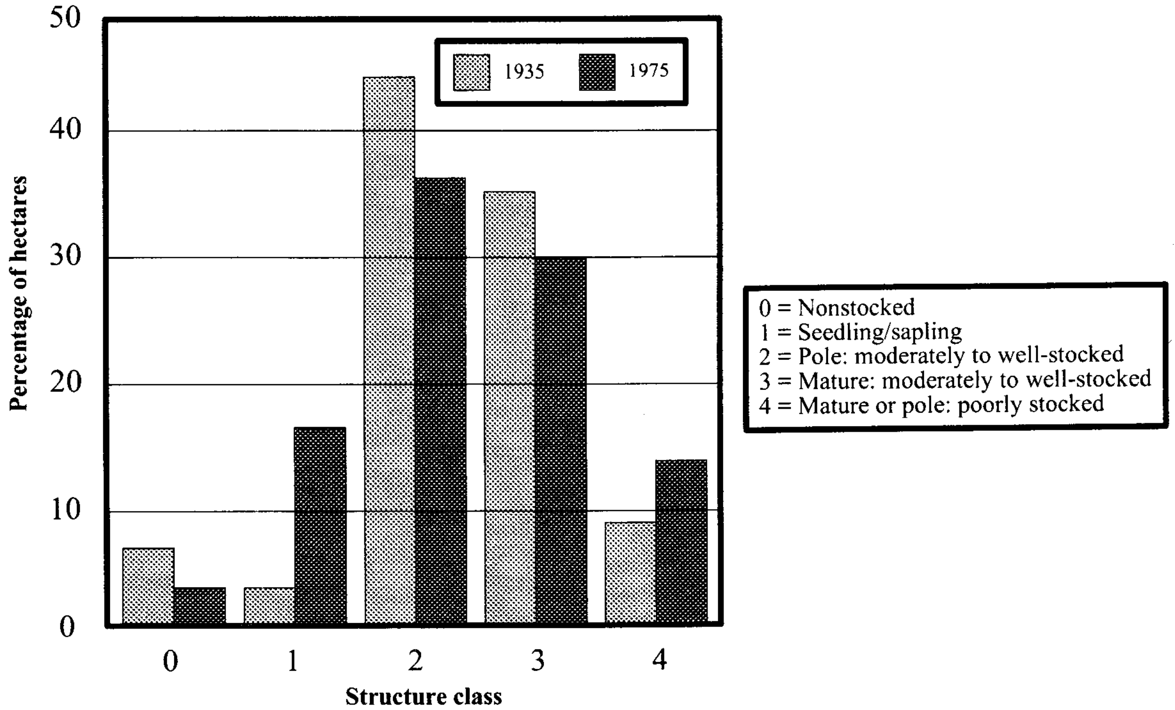


Figure 3: Net changes in structure class at high levels of pathogen and insect influence, 1935 era to 1975 era, ecosection M332a.

M333d

Pathogen- and insect-influenced cover type changes that occurred in this ecosection were similar to those in M332a: an increase in later-seral species cover types and a decrease in early seral cover types (Figure 4). But the amount of change was greater, and there were a few other differences. There were larger amounts of western white pine cover type and of nonforest (mostly recent burns) in the M333d sample from the 1935 era, and less ponderosa pine, reflecting more moist habitats and greater area with recent stand-replacing fires. The amount of lodgepole pine type increased in this area because of the loss of western white pine in mixed white pine/lodgepole pine stands that converted to lodgepole. The biggest structural changes were decreases in nonstocked and mature well-stocked stages, and a major increase in pole and mature poorly stocked stands (Figure 5).

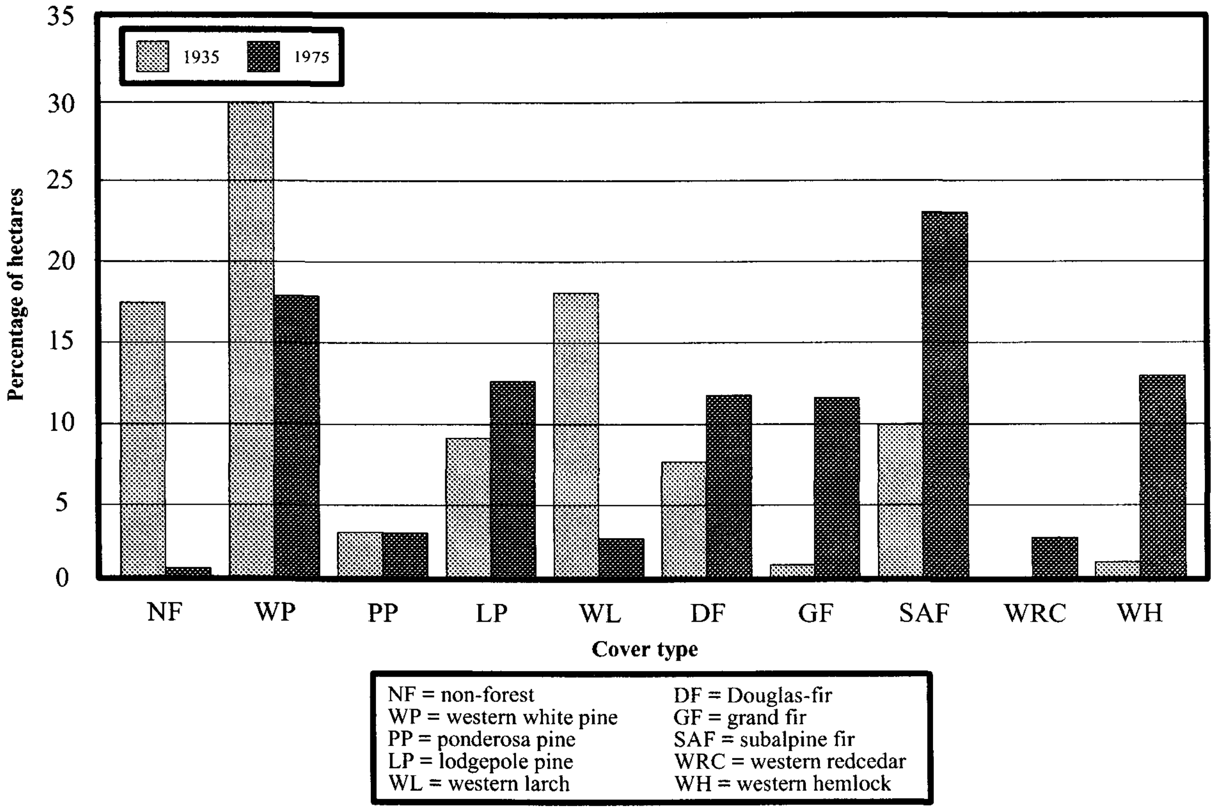


Figure 4: Net changes in cover type at high levels of pathogen and insect influence, 1935 era to 1975 era, in ecosection M333d.

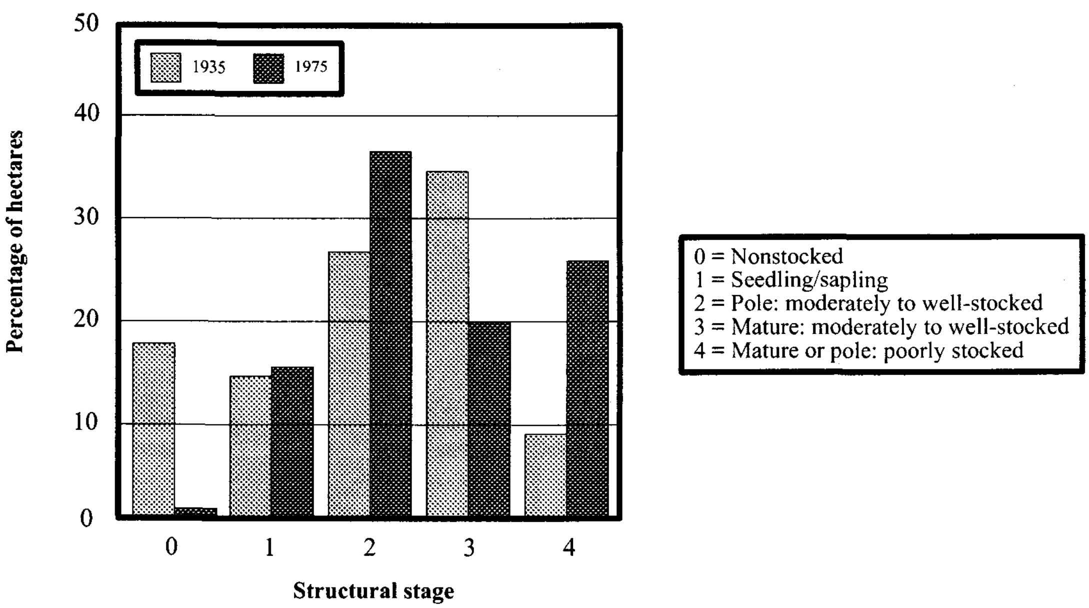


Figure 5: Net change in structure class at high levels of pathogen and insect influence, 1935 era to 1975 era, ecosection M333d.

The trends observed between 1935 and 1975 eras for cover types in both zones were consistent with more recent data on changes from all causes published by others (Brown and Chojnacky 1996, Zack personal communication). Changes in structure class are also similar among these studies, but the authors cited above show less accumulation of mature forest (classes 3 and 4), presumably due to the longer time-period for insects and pathogens to act on them, and to other causes, such as harvesting, fire, and silvical succession.

SUCCESSIONAL INFLUENCES OF PATHOGENS AND INSECTS

Most of the changes in forest conditions in our sample from 1935 to 1975 eras were consistent with the effects of pathogens and insects. In M332a, nearly 80 percent of transitions were considered to have been largely functions of pathogens and insects. Table 2 summarizes the influences of individual pathogens and insects on cover type and structure in that ecosection. Similarly, 85 percent of transitions in M333d were pathogen- and/or insect-influenced. Influences of individual agents in this ecosection are summarized in Table 3.

Table 2: Influences of pathogens and insects from 1935 to 1975 eras, ecosection M332a.

Pathogen/insect	Proportion of ha[1]	Primary Cover Effects (proportion)[2]	Primary Structure Effects (proportion)[2]
Root pathogens	.47	Increase climax (.70) Maintain early seral (.23)	Toward immature (.38) Prevent closure (.35) No effect (.24)
Mountain pine beetle in lodgepole pine	.19	Increase climax (.97)	Toward immature (.35) No effect (.29) Prevent closure (.29)
Douglas-fir beetle	.14	Increase climax (.54) Maintain early seral (.27)	Prevent closure (.46) Toward immature (.23) No effect (.22)
Douglas-fir beetle and root diseases, combined	.12	Increase climax (.54) Maintain early seral (.25) No effect (.22)	Prevent closure (.52) No effect (.23) Toward immature (.21)
White pine blister rust	.10	Increase climax (.94)	No effect (.53) Prevent closure (.33)
Mountain pine beetle/western pine beetle in ponderosa pine	.06	Increase climax (.78)	Toward immature (.46) Prevent closure (.27)
Mountain pine beetle in western white pine	.02	Increase climax (1.0)	Prevent closure (.58) Toward immature (.42)
Douglas-fir dwarf mistletoe	.04	No effect (.50) Maintain early seral (.44)	Prevent closure (1.0)
Lodgepole pine dwarf mistletoe	.01	Increase climax (.98)	Prevent closure (.98)
Western larch dwarf mistletoe	.01	Increase climax (1.0)	Prevent closure (1.0)
Stem decays	.03	Maintain early seral (.52) No effect (.39)	Prevent closure (.64) Decrease density (.30)
Spruce beetle	.01	Maintain early seral (.54) Increase climax (.46)	No effect (.51) Toward immature (.39)
Spruce budworm	.03	Maintain early seral (.46) No effect (.45)	Prevent closure (.84)

1 Proportion of hectares in M332a that were strongly influenced by each pathogen or insect.
2 Of the hectares most affected by the pathogen or insect, the proportion likely to show each successional effect.

Table 3: Influences of pathogens and insects from 1935 to 1975 eras, ecosection M333d.

Pathogen/insect	Proportion of ha	Primary Cover Effects (proportion)[2]	Primary Structure Effects (proportion)[2]
White pine blister rust	.43	Increase climax (.76) Maintain early seral (.21)	No effect (.52) Toward immature (.29) Prevent closure (.16)
Root pathogens	.48	Increase climax (.7) Maintain early seral (.24)	Toward immature (.46) No effect (.30) Prevent closure (.21)
White pine blister rust and root disease combined	.30	Increase climax (.75) Maintain early seral (.21)	Toward immature (.44) No effect (.33) Prevent closure (.23)
Douglas-fir beetle	.04	Increase climax (.64) Increase early seral (.20) No effect (.15)	Prevent closure (.57) Toward immature (.28)
Mountain pine beetle in lodgepole pine	.03	Increase climax (.63)	Toward immature (.56) No effect (.29)
Mountain pine beetle/western pine beetle in ponderosa pine	.02	Increase climax (.64) Maintain early seral (.36)	Toward immature (.66) Prevent closure (.24)
Mountain pine beetle in western white pine	.04	Increase climax (.81) Maintain early seral (.14) No effect (.04)	No effect (.50) Decrease density (.24) Prevent closure (.07)
Douglas-fir dwarf mistletoe	.02	Increase climax (.60) No effect (.29)	Prevent closure (.97)
Lodgepole pine dwarf mistletoe	<.01	Maintain early seral (1.0)	Prevent closure (1.00)
Western larch dwarf mistletoe	.01	Increase climax (.92)	Prevent closure (1.00)
Stem decays	.01	No effect (.50) Increase climax (.38)	Prevent closure (.82)
Spruce beetle	.02	No effect (.50) Increase climax (.49)	Toward immature (.72) Prevent closure (.15)
Spruce budworm	<.01	No effect (.59) Maintain early seral (.38)	Prevent closure (1.00)

[1] Proportion of hectares in M332a that were strongly influenced by each pathogen or insect.
[2] Of the hectares most affected by the pathogen or insect, the proportion likely to show each successional effect.

The most important functions in both ecosections were to accelerate change toward climax species composition, to stall development in immature stages, and reduce or prevent canopy closure (Figures 6 and 7). Pathogens and insects effectively suspended succession in small-tree structure classes or caused changes from large-tree to small-tree structures on 30 percent of the area during the 40-year interval. Such structural changes were seen in 32 percent of the area in habitat type group 5 in M333d, which was the predominant habitat type. A high percentage (62 percent in M332a and 58 percent in M333d) of pathways were identified as likely unique to those produced by pathogens and insects. The combined or independent functions of root disease, Douglas-fir beetle, and mountain pine beetle accounted for most transitions in M332a (Figure 6) and the combined functions of root disease and blister rust accounted for most transitions in M333d (Figure 7).

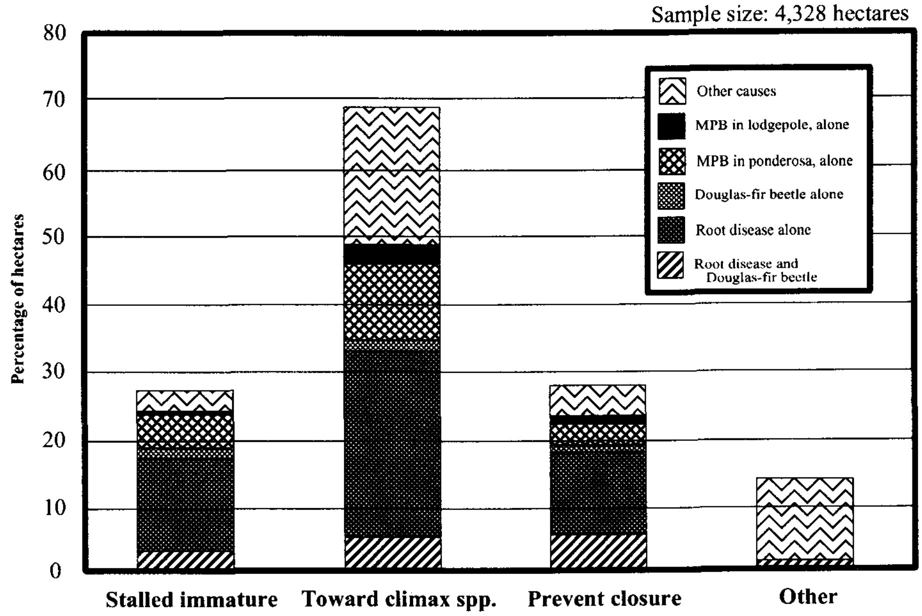


Figure 6: Transitions caused by combined or independent functions of root disease, Douglas-fir beetle, and mountain pine beetle, M332a.

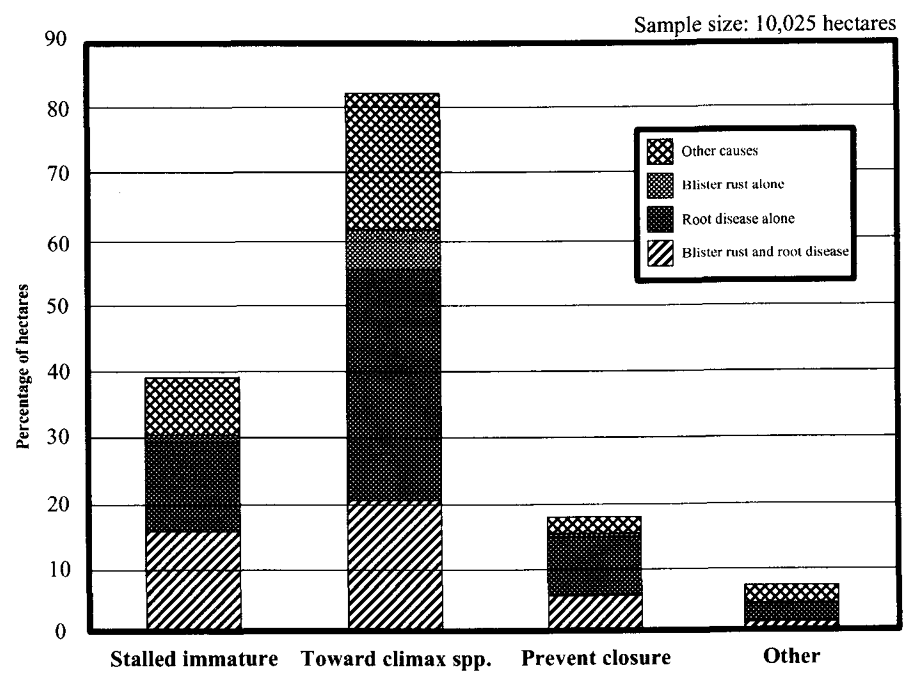


Figure 7: Transitions caused by root disease and blister rust, habitat type group 5, M333d.

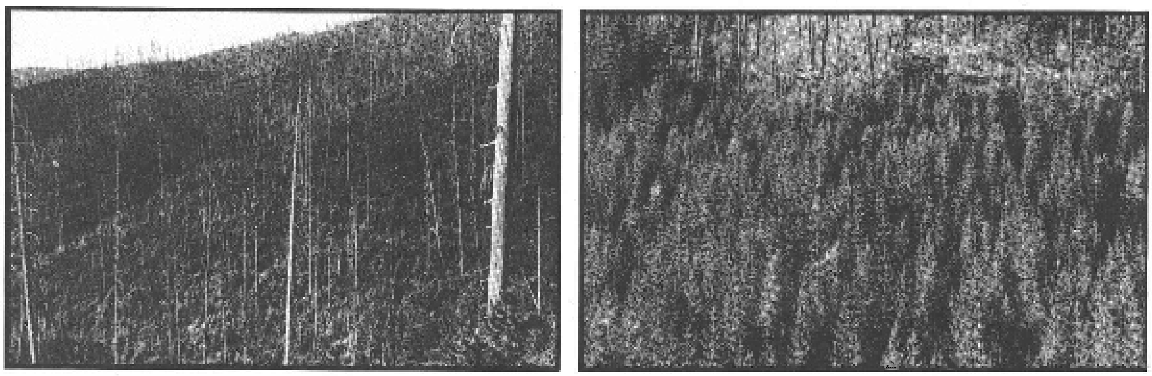
White Pine Blister Rust

White pine blister rust, caused by an introduced pathogen, has had a major, devastating impact on western white pine, whitebark pine, and other white pine species since it's introduction to western North America in the early 1900s. The rust was first found in Idaho in the 1920s, and by the 1940s, it was causing widespread mortality of western white pine.

Prior to the arrival of blister rust, white pines were common on all but the driest Douglas-fir and ponderosa pine habitat types. Western white pine was especially abundant in riparian areas and lower slopes in the mid-elevation, moist types, but was also common in the lower subalpine types. Whitebark pine, also a white pine species, occurs at even higher elevations. Western white pine was the most abundant cover type in ecosection M333d in the 1935 era, comprising about 35 percent of the sample. Western white pine cover type was a minor cover type in M332a.

Blister rust influenced succession on 43 percent of the ecosection M333d, both through changing white pine cover types to other species and by preventing white pine cover type from forming, mainly on recently burned shrub cover types. On 30 percent of this area, root disease was also an influence.

Historically, western white pine forests developed after large fires created openings that regenerated by seed from mature trees that escaped the fires (Figure 8a). Sometimes, regeneration was primarily to western white pine (Figure 8b). At other times, it was composed of mixed species, but since white pine usually lived longer than the other species, many additional acres became predominantly white pine after about 150 years. Western white pine that escaped stand-replacing fires could live over 300 years, but were eventually killed by mountain pine beetle or fire.

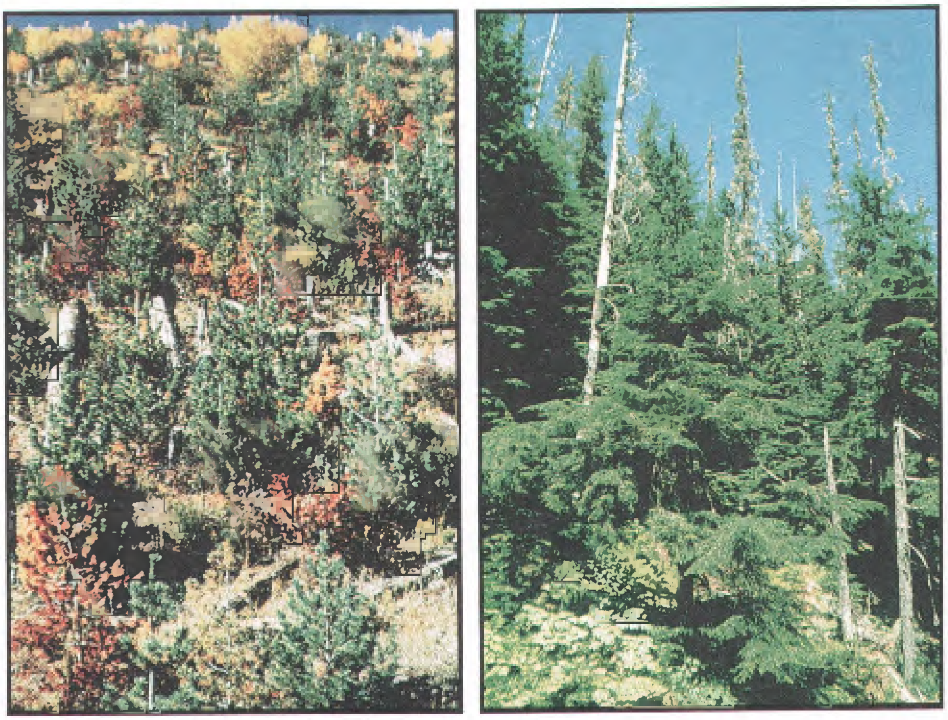


Figures 8a and 8b. Forest regeneration. In the past, large fires that were common in the ecosections studied created conditions that allowed pines, larch, and other shade-intolerant species to regenerate and grow. Pathogens and insects also killed trees, but in the absence of fire, the primary effect was to favor shade-tolerant species. **a.** Regeneration became established following a fire that killed the original, mature forest. **b.** A young western white pine stand has colonized a burned site. Western white pine was the most abundant tree species in ecosection M333d in the mid-1930s, one of the most abundant species in the 1970s, but only a minor species today.

M333d covers much of the historic range of western white pine in Idaho and Montana. Of the 22,000-hectare sample of western white pine cover type, the highest rust hazard (level 4) was assigned to 46 percent of the area, level 3 to 12 percent, level 2 to 27 percent, level 1 to 1 percent, and level 0 to 15 percent. This high level of hazard in susceptible native white pine stands explains the high level of mortality that resulted.

The most common result of blister rust in stands from the 1935 to the 1975 eras was to accelerate changes in species composition toward later-seral or climax cover types (57 percent of the hectares). This was usually combined with the stands either remaining in seed and sapling or pole structures over the 40-year interval, or losing the large-tree components if they were mature and moving backward to seedling/sapling or pole structures.

Large areas of M333d burned in the late 1800s and in 1910, so there were large expanses where white pine would have seeded in sapling or pole-sized stands by the mid-1930s. Blister rust would have rapidly intensified in these stands, causing widespread mortality of these vulnerable, young trees (Figure 9a). In stands that contained large amounts of mid- to late-seral species, such as grand fir, cedar, or hemlock, the loss of white pine accelerated succession toward late-seral species (Figure 9b). In our sample, nearly all seedling/sapling western white pine stands were changed to another cover type, either lodgepole pine or mid- to late-seral species (Figure 10).



Figures 9a and 9b. White pine blister rust-caused mortality. The introduced white pine blister rust was epidemic by the 1940s. **a.** Young stands such as this were killed within a few years, although larger trees lived longer. Even so, three-fourths of the well-stocked, mature white pine stands had been changed to a different type by the mid-1970s, mainly by blister rust and the native mountain pine beetle. **b.** The aftermath of the blister rust epidemic. Only snags remain in what was formerly a young stand of white pine stand. The stand has transitioned to shade-tolerant western hemlock and grand fir.

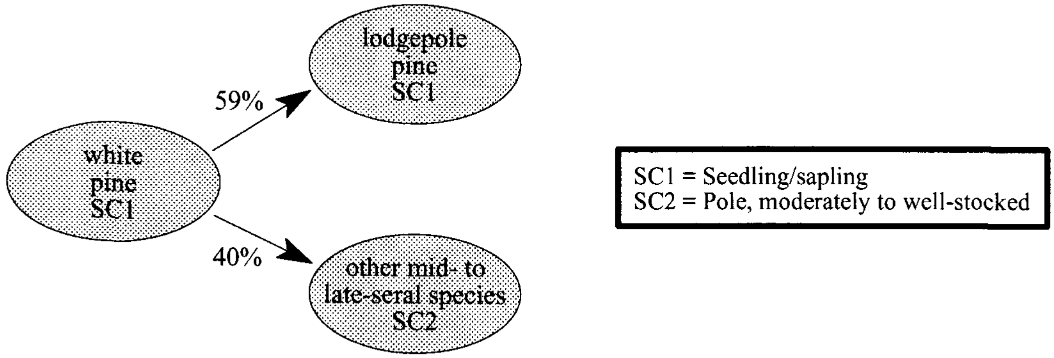


Figure 10: Conversion of white pine cover type in structure class 1, ecosection M333d.

Pole-sized white pine stands would be expected to grow into mature white pine classes, but pole-sized white pines are highly vulnerable to the rust. In our sample, about half of the pole-sized western pine stands were converted to mid- to late-seral cover types.

In mature stands where western white pine dominated, mortality from blister rust and other agents also resulted in a change in cover type and structure class. About three-fourths of the well-stocked stands and two-thirds of the low-density stands in our sample were converted to mid- to late-seral species (Figure 11 shows results for low-density stands). While the cause of cover type change of seedling/sapling stands was attributed to white pine blister rust, changes in mature stands were attributed to the combined effects of the rust and mountain pine beetle.

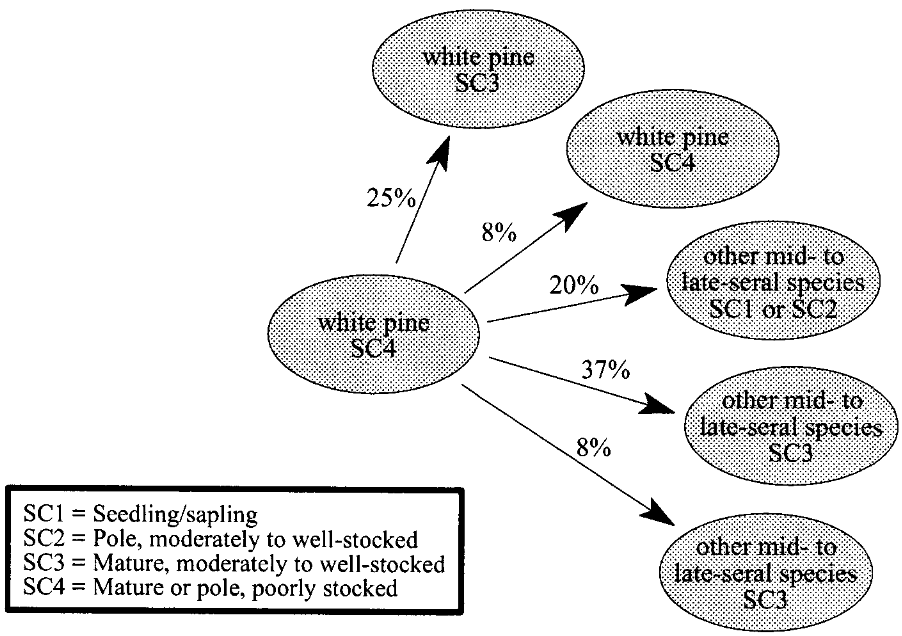


Figure 11: Conversion of white pine cover type in structure class 4 by blister rust, ecosection M333d.

In all, over 80 percent of the hectares with rust influence transitioned toward climax cover type, and only 17 percent followed a "normal" progression. Only about a third of the hectares that were classified as white pine cover type in the 1935 era were still classified as white pine in the 1975 era.

In conclusion, our analysis has shown that white pine blister rust severely impacted young western white pine during the first 40 years following its introduction. This impact has successfully short-circuited many historical succession pathways. Mixed-conifer stands that regenerated on suitable sites following stand-replacing fires typically converted to white pine cover type for up to 300 years before moving to climax grand fir, cedar, western hemlock, or subalpine cover types (which was uncommon because stands were usually regenerated again by fire before reaching a climax condition). In the presence of blister rust, these stands converted mainly to lodgepole pine, Douglas-fir, and grand fir at the seedling/sapling stage. Given the relatively short-lived nature of these early seral species due to root diseases and bark beetles, many pole-sized stands moved directly from western white pine to climax cover types.

Blister rust will continue to convert remaining western white pine stands to other species during the subsequent 40 years, but the rate is likely to decrease as the amount of the white pine in the most vulnerable young stands decreases. Regeneration of the species will be hindered by the lack of fire and by the rust, which will tend to kill young stands that do regenerate at an early age.

Long-term effects on white bark pine ecosystems are not entirely known, but much of the whitebark pine cover type in M332a and M333d have very high levels of infection and extensive mortality.

Root Disease

Root disease in northern Idaho and western Montana is caused by a number of native pathogens, most notably *Armillaria ostoyae, Heterobasidion annosum, Innonotus sulphurascens* (formerly *Phellinus weirii),* and *Phaeolus schweinitzii.* They kill or decay tree roots, eventually leading to the death of infected trees. Douglas-fir, subalpine fir, and grand fir are most susceptible to the diseases.

Root diseases are abundant and they are major agents of forest change in Idaho north of the Salmon River and in Montana west of the Continental Divide. Literature, observations, and permanent plot data indicate they play important successional roles. Root pathogen individuals can be very old, in excess of 1,500 years, and cover many acres. Thus, they can outlive many generations of trees, persisting between rotations in the roots of dead trees and stumps. Pathogen activity fluctuates slowly over time, however, and fungus biomass increases or decreases depending on the relative abundance of hosts.

The independent effects of individual pathogens is poorly understood in northern Idaho and western Montana because of the strong tendency of multiple pathogens to occur on one site, even in the same tree. Their combined effects are readily apparent, however, in the pattern of mortality. The typical pattern is chronic mortality of the Douglas-fir, grand fir, or subalpine fir overstory, and subsequent mortality of regeneration that forms in openings caused by the killing of the overstory. At any one time, one sees a mosaic of overstory and openings, and trees of all ages in various stages of decline and decay.

The prevalence of root disease in both ecosections is evident in the high frequency of significant severity ratings. Only 2 percent and 6 percent of hectares of M332a and M333d sample polygons, respectively, were assigned severity level 0 (on a scale of 0 to 9). Yet, the most severe levels were also uncommon, occurring in only 1 percent of ecosection M332a and 3 percent of M333d. The average severity was 4.0 in M333d and 3.9 in M332a. At this severity, the canopy has been reduced by 20 to 30 percent. Root disease was most severe in habitat groups with moderate levels of moisture and moderate to cold temperatures.

Cover types with the most root disease-susceptible tree species in 1935-era stands generally had highest severities of root disease 40 years later. Ponderosa pine and lodgepole pine generally had low root disease severities 40 years later. Grand fir, larch/fir, white pine, subalpine fir, Douglas-fir, and ponderosa pine mixed with Douglas-fir had the highest average root disease severities after 40 years. The high level of root disease that developed in white pine stands in the 1935 era is likely due, in part, to an increase in root disease-susceptible hosts following mortality of western white pine from blister rust.

Root disease was the most frequent cause of successional change in both ecosections (see Figures 6 and 7), influencing change on nearly half of the area in each ecosection. The most severe effects from root disease were stalling the forest in an early structure class, such as seedling/sapling or pole, or moving a stand from a more advanced structure class to a class with smaller, younger trees (Figure 12a). Decreasing density of large-tree classes or preventing canopy closure in stands that are progressing from seedling/sapling or pole classes to large-tree stands were also common functions of root pathogens. Most common, but harder to discern from silvical succession, was pushing the species composition toward the "climax" tree species. It was common for forest type to change to a later-seral stage, which was also smaller sized or more open. Succession functions of root pathogens varied considerably by habitat type.

Figure 12a and 12b. Root disease- and bark beetle-caused mortality. Root diseases and bark beetles were the most frequent native causes of successional change. Combinations of two or more agents, such as root diseases and Douglas-fir beetle, were active in 60 percent of the stands. **a.** A severe effect of root disease was to remove a mature Douglas-fir or true fir stand, thereby converting the stand to a class of smaller, younger trees. Subsequent continuing mortality of the regenerated trees often stalled the forest at an immature stage. **b.** Douglas-fir beetles killed mature Douglas-fir in groups, usually following windthrow or another disturbance, or single trees at other times. The effect of Douglas-fir beetle, alone or with root disease, was to cause transition to another forest type or to produce a more open stand.

Root pathogens are expected to continue as the most important successional influences during the next 40 years, but somewhat less effect on cover type is expected from root pathogens. The primary reason is that much of the area moved to later-seral cover types during the first 40 years, and will remain in these types until fire or harvesting occurs. Out of roughly half of the hectares in each ecosection with significant root disease effects, about 60 percent of

M332a and 80 percent of M333d are expected to be stalled in pole-sized or small tree stands or mature tree stands with low density.

Dwarf Mistletoes

Dwarf mistletoes are parasitic plants that extract water and nutrients from living conifer trees, having co-evolved with their hosts for millions of years. The different species of dwarf mistletoes are generally host-specific. Lodgepole pine, Douglas-fir, and western larch dwarf mistletoes occur throughout the range of their respective hosts in M332a and M333d.

The parasitic activity of dwarf mistletoes causes reduced tree diameter and height growth, direct tree mortality, and predisposition to other pathogens and insects. Dwarf mistletoe effects on individual trees are quite gradual, so ecosystem functions are the result of long-term infection.

Although each of the three dwarf mistletoe species affected succession only on a small proportion of the total area analyzed, results indicate that they did have significant effects on some pole to mature stands of the host type. Overall, the functions of dwarf mistletoes in forest succession were similar: they generally increased the rate of conversion to later-seral species and produced mature stands with relatively low stocking.

In M332a, overall influence from dwarf mistletoes was expected to stay about the same for the period from 1975 to 2015. In M333d, a small increase may be seen in both Douglas-fir and larch dwarf mistletoes as both species mature. Dwarf mistletoes can also *indirectly* influence succession in that period. Large and numerous brooms on sites heavily infected with dwarf mistletoe can increase the flammability of the site, which in turn can influence fire behavior.

Lodgepole pine dwarf mistletoe

Eighteen percent of the area covered by lodgepole pine structure classes 2, 3, or 4 in M332a and 6 percent of those classes in M333d were rated moderate or high for dwarf mistletoe activity. However, successional effects were attributed to dwarf mistletoes on only 1 percent of the total hectares analyzed within M332a and even less in M333d.

Douglas-fir dwarf mistletoe

Similarly, 16 percent of the area of Douglas-fir cover type in structure classes 2, 3, and 4 had a high probability of mistletoe activity. But Douglas-fir dwarf mistletoe potentially influenced succession on only 4 percent of the area in M332a and 2 percent in M333d.

Larch dwarf mistletoe

Queries identified high or moderate API values for dwarf mistletoe for only 1 percent of the hectares in M333d and even less in M332a. This amounted to 16 percent and 10 percent, respectively, of the area in structure classes 2, 3, and 4 of the host type. Dwarf mistletoe was the only agent associated with most changes in the western larch cover type, and it appeared to play a very significant successional role where western larch was a component in the 1935 era. Western larch often occurred in stands as widely-spaced, mature trees. These trees are often severely infected and have very poor crowns, which likely contribute to early mortality and reduced seed for regeneration. However, other causes were almost certainly responsible for much of the decrease in western larch that occurred between 1935 and 1975 eras. These include other causes of larch mortality and increases in abundance of other species, which then became the predominant species in the stands.

Stem Decays

Stem decay in living trees is caused by several native fungi. In most cases, decay increases with stand age and differs with host species. Stem decays are important in the creation of wildlife habitat in living and dead trees. Wounds are thought to be needed for stem decay to gain entry to trees, or to activate decay from pathogens already present.

Although heartwood decay is not thought to directly impact the growth or vigor of the tree, it does make trees more susceptible to stem breakage. The greater the amount of decay, the more susceptible the tree is to breakage.

High decay succession functions were found on 3 percent of the area in ecosection M332a and 1 percent in M333d. Stem decays tend to be significant in a very few stands. Where significant, their most important outcome was to produce mature stands with low canopy closure. Stem decays have little effect on species composition, but are significant in causing a break-up of the canopy.

Results indicate Indian paint fungus was more prevalent in the 1975 era than in the 1935 era. The hectares with high levels of influence from this pathogen increased from about 6 percent to 15 percent in both ecosections. This is due to the increase in host cover types and multiple-storied stands that favors infection in the understory.

The API values changed little for the other two stem decays over the last 40 years. But there has been a decrease in ponderosa pine and western larch cover types. These species are the most important for cavity nesting species, so has resulted in loss of cavity-nester habitat. This trend is expected to continue over the next 40 years.

Douglas-fir Beetle

The Douglas-fir beetle is a native bark beetle that kills large-diameter, mature Douglas-fir (Figure 12b). When populations are low, individual trees or small groups of trees are infested and killed (called the "weeding" function of bark beetle attack). Infested trees are typically those weakened by drought, defoliation, or root disease. Large-scale outbreaks that attack whole stands (resulting in a group-killing action) are usually triggered by a large-scale windthrow event. The availability of fire-weakened trees or those defoliated by western spruce budworm or Douglas-fir tussock moth may also contribute to an outbreak.

The Douglas-fir outbreak that started in northern Idaho in 1998 is a good example of an outbreak initiation. Bark beetle populations built up in trees downed by an ice storm and heavy snowfalls during the winter of 1996-1997. The beetles infested the trees in the spring of 1997, and emerged and attacked standing green trees in the spring of 1998. Groups of 50 to several hundred trees were attacked in infested areas, and major changes in stand cover and structure can now be expected during the two- to four-year outbreak cycle.

Twenty percent of the hectares analyzed for transitions in M332a were assigned a high, moderate, or low probability of transition due to Douglas-fir beetle (20 percent, high; 48 percent, moderate; and 32 percent, low). In M333d, 11 percent of the total hectares was assigned a high, moderate, or low probability of transition due to Douglas-fir beetle (6 percent, high; 42 percent, moderate; and 53 percent, low).

Douglas-fir beetle influenced succession on 14 percent of the area in M332a and 4 percent in M333d. The transitions attributed to Douglas-fir beetle were very similar in the two ecosections. The most common changes were from mature Douglas-fir cover type to a forest type of another, most often a climax, species and a change in structure to a younger class or more open forest canopy.

The functions of Douglas-fir beetle weeding and group-killing actions were similar but differed in magnitude. Douglas-fir beetle group-killing resulted in a higher probability of transition than did the weeding action.

It was uncommon for significant Douglas-fir beetle function to occur in the absence of root diseases, but it did occur on 3 percent of the hectares in M332a and less than 1 percent of M333d during the 40 years examined. Many stands that rated high or moderate for root disease also rated low (but not 0) for Douglas-fir beetle function because they contained only a few Douglas-fir large enough for beetle attack. The combination of the two agents will increase the probability of transition. Although not as dramatic as group-killing actions during outbreaks, endemic Douglas-fir beetle populations in conjunction with root disease caused significant changes on the landscape over time.

Douglas-fir beetle will continue to be a major agent of change during the next 40 years. In ecosections M333d and M332a, respectively, 40 percent and 46 percent of the areas are currently in pure or mixed Douglas-fir types in structure classes 2, 3, or 4. Approximately one-fifth of the area in each ecosection rated high or moderate probability for significant successional effects in the 1975 era.

Mountain Pine Beetle in Lodgepole Pine

The mountain pine beetle is a native bark beetle that kills lodgepole and other pine species. Most years, mountain pine beetle populations persist in small pockets of dead trees. Outbreaks, however, periodically occur that can kill most lodgepole pines in susceptible stands over quite large areas (Figure 13a).

Mountain pine beetle in lodgepole pine altered succession on 19 percent of M332a and 3 percent of M333d. The most common successional transition was to change species composition to another type, usually subalpine fir. Of the lodgepole pine cover types in the 1935 era, 50 percent of the area in M332a and 57 percent in M333d stayed lodgepole pine, and the rest transitioned to various other cover types.

There were significant changes in structure class distributions in lodgepole pine between the 1935 and 1975 eras. In general, the amount of structure class 1 decreased, presumably due to reduced stand-replacing fire. The amount of structure class 2 increased considerably, primarily due to growth of young stands. The amount in structure class 4 decreased in M332a and stayed essentially the same in M333d. There was little structure class 3 in either sample. Structure classes 3 and 4 represent larger diameters than lodgepole pine stands usually achieve.

Most of the transitions in lodgepole pine cover type in the 1935 era were consistent with mountain pine beetle activity. In lodgepole pine cover types, 98 percent of cover and structure changes in M332a were associated with mountain pine beetle. This is true of 60 percent of the changes in M333d.

Given conditions in the 1975 era, ecosection M333d should see an increase in mountain pine beetle influence by 2015 to about 12 percent of the hectares, while M332a may see a small decrease to about 10 percent. More than 80 percent of the lodgepole pine stands in each ecosection were in the most susceptible size class, but without fire or regeneration, harvesting the total amount of lodgepole pine will continue to decrease.

Mountain Pine Beetle and Western Pine Beetle in Ponderosa Pine

The mountain pine beetle and western pine beetle are the two most significant bark beetles of ponderosa pine in the United States. Successful attacks kill the host: either single, large, slow-growing old ponderosa pines or groups of younger trees in overly dense stands.

One or both beetles were associated with successional changes on 6 percent of the area in M332a and 2 percent in M333d. The most common function of the two beetles was to push toward late-seral species. A major loss of ponderosa pine cover type occurred between 1935 and 1975 eras. In M332a, 52 percent changed to another type and, in M333d, 68 percent changed. The changes were mainly attributed to mountain pine and western pine beetles, acting on stands of increased density due to fire suppression. In the absence of fire, not only have stand densities increased, but the amount of fire-susceptible Douglas-fir and grand fir increased.

The overall activity of pine bark beetles will decline during the next 40 years, because of reduced amounts of pine cover types. But they will remain active where susceptible pine type occurs, which is highly significant given the already depleted condition of stands of large pines.

Mountain Pine Beetle in Western White Pine

Mountain pine beetle attacks and kills mature western white pine (Figure 13b), and played a significant role in historical western white pine forests. Major outbreaks were recorded in the early 1900s, providing information on this role.

Figures 13a and 13b. Mountain pine beetle-caused mortality. Mountain pine beetle-influenced succession in lodgepole pine, western white pine. **a.** Outbreaks killed lodgepole pine over large areas, typically converting these stands to another forest type, usually subalpine fir. **b.** Mature western white pine stands were killed by beetle outbreaks in the early 1900s, which created fuels to support stand replacement fires that were common then. Today, mature white pine stand are uncommon, but mountain pine beetle continues to remove the last of the mature white pines from mixed-species stands.

The loss of white pine in pine cover types either accelerated succession to a later-seral species composition, or changed cover types to other seral species. Forest structure class was also affected by mountain pine beetle. Selective killing of white pine opened up stands, changing them from a mature closed canopy (structure class 3) to an open canopy (structure class 4). Beetles may also have affected forest structure in structure class 4 by continually killing trees and keeping the canopy open.

Mountain pine beetle influenced succession of western white pine on 2 percent of the area in M332a and 4 percent in M333d. The highest mountain pine beetle API values occurred in western white pine cover types with mature closed canopy (structure class 3) in ecosection M333d.

These functions are probably similar to those played by mountain pine beetle in the past, even in prehistoric times. However, in the past, this insect likely played a larger role in resetting succession by creating fuels that predisposed forests to stand-replacing fires. Such fires were responsible for regeneration of western white pine, a function that has been greatly limited today.

1975-era data show only a small amount of western white pine cover type, and even less that is in structure classes susceptible to mountain pine beetle. Therefore, mountain pine beetle's successional activity is expected to be very low in the next 40 years. However, the beetle will likely continue to play a critical role in removing the last old-growth white pine stands and most of the mature, potentially blister rust-resistant trees from mixed species stands.

Spruce Beetle

The spruce beetle is a native insect that infests all species of spruce. In the ecosections we analyzed, Engelmann spruce is its most common host. Most outbreaks occur following a population buildup in large-diameter windthrown spruce. Standing trees most susceptible to attack are mature, large-diameter (greater than 16 inches) trees, growing in dense stands with a large component of spruce, and which exhibit a slower-than-average growth rate in recent years.

There were no large expanses of spruce in either ecosection analyzed. Transitions occurring in M332a that were attributed to spruce beetle covered less than 1 percent of the total sample area, and in M333d, they occurred on only 2 percent of the area. The majority of transitions in both ecosections resulted in conversion to later-seral species with the loss of spruce, and a change to a more open canopy.

Spruce beetle activity in riparian areas will add large woody debris to streams, but also cause a loss of solar insolation. Endemic spruce beetle activity is probably beneficial by slowly creating high-quality snags over time. Outbreaks cause the loss of spruce component in a few years time, and also cause rapid change in dominant tree species and forest structure. These areas will be dominated by climax species, and forest structure will change to younger age classes or open canopies. A loss of large-diameter snags to replace woody debris in streams may result.

Western Spruce Budworm

Western spruce budworm-associated successional changes were observed in 3 percent of the area in M332a and in less than 1 percent of the area in M333d. The most significant budworm damage occurs on warm, dry sites. As a stand matures, budworm kills pockets of regeneration and pole-sized trees, thus allowing seral components of the stand and larger Douglas-fir to remain in a dominant position. Douglas-fir dwarf mistletoe, stem decay, root disease, or Douglas-fir beetle had moderate to high probabilities in all transitions with moderate to high budworm probabilities.

Significant Combinations of Agents

The majority of sampled stands had conditions that could support a variety of pathogen and insect activities. Based on the co-ocurrence of moderate to high API values for two or more agents, combined effects in the 1975 era were indicated in 60 percent and 62 percent of hectares in M332a and M333d, respectively. Co-occurrent combinations are summarized in Tables 4 and 5. Nine pairs of pathogens and/or insects co-occurred in at least 5 percent of the sample in each of the ecosections.

Table 4: Co-occurrence of moderate to high index values for insects and pathogens in the 1975 sample polygons for ecosection M332a.

M332a: Combinations of moderate to high APIs; percent of total hectares in 1975.			
First Agent		**Second Agent**	**Percent of Hectares**
Douglas-fir dwarf mistletoe	and	Root disease	21
Root disease	and	Stem decay in true firs/hemlocks	13
Douglas-fir dwarf mistletoe	and	Douglas-fir beetle	13
Douglas-fir beetle	and	Root disease	12
Spruce beetle	and	Root disease	11
Stem decay in lodgepole pine	and	Mountain pine beetle in lodgepole pine	7
Spruce beetle	and	Stem decay in true firs/hemlocks	7
Douglas-fir dwarf mistletoe	and	Mountain pine beetle in ponderosa pine	5
Douglas-fir dwarf mistletoe	and	Western spruce budworm	5

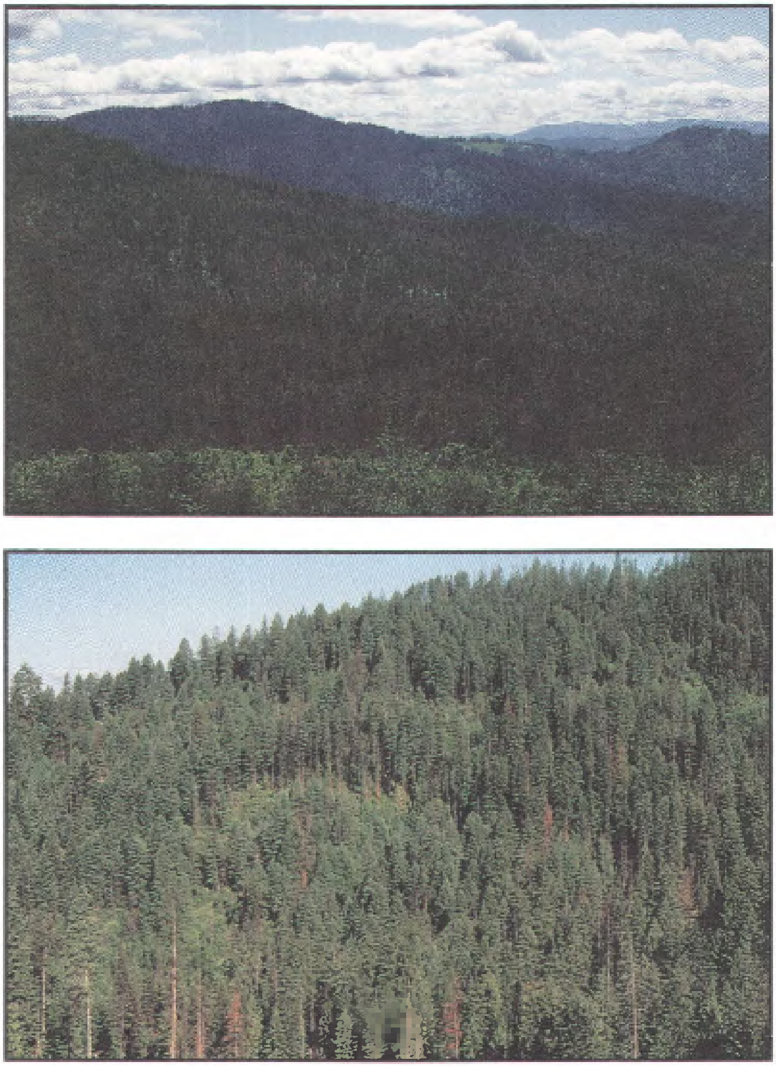
Table 5: Co-occurrence of moderate to high index values for insects and pathogens in the 1975 sample polygons for ecosection M333d.

M333d: Combinations of moderate to high APIs; Percent of total hectares in 1975.			
First Agent		**Second Agent**	**Percent of Hectares**
Douglas-fir dwarf mistletoe	and	Root disease	16
Root disease	and	Mountain pine beetle in western white pine	11
White pine blister rust	and	Douglas-fir beetle	8
White pine blister rust	and	Mountain pine beetle in western white pine	7
Stem decay in true firs/hemlocks	and	Mountain pine beetle in western white pine	7
Douglas-fir dwarf mistletoe	and	Western spruce budworm	6
Douglas-fir beetle group	and	Douglas-fir dwarf mistletoe	6
Root disease	and	Douglas-fir beetle group	5
Root disease	and	Lodgepole pine dwarf mistletoe	5

Where more than one pathogen or insect was active in a stand, their effects were either similar or opposing. When agents co-occurred, the succession function was due to combined actions of the agents. Examples of agents with additive effects were: root diseases and Douglas-fir beetle, root diseases and Douglas-fir dwarf mistletoe, and white pine blister rust and mountain pine beetle. Examples of agents with opposing effects were: bark beetles killing ponderosa pine and root diseases killing Douglas-fir in the same stands, and white pine blister rust killing white pine and root diseases killing Douglas-fir and grand fir in the same stands.

NET CHANGES FOR 1935-1975 ERAS AND PREDICTIONS FOR 1975-2015

If we assume that pathogen and insect effects will be similar in the future to what they were in the past, then a rough estimate of probable future conditions can be predicted for lands that are neither harvested or burned. Figures in this section show net changes in cover type and structure class from all causes between the 1935 and 1975 eras, with projections for the subsequent 40 years based on similar trends. Root pathogens and bark beetles are expected to cause most of the change during subsequent decades (Figures 14a and 14b), but other agents will also be highly significant because they reduce the amount of already declining types.



Figures 14a and 14b. Mortality patterns. Root pathogens and bark beetles are expected to cause the most forest change in future decades. **a.** The susceptibility of current forests to Douglas-fir beetle is illustrated by the widespread mortality in the Coeur d'Alene area following the ice storm of 1996-1997. **b.** Root pathogen effects are easily overlooked because they kill only a few large trees per acre each year, but over time root disease can create large openings. Our results indicate that the less-noticeable, annual mortality caused by root diseases and lower populations of bark beetles causes even greater change on the landscape over the long term than outbreaks. In the absence of fire or management, the net outcome of pathogens, insects, and silvical succession will be continued losses of shade-intolerant pines and larch, nonforest shrubfields, and seedling-sapling structure classes.

The most important future successional influence will be continued acceleration toward climax. As the amount of later-seral forest increases, largely in mature forest classes, increased mortality in these stands can be expected to produce more open canopies. The amount of nonforest and young, seedling/sapling stands is expected to decrease. It is unclear how well

Table 7: Expected trends; influences of pathogens and insects in ecosection M333d from 1975 to 2015.

Pathogen/Insect	Proportion of ha[1]	Primary Cover Effect (proportion)[2]	Primary Structure Effect (proportion)[2]
White pine blister rust	.35	Increase climax (.6)	No effect (.4) Prevent closure (.4)
Root pathogens	.66	Increase climax (.6)	Toward immature (.4) Prevent closure (.4)
Douglas-fir beetle	.18	No effect (.5) Increase climax (.40)	Prevent closure (.6) Toward immature (.3)
Mountain pine beetle, lodgepole pine	.12	Increase climax (.7)	Toward immature (.6)
Mountain pine beetle/ western pine beetle in ponderosa pine	.08	Increase climax (.9)	Toward immature (.5) Prevent closure (.5)
Mountain pine beetle, western white pine	.03	No effect (.7)	Prevent closure (.9)
Douglas-fir dwarf mistletoe	.19	No effect (.6)	Prevent closure (>.9)
Lodgepole pine dwarf mistletoe	>.01	Maintain seral (>.9)	Prevent closure (>.9)
Western larch dwarf mistletoe	.03	Increase climax (>.9)	Prevent closure (>.9)
Stem decays	.08	No effect (.6)	Prevent closure (.9)
Spruce beetle	.02	No effect (.7)	Prevent closure (.5) Toward immature (.4)
Spruce budworm	.04	No effect (>.9)	Prevent closure (>.9)

[1] Proportion of hectares in M332a that are expected to be strongly influenced by the pathogen or insect.
[2] Of the hectares expected to be most affected by the pathogen or insect, the proportion likely to show each successional effect.

Overall, observed trends are expected to continue (Figures 17 and 18). Blister rust effects on existing western white pine stands will decrease because of a reduced amount of susceptible young western white pine, but white pine that naturally regenerates will continue to be killed. Effects from root diseases and bark beetles will increase. Eighty percent of the stands are expected to progress to climax or remain in climax classes, with only 20 percent expected to remain in seral cover types. About one third of the area is expected to have low canopy density, remain stalled in small, young tree classes, or move into small, young tree structures as a result of pathogen and insect activity.

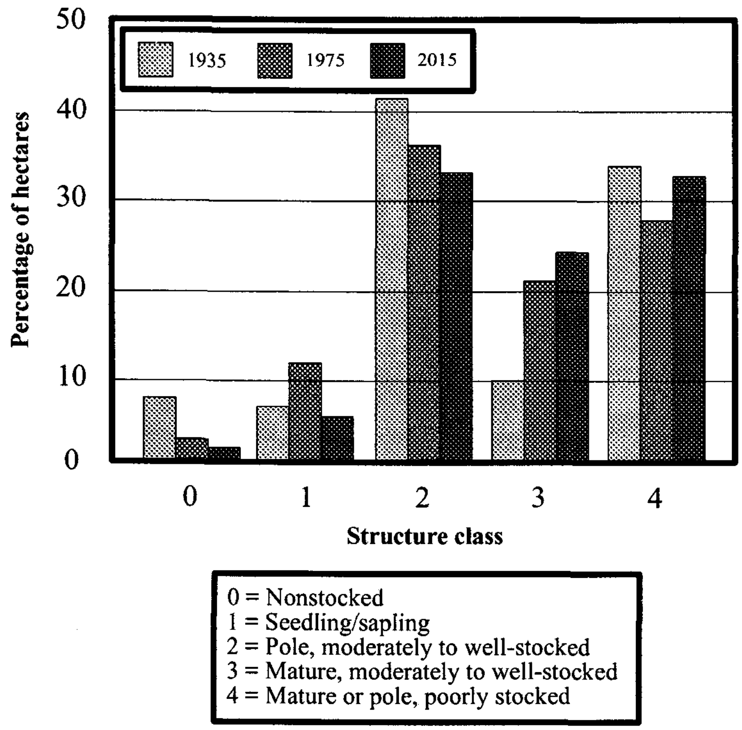


Figure 16: 1935-1975 eras' changes in structure classes from all causes, projected to 2015, M332a.

M333d

Root diseases and white pine blister rust will continue to cause most of the change during the next 40 years (Table 7). In addition, Douglas-fir beetle and mountain pine beetle are expected to increase dramatically. Douglas-fir dwarf mistletoe and stem decays are likely to increase as well.

Continued loss of the major seral species (ponderosa pine, western larch, and lodgepole pine) is expected, along with an increase in later-seral species (grand fir and subalpine fir) (Figure 15). Douglas-fir is expected to peak and begin to decline. Overall, 45 percent of the 1975-era sample is expected to remain in later-seral or climax cover types, and another 24 percent is expected to reach those classes. The rate of accumulation of large tree, dense stands may decline greatly as pathogens and insects remove stands from this class and prevent many others that would normally go there from reaching it (Figure 16).

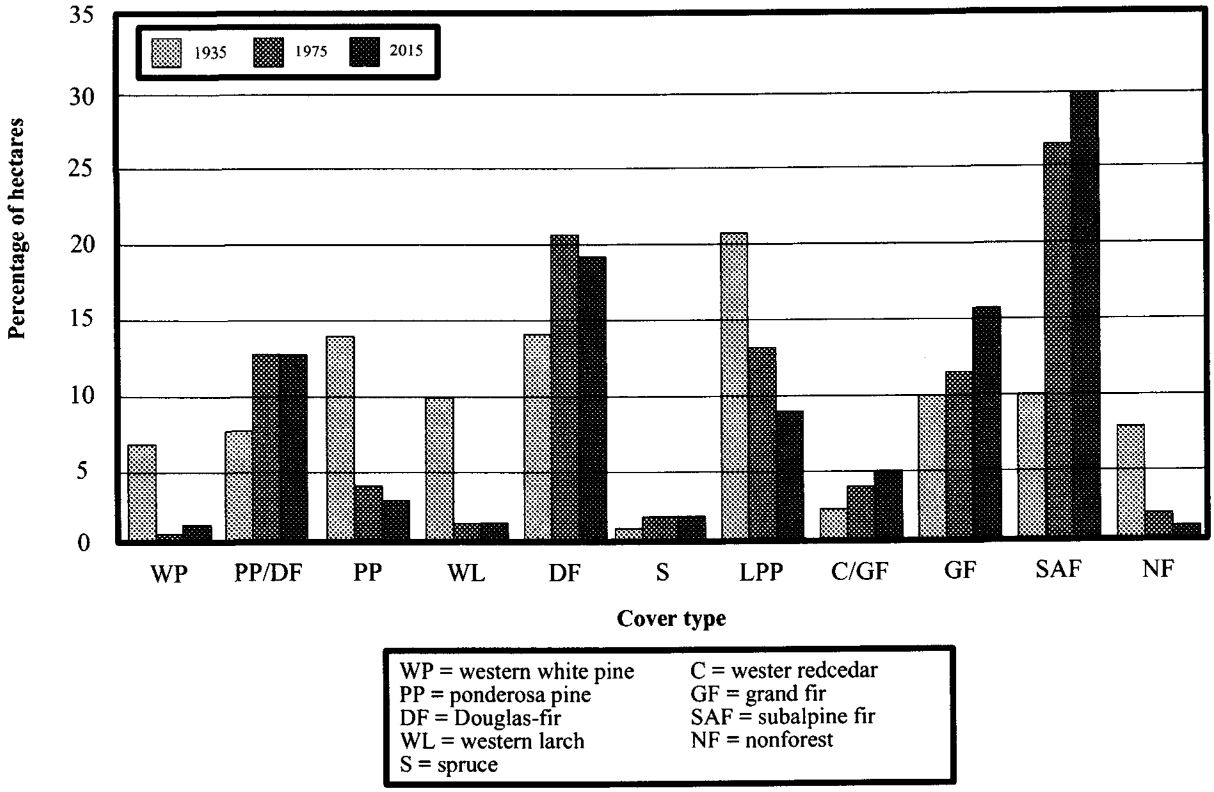


Figure 15: 1935-1975 eras' changes in cover type from all causes, projected to 2015, M332a.

western hemlock, western redcedar, and grand fir will perform over the long term: amounts of these cover types present on the landscape today are unprecedented. Grand fir, in particular, is susceptible to root pathogens and bark beetles. Western redcedar has decline symptoms in some areas, a condition that appears to be due in part to root disease. All of these species are highly susceptible to drought, stem decays, and fire. Past experience indicates that the influence of pathogens, insects, and other factors increases when there is a major increase in climax cover types.

M332a

Root diseases and Douglas-fir beetle are expected to cause most of the successional change between 1975-2015 (Table 6).

Table 6: Expected trends in influences of pathogens and insects in ecosection M332a from 1975 to 2015.

Pathogen/Insect	Proportion of ha[1]	Primary Cover Effect (proportion)[2]	Primary Structure Effect (proportion)[2]
White pine blister rust	<.01		
Root pathogens	.43	Increase climax (.6) Maintain seral (.2)	Toward immature (.3) Prevent closure (.3) No effect (.3)
Douglas-fir beetle	.18	Increase climax (.6)	Prevent closure (.4) No effect (.3)
Mountain pine beetle in lodgepole pine	.09	Increase climax (.9)	No effect (.7)
Mountain pine beetle/ western pine beetle in ponderosa pine	.05	Increase climax (.8)	Toward immature (.5) Prevent closure (.3)
Mountain pine beetle in western white pine	<.01		
Douglas-fir dwarf mistletoe	.04	No effect (.5) Maintain seral (.4)	Prevent closure (>.9)
Lodgepole pine dwarf mistletoe	<.01		
Western larch dwarf mistletoe	<.01		
Stem decays	.04	No effect (.5) Maintain seral (.4)	Prevent closure (.9)
Spruce beetle	.06	Increase climax (.9)	No effect (.9)
Spruce budworm	.03	No effect (.6)	Prevent closure (>.9)

[1] Proportion of hectares in M332a that are expected to be strongly influenced by the pathogen or insect.
[2] Of the hectares expected to be most affected by the pathogen or insect, the proportion likely to show each successional effect.

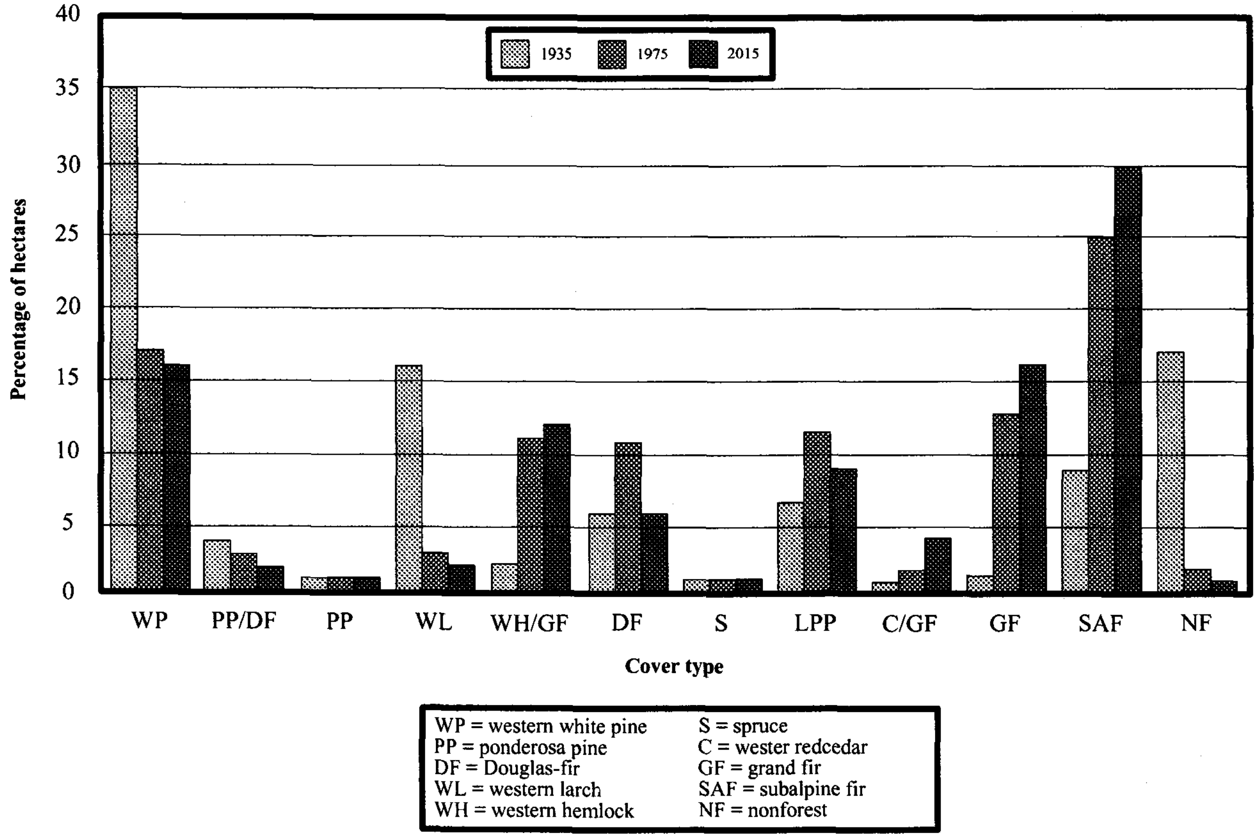


Figure 17: 1935-1975 eras' changes in cover type, projected to 2015, M333d.

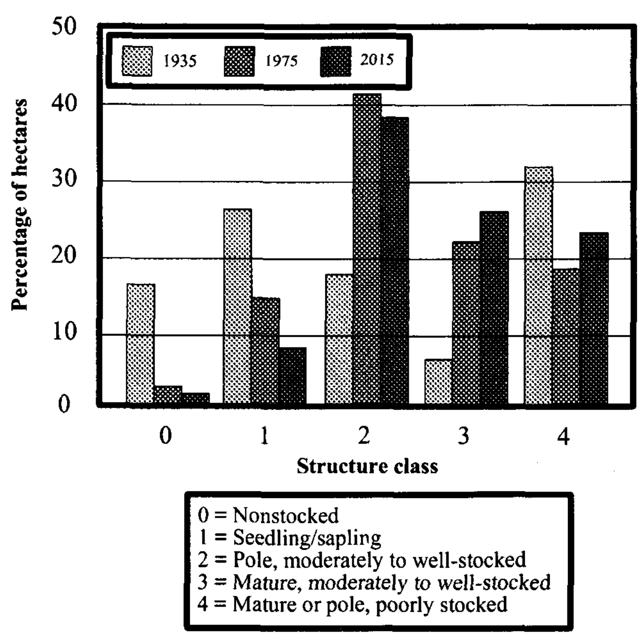


Figure 18: 1935-1975 eras' changes in structure classes, projected to 2015, M333d.

SUMMARY, CONCLUSIONS, AND IMPLICATIONS

The analysis began with three questions: what is the rate of change in forests in the absence of fire or active management? how significant are the roles of pathogens and insects in this change? how do pathogens and insects influence forest succession? These questions have significant management implications.

The rates of change were very significant. More than 90 percent of the sample stands changed to a different cover type, structure type, or both during the 40-year period between 1935 and 1975 eras. It was during this time that white pine blister rust became epidemic in western white pine forests and fire suppression policies were implemented. These results show the dynamic nature of forests in the analysis area, even in the absence of fire or management.

Pathogens and insects were involved with 75 percent or more of the observed changes. The most significant cause of successional change was the introduction of white pine blister rust, which resulted in widespread killing of western white pine.

Native pathogens and insects played major successional roles in both ecosections. Root diseases and bark beetles caused the most change, but many other agents caused significant changes in susceptible forest types and structure classes. The most common succession function of pathogens and insects was to accelerate the change to later-seral, more shade-tolerant species by killing early seral, shade-intolerant species, often while reducing stand density or preventing canopy closure. In particular, root diseases maintained lower stand densities and smaller trees. A less common but ecologically important function was to prolong early seral types by killing shade-tolerant species.

The trend toward mature, dense, climax forest is projected to decrease substantially with greater accumulations occurring in low-density mature and younger pole-sized stands that result from root disease- and bark beetle-caused mortality. A decrease can be expected in Douglas-fir, with the aging of 1975-era stands, making them susceptible to Douglas-fir beetle in addition to root diseases. Although root pathogens and bark beetles are expected to cause the most change, other agents will be highly significant because they decrease the amount of already declining types. In ecosection M333d, only 20 percent of the cover will be in early seral species, and only about 30 percent of M332a is expected to be seral.

In general, non-forest and seedling-sapling structures will continue to decrease. The amount of pole stands increased greatly in M333d from the 1935 era to the 1975 era, and large increases in mature, well-stocked stands occurred in both ecosections. Our evidence indicates that this trend will slow down and perhaps reverse during the next 40 years as bark beetles and root diseases reduce stand densities.

Vegetation changes have very significant implications for wildlife, biodiversity, productivity, watershed, and other resource values (Atkins et al. 1999). Management decisions should consider the predicted trends in forest condition with reference to desired conditions, which may be different from either historic or current conditions.

Results are applicable for forest planning at a variety of scales. Results specifically addressed the effects of the "no-action alternative" at the ecosection scale: our information can be used by managers to consider the effects of "no-action" policies on long-term vegetation trends. The information can be used directly, or further analysis can be done in planning units using technology developed for this assessment.

Results of this study underscore the relevance of pathogens and insects to forest planning and forest management. It is important to consider the pathogen and insect effects at broad scales of planning. They cause large changes at the landscape scale, which can affect planned objectives and change priorities. The introduction of white pine blister rust greatly reduced the abundance of western white pine (Neuenschwander et al. 1999). Our assessment indicated that native "outbreak insects" also produced significant changes. The cumulative effects of less-apparent agents such as root pathogens and endemic bark beetles caused even more significant successional changes over the long term than many short-term, intensive outbreaks.

The ecological effects of native pathogen and insect activities are sometimes desirable and sometimes not. We should consider whether they help maintain desired conditions or create less desirable conditions in deciding whether or not to alter their influence through management.

Different influences produce different successional effects. It is important to consider the effects of combined influences, especially including management, insects, pathogens, and fire. In the past, the origin of western white pine, western larch and other seral species in these analysis areas can be traced to large stand replacement and mixed severity fires (Smith and Fischer 1997). Pathogens and insects can complement fire by helping to maintain early seral species.

In the absence of fire, pathogens and insects generally reduce the abundance of seral tree species, and significant trends toward late successional stages can occur within a few decades. Although insects and diseases kill overstory trees, leading to regeneration or release, mostly mid- or late-seral species are regenerated or released. Thus, in the absence of fire or active management to favor historic and prehistoric cover types and structure classes, these types and structures will not be maintained or recruited.

We found that pathogens and insects can have large effects on forest succession. The economic impacts of pathogens and insects on resource production have been well documented; with this analysis, we have begun to understand and quantify their successional effects

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APPENDIX A: TABLES OF CONTENTS, VOLUMES 1 AND 2

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