FIRE-INSECT-DISEASE RELATIONSHIPS OF A LODGEPOLE PINE ECOSYSTEM IN SOUTH-CENTRAL OREGON

Final Report on
National Science Foundation Grant DEB-8109813

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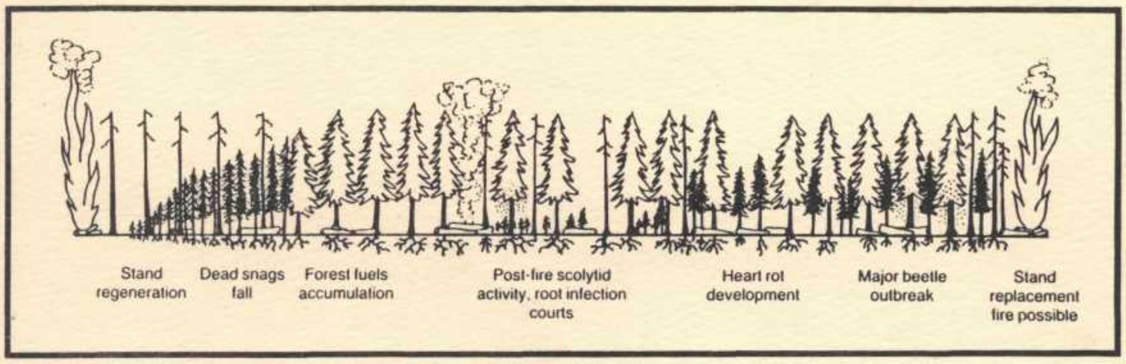

College of Forest Resources
University of Washington
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July 1985

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EXHIBIT VI-1

NATIONAL SCIENCE FOUNDATION
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FINAL PROJECT REPORT
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PART I–PROJECT IDENTIFICATION INFORMATION

1. Institution and Address College of Forest Resources University of Washington Seattle, WA 98195	**2. NSF Program** Ecology Program	**3. NSF Award Number** DEB 8109813
	4. Award Period From 7/1/81 To 12/31/84	**5. Cumulative Award Amount** $170,000

6. Project Title
Fire-Insect-Disease Relationships of a Lodgepole Pine Ecosystem in South Central Oregon

PART II–SUMMARY OF COMPLETED PROJECT *(FOR PUBLIC USE)*

Our goal was to quantify the relative roles fires, fungi, and mountain pine beetle (MPB) play in establishment and development of a climax lodgepole pine stand in south-central Oregon, and integrate these results into a descriptive stand model to reflect the consequences of each process and the impact of random environmental events or specific intervention measures. This required basic research in the following areas: 1) lodgepole pine regeneration; 2) fire behavior in lodgepole pine stands; 3) fire effects on lodgepole pine; 4) fire dependent fungal pathogen complexes; 5) MPB brood production and host selection patterns; and 6) fire-fungal-MPB interactions.

We found that trees became established after moisture competition was reduced by overstory mortality by fire or insects. Fire spread is limited by low fuel production in these low productivity stands, and that fires burn primarily along old logs. Along such corridors roots can be killed, which causes immediate stress and insect attack, or scarred which creates infection courts for fungi that later reduce tree vigor. Decades later, then trees may be "focus" trees for mountain pine beetles, and determine the magnitude of subsequent beetle outbreaks.

Our current research provides evidence that the interactions of fire, fungi and mountain pine beetle attacks are all tightly woven together in an ecosystem that perpetuates lodgepole pine in the tephra-derived soils of south central Oregon. Understanding the interactions of fire, fungi and mountain pine beetle populations are advantages forest managers now have in their attempt to minimize the effects of scolytid epidemics, and to determine the optimum time to harvest trees, conduct prescribed burns, or artificially intervene in the normal dynamics of the forest ecosystem.

PART III–TECHNICAL INFORMATION *(FOR PROGRAM MANAGEMENT USES)*

1. ITEM *(Check appropriate blocks)*	NONE	ATTACHED	PREVIOUSLY FURNISHED	TO BE FURNISHED SEPARATELY TO PROGRAM	
				Check (✓)	Approx. Date
a. Abstracts of Theses		X			
b. Publication Citations		X			
c. Data on Scientific Collaborators		X			
d. Information on Inventions	X				
e. Technical Description of Project and Results	▨	X			
f. Other *(specify)*	▨				

2. Principal Investigator/Project Director Name *(Typed)* Robert I. Gara	**3. Principal Investigator/Project Director Signature** James K Agee FOR R.I. GARA	**4. Date** 8/8/85

Background

Lodgepole pine covers some 3 million acres of commercially important and scenic lands of the Pacific Northwest. The species, *Pinus contorta* var. *murrayana* (Grev. and Balf.) Engelm., has a wide ecological amplitude, and as such, it represents a valuable timber species of the region although its past commercial value has been low. Its positive establishment following fires and its rapid juvenile growth offer promise that the species can be used in short rotation management schemes (Wellner 1973, Cole 1973, Dahms 1973). Besides their potential for timber production, lodgepole pine forests provide vast recreation and wilderness areas (Despain 1973, Litton 1973), important water source areas (Hoover 1973), and range and wildlife habitats (Dealy 1973).

Lodgepole pine was one of the pioneering species to occupy infertile tephra deposits at the close of the last glacial period in the southern Oregon Cascades (Hansen 1946). Franklin and Dyrness (1973) consider the virtually pure lodgepole pine stands to be an edaphic climax community on many sites of this so-called pumice plateau of south-central Oregon.

Under certain circumstances the dynamics of these forests are controlled by the interacting effects of fires, the mountain pine beetle (*Dendroctonus ponderosae* Hopk.), and fungal pathogens (Geiszler et al. 1980).

Project Objectives

Our main research goal was to quantify the relative roles fires, fungi, and mountain pine beetle (MPB) play in establishment and development of a climax lodgepole pine stand in south-central Oregon. Furthermore, we proposed to integrate these results into a descriptive stand model to reflect the consequences of each process and the impact of random environmental events or specific intervention measures. Accordingly, the development of the chronosequence and interaction that are inherent to this dynamic scenario required basic research in the following areas:

1) lodgepole pine regeneration;
2) fire behavior in lodgepole pine stands;
3) fire effects on lodgepole pine;
4) fire dependent fungal pathogen complexes;
5) MPB brood production and host selection patterns;

and

6) fire-fungal-MPB interactions.

The research results summarized below reflect the current status of our knowledge concerning the dynamics of climax lodgepole pine stands in south-central Oregon.

Research Sites

Our research sites within the Fremont National Forest and adjacent areas encompassed several discrete fire sites; these areas have been the scene of recurring mountain pine beetle infestations (R.E. Dolph, pers. comm. 1980). These burned sites included: 1) Bald Mt.--a prescribed fire of 1982; 2) Wickiup Springs--a prescribed fire of 1976; 3) Lookout Point--a stand replacement fire that occurred in 1839 and a moderate fire in 1898; 4) a 1980 fire at Crater Lake National Park that burned through climax lodgepole pine in the Sharp Peak area of the park; and 5) the 1982

Desert Cone fire which ignited naturally in an area near the north park boundary.

All study areas were about 1,800m elevation with soils derived from Mt. Mazama pumice and ash, which was deposited about 6,600 years ago. The area received an additional tephra deposit from the Paulina Peak eruption ca. 4,000 years ago. Annual precipitation, largely as snow, averages 60 cm. Because of the coarse textured surface soil and low rainfall, plant species diversity of this pumice plateau is low, and trees, shrubs, and herbs are shallow rooted.

As described by Volland (1982), large areas of these infertile, harsh sites support sparse *P. contorta* stands growing in lodgepole pine/needlegrass basin communities--essentially topoedaphic climaxes (Franklin and Dyrness 1973).

Plots established at Lookout Point and various other locations were intensively sampled for: 1) incidence of fire scars, 2) diameters of trees, 3) MPB attack status, 4) amount of fire damage, 5) regeneration patterns, 6) fungal pathogens, and 7) dendrochronological data.

Results

Regeneration Patterns--Studies were established at Wickiup Springs using a stratified random sample design to test for: the spatial pattern of seed dispersal and the number of seeds dispersed. At the same time cones were collected for subsequent germination trials.

Site characteristics which were measured included temperature profiles and soil moisture analyses taken during July and September 1981 at depths of 3, 8, and 15 cm from four ecological zones: under the canopy; from the seedling groups; in the open; and from the 1976 burn site. Plant moisture stress was evaluated for seedlings established after the 1976 burn, seedlings found in clusters around previous MPB-killed trees, and those growing under the canopy.

The effects of MPB activity or previous fires on regeneration patterns was investigated by destructively sampling seedlings for dry weights, foliar nutrients, and percent live fuel moisture. In addition an experiment designed to determine the effects of soil moisture and microclimate on first-year seedling survival was established. The treatment groups included seedlings growing under the canopy, those growing in groups around MPB-killed snags, those growing in the open, and the ones established during the 1976 burn. The treatment applied to each of these groups included: trenching around the seedlings--to destroy root competition from surviving trees; application of slash--to observe seedling establishment in association with a "protective niche" provided by the slash, trenching and slash, and controls. The results of these regeneration studies have been published elsewhere in greater detail (Stuart 1982). Some of the major conclusions from these studies show that:

1). Stratified lodgepole pine seeds germinated readily (95% success).

2). Seedling establishment was negligible in open areas, low under the canopy, successful in the area of the 1976 burn, and highest in clusters around the base of MPB-killed trees.

3). The pattern of seedling establishment correlated closely with soil moisture transects, i.e. lowest soil moisture in the open and under the canopy and highest among clustered seedlings.

4). Seedlings, however, with the least moisture stress were those established in the 1976 burn; those in the seedling clusters were moderately stressed; those growing under the healthy canopy were most most severely stressed (Table 1).

5). Seedlings established in the 1976 burn were the most thrifty of all those sampled. Although the burn-established-seedlings had no significant differences in foliar nutrients, they had a 10 fold higher dry weight and significantly higher percent fuel moisture than any other seedlings.

6). The main reason seedling establishment doesn't occur, either in openings or directly under the lodgepole canopy, is that the extensive rooting system of the established trees effectively utilizes all available moisture.

7). Seedlings, therefore, establish after root competition is eliminated following fire or from around individual MPB-killed trees.

Table 1. Scholander pressure bomb readings (absolute values in bars) of 1-year old needles taken at solar noon 8/26/81, Wickiup Springs, Fremont National Forest, Oregon; mean of 5 seedlings per treatment.

Seedlings in '76 burn	Seedlings Groups under MPB-killed trees	Seedlings under healthy canopy
17.6	19.0	22.2*

* Nested Anova test reveals significant differences between groups (0.10<P>0.025) and subgroups (P<.001).

<u>Fire Behavior</u>--Limited information exists on fire behavior of climax lodgepole pine stands. Some experimental burning was done in 1976 at Wickiup Springs, and at two fires within Crater Lake National Park.

Climax lodgepole pine forests are more fuel-limited than other forested communities in the Pacific Northwest. The exceptionally low wood productivity (1-2 m^3/ha yr) and leaf area (1-2 m^2/m^2) result in little fuel accumulation, particularly of fine fuels that usually carry the fire. Both prescribed and natural fires in summer months have been observed to spread widely across red fir (<u>Abies magnifica</u> var <u>shastensis</u> Lemm.) and ponderosa pine (<u>Pinus ponderosa</u> Doug. ex Loud.) forests without entering adjacent climax lodgepole pine stands. Where spread into lodgepole pine stands occurred, it was always along corridors of partially-decayed logs, remnants of a disturbance several decades earlier (Agee 1981). Under the conditions we have observed, fire presence and behavior in lodgepole pine forests is more closely linked to coarse fuel dynamics than to fine fuel dynamics, and thus to the history of past disturbances.

Logs often have higher fuel moistures than associated fuel classes, but the quantity and arrangement of these other fuel classes are such that they rarely carry the fire. For example, in the Crater Lake 1982 prescribed fire, litter and fine fuel moistures ranged from 4 to 10 percent, but the fuel was too discontinuous to sustain fire spread. The highest dead fuel moisture content (42 percent dry wt.) was measured in the interior of a decayed log, and this was the only fuel that would carry the fire.

Agee (1981) describes two primary mechanisms which are responsible for fire spread along these moist, partially decayed logs. First, the decayed interior of the log is usually surrounded by a less-decayed rind of sapwood. This allows for reasonable air circulation while the rind helps conserve heat by reducing convective heat loss from the log interior. As the interior portion flames or smolders, the sapwood rind may collapse and be consumed, or may be left as charred residue as the fire slowly moves along the log. The second characteristic of these logs is that rotten wood generally requires less energy to produce the combustible gases required for ignition (Susott 1982). These physical and chemical characteristics appear to favor partially decayed logs as fire corridors under most conditions. Less-decayed logs would be more likely to burn in years of extended drought when fuel moisture is very low. The result of this typical fire spread pattern is a matrix of burned log corridors with unburned areas in the gaps between logs (Figure 1).

Several implications for fire behavior in climax lodgepole pine can be made from our studies to date, including:

1). Fire spread is fuel limited because of low stand productivity.

2). Partially decayed logs appear to have physical and chemical characteristics that allow energy produced in the exothermic phases of combustion to be efficiently utilized.

3). Downed logs tend to be the corridors along which fire spreads under moderate fire weather conditions--a link to past stand disturbances (MPB, pathogens, fire).

Fire Effects--By standard dendrochronological methods (Stokes and Smiley 1978) we determined that the lodgepole pine stand at Wickiup Springs largely regenerated after an 1839 stand-replacement fire. In 1898, a low intensity fire wounded many of the then 60-year old trees, providing a set of scars for morphological examination. Fire was established as the scarring agent by the presence of surface charcoal, cross-dating scars of the same age in a nearby ponderosa pine stand, and multiple-scarred lodgepole pine within our study site. These latter trees had charcoal on the face of the pre-1898 scars, with no scars after 1898, indicating that the 1898 dated scar was caused by fire. Moreover, the distribution of these multiple fire-scarred lodgepole pines served as a chronicle of the area's fire history.

Recent tree wounds were observed from prescribed fires in 1976 and 1982 at Wickiup Springs and Bald Mt. respectively, and from 1980 fires in Crater Lake National Park. Time-temperature profiles were obtained within and underneath burning logs at the 1982 Crater Lake fire using shielded thermocouples.

After the prescribed fires, we excavated around the bases of fire charred and uncharred trees. We also removed charred bark and thus

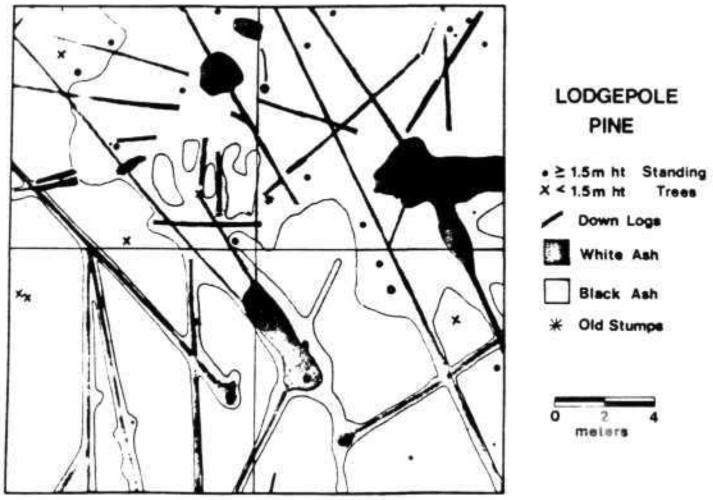

Figure 1. Fire spread at the 1980 Sharp Peak fire in a climax lodgepole pine stand; fire smoldered along decayed logs with some litter consumption. The "white ash" areas were corridors along which logs were completely consumed, imposing a "pick-up sticks" matrix of fire spread across the landscape (from Agee 1981).

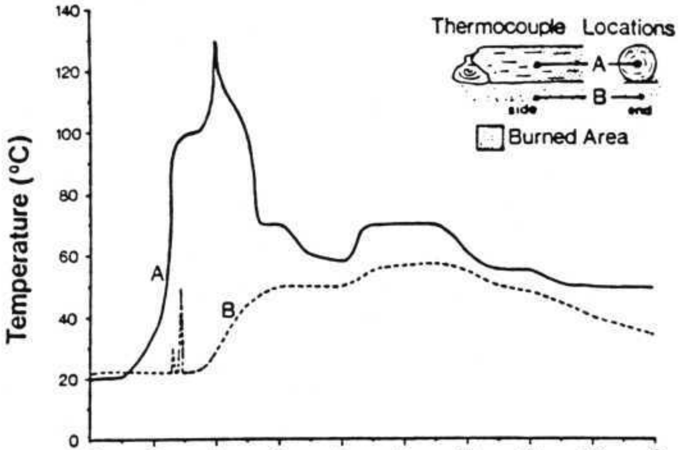

Figure 2. Time temperature profiles recorded by a shielded thermocouple placed inside a smoldering lodgepole pine log (A) and one buried 5 cm below the log (B) at a 1980 Crater Lake NP fire.

delineated the limits of fire-killed tissue. Comparable techniques were used to uncover damage on much older fire sites.

The 1980 and 1982 prescribed fires spread primarily along well-decayed logs in a manner previously described (Agee 1981). Less decayed logs produce higher flames but generally char around the exterior with little internal heat transfer. In contrast, when well-decayed logs are consumed at the soil surface, heat is transmitted into the soil. A thermocouple at 5 cm depth (at the top of the rooting zone) below a burning log recorded a short, rapid temperature pulse caused by smoldering litter at the edge of the log. Then a relatively smooth increase in soil temperature occurred, exceeding 50°C for over 3 hours (Figure 2). This temperature would be sufficient to kill at least the top portion of shallow tree roots (Hare 1961, Wright and Bailey 1982). Root fungal infection courts may thus be created as the logs burn along the soil surface.

Fire may cause damage to the tree bole as well as to tree roots. From the recently observed fires, wounds were classified into tree distinct types: low basal, tapering basal, and ellipsoid (Figure 3). Low basal wounds were generally caused by logs smoldering near a tree base; tapering basal wounds were caused by flaming logs; and ellipsoid wounds were caused by radiant heat from flare-ups of fine fuels or intensely-burning logs.

The percentage of cambial circumference killed declined successively for tapering basal, low basal, and ellipsoid wound types. Degree of associated root damage was essentially the same for basal wounds, but substantially less for ellipsoidal wounds. In addition, 20% of the outwardly unwounded trees surveyed had at least one major lateral root killed by fire (Table 2).

Scarred trees that survived the fires and subsequent insect attack initiated the wound-healing phase. We observed in the 1976 burn that

Figure 3. Appearance of a tapering basal fire wound on a lodgepole pine after the 1980 Sharp Peak fire (left) as compared with a fire scar by an 1898 fire wound at Lookout Point (right).

Table 2. Fire damage observed on surviving lodgepoles 2 years after the 1980 Sharp Peak burn. Results obtained from 10 (10x30m) plots established randomly throughout the burned area ±SE.

Wound Classification	$\bar{X}$ Diameter (cm)	% Tree Circumference Killed	% Trees with Damaged Roots
Tapered Basal n=13	21 ± 2	51 ± 5	79
Basal n=13	19 ± 3	39 ± 6	85
Ellipsoid n=8	14 ± 2	19 ± 4	16
Unwounded n=28	16 ± 2	–	18

cambial tissue is killed when heat is sufficient to char the bark. This charred bark covers the dead tissue for about 3-5 years, then exfoliates exposing the wound surface and wound-callus tissue. Lachmund (1921) recorded similar results for other western coniferous species. In subsequent decades, the exposed scars are subjected to deterioration by insect attack, fungal infection, and physical weathering; these scar faces then become surrounded by continual cambial growth. Using this sequence as a model, we matched a series of 85-year old scar types (Figure 4 E,F,G) with corresponding wound types (Figure 4 A,B,C,D) (Gara et al. 1985).

Our observations confirm that lodgepole pine is a fire-sensitive species, and that a light ground fire severely wounds many trees. Wounded trees should be more susceptible to bark beetle infestations after such a fire event. Immediate, post-fire scolytid-caused mortality would be another element of the catenary process that influences the permanence of lodgepole pine on these pumice plateau sites. Accordingly, in a companion study we investigated the relationship between newly fire-damaged trees and subsequent bark beetle activity.

Patterns of post-fire scolytid activity were studied after a ground fire burned through the climax lodgepole pine stands; the 1980 Sharp Peak and 1982 Bald Mt. burns. During 1982 and 1983, we established surveys to determine scolytid activity. Ten randomly established plots were laid out at Bald Mt. with a total of 176 living trees tallied. Two separate surveys were established at Sharp Peak; each consisted of about 25 randomly placed plots. We recorded 63 living trees in survey (A) and 164 living or dead trees in survey (B). The trees were placed into four fire-damage categories: undamaged, light, moderate, and heavy. The undamaged category indicated no charred bark and no burned fuels at the base of the tree; light damage indicated that 1/3 or less of the tree's basal circumference

Figure 4. Formation of basal (A), tapering basal (B,C) and ellipsoidal (D) fire wounds on lodgepole pine after a 1980 fire at Crater Lake NP, 1980. These wounds are compared with fire scars (E-H) formed by an 1898 fire near Wickiup Springs, Fremont NF, Oregon.

Table 3. Fire damage observed on surviving lodgepole pines 2 years after the Sharp Peak burn (1980) near Crater Lake, Oregon. Results (+SE) obtained from 10 (10x30m) plots established randomly throughout the burned area.

Wound Classification	Number of Trees	Mean Diameter of sampled trees	Tree Circumference Killed	Trees with Damaged Roots
		----cm----	------percent------	
Tapered Basal	13	21 ± 2	51 ± 5	79
Basal	13	19 ± 3	39 ± 6	85
Ellipsoid	8	14 ± 2	19 ± 4	16
Unwounded	28	16 ± 2	---	20

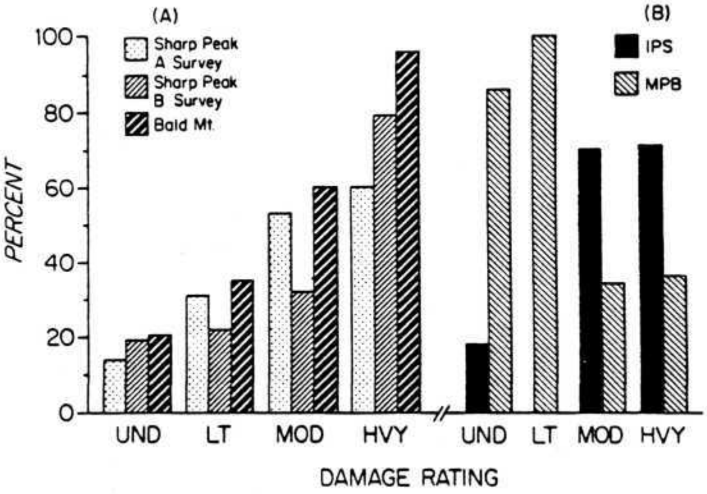

Figure 5. (A) Percentage of lodgepole pine infested by scolytids as related to fire damage rating (undamaged, light, moderate and heavy); data recorded 2 years after the 1980 Sharp Peak fire (surveys A and B) and one year after the Bald Mt. Fire. (B) Percent of trees infested by *Ips* and mountain pine beetles (MPB) as related to damage rating; data from Sharp Peak A survey (from Geiszler, *et al.*, 1984).

was charred. Moderately damaged trees had between 1/3-2/3 of their basal circumference burned, while heavily damaged trees had over 2/3 of their basal circumference charred. The root systems of trees within each plot were excavated in a meter radius around each stem in order to determine the percentage of lateral roots damaged or killed by fire. The height of fire-caused wounds also was determined on all trees. The extent of root damage was not surveyed in Sharp Peak (B) survey, however, the extent of direct tree mortality due to fire per se was determined. The presence of D. ponderosae and Ips pini (Say) on sampled trees was analyzed by removing bark and noting gallery characteristics and identifying adult specimens.

The results of these surveys showed that between 44.4-52.8% of all surveyed trees had no bole damage; the proportion of other bole damage classes varied between plots. More importantly, 14.3-33.3% of the unscorched trees had fire-killed roots, and the percentage of root kill increased conspicuously with severity of bole damage (Table 3).

Scolytids began to attack trees two weeks after the Bald Mt. burn; although not witnessed, we surmise that attacks also began shortly after the Sharp Peak burn. A year later, 42% of the trees at the Bald Mt. site were beetle infested and three years after the Sharp Peak fire a third of the trees there were attacked. In general, there was a direct relationship between the proportion of infested trees in an area and degree of bole damage (Figure 5).

As noted at Bald Mt., most of the I. pini and D. ponderosae infestations occurred on the heavily fire damaged trees. This relationship is shown by the high positive correlations between the frequency of infested trees and percent of root-kill, bole damage, or wound height (Table 4). In addition to correlation analysis, we also used discriminant analysis (Nie et al. 1975) to develop predictive equations that would discern whether or not a damaged tree would be attacked by *Ips* and/or mountain pine beetles. The discriminant analysis examined the contribution of percent basal kill, percent root kill, wound height and tree diameter in forming the "best" linear combination of discriminating variables in a stepwise fashion (Table 5). Percent root kill and tree diameter correctly classified 74% of the trees infested with *D. ponderosae*. Percent basal kill and tree diameter correctly classified 84% of the trees infested with *I. pini* attacks (Table 5).

The magnitude of a coefficient associated with a predictive equation represents the relative contribution of a variable, while the sign of a coefficient classifies the variable as making a positive or negative contribution to the equation. Thus, for *Ips* (Table 5, eq. 1), the percent basal kill is about twice as important as tree diameter, and *Ips* tend to attack the smaller diameter trees. Alternatively, mountain pine beetles tend to attack larger diameter trees and diameter is only about 30% less important than percent kill (Table 5, eq. 3).

Percent root kill or percent basal kill seem to be equally serviceable as discriminant variables in predicting scolytid attack (*Ips* and/or *Dendroctonus*). Since both these variables are highly associated with each other, we computed each "best" or "next best" discriminant analysis equation by using the alternative variable. There was little difference in the canonical correlation values for either of these equations. Thus, either percent basal kill or root kill is nearly equally associated with scolytid attack (Table 5, eqs. 5 and 6).

We observed that a higher proportion of undamaged and lightly damaged trees were attacked by mountain pine beetles than the more severely

Table 4. Adjusted r^2 values from correlation analysis between the percent of trees attacked by scolytids per damage class and the percent fire damage; data from 1983 Bald Mt. survey.

	Adjusted r^2 values	
Fire damage	*Ips*	MPB
Wound height	.74	.79
Percent root kill	.74	.91
Percent bole kill	.96	.91

Table 5. Three discriminant analyses used to discriminate between the eff of percent basal kill (PBK), percent root kill (PRK) and tree diameter (on whether or not the affected trees are attacked by *Ips*, *D. ponderosae* or both (Scolytids). Data taken from the 1983 Bald Mountain survey. All equations significant at .0000.

Bark Beetles	Equations[1] with Standardized Coefficients	Equation Quality	Canonical Correlation	Percent Correctly Classified
IPS	(1) D = .960 PBK - .513 DBH	Best	.6079	83.72
	(2) D = .873 PRK - .615 DBH	Next Best	.5602	84.30
MPB	(3) D = .898 PRK + .627 DBH	Best	.5101	73.84
	(4) D = .825 PBK + .765 DBH	Next Best	.4247	65.70
Scolytids	(5) D = 1.00 PRK	Best	.6424	73.26
	(6) D = 1.00 PBK	Next Best	.5597	77.33

[1] D = the discriminant score used to classify whether a tree will be either attacked or unattacked.

fire-damaged trees, while *Ips* preferred the moderate to heavily fire-damaged trees (Figure 5). These results highlight the ecological separation of *Ips* and *Dendroctonus*; the former preferring only dead or dying small diameter trees; the latter attacking less severely damaged but larger hosts.

In summary, light surface fires drastically thin the climax lodgepole pine stands of south central Oregon, as well as extensively damaging the roots and boles of many surviving trees. Shortly thereafter, pulses of scolytid activity further thin stands of the most weakened trees. These fires, together with scolytids, serve to release stands from root and crown competition, which allows regeneration to establish and concentrates growth on the remaining stand (Stuart 1983; Waring and Pitman 1983; Larsson et al. 1983). These fires also serve to:

1). Maintain a resident mountain pine beetle population;

2). Establish fungal infection courts that temporally link fire events with future *D. ponderosae* outbreaks (Geiszler et al. 1980), through fire-killed roots;

and

3). Provide fuel beds for succeeding fires.

Fungal Pathogens--Few studies, with the exception of Nordin (1958) and Paine (1966), have investigated the development of fungal infections in fire-damaged lodgepole pine. Accordingly, we began this study to investigate: 1) the establishment of fungal infection courts in fire-damaged trees; 2) the succession of fungal flora invading fire wounds; 3) the development of decay columns over time in these trees; and 4) possible relationships between decayed trees and mountain pine beetle infestations.

Between 1982-84 we sampled about 150 trees from the various fire sites already mentioned, plus two additional sites where natural fires occurred, namely: Bald Mt. 1870 and Jungle Springs 1920. These trees were in two groups: those with no visible above ground fire-caused damage, and trees with either basal wounds caused by recent fires or scarred trees that were wounded by previous fires. To detect possible root damage caused by fire, the roots of all sampled trees were exposed for a meter radius around each tree. Subsequently, all trees were felled and serially sectioned every 1.5 m to determine the origin and height of any fungal decay or stain column.

The fungal status of each sampled tree was determined by taking chips from bole and root material and culturing the chips on 2% malt extract media. Basidiomycete fungi were identified in accordance to methods and keys published by Nobles (1965) and Stalpers (1979). When available, fungal fruiting bodies were collected and sent for identification to Dr. R. L. Gilbertson, University of Arizona.

The enzymatic capabilities of fungi were identified in order to characterize whether they were white or brown rots. These enzymatic determinations were made by inoculating 2% malt agar media with fungi isolated from fire damaged root tissues and decay columns. Each inoculation was replicated three times and the petri dishes containing the materials were incubated at 25°C for three weeks. After this period, reagents were applied to each culture in accordance with Stalper's (1979) methods. The presence of brown or white rots was then easily detectable by noting the color of the stained material.

The comparative growth rates of white-rot fungi vs. brown-rot fungi were determined by plating fungal isolates from fire-damaged roots and heart-rot columns on 2% malt agar. These cultures were incubated at 25°C for two weeks and the mean growth rate (mm day-1) of each colony was determined (Littke 1982).

The impact of developing decay columns on annual radial increment was investigated in the 140-year old stands of Lookout Point (trees established by the 1839 fire). Sixteen paired trees were located: one member of each pair contained a viable rot column and the other was an uninfected control. The fungal status of each tree was predetermined by drilling the lower bole with a gasoline-powered auger (Blair and Driver 1977). These paired trees then were felled and disks removed at the base, at 137 cm height and near mid-crown. Disks were sanded and the growth increment for each year was determined to the nearest 0.01 mm at two points 180 degrees apart along the circumference. In this manner, growth differences between infected and uninfected trees were determined over the time elapsed since fire damage.

We found that fungi imperfecti were consistently isolated from the zone immediately behind weathered above-ground fire scars, while Basidiomycete fungi were only isolated from the heartwood zone. In other words, there were no Basidiomycetes in the continuum between fire scar tissues and developing heart-rot columns. These decay columns, therefore, were not established directly through fire scars on the boles of trees as suggested by Nordin (1985) and Geiszler et al. (1980).

The presence of two spatially distinct fungal floras and the conical shape of the heart-rot column suggested that these decay columns originated below-ground. After serially sectioning ca 30 trees having heart-rot columns, we found that fire-killed roots were the infection courts through which invading fungi had become established. In fact, ca 70% of the fire-scarred trees at Lookout Point had root damage and these damaged roots invariably were decayed. A Chi square test showed that trees with fire-damaged roots were significantly more likely to have butt rot than trees with undamaged roots (Table 6). Additionally, about 33% of the unscarred trees also had fire-damaged roots and over 20% of these trees had active heart-rot columns (Figure 6).

While an abundance of brown-rot Basidiomycetes species were found in trees with advanced root and butt decay, recently fire-damaged tissues were infected with fungi imperfecti and white-rot Basidiomycetes (Table 7). By culturing fire-damaged root material associated with fires of different ages, we found that the white-rot fungus *Pholiota carbonicola* was the primary invader of freshly scorched lodgepole pine roots. This fungus is known to gregariously fruit in conifer stands following fire. In agreement with Grund (1962), we noticed a peak of *P. carbonicola* sporocarp production 3 years after the Sharp Peak fire.

In contrast, a mixed population of white- and brown-rot Basidiomycetes characterized the flora of roots killed 6 years after the Wickiup Springs 1976 fire, these included *Poria subacida*. *Heterobasidion annosum*, *Lentinus lepideus*, and *Sistrotrema brinkmanni*. Little intact root material, suitable for fungal isolation, could be found from roots damaged by the 1898 Lookout Point fire. However, we were able to trace decay columns in these trees by locating rot inception in fire-killed roots and by then following the decay columns into the boles of these trees (Figure 7). The fungi isolated from these heart-rot columns were: *Poria asiatica*, *Gleophyllum odoratum*, *Tyromyces leucospongia* and others (Table 7). These fungi were also a major part of the lignicolous fungal flora of the surrounding area (Table 8).

Poria asiatica may be the most significant brown-rot species inhabiting the heart-rot columns. This fungus has been characterized as an

Table 6. The relationship between fire-killed roots and the incidence of bole decay in 49 lodgepole pine that survived the 1898 Lookout Point fire.

Lodgepole Pine Roots	Bole Status		Chi-square Statistics
	Decayed	Undecayed	
Fire killed	24	4	X(1)=10.81
Undamaged	6	15	P=0.005

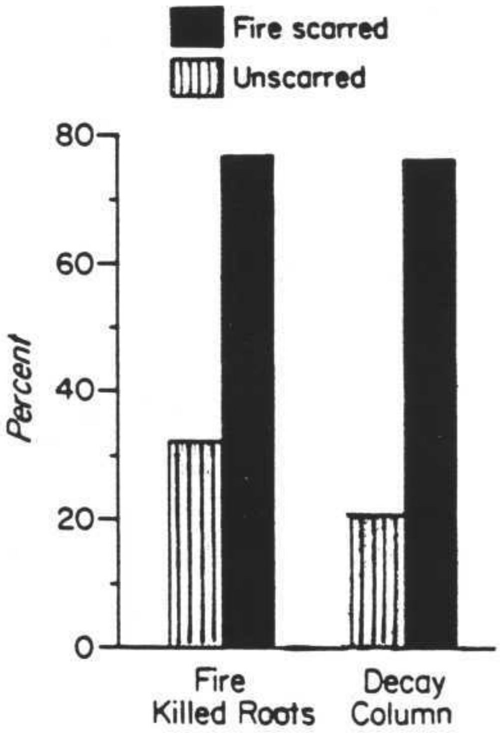

Figure 6. The percentage of fire-scarred and unscarred lodgepole pines with fire-killed roots (left), and those with active decay columns (right); data from 44 trees sampled at the 1898 Lookout Point fire (from Littke and Gara 1984).

Figure 7. A 140-yr. old, unscarred lodgepole pine growing in the 1898 Lookout Point fire site with fire-scarred root (left). A crossection of the bole showing decay column associated with the fire-damaged root (right).

Table 7. Fungal isolates identified from lodgepole pines damaged during the 1980 Sharps Peak fire, 1976 Wickiup Springs fire and 1898 Lookout Point fire; isolations made from tissues associated with butt decay in fire-scarred (FS) trees, fire-killed (FK) roots, and down logs (DL), from Littke and Gara 1984.

Burn site	Years after fire	Fungal species	Rot[1]	%[2]	Material
Sharp Peak	2	*Pholiota carbonicola*	W	24	FK roots
		Trametes carbonaria	W	5	"
		Misc. fungi imperfecti etc.	–	71	
Wickiup	6	*Poria subacida*	W	25	FS trees/DL
		Heterobasidion annosum	W	6	FS trees/DL
		Lentinus lepideus	B	6	FK roots
		Sistotrema brinkmanni	B	6	FK roots
		Unid.	W	57	FS/FK trees
Lookout Point	84	*Poria asiatica*	B	13	FS trees
		Gloeophyllum odoratum	B	10	FS trees/DL
		Lentinus lepideus	B	3	FS trees
		Tyromyces Leucospongia	B	8	DL
		Poria taxicola	B	3	FS trees
		Poria subacida	W	3	DL
		Coniophora sp.	B	5	DL
		Unid. Basidiomycetes[3]	B	38	FS trees

[1] Rot type: W = white rot; B = brown rot.

[2] Percent total isolations per site, usually 8 isolations per specimen.

[3] Unidentified Basidiomycetes – usually isolated once, each species less than 1% of total isolates.

Table 8. Occurrence of brown- and white-rot Basidiomycete fruiting bodies on substrates of different decay status.

Fungal Species	Fungal Occurrence by Substratum[1] Live Tree (Heart Rots)	Standing Dead (Dead 1-5 Yrs)	Dead/Down (Dead 5-10 Yrs)	Dead/Down Moderately Decayed (Dead 10 + Yrs)	Dead and Extensively Decayed
Brown Rot Basidiomycetes					
Amylocystis lapponica	-	+	+	+	-
Chaetoderma luna	-	-	+	+	-
Columnocystis abietina	-	-	+	+	-
Crepidotus stratosus	-	-	+	+	-
Gloephyllum odoratum	+	+	+	+	+
Guepiniopsis alpina	-	+	+	+	-
Inonotus circinatus	-	-	+	+	-
Phellinus ferruginosus	-	-	+	+	-
Poria asiatica	+	+	+	+	+
Poria albobrunnea	-	-	+	+	-
Poria crassa	+	+	+	+	-
Poria odora	-	-	-	+	+
Tublicrinus subulatus	-	-	-	+	+
Tyromyces leucospongia	-	-	+	+	+
White Rot Basidiomycetes					
Cylindrobasidium corrugum	-	+	+	+	-
Heterobasidion annosum	+	+	+	+	+
Poria romellii	-	-	+	+	-
Tricholomopsis rutilans	-	-	-	+	+
Scytinostroma corrugum	-	-	-	+	+

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[1] Fungi collected over period of two years at Lookout Point research site, Fremont National Forest, south-central Oregon. Fungi verified by Dr. R.L. Gilbertson, Univ. Arizona, Tuscon.

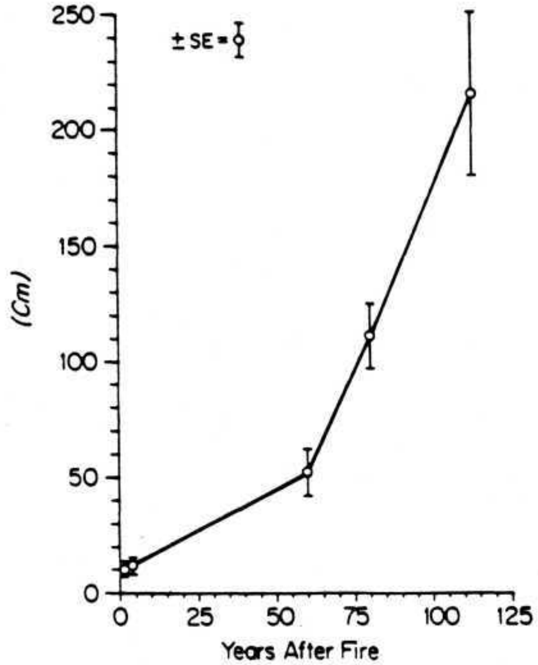

Figure 8. Vertical development over time of active decay columns in lodgepole pine whose lateral roots were damaged by fires in 1870, 1898, 1920, 1976, or 1980 respectively (from Littke and Gara 1984).

opportunistic invader of fire wounds (Buckland 1946, Robinson-Jeffery and Loman 1963). Furthermore, Buckland (1946) observed that this fungus could grow simultaneously with, and eventually outcompete and succeed various white-rot fungal species.

Early work by Hepting (1935) suggested that decay columns in stems of fire-scarred eastern hardwoods progress upward at a linear rate. However, by observing decay column development in a 113-year time series for fire-scarred lodgepole pine, we found that two years after a fire, decay was confined to fire-killed roots and possibly the lower root collar; after six years the decay column extended into the main stem. In subsequent years, the rate of upward extension of the heart-rot columns was exponential (Figure 8).

Decay development rate, within the first few years after the fire, may be controlled largely by the dynamics of fungal succession (Bouchier 1961). We suggest that white-rot fungal species and fungi imperfecti are initial invaders of freshly fire-killed root tissues as evidenced by their fast growth rate and numerical dominance. In time, white-rot fungi was displaced by slower growing brown-rot species (Table 9). Most likely, these initial invaders can tolerate tree defensive reactions while at the same time paving the way for the later successional species.

Later, an increased decay rate may reflect a depletion in available energy for host defenses or establishment of a metabolic sink as host compartmentalization occurs in an attempt to suppress the pathogen (Hoque 1982, Shortle 1969). Such a shift in energy allocation from growth to defense may be seen when we compared the mean annual increment of P. asiatica infected trees with the growth increment in similar sized, adjacent uninfected trees (controls). Infected trees grew significantly

(T-test, P=0.05) slower than the controls. The comparative effects of the 1898 Lookout Point fire on growth of trees that escaped injury with those injured and subsequently infected were as follows: all trees showed the effects of stand release during 1900 to 1910 as both groups increased diameter growth; the possible effects of fungal establishment became evident ca 1920 in the infected trees as annual increment started to decline; and during the next 60 years, the decaying trees grew conspicuously slower than uninfected ones (Figure 9).

In summary we found that ca 6-7 decades after the 1898 Lookout Point fire, the pure lodgepole pine stands of this area were a mosaic of *P asiatica* infected and uninfected trees. At this state in stand development, we observed that mountain pine beetles preferentially selected diseased trees (focus trees), and as the beetle outbreak developed more infected than uninfected trees were killed by the mountain pine beetle (Gara et al. 1985, Geiszler et al. 1980).

These results established the temporal link between past fire events and subsequent mountain pine beetle outbreaks in the Lookout Point area. Our conclusions based upon this research suggests that:

1). Fire-killed root material rapidly becomes invaded by fungi imperfecti and white-rot Basidiomycetes.

2). Secondary fungal succession occurs establishing brown-rot Basidiomycetes, which develop heart-rot over several decades.

3). Trees with active heart-rot columns were "going down hill" when compared with uninfected lodgepole pine.

4). After 6-7 decades since the fire the stand was a heterogenous mixture of infected and uninfected trees.

5). Mountain pine beetles preferentially selected infected trees (focus trees).

6). The number and special distribution of focus trees may be associated with the initiation and subsequent magnitude of mountain pine beetle outbreaks.

Table 9. Mean fungal radial growth rate (mm day^{-1}) in vitro and percentage of white- and brown-rot fungi isolated from living fire-scarred lodgepole pines from 3 fire sites in south-central Oregon.

	Mean growth rate	% Fungi	
Fire event	(mm/day)	brown-rots	white-rots
Sharp Peak 1980	2.3	0	100
Wickiup Springs 1976	1.7	12	88
Lookout Point 1898	1.4	80	20

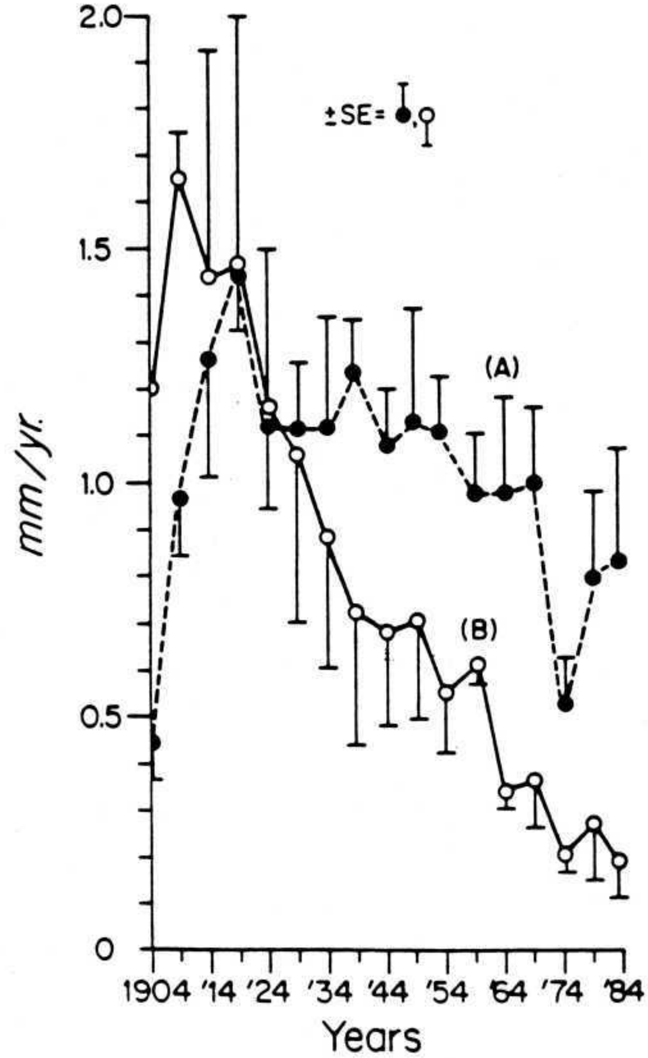

Figure 9.–Mean annual increment (mm•yr^{-1}) of adjacent pairs of similar diameter lodgepole pines following the 1898 Lookout Point fire. One member of each pair was undecayed and unscarred (A); the other member was fire-scarred and had an active decay column (B) (Littke and Gara 1984).

MPB Brood Production--We investigated brood production by *D. ponderosae* in trees killed during the 1982 attack season. Individual trees (n=49) were equipped with 1M long nylon emergence cages (Gara 1967). These cages were placed on the trees prior to beetle emergence. Emerging beetles were collected and recorded daily.

We observed that seasonal emergence followed a single peak pattern centered around mid-July (Figure 10). Beetles were collected as early as the first week of June, and as late as mid-September. Clearly this type of emergence pattern supports the MPB attack dynamics observed in later studies (see discussion below).

There were quantitative differences in daily emergence form individual trees (Figure 11). Typically, emerging beetles appeared earlier from larger diameter trees than from corresponding smaller diameter trees. Additionally, over the season these large trees subsequently produced more beetles. The relationship between daily mean high temperature and beetle emergence is shown in Figure 11(A & B). A 10° drop in the daily mean air temperature resulted in a near cessation of beetle emergence. Subsequently, rising temperatures resulted in increased emergence.

Host Selection Patterns--*Dendroctonus ponderosae* is the most destructive insect pest of lodgepole pine forests in western North America. Mountain pine beetle populations select suitable and/or susceptible hosts during their dispersal flights. However, there is considerable controversy whether the initial selection of hosts by dispersing bark beetles is random (beetles landing indiscriminately on hosts) or directed (beetles landing preferentially on weakened host trees) (review in Wood 1982). Preferential landings on hosts, presumably in response to olfactory cues emanating from weakened hosts, is termed primary attraction (Moeck et al. 1981).

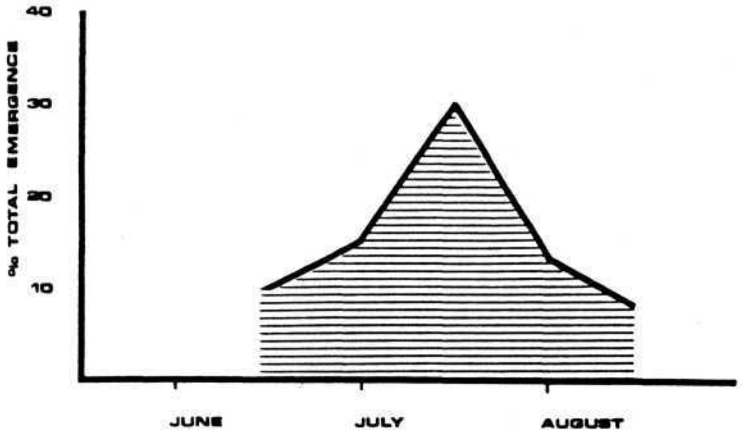

Figure 10. Seasonal emergence pattern of *D. ponderosae* from trees attacked in 1982, Wickiup Springs locale, Fremont NF, Oregon.

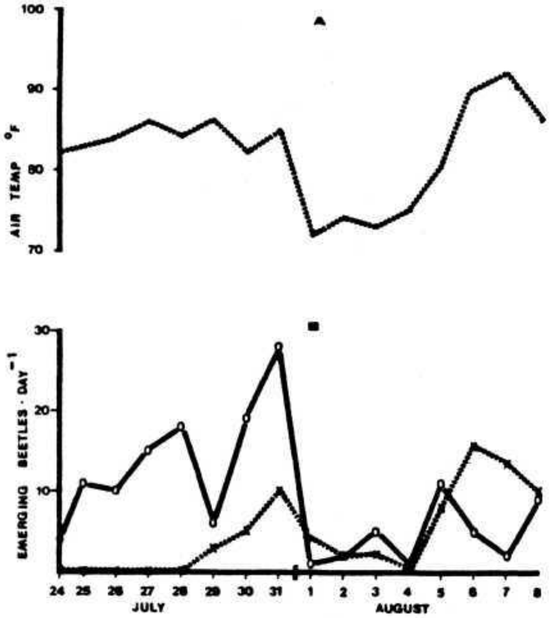

Figure 11. Daily emergence pattern of *D. ponderosae* from individual trees in Fremont NF, Oregon.

We have shown that during the first few years of an outbreak more fire-scarred than unscarred trees are killed by MPB's, and, moreover, fire-scarred trees have significantly more advanced decay and fungal stain than unscarred trees (Geiszler et al. 1980). The most common fungus in fire-scarred lodgepole pine of our study area is P. asiatica (Littke and Gara 1983). The question remains, however, whether or not dispersing beetles preferentially land on these infected trees.

We investigated this question during the summers of 1981-1983, before the MPB dispersal flight by attaching window-barrier traps (Chapman and Kinghor 1955) to an approximately equal number of fire-scarred and unscarred trees, a total of 104 test trees. All test trees were on the average 23 cm in diameter, the preferred diameter for MPB attack in this area (Geiszler et al. 1980. When the dispersal flights commenced, we removed the trapped beetles daily. We stopped counting beetles on a trap when the test tree or trees adjacent to it were attacked. We felt that once aggregating pheromones were present, the particular test tree was of no further value. After completion of the landing study, we cut all test trees and investigated their fungal status.

As the number of test trees "available for landing" changed during the season we used the joint binomial distribution to compute the probabilities of a MPB landing on a fire-scarred tree--we term this type of landing a "success". The joint binomial distribution takes into consideration that the probability of a success can be different for changing (or different) sample sets. This distribution can be described as:

$$P(S<s) = \sum \prod_{i=1}^{K} \binom{N_i}{M} \quad p^{M_i} (1-p_i)^{N_i - M_i}$$

where S is a random variable for the number of successes, s is the observed number of successes, K is the number of sample sets taken, N_i is the number of samples in the i^{th} set, m_i is the observed number of successes in the i^{th} set, and p_i is the probability of a success in the i^{th} set. The summation (Σ) is taken over all values of M_i such that $S = \sum_{i=1}^{K} M_i$ is greater than $s = \sum_{i=1} m_i$ and) $\leq M_1 \leq N_i$ (from Gara *et al.*, 1984).

where S is a random variable for the number of successes, s is the observed number of successes, K is the number of sample sets taken, Ni is the number of samples in the ith set, mi is the observed number of successes in the ith set, and pi is the probability of a success in the ith set. The summation (Z) is taken over all values of Mi such that S=$\overset{k}{\underset{i=1}{Z}}$Mi is greater than s=$\overset{k}{Z}$mi and 0<Mi<Ni.

The results indicate that dispersing beetles preferentially select fire scarred trees (P = 0.023) and trees primarily with P. asiatica (P = 0.008) (Figure 12). Apparently, MPB's in dispersal flight can detect host selection cues, which may be volatile materials produced by interactions between the decay fungi and host constituents. These results also confirm the existence of preferred focus trees--trees initially selected by flying D. ponderosae at a time before the population is concentrating in response to pheromones.

To simulate the concentration phase of the D. ponderosae host selection pattern, we placed window traps and synthetic pheromones (Trans-verbenol + alpha-pinene + myrcene) on 25 pairs selected hosts (focus trees). Trees over 20cm dbh that surrounded these baited trees (recipient trees) also were supplied with window traps. The synthetic pheromone was removed when at least 10 attacks occurred on the baited trees; further attacks on these trees augmented naturally. Attacks were tallied hourly

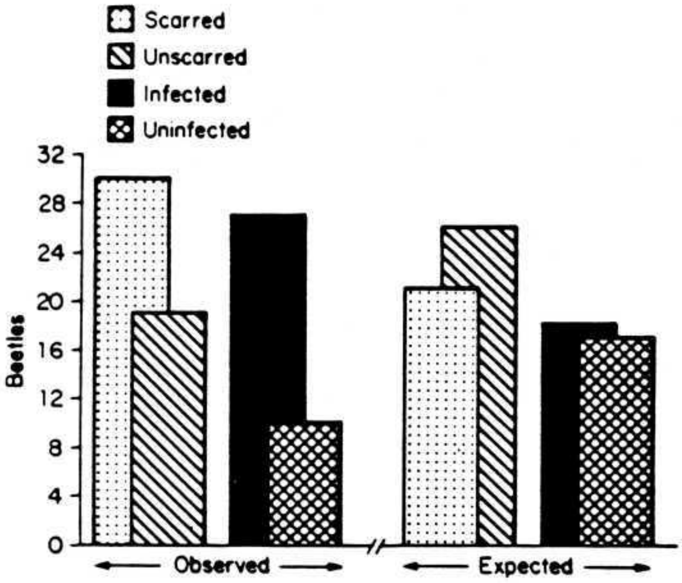

Figure 12. Observed number of *D. ponderosae* landings and expected number of landings (assuming random selection) on fire-scarred and unscarred as well as fungus-infected and uninfected lodgepole pine at Lookout Point.

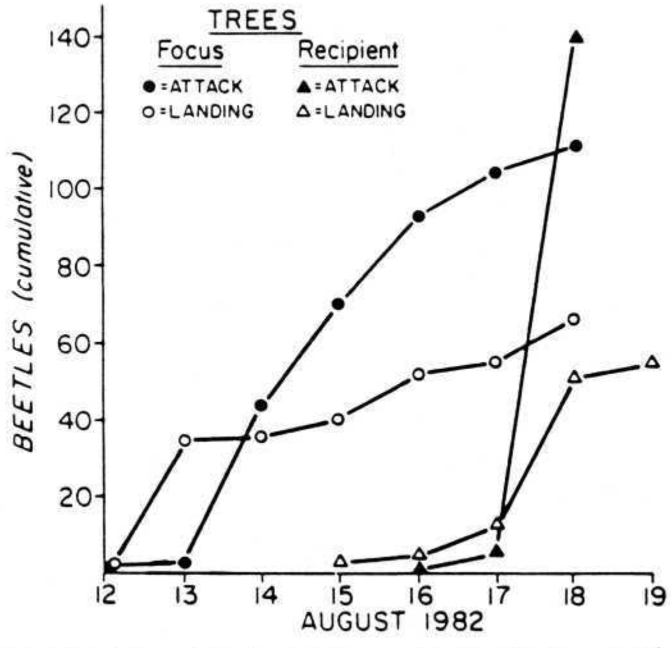

Figure 13. Cumulative numbers of *D. ponderosae* landings and attacks on lodgepole pines initially baited with synthetic pheromones (focus trees) and later on adjacent stems (recipient trees); studies conducted at Lookout Point area.

within a 2m band, 1.2m above the ground. Similarly, window traps were emptied and beetles recorded every hour. The sequential progression of attacks and landings on bait trees and adjacent trees was followed for several days.

We found the rate of beetle landings on the bait trees was synchronous with the attack pattern. When the attack rate on the baited trees leveled off, presumably in response to antiaggregants, a few beetles landed on a neighboring tree. Almost immediately these recipient trees in turn were mass attacked (Figure 13).

These observations demonstrate that once a focus tree is selected and attacked, recipient trees are precipitously attacked by interactions between pheromones; moreover, diameters and distance of adjacent stems play important roles in this serial attack pattern--in essence the switching mechanism described by Geiszler and Gara (1978). Following this scenario the potential for _D. ponderosae_ outbreaks increases proportionally with the abundance of focus trees and the spatial distribution of suitable neighboring hosts (Amman and Cole 1983).

Additionally, we felt that tree vigor (Waring and Pitman 1980) was not the only factor in the continuation of a MPB outbreak in lodgepole pine--at least in our research area. Rather the maintenance of an outbreak is conditioned by distribution and number of focus trees--in our case a link to the fire history of the area--and the diameter and "spacing-geometry" of recipient trees. Accordingly, we established four 60 x 30m plots in lodgepole pine stands that were 2 km from the main outbreak area. Each plot was divided in half; one half was thinned so that each tree was about 6m from an adjacent tree. The other half of each plot was unthinned and served as a control.

Increment cores were taken from trees within the thinned and unthinned half of each plot; the average vigor ratings (Waring and Pitman 1980) of both the treated and untreated portion of plot were then determined. A tree in each half plot was baited with synthetic MPB attractant.

In the most heavily thinned half plots (plots A at 222 trees/ha and plot B at 189 trees/ha) only 11% of the unbaited trees were attacked, while the trees in the corresponding unthinned half plots had 43% of the unbaited trees attacked ($P<.001$). In plot D (356 trees/ha) the trees were more closely spaced and 32% of the unbaited trees were attacked in the thinned plot. In other words, even though each half of a particular plot had essentially the same vigor ($P>.33$), the outbreak expanded primarily in the unthinned areas. These results further strengthen the notion that outbreaks do not terminate only because of a general increase in stand vigor (e.g. in the applied sense, by thinning regimes based on vigor parameters) but also by the elimination of focus trees and increased spacing between trees.

Results from these experiments suggest some important features concerning the emergence pattern, host selection, and attack dynamics of _D. ponderosae_. These can be summarized as:

1). Beetles emerge in a single wave pattern throughout the flight season. Such a pattern allows for large numbers of beetles to initiate and more importantly to sustain the attack rates on surrounding recipient trees.

2). Considerable quantitative variation occurs between trees in regards to daily emergence patterns. Presumably, this is a function of diameter, phloem thickness, and previous attack date. Wide fluctuations in daily mean air temperature results in decreased beetle emergence and possibly adversely affect ongoing attack rates.

3). During the first years of an outbreak we observed a preference by MPB for fungal infected trees. Subsequent landing studies showed that preferential landings occurred on fungal infected trees relative to uninfected controls.

4). Initial beetle attacks on the focus tree precipitate greater attack rates on surrounding recipient trees, findings supporting the "switching" mechanism.

5). MPB attack dynamics were significantly affected by disruption of the diameter-distance spatial geometry than by changes in the vigor of the stand. This suggests that outbreaks expend where the focus tree are more numerous and where the spatial distribution of surrounding potential recipient trees lies within some critical value.

Fire-Fungal-MPB Interactions--Lodgepole pine reproduction of our study areas occurs when root competition between trees is drastically reduced: a situation following mountain pine beetle outbreaks and fire events. This seedling establishment pattern has been shown to be tied to increased moisture availability in the vicinity of recently-killed tree clumps and a relatively favorable microclimate provided by logs and standing dead trees--both of which favor seedling establishment (Stuart 1983). We therefore attempted to link current stand structure with previous fires and MPB disturbances. Accordingly, we established plots in areas of widely divergent fire histories and collected dendrochronological data associated with fire scars, D. ponderosae outbreak history (for methods see Stuart et al. 1982, Mitchell et al. 1982) and subsequent regeneration patterns.

While suitable hosts were randomly spaced, beetle-killed trees were usually found in statistically-clumped patterns (Stuart 1983), a finding supporting the MPB-switching mechanism (Geiszler and Gara 1978). Therefore, seedlings establishment should be closely associated with these clumps of beetle-killed trees. This was tested by mapping seedling groups and groups of recently killed trees. Seedling groups were defined by the presence of beetle-killed trees and their zone of competitive influence (half the distance between a beetle-killed tree and the nearest live tree). Maps of both these groups were superimposed on one another. A variety of statistical tests of association, including the chi-square tests of independence, showed that there was statistical association of seedling groups with groups of beetle-killed trees (Stuart 1983). Therefore, regeneration patterns would be closely associated with these clumps of beetle-killed trees. Since beetle outbreaks historically continue for several years, regeneration patterns would temporally follow these outbreak periods.

Similarly, fires also are important in creating growing space for seedling regeneration. Depending on fire behavior, individual trees to entire stands may be killed; and this is reflected in subsequent regeneration patterns. A single light ground fire (Agee 1981) would maintain a predominance of two age classes. As a consequence of fuel patterns, stands that develop after these light fires tend to be a mosaic of surviving older residual trees and younger regeneration that occurs either randomly or in discrete patches. An intense fire would create conditions for a single age-class stand to develop.

A series of line transects within the Lookout Point area was used to describe regeneration patterns associated with past fire and mountain pine beetle activity. These transects crossed four distinct areas defined by community structure and fire history: 1) a ridgetop ponderosa pine community characterized by a varied fire history; 2) an ecotonal area zone between the ponderosa pine ridgetop and the climax lodgepole pine situation in the flats below; 3) the climax lodgepole pine flats, which experienced an 1839 stand regeneration fire and 1898 light ground fire; and 4) an adjacent climax lodgepole pine area that had not had a fire for at 350 years.

Based on the distribution and ages of single and multiple fires scars, we found that, historically, fires originated in the ponderosa pine ridgetop and ecotonal zone and moved into the climax lodgepole pine flats in accordance with the smoldering log-fire mode. Regeneration patterns of the ridgetop and ecotonal areas were heterogenous, reflecting seedling establishment after a series of fires that spanned the last three centuries (Figure 14; A,B,C). In contrast regeneration patterns of the lodgepole pine flats, which experience only two fires were bimodal--trees initiated in 1840 and 1899. The climax lodgepole pines stand that had no fires in the 350 years had a variety of age classes (85 to 350 years) that occurred in clumps. Since fire scars were absent in this stand, we feel that this clumped regeneration pattern resulted from sporadic removal of trees by *D. ponderosa*.

Synthesis--We propose the following conceptual model that integrates the effects of fire, fungi and mountain pine beetles in development on lodgepole pines stand in the Lookout Point area (Fig. 15). During 1839, fuel conditions and weather were ideal for spread of a stand replacement fire throughout the Lookout Point area. This fire eliminated root competition between trees and a new lodgepole pine stand was established. As this fast growing new stand emerged, there developed a strong competition for light and moisture, resulting in mortality of suppressed trees. Over the next 60 years, these small dead trees provided low decay type fuels that laid on top of more decayed logs that were remnants of the 1839 fire.

In 1898 the fuel bed was optimal for spread of a slow moving fire, similar to that described by Agee (1981) at Sharp Peak and noted in the 1982 Bald Mountain fire. This is the type of fire that not only further thinned the stand (i.e., through outright killing of trees and subsequent scolytid attack), established reproduction patches, but also wounded major lateral roots and boles of many of the residual trees. This root wounding

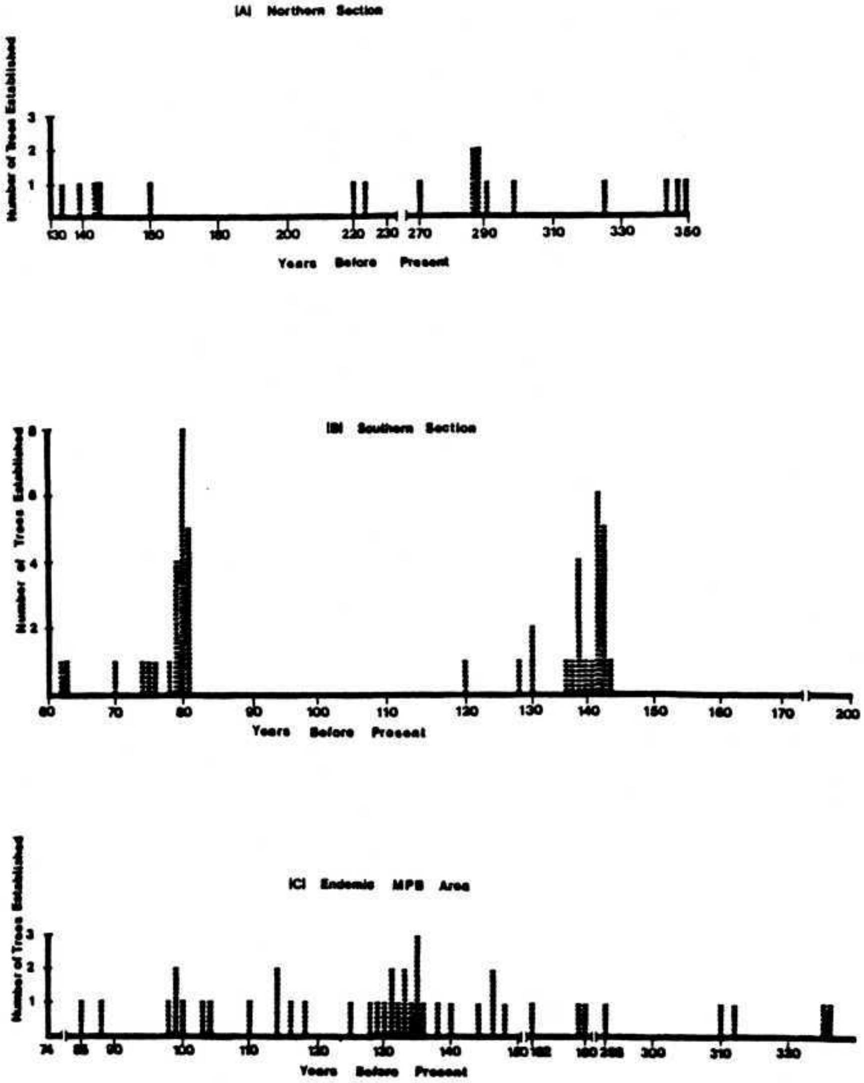

Figure 14. Lodgepole pine establishment at: (A) the northern, and (B) the southern section of the Lookout Point area; (C) represents establishment at the "endemic MPB area."

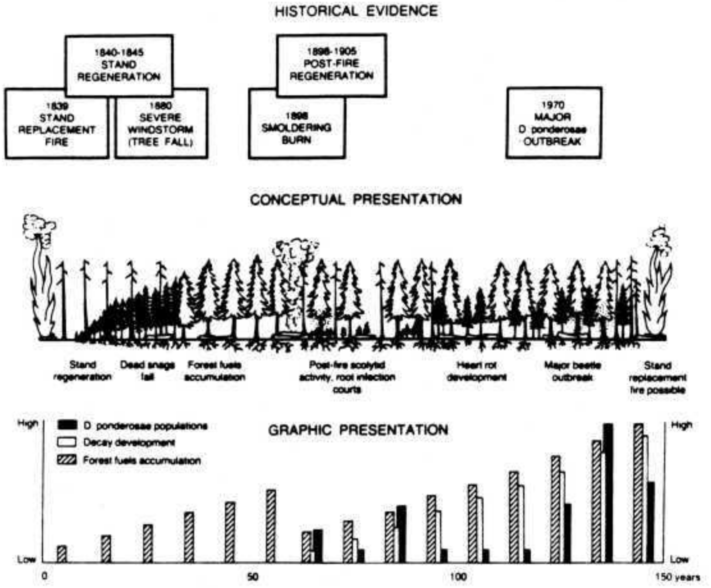

Figure 15. Interactions between fires, fungi, and mountain pine beetles observed at Lookout Point--a climax lodgepole pine forest of the Oregon pumice plateau.

Table 10. A comparison of lodgepole pine stands of the "no-fire area" with those of the climax lodgepole pine flats of the Lookout Point site.

Characteristics	"No-Fire Area"	Lookout Point
D. ponderosae status	single or small group kills	recent massive outbreak
Potential focus trees	scattered	predictable and generally the large diameter fire-scarred trees
Fire scars	none	plentiful as over 50% of the stems scarred by the 1898 fire
Fungal status	variable and mainly found in trees selected by *D. ponderosae*	fire-scarred dominants with advanced *P. asiatica* infection
Age structure	tree patches of variable ages with 200-yr-old dominants	dominants predominately 142 years old with scattered 84-yr-old reproduction patches

provided infection courts for invading white-rot fungi. Afterwards, a succession of fungi conditioned the root tissues for infection by the brown-rot complex with *P. asiatica* being one of the principal agents. In time, the impact of this fungal action essentially created trees that were susceptible to attack by dispersing mountain pine beetles (focus trees).

During development of the beetle outbreak at Lookout Point, the beetles preferentially attacked the largest diameter trees with advanced butt rot. In subsequent years the largest of the remaining trees were killed until the remaining stems were too small to support beetle populations (also see Cole and Amman, 1980).

A different set of fire-fungi-*D. ponderosae* interactions occurred in the fourth transect area, which did not experience either the 1839 or 1898 fires (Table 10). While the Lookout Point area underwent a recent mountain pine beetle outbreak, the "no fire" area has had no outbreak. Fungal-infected trees over 200 years old were being killed either singly or in small groups by beetles, and tree regeneration was establishing in the same pattern. The more diverse structure of this stand has apparently conditioned it to experience frequent by minor beetle disturbances, in contrast to the more wave-related fire, fungi and beetle disturbances at Lookout Point.

Conclusions

Our current research provides evidence that the interactions of fire, fungi and mountain pine beetle attacks are all tightly woven together in an ecosystem that perpetuates lodgepole pine in the tephra-derived soils of south central Oregon. All other stand factors being equal (stocking, competition, nutrients, and so forth), the spatial arrangement of decayed trees (focus trees) and adjacent trees of suitable size in the stand ultimately dictates the magnitude of *D. ponderosae* outbreak.

Understanding the interactions of fire, fungi and mountain pine beetle populations are advantages forest managers now have in their attempt to minimize the effects of scolytid epidemics. In particular, understanding the dynamics of lodgepole pine stands will make it possible for managers to project ahead to the optimum time to harvest trees, conduct prescribed burns, or artificially intervene in the normal dynamics of the forest ecosystem.

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DEB 8109813

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INFLUENCE OF FIRES, FUNGI AND MOUNTAIN PINE BEETLES ON DEVELOPMENT OF A LODGEPOLE PINE FOREST IN SOUTH-CENTRAL OREGON[1]

R. I. Gara, W. R. Littke, J. K. Agee, D. R. Geiszler, J. D. Stuart, and C. H. Driver

ABSTRACT

Virtually pure lodgepole pine stands form an edaphic climax community over large areas of the infertile "pumice plateau" of south-central Oregon. During our ongoing studies on the dynamics of these forests we developed the scenario that periodic fires create fungal infection courts in damaged roots; in time, advanced decay develops in the butts and stems of these trees. The mountain pine beetle preferentially selects and kills these trees during the flight season. As these outbreaks develop, additional uninfected trees are attacked. In time, the stage is set for subsequent fires as needles drop, snags fall, and logs decay.

INTRODUCTION

Lodgepole pine covers some 3 million acres of commercially important and scenic lands of the Pacific Northwest. The species, *Pinus contorta* var. *murrayana* (Grev. and Balf.) Engelm., has a wide ecological amplitude, and as such, it represents a valuable timber species of the region although its past commercial value has been low. Its positive establishment following fires and its rapid juvenile growth offer promise that the species can be used in short rotation management schemes (Wellner 1973, Cole 1973, Dahms 1973). Besides their potential for timber production, lodgepole pine forests provide vast recreation and wilderness areas (Despain 1973, Litton 1973), important water source areas (Hoover 1973), and range and wildlife habitats (Dealy 1973).

Lodgepole pine was one of the pioneering species to occupy infertile tephra deposits at the close of the last glacial period in the southern Oregon Cascades (Hansen 1946). Franklin and Dyrness (1973) consider the virtually pure lodgepole pine stands to be an edaphic climax community on many sites of this so-called pumice plateau of south-central Oregon. Under certain circumstances the dynamics of these forests are controlled by the interacting effects of fires, the mountain pine beetle (*Dendroctonus ponderosae* Hopk.), and fungal pathogens (Geiszler *et al.*, 1980). The main goal of the research summarized here was to assess the relative roles these ecological events play in the establishment and development of a climax lodgepole pine forest in south-central Oregon.

RESEARCH SITES

Our research sites within the Fremont National Forest and adjacent areas encompassed several discrete fire sites; these areas have been the scene of recurring epidemic infestations of the mountain pine beetle (R. E. Dolph, pers. comm. 1980). These burned sites included: 1) Bald Mt. – a prescribed fire of 1982; 2) Wickiup Springs – a prescribed fire of 1976; 3) Lookout Point – a stand replacement fire that occurred in 1839 and a moderate fire in 1898; and 4) a 1980 fire at Crater Lake National Park that burned near the northern boundary of the park and eventually spread through a climax lodgepole pine stand in the Sharp Peak area of the Park.

All study areas were about 1,800 m elevation with soils derived from Mt. Mazama pumice and ash, which were deposited about 6,600 years ago. The area received an additional tephra deposit from the Paulina Peak eruption ca. 4,000 years ago. Annual precipitation, largely as snow, averages 60 cm. Because of the coarse-textured surface soil and low rainfall, plant species diversity of this pumice plateau is low, and trees, shrubs and herbs are shallow rooted.

The research results summarized below reflect the current status of our knowledge concerning the dynamics of these climax lodgepole pine stands.

RESULTS

Fire Behavior. – Climax lodgepole pine forests are more fuel-limited than other forested communities in the Pacific Northwest. The exceptionally low wood productivity (1-2 $m^3 \cdot ha^{-1} \cdot yr^{-1}$) and leaf area (1-2 $m^2 \cdot m^{-2}$) result in little fuel accumulation, particularly of fine fuels that usually carry the fire. Both prescribed and natural fires in summer months have been observed to spread widely across red fir (*Abies magnifica* var. *shastensis* Lemm.) and ponderosa pine (*Pinus ponderosa* Doug. ex Loud.) forests without entering adjacent climax lodgepole pine stands. Where spread into lodgepole pine stands occurred, it was always along corridors of partially-decayed logs, remnants of a disturbance several decades earlier (Agee 1981). Under the conditions we have observed, fire presence and behavior in lodgepole pine forests is more closely linked to coarse fuel dynamics than to fine fuel dynamics, and thus to the history of past disturbances.

Logs often have higher fuel moistures than associated fuel classes, but the quantity and arrangement of these other fuels are such that they rarely carry the fire. For example, in the

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Crater Lake prescribed fire, litter and fine twig fuel moistures ranged from 4 to 10 percent, but the fuel was too discontinuous to sustain fire spread. The highest dead fuel moisture content (42 percent dry wt.) was measured in the interior of a decayed log, and this was the only fuel that would carry the fire.

Two primary mechanisms are responsible for fire spread along these moist, partially-decayed logs. First, the decayed interior of the log is usually surrounded by a less-decayed rind of sapwood. This allows for reasonable air circulation while the rind helps conserve heat by reducing convective heat loss from the log interior. As the interior portion flames or smolders, the sapwood rind may collapse and be consumed, or may be left as charred residue as the fire slowly moves along the log. The second characteristic of these logs is that rotten wood generally requires less energy to produce the combustible gases required for ignition (Susott, 1982). These physical and chemical characteristics appear to favor partially decayed logs as fire corridors under most conditions. Less-decayed logs would be more likely to burn in years of extended drought when fuel moisture is very low. The result of this typical fire spread pattern is a matrix of burned log corridors with unburned areas in the gaps between logs.

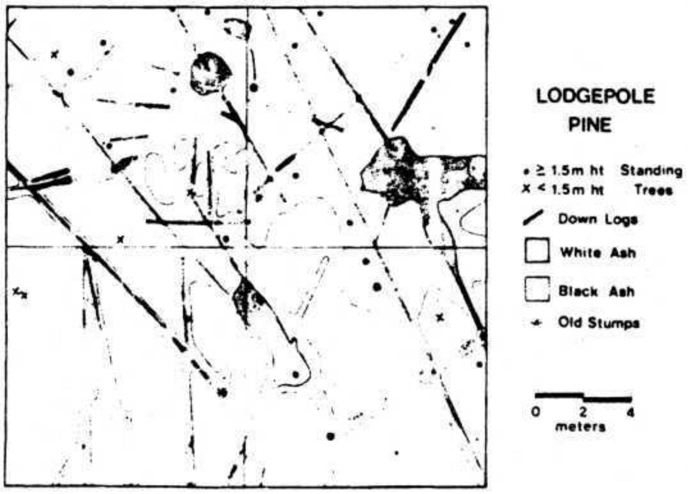

Figure 1. – Fire spread at the 1980 Sharp Peak fire in a climax lodgepole pine stand; fire smoldered along decayed logs with some litter consumption. The "white ash" areas were corridors along which logs were completely consumed, imposing a "pick-up sticks" matrix of fire spread across the landscape (from Agee 1981).

Fire Effects. – This unusual log-to-log smoldering pattern causes both above-ground and below-ground ecological effects. Above-ground effects include crown scorch and complete or partial girdling of the bole. In some cases, the below-ground impacts are even more significant. Where logs are consumed by fire, considerable heat is transferred into the soil (Figure 2), which may damage or kill the tops of tree roots that occur in these shallow-rooted forests (Hare 1961, Wright and Bailey 1982). Immediately after a fire many of the damaged trees are stressed and attacked by bark beetles. Accordingly, we chose three fire events (Bald Mt. 1982, Sharp Peak 1980, and Lookout Point 1898) to compare and develop a chronosequence of fire wound initiation, scar formation and immediate post-fire scolytid activity.

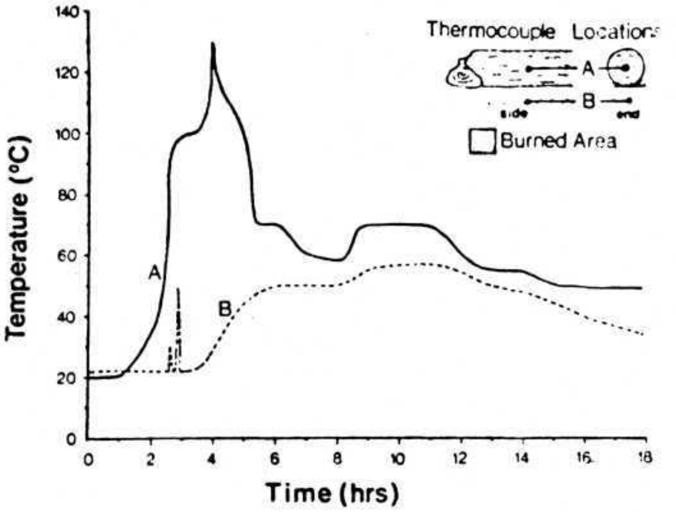

Figure 2. – Time temperature profiles recorded by a shielded thermocouple placed inside a smoldering lodgepole pine log (A) and one buried 5 cm below the log (B) at a 1980 Crater Lake NP fire.

After the Bald Mt. and Sharp Peak fires, surviving trees were classified into a series of bole damage types. Low basal wounds resulted from logs smoldering near a tree base; tapering basal wounds were caused by flaming logs; and ellipsoidal wounds, which did not have ground contact, were caused by radiant heat from flare-ups of fine fuels or intensely-burning logs. Typically, the amount of cambial circumference killed and associated root damage declined successively in tapering basal, low basal, and ellipsoid wound types. Furthermore, an additional 20% of the unwounded trees surveyed had at least one major lateral root killed by fire (Table 1).

In agreement with observations on other western conifers (Lachmund 1921), we found that charred bark covering dead tissues exfoliates within 3-5 yrs, thus exposing the wound surface and wound-callus tissue (scar formation). In subsequent decades, the exposed scars deteriorate by insect attack, fungal infection, and physical weathering; these scar faces then become surrounded by continual cambial growth. Using this sequence as a model, we matched a series of 85-yr-old scar types from the Lookout Point burn with corresponding wound types; an example of this morphological comparison is seen in Figure 3.

A year after the Bald Mt. fire and two years following the Sharp Peak fire, we established surveys to determine relationships between fire-damaged lodgepole pine and subsequent tree killings by *Ips pini* (Say) and *D. ponderosae.* Scolytid activity began within two weeks after the Sharp Peak and Bald Mt. fires and the proportion of infested trees increased with higher degrees of bole damage (Fig 4A). Furthermore, a higher proportion of undamaged and lightly damaged trees were attacked by *D. ponderosae* than the more severely fire-damaged trees, while *Ips* preferred the moderate to heavily fire-damaged trees (Fig. 4B). These scolytid attacks were correlated with percent bole damage, wound height, and percent root kill (Table 2). By using discriminant analysis methods, we showed that percent root kill was the most important fire-related variable associated with combined *Ips* and *Dendroctonus* attack. In addition to being correlated with degree of fire damage, *I. pini* attacks were negatively correlated with tree diameter, while *D. ponderosae* primarily attacked large diameter trees.

Table 1.—Fire damage observed on surviving lodgepole pines 2 years after the 1980 Sharp Peak burn. Results obtained from 10 (10 × 30m) plots established randomly throughout the burned area ± SE.

Wound Classification	$\bar{X}$ Diameter (cm)	% Tree Circumference Killed	% Trees with Damaged Roots
Tapered Basal n = 13	21 ± 2	51 ± 5	79
Basal n = 13	19 ± 3	39 ± 6	85
Ellipsoid n = 8	14 ± 2	19 ± 4	16
Unwounded n = 28	16 ± 2	–	18

Figure 3.—Appearance of a tapering basal fire wound on a lodgepole pine after the 1980 Sharp Peak fire (left) as compared with a fire scar by an 1898 fire wound at Lookout Point (right).

Fungal Patho[illegible] rder to [illegible] k fires with establishment of fungal infec[illegible], in [illegible] oles of trees (Geiszler *et al.*, 1980, Nordin 19[illegible] iall[illegible] ectioned the boles and exposed the roots of abo[illegible] tree[illegible] hat survived the various fires in our study area. We noted that within a year, newly fire-damaged root tissues were infected with fungi imperfecti and white-rot Basidiomycetes. In contrast, material from older fires yielded an abundance of brown-rot Basidiomycetes (Table 3).

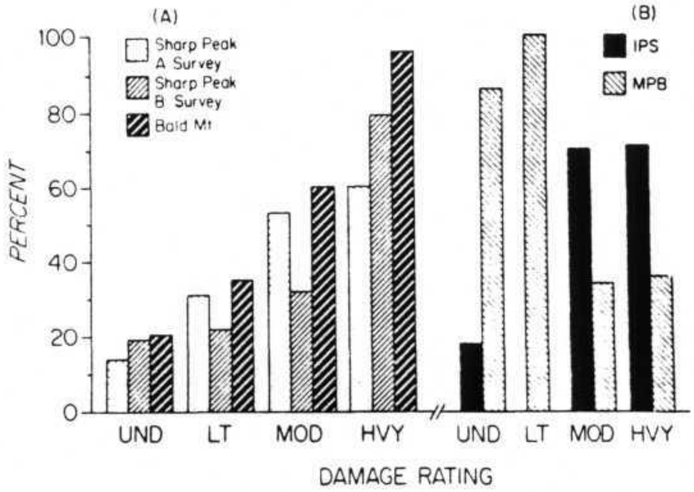

Figure 4.—(A) Percentage of lodgepole pine infested by scolytids as related to fire damage rating (undamaged, light, moderate and heavy); data recorded 2 years after the 1980 Sharp Peak fire (surveys A and B) and one year after the Bald Mt. fire. (B) Percent of trees infested by *Ips* and mountain pine beetles (MPB) as related to damage rating; data from Sharp Peak A survey (from Geiszler *et al.*, 1984).

Table 2.—Adjusted r^2 values from correlation analysis between the percent of trees attacked by scolytids per damage class and the percent fire damage, data from 1983 Bald Mt. survey.

	Adjusted r^2 values	
Fire damage	*Ips*	*MPB*
Wound height	.74	.79
Percent root kill	.74	.91
Percent bole kill	.96	.91

Fungal isolations made from tissues in the continuum between fire scars and the heart rot columns, of trees fire-scarred in 1898, yielded only fungi imperfecti and not wood-decaying Basidiomycetes. These fungi imperfecti were mostly *Leptographium* and *Paceliomyces* species associated with cerambycid and scolytid activity. In contrast the Basidiomycetes, *Poria asiatica, Gleophyllum odoratum, Lentinus lepideus, Pereniporia subacida* and *Tyromyces leucospongia* were consistently isolated only from decay columns. Among these later-occurring heart rot fungi, *P. asiatica* is ecologically most significant because it characteristically invades fire wounds and in doing so outcompetes contemporaneous white-rot species (Robinson-Jeffery and Loman 1963, Buckland 1946).

The presence of these two spatially distinct fungal floras together with the conical shape of the butt rot column strengthened the notion that these decay columns originated in fire-killed roots. Moreover, by tracing the development of fungal decay in fire-killed roots and subsequent decay spread into the stems of these trees, we substantiated the fact that fire-killed root tissues are the fungal entry courts and not above-ground bole damage (Fig. 5). For example, we found that 75% of trees at Lookout Point with fire scars also had fire-killed roots, as did 32% of the unscarred trees. In fact, there was a strong association ($\chi^2(1) = 16.5$, $P = .001$) between existing decay columns and the presence of fire-killed roots (Fig. 6).

Table 3. – Fungal isolates identified from lodgepole pines damaged during the 1980 Sharps Peak fire, 1976 Wickiup Springs fire and 1898 Lookout Point fire; isolations made from tissues associated with butt decay in fire-scarred (FS) trees, fire-killed (FK) roots, and down logs (DL), from Littke and Gara 1984.

Burn site	Years after fire	Fungal species	Rot[1]	%[2]	Material
Sharp Peak	2	*Pholiota carbonicola*	W	24	FK roots
		Trametes carbonaria	W	5	"
		Misc. fungi imperfecti etc.	–	71	
Wickiup	6	*Poria subacida*	W	25	FS trees/DL
		Heterobasidion annosum	W	6	FS trees/DL
		Lentinus lepideus	B	6	FK roots
		Sistotrema brinkmanni	B	6	FK roots
		Unid.	W	57	FS/FK trees
Lookout Point	84	*Poria asiatica*	B	13	FS trees
		Gloeophyllum odoratum	B	10	FS trees/DL
		Lentinus lepideus	B	3	FS trees
		Tyromyces Leucospongia	B	8	DL
		Poria taxicola	B	3	FS trees
		Poria subacida	W	3	DL
		Coniophora sp.	B	5	DL
		Unid. Basidiomycetes[3]	B	38	FS trees

[1] Rot type: W = white rot; B = brown rot.

[2] Percent total isolations per site, usually 8 isolations per specimen.

[3] Unidentified Basidiomycetes – usually isolated once, each species less than 1% of total isolates.

Within the first few years after a fire, the development of decay in trees may be largely controlled by the dynamics of fungal succession (Bourchier 1961). However, later, an increase in rate of decay development may relfect changes in host energy allocation patterns (Hoque 1982, Shortle 1979) (Fig. 7). In any case, ca. 5-6 decades after the Lookout Point 1898 fire, *P. asiatica* infected trees were growing significantly slower (P = 0.05) than uninfected neighboring trees of equal diameter and age class (Fig. 8). The existence of a stand comprised of a mosaic of infected and uninfected trees will have important consequences with regard to mountain pine beetle population dynamics.

Figure 5. – A 140-yr-old, unscarred lodgepole pine growing in the 1898 Lookout Point fire site with fire-scarred root (left). A crossection of the bole showing decay column associated with the fire-damaged root (right).

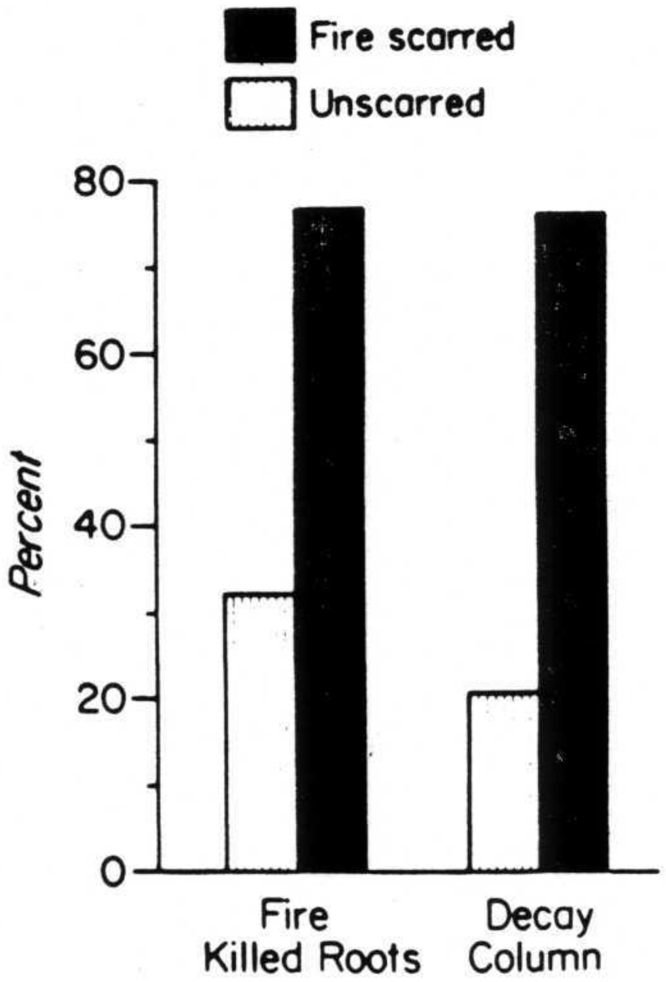

Figure 6. – The percentage of fire-scarred and unscarred lodgepole pines with fire-killed roots (left), and those with active decay columns (right); data from 44 trees sampled at the 1898 Lookout Point fire (from Littke and Gara 1984).

Host Selection Patterns. – During the first few years of an outbreak more fire-scarred than unscarred trees are killed by *D. ponderosae*, and, moreover, fire-scarred trees have more advanced decay and fungal stain than unscarred trees (Geiszler *et al.*, 1980). An important remaining question is whether or not dispersing beetles preferentially land on fungal infected trees.

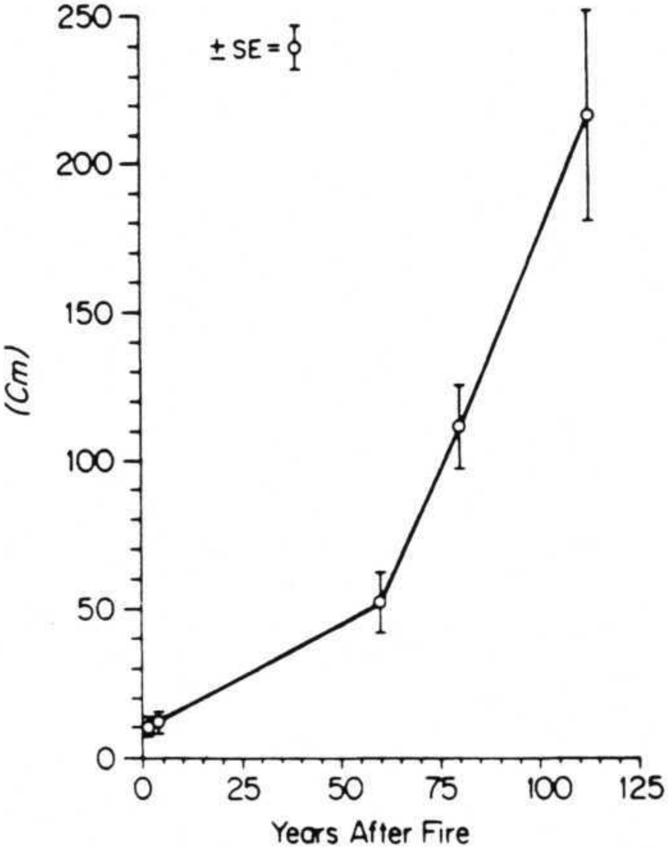

Figure 7. Vertical development over time of active decay columns in lodgepole pine whose lateral roots were damaged by fires in 1870, 1898, 1920, 1976, or 1980 respectively (from Littke and Gara 1984).

We investigated this question by establishing modified window traps (Chapman and Kinghorn 1955) on *P. asiatica* infected [illegible]fected trees. These tests were done at a time before trees throughout the Lookout Point area were being attacked. These studies (Fig. 9) indicated that dispersing beetles preferentially landed on fire-scarred trees (P = .03) and particularly on trees with fungal decay (= .003) (Gara *et al.*, 1984). These results confirm the existence of preferred focus trees – trees initially selected by dispersing beetles at a time before the population is concentrating.

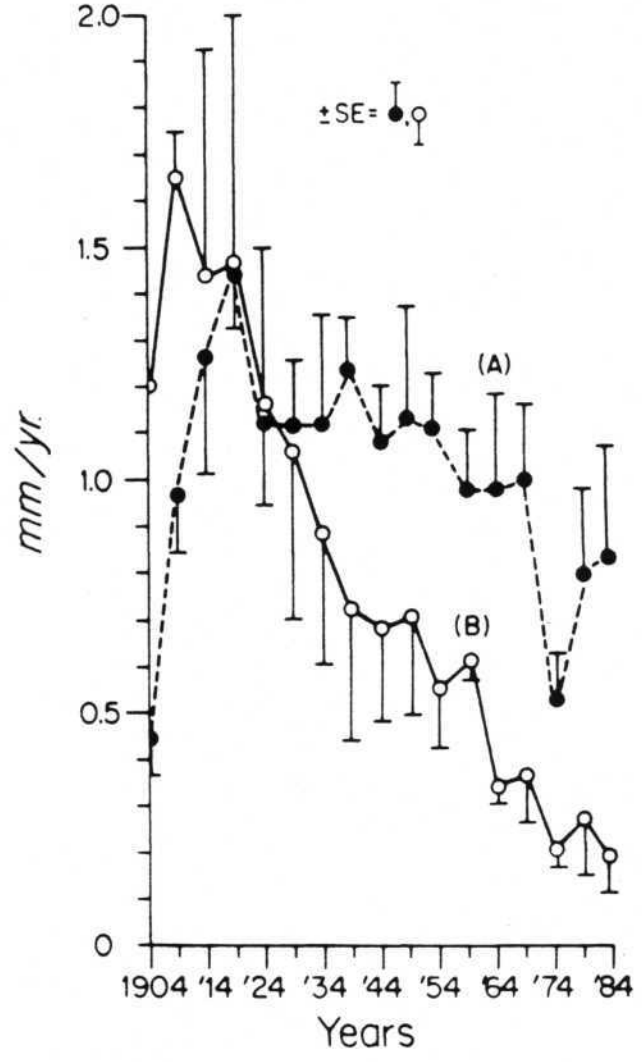

Figure 8. – Mean annual increment ($mm \cdot yr^{-1}$) of adjacent pairs of similar diameter lodgepole pines following the 1898 Lookout Point fire. One member of each pair was undecayed and unscarred (A); the other member was fire-scarred and had an active decay column (B) (Littke and Gara 1984).

To simulate the concentration phase of the *D. ponderosae* host selection pattern, we placed window traps and synthetic pheromones on selected hosts (focus trees). Trees over 20 cm dbh that surrounded these baited trees (recipient trees) also were supplied with window traps. The synthetic pheromone was removed when at least 10 attacks occurred on the baited trees; further attacks on these trees augmented naturally. Attacks were tallied hourly within a 2-m band, 1.2 m above the ground. Similarly, window traps were emptied and beetles recorded every hour. The sequential progression of attacks and landings on bait trees and adjacent trees was followed for several days.

The rate of beetle landings on the bait tree was synchronous with the attack pattern. When the attack rate on the baited trees leveled off, presumably in response to antiaggregants, a few beetles landed on a neighboring tree. Almost immediately these recipient trees in turn were mass attacked (Fig. 10).

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APPENDIX

As the number of test trees "available for landing" changed during the study (Fig. 9) we used the joint binomial distribution to compute the probabilities of a *D. ponderosae* landing on a fire-scarred tree – we term this type of landing a "success." The joint binomial distribution takes into consideration that the probability of a success can be different for changing (or different) sample sets. This distribution can be described as

$$P(S<s) = \Sigma \prod_{i=1}^{K} \binom{N_i}{M} p^{M_i} (1-p_i)^{N_i - M_i}$$

where S is a random variable for the number of successes, s is the observed number of successes, K is the number of sample sets taken, N_i is the number of samples in the i^{th} set, m_i is the observed number of successes in the i^{th} set, and p_i is the probability of a success in the i^{th} set. The summation (Σ) is taken over all values of M_i such that $S = \sum_{i=1}^{K} M_i$ is greater than $s = \sum_{i=1} m_i$ and $) \leq M_1 \leq N_i$ (from Gara *et al.*, 1984).

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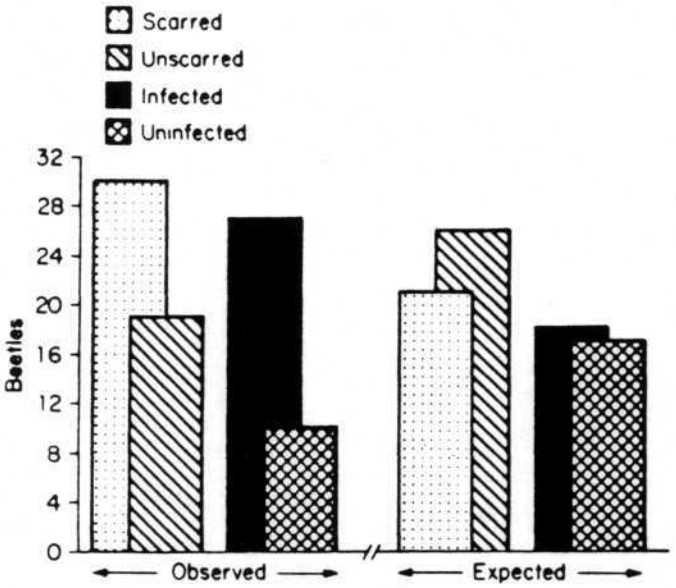

Figure 9. – Observed number of *D. ponderosae* landings and expected number of landings (assuming random selection) on fire-scarred and unscarred as well as fungus-infected and uninfected lodgepole pine at Lookout Point (see appendix).

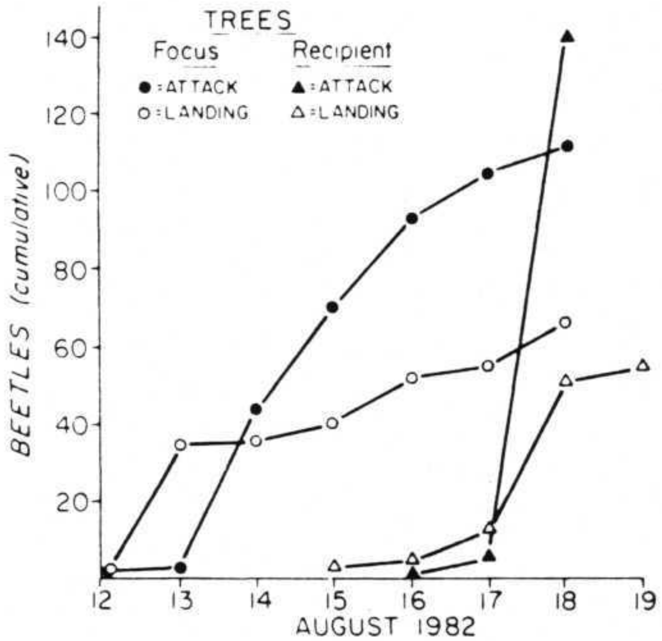

Figure 10. – Cumulative numbers of *D. ponderosae* landings and attacks on lodgepole pines initially baited with synthetic pheromones (focus trees) and later on adjacent stems (recipient trees); studies conducted at Lookout Point area.

These observations demonstrate that once a focus tree is selected and attacked, recipient trees are precipitously attacked by interactions between pheromones; moreover, diameters and distance of adjacent stems play important roles in this serial attack pattern – the switching mechanism described by Geiszl and Gara (1978). Thus the potential for *D. ponderosae* outbreak increases proportionately with the abundance of focus trees and the spatial distribution of suitable neighboring hosts (Amman and Cole 1983).

Stand Structure. – Lodgepole pine reproduction of our study areas occurs when root competition between trees is drastically reduced: a situation following mountain pine beetle outbreaks and fire events. This seedling establishment pattern was due to increased moisture availability in the vicinity of recently-killed tree clumps and a relatively favorable microclimate provided by logs and standing dead trees – both of which favor seedling establishment (Stuart 1983). We therefore attempted to link current stand structure with previous fires and *D. ponderosae* disturbances. Accordingly, we established plots in areas of widely divergent fire histories and collected dendrochronological data associated with fire scars, *D. ponderosae* outbreak history (for methods see Stuart *et al.*, [1982], Mitchell *et al.*, [1982]) and subsequent regeneration patterns.

While suitable hosts were randomly spaced, beetle-killed trees were usually found in statistically-clumped patterns (Stuart 1983), a finding in support of the switching mechanism (Geiszler and Gara 1978). Therefore, seedling establishment should be closely associated with these clumps of beetle-killed trees. This was tested by mapping seedling groups and groups of recently killed trees. Seedling groups were defined by the presence of beetle-killed trees and their zone of competitive influence (half the distance between a beetle-killed tree and the nearest live tree). Maps of both of these groups were superimposed on one another. A variety of statistical tests of association, including the chi-square test of independence, showed that there was statistical association of seedling groups with groups of beetle-killed trees (Stuart 1983). Therefore, regeneration patterns would be closely associated with these clumps of beetle-killed trees. Since beetle outbreaks historically continue for several years, regeneration establishment would temporally follow these outbreak periods.

Similarly, fires also are important in creating growing space for seedling regeneration. Depending on fire behavior, individual trees to entire stands may be killed; and this is reflected in subsequent regeneration patterns. A single light ground fire (Agee 1981) would maintain a predominance of two age classes. As a consequence of fuel patterns, stands that develop after these light fires tend to be a mosaic of surviving older residual trees and younger regeneration that occurs either randomly or in discrete patches. An intense fire would create conditions for a single age-class stand to develop.

A series of line transects within the Lookout Point area were used to describe regeneration patterns associated with past fire and mountain pine beetle activity. These transects crossed four distinct areas defined by community structure and fire history:

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MOUNTAIN PINE BEETLE SCARRING OF LODGEPOLE PINE IN SOUTH-CENTRAL OREGON

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ABSTRACT

Stuart, J.D., Geiszler, D.R., Gara, R.I. and Agee, J.K., 1983. Mountain pine beetle scarring of lodgepole pine in south-central Oregon. *For. Ecol. Manage.*, 5: 207–214.

Three forest disturbance periods, 1973–present, 1922–29, and 1827–46 were determined by aging scars on stems of lodgepole pine trees. All of the scars from the 1970's and 1920's, and most of the scars from the 1820's–40's were determined to be caused by the mountain pine beetle. A few scars from the earliest period may be the result of fire. Diagnostic characteristics of beetle scars are: resemblance to fire scars, pitch tubes, beetle emergence holes, blue stain, beetle galleries, retained bark on the scar face, and an orange or red discoloration around healthy sapwood. Beetle attacks tend to have a northeastern aspect and extend approximately two-thirds around tree boles at breast height.

By recognizing beetle scars it is possible to accurately age previous mountain pine beetle attacks. Many scars which had been thought to be of fire origin are actually caused by the mountain pine beetle.

INTRODUCTION

Lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *murryana* Grev. and Balf.) is ubiquitous in south-central Oregon. Over most of its range it is a seral species in climax communities dominated by ponderosa pine (*Pinus ponderosa* Dougl. ex Loud.), Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), mountain hemlock (*Tsuga mertensiana* [Bong.] Carr.), and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.). In flat areas or in depressions where there is cold air damming, and on waterlogged soils, lodgepole pine is considered climax (Franklin and Dyrness, 1973). There is good evidence to suggest that most seral lodgepole pine stands become established following fire. In climax lodgepole stands, however, the role of fire is not as clear. The presence of apparent fire scars suggests that fire may well be important in such stands. Agee (1981) has proposed a hypothesis for the mechanism of fire scarring of climax lodgepole pine in Crater Lake National Park. During a prescribed burn in the summer of 1980, he observed that as the fire moved from ponderosa pine stands into climax lodgepole pine stands, it burned slowly by conduction along downed logs. Spread occurred primarily from log to log with only occasional patches of litter being burned. It was suggested that fire scarring could occur if a live tree was close enough to a burning log to have a portion of its cambium killed by radiant heat. Fire scarring was observed one year after the fire. However, the fire scarred fewer trees than typically seen in climax lodgepole pine stands. Furthermore, in some of the climax lodgepole pine stands there is little charcoal on, and beneath the soil surface. For these reasons we began to look more carefully at the "fire scars" in climax lodgepole pine stands to determine if they could be of non-fire origin. The most likely agent appeared to be the mountain pine beetle (MPB, *Dendroctonus ponderosae* Hopk.).

Mountain pine beetle epidemics have been recurrent in lodgepole pine stands in eastern Oregon. Relatively dense stands with trees of low vigor are attacked when trees average between 20–30 cm in diameter at breast height. (Cole and Amman, 1980; Geiszler et al., 1980; Waring and Pitman, 1980). Not all attacked trees are killed by the beetles, and those that survive may incur visible permanent injuries to their boles. The objective of this study was to reconstruct disturbance dates by aging scars, to determine if mountain pine beetle attacks can cause scarring, to estimate the amount of scarring, and to develop diagnostic characteristics which can be used to differentiate a beetle scar from a fire scar.

STUDY AREA

The study was conducted in July, 1981 in an old-growth lodgepole pine stand growing at 1800 m elevation near Wickiup Springs on the Fremont National Forest, OR. Soils are relatively infertile, well-drained, loamy sands, developed from Mt. Mazama eolian ash and pumice. The climate during the growing season is characterized by warm, dry days and cold nights. Summer temperatures range from lows of −7°C at night to highs of 41°C during the day. Yearly precipitation ranges from 38–76 cm, with most falling as snow from November through April (Wenzel, 1979).

The site was located on a 0–10% slope. The understory is extremely depauperate, with only a few scattered individuals (cover less than one percent) of bitterbrush (*Purshia tridentata* [Pursh] DC.), long-stolon sedge (*Carex pensylvanica* Lam.), western needlegrass (*Stipa occidentalis* Thurb. ex Wats.), sulfur buckwheat (*Eriogonum umbellatum* Torr.), and pussypaws (*Spraguea umbellata* Torr.). According to Volland (1976) the potential wood productivity on this site would be approximately 1 $m^3 ha^{-1} year^{-1}$. Mountain pine beetle epidemics have occurred in the 1920's and the 1970's (Geiszler et al., 1980; R.E. Dolph, U.S. Forest Service, Portland, OR, personal communication, 1981). Fires larger than 0.10 ha in the surrounding forest have not been reported for at least 30 years (USFS, 1981).

METHODS

Stand disturbance events were determined by aging scars in a manner similar to that developed by McBride and Laven (1976) and Arno and Sneck (1977). Forty-three scarred trees were selected, and cross-sectional wedges, which included scars, were removed with a chainsaw from the larger trees. Scars on smaller trees were removed by sawing discs out of felled trees. After sanding the wedges and discs to a polish, ages of disturbances as denoted by scars were determined by counting annual growth rings under a microscope.

To establish whether the mountain pine beetle can cause scarring, a randomly oriented line transect was established in a stand that had been experiencing a mountain pine beetle epidemic for the last 8 years. Any live tree with pitch tubes (indicating an attack had occurred) within 10 m of the line was examined. The following information was collected: (1) the aspect of the pitch tubes on the tree; (2) the aspect of beetle emergence holes; (3) the presence of spiral scars; (4) the presence of blue stain (a fungal infection introduced by bark beetles); and (5) the aspect of dead bole tissue. Dead bole tissue and presence of blue stain were determined by coring into the bole in four locations: two on the north side, and two on the south side. North and south aspects were chosen since a reconnaissance had shown that pitch tubes on live trees were primarily on north aspects. The objective was to see if bole tissue associated with pitch tubes was dead and whether areas with no pitch tubes (i.e. south sides) had live cambium.

A related survey was conducted to determine the mean aspect and size of beetle attacks. A random sample consisting of 50 plots (12 m × 12 m) was established in a 15 ha area. Tree diameter, attack length, attack arc, and damage class were recorded for each tree larger than 3.5 cm diameter at breast height. Mid-circumference arc aspects were assigned to trees where attacks did not completely circumscribe the tree.

RESULTS AND DISCUSSION

Scars resembling fire scars (wide at the base and tapering up the bole) were formed following recent non-lethal bark beetle attacks (Tables I and II). Beetle emergence holes, blue stain, and ascending scars spiralling with the

TABLE I

Percent occurrence of *D. ponderosae* scar characteristics by bole aspect resulting from an outbreak that began ca. 1973 near Wickiup Springs, Fremont National Forest, OR ($N = 20$)

Bole aspect	Presence of dead tissue	Pitch tubes	Emergence holes	Spiral scar	Multiple spiral scar
North	95	100	80	60	10
South	0	20	0	0	0

TABLE II

Comparison of incidence of blue stain with emergence holes for mountain pine beetle attacked trees during the 1973–80 outbreak at Wickiup Springs, Fremont National Forest, OR

		Emergence hole			
		yes	no		sum
Blue	yes	13	0		13
Stain	no	3	4		7
	sum	16	4	Total =	20

$\chi^2 = 9.29$
$P = 0.0022$

tracheid alignment (Vité, 1961) were associated with the newly forming scars. Other characteristics of these young scars were that the bark was retained for many years (in contrast to bark peeling off on a fire scar), and mountain pine beetle galleries were evident. All of the trees which had blue stain had beetle emergence holes (Table II). Multiple scars, where live and dead cambium strips alternate, had no blue stain and no emergence holes.

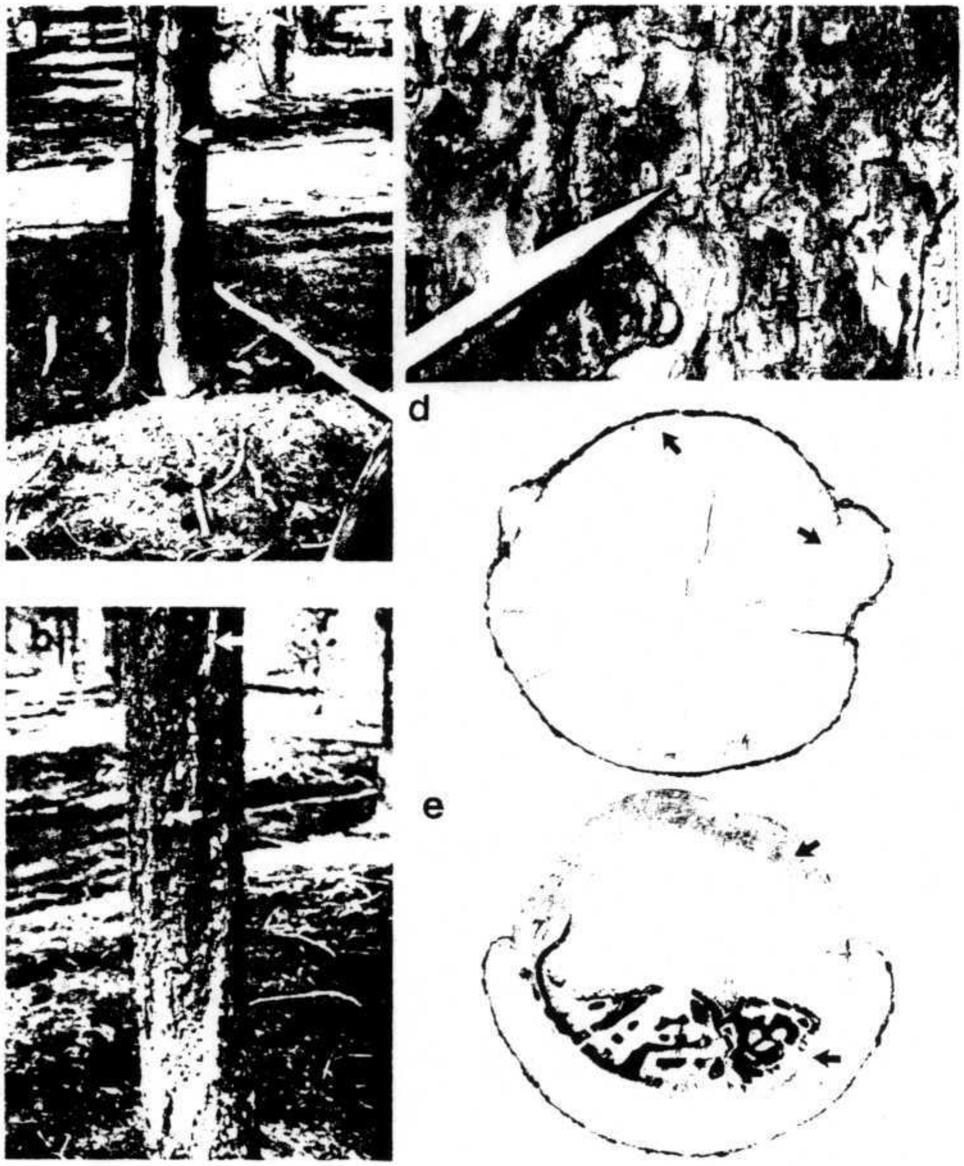
TABLE III

Characteristics of mountain pine beetle scars in a climax lodgepole pine stand at Wickiup Springs, Fremont National Forest, OR

(1) resembles a fire scar (Fig. 1a)
(2) bark retention in face of scar (Fig. 1a)
(3) may have spiral scar (Fig. 1b)
(4) recent scars will have pitch tubes (Fig. 1b)
(5) may have emergence holes (Fig. 1c)
(6) may have blue stain (Fig. 1d, e)
(7) may have an orange or red discoloration around healthy sapwood (presumably a tree defense against blue stain) (Fig. 1d,e)
(8) may have mountain pine beetle galleries
(9) will probably be on the north or northeast side of the bole.

Fig. 1. Characteristics of mountain pine beetle scars seen on lodgepole pine at Wickiup Springs, Fremont National Forest, OR: (a) lodgepole pine tree with beetle scar similar in appearance to a fire scar; arrow shows area of bark retention in the face of a 55-year-old scar; (b) lodgepole pine tree with arrows depicting MPB pitch tubes and callus tissue ascending along spiral tracheids of a 1973 scar; (c) MPB emergence hole in a 1973 scar face; (d) cross section at stump height of a 1973 MPB attacked tree; arrows point to zone of discoloration around healthy sapwood (near callus tissue) and to zone of blue stain between lobes of callus tissue; and (e) cross section at stump height of a 1925 MPB-attacked tree; arrows point to a ring of discolored wood coincident with healthy sapwood and to zone of blue stain. Excavations in heartwood are from insects of the Cerambycidae family.

Scars were formed on the north side of trees as a result of the 1970's mountain pine beetle epidemic (Table I). These scars exhibit a range of diagnostic characteristics, but other than pitch tubes, none of these characteristics were found on every scarred tree. For example, only 65% of sampled trees had blue stain (Table II). Relying on presence of blue stain alone as a diagnostic characteristic for beetle scars would underestimate this source of scarring. Scars without blue stain might be incorrectly attributed to other



sources. Validation of beetle scarring should occur only if there is a combination of characteristics present.

Diagnostic characteristics which help to classify scars caused by the mountain pine beetle are listed in Table III and are shown in Fig. 1. With time, some characteristics become less prominent. It appears that blue stain fades after 75 to 100 years, and that beetle galleries will erode from exposed surfaces after 50 years or so. Therefore, the source of disturbance is more difficult to determine on scars exceeding 50—100 years in age.

In the 1973—81 outbreak (Table IV) 36% of the sampled trees had been attacked by the mountain pine beetle. Whether trees attacked in 1981 will die, develop scars, or be unaffected can not be determined until at least 1982; at least one growing season is required for scarring symptoms to become apparent. However, 41% of those trees attacked between 1973—80, or 9% of the total population, are developing scars. A previous study (Geiszler et al., 1980) in a similar climax lodgepole pine stand showed that 50—80% of trees larger than 10 cm [diameter (at breast height)] were killed during a mountain pine beetle epidemic, and that approximately 50% of live trees had been previously fire scarred. It now appears, however, that some of these trees were actually MPB scarred. It is expected that some of the 86 trees attacked

TABLE IV

Abundance of trees in each mountain pine beetle (MPB) damage class resulting from the 1973—81 outbreak at Wickiup Springs, Fremont National Forest, OR

Damage class	Tree count	Percent
Not attacked	432	64
Attacked in 1981	86	13
Killed in last 8 years	95	14
Green trees with MPB emergence	37	5
Heavy attach and pitchout — an unsuccessful attack	29	4
Total	679	100

TABLE V

Mountain pine beetle attack statistics of circumferential arc and azimuth on killed and surviving lodgepole pines measured at breast height. Data collected in 1981 from beetle attacks at Wickiup Springs, Fremont National Forest, OR

	Mean x	Standard deviation S	Minimum	Maximum
Attack arc	261.2	106.7	5	360
Mid-arc azimuth	33.2	37.2	289	174

in 1981 will develop scars, and that scarring will continue until the outbreak collapses. Scarred trees as a percent of the total number of live trees in the stand should increase not only because more scarring takes place, but also because, over time, more trees will be killed by subsequent MPB attacks.

Attack length, extent of attack arc, and attack aspect were compared between mountain pine beetle killed trees and survivors with a *t*-test. There were no statistical differences between scarred and dead trees for extent of arc ($P = 0.3603$), or attacked aspect ($P = 0.5943$). However, the killed trees had attacks extending higher on their stems ($\bar{x} = 4.73$ m, $s = 2.36$) than the surviving attacked trees ($\bar{x} = 3.53$ m, $s = 2.14$) ($P = 0.0001$). Most of the attacked arcs are centered in the northeast quadrant of the trees, and usually extend around two-thirds of the circumference of the trees (Table V).

Identification of beetle scars has enabled past mountain pine beetle epidemics to be differentiated from fires. It has also made possible accurate dating of beetle outbreaks here and other central Oregon location (R.G. Mitchell, R.E. Martin and J.D. Stuart, manuscript in preparation: Catfaces on lodgepole pine-fire scars or strip-kills by the mountain pine beetle). On our study area, the documented 1920's and 1970's outbreaks have been independently verified by scar analysis (Table VI). Examination of scars from the 1827—46 disturbance(s) has shown that there was a mountain pine beetle outbreak during this period. Some of these 1820's—40's scars, however, provide inconclusive evidence of beetle scarring, and leave open the possibility a fire may have been responsible.

TABLE VI

Lodgepole pine scar age ranges and types of disturbance seen at Wickiup Springs, Fremont National Forest, OR

Age range of scars (Sample size in parentheses)	Disturbance Type
1973—75 (25)	Mountain pine beetle
1922—29 (10)	Mountain pine beetle
1827—46 (8)	Mountain pine beetle and fire

CONCLUSIONS

Mountain pine beetle scars on lodgepole pine can be differentiated from fire scars if some, or all, of the following characteristics are present: pitch tubes, beetle emergence holes, blue stain, larval galleries, retained bark on the scar face, and an orange or red discoloration around healthy sapwood.

Mountain pine beetle scars are generally found on the north and northeast sides of lodgepole pine stems.

Mountain pine beetle attacks extend approximately two-thirds of the way around the bole.

After 50—100 years, blue stain, bark retention, and beetle galleries become less prominent on scarred trees.

Mountain pine beetle outbreaks have been verified by scar analysis for disturbances in the 1970's, the 1920's and the 1820's-40's.

ACKNOWLEDGEMENT

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Hazard rating of lodgepole pine stands to mountain pine beetle outbreaks in southcentral Oregon

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STUART, J. D. 1984. Hazard rating of lodgepole pine stands to mountain pine beetle outbreaks in southcentral Oregon. Can. J. For. Res. **14**: 666–671.

Stand structure and vigor variables were used to develop a model for predicting the development of a *Dendroctonus ponderosae* Hopk. outbreak in climax *Pinus contorta* Dougl. ex Loud. var. *murrayana* Grev. and Balf. stands in south central Oregon. Stepwise discriminant analysis indicated the significant predictor variables were quadratic mean diameter and the number of rings in the outermost centimetre of radial growth at breast height ($p = 0.00001$, canonical correlation coefficient = 0.77235). Ninety-three percent of the stands were correctly classified into their appropriate groups (attacked versus unattacked). None of the five indices of competition tested ((*i*) Waring and Pitman's tree vigor index, (*ii*) Mahoney's periodic growth ratio, (*iii*) Krajicek's crown competition factor, (*iv*) Hegyi's competition index, and (*v*) Curtis's stand density index) were significant discriminators.

STUART, J. D. 1984. Hazard rating of lodgepole pine stands to mountain pine beetle outbreaks in southcentral Oregon. Can. J. For. Res. **14**: 666–671.

La structure du peuplement et des variables de vigueur ont été utilisées pour la mise au point d'un modèle prédisant le développement d'une épidémie de *Dendroctonus ponderosae* Hopk. dans les peuplements climaciques de *Pinus contorta* Dougl. ex Loud. var. *murrayana* Grev. and Balf. du centre sud de l'Oregon. L'analyse discriminante par étape a indiqué que les variables de prédiction significatives étaient la moyenne quadratique en diamètre et le nombre d'anneaux dans le centimètre externe de la croissance radiale à hauteur de poitrine ($p = 0{,}00001$, coefficient de corrélation canonique = 0,77235). Quatre-vingt-treize pourcent des peuplements ont été correctement classés dans leurs groupes appropriés (attaqués versus non attaqués). Aucun des cinq indices de compétition évalués ((*i*) indice de vigueur de l'arbre de Waring et Pitman, (*ii*) rapport de croissance périodique de Mahoney, (*iii*) facteur de compétition de cime de Krajicek, (*iv*) indice de compétition de Hegyi, (*v*) indice de densité de peuplement de Curtis) n'avait un pouvoir discriminant significatif.

[Traduit par le journal]

Introduction

Researchers have developed a variety of hazard rating schemes designed to predict if mountain pine beetle (*Dendroctonus ponderosae* Hopk.) (MPB) outbreaks may occur in lodgepole pine (*Pinus contorta* Dougl. ex Loud.) forests. Most hazard rating schemes were developed for *Pinus contorta* var. *latifolia* and are yet untested for *P. contorta* var. *murrayana* stands. The simplest system plots historical infestations on a map from which land managers can determine areas prone to MPB attack (Crookston *et al.* 1977). Other hazard rating systems have been based on the following parameters: climate (Safranyik 1978); tree age, diameter, and climatic zone (Shrimpton 1975; Safranyik *et al.* 1975); habitat types, tree diameter, and elevation (Roe and Amman 1970; McGregor 1978); phloem thickness and diameter (Cole 1978; Cole and Cahill 1976); periodic growth ratio (Mahoney 1978); crown competition factor (Schenk *et al.* 1980); tree vigor (Waring and Pitman 1980); and phloem thickness, tree vigor, and MPB population dynamics (Berryman 1982). Cole and Amman (1980) developed an integrative hazard rating system with the following variables: (*i*) climatic suitability of stand location; (*ii*) average tree diameter 20.5 cm or more; (*iii*) average age 80 years or more; (*iv*) 25% or more of the trees have a diameter at breast height of 20.5 cm or more and a phloem thickness of 2.79 mm or more; (*v*) high crown competition factors and declining periodic growth ratios in some western Montana and northwest Idaho habitat types.

The study described in this paper was made to determine which stand structure variables and (or) hazard rating indices could be used to predict if a MPB outbreak would occur in the study area. Two types of indices were included: (*a*) those used in previous MPB hazard ratings in lodgepole pine forests, and (*b*) those adapted from competition indices used in tree and stand growth simulation. The latter index type was included since competition has been linked to declining tree vigor and a weakening of host defenses (Rudinsky 1962; Schenk *et al.* 1980; Berryman 1982). Two indices based on tree size – density relationships were chosen as examples of this type. The study was limited to the onset of an outbreak. Once an outbreak had started it was felt the predictive value of the stand structure variables and hazard rating indices would be lessened because of confounding effects of MPB population dynamics.

Methods

Study area

The study was conducted in the summer of 1982, in unlogged climax lodgepole pine stands growing at 1800 m elevation near Wickiup Springs on the Fremont National Forest, Oregon. Soils are relatively infertile, well drained, loamy sands, developed from Mount Mazama eolian ash and pumice. The climate during the growing season is characterized by warm, dry days and cold nights. Summer temperatures range from lows of −7°C at night to highs of 41°C during the day. Yearly precipitation ranges from 38–76 cm, with most falling as snow from November through April (Wenzel 1979).

Infestation history

Lodgepole pine forests in south central Oregon have experienced recurring mountain pine beetle outbreaks. Stuart *et al.* (1983) established that outbreaks occurred in climax lodgepole pine stands on the northern portion of the Fremont National Forest in the late 1820's to

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TABLE 1. Year of mountain pine beetle (MPB) outbreak, number of paired plots per outbreak year, density of mountain pine beetle killed trees in outbreak stands, and approximate year of lodgepole pine establishment for sampling sites located near Wickiup Springs, Fremont National Forest, OR

Year of MPB outbreak	Number of paired plots (group 1 + group 2)	Number of MPB-killed trees per group 2 plot	Approximate year of tree establishment
1967	1	5	1899
1968	2	8, 5	1899, 1840
1970	1	4	1750
1972	3	5, 4, 4	1840, 1840, 1840
1973	7	6, 2, 4, 4, 6, 4, 4	1840, 1840, 1750, 1840, 1750, 1840, 1840
1981	1	5	1899

1840's, the 1920's, and from the late 1960's to present. Stuart (1983) suggests that there may have been outbreaks in these stands in ca. 1620 and in ca. 1750. Fires occurred in 1840 and 1899 (Stuart 1983).

The most recent MPB outbreak was first reported in 1956 approximately 10 km south (latitude 43°15′N, longitude 121°22′W) of the study site and encompassed 80 ha. The outbreak area slowly increased northward, peaked in 1968, and covered approximately 75 000 ha (Dolph 1972). By 1981 all of the study area had been affected. Tree mortality was ubiquitous. However, interspersed among the stands which experienced tree mortality were smaller stands having no MPB-killed trees. The intimate mosaic pattern of stands which had outbreaks with those that did not have outbreaks suggests both kinds of stands had an equal opportunity to experience an outbreak.

Study design

The study was located in climax lodgepole pine stands in the general vicinity of Wickiup Springs and Bald Mountain. Sampling sites were located such that plots could be established in stands that (1) escaped an outbreak (group 1), and (2) those that experienced an outbreak (group 2). Paired plots in adjacent stands were used so that tree and stand parameters could be corrected to the year prior to an outbreak (Table 1). All trees in group 2 stands were killed in the same year. Average tree age was identical for each pair of plots, although tree ages differed among sampling sites (83−232 years) (Table 1). Group 1 stands were relatively scarce and were, therefore, used to define the location of sampling sites. Fifteen group 1 stands were identified along United States Forest Service roads 2516 and 256.

After locating the sampling sites, plot centers were randomly located. Data collected from the 15 paired circular 0.01-ha plots (15 group 1 and 15 group 2 plots) included the following: (*i*) the DBHs, to the nearest 0.5 cm, of all trees greater than or equal to 2 cm DBH; (*ii*) MPB-induced tree mortality; (*iii*) the sapwood thicknesses of the five largest trees, determined by measuring the widths of the transluence or the widths of blue stain of increment core samples; (*iv*) information required to calculate Hegyi's index of competition (Daniels 1976), i.e., (*a*) the number of competitors per subject tree; (*b*) the distance, to the nearest centimetre, from the subject tree to each competitor; (*c*) the DBHs, to the nearest 0.5 cm, of subject trees and their competitors. The subject trees were the five largest in each plot. The competitors of each subject tree were those "in" trees found by sighting through a metric wedge prism (basal area factor (BAF) of 2.3) from a point as close to the subject tree as possible.

In addition, increment cores were extracted from the subject trees for growth analysis. In the laboratory the cores were sanded to a polish and cross-dated under a microscope to determine when MPBs had been active in the vicinity of the plot. The number of rings, rings per centimetre, and measurements of annual growth were made for those years immediately prior to when MPBs were present. Ring widths were measured on a Bannister incremental measuring machine.

The hazard rating indices used in the analysis were as follows: (*i*) Waring and Pitman's tree vigor index (V) (Waring and Pitman 1980; Mitchell *et al.* 1983); (*ii*) Mahoney's periodic growth ratio (PGR) (Mahoney 1978); (*iii*) Krajicek's crown competition factor (CCF) (Krajicek *et al.* 1961); for lodgepole pine in south-central Oregon Dahms (1971) modified Krajicek's model to:

$$[1]\quad \mathrm{CCF} = 1/A0.0192(n) + 0.0168 \sum_{i=1}^{n} (D) + 0.0036 \sum_{i=1}^{n} (D^2)$$

where A = plot area in acres, n = the number of trees, and D = diameter outside bark. (*iv*) Hegyi's competition index (HEGYI) (Daniels 1976); Daniels proposed a modification of Hegyi's index which would select competitors based on their size and distance from the subject tree; he found that an angle guage with a BAF of 2.3 gave the highest correlations between observed diameter increment and observed total height increment with the calculated competition index value; (*v*) Curtis's stand density index (SDI) (Curtis 1982).

The stand structure variables used in the analysis were as follows: (*vi*) quadratic mean diameter (QUADMN); (*vii*) stand density (DENSITY); (*viii*) mean diameter of the five largest trees in the plot (DBH); (*ix*) mean number of rings in the outermost centimetre of radial growth at breast height for the five largest trees per plot (RINGCM); (*x*) mean number of competitors per plot using Hegyi's index (NUMCOM); (*xi*) basal area per plot (BA); (*xii*) mean basal area of the five largest trees per plot (TREEBA); (*xiii*) mean diameter of all trees in the plot (AVGDBH); (*xiv*) basal area percentage (BAPRCNT), where basal area percentage equals the mean increase in basal area over the past 10 years' growth as a percentage of the basal area for the five largest trees in a plot.

Differences between group means for each variable were determined with 2-tailed *t*-tests.

A discriminant analysis approach was used to develop a stand hazard rating model which would predict, within certain bounds of probability, whether a climax lodgepole pine stand would be susceptible to a MPB outbreak. It was hypothesized that a combination of stand structure characteristics and some hazard rating indices would be significant predictors. The two group discriminant analyses were run using SPSS (Statistical Package for the Social Sciences) procedures (Nie *et al.* 1975). All analyses were done stepwise, with the possibility of entering and removing variables at each step. Some analyses were run in which each of the five indices of competition were "forced in" and could not be removed. The objective was to determine what the relative contribution of these indices would be once all significant variables had been entered.

Results and discussion

Five hazard rating indices and the nine stand structure variables were entered into a correlation analysis to determine which variables would be best to use in the discriminant analysis. From inspection of the pooled within-groups correlation matrix (Table 2), it was judged that four of the stand structure variables (DBH, AVGDBH, TREEBA, and BA) should be removed from subsequent analyses because of their high correlations with other variables: DBH, AVGDBH, and TREEBA with QUADMN; and BA with CCF. Quadratic mean diameter

TABLE 2. Pooled within-group correlation matrix of stand structure and vigor variables used in analysis to assess mountain pine beetle outbreak hazard in climax lodgepole pine stands near Wickiup Springs, Fremont National Forest, OR[a]

	DBH	RINGCM	NUMCOM	HEGYI	DENSITY	BA	TREEBA	PGR	CCF	QUADMN	SDI	BAPRCNT	AVGDBH	V
DBH	1.00000													
RINGCM	−0.33633	1.00000												
NUMCOM	−0.16032	0.03193	1.00000											
HEGYI	−0.56556	0.12515	0.76133	1.00000										
DENSITY	−0.38044	−0.00061	0.54870	0.63047	1.00000									
BA	0.46274	−0.27464	0.61985	0.32447	0.49148	1.00000								
TREEBA	0.97945	−0.35785	−0.22098	−0.54434	−0.37379	0.44523	1.00000							
PGR	0.03604	−0.07893	−0.26069	−0.22247	−0.13753	−0.12489	0.06457	1.00000						
CCF	0.30993	−0.29433	0.66026	0.39325	0.64006	0.98057	0.29277	−0.16463	1.00000					
QUADMN	0.81975	−0.28599	−0.27720	−0.56616	−0.63778	0.19884	0.82541	−0.05687	0.06026	1.00000				
SDI	0.13843	−0.13457	0.71869	0.56064	0.73541	0.91997	0.11743	−0.13074	0.91341	−0.16834	1.00000			
BAPRCNT	−0.26892	−0.55239	−0.20150	0.12554	−0.07984	−0.25334	−0.18019	0.12512	−0.17688	−0.07178	−0.26629	1.00000		
AVGDBH	0.78358	−0.19762	−0.17718	−0.45930	−0.60295	0.25827	0.77938	−0.08154	0.08901	0.97505	−0.07503	−0.15042	1.00000	
V	0.02037	−0.45033	−0.27682	−0.07121	−0.14509	−0.10934	0.11665	0.57413	−0.12332	−0.00020	−0.15918	0.69231	−0.07408	1.00000

[a] See Methods section for variable descriptions.

TABLE 3. Means of variables used in analysis to assess mountain pine beetle (MPB) outbreak hazard in climax lodgepole pine stands near Wickiup Springs, Fremont National Forest, OR (group 1, stands not attacked by MPBs; group 2, stands attacked by MPBs)

Group No.	Group means													
	DBH**	RINGCM**	NUMCOM	HEGYI*	DENSITY**	BA	TREEBA**	PGR	CCF	QUADMN**	SDI	BAPRCNT**	AVGDBH**	V**
1	20.45333	21.57333	10.84000	3.28027	27.63333	3555.64067	345.33404	0.93014	217.96355	13.75936	3.20972	9.95243	12.66723	30.22736
2	24.87333	27.22667	10.14667	2.59827	12.33333	3598.65133	511.60531	0.89564	205.73965	20.08135	2.71571	6.84259	18.67978	22.87541
Total	22.86333	24.40000	10.49333	2.93027	19.93333	3576.14600	428.46968	0.91280	211.85160	16.92036	2.96271	8.29750	15.67350	26.55139

NOTE: See Methods section for variable descriptions. *, 5% significance level; **, 1% significance level.

TABLE 4. Discriminant function classification coefficients used in analysis to assess mountain pine beetle hazard in climax lodgepole pine stands near Wickiup Springs, Fremont National Forest, OR

Variables	GRPNUM 1	GRPNUM 2
QUADMN[a]	1.268654	1.779806
RINGCM[b]	1.369873	1.774615
(CONSTANT)	−24.19745	−42.72203

[a] Quadratic mean diameter.

[b] Rings per centimetre.

was expected to best represent the diameter classes preferred by the MPB and, since phloem thickness has been shown to be positively correlated with diameter (Amman 1969, 1975; Cole 1973), to best represent phloem thickness. Two of the hazard rating indices (CCF and SDI) had a high correlation coefficient ($r = 0.913$), but since a primary objective of the study was to compare the effectiveness of these indices as discriminators, they were left in the analysis.

A comparison of the means of the 14 variables (Table 3) showed that the stands which did not experience the recent MPB outbreak (group 1) had trees which were denser ($p = 0.0016$) and smaller in diameter ($p = 0.0004$) than stands attacked by MPBs (group 2). The basal area of both groups was essentially the same ($p = 0.916$). Two variables based on tree vigor showed that group 1 stands experienced less competition (Waring and Pitman's index, $p = 0.0068$; number of rings per centimetre, $p = 0.0020$). Another vigor variable, Mahoney's periodic growth ratio, showed no statistical difference between groups ($p = 0.368$). The variables based on mensurational parameters such as diameter−density relationships (CCF), quadratic mean diameter and basal area (SDI), and intertree distances and diameters of trees selected by a wedge prism (HEGYI) gave inconclusive results. Hegyi's index showed that group 1 stands experienced greater competition ($p = 0.0471$), while the crown competition factor and the stand density index showed no statistical differences between groups ($p = 0.605$ and $p = 0.161$, respectively). The vigor variables were thought to better represent competition, as they directly measure tree growth. The other indices of competition are indirect measures of competition, and are therefore not as reliable.

The five remaining stand structure variables and the five hazard rating indices determined to be suitable for further analysis were entered in a stepwise discriminant analysis. The most significant variable (highest F, equal to or greater than 1.0) was entered at each step. It was possible to remove previously entered variables if, because of the addition of new variables, their significance levels fell below an F value of 1.0.

The variables that the discriminant analysis selected as statistically significant discriminators of groups were measures of tree diameter (quadratic mean diameter) and of tree vigor (rings per centimetre), ($p = 0.00001$, canonical correlation coefficient = 0.77235). Group centroids were separated by 2.35 standard deviations.

The selection of quadratic mean diameter and of the number of rings per centimetre as variables to predict whether a lodgepole pine stand would be attacked by MPBs is consistent with what Cole and Amman (1980) found.

The adequacy of the derived discriminant functions was tested by classifying the stands used to derive the functions in the first place, and comparing these predicted group memberships with actual group memberships. Using coefficients from Fisher's linear discriminant functions (Table 4) it was possible to calculate probabilities of group membership for each stand. A stand was classified into a particular group if its probability of membership was greater than 0.5. An incorrect classification occurred if a stand was classified into group 1, for example, yet actually belonged to group 2. In this analysis 93.33% of the stands were correctly classified.

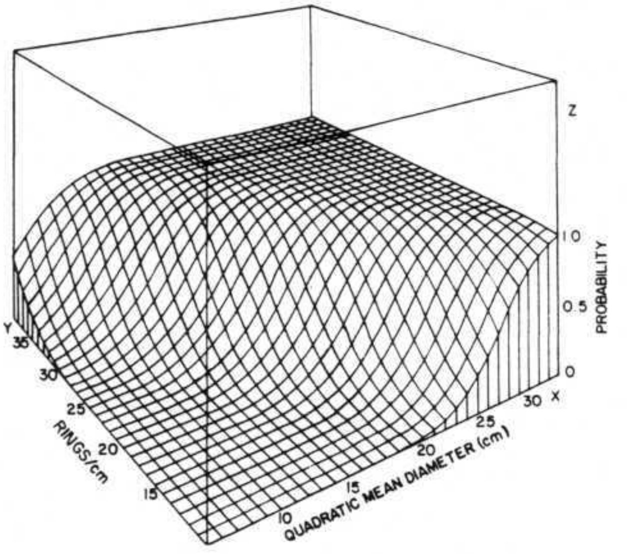

FIG. 1. Three dimensional surface indicating the probability a climax lodgepole pine stand near Wickiup Springs, Fremont National Forest, OR, may incur a mountain pine beetle outbreak based on the quadratic mean diameter and the number of rings per centimetre.

Given that the discriminant analysis did a good job of separating the groups, and that the predictor variables were ecologically appropriate, a model based on the classification scores was developed to predict whether a particular stand would be susceptible to MPB attacks. The model calculates the posterior probabilities that a stand belongs to group 2 based on the Fisher linear discriminant function classification coefficients. By using the quadratic mean diameter and the number of rings per centimetre for a climax lodgepole pine stand from the general vicinity of Wickiup Springs, it was possible to determine the posterior probability that the stand would be attacked by MPBs. Posterior probabilities were calculated by

$$[2]\quad P = \exp(S_{ij}) / \sum_{k=1}^{a} \exp(S_{ij})$$

where S = the classification score for stand i of group j, and a = the number of groups (Dixon and Brown 1981).

For example, the posterior probability that a stand belongs to group 2 is

$$[3]\quad P = [\exp(-42.722 + 1.779(\mathrm{QUADMN}) + 1.775(\mathrm{RINGCM}))] / [\exp(-42.722 + 1.779(\mathrm{QUADMN}) + 1.775\,(\mathrm{RINGCM})) + \exp(-24.197 + 1.269(\mathrm{QUADMN}) + 1.369(\mathrm{RINGCM}))]$$

By calculating an array for posterior probabilities for the two variables, it was possible to develop a three-dimensional representation of the probability surface (Fig. 1). Estimating the probability that a stand will be attacked by MPBs is easier and

TABLE 5. Contributions of five hazard rating indices used in discriminant analysis models to predict if a mountain pine beetle outbreak will occur in a climax lodgepole pine forest near Wickiup Springs, Fremont National Forest, OR

Index of competition	Wilks lambda	R^2	F	Added contribution to canonical correlation coefficient with all significant variables in the model
Waring and Pitman	0.7660	0.234	0.0068	0.0020
Hegyi	0.8665	0.134	0.0471	0.0014
Stand density index	0.9312	0.069	0.1613	0.0001
Periodic growth ratio	0.9709	0.029	0.3675	0.0001
Crown competition factor	0.9903	0.009	0.6045	0.0015

faster by interpolation from Fig. 1 than by using the formula. If it is necessary to know the exact probability of MPB attack, the formula should be used.

Users of the results of this discriminant analysis and prediction equations should note that the numerical relationships are valid only for stands in the general vicinity of Wickiup Springs. If one needed to know the probability that a stand will be attacked by MPBs in a different region, a new set of data would have to be collected and the corresponding predictive equations developed using the method outlined above.

The relative importance of the hazard rating indices was determined by forcing them into separate stepwise discriminant analyses. In each analysis the first variable entered was one of the hazard rating indices. Subsequent steps brought in the next most significant (F equal to or greater than 1) variables. It was possible for a variable to be removed from the analysis if its significance level dropped below an F of 1.0. The hazard rating index, however, could not be removed from the analysis, regardless of its F value. By examining the summary table for the first step in each analysis, it was possible to determine the significance level and the percentage of the explained variation [(1 − Wilk's lambda) (100)] for each index of competition. Waring and Pitman's tree vigor index and Hegyi's index were the only indices that were statistically significant ($p = 0.0068$ and $p = 0.0471$, respectively), although they explained less than 25% of the variation in the data (23.4 and 13.4%, respectively) (Table 5). The other indices explained even less of the variation, with the stand density index accounting for 6.9%, the periodic growth ratio accounting for 2.9%, and the crown competition factor explaining only 0.93%. The contribution of the hazard rating indices as discriminators was negligible once all the significant variables had been entered. Waring and Pitman's index was the best of the five, although it improved the canonical correlation index by only 0.0020. The added contributions of the other four indices were, in descending order: crown competition factor (0.0015), Hegyi's index (0.0014), periodic growth ratio (0.0001), and stand density index (0.0001).

Conclusions

The variables determined to be significant predictors of whether a climax lodgepole pine stand will be attacked by MPBs were the quadratic mean diameter and the number of rings in the outermost cm of radial growth. None of the other hazard rating indices were significant. A possible reason why the hazard rating indices were not significant could be that none of them incorporated both vigor (growth) and tree size: Waring and Pitman's and Mahoney's indices were based on growth, Curtis's index was based on tree size, Hegyi's and Krajicek's indices were based on tree size and density. It may be possible to develop a better predictive model if one of the vigor indices were modified to incorporate tree size.

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Primary Attraction of the Mountain Pine Beetle to Lodgepole Pine in Oregon

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ABSTRACT Dispersing *Dendroctonus ponderosae* landed preferentially on lodgepole pines with fire scars and decay ($P = 0.023$ and $P = 0.008$, respectively, by joint binomial distribution analysis).

THE MOUNTAIN PINE BEETLE (MPB), *Dendroctonus ponderosae* Hopkins, is the most destructive insect pest of lodgepole pine (*Pinus contorta* Douglas) forests in western North America. Mountain pine beetles select suitable or susceptible hosts during their dispersal flights. However, there is considerable controversy over whether the initial selection of hosts by dispersing bark beetles is random (beetles landing indiscriminately on hosts) or directed (beetles landing preferentially on weakened host trees) (*see* review in Wood [1982]). Preferential landing on hosts, presumably in response to olfactory cues emanating from weakened hosts, is termed primary attraction (Moeck et al. 1981).

We have shown that during the first few years of an outbreak, more fire-scarred than unscarred trees are killed by MPBs, and, moreover, fire-scarred trees have significantly more advanced decay and fungal stain than unscarred trees (Geiszler et al. 1980). The most common fungus in fire-scarred lodgepole pine in our study area was *Poria asiatica* (Pilat) Overholts (Littke and Gara 1983). The question remains, however, whether or not dispersing beetles preferentially land on decayed trees.

We investigated this question in a topoedaphic climax *P. contorta* var. *murrayana* (Grev. and Balf.) stand growing on tephra-derived soils of southcentral Oregon (Franklin and Dyrness 1973). These stands have been host to a MPB population since ca. 1970. During the summers of 1981 and 1982, before the MPB dispersal flight, we attached window-barrier traps (Chapman and Kinghorn 1955) to approximately equal numbers of fire-scarred and unscarred trees (78 trees in 1981, 26 in 1982). All test trees were on the average 23 cm in diameter, the preferred diameter for MPB attack in this area (Geiszler et al. 1980). When the dispersal flights commenced, we removed the trapped beetles daily. We stopped counting beetles on a trap when the test tree or trees adjacent to it were attacked. We felt that once aggregating pheromones were present, the particular test tree was of no further value. After completion of the landing study, we cut all test trees and investigated their fungus status.

As the number of test trees "available for landing" changed during the season, we used the joint binomial distribution to compute the probabilities of a MPB landing on a fire-scarred tree—a type of landing we termed "success." The joint binomial distribution takes into consideration that the probability of a success can be different for changing (or different) sample sets. This distribution can be described as

$$P(S > s) = \sum \prod_{i=1}^{K} \binom{N_i}{M_i} p_i^{M_i}(1 - p_i)^{N_i - M_i}$$

where S is a random variable for the number of successes, s is the observed number of successes, K is the number of sample sets taken, N_i is the number of samples in the i^{th} set, m_i is the observed number of successes in the i^{th} set, and p_i is the probability of a success in the i^{th} set. The summation ($\sum$) is taken over all values of M_i such that

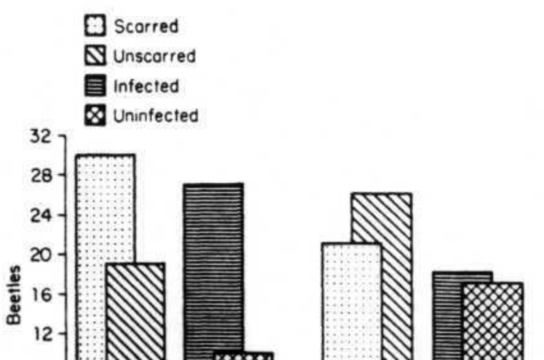

Fig. 1. Observed number of *D. ponderosae* landings and expected number of landings (assuming random selection) on scarred and unscarred as well as fungus-infected and uninfected lodgepole pines. Studies done near Wickiup Springs, Fremont Natl. For., Oreg.

$$S = \sum_{i=1}^{k} M_i \text{ is greater than } s = \sum_{i=1}^{k} m_i$$

and $$0 \le M_i \le N_i$$

The results indicate that dispersing beetles preferentially select fire-scarred trees ($P = 0.023$) and primarily trees with *P. asiatica* ($P = 0.008$) (Fig. 1). Apparently MPBs in dispersal flight can detect host cues, which may be volatile materials produced by interactions between the decay fungi and host constituents. These results also confirm the existence of preferred focus trees—trees initially selected by flying *D. ponderosae* at a time before the population aggregates in response to pheromones.

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Stand Structure and Development
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in South-Central Oregon

by

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Abstract

STAND STRUCTURE AND DEVELOPMENT
OF A CLIMAX LODGEPOLE PINE FOREST
IN SOUTH-CENTRAL OREGON

by John David Stuart

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Stand structure of south-central Oregon lodgepole study sites was characterized as being: (a) multi-sized (bimodal height and platykurtic DBH distributions), (b) multi-aged (regeneration peaks circa 1750, 1840, 1900, 1925, and late 1970's), and (c) overwhelmingly dominated by the circa 1840 age class. The mean height (8.45 m), DBH (15.01 cm) and basal area (19.52 m^2 ha^{-1}) of these stands were small. Every regeneration peak since 1750 was associated with a period of slow growth and either a mountain pine beetle (MPB) outbreak (1827-1846, 1920's, 1970's) or a fire (1840, 1899). It is likely that a neighboring 1620 and the 1750 regeneration pulses were associated with MPB outbreaks. Past MPB outbreaks were determined by aging scars on stems of lodgepole pine trees. No tree of less than 10 cm DBH was killed in the recent MPB outbreak. Of those trees larger than 10 cm DBH, 31.7% were killed by the MPBs, representing 38.3% of basal area and 44.0% of leaf area.

Development of climax lodgepole pine stands was found to be dependent on the limiting factors of the site and disturbance events such as MPB outbreaks or fire. Rates of growth and the degree of competitive interaction between trees and seedlings were limited by severe microclimates and/or lack of soil moisture. Seedlings

growing on sites with favorable microclimates and reduced competition for soil moisture had significantly higher survival rates, lower internal moisture stress, and greater biomass production.

A discriminant analysis to determine what stand structural variables and/or indices of competition could be used to predict when a MPB outbreak would occur showed that quadratic mean diameter and number of rings cm^{-1} in the outermost cm of radial growth were the best predictors. Fire occurrence was found to be limited to periods of time when there were enough intersecting U.S.F.S. decay class 4 logs for fire spread.

A conceptual model was made which describes how fire, MPB outbreaks, decay, and drought affect stand structure and development.