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INFLUENCE OF FIRES, FUNGI AND MOUNTAIN PINE BEETLES ON DEVELOPMENT OF A LODGEPOLE PINE FOREST IN SOUTH-CENTRAL OREGON¹

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 ($1-2 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) and leaf area ($1-2 \text{ m}^2 \cdot \text{m}^{-2}$) 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

¹Study supported by NSF grant DEB 8209813

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.

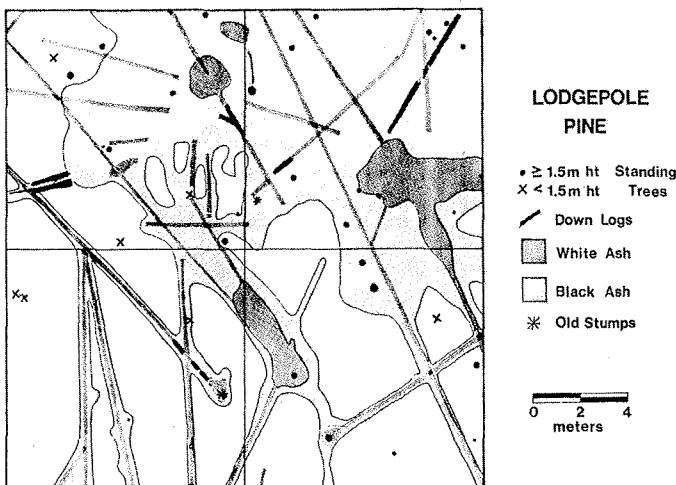


Figure 1.—Fire spread at the 1980 Sharp Peak fire in a climax lodgepole pine stand; fire smoldered along decayed logs with some litter consumption. The “white ash” areas were corridors along which logs were completely consumed, imposing a “pick-up sticks” matrix of fire spread across the landscape (from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

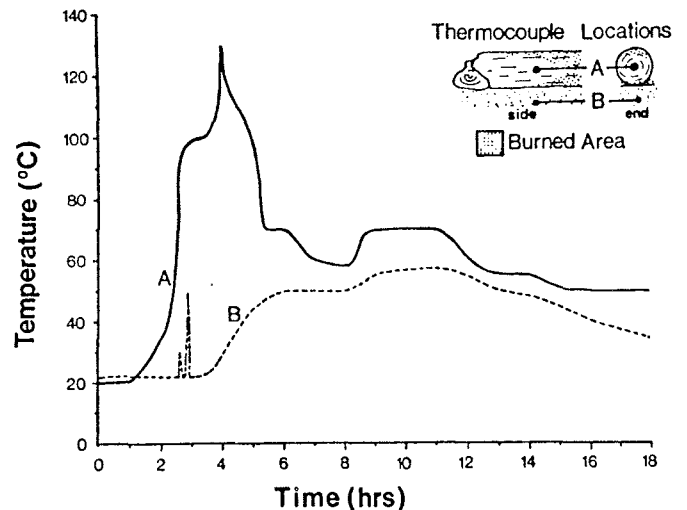


Figure 2.—Time temperature profiles recorded by a shielded thermocouple placed inside a smoldering lodgepole pine log (A) and one buried 5 cm below the log (B) at a 1980 Crater Lake NP fire.

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 Pathogens.—In order to link fires with establishment of fungal infection courts in the boles of trees (Geiszler *et al.*, 1980, Nordin 1958), we serially sectioned the boles and exposed the roots of about 100 trees that 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).

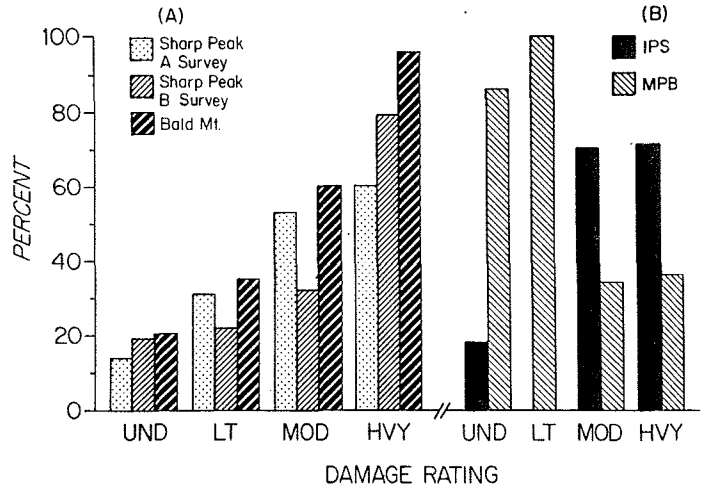


Figure 4.—(A) Percentage of lodgepole pine infested by scolytids as related to fire damage rating (undamaged, light, moderate and heavy); data recorded 2 years after the 1980 Sharp Peak fire (surveys A and B) and one year after the Bald Mt. fire. (B) Percent of trees infested by *Ips* and mountain pine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

Fire damage	Adjusted r^2 values	
	<i>Ips</i>	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 *Lep-tographium* 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 out-competes 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	<i>Pholiota carbonicola</i>	W	24	FK roots
		<i>Trametes carbonaria</i>	W	5	"
		Misc. fungi imperfecti etc.	—	71	
Wickiup	6	<i>Poria subacida</i>	W	25	FS trees/DL
		<i>Heterobasidion annosum</i>	W	6	FS trees/DL
		<i>Lentinus lepideus</i>	B	6	FK roots
		<i>Sistotrema brinkmanni</i>	B	6	FK roots
		Unid.	W	57	FS/FK trees
Lookout Point	84	<i>Poria asiatica</i>	B	13	FS trees
		<i>Gloeophyllum odoratum</i>	B	10	FS trees/DL
		<i>Lentinus lepideus</i>	B	3	FS trees
		<i>Tyromyces Leucospongia</i>	B	8	DL
		<i>Poria taxicola</i>	B	3	FS trees
		<i>Poria subacida</i>	W	3	DL
		<i>Coniophora</i> sp.	B	5	DL
		Unid. Basidiomycetes ³	B	38	FS trees

¹Rot type: W=white rot; B=brown rot.

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

³Unidentified 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 reflect 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 crosssection of the bole showing decay column associated with the fire-damaged root (right).

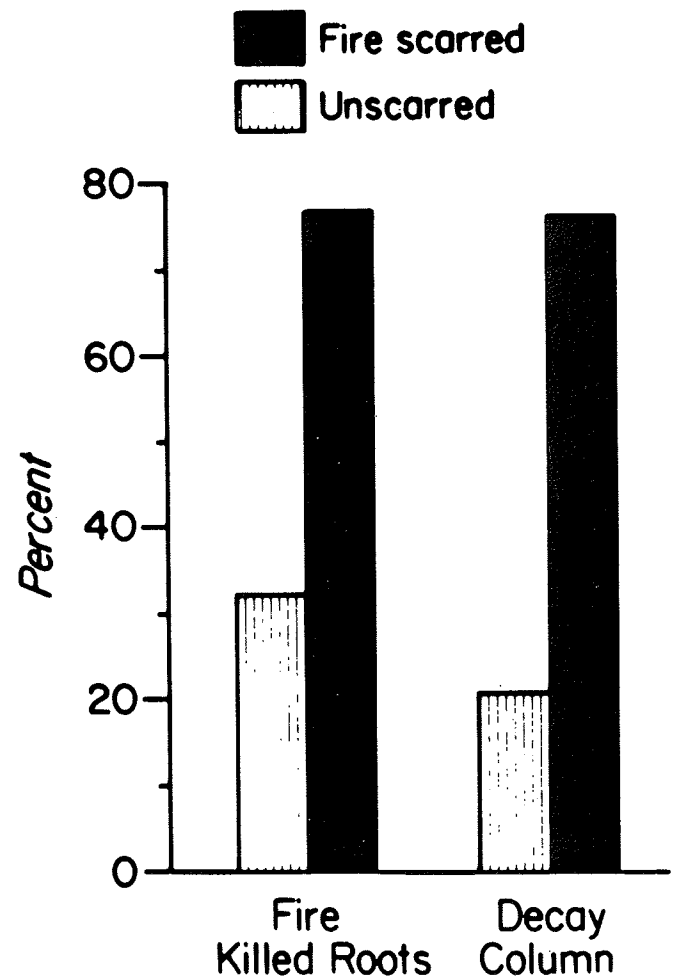


Figure 6.—The percentage of fire-scarred and unscarred lodgepole pines with fire-killed roots (left), and those with active decay columns (right); data from 44 trees sampled at the 1898 Lookout Point fire (from Littke and Gara 1984).

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.

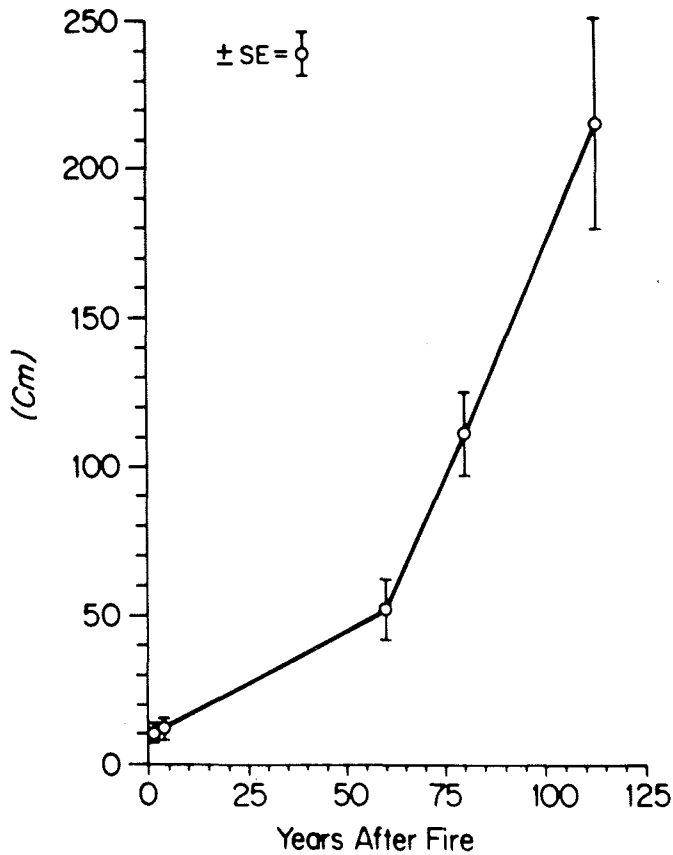


Figure 7. Vertical development over time of active decay columns in lodgepole pine whose lateral roots were damaged by fires in 1870, 1898, 1920, 1976, or 1980 respectively (from Littke and Gara 1984).

We investigated this question by establishing modified window traps (Chapman and Kinghorn 1955) on *P. asiatica* infected and uninfected 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.

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

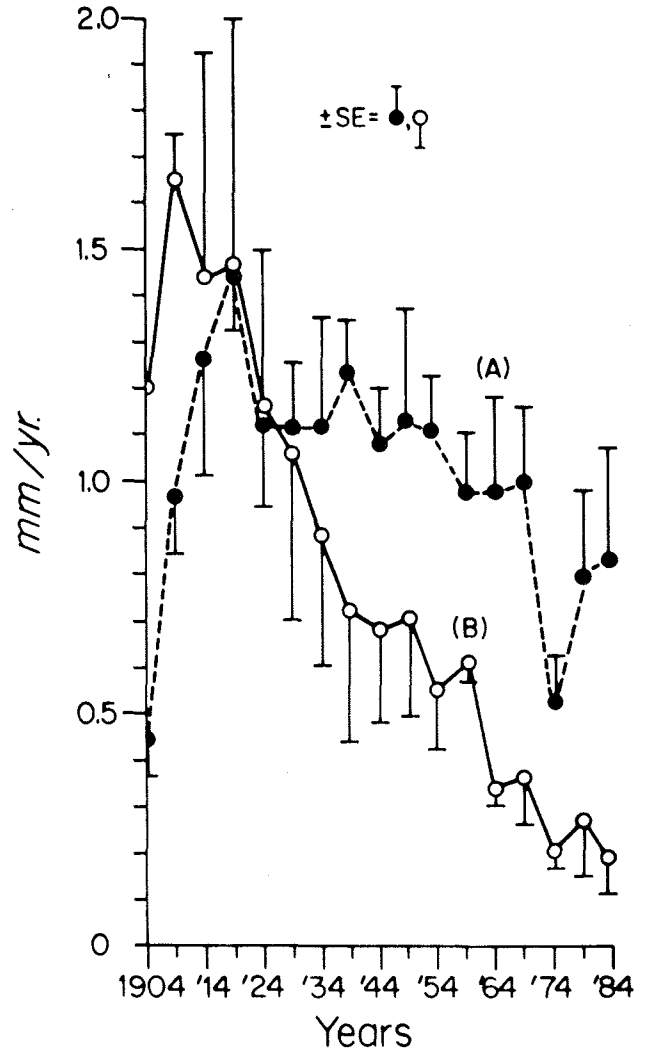


Figure 8.—Mean annual increment ($\text{mm}\cdot\text{yr}^{-1}$) of adjacent pairs of similar diameter lodgepole pines following the 1898 Lookout Point fire. One member of each pair was undecayed and unscarred (A); the other member was fire-scarred and had an active decay column (B) (Littke and Gara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

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).

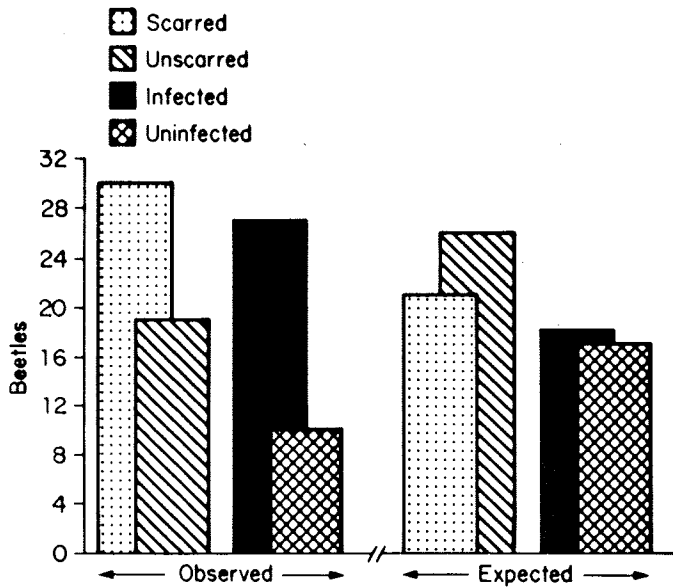


Figure 9.—Observed number of *D. ponderosae* landings and expected number of landings (assuming random selection) on fire-scarred and unscarred as well as fungus-infected and uninfected lodgepole pine at Lookout Point (see appendix).

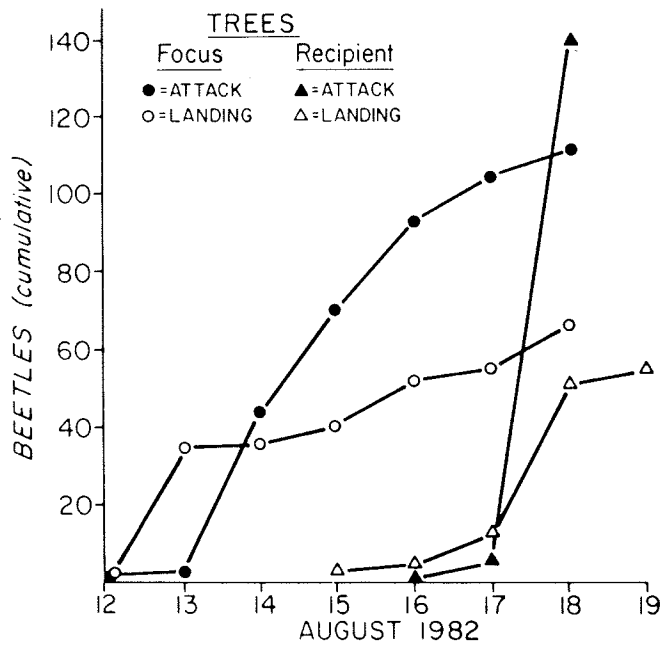


Figure 10.—Cumulative numbers of *D. ponderosae* landings and attacks on lodgepole pines initially baited with synthetic pheromones (focus trees) and later on adjacent stems (recipient trees); studies conducted at Lookout Point area.

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 Geiszler and Gara (1978). Thus the potential for *D. ponderosae* outbreaks 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:

(1) a ridgetop ponderosa pine community characterized by a varied fire history; (2) an ecotonal zone between the ponderosa pine ridgetop and the climax lodgepole situated in the flats below; (3) the climax lodgepole pine flats, which experienced an 1839 stand regeneration fire and an 1898 light ground fire; and (4) an adjacent climax lodgepole pine area that had not had a fire for at least 350 years.

Based on the distribution and ages of single and multiple fire 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 model. Regeneration patterns of the ridgetop and ecotonal areas were heterogenous, reflecting the seedling establishment after a series of fires that spanned the last three

centuries. In contrast, regeneration patterns of the lodgepole pine flats, which experienced only two fires, were bimodal—trees initiated in 1840 and 1899. The climax lodgepole pine stand that had no fires in the last 350 years had a variety of age classes (85 to 350 yrs) 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. ponderosae*.

Synthesis.—We propose the following conceptual model that integrates the effects of fire, fungi and mountain pine beetles in development of lodgepole pine stands in the Lookout Point area (Fig. 11). During 1839, fuel conditions and weather were ideal for spread of a stand replacement fire throughout a large portion of the Lookout Point area. This fire eliminated root

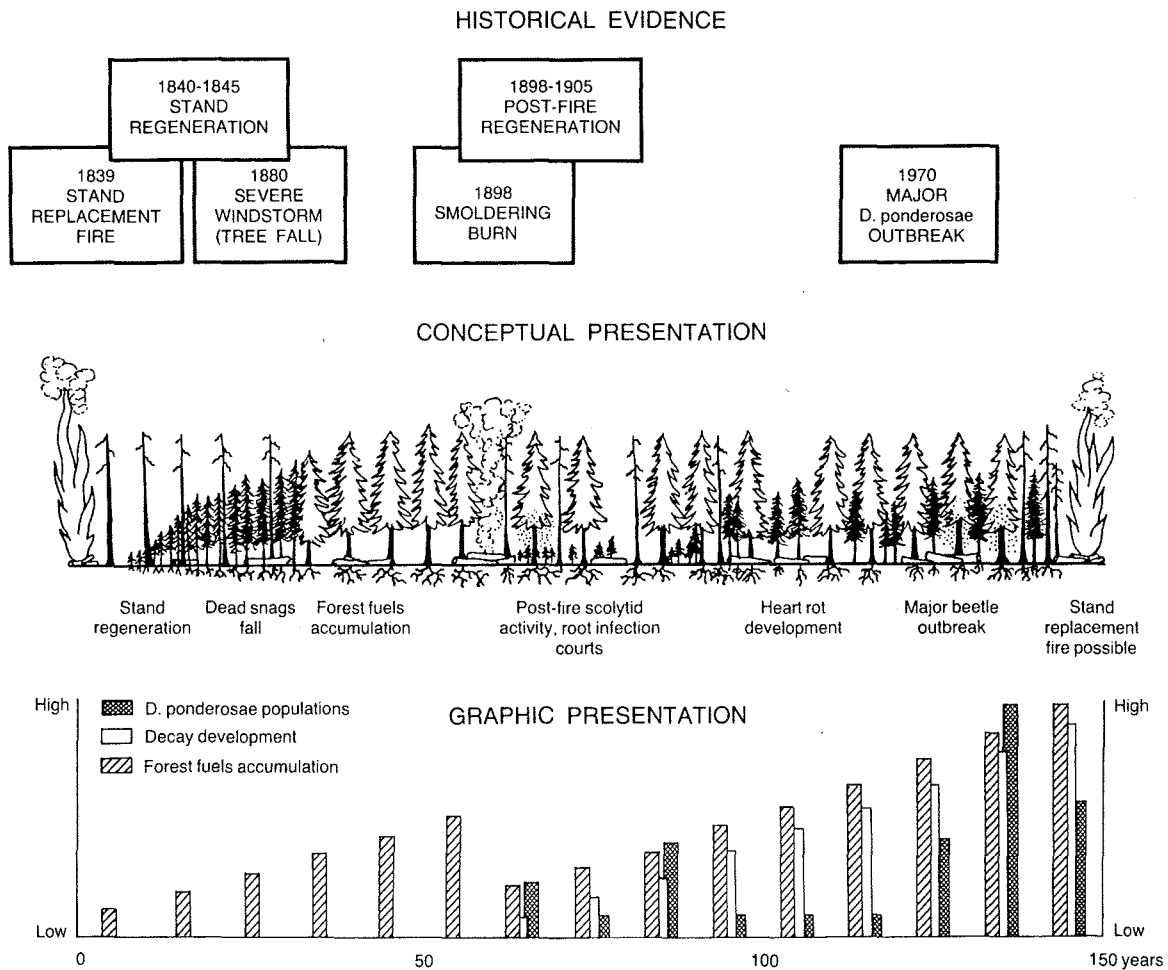


Figure 11.—Interactions between fires, fungi, and mountain pine beetles observed at Lookout Point—a climax lodgepole pine forest of the Oregon pumice plateau.

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 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 4). 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 but 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 actions 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 would have in their attempt to minimize the effects of scolytid epidemics. In particular, understanding the dynamics of lodgepole pine stands would 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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Table 4. -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
<i>D. ponderosae</i> 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 <i>D. ponderosae</i>	fire-scarred dominants with advanced <i>P. asiatica</i> 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

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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

$$P(S < s) = \sum_{i=1}^K \prod_{j=1}^i \binom{N_j}{M_j} p^{M_j} (1-p_j)^{N_j-M_j}$$

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)

K

is taken over all values of M_i such that $S = \Sigma_{i=1}^K M_i$ is greater

$i=1$

than $s = \Sigma_{i=1}^K m_i$ and $M_i \leq N_i$ (from Gara *et al.*, 1984).

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