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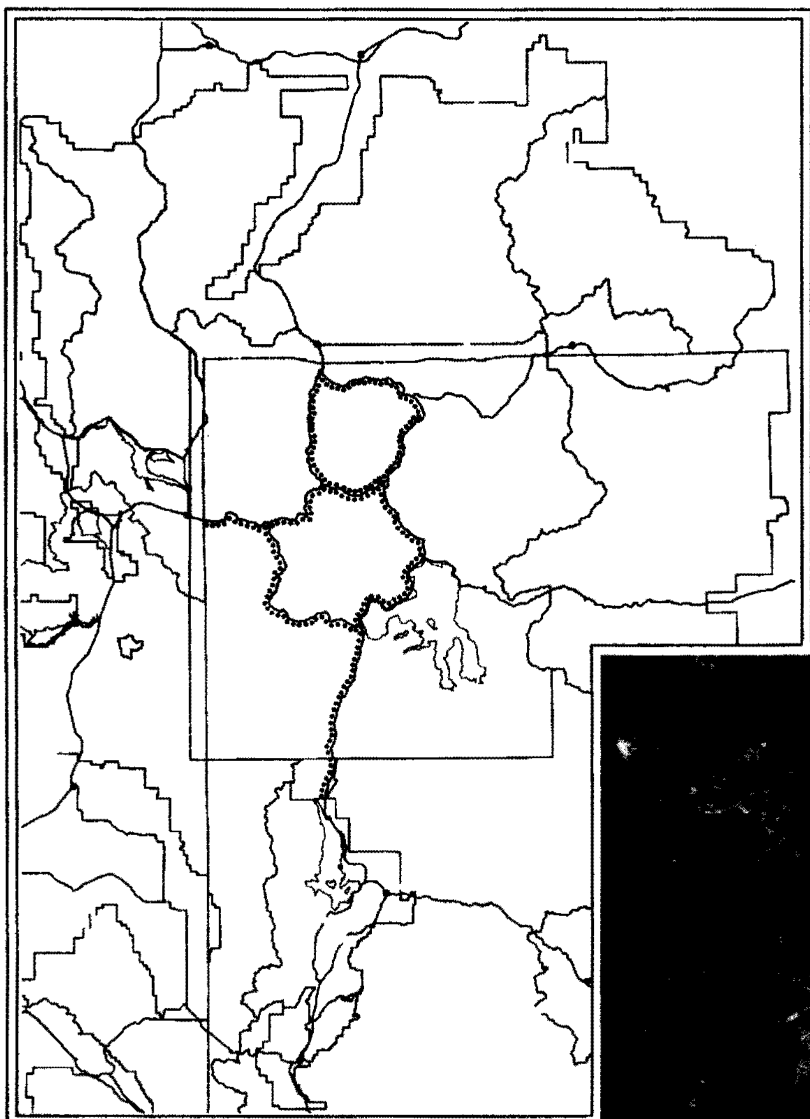

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Research Summary

Extensive surveys of bark beetle and wood borer infestation in the Greater Yellowstone Area were conducted in 1991 through 1993. The study objectives were to determine the effect of delayed tree mortality following the 1988 fires on mosaics of fire-killed and green tree stands, the relationship between fire injury and subsequent infestation, and the effect of insect buildup in fire-injured trees on infestation rates for uninjured trees. Surveys were conducted adjacent to roads, and plots were selected randomly. In 1991, 321 plots were measured, 198 plots in 1992, and 127 plots in 1993. Insects killed 12.6 percent of the Douglas-fir (*Pseudotsuga menziesii*), 17.9 percent of the lodgepole pine (*Pinus contorta*), 6.6 percent of the Engelmann spruce (*Picea engelmannii*), 7.5 percent of the subalpine fir (*Abies lasiocarpa*), and 2.8 percent of the whitebark pine (*Pinus albicaulis*). Delayed mortality attributed to fire injury accounted for more mortality than insects. Both types of mortality greatly altered the original fire-killed/green tree mosaics that were apparent immediately after the 1988 fires. Insect infestation was strongly and positively correlated with the percent of the basal circumference of the tree that was fire killed in all species, except in Engelmann spruce where infestation peaked in the middle fire-injury class. Infestation in Douglas-fir, lodgepole pine, and Engelmann spruce increased through 1992 then declined in 1993. Although it cannot be said with certainty that insects built up in fire-injured trees and then caused increased infestation of uninjured trees, the high level of infestation suggests this is the case.

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Survival of conifers following fire depends on the type and degree of injuries, initial tree vigor, and the postfire environment, which includes the influence of insects, diseases, and weather. As fire injury increases, the probability of death due to one or more of these causes also increases.

Bark beetles of the family Scolytidae and wood borers of the families Buprestidae and Cerambycidae are frequently associated with tree mortality following fire. In the absence of significant bole or root injuries, the probability of attack by primary bark beetles (those attracted to healthy trees) is low when light defoliation by fire occurs and the probability usually declines further with complete defoliation (Furniss 1965; Miller and Keen 1960; Mitchell and Martin 1980; Wagener 1961). Secondary bark beetles (those commonly attracted to severely weakened or recently killed trees) and wood borers are drawn to burned trees, but their contribution to mortality, while thought to be minor (Mitchell and Martin 1980) is largely unknown.

Observations on permanent plots that were established in the Greater Yellowstone Area in 1989 and 1990 showed increased susceptibility of insect infestation with increased fire injury for most tree species. However, trees that were completely defoliated by canopy fires that also resulted in complete burning or severe scorching of the inner bark, especially in thin-barked trees, were no longer suitable for bark beetle infestation (Amman 1991; Amman and Ryan 1991). Insect contribution to tree mortality is sometimes difficult to determine because of nonobvious bole and root injuries by fire. These injuries result in inaccurate mortality predictions from existing models based on crown scorch alone (Ryan and Amman 1994).

Because of the small number of permanent plots used to follow tree mortality pertaining to fire injury in the Greater Yellowstone Area, surveys for insect activity were conducted to obtain a larger sample on which to investigate interactions between insects and fire-injured trees. The objectives of our study were to determine delayed tree mortality attributed to fire injury and bark beetles and the effects on mosaics of fire-killed and green (live) trees, the relationship between fire injury and subsequent infestation by bark beetles and wood borers, and the buildup of bark beetles in fire-injured trees and subsequent infestation of uninjured trees.

Methods

Extensive surveys for bark beetle activity were conducted in 1991, 1992, and 1993. The surveys followed roads in Yellowstone Park and Rockefeller Memorial Parkway (fig. 1); limited resources prevented a more complete survey that would have included back country and areas closer to roads. The plot locations were randomized by selecting random distances to be driven down a road, flipping a coin to determine whether plot establishment would be on the left or right side of the road, and selecting at random the distance the plot would be located from the road (40 to 100 m).

To be used in our study, the plot must have contained some trees with green foliage. Canopy fires that caused complete defoliation usually resulted in complete burning or severe scorching of the inner bark, especially in thin-barked species. Trees with this type of injury were no longer suitable for bark beetle infestation (Amman 1991). Therefore, our sampling focused on areas where canopy fires had not occurred and on adjacent unburned forest. If the trees in the plot were dead or faded, the location was moved to the next

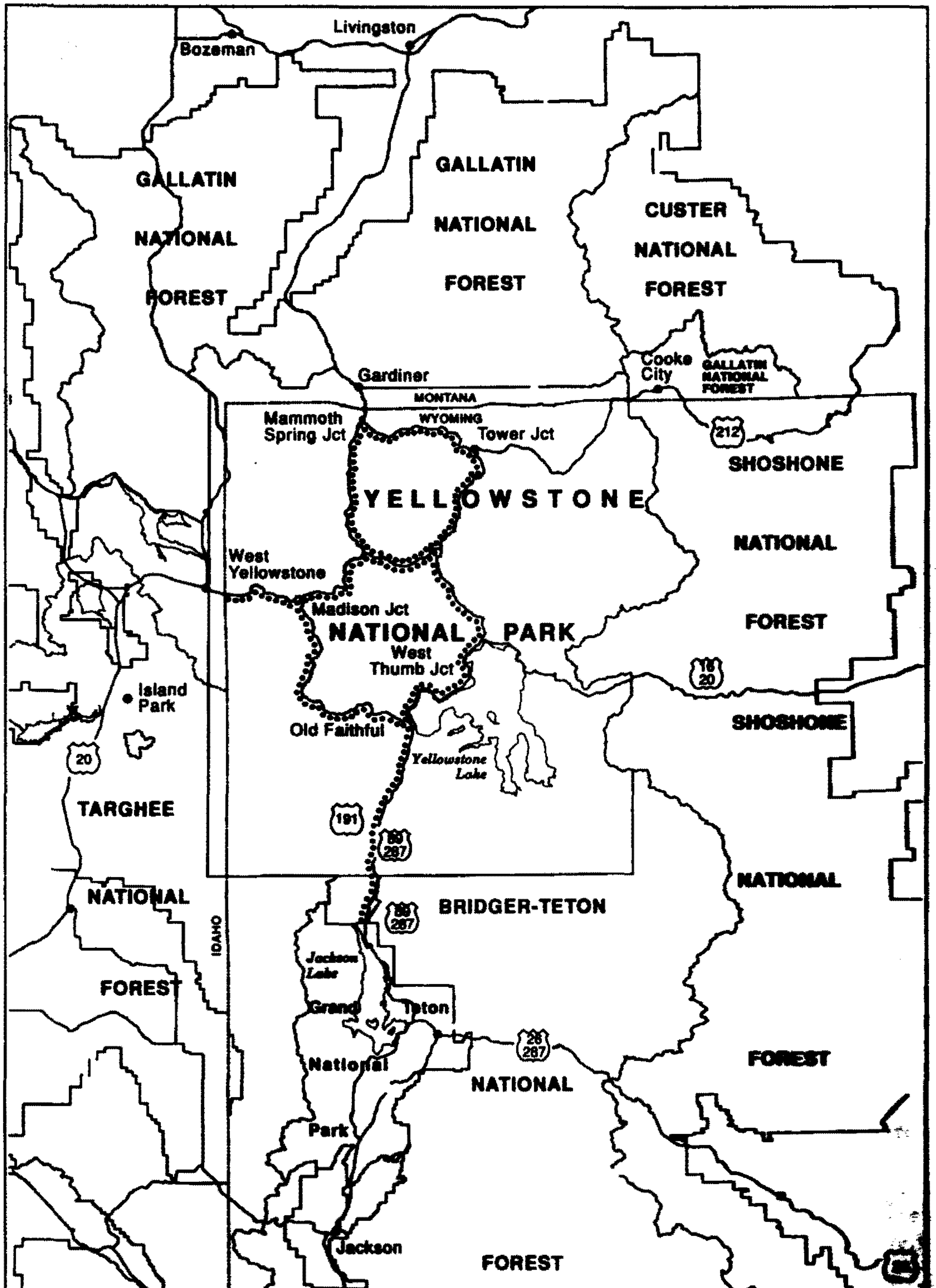

Figure 1—Roads where plots were established (dotted lines) in the Greater Yellowstone Area.

even chain distance. A 10 basal area factor variable plot was installed at each location. All trees in the plot were examined and classified alive or dead based on the presence or absence of living foliage, the percentage of basal circumference girdled by fire, and insect infestation. The numbers of plots examined were 321 in 1991, 198 in 1992, and 127 in 1993. Plot placement in 1992 and 1993 was along the same roads surveyed in 1991, but they became more widely spaced in succeeding years. Low elevations between 2,040 and 2,485 m delineated plot locations; therefore, trees consisted mostly of lodgepole pine and Douglas-fir.

Tree observations included species, diameter at breast height (d.b.h.), degree of fire injury, presence of insect attack, and insect species. Tree injury was measured as the percentage of basal circumference in which the cambium was killed. Injuries attributed to fire effects included trees with 100 percent stem girdled by fire, while trees that were not 100 percent girdled but showed signs of infestation by bark beetles or wood borers had injuries attributed to insects. Cambium injury was determined by removing small sections of bark and visually inspecting tissues. Boring frass expelled from the bark was the usual sign of insect infestation. Some bark was removed so that the insects could be identified, and insect observations were made on the lower 2 m of the trees. Insects were classified according to whether they were primary or secondary bark beetles, wood borers, or other insects.

The year in which a tree died was estimated from foliar characteristics. We estimated year of death only for Douglas-fir and lodgepole pine because other tree species were present in such small numbers that loss by year would not be meaningful.

For Douglas-fir, trees infested the year of the survey had green foliage and fresh boring frass on the bole of the tree; the previous year's trees had mostly red foliage with some needle loss occurring. Trees infested 2 years previously had some red needles remaining, but most needles had dried and fallen. Trees infested 3 years previously essentially had no needles remaining, and some of the finer twigs had fallen.

This method is not accurate in all cases because Bedard (1950) stated that Douglas-fir varies greatly in the elapsed time between Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) infestation and foliage discoloration. Some trees maintain red foliage for a year or longer after beetles have emerged from them. An occasional tree may exhibit some fading in the fall following infestation, but it may appear mottled and may be confined to a few scattered branches (Furniss 1959).

In lodgepole pine we used the characteristics presented by Cole and Amman (1969) to estimate how long since a tree had been killed by bark beetles: (1) tree killed in current year—foliage green, fresh boring frass, larvae or adults present; (2) tree killed in previous year—foliage bright orange to straw color; (3) tree killed in second year past—foliage dull orange and most retained; (4) tree killed in third year past—foliage dull orange to gray and most lost. This dates trees back to 1988, the year of the fires and the year that there was little infestation (Amman 1991). As with Douglas-fir, some errors could occur. For example, a tree with little foliage or on a dry site would fade faster than a tree with a large crown or on a moist site.

An intensive study by Schmid (1976) shows that the problem of fading in Engelmann spruce is more complicated than in Douglas-fir and lodgepole pine. Needles usually turn greenish-yellow and fall approximately a year after spruce beetles infest the tree. However, some trees remain green until the fall of the second year (Massey and Wygant 1954). A particularly complicating factor is that branches of some infested trees develop new growth in the summer following the year of infestation (Schmid 1976). The density of attacking beetles, and hence completeness of blue stain fungal inoculation, are considered factors affecting rate of needle drying and dropping in spruce (Schmid 1976).

Because there was no additional insect-caused mortality tallied in 1993, except for a small amount caused by Douglas-fir beetle, 1993 data will not be included in the figures. Percent basal girdling was observed continuously and placed into classes, then data were subjected to weighted regression analyses, because of differing sample sizes, to show differences.

Results and Discussion

Fire injury and bark beetle infestation, not only of fire-injured trees but also of uninjured trees, resulted in considerable change to mortality estimates and to the mosaics of fire-killed and green tree stands following the 1988 fires.

Tree Mortality by Cause

Douglas-fir mortality consisted of 31.7 percent of the 1,012 trees examined, with 18.5 percent attributed to delayed effect of fire injury, 12.6 percent attributed to bark beetle and wood borer infestation, and 0.6 percent due to unidentified causes (fig. 2). Mortality in trees that were 100 percent stem girdled by fire was attributed to fire effects. Those that were not 100 percent girdled, but became infested by bark beetles or wood borers, had mortality that was attributed to insects.

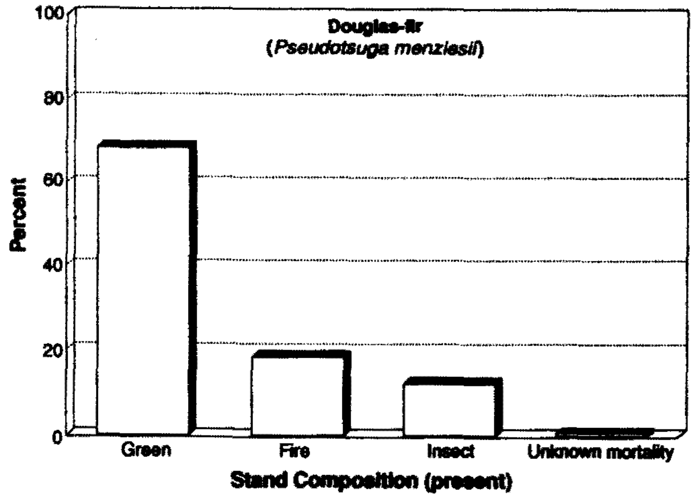

Figure 2—Alive (green) and dead Douglas-fir by cause of mortality.

Most infestation was by the Douglas-fir beetle. Additional mortality, especially of small diameter trees, was caused by *Pseudohylesinus nebulosus* LeConte and wood borers.

These data show that almost one-third of the Douglas-fir that were green and considered alive following the 1988 fires died from delayed effects of fire or insect infestation. Where mortality is evenly distributed, the fire-killed and green Douglas-fir mosaics appear slightly affected. However, where mortality is concentrated, drastic altering of the mosaic is apparent.

On the other hand, lodgepole pine mortality consisted of 51.6 percent of the 4,758 sampled trees. This breaks down to 30.5 percent due to fire injury, 17.9 percent due to insects, and 3.2 percent to unidentified causes (fig. 3). All trees retaining green foliage after the 1988 fires may be considered survivors of the fires. However, even though they still had green foliage, green phloem, and appeared alive, almost two-thirds of the lodgepole that subsequently faded had been completely girdled by light ground fires. Many of these trees' deaths from fire injury were not apparent even 3 to 4 years after the fires, and quite often not until the lodgepole were infested by the pine engraver (*Ips pini* [Say]) or the twig beetles, *Pityophthorous confertus* Swaine and *Pityogenes knecteli* Swaine, did rapid fading occur. Of all the lodgepole pine that died from all causes, including fire injury, 44 percent were infested by the pine engraver. Mountain pine beetle, *Dendroctonus ponderosae* Hopkins, infested only 0.8 percent of the lodgepole.

In this data set, and as observed by others (Blackman 1931; Hopkins 1905), mountain pine beetle is not strongly attracted to fire-injured trees. In addition to the stress of fire injury, trees had been subjected to drought for several years. These stress factors did not significantly increase nor precipitate an outbreak of mountain pine beetles, which again points to uniqueness in terms of lack of response to stress factors that are commonly associated with Douglas-fir beetle and pine engraver infestations.

Mortality of Engelmann spruce totaled 41 percent of the 439 trees in the sample: 31.9 percent were killed by fire injury, 6.6 by insects, and 2.5 percent died from unidentified factors (fig. 4). Spruce beetle (*Dendroctonus rufipennis* [Kirby]) killed almost one-half of the spruce killed by insects. Other insects that caused spruce death were *Ips pilifrons* Swaine and wood borers of families Buprestidae and Cerambycidae. The high loss of spruce to fire injury is related to thin bark, which causes them to be easily killed by fire.

Subalpine fir had 37.3 percent survival of the 134 trees in our sample. Most mortality was attributed

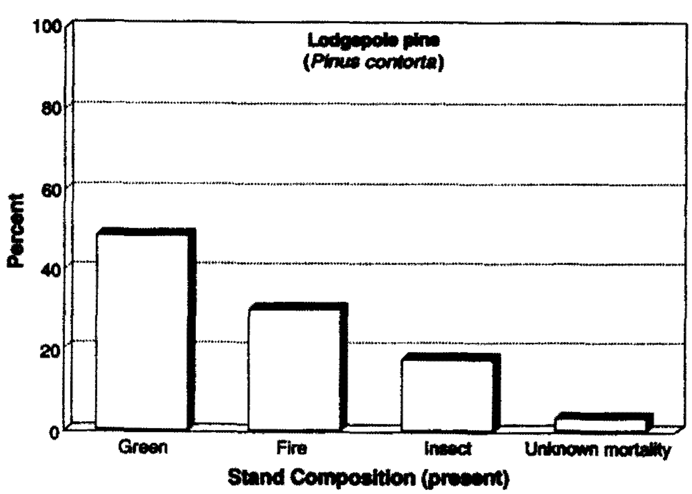

Figure 3—Alive (green) and dead lodgepole pine by cause of mortality.

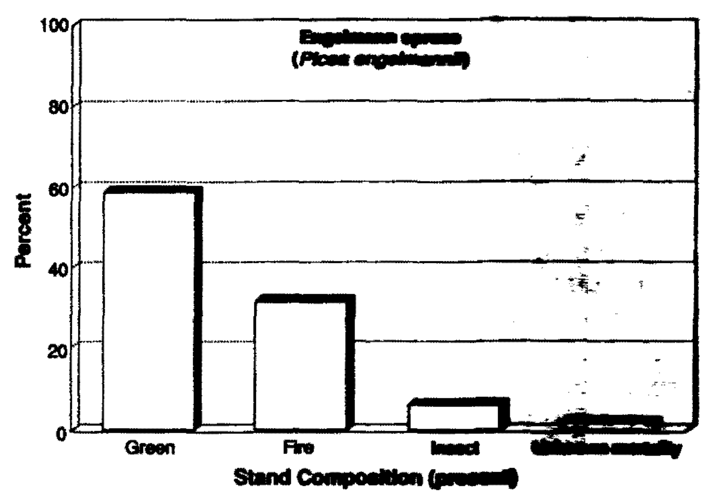

Figure 4—Alive (green) and dead Engelmann spruce by cause of mortality.

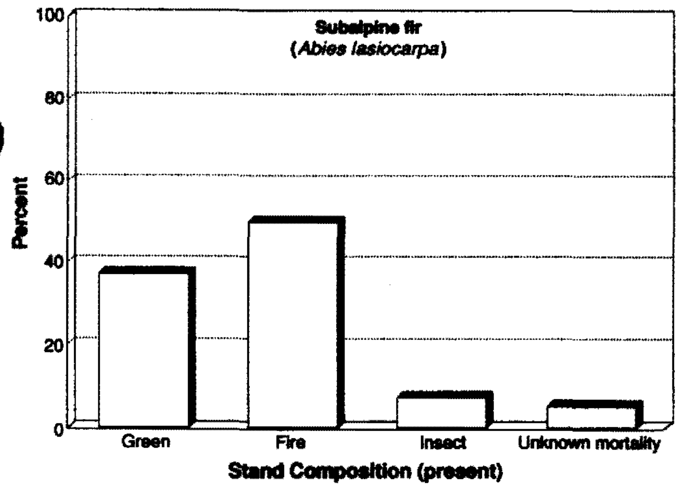

Figure 5—Alive (green) and dead subalpine fir by cause of mortality.

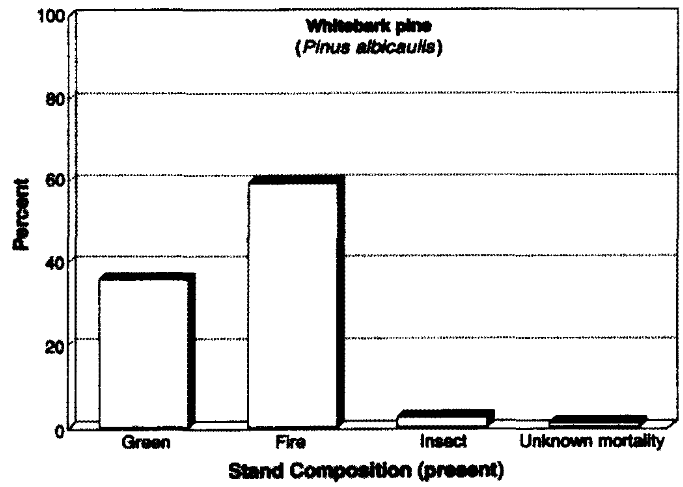

Figure 6—Alive (green) and dead whitebark pine by cause of mortality.

to fire injury (50 percent), with insects accounting for only 7.5 percent and unidentified causes 5.2 percent (fig. 5). Subalpine fir is the most sensitive to fire injury of the tree species in this study (Ryan and Amman 1994). Most insect-caused mortality of subalpine fir was caused by wood borers in the families Cerambycidae and Buprestidae.

Whitebark pine also appears sensitive to fire injury in the fire types that occurred in the Greater Yellowstone Area in 1988, with only 36.1 percent of the 144 trees in our sample surviving. Mortality in trees was attributed to the following causes: 59.7 percent to fire injury, 2.8 percent to insects, and 1.4 percent to unidentified causes (fig. 6). Whitebark pine was usually killed by mountain pine beetle and pine engraver.

Delayed mortality from fire injury and insects ranged between 41 and 64 percent in the tree species represented in this study. This mortality resulted in drastic changes in dead and green tree mosaics that were observed immediately following the 1988 fires. Losses to fire injury could be determined shortly after the fires by examining trees for complete basal girdling; however, predicting losses to insect infestation was more difficult. Observations in the next section provide the basis for making such predictions.

Infestation in Relation to Fire Injury

Insect infestation was positively related to the percent of the basal circumference killed by fire in Douglas-fir, lodgepole pine, and Engelmann spruce. Meaningful relationships were not established for subalpine fir and whitebark pine because of the small amount in our sample.

Our sample of lodgepole pine showed that a total of 43.9 percent of all fire-injured trees were infested by insects. Infestation ranged from a low of 21.7 percent in lodgepole with no injury to a high of 66.6 percent in trees with 81 to 100 percent basal girdling by fire (fig. 7). The pine engraver accounted for the most lodgepole pine infestation, ranging from 16.6 percent of trees in the uninjured class to 44.8 percent of trees in the 81 to 100 percent basal injury class (fig. 8). Twig beetles (*Pityphthorous* and *Pityogenes*) were the next most common, with the wood borers (Cerambycidae and Buprestidae) infesting a few trees. Regressions showing the relationships of infestation to fire injury are given in figure 9. Infestation increased in all injury classes in 1992 (fig. 10). The increase in the uninjured class indicates a possible jump in pine engraver populations within fire-injured trees in previous years resulting in the increase in infestation of uninjured trees.

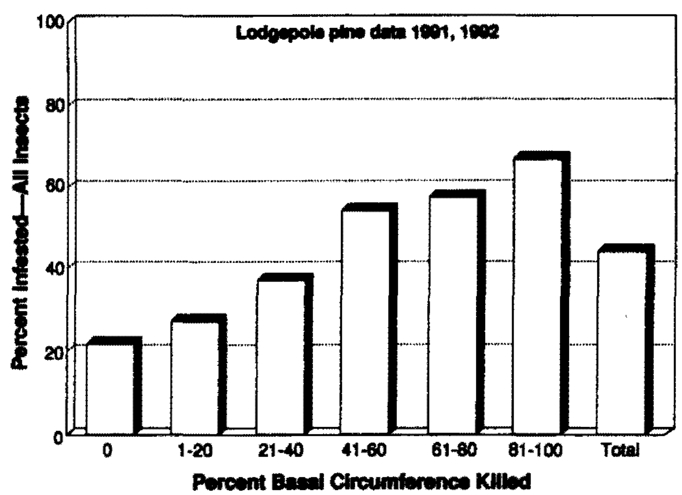

Figure 7—Percent insect infestation of lodgepole pine by fire-injury class.

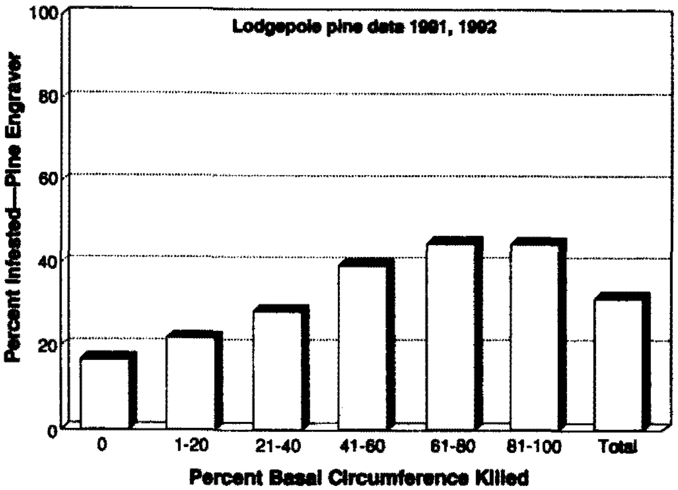

Figure 8—Relationship of pine engraver infestation to basal fire injury of lodgepole pine.

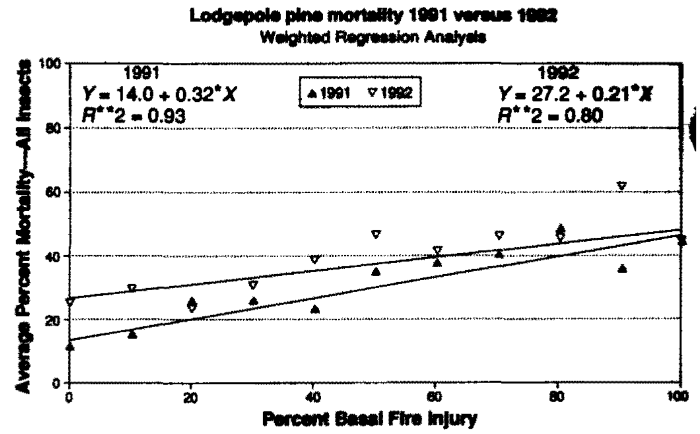

Figure 10—Relationship of insect infestation to basal fire injury of lodgepole pine, 1991 versus 1992.

Mountain pine beetle infested only a small number of lodgepole pine and did not show much preference for any fire-injury class. Infestation ranged between 0.3 percent of the trees in the 61 to 80 percent basal injury class to 1.2 percent of the uninjured tree class (fig. 11), which is consistent with previous measurements in the Greater Yellowstone Area (Amman and Ryan 1991) and other studies (Blackman 1931; Hopkins 1905). Mountain pine beetle appears not to respond to trees stressed by fire or drought, since both were present in the Greater Yellowstone Area during this study. An alternative hypothesis is that beetles respond to stressed trees but are unable to build up populations in them. Schmitz (1988) observed mountain pine beetle infesting diseased lodgepole pine when beetle populations were at an endemic level, but brood production was low which prevented buildup of the beetle population. Not until mountain pine beetles infest better quality lodgepole pine (those growing faster and having thicker phloem, which is the food of developing larvae) does the population build to a potential outbreak.

Our sample of Douglas-fir (1991 and 1992 surveys combined) showed that 41.6 percent of all fire-injured trees were infested by insects. Infestation ranged from a low of 18.4 percent of uninjured trees to a high of 79.7 percent of trees having 81 to 100 percent of the basal circumference girdled by fire (fig. 12). The Douglas-fir beetle accounted for the most infestation, ranging between 16.3 percent of the uninjured trees to 47.0 percent of trees having 81 to 100 percent basal

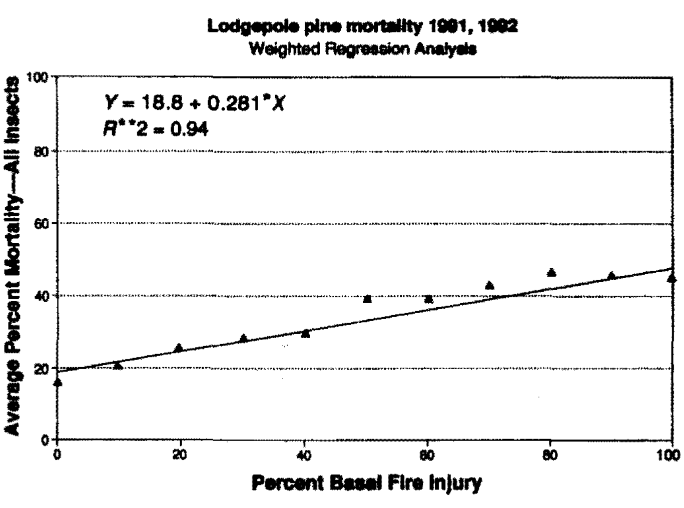

Figure 9—Relationship of insect infestation to basal fire injury of lodgepole pine.

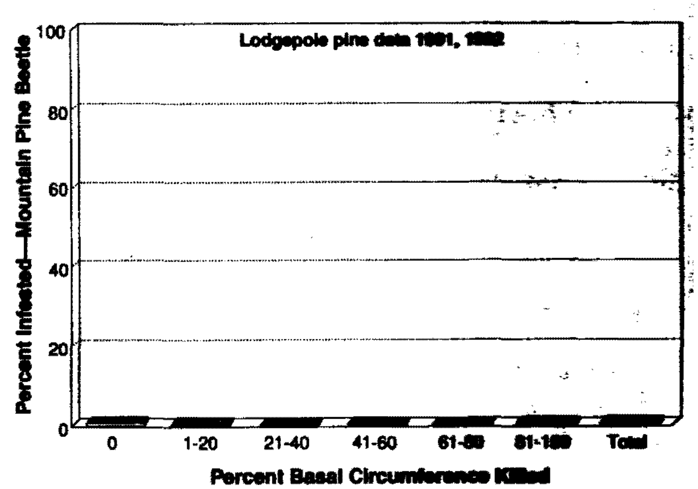

Figure 11—Relationship of mountain pine beetle infestation to basal fire injury of lodgepole pine, 1991 and 1992.

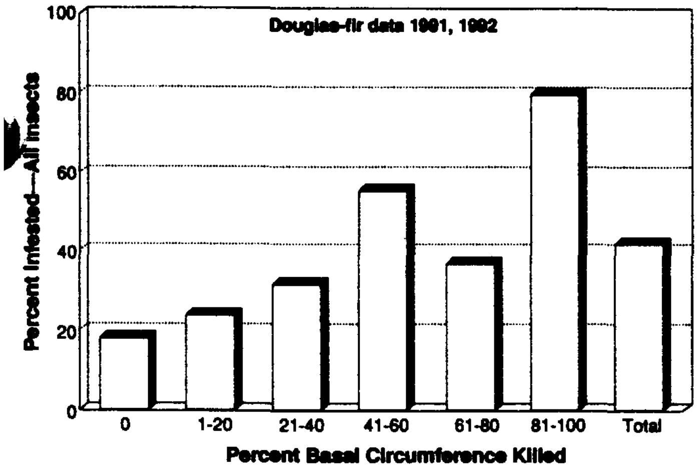

Figure 12—Percent insect infestation of Douglas-fir by fire-injury class.

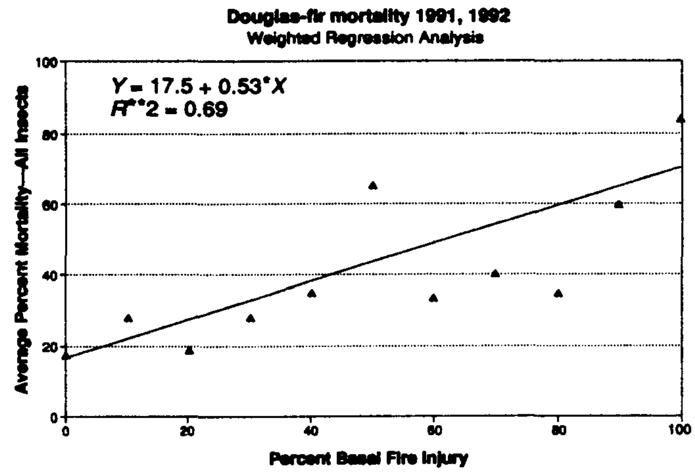

Figure 14—Relationship of insect infestation to basal fire injury of Douglas-fir.

injury (fig. 13). *Pseudohylesinus nebulosus* was the second most common bark beetle infesting Douglas-fir, followed by the wood borers. Regression relationships between basal girdling by fire and infestation are shown in figure 14.

Our sample of Engelmann spruce for 1991 and 1992 combined show that 28.7 percent of trees across all injury classes were infested by insects. Infestation ranged from 10.1 percent of the uninjured trees to 53.6 percent of trees having 41 to 60 percent of their basal circumference killed by fire (fig. 15). Spruce beetle accounted for almost one-half of the infested trees (13.9 percent). Infestation by spruce beetle ranged between 5.8 percent of uninjured trees to 39.3 percent of trees having 41 to 60 percent basal girdling; the infestation is usually limited to the lower 20 ft of the trunk (Schmid 1976). Therefore, bark scorching in the injury classes exceeding 60 percent girdling of the basal circumference may deter beetles from infesting such heavily injured trees (fig. 16).

Our samples of subalpine fir (134 trees) and whitebark pine (144 trees) were too small to draw meaningful conclusions about insect response to different fire injury levels. However, it does appear that insects, mostly wood borers, prefer the more severely injured subalpine fir (fig. 17).

No strong relationship between fire injury and infestation existed in the whitebark pine data (fig. 18).

Buildup of Insects in Fire-Injured Trees

The insect buildup in fire-injured trees and subsequent increase in infestation of trees uninjured by fire was studied by relating infestation to the year of occurrence. Dating infestation in 1989 and 1990 depended on foliage coloration; 1991 and 1992 were

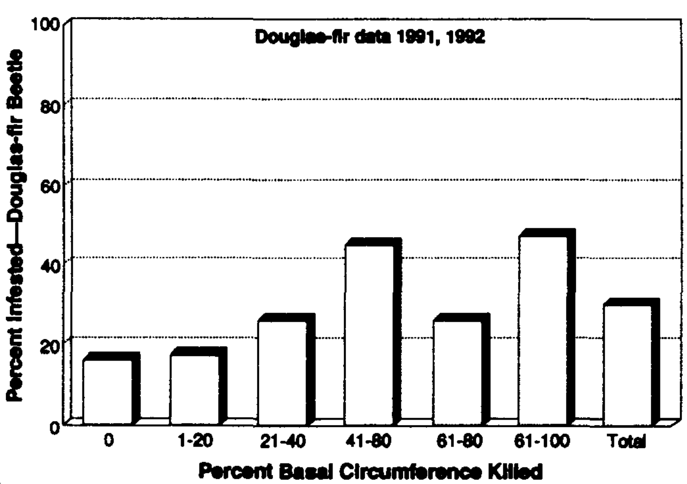

Figure 13—Percent Douglas-fir beetle infestation of Douglas-fir by fire-injury class.

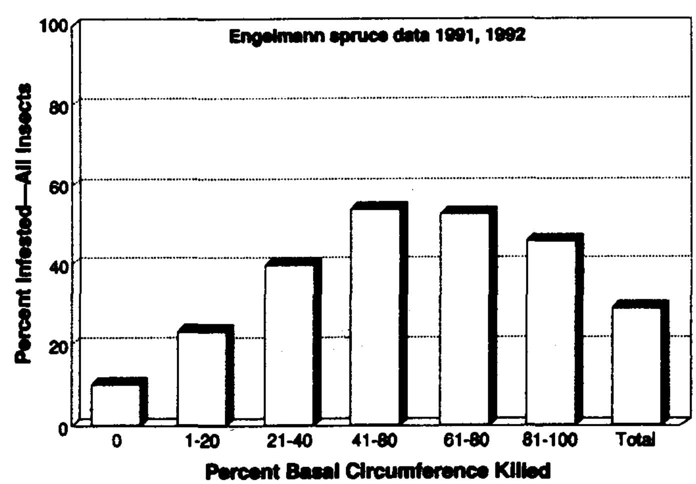

Figure 15—Relationship of all insect infestation to basal fire injury of Engelmann spruce.

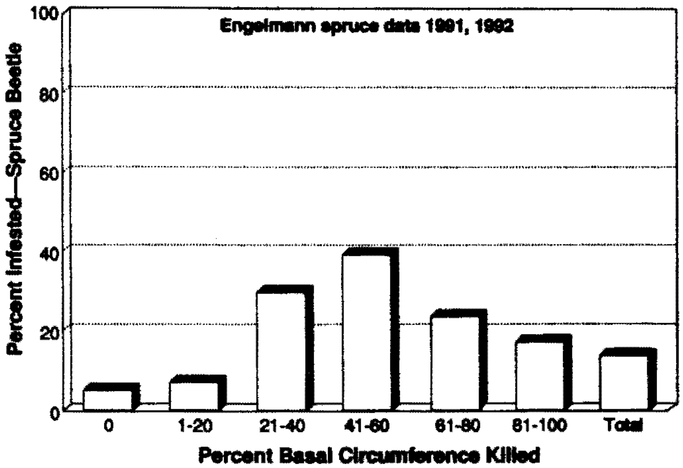

Figure 16—Relationship of spruce beetle to basal fire injury of Engelmann spruce.

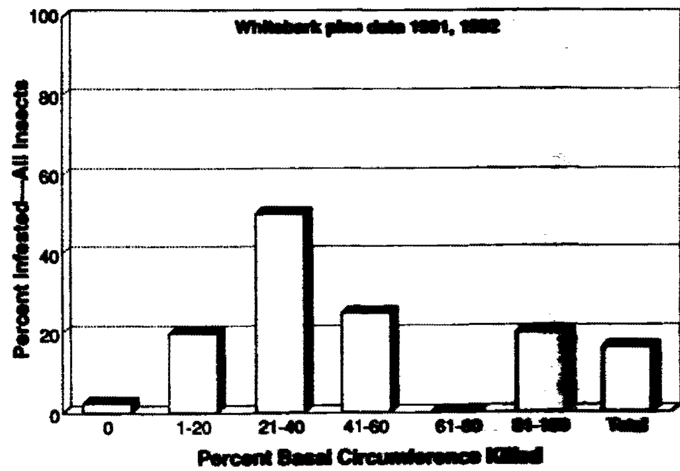

Figure 18—Percent insect infestation of whitebark pine by fire-injury class.

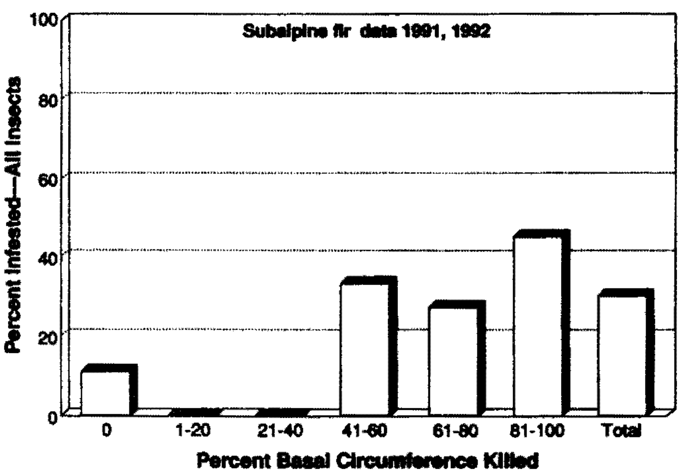

Figure 17—Percent insect infestation of subalpine fir by fire-injury class.

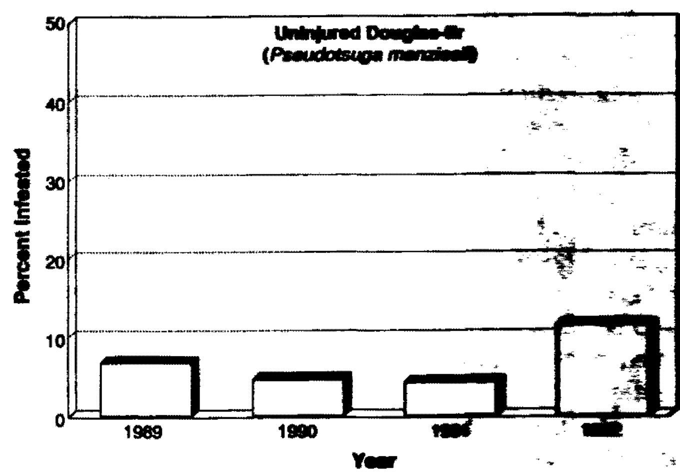

Figure 19—Percent Douglas-fir mortality caused by insect infestation during 4 postfire years.

based on actual infestation of green trees observed during the 1991, 1992, and 1993 surveys.

In Douglas-fir, insects—particularly Douglas-fir beetle—infested uninjured trees on permanent plots starting in 1989, the first postfire year (Amman 1991). This trend continued in 1990, Amman and Ryan (1991) showed 46 percent of the uninjured Douglas-fir as infested. Results of the extensive surveys in 1991 and 1992 show that infestation of uninjured trees was high in 1989, but was somewhat lower in 1990 and 1991. However, a substantial increase occurred in infestation rates from 1991 and 1992: 4 to 12 percent (fig. 19). Most of the 1992 increase was due to Douglas-fir beetle.

Although we did not sample Douglas-fir beetle populations by removing bark, observations by Pasek and Schaupp (1992) in the Clover Mist Fire areas located in the Shoshone National Forest, which is adjacent to Yellowstone National Park, have general application. They observed brood reduction from 1990 levels that was attributed to prolonged extreme cold temperatures. Reduced brood survival could account for the low tree mortality occurring in 1991. We observed the large increase in Douglas-fir mortality in 1992 is close to the upper limit of the 1.5 to 3.0 fold increase predicted by Pasek and Schaupp (1992) based on their sampling of Douglas-fir beetle populations.

In lodgepole pine, infestation of uninjured trees changed from 2 percent in 1991 to 7 percent in 1992. Most of this was attributed to pine engraver. A pattern of infestation by year is similar to that in Douglas-fir. Although infestation of lodgepole was high in 1989, a decline was observed from 1990 through 1991; however, a substantial increase occurred in

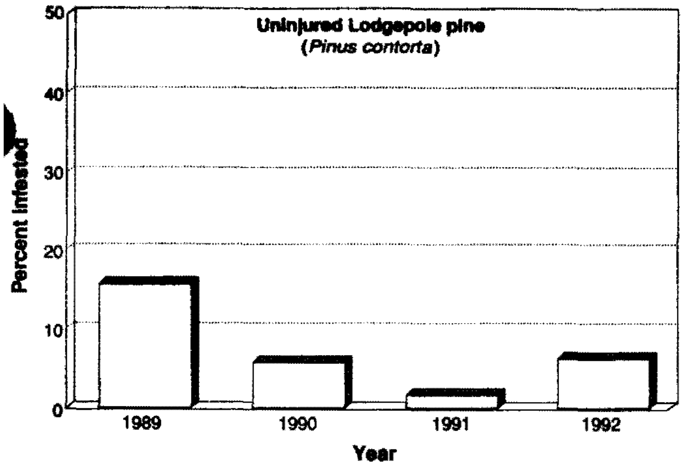

Figure 20—Percent lodgepole pine mortality caused by insect infestation during 4 postfire years.

1992 (fig. 20). Perhaps the prolonged extreme cold temperatures that Pasek and Schaupp (1992) attributed to Douglas-fir beetle mortality also affected pine engraver survival. The 1992 upward swing in infestation ended, and no additional mortality of uninjured trees was tallied in 1993.

In Engelmann spruce, infestation of uninjured trees showed a steady increase during each of the 4 postfire years (fig. 21). Spruce beetle accounted for most of this infestation. The increase of 2 percent in 1991 to 8 percent in 1992 suggests that beetles probably built up in fire-injured trees and began infesting more of the uninjured trees. Because spruce beetle have a 2-year cycle, the large increase in 1992 would be the result of populations surviving in trees infested in 1990.

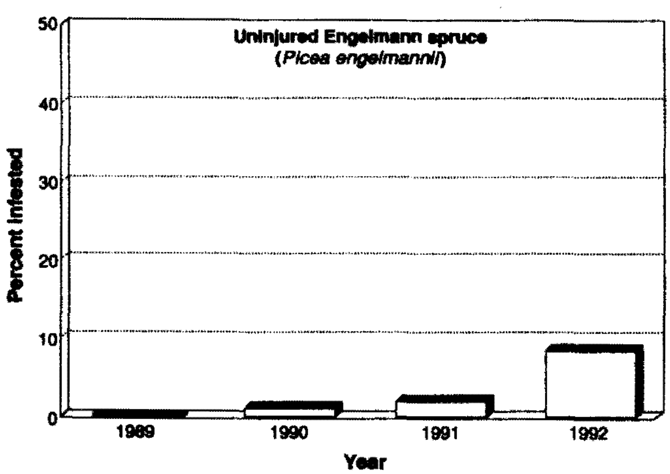

Figure 21—Percent Engelmann spruce mortality caused by insect infestation during 4 postfire years.

Although infestation figures for 1992 were higher than those for 1991, there was a decline in 1993. However, with drought conditions continuing to prevail in the Greater Yellowstone Area, Douglas-fir beetle may continue to kill large numbers of trees. Off-plot observations showed considerable infestation of trees in unburned stands, but pine engraver populations probably will decline after the year that they infest standing, uninjured trees (Sartwell and others 1971).

Conclusions

From the extensive surveys conducted in 1991, 1992, and 1993, we conclude that bark beetle and delayed tree mortality due to fire injury significantly alter mosaics of green and fire-injured trees, that insect infestation increases with the percent of basal circumference killed by fire, and that bark beetle populations appear to increase in fire-injured trees and then infest uninjured trees.

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Surveys of bark beetle and wood borer infestation in the Greater Yellowstone Area were conducted from 1991 through 1993 to determine the effect of delayed tree mortality on mosaics of fire-killed and green tree stands, the relationship between fire injury and infestation, and the effect of insect buildup in fire-injured trees on infestation rates for uninjured trees. Fire injury accounted for more delayed mortality than insect infestation, but both types of mortality greatly altered the mosaics immediately apparent after the 1988 fires. The high level of infestation suggests that insects built up in fire-injured trees and then caused increased infestation of uninjured trees.

Keywords: fire injury, Yellowstone fires, Douglas-fir, lodgepole pine, Engelmann spruce, whitebark pine, subalpine fir, mosaic patterns

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