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Abstract. After the 1988 Greater Yellowstone Area fires two studies were begun to monitor beetle activity in burned and unburned conifers and to evaluate the susceptibility of fire-injured trees to bark beetle attack. An intensive survey was conducted annually from 1989 through 1992 on 24 permanent plots located in or near stands burned by surface fire. Stands were located adjacent to areas of extensive crowning and torching. By August 1992, 79% of the 125 Douglas-fir had been infested by bark beetles (primarily by the Douglas-fir beetle) and wood borers; 62% of the 151 lodgepole pine were infested (primarily by the pine engraver); 94% of the 17 Engelmann spruce were infested (primarily by the spruce beetle); and 71% of the 17 subalpine fir were infested (primarily by wood borers). Fire injury combined with subsequent insect attack killed 77% of the Douglas-fir, 61% of the lodgepole pine, 94% of the Engelmann spruce, and all of the subalpine fir. An extensive survey was conducted in 1991 and 1992 on 519 randomly located plots throughout the area. Plots were located in unburned and surface fire-burned areas. Insects killed 13% of the 1,012 Douglas-fir, 18% of the 4,758 lodgepole pine, 7% of the 439 Engelmann spruce, 8% of the 134 subalpine fir, and 3% of the 144 whitebark pine. For all species, insect infestation increased with the percent of the basal circumference killed by fire, except for Engelmann spruce where infestation was greatest with 40 to 80 % of the basal circumference girdled. Infestation in Douglas-fir, lodgepole pine, and Engelmann spruce increased with time. The high level of infestation suggests that insect populations increased in fire-injured trees and then spread to uninjured trees. Increases from 1991 to 1992 suggest that additional tree mortality will occur in 1993, and that a major outbreak could occur in Engelmann spruce. Delayed tree mortality attributed to fire injury accounted for more mortality than insects. Both types of mortality greatly altered the original mosaics of green trees and dead trees that were apparent immediately after the 1988 fires.

Keywords: *Abies lasiocarpa*; Buprestidae; Cerambycidae; *Dendroctonus ponderosae; Dendroctonus pseudotusgae; Dendroctonus rufipennis; Ips pini; Picea engelmannii; Pinus albicaulis; Pinus contorta; Pseudotsuga menziesii.*

Introduction

Conifer survival following fire depends on the type and degree of tree injuries, initial tree vigor, and the postfire environment. Postfire environment includes the influence of insects, diseases, and weather on tree survival. As fire injury increases, the probability of death due to one or more causes increases (Peterson and Arbaugh 1986, Ryan and Reinhardt 1988, Ryan and Amman 1994). Delayed mortality associated with fire injuries and subsequent insect infestation significantly alters forest structure.

In 1988 crown fires in the Greater Yellowstone Area (GYA) burned roughly 350,000 ha, while surface fires burned an additional 200,000 ha (Greater Yellowstone Post-Fire Resource Assessment Committee, Burned Area Survey Team 1988). Crown fires badly charred trees, instantly killing most of them. Surface fires caused varying degrees of crown and bole injury, increasing susceptibility to insect attack. Increases in insect populations in fire-injured trees create the possibility insects can spread to unburned trees. After the 1988 fires, we began 2 surveys to improve our understanding of fire injury and insect interactions in the GYA. The first study began in 1989 and focused on determining the species of insects associated with varying degrees of fire injury and the way insect attack and tree survival changed over time. In 1991 a second study was begun to cover a larger area and assess the potential for build-up of bark beetle populations and their spread to adjacent unburned trees. The objectives of the second study were to determine delayed tree mortality resulting from fire injury, bark beetles, and wood borers; and to assess if the build-up of insects in fire-injured trees led to subsequent infestation of uninjured trees.

Methods

Intensive Survey

Canopy fires usually completely burned or severely scorched the phloem and cambium, especially in thin-barked trees. Because bark beetles feed on the phloem and cambium, such trees were no longer suitable for bark beetle infestation. The intensive survey focused on sampling in stands along the boundary between unburned forests and forests burned by surface fires. We made observations on 24 Bitterlich point-sample plots (Avery 1967) using a 2.23 m^2ha^{-1} basal area factor prism. Plots were located within the North Fork, Snake River, Huck, and Hunter fires. Fuel (Hartford and Rothermel 1991), weather (Bushey 1989), and fire behavior (Rothermel et al. 1994) conditions have been previously described for the GYA. Plots were located in lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*) forests between 2,000 and 2,500 m elevation, and within a few hundred meters of roads. In addition to lodgepole pine and Douglas-fir, we encountered a few Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Measurements were made of tree diameter at breast height, crown scorch, and the percentage of the circumference killed at the base. Crown scorch was estimated visually and expressed as the percentage of the prefire crown volume killed. We determined cambium injury by removing small sections of bark and visually inspecting tissues. We classified insects attacking trees as primary (those that can infest and kill healthy trees) or secondary bark beetles (those commonly attracted to weakened or recently killed trees), wood borers of the families Buprestidae and Cerambycidae, or other insects (Table 1). Observations of insects were restricted to the lower 2 m of the bole. We detected insect attack by inspecting for boring dust and for insect entrance and exit holes. Insect species were identified by removing a small portion of bark, exposing the phloem and cambium. Annual observations were made of insect attack and tree mortality from 1989 through 1992. Trees were classified as alive or dead based on the presence or absence of living foliage. Additional details on plot location, measurements, and preliminary observations are contained in Amman and Ryan (1991) and Ryan and Amman (1994).

Extensive Survey

An extensive survey for bark beetle activity was conducted in 1991 and 1992. Plots were located throughout the burned/unburned mosaic at random distances along the roads in Yellowstone Park and the Rockefeller Memorial Parkway. Plots were in unburned or lightly burned forests primarily between 2,000 and 2,500 m elevation. To be included in the study, a plot had to contain green trees. In 1991, 321 plots were examined, in 1992 198 were examined. Additional details of plot locations and descriptions are outlined in Rasmussen et al. (1996). The survey consisted of 4,758 lodgepole pine, 1,012 Douglas-fir, 439 Engelmann spruce, 134 subalpine fir, and 144 whitebark pine (*Pinus albicaulis*). Sampling was conducted on variable radius plots as outlined in the intensive survey. All trees in the plot were examined and classified as alive, fire killed, or insect killed, based on the presence or absence of living foliage, the degree of girdling by the fire, and degree of insect infestation. Fire injury was grouped into six classes based on the percent of the circumference girdled by heat: unburned, 1 to 20 %, 21 to 40 %, 41 to 60 %, 61 to 80 %, and 81 to 100 %.

Observations of each tree included species, diameter at breast height, presence or absence of insect attack, insect species, and the percentage of basal circumference in which the cambium was killed by fire. Trees in which the cambium was killed for 100 percent of the basal circumference (completely girdled), were considered to have been killed by the fire. Those that were not com-

Table 1. Bark beetles and wood borers infesting trees in the Greater Yellowstone Area after the 1988 fires

	Bark beetles			
Host	Primary	Secondary	Borers	Other
Lodgepole pine	*Dendroctonus ponderosae*	*Ips pini* *Dendroctonus valens* *Pityophthorus spp.* *Pityogenes spp.*	Buprestidae Cerambycidae	Ambrosia *Hylurgops* spp. *Hylastes* spp.
Whitebark pine	*Dendroctonus ponderosae*	*Ips* spp.	Buprestidae Cerambycidae	
Douglas-fir	*Dendroctonus pseudotsugae*	*Pseudohylesinus* spp.	Buprestidae Cerambycidae	
Engelmann spruce	*Dendroctonus rufipennis*	*Ips pilifrons* *Scierus* spp.	Buprestidae Cerambycidae	Siricidae Ambrosia
Subalpine fir			Buprestidae Cerambycidae	

pletely girdled but became infested by bark beetles or wood borers were attributed to insect mortality. Cambium injury and insect attack were determined using procedures outlined in the intensive survey methods. The build-up of insects in fire-injured trees and the subsequent increase in infestation of unburned trees were determined by relating infestation to the year of its occurrence. Dating the year of insect attack for 1989 and 1990 was estimated from foliar characteristics criteria described in Rasmussen et al. (1996). Dates for the next two years were based on the actual observation of infestation of green trees.

Results

Intensive survey

Detailed descriptions of fire injury and preliminary results of the intensive survey were reported in Amman and Ryan (1991) and Ryan and Amman (1994). The results presented here are the final insect attack and tree mortality observations.

Douglas-fir

By 1992, 79% of the 125 Douglas-fir in the intensive survey were attacked by 1 or more species of insects, and 77% had died (Tables 2, 3). Both live and dead Douglas-fir were similar in size and, therefore, resistance to fire injury. However, dead trees suffered greater crown and bole injury, indicating that these trees experienced more extreme fire behavior. Seventy-one percent of the insect attacks were by the Douglas-fir beetle (*Dendroctonus pseudotsugae*). Of the dead Douglas-fir, 83% were attacked by insects (Table 2), primarily Douglas-fir beetles (n = 73). Larvae of Buprestidae and Cerambycidae wood borers infested 23% of the Douglas-fir. Dead trees that were not attacked by Douglas-fir beetles were generally small diameter and too severely burned to make suitable habitat for the beetles. Two-thirds of the surviving trees were attacked. These were primarily "strip" attacks (narrow vertical areas of infestation) of Douglas-fir beetles (n = 15) in green phloem and wood borer attacks (n = 9) in dead phloem. The average basal girdling of surviving burned Douglas-fir was 59% of the circumference. Except in the smaller diameter trees, injury to the phloem and cambium was restricted primarily to narrow bands near the root crown. This resulted when duff concentrations beneath the trees burned.

Table 2. The number of trees that were alive or dead and whether they had been infested by insects or not.

Species/status	Alive	Dead	Total
Douglas-fir			
Infested	19	80	99
Noninfested	10	16	26
Total	29	96	125
Engelmann spruce			
Infested	1	15	16
Noninfested	0	1	1
Total	1	16	17
Lodgepole pine			
Infested	13	80	93
Noninfested	46	12	58
Total	59	92	151
Subalpine fir			
Infested	0	14	14
Noninfested	0	3	3
Total	0	17	17

Table 3. Cumulative percent insect attack and mortality by year for the intensive survey.

	Year			
Species/status	1989	1990	1991	1992
Douglas-fir (n = 125)				
Infested	24	62	76	79
Dead	12	37	52	77
Engelmann spruce (n = 17)				
Infested	65	82	82	94
Dead	12	82	82	94
Lodgepole pine (n = 151)				
Infested	24	44	58	62
Dead	18	48	58	61
Subalpine fir (n = 17)				
Infested	37	65	71	71
Dead	76	100	100	100

Douglas-fir beetles preferred trees with more than 50% basal girdling, ample green phloem, and less than 75% crown scorch (Table 4). Wood borers initially attacked phloem that was not suitable for Douglas-fir beetles or delayed attack until those beetles were well established. The role of other beetles in Douglas-fir was minor and usually associated with Douglas-fir beetles. Douglas-fir beetles initially attacked severely injured trees, then attacked more lightly injured trees during 1991 and 1992. The major increase in cumulative insect attack occurred in 1990, when 38% of the trees were attacked, compared with 14% in 1991 and 3% in 1992 (Table 3). Mortality was substantially higher in trees with more than 50% crown scorch or more than 75% basal girdling (Table 4). Most trees that died in 1989 suffered both severe crown and severe bole injury. The majority of subsequent mortality occurred among trees that suffered little crown injury but had more than 50% basal girdling.

Table 4. Number of trees, percent mortality, and number of trees infested by insects by species and fire injury.

Species	Crown scorch (%)	Basal girdling (%)[a]			
		0-25	26-50	51-75	76-100
Douglas-fir (n = 125)	0-25	11(82) 8[b]	14(64)12	13(46)11	17(76)17
	26-50	-	6(33) 6	4(50) 4	5(100) 5
	51-75	1(100) 1	3(0) 2	4(75) 4	12(100)12
	76-100	-	8(88) 4	1(100)1	26(100)15
Engelmann spruce (n = 17)	0-25	1(0) 0	-	-	4(75) 4
	26-50	-	-	-	3(100) 3
	51-75	-	-	-	5(80) 5
	76-100	-	-	-	4(100) 4
Lodgepole pine (n = 151)	0-25	30(13) 2[c]	15(13) 5	15(13) 4	59(88)54
	26-50	-	-	-	8(100) 6
	51-75	-	-	-	6(100) 4
	76-100	-	-	1(100) 1	17(100)14
Subalpine fir (n = 17)	0-25	-	1(100) 1	-	4(100) 4
	26-50	-	-	-	1(100) 1
	51-75	-	-	-	1(100) 1
	76-100	-	-	-	10(100) 9

[a] The first number is the number of burned trees in the survey, the number in parentheses is the percentage of trees that died, and the third number is the number of trees infested by insects.
[b] Includes nine trees from an unburned patch of forest. Six of these were attacked by Douglas-fir bark beetles and died.
[c] Includes 25 unburned trees, two of which died. These trees were not attacked by insects and their deaths appear unrelated to the fires.

Lodgepole Pine

Of the 151 lodgepole pine in the intensive survey, 62% were attacked by one or more species of insects, and 61% died (Tables 2, 3). The majority of dead trees were extensively fire girdled (greater than 75% of the circumference) and heavily insect infested (Table 4). Both live and dead trees were similar in size, but dead trees had suffered greater fire injury. Surviving trees received less than 25% crown scorch. Burned living trees averaged 56% basal girdling. Because lodgepole pine is a thin-barked species, severe crown injury was associated with severe bole injury. Severely injured bole tissues were not suitable for bark beetles. The dominant fire injury to sample trees was to the phloem and cambium in the lower 0.5 m of the bole. Frequently, only a 2- to 4-cm high band at the root crown was killed. Of the 25 unburned lodgepole pine in the survey, two trees died. Their deaths appear to be unrelated to the fires.

The majority of insects attacking lodgepole pine (Table 2) were pine engravers (*Ips pini*). Of the 70 trees attacked by pine engravers, 62 died. Most trees infested by pine engravers had more than 75% basal girdling but less than 50% crown scorch. The twig beetle (*Pityophthorus confertus*) attacked 18 trees, while mountain pine beetle (*D. ponderosae*) attacked eight trees. Seven of these pines died. However, mountain pine beetle attack densities appeared to be low. Red turpentine beetle (*D. valens*) attacked two trees and one died. Wood borers attacked 21 of the fire-injured lodgepole pine. Five of these pines lived and 16 died. The lodgepole pine that survived attacks primarily experienced strip attacks. When insect attacks occurred above the ungirdled portion of the bole, the tree generally died. The cumulative percent of lodgepole pine infested by insects increased by 20% between 1989 and 1990, by 14% between 1990 and 1991, and by 4% between 1991 and 1992 (Table 3). Cumulative mortality followed a similar trend (Table 3).

Engelmann Spruce and Subalpine Fir

We encountered only 17 Engelmann spruce and 17 subalpine fir in the intensive survey because we focused on Douglas-fir and lodgepole pine forests. By August 1992, all but 1 spruce had died (Table 2). The 14 spruce trees that died before 1991 were completely girdled. The 2 trees that died between 1991 and 1992 were 90% girdled and heavily infested with spruce beetle (*D. rufipennis*) in 1991. Spruce beetle infested 24% of the spruce. Thirteen of the subalpine fir suffered basal girdling in excess of 75% of the circumference and died by 1989. All of the subalpine fir died by 1990. Wood borers infested 74% of the spruce and fir.

Extensive Survey

By 1991, when the extensive survey began, most trees that suffered severe crown scorch or severe bole injury had died. Subsequent bark beetle infestation of less severely burned and unburned trees resulted in considerable delayed mortality. Delayed mortality from fire injury and insects in the tree species represented in this study ranged between 41 and 64%. This mortality altered the visual appearance of the stands during the years after the 1988 fires. Infestation by insects was positively related to the percentage of the basal circumference of the tree that had been killed by fire in Douglas-fir, lodgepole pine, and Engelmann spruce (Figure 1). Meaningful relationships were not established for subalpine fir and whitebark pine because of the small numbers of those species in our sample. For uninjured trees, insects attacked 22% of the lodgepole pine, 18% of the Douglas-fir, 11% of the subalpine fir, 10% of the Engelmann spruce, and 3% of the whitebark pine (Figure 1).

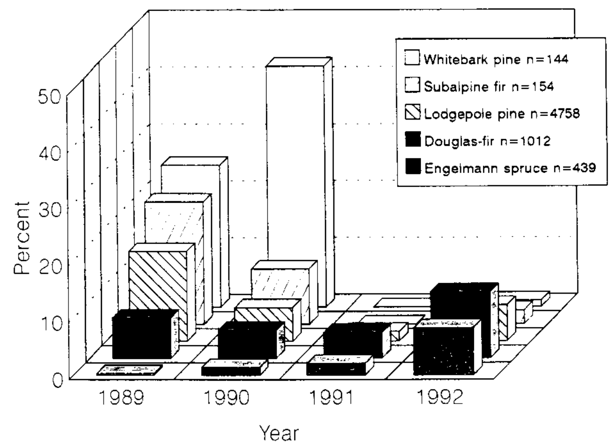

Figure 1. Percentage of trees infested by insects for five conifer species and percentage of basal circumference killed. Data are from the extensive survey of the 1988 Greater Yellowstone Area fires.

Douglas-fir

Of the 1,012 Douglas-fir examined, 32% were dead. Almost one-third of the Douglas-fir that were green and appeared to be alive following the 1988 fires died from the delayed effects of fire injury or were killed by insects. Of the delayed mortality, 19% was attributed to fire injury, while 13% was attributed to bark beetle and wood borer infestation. The cause of death could not be identified in 1% of the trees (Figure 2). Most infestation was by the Douglas-fir beetle. Additional mortality, especially of small diameter trees, was associated with Douglas-fir pole beetle (*Pseudohylesinus nebulosus*) and wood borers.

An average of 42% of the Douglas-fir in all fire-injury classes combined was infested by insects. Infestation increased from 18% in the unburned class to 80% in trees with 81-100% of the basal circumference girdled by fire (Figure 1). Douglas-fir beetle accounted for most of the infestation, which ranged between 16% of the trees in the uninjured class to 47% in the 81-100% basal injury class.

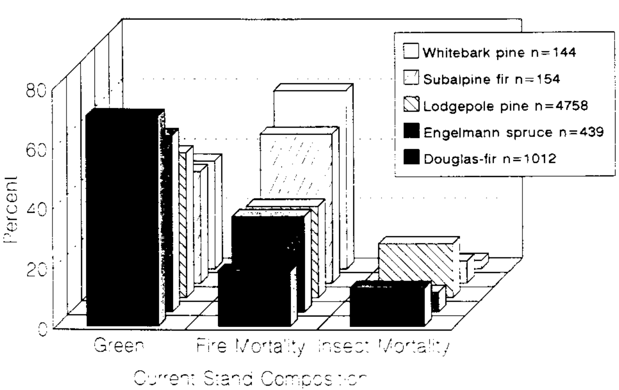

Figure 2. Percentage of healthy (green) trees versus fire-killed and insect-killed trees for the extensive survey of the 1988 Greater Yellowstone Area fires.

The second most common bark beetle infesting Douglas-fir was *P. nebulosus*; wood borers were the next most common insect infesting Douglas-fir.

In Douglas-fir, insects, particularly Douglas-fir beetles, began infesting uninjured trees the first year after the fire. Infestation of uninjured trees declined somewhat in 1990 and 1991. Then the infestation increased from 4% in 1991 to 12% in 1992 (Figure 3). Most of this was due to Douglas-fir beetle.

Lodgepole Pine

Lodgepole pine mortality was 52% of the 4,758 sampled trees. Of tree mortality, 31% was due to fire-injury, 18% was due to insects, and 3% was due to unidentified causes (Figure 2). Because of green foliage after the 1988 fires, many of these trees appeared to have survived the fires. However, almost two-thirds of the lodgepole pine that subsequently became infested and died had been completely girdled by light ground fires. The foliage on many of these trees did not fade until they were infested by pine engravers or twig beetles (*Pityophthorus confertus* and *Pityogenes knechteli*) three or four years after the fires. Of the dead lodgepole pine, 44% were infested by pine engravers. Total insect infestation ranged from a low of 22% of lodgepole with no injury to 67% of lodgepole with 81-100% of their basal circumference girdled by fire (Figure 1). Pine engravers accounted for most lodgepole pine infestation, ranging from 17% of trees in the uninjured class to 45% of trees in the 81-100% basal injury class. Twig beetles were the next most common, with the wood borers infesting a few trees. Mountain pine beetles infested less than 1% of the lodgepole pine and did not show much preference for any fire-injury class.

In lodgepole pine, infestation of uninjured trees increased from 2% in 1991 to 7% in 1992. Most of this was attributed to pine engravers. The pattern of infestation by year is similar to that in Douglas-fir. Infestation of lodgepole was high in 1989, then declined through 1991. A substantial increase occurred in 1992 (Figure 3).

Engelmann Spruce, Subalpine Fir, and Whitebark Pine

Mortality of Engelmann spruce totaled 41% of the 439 trees in the sample. Of these, 32% were killed by fire injury, 7% by insects (Figure 2); 2% died from unidentified factors. Spruce beetles killed almost half of the spruce that were killed by insects. Other insects that killed spruce were the pine engravers (*Ips pilifrons*) and wood borers.

Across all basal injury classes, 29% of the Engelmann spruce were infested by insects. Infestation ranged from 10% of the uninjured class to 54% of trees having 41-60% of their basal circumference girdled by fire (Figure 1). Spruce beetles accounted for almost half of the infested trees (14%). Infestation by spruce beetle ranged between 6% of the uninjured class to 39% of trees having 41-60% basal girdling.

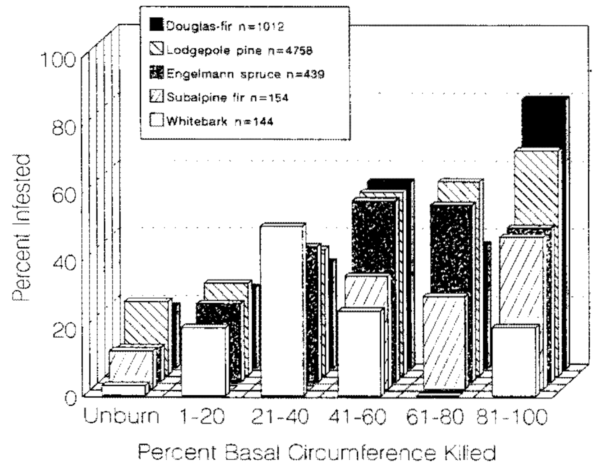

Figure 3. Percentage of trees infested by insects for 5 conifer species in the Greater Yellowstone Area for 4 years after the 1988 fires. Data are from the extensive survey of the 1988 Greater Yellowstone Area fires.

Mortality of the 134 subalpine fir totaled 63%. Fire injury accounted for 50% of the mortality, whereas insects accounted for 8% and unidentified causes accounted for 5% of the mortality (Figure 2). Wood borers accounted for most of the insects attacking subalpine fir.

Of the 144 whitebark pine in the extensive sample, 64% died; 60% died from fire injury, 3% died from insect attacks, and 1% died from unidentified causes (Figure 2). Mountain pine beetle and a pine engraver, probably *Ips montanus*, were the most common insects killing whitebark pine.

Our samples of subalpine fir and whitebark pine were too small to draw meaningful conclusions about insect response to different fire-injury classes. However, it appeared that insects consisting mostly of wood borers preferred the more severely injured subalpine fir (Figure 1). No strong relationship between fire injury and infestation existed in the whitebark pine data (Figure 1).

Discussion

The results of both the intensive and extensive surveys indicate that several insect species were attracted to trees stressed by fire injury. These attacks contributed to delayed mortality throughout the GYA. Few of the burned trees had more than half of their crown injured by fire. Many had no crown injury at all. In an analysis of the mortality of seven western conifers, including all of the species in this study except whitebark pine, Ryan and Reinhardt (1988) found little difference in mortality among species due to crown scorch. With less than 70% crown scorch, and in the absence of bole or root injury, trees of normal vigor are more likely to live than die (Ryan 1990). Studies of girdling by mechanical means (Noel 1970) and heat (Ryan and Frandsen 1991, Ryan 1993) indicate that trees have a high probability of surviving until nearly all of the phloem is severed. Ryan (1993) found basal girdling up to 80% of the circumference had no effect on seasonal water relations and only minor effects on allocation of carbon to growth. The high mortality in trees with minor crown and bole injury indicates that insects contributed to significant mortality in the GYA. The relatively high infestation of unburned trees in 1991 and 1992 compared to endemic attack rates further demonstrates that insects contributed to increased mortality after the 1988 fires.

We observed few trees infested by mountain pine beetles and those that were infested appeared to have few beetles. The lack of significant mountain pine beetle activity may be due to low population levels or habitat preference. Populations of mountain pine beetles were low in the GYA in 1988 (Knapp et al. 1988, Gibson and Oakes 1989). Also, mountain pine beetles do not prefer trees stressed by fire or drought (Rasmussen et al. 1996). Although some mountain pine beetles were present in the GYA during this study, populations did not increase in the stressed trees. Schmitz (1988) observed mountain pine beetles infesting diseased lodgepole pine when beetle populations were at an endemic level; brood production was very low, preventing the beetle population from building up. Population build-up and a full-scale outbreak appears to require faster growing trees with thicker phloem, the larvae's food source.

Although we did not sample Douglas-fir beetle populations by removing bark, Pasek and Schaupp (1992) did remove bark in areas of the Clover Mist Fire in the Shoshone National Forest adjacent to Yellowstone National Park. They observed that broods were reduced from 1990 levels; they attributed the reduction to prolonged, extremely cold temperatures. Reduced brood survival could account for low infestation in 1991. The large increase in Douglas-fir infestation in 1992 (Figure 3) is close to the upper limit of the 1.5- to 3-fold increase predicted by Pasek and Schaupp (1992), based on their sampling of Douglas-fir beetle populations. Infestation figures for 1992 are higher than those for 1991, but we don't know that all of these infested trees will die. However, it appears that fewer fire-injured trees are available for infestation, increasing infestation of uninjured trees. The attack trends from the extensive survey suggest increased infestation in 1993. However, Douglas-fir beetle outbreaks generally coincide with periods of drought. Increased precipitation in 1993 could alter the apparent trend.

In Engelmann spruce, infestation steadily increased in each of the four years after the fire (Figure 3). Spruce beetles accounted for most of this infestation. The large increase from about 2% in 1991 to 8% in 1992 suggests that beetles probably built up in fire-injured trees and are now infesting more of the uninjured trees. The steady increase in infestation of uninjured spruce indicates that the spruce beetle population could be poised for a major outbreak. Because the spruce beetle has a 2-year life cycle, the large increase in 1992 would be the result of populations surviving in trees infested in 1990. Should survival be as high in the spruce infested in 1991 beetles could infest a higher percent of the uninjured spruce than they infested in 1992. With good survival, beetles emerging in 1994 could continue the high level of infestation.

Delayed mortality resulting from lethal underburning and the subsequent insect-caused mortality in surviving underburned and adjacent unburned forests changed the 1988 postfire forest mosaic. Delayed mortality creates diverse habitats for fauna (McEneaney 1996), affects regeneration (Anderson et al. 1996) and nutrient cycling, and confounds efforts to survey burned forests using remote sensing (White et al. 1994). Recent evidence suggests that 60% of the area burned in stand-replacement fires in the Selway-Bitterroot Wilderness in Idaho and Montana occurred as lethal understory fires, with the remainder occurring as crown fires (Brown et al. 1994). Our surveys were not designed to quantify the area of delayed mortality in the GYA. However, photographs taken periodically since 1988 and our survey data suggest that delayed mortality was extensive.

Conclusions

The results of both the intensive and extensive surveys indicate that stress resulting from fire injury led to increased bark beetle activity in the GYA. Lethal basal girdling coupled with insect attacks of unburned and lightly burned trees caused considerable delayed mortality. Delayed mortality altered the visual appearance of the burn mosaic. Lethal underburning alters a number of ecosystem processes that can have long-lasting effects on forested ecosystems. Additional research is needed to better understand how fires of varying severity alter forest structure and insect ecology.

Trees with severe crown scorch tended to have more heat-killed cambium and to succumb more rapidly. These trees tended to not to be favorable habitat for bark beetles but frequently were attacked by wood borers. In contrast, trees with light crown scorch and basal girdling were attacked more frequently first by primary and secondary bark beetles and were later attacked by woodborers. Bark beetle infestation increased with the percent of basal circumference killed by fire. The relative importance of factors affecting beetle response such as insect populations before the fire, trees' reduced resistance to attack, increased nutritional value of phloem, weather after the fire, and predation are unknown.

Bark beetle populations appear to have increased in fire-injured trees and then infested uninjured trees. Whether some beetle species will continue to spread to unburned forests is uncertain. However, historic evidence from other fires suggests major epidemics are unlikely in the absence of additional stress from drought or other sources.

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