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Kevin C. Ryan

Gene D. Amman

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Interactions Between Fire-injured Trees and Insects in the Greater Yellowstone Area

Kevin C. Ryan
Intermountain Research Station
U.S. Department of Agriculture, Forest Service
Intermountain Fire Sciences Laboratory
P.O. Box 8089
Missoula, MT 59807

Gene D. Amman
Intermountain Research Station
U.S. Department of Agriculture, Forest Service
Ogden Forestry Sciences Laboratory
507 25th Street
Ogden, UT 84401

Abstract. After the 1988 Greater Yellowstone Area (GYA) fires, 24 permanent plots were established at 6 sites within 4 different burned areas. The purpose was to evaluate the effects of fire injury on susceptibility to insect attack and tree survival. Mensuration, fire injury, and insect attack data were collected on four species of burned conifers. By July 1991 76 percent of the 125 Douglas-fir had been infested by bark beetles (primarily by the Douglas-fir beetle) and wood borers; 58 percent of the 151 lodgepole pine were infested (primarily by the pine engraver); 82 percent of the 17 Engelmann spruce were infested (primarily by the spruce beetle); and 88 percent of the 17 subalpine fir were infested (primarily by wood borers). Fire injury combined with subsequent insect attack resulted in death to 55 percent of the Douglas-fir, 69 percent of the lodgepole pine, 82 percent of the Engelmann spruce, and all of the subalpine fir.

Mountain pine beetles have not been attracted to fire-injured lodgepole pine nor do such trees appear susceptible to a significant buildup of this insect. However, pine engraver beetles are attacking girdled and partially girdled lodgepole pine. Mortality of Douglas-fir is associated with a significant buildup of Douglas-fir bark beetles. The data, while not conclusive, suggest that insect populations are increasing in fire-injured trees and spreading to nearby uninjured trees, particularly in Douglas-fir.

These data were used as an independent test of a tree mortality model developed from data previously collected following prescribed fires. The model accurately predicted the death of Engelmann spruce and subalpine fir, but predicted mortality was too low for Douglas-fir and too high for lodgepole pine. Model failures can be partially explained by

differences in the fire behavior experienced by trees in the two data sets, but interpretations are confounded by insect interactions.

Introduction

The type and degree of fire injury, tree vigor, and the postfire environment determine conifer survival after fire. Heat-caused injury to the canopy is the most common source of tree death (Peterson 1985; Peterson and Arbaugh 1986, 1989; Ryan 1990; Ryan, Peterson, and Reinhardt 1988), but injuries to bole cambium and roots may be more important in some cases (Ferguson, Gibbs, and Thatcher 1960; Ryan and Frandsen 1991; Ryan, Peterson, and Reinhardt 1988; Ryan and Reinhardt 1988; Swezy and Agee 1991). Mortality resulting from excessive crown injury normally occurs during the first two growing seasons following fire, while death resulting from bole and root injury often does not occur for two or more growing seasons (Ferguson, Gibbs, and Thatcher 1960; Ryan and Frandsen 1991; Ryan, Peterson, and Reinhardt 1988). Vigorous trees are more likely to survive moderate fire injuries than stressed, slow growing trees (Ryan 1990).

Based on data collected on 2,356 trees burned in 43 prescribed fires, Ryan and Reinhardt (1988) developed a logistic regression model to predict mortality of fire-injured conifers in the Northwestern United States. The model is contained in the BEHAVE fire behavior program (Andrews and Chase 1989) and is used by managers to predict and control mortality from prescribed fires. Following recent wildfires, managers also used the equation to predict mortality along travel corridors and in burned commercial forests. However, its use following wildfires has not been tested with independent data.

After publication the mortality model in Ryan and Reinhardt (1988) was reformulated by changing the functional form for including the effect of increasing bark thickness. The current equation fits the data as well and is more robust for management application. The model as it is currently formulated is

$$P_m = 1/\{1 + e^{[-1.941+(\text{bark factor} + \text{crown factor})]}\} \tag{1}$$

where: P_m = the probability of mortality (0 to 1.0);
bark factor = $6.316[1 - e^{(-0.3937BT)}]$, BT is bark thickness (cm);
crown factor = $-0.000535CSC^2$, CSC is crown volume scorched (%)

Logistic models such as equation (1) can be used either to estimate the likelihood that an individual tree will die or to estimate the proportion of a similar population that can be expected to die (Ryan, Peterson, and Reinhardt 1988).

Insects are an important aspect of the postfire environment that affects tree survival. But because it is difficult to assess fire injuries to bole and roots adequately, it is often unclear whether insects are attacking mortally injured trees or are themselves a primary source of death. In the absence of significant bole or root injuries, the probability of attack by primary bark beetles, those that can infest and kill healthy trees, is initially low with light defoliation, increases with moderate to heavy defoliation, but often drops with complete defoliation (Furniss 1965; Miller and Keen 1960; Mitchell and Martin 1980; Wagener 1961). Bark beetles also attack trees with cambium injury but are thought to contribute little to mortality, except in conjunction with defoliation or when a large proportion of the circumference is killed (Ferguson, Gibbs, and Thatcher 1960; Ryan and Frandsen 1991; Wagener 1961). Secondary bark beetles (those commonly attracted to severely weakened or recently killed trees) and wood borers are often attracted to burned trees when suitable populations exist in the vicinity of the fires (Fellin 1980; Furniss and Carolin 1977). Their contribution to mortality, while thought to be minor (Mitchell and Martin 1980), is largely unknown. Host/insect species relationships and the degree to which fire-injured trees lead to a buildup of populations capable of attacking nearby unburned trees have not been determined for most species.

In 1988 canopy-consuming 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 and instantly killed most trees. Trees burned in surface fires received varying degrees of crown and bole injury. In 1989 we initiated a survey to improve our understanding of fire injury and insect interactions in the GYA. The objectives were to (1) examine short-term mortality of partially burned trees, (2) determine which insect species attacked fire-injured trees, (3) test the ability of equation (1) to predict mortality following uncontrolled fires in the Northern Rocky Mountains, and (4) make a preliminary assessment of the potential for build-up of bark beetle populations and their spread to adjacent unburned trees.

Methods

Canopy fires usually resulted in complete burning or severe scorching of the inner bark, especially in thin-barked trees. Because such trees are no longer suitable for bark beetle infestation, we focused our sampling on surface burned and adjacent unburned forests. We made observations on 24 variable radius plots (2.23 m^2ha^{-1} basal area prism factor) within areas covered by four fires (table 1). Plots were located in lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*) forests at elevations between 2,000 and 2,500 m. In addition to lodgepole pine and Douglas-fir, we encountered a few Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Individual trees were numbered with aluminum tags, except in the heavily used Madison River area, where successive observations were made by comparing tree diameter and location. Measurements were made of tree diameter at breast height, the percentage of the crown volume scorched, and the percentage of the circumference killed at the base. Crown scorch was ocularly assessed 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. Bark thickness was computed from tree diameter and species dependent equations (Ryan and Reinhardt 1988).

We classified insects attacking trees according to whether they were primary or secondary bark beetles, wood borers, or other insects (table 2). Observations of insects were restricted to the visible lower bole (c. 2 m). We detected insect attack by inspecting for boring dust and for entrance and exit holes. Species were identified by removing a small portion of bark, exposing the phloem and cambium. Ovservations were made of insect attack and mortality from 1988 through 1991. Trees were classified as alive or dead based on the presence or absence of living foliage. We evaluated the performance of equation (1) by comparing the predicted status (alive or dead) with the observed tree status in 1991. The expected fate of an individual tree was determined by inspecting its probability of mortality. If the probability of mortality exceeded 0.5, we predicted the tree would die. Otherwise, we predicted it would live. The expected number of dead trees in a stand was the product of the probability of mortality and the number of trees.

Additional details on plot location, measurements, and preliminary observations based on the first two growing seasons are contained in Amman and Ryan (1991).

Table 1. Location of plots and number of trees by species in the fire-injury and insect interaction survey of the 1988 Yellowstone fires

Fire	Location	No. plots	Species	No. trees
North Fork	Bunsen Peak	3	Douglas-fir	52
	Madison River	4[a]	Douglas-fir	43
			Lodgepole pine	6
Snake River	Grant Village	1	Lodgepole pine	12
Huck	Rockefeller Parkway	9	Douglas-fir	26
			Engelmann spruce	2
			Lodgepole pine	75
			Subalpine fir	9
Hunter[b]	Ditch Creek	7	Douglas-fir	4
			Engelmann spruce	15
			Lodgepole pine[c]	58
			Subalpine fir	8
Total		24		310

[a]One plot on the Madison River was completely unburned and contained 9 Douglas-fir and 6 lodgepole pines.
[b]The Hunter fire occurred on the Bridger-Teton National Forest, about 50 km south of Yellowstone Park.
[c]Includes 19 lodgepole pines that were completely unburned.

Results and Discussion

Douglas-fir

Of the 125 Douglas-fir in the survey, 116 trees were burned to varying degrees. The remaining nine trees were in an unburned patch of forest and were not directly affected by fire. Mortality increased annually to 55 percent in late July 1991 (figure 1). We found no difference in tree diameter between living and dead Douglas-fir, but dead trees suffered greater crown scorch and basal girdling (table 3), indicating that they were exposed to more severe fires. Most trees that died in 1989 suffered both severe crown and bole injury. The majority of additional mortality between 1989 and 1991 occurred among trees that suffered little crown injury but had greater than 50 percent basal girdling. Mortality was substantially higher in trees with more than 50 percent crown scorch or more than 75 percent basal girdling (table 4).

Of the 116 Douglas-fir that burned, 26 percent were infested by insects in 1989, primarily the Douglas-fir beetle (DFB) (*Dendroctonus pseudotsugae*) and a few wood borer larvae of Buprestidae and Cerambycidae (Amman and Ryan 1991). Most infested Douglas-fir in 1989 had 50 percent or more stem girdling by fire. In 1990 infestation increased to 67 percent of the trees (Amman and Ryan 1991). By 1991 76 percent of the trees were infested (table 5). The Douglas-fir beetle was active at all survey locations to burned trees when suitable populations exist in the vicinity of the fires (Fellin 1980; Furniss and Carolin 1977). Their contribution to mortality, while thought to be minor (Mitchell and Martin 1980), is largely unknown. Host/insect species relationships and the degree to which fire-injured trees lead to a buildup of populations capable of attacking nearby unburned trees have not been determined for most species.

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Table 2. Bark beetles and wood borers infesting trees in the Greater Yellowstone Area following the 1988 fires

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

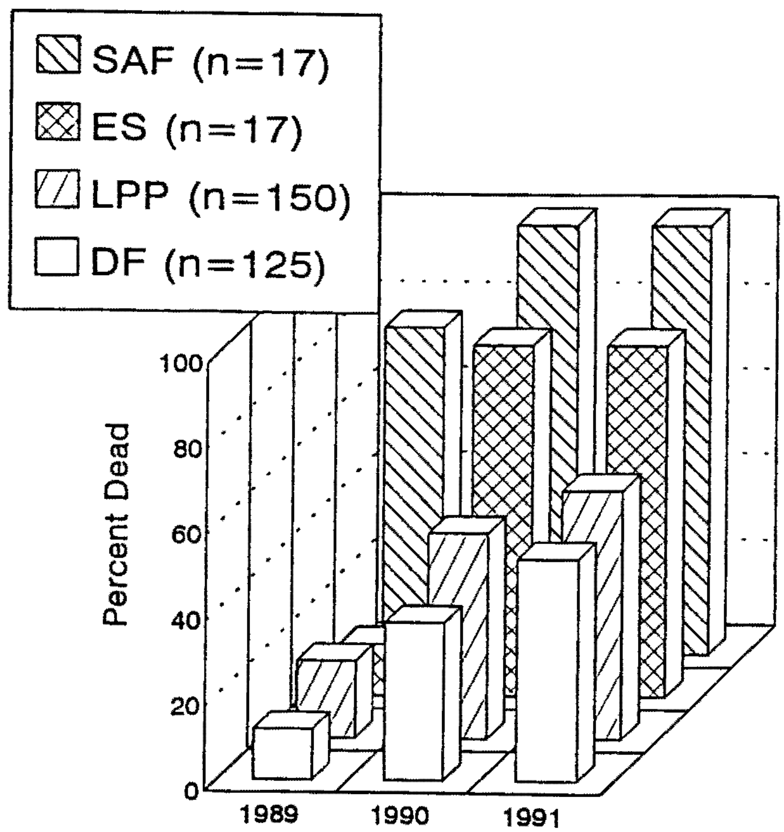

Figure 1. Percent mortality by species and year for trees burned in the 1988 Greater Yellowstone Area fires. SAF = subalpine fir, ES = Engelmann spruce, LPP = lodgepole pine, DF = Douglas-fir.

There appears to be a pattern where DFB initially attacked severely injured trees, then attacked more lightly injured ones. Peterson and Arbaugh (1986) found that the level of insect attack was an important factor in the death of burned Douglas-fir in the northern Rocky Mountains. In later work they found insect attack was unimportant for predicting the fate of fire-injured Douglas-fir in the Cascade Mountains (Peterson and Arbaugh 1989), possibly because beetle populations were low. Our results confirm the co-occurrence of fire injury and insect attack. With our data it is not possible, however, to determine whether the spread of DFB to more lightly injured trees results from a gradual decline in those trees' resistance to attack or whether DFB populations increased and overwhelmed the trees' defensive capabilities. We suspect that DFB is a significant source of additional mortality.

Table 3. Average tree diameter, percentage crown scorch, and percentage basal girdling, and predicted probability of mortality ($P_{mort.}$), by species and status

Species/status	No. trees	Diameter (cm)	Crown scorch (%)	Basal girdling (%)	$P_{mort.}$[a]
Douglas-fir					
Alive	52	38.9	25.6	68.3	0.27
Dead	64	36.9	67.6	81.4	0.65
Engelmann spruce					
Alive	3	35.6	24.3	66.7	0.59
Dead	14	35.7	55.0	100.0	0.80
Lodgepole pine					
Alive	39	25.7	1.2	60.2	0.72
Dead	87	25.3	29.9	94.3	0.81
Subalpine fir					
Alive	0	—	—	—	—
Dead	17	25.7	67.2	96.5	0.92
Total	276	31.3	37.3	81.7	0.66

[a]Calculated from equation (1).

In addition to the unburned trees on our plots that are infested, we have observed DFB successfully attacking trees in unburned areas near our Madison River plots. Spread of DFB to unburned trees is contrary to observations by M. Furniss (1965), who found DFB established offspring in 88 percent of fire-injured Douglas-fir following a fire in Idaho, but found the number of offspring small because of pitch invasion of galleries and sour sap condition. He did not report any infestation after the first postfire year. However, R. Furniss (1941) observed DFB buildup in Douglas-fir in Oregon following the 1933 Tillamook fire. Beetles killed large numbers of uninjured trees in 1935 and 1936. R. Furniss thought that frequent fires provided large numbers of injured trees for successive generations, thus allowing the DFB population to increase and overcome healthy trees' resistance. Our preliminary survey of fire and insect interactions was not designed to address questions of population buildup and beetle migration. However, the observed beetle activity prompted a more extensive survey of the GYA in 1991. Preliminary results indicate that extensive buildup of DFB is occurring in scorched trees (Amman unpublished data). It should also be noted that populations of DFB were increasing in the GYA at the time of the 1988 fires (Gibson and Oakes 1989; Knapp et al. 1988).

Table 4. Number of trees, percentage 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	0-25	2(100)2	12(42)10	14(21)9	18(22)13
	26-50	—	6(17)6	4(50)4	5(40)4
	51-75	1(100)1	3(0)1	4(25)1	12(60)4
	76-100	—	8(88)2	1(0)1	26(100)8
Engelmann spruce	0-25	1(0)0	—	—	4(75)2
	26-50	—	—	—	3(100)3
	51-75	—	—	—	5(80)1
	76-100	—	—	—	4(100)1
Lodgepole pine	0-25	5(40)1	16(19)5	14(7)3	59(83)38
	26-50	—	—	—	8(100)6
	51-75	—	—	—	6(100)3
	76-100	—	—	1(100)1	17(100)6
Subalpine fir	0-25	—	1(100)1	—	4(100)3
	26-50	—	—	—	1(100)0
	51-75	—	—	—	1(100)1
	76-100	—	—	—	10(100)6

[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.

Equation (1) predicts that 48 percent of all Douglas-fir in the survey will die. This number is 7 percent less than observed through July 1991. On an individual tree basis, equation (1) accurately predicted the July 1991 status of three-fourths of the trees (table 7). The majority of trees missclassified are those expected to live but that are already dead. Equation (1) consistently underpredicted the death of trees with low crown injury and high basal girdling. Further, equation (1) cannot account for future deaths among current living but DFB-infested trees. The failure of equation (1) to predict the death of low crown-injury trees accurately may reflect a bias in the data used by Ryan and Reinhardt (1988) to build the model. Their data came predominantly from moderate-intensity surface fires where duff moisture was generally too high to support the sustained burning that leads to basal injury in thick-barked trees. Extended drought in 1988 dried the duff around the bases of most Douglas-fir. Heat from burning duff killed the cambium around much of the circumference of these trees. Equation (1) does not give adequate weight to predicting mortality resulting from such heating. The underprediction of mortality may also be associated with the high incidence of attack by DFB.

Table 5. Cumulative distribution of insect infestation through 1991, by species

Species	Number	Percent infested				
		Primary	Secondary	Other	Borers	Total[a]
Douglas-fir	125	62	0	0	20	76
Engelmann spruce	17	24	6	18	65	82
Lodgepole pine	151	5	41	13	13	58
Subalpine fir	17	24	0	6	65	88
Total	310					

[a]Total percentage of trees attacked regardless of insect species. Many trees suffered attack from more than one species of insect.

Lodgepole Pine

Of the 151 lodgepole pine in the survey, 126 were burned. Death of fire-injured lodgepole pine was low in 1989 but increased substantially in 1990 (figure 1). Dead trees were similar in size to live trees but suffered greater fire injury (table 3). By late July 1991 69 percent of the burned lodgepole pine were dead even though most trees received less than 25 percent crown scorch (table 4). A total of 71 percent of the lodgepole pine were more than 75 percent girdled, and most of these died. All of the surviving trees received less than 25 percent crown scorch. Of the 25 unburned lodgepole pine in the survey, 2 trees died. Their death appears to be independent of the fires.

By 1991 58 percent of the 151 lodgepole pine were attacked by insects (table 5). This is a continuation of the trend for an annual increase in the cumulative number of attacked trees. We previously reported that 24 percent of these trees had been attacked in 1989 and 44 percent by 1990 (Amman and Ryan 1991). Mountain pine beetle (MPB), *D. ponderosae*, attacked eight trees. All MPB attacks occurred on the Hunter fire on the Bridger-Teton National Forest. In these trees MPB was mixed with the pine engraver (PE) (*Ips pini*) and the twig beetle (*Pityophthorous confertus*). Wood borers, both Buprestidae and Cerambycidae, were found occasionally in fire-injured lodgepole pine. Pine engravers accounted for the majority of insects attacking lodgepole pine. Most trees infested by PE had greater than 75 percent basal girdling but less than 50 percent crown scorch. Our sample size is small but suggests that PE is not strongly attracted to trees with high crown scorch, perhaps because high crown scorch in lodgepole pine is frequently accompanied by high bole injury, and dead cambium is not suitable PE habitat. The primary fire injury associated with insect infestation and subsequent death of these trees is basal girdling. As of July 1991 8 of the 64 living lodgepole pine were infested with PE. Pine engravers were active at all survey locations except Madison, which has a small sample size (table 6).

The lack of significant MPB activity is probably due to low population levels and habitat preference. Populations of MPB were low in the GYA in 1988 (Gibson and Oakes 1989; Knapp et al. 1988). Also, observations over the years suggest that MPB is not strongly attracted to fire-scorched trees. Mitchell and Sartwell (1974) report that mountain pine beetles seldom breed in fire-injured trees in numbers sufficient to cause an increase in the population. Hopkins (1905) found no MPB in fire-injured ponderosa pine in the Manitou Park area of Colorado. Blackman (1931), working on the Kaibab National Forest in northern Arizona, found MPB unattracted to fire-scorched trees because the scorched phloem did not offer favorable conditions for beetle offspring. Rust (1933) reported that fire-injured ponderosa pine were infested by MPB the first year following a fire in northern Idaho. However, the infestation declined the next year. Following fires in eastern Oregon, Geiszler et al. (1984) observed MPB mostly in larger diameter lodgepole pine that experienced some root injury or basal injury to less than one-third of the circumference. This behavior was in direct contrast to PE, which preferred smaller diameter lodgepole pine and those with more than one-third of the basal circumference killed.

Table 6. Cumulative insect infestation and observed mortality through July 1991 and expected mortality by location

Location	Species	No. trees	Infested[a]	Killed	
				Observed	Expected[b]
			Percent		
Bunsen Peak	Douglas-fir	52	81	40	38
Madison River	Douglas-fir	43	63	58	35
	Lodgepole pine	6[c]	0	33	0
Grant Village	Lodgepole pine	12	58	42	100
Rockefeller Parkway	Douglas-fir	26	96	69	62
	Engelmann spruce	2	50	100	100
	Lodgepole pine	75	45	44	75
	Subalpine fir	9	89	100	100
Ditch Creek	Douglas-fir	4	25	50	100
	Engelmann spruce	15	87	80	80
	Lodgepole pine[d]	58	79	84	100
	Subalpine fir	8	88	100	100
Total		310			

[a]Total percentage of trees infested regardless of insect species and including both burned and unburned trees.
[b]Expected mortality is based on the individual burned tree's expected status ($P_m \geq 0.5$ = dead) as computed by equation (1).
[c]All 6 lodgepole pine were completely unburned.
[d]Includes 19 lodgepole pines that were completely unburned.

Given the diameters and severity of basal girdling of our lodgepole pine (table 3), the high incidence of PE in this survey is consistent with the observations of Geiszler et al. (1984). Also, the large number of trees infested by pine engraver is not surprising because these beetles are able to reproduce in wind-broken material, including large branches, and in decadent trees (Sartwell et al. 1971). Such material is plentiful throughout the GYA. Consequently, although PE was not causing noticeable tree mortality in 1988, sufficient numbers were probably present to infest the fire-injured lodgepole pine in the spring of 1989.

Table 7. Observed vs. expected mortality for four species

Species	Observed	Predicted[a]		
		Alive	Dead	Total
Douglas-fir	Alive	44	8	52
	Dead	21	43	64
Engelmann spruce	Alive	2	1	3
	Dead	1	13	14
Lodgepole pine	Alive	0	39	39
	Dead	0	87	87
Subalpine fir	Alive	0	0	0
	Dead	0	17	17
Total		68	208	276

[a]Predicted mortality based on the number of trees with a calculated probability of mortality greater than 0.5.

When equation (1) was used to predict the probability of mortality for all lodgepole pine in the survey, it predicted that 78 percent of the trees would die. This result compares to the observed 69 percent mortality. However, when applied on an individual tree basis, equation (1) completely failed to predict the survival of partially injured trees (table 7). Because lodgepole pine has thin bark, the calculated probability of mortality exceeded 0.5, with the result that all trees were predicted to die. Equation (1) was developed from data collected on moderate-intensity surface fires that were relatively uniform in their spatial coverage. Because of its thin bark, lodgepole pine is relatively sensitive to fire. Any fire vigorous enough to bathe the bole in flames for more than a few seconds should cause extensive cambium injury. Because our survey was conducted along the margin between canopy-burned and unburned forests, many trees were lightly scorched only on a portion of their circumference, and survival was greater than predicted. This was particularly true on the plot near Grant Village, where equation (1) performed most poorly (table 6).

Engelmann Spruce

Because our survey focused on Douglas-fir and lodgepole pine forests, we encountered only 17 Engelmann spruce on our plots. By July 1991 spruce mortality was 82 percent (figure 1). As expected for a thin-barked species, mortality did not vary by tree diameter (table 3). Dead trees, however, received more crown and bole injury. The 14 trees that died were completely girdled. Two of the surviving trees are 90 percent girdled, infested with spruce beetle (SB) (*D. rufipennis*), and expected to die. This result compares favorably with equation (1), which predicts that two trees will live (table 7). Insects infested 65 percent of the trees in 1989, increasing to 82 percent in 1990 (Amman and Ryan 1991). No additional trees were attacked in 1991 (table 5). Dry duff around the base of the spruce resulted in slow-burning fires that often burned off the roots or so weakened them that the trees were easily toppled by wind. Windthrown spruce with unscorched trunks created an ideal habitat for the SB, which prefers windthrown trees (Schmid and Hinds 1974). The small additional SB infestation in 1990 probably occurred because the spruce beetle has a two-year cycle in the GYA. We expected a buildup of SB when beetles from trees infested in 1989 emerged in 1991. However, we found high winter-caused beetle mortality in our small sample. Partially burned spruce near our plots contain some SB, but there is little evidence of a major population buildup.

Subalpine Fir

Subalpine fir are noted for their lack of fire resistance, primarily because of their thin bark (Ryan 1990; Ryan and Reinhardt 1988). Virtually any fire vigorous enough to scorch the bark will cause cambium inujry, followed by sloughing of the dead bark. Wood borers (Buprestidae and Cerambycidae) infested 35 percent of our subalpine fir in 1989. This infestation increased to 71 percent in 1990 (Amman and Ryan 1991) and to 88 percent in 1991 (table 5). Sixteen of the fir suffered basal girdling in more than 75 percent of the circumference. Most of the bark on subalpine fir was badly burned and not conducive to bark beetle infestation. All 17 subalpine fir died following the fires. Equation (1) accurately predicted the fate of these trees (table 7).

Conclusions

The 1988 fires in the Greater Yellowstone Area killed many trees outright. Many more were partially injured but still provided suitable habitat for insects. Some trees escaped fire injury but were exposed to insect attack from nearby infested trees. It is difficult to assess all fire injuries adequately, so the extent to which insects contributed to tree death is uncertain. Additional research is needed to focus on the physiological responses of fire-injured trees and their relationships with insect ecology. Although our sample of trees is small compared with total for the GYA, these observations suggest a trend for continued bark beetle infestation of both fire-injured and uninjured trees for 1991. Whether or not infestations extend beyond 1991 will depend in part on the availablity of suitable host material, which in many areas has been exhausted.

Preliminary indications are that existing models for predicting fire-caused mortality of these species should be used with caution following wildfires, particularly in areas of uneven burning near the edges of more severely burned forests. Equation (1) may be applied to populations but should not be applied to individual trees when fuels and fire behavior result in a patchy burn or when duff around the base of trees is deep and dry enough to burn. The failure of the model to predict the survival of partially girdled trees illustrates the need to develop additional models that predict mortality directly from girdling rather than from bark thickness. Morphological factors related to potential resistance to cambium injury may be adequate for planning a prescribed burn, but are a weak substitute for actual measurement of injuries when making postfire predictions of individual tree mortality.

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Editor
Don G. Despain

Technical Assistance and Logistics
Sarah Broadbent
Renee Evanoff

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