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BARK BEETLE—FIRE ASSOCIATIONS IN THE GREATER YELLOWSTONE AREA

Gene D. Amman[1]

Abstract—The large forest fires in and around Yellowstone National Park in 1988 bring up many ecological questions, including the role of bark beetles. Bark beetles may contribute to fuel buildup over the years preceding a fire, resulting in stand replacement fires. Fire is important to the survival of seral tree species and bark beetles that reproduce in them. Without fire, seral species are ultimately replaced by climax species. Following fire, bark- and wood-boring beetles respond to fire-injured trees. Because of synchrony of the fires and life cycles of the beetles, beetle infestation in 1988 was not observed in fire-injured trees. However, endemic populations of beetles, upon emergence in 1989, infested large numbers of fire-injured trees. Of the trees examined in each species, 28 to 65 percent were infested by bark beetles: Pinus contorta (28 percent) by Ips pini; Pseudotsuga menziesii (32 percent) by Dendroctonus pseudotsugae; Picea engelmannii (65 percent) by Dendroctonus rufipennis; and Abies lasiocarpa (35 percent) by Buprestidae and Cerambycidae. Most trees infested by bark beetles had 50 percent or more of their basal circumference killed by fire. Bark beetle populations probably will increase in the remaining fire-injured trees.

INTRODUCTION

Insects and diseases are important in modifying the age structure and species composition of many forests. Their activities contribute to accumulation of dead fuels that make large-scale fires possible--resulting in new stands of the host tree. The stands are then temporarily free of attack (Kilgore 1986). The mosaics of different-aged stands created as the result of fires assure survival of both trees and insects that infest them. However, fire is more important to the survival of some ecosystems than others. Following fires, injured trees are susceptible to infestation by bark beetles. Subsequent buildup of bark beetle populations can result in killing of uninjured trees.

In this paper I will discuss bark beetle ecology (1) as it may contribute to fuel buildup and fire intensity and (2) as it relates to fire-injured trees in the aftermath of forest fires. Lodgepole pine (Pinus contorta Douglas), the most prevalent tree species in the Greater Yellowstone Area (GYA) and one that we know the most about with respect to bark beetle-tree interactions, will be discussed more fully than other species.

BARK BEETLES AS CONTRIBUTORS TO FUEL BUILDUP

Pfister and Daubenmire (1975) recognized four basic successional roles for lodgepole pine: minor seral, dominant seral, persistent, and climax. Large areas of lodgepole pine in the GYA have almost no spruce-fir component. Despain (1983) concludes these are essentially self-perpetuating climax lodgepole pine stands that often exceed 300 to 400 years of age, with no evidence of fire since establishment.

Mountain pine beetle (MPB) infestation characteristics differ by lodgepole pine successional roles. In stands where lodgepole pine is seral and stands have been depleted by beetle infestations, lodgepole will be replaced by the more shade-tolerant species in the absence of fire. These shade-tolerant species consist primarily of Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) at the lower elevations and subalpine fir (Abies lasiocarpa [Hook.] Nutt.) and Engelmann spruce (Picea engelmannii Parry) at the higher elevations. Starting with the stand generated by fire, lodgepole pine grows rapidly and occupies the dominant position in the stand. Fir and spruce seedlings also become established in the stand but grow more slowly than lodgepole pine.

Once the lodgepole reach susceptible size, MPB infestations kill 30 to over 90 percent of trees 12.7 cm and larger diameter at breast height (Cole and Amman 1980; McGregor and others 1987). After each infestation, both residual lodgepole pine and the shade-tolerant species increase their growth (Roe and Amman 1970). Infestations are repeated as the residual lodgepole pines reach size and phloem thickness conducive to beetle infestation and survival (Amman 1977). This cycle is repeated at 20- to 40-year intervals, depending upon growth of the trees (Roe and Amman 1970). Although size and phloem thickness are the variables necessary for beetle epidemics to occur, some authors (e.g., Berryman 1978) believe trees must be weakened before MPB can infest them. However, this has not been demonstrated, and will require detailed studies of beetle populations progressing from low level into the early phases of an epidemic (Schmitz 1988). Fuel levels and fire hazard continue to increase with each beetle infestation (Brown 1975; Flint 1924; Gibson 1943; Roe and Amman 1970) until lodgepole pine is

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eliminated from the stand, or until a fire occurs that kills most trees (including thick-barked, fire-resistant species), and the stand regenerates to lodgepole pine.

Where lodgepole pine is persistent or climax (Pfister and Daubenmire 1975), the association of lodgepole pine and mountain pine beetle is somewhat different. In these cases, the forest consists of lodgepole pine of different sizes and ages, ranging from seedlings to a few overmature trees. In these forests, MPB infests and kills many of the pines as trees reach large size. Openings created in the stand, as a result of the larger trees being killed, are seeded by lodgepole pine. The cycle is then repeated as other lodgepole pines reach sizes and phloem thicknesses conducive to increases in beetle populations (Amman 1977).

Amman (1977) hypothesized that periodic MPB infestations continue the multi-aged nature of the stands. A mosaic of small clumps of different ages and sizes may occur. The overall effect is likely to be more chronic infestation by the beetle because of the more constant source of food. Beetle infestations in such forests may result in the death of fewer trees per hectare during each infestation than would occur in even-aged stands (caused by stand replacement fires) and in those stands where lodgepole pine is seral. Fires in uneven-aged persistent and climax lodgepole pine forests should not be as hot as fires where widespread epidemics of beetles have occurred because smaller, more continuous deposits of fuel are added to the forest floor under chronic beetle infestations. Thus, with lighter accumulations of fuel, fires tend to eliminate or weaken some of the trees but do not cause total elimination and complete regeneration of the stand. An example is the situation described by Gara and others (1985) in south-central Oregon, where lodgepole pine forms an edaphic climax. Here, fires are slow moving, and the heat of smoldering logs scorches roots and sides of trees. Later these injured trees are invaded by fungi that work their way up the roots into the trunks. Subsequently, mountain pine beetles are attracted to and kill these trees. As the dead trees rot and fall over, the stage is set for another fire.

Most fires that occur in lodgepole pine are either slow and smoldering or are rapidly moving, intense crown fires (Lotan and others 1985). High-intensity fires tend to favor lodgepole pine over such species as Douglas-fir (Kilgore 1986) and would likely occur following epidemic beetle infestations. Brown (1975) states that the major vegetation pattern found in lodgepole pine today was caused by stand replacement fires, although many uneven-aged lodgepole pine stands result from lower intensity surface fires.

In south-central Oregon, Stuart and others (1989) have related lodgepole pine regeneration pulses to mountain pine beetle and fire disturbances. They observed that (1) stands that experienced periodic MPB epidemics accompanied by a fire had an even-aged structure; (2) stands that had periodic MPB epidemics and no fire had a storied, bimodal size structure; and (3) stands that experienced mortality by low level MPB populations, with or without low intensity fire, had multi-aged structure.

Romme and others (1986) examined the effects of beetle outbreaks on primary productivity in forests dominated by lodgepole pine in northwestern Wyoming. They concluded that the mountain pine beetle does not regulate primary productivity. Even though MPB has drastic effects upon stands (considering the forest landscape comprises a mosaic of stands in various stages of succession), annual productivity for the landscape is relatively constant despite continual fluctuations of individual stands. The sudden and massive death of a large proportion of the biomass leads to only a brief drop in primary productivity and to a more equitable distribution of biomass and resources. Therefore, the primary function of large MPB infestations and the death of large numbers of lodgepole pine appears to be survival of host and beetle by creating large amounts of fuel for fire that, when ignited, eliminate competing vegetation and regenerates lodgepole pine (Amman 1977; Roe and Amman 1970; Romme and others 1986).

The mosaic of stands of different ages created by the action of MPB and fire is ideal for MPB survival. Because stands are coming into sizes conducive to continual MPB infestation and survival, a continual supply of food is provided. However, an ideal mosaic for MPB probably did not occur following the 1988 GYA fires because fire behavior was influenced more by drought and wind than by fuels. Virtually all forest age and fuel categories burned (Christensen and others 1989).

Romme and Despain (1989) state that the mosaic created by the 1988 fires will be more homogeneous than the mosaic created by fires in the early 1700's, and few ecological consequences will be incurred because succession is slow. One consequence is likely to be a major MPB infestation in 80 to 120 years because at this age many lodgepole pine stands sustain their first beetle outbreak, again creating a large amount of dead fuel in a relatively short period, setting the stage for another stand replacement fire (Roe and Amman 1970). The timing of MPB infestations, when lodgepole pine are mature in seral stands, not only assures large amounts of fuel from the dead trees for a stand replacement fire but also adequate seed to regenerate the stand (Peterman 1978). Peterman suggests the ecological role of MPB could be to decrease the probability of lodgepole stands, with a high degree of serotiny, producing stagnant stands of offspring. By preventing the stand from getting too old, much less seed would be available. Such a mechanism could have evolutionary significance to lodgepole pine because stagnant stands do not reproduce well, and the stand following the stagnant stand could be outcompeted by climax tree species. Peterman further points out that prevention of stagnant stands would be advantageous to MPB because the beetle does not reproduce well in small, stagnant trees.

The contribution of dead fuel buildup, a result of the 391 000 ha infestation of MPB in Yellowstone National Park that was still active in 1982 (Gibson and Oakes 1987), to behavior of the 1988 fires was masked by the extreme fire conditions (Christensen and others 1989). Studies of small fires in portions of Yellowstone not involved in the 1988 fires probably would elucidate interactions of MPB infestations, dead fuel buildup, and fires. A relationship similar to MPB, lodgepole pine, and fire has been proposed for southern pine beetle (SPB) (D. frontalis Zimmermann) and pines in the Southern United States. There, pines are replaced by hardwood tree species in the absence of fire (Schowalter and others 1981). Therefore, survival of SPB and its host in natural stands is dependent upon frequent fires.

Bark beetles infesting climax tree species would not have the same need for a close relationship with forest fires as those infesting seral species. The spruce beetle (SB) (D. rufipennis [Kirby]) and the Douglas-fir beetle (DFB) (D. pseudotsugae) usually kill small groups of trees. However, occasionally they also cause heavy mortality, favoring large trees over vast areas, after building up in windthrown trees. For example, SB killed millions of Engelmann spruce in Colorado between 1939 and 1951 (Massey and Wygant 1954) and white spruce (P. glauca [Moench] Voss) in Alaska between 1960 and 1973 (Baker and Kemperman 1974). Schmid and Hinds (1974) describe the scenario in spruce-fir stands in the central Rocky Mountains following spruce beetle infestations. Following a spruce-beetle outbreak, the percentage of subalpine fir in the stand increases, with fir dominating the stand. As fir reach 125 to 175 years of age, they begin to die, with the bark beetle Dryocoetes confusus Swaine being one of the mortality factors. Young spruce and fir increase their growth as overstory fir die. The less shade-tolerant spruce is then favored over fir as the original canopy fir are killed. Spruce becomes dominant as it outlives fir and gains greater size. Eventually, the cycle is repeated. Spruce beetle generally live in moist forests where fires are less frequent and intense because of moist, sparse fuels (Arno 1976). Small fires in the spruce-fir type would expose mineral soil and probably favor establishment of spruce.

The Douglas-fir beetle seldom creates widespread destruction in the Rocky Mountains, generally killing groups of dense mature Douglas-fir (Furniss and Orr 1978). These groups are usually widely separated, and the space created by death of some overstory trees usually regenerates to Douglas-fir.

These observations suggest coadaptive or coevolutionary relationships between bark beetles and their host trees, and the importance of fire in maintaining these relationships for seral tree species.

BARK BEETLE/FIRE-INJURED TREE ASSOCIATIONS

Following the 1988 GYA fires, large numbers of trees girdled or partially girdled by heat remained at the burn perimeter and are providing infestation opportunity to bark beetles. Beetles may increase to large numbers and infest uninjured trees after most of the fire-injured trees are killed.

The bark beetle situation in the GYA at the time of the 1988 fires shows that the species were at low population levels, except the DFB. The massive infestations of MPB that covered over 391 000 ha in Yellowstone Park in 1982 had declined to only 125 ha by 1986 (Gibson and Oakes 1987) and to no infested trees in 1987 (Gibson and Oakes 1988). In 1988, insect detection flights over the park were not made because of fire fighting efforts and smoke (Gibson and Oakes 1989). However, on the nearby Bridger-Teton National Forest, MPB infestation had declined from 1,296 ha in 1987 to 364 ha in 1988 (Knapp and others 1988).

Although no survey estimates are available for other bark beetle species in Yellowstone Park, surveys of adjacent areas showed only the DFB was increasing, whereas spruce beetle infestation was light (Knapp and others 1988) and pine engraver (Ips pini Say) populations had declined (Gibson and Oakes 1989).

The small populations of bark beetles in the GYA at the time of the 1988 fires, coupled with timing of the fires in relation to life cycles of bark and wood infesting beetles, resulted in few fire-injured trees being infested in 1988. The SB, DFB, and pine engraver all emerge to infest new material in the spring, prior to occurrence of the fires. The MPB emerges in late July and early August, but few were in the GYA.

Studies were started in 1989 to determine bark beetle infestation of fire-injured trees and potential buildup of beetle populations. Observations were made in three areas: (1) near the Madison River, approximately halfway between Madison Junction and West Yellowstone (the North Fork fire); (2) along the John D. Rockefeller, Jr., Memorial Parkway, south of Yellowstone's South Gate (the Huck fire); and (3) in the Ditch Creek area of the Bridger-Teton National Forest (Hunter fire). In each area, variable plots (10 basal area factor) were established: area 1, three plots; area 2, nine plots; and area 3, seven plots. All trees in the plots were numbered so that survival of individual trees can be followed for several years. Survival of scorched trees can be predicted from volume of crown scorch (Ryan and others 1988). Peterson and Arbaugh (1986) found crown scorch and basal scorch were best predictors for lodgepole pine survival, and crown scorch and insect attack were most important as predictors of survival of Douglas-fir. However, the researchers did not identify the insects. I used the percentage of basal circumference in which the cambium was killed, rather than relating infestation to crown scorch, because of the high sensitivity of lodgepole and spruce to even light ground fire. Some bark was removed from trees infested by insects so that insects could be identified. Because our plots were mostly at low elevations (2 050 to 2 400 m), trees consisted mostly of lodgepole pine and Douglas-fir. The limited nature of our observations preclude their use for making predictions of bark beetle activity beyond our plots. Greater coverage of the burned area is planned in 1990.

Lodgepole Pine

Lodgepole pine is the most abundant tree in the samples. Overall, 28 percent of the trees were infested by the pine engraver (*Ips pini* Say) (table 1). Of the trees infested, only one had not been scorched by fire. All others had 50 percent or more basal girdling (phloem killed by fire). Most commonly, trees infested by the pine engraver had 100 percent basal girdling (table 2). Many of these trees showed little evidence of scorch and looked healthy except for boring frass made by the beetles. Upon closer inspection, however, the trees were completely girdled at the base by a light ground fire. Geiszler and others (1984) also found most lodgepole pine infested by pine engraver were moderately to heavily injured following a fire in Oregon.

It is not surprising that a large number of trees were infested by pine engraver because they are able to reproduce in wind-broken material (including large branches) and in decadent trees near death (Sartwell and others 1971). There always seems to be plenty of such material available. Consequently, the engraver is almost always present in substantial numbers, although not necessarily causing noticeable tree mortality.

Only one tree containing MPB was observed (Hunter fire on the Bridger-Teton National Forest) and it was not on a plot. Observations over the years suggest that MPB is not strongly attracted to fire-scorched trees, so few trees would be infested even if a large population had been present in the GYA. The MPB seldom breeds in trees injured or killed by fire 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. However, he did observe several secondary species, including the red turpentine beetle (*D. valens* Lec.). In a subsequent publication concerning insect damage in the National Parks, Hopkins (1912) stated that forest fires contribute, to a limited extent, to the multiplication of certain species that breed in fire-scorched trees, but as a rule forest fires kill more beetles

Table 1.--Number of trees examined and the percentage infested by bark- and wood-boring beetles for plots located in three fires in the Greater Yellowstone Area, 1989

	Fire							
Tree species	North Fork		Huck		Hunter		All fires	
	No.	Pct	No.	Pct	No.	Pct	No.	Pct
Lodgepole pine	0	0	67	24	58	33	125	28
Douglas-fir	34	18	25	52	4	25	63	32
Engelmann spruce	0	0	2	50	15	67	17	65
Subalpine fir	0	0	9	33	8	38	17	35
All species	34	18	103	31	85	38	222	32

Table 2.--Number and percentage of trees infested by bark- and wood-boring beetles in different fire-injury categories, Greater Yellowstone Area, 1989

	Percentage of basal circumference killed by fire									
Tree species	0		1-25		26-50		51-75		76-100	
	No.	Pct	No.	Pct	No.	Pct	No.	Pct	No.	Pct
Lodgepole pine	21	5	4	0	15	0	12	25	73	41
Douglas-fir	17	28	3	0	10	30	11	36	22	41
Engelmann spruce	0	0	1	0	0	0	0	0	16	69
Subalpine fir	0	0	0	0	0	0	0	0	17	31
All species	38	16	8	0	25	12	23	30	128	43

than they protect (by protect, he probably meant provide breeding habitat). Swaine (1918), referring to Canadian conditions, wrote that ground fires that injure and kill large numbers of trees may provide material for rapid development of bark beetles. He thought this was particularly true if fires occur year after year in neighboring localities. Apparently the proximity of fires would allow beetles to continue to build up their populations for several consecutive years. Blackman (1931), working on the Kaibab National Forest in northern Arizona, found MPB did not prefer fire-scorched trees. He thought the scorched phloem did not offer favorable conditions for beetle offspring. The MPB has fairly limited requirements of phloem thickness and moisture in order to reproduce (Amman and Cole 1983).

In agreement with most observations in the Rocky Mountains that MPB are not attracted to fire-scorched trees, Geiszler and others (1984) observed MPB mostly in trees uninjured or lightly injured by fire, in direct contrast to pine engraver in moderate to heavily injured trees. Rust (1933) reported fire-injured ponderosa pine were infested by MPB the first year following a fire in northern Idaho; however, the infestation declined the next year.

The wood borers, both Buprestidae and Cerambycidae, were found occasionally in fire-injured lodgepole.

Douglas-fir

Douglas-fir was the second most common tree found on the plots. Of the trees examined, 32 percent were infested by insects, mostly DFB and a few wood borer larvae of Buprestidae and Cerambycidae (table 1). Most infested Douglas-fir had 50 percent or more girdling by fire (table 2). Some Douglas-firs that had needles and limbs completely burned were infested by DFB in the base where the bark was thick enough to protect the phloem from complete incineration or from drying so excessively that beetles would not construct egg galleries in it. Phloem in such trees was completely brown, and larvae probably will not complete development in such trees.

Furniss (1965) studied the susceptibility of fire-injured Douglas-fir to bark beetle attack after a large fire in southern Idaho. He found 70 percent of the trees were infested by DFB 1 year after the fire. And even small or lightly burned trees attracted the beetles. He found incidence of attack increased with tree size and severity of crown and cambium injury by fire. However, infestation decreased sharply with outright tree killing by fire. Although beetles established brood in 88 percent of the trees, offspring numbers were small because of pitch invasion of the galleries and sour sap condition.

Furniss (1965) did not report on DFB infestation in fire-scorched Douglas-fir beyond the first postfire year. However, following the Tillamook fire of 1933 in the coastal range of Oregon, DFB buildup in fire-injured Douglas-fir occurred. Beetles then killed large numbers of uninjured trees in 1935 and 1936, but the infestation soon subsided (Furniss 1941). Furniss thought beetles were able to increase because frequent fires in the Tillamook area provided large numbers of injured trees in which the beetles could reproduce.

Connaughton (1936) observed that delayed mortality of fire-injured Douglas-fir was mostly caused by insects (probably DFB) and fire damage to roots. He found Douglas-fir had a thick layer of duff around the trunk that burned slowly, heating the soil and badly injuring the roots. The evidence for root injury did not show up until a year or two after the fire in west-central Idaho.

Engelmann Spruce

Engelmann spruce constituted a small part of our tree sample, with only 17 trees examined. Spruce beetle infested 65 percent of the trees (table 1), and these were usually the larger diameter trees. Of the spruce, only those with 75 percent or greater basal girdling were infested (table 2). Some spruce burned similarly to Douglas-fir described by Connaughton (1936). Duff around the base resulted in a slow burning fire that often burned off the roots or so weakened them that the trees were easily blown over by wind. Windthrown trees with unscorched trunks created an ideal habitat for the SB, which shows a strong preference for windthrown trees (Massey and Wygant 1954; Schmid and Hinds 1974). Large numbers of spruce beetle larvae occurred in the spruce, as well as some larvae of Buprestidae and Cerambycidae.

Subalpine fir

Wood borers (Buprestidae and Cerambycidae) infested 35 percent of the 17 subalpine fir in the sample (table 1). All of the fir suffered 100 percent basal girdling. The bark was badly burned and not conducive to bark beetle infestation (table 2).

Whitebark Pine

Whitebark pine (P. albacaulis Engelm.), which is generally found at high elevations in GYA, did not occur in any of our plots. MPB infestations during the past 20 years caused considerable whitebark mortality (Bartos and Gibson 1990), but the number of infested trees was low at the time of the 1988 fires. Although MPB is not strongly attracted to fire-scorched lodgepole and ponderosa pines in the Rocky Mountains, Craighead and others (1931) state that it prefers weakened and fire-scorched western white pine (P. monticola Dougl.), one of the five-needle pines. Therefore, MPB may be more attracted to fire-injured five-needle pines, whitebark and limber (P. flexilis James), than to lodgepole pine.

CONCLUSIONS

Of the bark beetles in the GYA, MPB plays a significant role in converting live fuels to dead fuels in a relatively short period. This behavior probably promotes hot stand replacement fires that assure survival of lodgepole pine and, hence, survival of MPB. Fire is not as important in the ecology of bark beetles infesting climax tree species.

Although a limited number of fire-injured trees were sampled in the GYA, almost one-third were infested by bark beetles. Therefore, numbers of infested trees in the sampled areas likely will increase because of the remaining large numbers of fire-injured trees.

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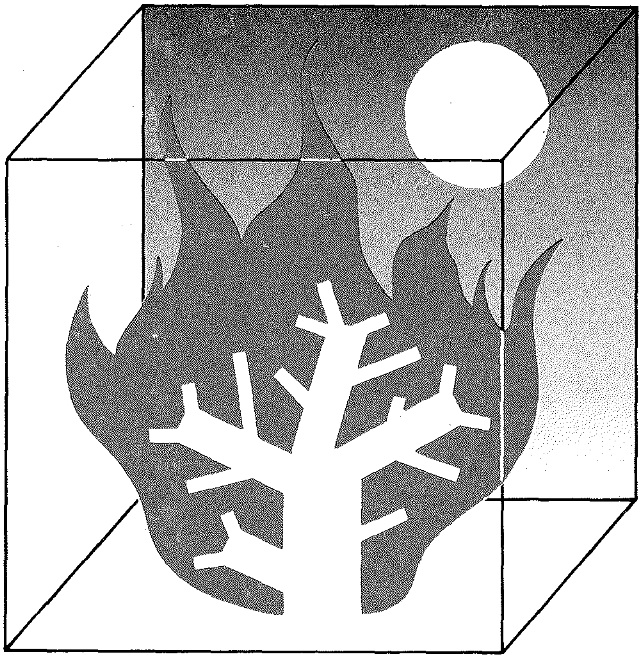

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