



Bark Beetle and Fire Interactions in Western Coniferous Forests: Research Findings

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Native bark beetles and wildfires are important disturbances in western coniferous forests. Bark beetles can colonize and kill trees of all species, ages, and sizes, but each species exhibits unique host preferences and impacts. Some bark beetles cause extensive levels of tree mortality (table 1), as demonstrated by mountain pine beetle (*Dendroctonus ponderosae*) in several pines, western pine beetle (*Dendroctonus brevicomis*) in ponderosa pine (*Pinus ponderosa*), Douglas-fir beetle (*Dendroctonus pseudotsugae*) in Douglas-fir (*Pseudotsuga menziesii*), and spruce beetle (*Dendroctonus rufipennis*) in several spruces. Other bark beetles are secondary agents that colonize stressed, dead, or dying trees. The impacts of these secondary agents often go unnoticed, while the former occasionally drive headlines in large newspapers.

Figure 1—Tree mortality following a bark beetle outbreak in the Sierra Nevada in California. California experienced a severe drought from 2012 to 2015, stimulating a large bark beetle outbreak in the central and southern Sierra Nevada. Most tree mortality was caused by western pine beetle (*Dendroctonus brevicomis*), which readily colonizes drought-stressed ponderosa pine (*Pinus ponderosa*), but other tree and shrub species were also affected. About 89 percent of the ponderosa pines in the three largest diameter classes were killed (Fettig and others 2019), representing the loss of an important structural component of these forests. Mortality of sugar pine (*Pinus lambertiana*), caused primarily by mountain pine beetle (*Dendroctonus ponderosae*), was also substantial (48 percent). In total, 49 percent of the trees died between 2014 and 2017. Photo: C. Fettig, USDA Forest Service.

In general, bark beetles require living phloem (the layer of cells within the inner bark that transports photosynthates (sugars) within the tree) to reproduce. When bark beetle populations are low, the beetles create small gaps in the forest canopy by colonizing and killing trees stressed by age or other factors. During bark beetle outbreaks, large numbers of trees can be

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Table 1—Bark beetles recognized as causing substantial levels of tree mortality during outbreaks in the Western United States.

Common name	Scientific name	Common host(s)	Current knowledge of effects on wildfire behavior and severity ^a
California fivespined ips	<i>Ips paraconfusus</i>	Lodgepole pine, sugar pine, ponderosa pine	Low
Douglas-fir beetle	<i>Dendroctonus pseudotsugae</i>	Douglas-fir	Moderate
Fir engraver	<i>Scolytus ventralis</i>	White fir, grand fir, California red fir	Low
Jeffrey pine beetle	<i>Dendroctonus jeffreyi</i>	Jeffrey pine	Low
Mountain pine beetle	<i>Dendroctonus ponderosae</i>	Whitebark pine, lodgepole pine, limber pine, sugar pine, western white pine, ponderosa pine	High
Northern spruce engraver	<i>Ips perturbatus</i>	White spruce, Lutz spruce	Low
Pine engraver	<i>Ips pini</i>	Lodgepole pine, Jeffrey pine, sugar pine, ponderosa pine	Low
Pinyon ips	<i>Ips confusus</i>	Pinyon pine(s)	Low
Spruce beetle	<i>Dendroctonus rufipennis</i>	Engelmann spruce, white spruce, Lutz spruce	Moderate
Western balsam bark beetle	<i>Dryocoetes confusus</i>	Subalpine fir	Low
Western pine beetle	<i>Dendroctonus brevicornis</i>	Ponderosa pine, Coulter pine	Low

a. Level (low, moderate, or high) defined in relation to knowledge of the effects imposed by mountain pine beetle outbreaks, which have been most intensively studied.

killed over extensive areas (fig. 1), often adversely affecting timber and wood fiber production, water quality and quantity, fish and wildlife populations, opportunities for outdoor recreation, and biodiversity and carbon storage, among other ecological goods and services (Morris and others 2018).

HISTORIC OUTBREAK LEVELS

The amount of tree mortality caused by bark beetles in the Western United States has exceeded that caused by wildfires in the last 3 decades (Hicke and others 2016), and several recent outbreaks are considered the most severe in history. Since 2000, for example, about 25.5 million acres (10.3 million ha) in the Western United States have been affected by mountain pine beetle. Activity peaked in 2009, with 8,842,698 acres (3,578,513 ha) affected in that year alone.

Bark beetles are cold-blooded organisms highly sensitive to changes in temperature, which influence their survival and population growth (Bentz and others 2010). Drought stress adversely affects the ability of conifers

to repel beetle attack (Kolb and others 2016). Accordingly, recent bark beetle outbreaks have been correlated with shifts in temperature and precipitation caused by climate change. In some forests, increases in tree density have exacerbated the effect by providing an abundance of hosts and by increasing competition among hosts for limited resources, making trees more vulnerable to beetle attacks.

Wildfires have sculpted many western forests for millennia, reducing the quantity and continuity of fuels, discouraging establishment of fire-intolerant tree species, and influencing the susceptibility of forests to bark beetle outbreaks and other disturbances. Climate change is increasing the number of large wildfires (fires greater than 1,000 acres (400 ha) in size), the frequency of wildfires, the length of the wildfire season (by up to 90 days in some locations), and the cumulative area burned (Vose and others 2018). Suppression costs and risks to homes and other infrastructure are also increasing (Flannigan and others 2006).

In this article, we consider two common interactions between bark beetles and wildland fires:

1. The effects of fuel reduction treatments (prescribed fire and mechanical thinning) and wildfires on bark beetles; and
2. The effects of bark beetle outbreaks and associated levels of tree mortality on fuels and wildfire behavior and severity.

We briefly describe the current state of knowledge and identify gaps in knowledge needed to make informed management decisions.

EFFECTS OF FUEL REDUCTION TREATMENTS ON BARK BEETLES

Tens of millions of acres of forest in the Western United States are classified as having moderate to high fire hazards. Efforts to lower hazards focus on reducing surface fuels, increasing the height to live crowns, decreasing crown bulk density, and retaining large trees of fire-resistant species such as

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ponderosa pine (Agee and Skinner 2005). When applied under prescription, planned ignitions and their mechanical surrogates (such as thinning from below) are generally effective in meeting fuel reduction goals (McIver and others 2013; Stephens and others 2012). For example, the effectiveness of prescribed fire for treating surface and ladder fuels to reduce the incidence of passive crown fire (that is, the torching of small groups of trees) is well supported by modeling of predicted fire behaviors (Stephens and others 2009) and by empirical research (Ritchie and others 2007). Furthermore, results from the National Fire and Fire Surrogate Study, the largest study of its kind (www.frames.gov/ffs/about), indicate that the incidence of active crown fire is best reduced by combining prescribed fire with mechanical fuel treatments (McIver and others 2013).

The type of fuel reduction treatments and their manner of implementation have different effects on the fuel matrix, which can influence the susceptibility of forests to bark beetles in different ways (Fettig and others 2007). For example, prescribed fire can affect the health and vigor of residual trees; the size, distribution, and abundance of preferred bark beetle hosts; and the physical environment within forests. Associated reductions in tree density can alter microclimates, affecting beetle fecundity (the ability to produce offspring) and fitness as well as the phenology (timing of life cycle events) and voltinism (number of generations per unit of time) of bark beetles and their predators, parasites, and competitors. Tree density reductions can also disrupt pheromone plumes that attract bark beetles to a tree during initial colonization.

Volatiles (volatile organic compounds) released from trees are known to influence the behavior of many bark beetles (Seybold and others 2006). Fettig

and others (2006) showed that chipping submerchantable and unmerchantable ponderosa pines and depositing the chips back into treated stands increases the risk of infestation by several species of bark beetles in the Southwestern United States. The effect was due to large amounts of monoterpenes being released during chipping, which enhanced attraction to bark beetles. Impacts were greater from chipping in spring (April–May) than in late summer (August–September) because spring is the time of peak flight activity for several species of bark beetles in the Southwestern United States as they search for new hosts. If possible, chipping should be conducted in fall to minimize tree losses to bark beetles if the chips will remain onsite.

PRESCRIBED FIRE

Following fire, tree mortality can be immediate due to consumption of living tissue or heating of critical plant tissues; or it can be delayed, occurring over the course of a few years as a result of fire injuries to the crown, bole, or roots (Hood and others 2018a). Levels of delayed tree mortality caused by bark beetles depend on numerous factors, including tree species; tree size; tree phenology; degree of fire-caused injuries; initial and postfire levels of tree vigor; the postfire environment; and the scale, severity, and composition of bark beetle populations and other tree mortality agents in the area.

A common management concern is that bark beetles might colonize and kill trees that were injured by prescribed fire and otherwise would have survived. These trees may then serve as a source of beetles and attractive semiochemicals as host volatiles are released by the boring activity of bark beetles. In addition to host volatiles, the pheromones produced by bark beetles might attract other beetles and result in additional levels of tree mortality over time.

Fettig and McKelvey (2014) monitored the effects of fuel reduction treatments on levels of tree mortality at Blacks Mountain Experimental Forest in California over a 10-year period. Twelve experimental plots (ranging from 190 to 356 acres (76–142 ha)) were established to create two distinct forest structural types: midseral stage (with low structural diversity) and late-seral stage (with high structural diversity). Following harvesting, half of each plot was treated with prescribed fire.

A total of 16,473 trees (9 percent of all trees) died. Mortality was concentrated:

- On plots with high structural diversity (64 percent);
- On burned-split plots (61 percent);
- Within the two smallest diameter classes (87 percent); and
- During the second sample period (3 to 5 years after prescribed burns).

Most mortality was caused by bark beetles (65 percent), notably fir engraver (*Scolytus ventralis*) in white fir (*Abies concolor*) and mountain pine beetle, western pine beetle, and pine engraver (*Ips pini*) in ponderosa pine. The authors concluded that this level of tree mortality did not interfere with management objectives aimed at increasing overall forest resilience.

Similarly, Douglas-fir beetle, pine engraver, and western pine beetle caused some tree mortality following prescribed fires in western Montana. Mortality occurred shortly after prescribed fires, and unburned plots were unaffected. However, following a regional mountain pine beetle outbreak that started about 5 years after treatments were completed, 50 percent of ponderosa pines in control (untreated) plots and 39 percent in prescribe-burned plots were colonized

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and killed. Almost no trees were killed by mountain pine beetle in thinned plots and thinned-and-prescribed-burned plots (Hood and others 2016). Thinning treatments, with or without prescribed fire, dramatically increased tree growth rates and production of resin ducts (a measure of conifer defense against bark beetles) relative to the control and prescribed fire treatments.

In some cases, concerns about maintaining large-diameter trees following prescribed fire have been justified. For example, Fettig and McKelvey (2014) reported that most tree mortality (78 percent) in the largest diameter class occurred during the first 5 years after prescribed fire and that 66 percent was caused by bark beetles. Tree protection treatments (such as insecticides and semiochemicals) can be selectively used to protect individual trees from colonization by bark beetles (Fettig and Hilszczański 2015). Furthermore, methods such as raking litter and duff from the bases of large-diameter trees have been shown to reduce prescribed fire severity and levels of tree mortality (Fowler and others 2010; Hood 2010). Additional research is needed to determine under what conditions large-diameter trees are most susceptible to delayed mortality following prescribed fire and when tree protection treatments are warranted.

The limited number of studies on the effects of season of burn (spring versus fall) on levels of tree mortality caused by bark beetles show mixed results. Some studies show increases in certain bark beetle species following fall treatments (that is, when fuels are drier and burns are more intense); see, for example, Fettig and others (2010). Other studies show stronger effects following early-season burns (that is, when bark beetles are more active); see, for example, Schwilk and others (2006). More research is needed to fully define these relationships in different forest types.

Although most of the tree mortality caused by bark beetles following prescribed fire occurs during the first few years, this pattern might differ in adjacent untreated areas. The reason, in part, is

that unburned areas do not benefit from the positive effects of prescribed fire (such as increased growing space due to reduced tree density), which affect tree vigor and susceptibility to colonization by bark beetles. Notable infestations in adjacent unburned areas are uncommon but can occur and should be watched for in case additional management is warranted to limit tree losses (Fettig and Hilszczański 2015).

MECHANICAL FUEL TREATMENTS

Factors such as stand density, host density, and average tree diameter are strong predictors of the severity of bark beetle infestations in the Western United States. High levels of beetle-caused tree mortality (for example, greater than 20 percent) should be expected following fuel reduction treatments

2006). Six and others (2002) showed that pine engravers are unable to colonize and reproduce in chips. Moreover, slash can be managed to minimize colonization of residual trees by bark beetles (DeGomez and others 2015).

EFFECTS OF WILDFIRES ON BARK BEETLES

Factors that influence tree mortality caused by bark beetles are the same after wildfires as after prescribed fires. Our distinction is based not on ignition type but largely on differences in fire intensity and fire severity: most wildfires are higher in intensity and severity than prescribed fires (though not always). Low-severity wildfires can induce tree defenses against bark beetles (Hood and others 2015). Resin-duct-related defenses take about 1 year after wildfire to form; during this time, fire-injured trees can be

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that retain high residual stand densities, regardless of treatment effects. Although thinning has long been advocated as a measure to reduce beetle-caused tree mortality (Fettig and others 2007), thinning prescriptions for fuel reduction differ from prescriptions for reducing susceptibility to bark beetles. In the latter, crown or selection thinning (that is, removal of larger trees in the dominant and codominant crown classes) is typically required to achieve target threshold densities and residual tree spacing as well as significant reductions in the abundance of preferred hosts. Nevertheless, thinning from below (for fuels reduction) does release growing space, reducing a stand's susceptibility to bark beetles.

A common concern following mechanical fuel treatments is that bark beetles could breed in logging residues (chips and/or slash) and emerge to colonize residual trees. However, most studies indicate that this is uncommon (see, for example, Fettig and others

more susceptible to colonization by bark beetles, which might help explain some of the near-term increases in levels of beetle-caused tree mortality after some wildfires and prescribed fires (Hood and others 2015, 2016). The level of tree injury influences bark beetle attraction, with moderately injured trees being most susceptible to colonization by bark beetles (see, for example, Hood and Bentz 2007; Lerch and others 2016; and Powell and others 2012).

High-severity wildfires generally reduce susceptibility to bark beetles by killing large numbers of host trees. For example, research in subalpine forests in Colorado shows that spruce beetle outbreaks are reduced for decades after high-severity wildfires (Bebi and others 2003), the dominant fire regime in these forests. As with prescribed fires, bark beetles routinely cause additional levels of tree mortality after wildfires, but infestations in adjacent unburned areas are uncommon (Davis and others 2012; Lerch and others 2016; Powell and others 2012).

EFFECTS OF BARK BEETLE OUTBREAKS ON FUELS AND FIRE BEHAVIOR AND SEVERITY

Although fuel reduction treatments and wildfires can affect bark beetles, the reverse is also true: bark beetles can alter wildfire behavior by changing fuel conditions. Of the bark beetle–host systems to consider, the effects of mountain pine beetle in lodgepole pine (*Pinus contorta*) have been most intensively studied (table 1), and for good reason: mountain pine beetle alone is responsible for almost half of the total area affected by bark beetles in the Western United States. All other bark beetle–host systems have received less attention, some little or none (table 1).

Fire behavior in beetle-affected forests largely depends on the severity of the outbreak (the proportion of trees colonized and killed) and the amount of time since the outbreak occurred. Jenkins and others (2008, 2014) use the term “bark beetle rotation” to describe the period from the start of a bark beetle outbreak to the next outbreak within susceptible forests. In the “endemic phase,” beetle-caused tree mortality is limited (for example, to less than 2 trees per acre per year) and generally isolated to stressed hosts. In the “epidemic phase,” beetles colonize and kill large numbers of susceptible hosts. In the “post-epidemic phase,” beetle populations subside and most beetle-killed trees fall to the forest floor. The endemic and post-epidemic phases can last for decades to centuries, whereas the epidemic phase usually lasts from 2 to 10 years.

Recently attacked trees are referred to as “green-infested” (fig. 2A). As needles fade, trees enter the “yellow” stage. In the “red” stage, needles on beetle-killed

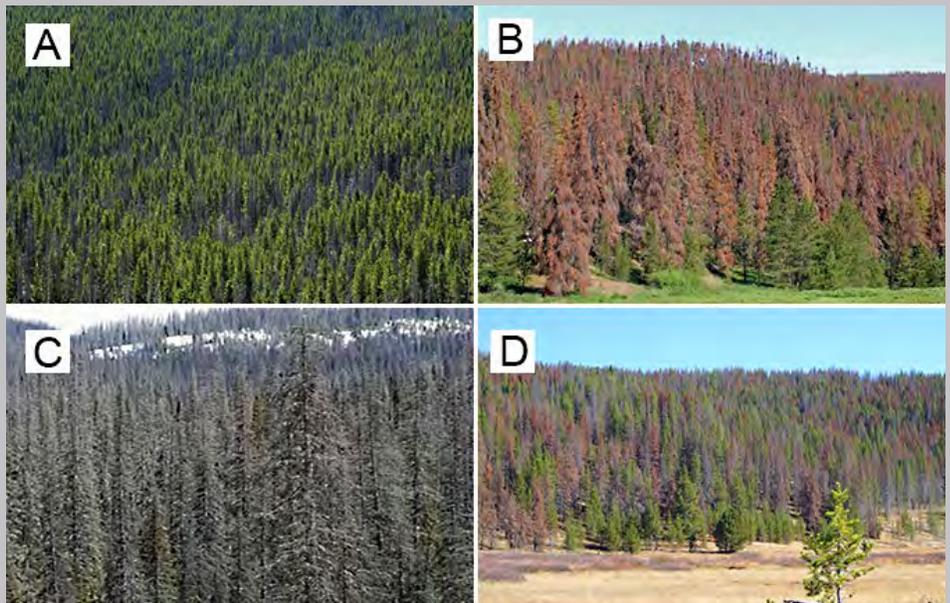


Figure 2—Bark beetles can cause dramatic changes to forest canopies in coniferous forests. For example, during and after mountain pine beetle (*Dendroctonus ponderosae*) outbreaks, lodgepole pine (*Pinus contorta*) canopies transition from the green-infested stage (A) to the red stage (B) in about 1 to 3 years and then to the gray stage (C), which lasts from about 3 to 25 years following the outbreak. The likelihood of crown and spot fires is greater during the red stage and possibly reduced during the gray stage. Bark beetle activity frequently results in a mosaic of green, red, and gray trees (D) as trees are attacked and killed over several years (usually 2 to 6 years for mountain pine beetle), which can complicate fire behavior prediction in these forests. Photos: J. Runyon, USDA Forest Service.

trees turn red (fig. 2B). The final stage is the “gray” stage, when needles fall off the trees (fig. 2C). The timing of needle fade and color change varies considerably by tree species, bark beetle species, and geographic location. For example, in the mountain pine beetle–lodgepole pine system, the green-infested stage lasts for about 1 year; the yellow and red stages last for about 1 to 3 years; and the gray stage lasts for about 3 to 25 years (Klutsch and others 2009). It is important to note that, during an outbreak, trees are attacked and killed over several years, and cumulative levels of tree mortality vary considerably even within the same bark beetle–host system. Therefore, a forest often contains trees and stands in multiple stages and phases of a bark beetle rotation at the same time (fig. 2D).

CROWN AND CANOPY FUELS

Not surprisingly, beetle-induced changes to foliar moisture have the greatest effects on flammability. This is because water is a heat sink and moisture in plant tissues increases the amount of

energy required for fuels to ignite and burn. Trees colonized and killed by bark beetles rapidly dry out and lose most of their water content by the first summer following attack as needles transition from green to red (fig. 2A, 2B). For example, the twigs and needles of lodgepole pine killed by mountain pine beetle lose 80 to 90 percent of their water content within 1 year of attack (Jolly and others 2012a; Page and others 2012). The loss of moisture increases flammability by shortening time to ignition, lowering temperature at ignition, and raising heat yields when burned (Jolly and others 2012a; Page and others 2012). Reduction in moisture content explains nearly 80 percent of the increase in needle flammability (Page and others 2012). Similar reductions in foliage moisture content and increases in flammability have been documented in Engelmann spruce (*Picea engelmannii*) killed by spruce beetle (Page and others 2014) and Douglas-fir killed by Douglas-fir beetle (Giunta 2016).

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Figure 3—Coarse woody fuel accumulations following a bark beetle outbreak in the Sierra Nevada in California. Based on a survey of 180 plots across 4 national forests, 31 percent of the dead trees fell to the forest floor within 4 years of being killed, which is much faster than reported elsewhere in the literature for other locations and bark beetle–host systems (Fettig and others 2019). Stephens and others (2018) concluded that a greater potential for “mass fires” exists for this region, driven by the amount, size, and continuity of dry combustible woody fuels, which could produce large, severe, and uncontrollable wildfires. Mass fires or “firestorms” (Finney and McAllister 2011) can occur when large areas burn simultaneously for long periods at high intensities, generating their own weather conditions. The science on mass fires (such as Countryman 1965) is limited and the risks are poorly understood. Photo: L. Mortenson, USDA Forest Service.

Bark beetles alter foliage flammability in other ways as well. The proportions of fat, fiber, lignin and cellulose, starches, and sugars change in needles after beetle colonization, and each factor can affect flammability (Jolly and others 2012a; Page and others 2012, 2014). Conifers also contain large amounts of flammable terpenes. Beetle attack generally increases the emission of terpenes and terpene concentrations within needles (Giunta and others 2016; Page and others 2012, 2014), which can shorten time to ignition, lower temperature at ignition, and increase the maximum rate of mass loss (an indication of burning rate) (Page and others 2012, 2014). Moreover, the emission of terpene “clouds” from plants has been linked to eruptive fire behavior in Europe (Barboni and others

2011; Courty and others 2012) but has not yet been studied in the Western United States. Firefighters have reported observations that support the existence of terpene clouds in western forests during the epidemic phase; additional research is warranted on terpene clouds and their potential effects on fire behavior in the Western United States.

Outbreaks also alter canopy fuel arrangement (Hicke and others 2012; Jenkins and others 2008). As trees move from the red to the gray stage (fig. 2B, 2C), canopy fuels decrease. As dead trees deteriorate and fall to the forest floor (fig. 3), canopy bulk density and canopy cover decline over time. The decrease in canopy fuel continuity also reduces the sheltering effect of the forest, causing higher wind speeds near

the ground (Hoffman and others 2015). Increased light and moisture availability resulting from mortality of dominant and codominant trees release smaller surviving trees that were unsuitable hosts for bark beetles, increasing ladder fuels during the post-epidemic phase.

LITTER, FINE FUELS, AND COARSE WOODY FUELS

Although dying and dead foliage is more flammable than live foliage, it remains in the canopy for only a short time (usually 3 years or less). The accumulation rate of canopy materials (foliage and twigs) on the forest floor can be of greater importance, influencing surface fuel loadings and associated fire hazards.

Stalling and others (2017) evaluated the effects of mountain pine beetle and Douglas-fir beetle outbreaks on fuel conditions in Montana and Idaho. Foliage deposition occurred mostly during the first 2 years of the epidemic phase. Unlike foliage, fine woody and nonwoody material tended to come down irregularly, deposited at essentially the same rate from year to year. Tree fall and accumulations of coarse woody surface fuels were limited over the 10-year period of study. These findings suggest that fire hazards in these forests were influenced less during the late epidemic and early post-epidemic phases than previously thought. Highly flammable dead foliage does not stay in the canopy for long, and accumulations of canopy materials on the forest floor do not exceed the annual rate of fuel decomposition (Stalling and others 2017).

Ultimately, all of the woody fuel from beetle-killed trees is transferred to the forest floor during the post-epidemic phase. This period varies considerably by site and tree species, among other factors, with half-lives (the time required for half of the dead trees to fall to the forest floor) ranging from years (such as for ponderosa pines killed by western pine beetle in the central and southern Sierra Nevada (fig. 3)) to decades (such as for lodgepole pines killed by mountain pine beetle in northeast Oregon (Harvey 1986)). Over time, medium and coarse woody fuels

gradually accumulate, increasing fuel bed depth. For example, Jenkins and others (2014) reported that medium and coarse woody fuels increased by a factor of about 2.5 to 8 in forests of the Intermountain West following mountain pine beetle outbreaks 20 years earlier.

FIRE BEHAVIOR AND SEVERITY

Modeling fire behavior in beetle-affected forests is challenging, largely because fire behavior model assumptions are violated (Hood and others 2018b; Jenkins and others 2012, 2014; Page and others 2014). The limited ability to use empirical data to evaluate model predictions (Alexander and Cruz 2013a) has fed controversy over whether epidemic and/or post-epidemic phases have more fire behavior hazards than the endemic phase (Jolly and others 2012a; Simard and others 2011, 2012).

Physics-based models suggest that bark beetle outbreaks increase wildfire rates of spread, with spread rates peaking during the red stage. Rates of spread remain higher than in the endemic phase even though canopy fuels decrease (Hoffman and others 2015). In an experiment on needle flammability, red needles from beetle-attacked trees ignited faster than green needles, which could lead to increased crown fire potential (Jolly and others 2012b). However, it is unknown whether the increase in flammability scales up to entire canopies and results in higher intensity crown fires (Alexander and Cruz 2013b). After a crown fire begins, fire behavior in lodgepole pine forests under dry, windy conditions is likely to be similar, regardless of bark beetle activity (Schoennagel and others 2012). Under most circumstances, severe fire weather conditions trump beetle-induced changes in fuel conditions.

Using a physics-based model, Sieg and others (2017) found higher fire severity (that is, tree mortality) in ponderosa-pine-dominated forests during the red stage than in the endemic phase but unchanged or even lower fire severity during the gray stage. The observed increases in fire severity attributed to the bark beetle outbreak declined under high wind conditions (Sieg and others 2017).

Fire severity, measured as change in vegetation, decreased over time following mountain pine beetle outbreaks in Washington and Oregon (Meigs and others 2016). By contrast, Prichard and Kennedy (2014) reported higher fire severity during the red stage following mountain pine beetle outbreaks in Washington.

Harvey and others (2014) reported similar levels of fire severity in red-stage and gray-stage lodgepole pine forests following mountain pine beetle outbreaks in the Northern Rockies. They evaluated several metrics of fire severity and found that only extreme fire weather conditions increased fire severity in terms of deep charring (that is, charring into the wood along tree boles and into crowns, with less than 5 percent of branches remaining) (Harvey and others 2014).

After forests enter the gray stage, evidence suggests that fire severity—and, presumably, the potential for heightened fire behavior—diminish for some time (Hicke and others 2012) (fig. 4). However, more research is needed to fully understand the potential for crown fires in the gray stage.

Although bark beetle outbreaks can influence fire behavior and severity, they have little effect on the extent of the area burned (see, for example, Hart and others 2015) or the likelihood or frequency of wildfire occurrence (Bebi and others 2003; Meigs and others 2015).

The effects on fire behavior and severity have important implications for fire management and firefighter safety. For example, the likelihood of torching, crowning, and spotting can be greater in forests containing an abundance of red



Figure 4—Gray-stage coniferous forest following a bark beetle outbreak. Fire behavior in beetle-affected forests largely depends on the proportion of trees killed and the amount of time since the bark beetle outbreak (that is, the “bark beetle rotation”). In the gray stage, fire severity—and, presumably, the potential for heightened fire behavior—is reduced. However, high-severity crown fires have been reported in some gray-stage forests (Agne and others 2016), especially after significant accumulations of coarse woody fuels. The science on fire behavior in gray-stage forests is limited. Photo: S. Hood, USDA Forest Service.

crowns (Schoennagel and others 2012; Jenkins and others 2014). Moreover, firefighters have observed “surprising” fire behavior in some forests during the epidemic and post-epidemic phases (Moriarty and others 2019; Page and others 2013). Rapid shifts from surface fires to crown fires pose safety risks to firefighters caused by increases in fireline intensities and spotting, which

fire interactions in western coniferous forests in the last 15 years. Much of this information has been synthesized in notable publications (such as Hicke and others 2012; Jenkins and others 2008, 2012, 2014; Kane and others 2017; and Stephens and others 2018). We encourage the reader interested in delving deeper into this topic to consult these publications.

small trees or big trees are killed and whether some trees or nearly all trees are killed);

- The dominant fire regime of the forest type;
- The spatial scale; and
- Limitations in the prediction of fire behavior in beetle-affected forests.

Furthermore, most studies are retrospective (rather than controlled experiments) and inherently have a lot of variability.

Given the implications for firefighter safety and fire suppression activities, work is needed to more accurately quantify relationships between bark beetle outbreaks and fire behavior and severity, especially in understudied forest types (table 1). Creating and maintaining forest structures that are more resilient to bark beetles and wildfires will go a long way toward addressing concerns regarding increases in fire behavior and severity following bark beetle outbreaks.

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might necessitate larger safety zones (Butler and Cohen 1998). Snags are an important safety concern, particularly during the post-epidemic phase (fig. 3). Accordingly, firefighters should anticipate the potential for unusual fire behavior (even during the green-infested stage) in beetle-affected forests and the unique suppression challenges that can result (such as increased difficulties in fireline construction and establishment of access, egress, and escape routes).

LOOKING FORWARD

A key finding of the recently published U.S. Fourth National Climate Assessment is that it is “very likely that more frequent extreme weather events will increase the frequency and magnitude of severe ecological disturbances, driving rapid (months to years) and often persistent changes in forest structure and function across large landscapes” (Vose and others 2018). As such, it is reasonable to assume that bark beetles and wildfires will increasingly interact to shape western forests.

Recognizing this, the fire science and forest health communities have largely bridged cultural and communication divides (Jenkins and others 2009) and have strengthened relationships with managers in hopes of delivering science of utmost relevance to managers’ concerns (Kocher and others 2012). A tremendous amount of knowledge has been developed on bark beetle and

The scientific community now has a pretty solid understanding of the effects of fuel reduction treatments on bark beetles, which tend to lead to fairly consistent responses among different forest types in the Western United States. Nevertheless, knowledge gaps exist and need to be addressed. Many initial fears concerning long-term increases in levels of delayed tree mortality caused by bark beetles were unfounded. Accordingly, one might view the associated increases in tree mortality as “short-term losses” suffered for “long-term gains” (Fettig and McKelvey 2014). This is especially true when considering that rates of tree mortality caused by bark beetles are generally low (less than 5 percent) and concentrated in small-diameter trees (that is, ladder fuels) and in fire-intolerant tree species (such as white fir).

Although the scientific literature shows mixed results, most suggests that bark beetle outbreaks can significantly change fuel profiles and fire behavior and severity during the epidemic and post-epidemic phases. Nevertheless, discussions of the effects of bark beetle outbreaks on fuels and fire behavior get unnecessarily complex and occasionally contentious if they ignore:

- The amount of time that has occurred since the outbreak (that is, the bark beetle rotation);
- The type and severity of the outbreak (including such factors as whether

LITERATURE CITED

- Agee, J.K.; Skinner, C.N. 2005. Basic principles of forest fuel reduction treatments. *Forest Ecology and Management*. 211: 83–96.
- Agne, M.C.; Woolley, T.; Fitzgerald, S. 2016. Fire severity and cumulative disturbance effects in the post-mountain pine beetle lodgepole pine forests of the Pole Creek Fire. *Forest Ecology and Management*. 366: 73–86.
- Alexander, M.E.; Cruz, M.G. 2013a. Limitations on the accuracy of model predictions of wildland fire behaviour: a state-of-the-knowledge overview. *The Forestry Chronicle*. 89: 372–383.
- Alexander, M.E.; Cruz, M.G. 2013b. Assessing the effect of foliar moisture on the spread rate of crown fires. *International Journal of Wildland Fire*. 22: 415–427.
- Barboni, T.; Cannac, M.; Leoni, E.; Chiaramonti, N. 2011. Emission of biogenic volatile organic compounds involved in eruptive fire: implications for the safety of firefighters. *International Journal of Wildland Fire*. 20: 152–161.
- Bebi, P.; Kulakowski, D.; Veblen, T.T. 2003. Interactions between fire and spruce beetles in a subalpine Rocky Mountain forest landscape. *Ecology*. 84: 362–371.
- Bentz, B.J.; Régnière, J.; Fettig, C.J. [and others]. 2010. Climate change and bark beetles of the Western United States and Canada: direct and indirect effects. *Bioscience*. 60: 602–613.
- Butler, B.W.; Cohen, J.D. 1998. Firefighter safety zones: a theoretical model based on radiative heating. *International Journal of Wildland Fire*. 8: 73–77.
- Countryman, C.M. 1965. Mass fire characteristics in large-scale tests. *Fire Technology*. 1: 303–317.
- Courty, L.; Chetehouna, K.; Halter, F. [and others]. 2012. Flame speeds of α -pinene/air and limonene/air mixtures involved in accelerating forest fires. *Combustion Science and Technology*. 184: 1397–1411.
- Davis, R.S.; Hood, S.; Bentz, B.J. 2012. Fire-injured ponderosa pine provide a pulsed resource for bark beetles. *Canadian Journal of Forest Research*. 42: 2022–2036.
- DeGomez, T.; Fettig, C.J.; McMillin, J.D.; Anhold, J.A.; Hayes, C. 2015. Managing slash to minimize colonization of residual leave trees by *Ips* and other bark beetle species following thinning in southwestern ponderosa pine (revised 10/2014). AZ1449. Tucson, AZ: University of Arizona, College of Agriculture and Life Sciences Bulletin. 12 p.
- Fettig, C.J.; McKelvey, S.R. 2014. Resiliency of an interior ponderosa pine forest to bark beetle infestations following fuel-reduction and forest-restoration treatments. *Forests*. 5: 153–176.
- Fettig, C.J.; Hilszczański, J. 2015. Management strategies for bark beetles in conifer forests. In: Vega, F.E.; Hofstetter, R.W. eds. *Bark beetles: biology and ecology of native and invasive species*. London: Springer: 555–584.
- Fettig, C.J.; McMillin, J.D.; Anhold, J.A. [and others]. 2006. The effects of mechanical fuel reduction treatments on the activity of bark beetles (Coleoptera: Scolytidae) infesting ponderosa pine. *Forest Ecology and Management*. 230: 55–68.
- Fettig, C.J.; Klepzig, K.D.; Billings, R.F. [and others]. 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. *Forest Ecology and Management*. 238: 24–53.
- Fettig, C.J.; McKelvey, S.R.; Cluck, D.L. [and others]. 2010. Effects of prescribed fire and season of burn on direct and indirect levels of tree mortality in ponderosa and Jeffrey pine forests in California, USA. *Forest Ecology and Management*. 260: 207–218.
- Fettig, C.J.; Mortenson, L.A.; Bulaon, B.M.; Foulk, P.B. 2019. Tree mortality following drought in the central and southern Sierra Nevada, California, U.S. *Forest Ecology and Management*. 432: 164–178.
- Finney, M.A.; McAllister, S.S. 2011. A review of fire interactions and mass fires. *Journal of Combustion*. 2011: Article 548328. DOI: 10.1155/2011/548328.
- Flannigan, M.D.; Amiro, B.D.; Logan, K.A. [and others]. 2006. Forest fires and climate change in the 21st century. *Mitigation and Adaptation Strategies for Global Change*. 11: 847–859.
- Fowler, J.F.; Sieg, C.H.; Wadleigh, L.L. 2010. Effectiveness of litter removal to prevent cambial kill-caused mortality in northern Arizona ponderosa pine. *Forest Science*. 56: 166–171.
- Giunta, A. 2016. Douglas-fir beetle mediated changes to fuel complexes, foliar moisture content, and terpenes in interior Douglas-fir forests of the central Rocky Mountains. Master's Thesis. Logan, UT: Utah State University. 161 p.
- Giunta, A.D.; Runyon, J.B.; Jenkins, M.J.; Teich, M. 2016. Volatile and within-needle terpene changes to Douglas-fir trees associated with Douglas-fir beetle (Coleoptera: Curculionidae) attack. *Environmental Entomology*. 45: 920–929.
- Hart, S.J.; Schoennagel, T.; Veblen, T.T.; Chapman, T.B. 2015. Area burned in the Western United States is unaffected by recent mountain pine beetle outbreaks. *Proceedings of the National Academy of Sciences*. 112: 4375–4380.
- Harvey, B.J.; Donato, D.C.; Turner, M.G. 2014. Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the U.S. Northern Rockies. *Proceedings of the National Academy of Sciences*. 111: 15120–15125.
- Harvey, R.D. 1986. Deterioration of mountain pine beetle-killed lodgepole pine in northeast Oregon. Pap. R6–86–13. Portland, OR: USDA Forest Service. 10 p.
- Hicke, J.A.; Johnson, M.C.; Hayes, J.L.; Preisler, H.K. 2012. Effects of bark beetle-caused tree mortality on wildfire. *Forest Ecology and Management*. 271: 81–90.
- Hicke, J.A.; Meddens, A.J.H.; Kolden, C.A. 2016. Recent tree mortality in the Western United States from bark beetles and forest fires. *Forest Science*. 62: 141–153.
- Hoffman, C.M.; Linn, R.; Parsons, R. [and others]. 2015. Modeling spatial and temporal dynamics of wind flow and potential fire behavior following a mountain pine beetle outbreak in a lodgepole pine forest. *Agricultural and Forest Meteorology*. 204: 79–93.
- Hood, S.M. 2010. Mitigating old tree mortality in long-unburned, fire-dependent forests: a synthesis. Gen. Tech. Rep. RMRS–GTR–238. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station. 71 p.
- Hood, S.M.; Bentz, B. 2007. Predicting post-fire Douglas-fir beetle attacks and tree mortality in the Northern Rocky Mountains. *Canadian Journal of Forest Research*. 37: 1058–1069.
- Hood, S.; Sala, A.; Heyerdahl, E.K.; Boutin, M. 2015. Low-severity fire increases tree defense against bark beetle attacks. *Ecology*. 96: 1846–1855.
- Hood, S.; Baker, S.; Sala, A. 2016. Fortifying the forest: thinning and burning increase resistance to a bark beetle outbreak and promote forest resilience. *Ecological Applications*. 26: 1984–2000.
- Hood, S.; Varner, M.; van Mantgem, P.; Cansler, C.A. 2018a. Fire and tree death: understanding and improving modeling of fire-induced tree mortality. *Environmental Research Letters*. 13: 113004.
- Hood, S.; Keane, R.E.; Smith, H.Y. [and others]. 2018b. Conventional fire behavior modeling systems are inadequate for predicting fire behavior in bark beetle-impacted forests. In: Potter, K.; Conkling, B., eds. *Forest health monitoring: national status, trends, and analysis 2017*. Gen. Tech. Rep. SRS–GTR–233. Asheville, NC: USDA Forest Service, Southern Research Station: 167–176.
- Jenkins, M.J.; Hebertson, E.; Page, W.; Jorgensen, W.P. 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. *Forest Ecology and Management*. 254: 16–34.
- Jenkins, M.J.; Fettig, C.J.; Hebertson, E.G. 2009. Bark beetles, fuels and fire: a synthesis of our present understanding and implications for management. In: Rideout-Hanzak, S.; Oswald, B.P.; Beierle, M., comps. *4th Annual International Congress on Fire Ecology and Management: Fire as a Global*

- Process. Leavenworth, WA: The Association for Fire Ecology.
- Jenkins, M.J.; Page, W.G.; Hebertson, E.G.; Alexander, M.E. 2012. Fuels and fire behavior dynamics in bark beetle-attacked forests in Western North America and implications for fire management. *Forest Ecology and Management*. 275: 23–34.
- Jenkins, M.J.; Runyon, J.B.; Fettig, C.J. [and others]. 2014. Interactions among the mountain pine beetle, fires, and fuels. *Forest Science*. 60: 489–501.
- Jolly, W.M.; Parsons, R.A.; Hadlow, A.M. [and others]. 2012a. Relationships between moisture, chemistry, and ignition of *Pinus contorta* needles during the early stages of mountain pine beetle attack. *Forest Ecology and Management*. 269: 52–59.
- Jolly, W.M.; Parsons, R.; Varner, J.M. [and others]. 2012b. Comment: Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? *Ecology*. 93: 941–946.
- Kane, J.M.; Varner, J.M.; Metz, M.R.; van Mantgem, P.J. 2017. Characterizing interactions between fire and other disturbances and their impacts on tree mortality in western U.S. forests. *Forest Ecology and Management*. 405: 188–199.
- Kocher, S.D.; Toman, E.; Trainor, S.F. [and others]. 2012. How can we span the boundaries between wildland fire science and management in the United States? *Journal of Forestry*. 110: 421–428.
- Kolb, T.E.; Fettig, C.J.; Ayres, M.P. [and others]. 2016. Observed and anticipated impacts of drought on forest insects and diseases in the United States. *Forest Ecology and Management*. 380: 321–334.
- Klutsch, J.G.; Negron, J.F.; Costello, S.L. [and others]. 2009. Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in Colorado. *Forest Ecology and Management*. 258: 641–649.
- Lerch, A.P.; Pfammatter, J.A.; Bentz, B.J.; Raffa, K.F. 2016. Mountain pine beetle dynamics and reproductive success in post-fire lodgepole and ponderosa pine forests in northeastern Utah. *Plos One* 11: e0164738.
- McIver, J.; Stephens, S.; Agee, J. [and others]. 2013. Ecological effects of alternative fuel reduction treatments: highlights of the national fire and fire surrogate study (FFS). *International Journal of Wildland Fire*. 22: 63–82.
- Meigs, G.W.; Campbell, J.L.; Zald, H.S.J. [and others]. 2015. Does wildfire likelihood increase following insect outbreaks in conifer forests? *Ecosphere*. 6: art118.
- Meigs, G.W.; Zald, H.S.J.; Campbell, J.L. [and others]. 2016. Do insect outbreaks reduce the severity of subsequent forest fires? *Environmental Research Letters*. 11: 045008.
- Moriarty, K.; Cheng, A.S.; Hoffman, C.M. [and others]. 2019. Firefighter observations of “surprising” fire behavior in mountain pine beetle-attacked lodgepole pine forests. *Fire*. 2: 34. DOI: 10.3390/fire2020034.
- Morris, J.L.; Cottrell, S.; Fettig, C.J. [and others]. 2018. Bark beetles as agents of change in social-ecological systems. *Frontiers in Ecology and the Environment*. 16(S1): S34–S43.
- Page, W.G.; Jenkins, M.J.; Runyon, J.B. 2012. Mountain pine beetle attack alters the chemistry and flammability of lodgepole pine foliage. *Canadian Journal of Forest Research*. 42: 1631–1647.
- Page, W.G.; Alexander, M.E.; Jenkins, M.J. 2013. Wildfire’s resistance to control in mountain pine beetle-attacked lodgepole pine forests. *The Forestry Chronicle*. 89: 783–794.
- Page, W.G.; Jenkins, M.J.; Runyon, J.B. 2014. Spruce beetle-induced changes to Engelmann spruce foliage flammability. *Forest Science*. 60: 691–702.
- Powell, E.N.; Townsend, P.A.; Raffa, K.F. 2012. Wildfire provides refuge from local extinction but is an unlikely driver of outbreaks by mountain pine beetle. *Ecological Monographs*. 82: 69–84.
- Prichard, S.J.; Kennedy, M.C. 2014. Fuel treatments and landform modify landscape patterns of burn severity in an extreme fire event. *Ecological Applications*. 24: 571–590.
- Ritchie, M.W.; Skinner, C.N.; Hamilton, T.A. 2007. Probability of tree survival after wildfire in an interior pine forest of northern California: effects of thinning and prescribed fire. *Forest Ecology and Management*. 247: 200–208.
- Schoennagel, T.; Veblen T.T.; Negron J.F.; Smith, J.M. 2012. Effects of mountain pine beetle on fuels and expected fire behavior in lodgepole pine forests, Colorado, USA. *Plos One*. 7(1): e30002.
- Schwilk, D.W.; Knapp, E.E.; Ferrenberg, S.M. [and others]. 2006. Tree mortality from fire and bark beetles following early and late season prescribed fires in a Sierra Nevada mixed-conifer forest. *Forest Ecology and Management*. 232: 36–45.
- Seybold, S.J.; Huber, D.P.W.; Lee, J.C.; Graves, A.D.; Bohlmann, J. 2006. Pine monoterpenes and pine bark beetles: a marriage of convenience for defense and chemical communication. *Phytochemistry Reviews*. 5: 143–178.
- Sieg, C.H.; Linn, R.R.; Pimont, F. [and others]. 2017. Fires following bark beetles: factors controlling severity and disturbance interactions in ponderosa pine. *Fire Ecology*. 13: 1–23.
- Simard, M.; Romme, W.H.; Griffin, J.M.; Turner, M.G. 2011. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? *Ecological Monographs*. 81: 3–24.
- Simard, M.; Romme, W.H.; Griffin, J.M.; Turner, M.G. 2012. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Reply. *Ecology*. 93: 946–950.
- Six, D.L.; Vander Meer, M.; DeLuca, T.H.; Kolb, P. 2002. Pine engraver (*Ips pini*) colonization of logging residues created using alternative slash management systems in western Montana. *Western Journal of Applied Forestry*. 17: 96–100.
- Stalling, C.; Keane, R.E.; Retzlaff, M. 2017. Surface fuel changes after severe disturbances in northern Rocky Mountain ecosystems. *Forest Ecology and Management*. 400: 38–47.
- Stephens, S.L.; Moghaddas, J.J.; Edminister, C. [and others]. 2009. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western U.S. forests. *Ecological Applications*. 19: 305–320.
- Stephens, S.L.; McIver, J.D.; Boerner, R.E.J. [and others]. 2012. The effects of forest fuel-reduction treatments in the United States. *Bioscience*. 62: 549–560.
- Stephens, S.L.; Collins, B.M.; Fettig, C.J. [and others]. 2018. Drought, tree mortality, and wildfire in forests adapted to frequent fire. *Bioscience*. 68: 77–88.
- Vose, J.M.; Peterson, D.L.; Domke, G.M. [and others]. 2018. Forests. In: Reidmiller, D.R.; Avery, C.W.; Easterling, D.R. [and others], eds. *Impacts, risks, and adaptation in the United States: fourth national climate assessment, volume II*. Washington, DC: U.S. Global Change Research Program: 223–258.