

fire & fuels management

Interactions Among the Mountain Pine Beetle, Fires, and Fuels

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Bark beetle outbreaks and wildfires are principal drivers of change in western North American forests, and both have increased in severity and extent in recent years. These two agents of disturbance interact in complex ways to shape forest structure and composition. For example, mountain pine beetle, *Dendroctonus ponderosae* Hopkins, epidemics alter forest fuels with consequences for the frequency and intensity of wildfires and, conversely, fire injury to trees can promote bark beetle attack and increase beetle populations. Given the great influence these processes have on forest ecosystems, a better understanding of how bark beetles and fires interact is needed to better manage forests and to predict and manage wildfires. Here we review current knowledge on how fire and bark beetles interact, focusing on the mountain pine beetle. We highlight research on how fuel reduction treatments and wildfires affect bark beetles and how bark beetles can affect wildfires by modifying the moisture content, chemistry, and structure of fuels. Last, we discuss the implications these findings have for fire management and firefighter safety.

Keywords: bark beetles, *Dendroctonus*, disturbance, fire behavior, flammability

Wildfires and outbreaks of native bark beetles (Coleoptera: Curculionidae, Scolytinae), such as the mountain pine beetle (MPB), *Dendroctonus ponderosae* Hopkins, are recognized as two primary disturbances in conifer forests of western North America. Wildfires have sculpted these 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 over time (Kulakowski et al. 2012). In recent decades, anthropogenic-induced changes in climate (Levinson and Fettig 2013) and very effective fire suppression (Agee and Skinner 2005), among other factors (Sibold et al. 2006, Baker 2009), have resulted in substantial changes in forest conditions over millions of hectares. Both the extent and severity of wildfires (Stephens and Ruth 2005) and bark beetle outbreaks (Meddens et al. 2012) have increased. Furthermore, projected increases in mean annual temperatures range from ~1 to 3.5° C by the 2050s in western North America, and although projected changes in precipitation patterns are more complex to model, more frequent and severe droughts are expected (Fettig et al. 2013). These conditions are expected to further increase the frequency and severity of wildfires (Westerling et al. 2006) and bark beetle outbreaks (Bentz et al. 2010) in susceptible forests. In this

article, we consider two common interactions between bark beetles and wildfire: the effects of fuel reduction treatments and mixed-severity wildfire on MPBs and the effects of MPB outbreaks on fuels and fire behavior described by semiempirical prediction models used in the United States. We also describe the current state of our knowledge and identify gaps for making informed management decisions.

Bark Beetle Dynamics

Millions of hectares of conifer forests in western North America have been affected by epidemic levels of bark beetles in the genus *Dendroctonus* since the 1990s, resulting in extensive tree mortality (Man 2010). For example, forests of inland Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, several pine species, and Engelmann spruce, *Picea engelmannii* Parry ex Engelm, have been affected from the southern Rocky Mountains through northern British Columbia, Canada (Meddens et al. 2012). In particular, recent outbreaks of MPBs have been severe, long lasting, and well documented (Bentz et al. 2009). This species ranges throughout British Columbia and portions of Alberta, Canada, and throughout much of the western United States and colonizes several pine species, most notably, lodgepole pine (*Pinus contorta* Dougl. ex Loud.), ponderosa

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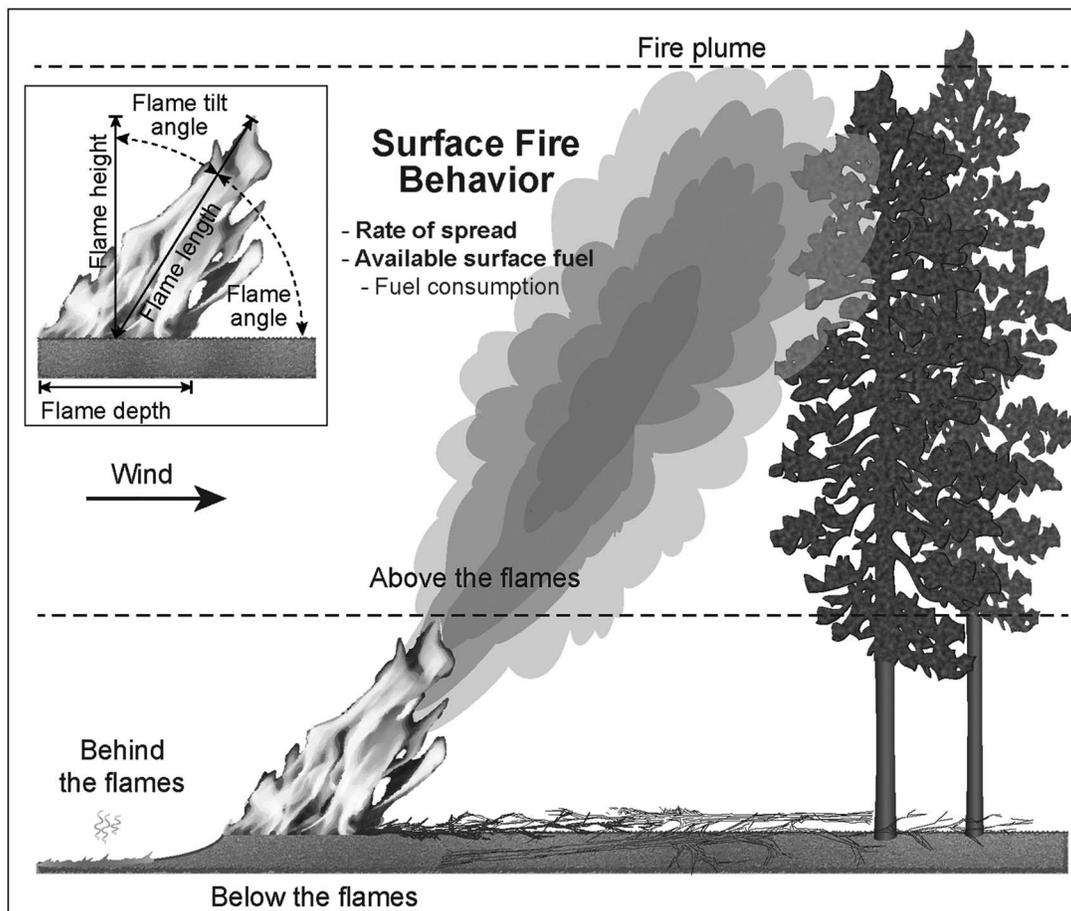


Figure 1. Changes to surface fuel load affected by mountain pine beetle activity influences surface fire behavior and the potential transition to crown fire. (Adapted with permission from Martin E. Alexander.)

pine (*Pinus ponderosa* Dougl. ex Laws.), sugar pine (*Pinus lambertiana* Dougl.), limber pine (*Pinus flexilis* E. James), western white pine (*Pinus monticola* Dougl. ex D. Don), and whitebark pine (*Pinus albicaulis* Engelm.) (Gibson et al. 2009). The extent of tree mortality resulting from *D. ponderosae* outbreaks may be limited to small spatial scales (e.g., small groups of trees) or affect entire landscapes.

Much has been written about the causes and consequences of bark beetle outbreaks in the western United States. The most susceptible stands are typically overmature and dense and are composed of a high percentage of large-diameter host tree species (Fettig et al. 2007). These stands also occur at latitudes and elevations favorable to bark beetle population development (see Bentz et al. 2014). The large geographic distribution of susceptible stands in many forest types has been attributed to a century of fire suppression, surface fuel reduction by domestic animal grazing, and homogeneous stand structure resulting from extensive stand replacing fire events during the late 1800s and early 1900s (Sibold et al. 2006, Baker 2009).

Bark beetle outbreaks are often initiated when bark beetle-susceptible forests are subjected to a period of short-term stress such as drought (Negrón et al. 2009, Chapman et al. 2012). During such periods, host tree resistance to bark beetle attack is reduced, yet phloem tissues still provide adequate nutrients to support rapid increases in bark beetle populations. Unseasonably warm temperatures also contribute to population growth by accelerating rates of bark beetle development and favoring brood survival (Raffa et al. 2008, Bentz et al., 2014). The effect of environmental factors may

be most acute in tree species growing on moist sites and/or at high elevations such as whitebark pine (Loehman et al. 2011, Bentz et al., 2014). Not surprisingly, it has been suggested that climate change is contributing to the current wave of MPB outbreaks (Bentz et al. 2010, Logan et al. 2010).

Wildland Fire Dynamics

Wildland fire behavior is the manner in which fuels ignite, flames develop, and fires spread (Merrill and Alexander 1987) and is driven by the interaction of fuels, weather, and topography (Figure 1). Topographic features important to fire behavior include aspect, elevation, slope, and the topographic configuration. Collectively, these affect the intensity, direction, and spread of wildfires (Rothermel 1983). Although topographic features are fixed in geological time, they interact with weather variables over very short or long distances and time scales (Schroeder and Buck 1970). Fire weather variables such as air temperature, relative humidity, and especially wind direction and velocity have dramatic effects on fire behavior over both diurnal and seasonal cycles (Cheney et al. 1993, Fernandes 2001). Long-term changes in fire weather such as seasonal drying interact with short-term fire weather to modify fuel moisture. Dead fuel moisture content mediates the influence of topographic position, time of year, and real-time fire weather on observed fire behavior and is determined by duration and time since precipitation, temperature, and relative humidity (Rothermel et al. 1986, Holden and Jolly 2011). Live fuel moisture is a function of plant

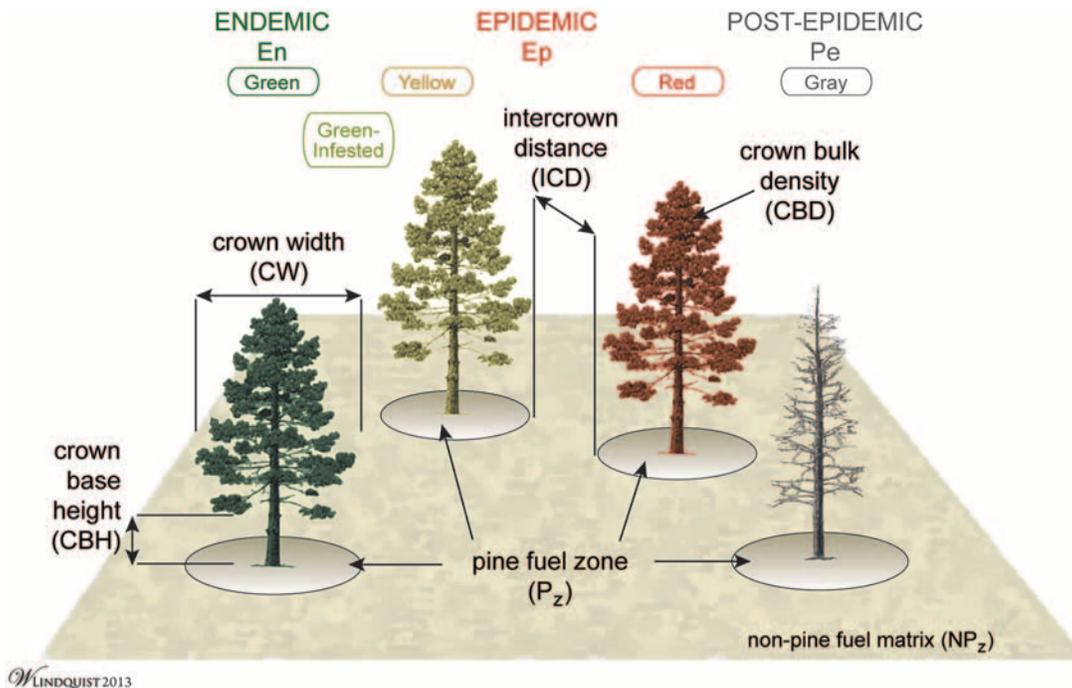


Figure 2. This graphic illustrates crown and canopy parameters and the changes to lodgepole pine needle condition occurring over the course of the bark beetle rotation (Jenkins et al. 2008).

species and seasonality and decreases as plants senesce and die (Blackmarr and Flanner 1968, Philpot and Mutch 1971).

Forest fuels are composed of plant material from trees including bark flakes, cones, needles and leaves, twigs, branches, stems and boles, and downed logs as well as understory vegetation such as grasses, mosses, forbs, and shrubs (Sandberg et al. 2001). Forest fuels are typically classified into four components: ground fuels, surface fuels, ladder or bridge fuels, and aerial or crown fuels. Ground fuels include material that has begun to degrade (F-layer) and humus consisting of largely unidentifiable organic matter (H-layer). Surface fuels include newly cast material (L-layer), down and dead woody fuels, herbaceous vegetation, and low shrubs (Pyne et al. 1996). This component may constitute a large fraction of the total biomass available for fire consumption. Ladder or bridge fuels composed of immature or suppressed trees and larger shrubs are sometimes present and may occupy the gap between surface and aerial fuels, providing a means by which fires can extend from the forest floor (surface fires) to the crown, resulting in crown fires (Agee and Skinner 2005). Aerial fuels are contained in the crowns of standing trees and are separated from surface fuels by a distinct vertical gap. The entire arrangement of ground, surface, ladder, and aerial fuels constitute the fuel complex. Characteristics important for classifying the fuel complex include the quantity, particle size, compactness, depth, chemistry, and distribution horizontally and vertically of each fuel stratum (Albini 1976, Keane 2012). Lodgepole pine forests can display highly variable fuel conditions, being especially dependent on successional status and disturbance history (Pfister and Daubenmire 1975) even in the absence of significant levels of tree mortality. The amount and arrangement of surface fuels can vary widely (Brown and See 1981), but several researchers have noted a lack of fine surface fuels and a sparse understory in mature stands of lodgepole pine (Habeck 1976, Gara et al. 1985).

Fire ignition and spread in lodgepole pine forests are primarily influenced by surface fuels (Figure 1). The surface fire spread rate

will increase as the fuelbed is exposed to wind and as the slope angle increases. Increases in surface fuel load and/or fuel flammability result in increases in fireline intensity commonly observed as longer flame lengths (Byram 1959). The transition to crown fire is possible when the surface fire is sufficiently intense to bridge the gap to aerial fuels and is influenced by canopy base height, the presence of ladder fuels, and foliar moisture content (Van Wagner 1977, Beighley and Bishop 1990), among other factors, most notably wind speed. Once the transition from the surface to crown occurs, the terminology to describe the type of crown fire usually follows the conventions proposed by Van Wagner (1977) with either passive, active, or independent crown fire behavior, depending on the rate of fire spread and the distance among crowns as reflected in the canopy bulk density (CBD) (Figure 2). In lodgepole pine forests, typical fire behavior can be wide-ranging, encompassing both low-intensity surface fires and high-intensity crown fires (Arno 1980, Lotan et al. 1985, Barrett et al. 1997). In more xeric, lower-elevation forests more frequent and less intense surface fires have been recorded (Arno 1980). In mesic, high-elevation forests long-interval, high-intensity crown fires are more common (Romme 1982).

Effects of Fuel Reduction Treatments on MPB Activity

Currently, >10 million hectares of forests are classified as having moderate to high fire hazards in the western United States (Stephens and Ruth 2005), and fuel reduction treatments have been widely promoted to reduce the severity of future wildfires. When applied under prescription, both prescribed fire and its mechanical surrogates (e.g., thinning) are generally effective in meeting short-term fuel reduction objectives as treated stands are more resilient to wildfire (Stephens et al. 2012, McIver et al. 2013). For example, the effectiveness of prescribed fire for treating surface and ladder fuels to reduce the incidence of passive crown fire (i.e., torching of small groups of trees) is well supported by modeling of predicted fire

behaviors (Stephens et al. 2009) and by empirical research (Ritchie et al. 2007). The potential for active crown fire is reduced most effectively by combinations of prescribed fire and mechanical fuel treatments (i.e., removal of smaller-diameter trees) (Stephens et al. 2012).

Fuel reduction treatments have functionally different effects on the fuel matrix and thus on the structure and composition of residual forests as well as their resiliency to bark beetle infestations (Fettig et al. 2007). For example, fuel reduction treatments may affect the health and vigor of residual trees; the size, distribution, and abundance of preferred hosts; and the physical environment within forests. Tree volatiles released during harvest operations and/or the application of prescribed fire are known to influence the physiology and behavior of many bark beetles (Seybold et al. 2006), to increase bark beetle colonization rates on trees (Fettig et al. 2006, Davis et al. 2012), and to increase levels of tree mortality attributed to bark beetles in ponderosa pine forests (DeGomez et al. 2008). Furthermore, associated reductions in tree density cause changes in microclimate that affect beetle fecundity and fitness, phenology, and voltinism as well as that of predators, parasites, and competitors (Bartos and Amman 1989) that may cause turbulences that disrupt pheromone plumes used for recruiting conspecifics during initial phases of host tree colonization (Thistle et al. 2004), thus negatively affecting host finding success. The propensity for many species of bark beetles to attack fire-injured trees has stimulated much research on the effects of fuel reduction treatments on the amount and distribution of bark beetle-caused tree mortality in the western United States.

Prescribed Fire

After prescribed fire, tree mortality may be immediate because of consumption of living tissue or heating of critical plant tissues or can be delayed, occurring over the course of a few years, as a result of fire injuries to the crown, bole, or roots (Hood et al. 2007b). Levels of delayed tree mortality attributed to bark beetles depend on numerous factors including tree species, tree size, phenology, degree of fire-caused injuries, initial and postfire levels of tree vigor, the post-fire environment, and frequency and severity of other predisposing, inciting, and contributing factors. A common management concern is that bark beetles may attack and kill trees that were injured by prescribed fire, but that otherwise would have survived. These trees may then serve as a source of beetles and attractive semiochemicals (i.e., host volatiles and aggregation pheromones produced by many bark beetle species, including MPB, during host colonization; see Progar et al. 2014) that attract other beetles into the vicinity, resulting in additional levels of tree mortality over time.

In comparison with that for other species of bark beetles, limited work on the effects of prescribed fire on MPB activity has been done. This is presumably because most recent research on MPB has concentrated on its impacts in lodgepole pine forests where prescribed fire is less often applied than, for example, in ponderosa pine forests. Fettig et al. (2010b) reported significant increases in the amount of tree mortality attributed to MPBs in ponderosa pine forests in California after late season burns but not early season burns. Mortality was concentrated in smaller-diameter ponderosa pines (Figure 3). Schwilk et al. (2006) found that the probability of bark beetle attack (several species) on pines did not differ between early and late season prescribed fires, whereas the probability of attack on red fir (*Abies magnifica* A. Murr.) and white fir (*Abies concolor* Gord. and Glend.) was greater after early season burns. Fettig et al. (2008) reported that the application of prescribed fire resulted in significant increases in

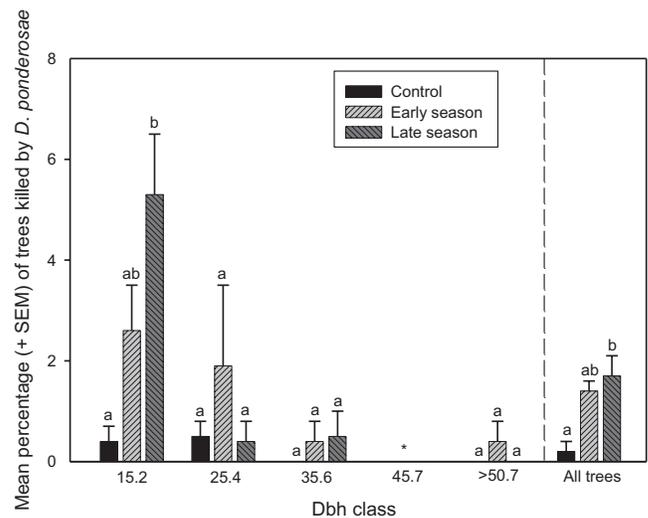


Figure 3. Mean percentage of trees killed by MPBs by diameter class (midpoint of 10-cm diameter classes shown except for largest diameter class) 3 years after the application of prescribed fire, Tahoe National Forest, California. Means (+SEM) followed by the same letter within groups are not significantly different (Tukey's honestly significant difference, $P > 0.05$). The asterisk denotes that no trees were attacked in that size class regardless of treatment. (Adapted from Fettig et al. (2010a).)

MPB-caused tree mortality in all but the two largest dbh classes (>49.6 cm dbh) in ponderosa pine in northeastern California. Similar results have been reported from mixed-conifer forests in the Southern Cascades (Fettig et al. 2010a). Although in some studies the MPB response to mixed-severity wildfire was minimal (Rasmussen et al. 1996, McHugh et al. 2003), recent studies attribute significant tree mortality to MPB after wildfire (see Effects of Mixed-Severity Wildfire on MPB).

Most of the delayed mortality attributed to MPBs occurs during the first few years after prescribed fire within treated areas (Fettig et al. 2010a), but this may differ for adjacent untreated areas. For example, Fettig and McKelvey (2010) reported large increases in the amount of bark beetle-caused tree mortality (several species) on unburned split plots compared with that on adjacent burned split plots 3–5 years after the application of prescribed fire in northeastern California. This is probably due to unburned areas not benefiting from the positive effects of prescribed fire (e.g., increased growing space) that affect tree vigor and thus susceptibility to bark beetle attack (Fettig et al. 2007). Interestingly, Fettig et al. (2006) observed a similar effect for mechanical fuel treatments involving chipping of sub- and unmerchantable trees whereby chipping increased plot risk to bark beetle attack (several species) in the short term by the production of large amounts of attractive monoterpenes. In the longer term, however, it decreased hazard by increasing the amount of growing space allocated to each residual tree by reducing stand density through thinning. Surveys along the perimeter of chipped plots revealed large numbers of recently attacked trees (including from MPBs) in untreated areas that did not benefit from the positive effects of thinning but had a similar level of risk associated with high levels of monoterpenes beneath the forest canopy (Fettig et al. 2006).

Mechanical Fuel Treatments

Although thinning has long been advocated as a preventive measure to reduce the amount of bark beetle-caused tree mortality that

occurs, prescriptions for fuel reduction (i.e., reduction of surface fuels, increasing the height to live crown, decreasing crown density, and retaining large trees of fire-resistant species) (Agee and Skinner 2005) differ from those implemented specifically for reducing stand susceptibility to bark beetle infestation. In the latter case, crown or selection thinning (i.e., removal of larger trees in the dominant and codominant crown classes) is typically required to achieve target threshold stand densities, residual tree spacing, and significant reductions in the abundance of preferred hosts necessary to reduce susceptibility to MPB (Fettig et al. 2007, Gillette et al., 2014). Despite these factors, thinning to reduce fuels may have the added benefit of reducing stand susceptibility to MPB (see Fettig et al., 2014) because MPB infestations have been associated with high stand densities in lodgepole pine (Mitchell et al. 1983), ponderosa pine (Fiddler et al. 1989, Negrón and Popp 2004), and whitebark pine forests (Perkins and Roberts 2003), presumably because below-ground competition for nutrients and water leads to reductions in host vigor (Fettig et al. 2007), among other factors. For example, Waring and Pitman (1985) observed that lodgepole pine with low vigor were more heavily attacked by MPBs and that some produced no resin on attack, which is the primary defense mechanism of pines against bark beetle colonization. Although carelessly implemented thinning may result in physical damage to residual trees, perhaps increasing the likelihood of tree colonization by bark beetles (Fettig et al. 2007), this has not been observed for MPBs after applications of mechanical fuel reduction treatments.

Effects of Mixed-Severity Wildfire on MPBs

Early in the last century MPBs were observed attacking fire-injured trees after wildfire (Rust 1933), although there were also reports of wildfire with no response by MPBs (Hopkins 1905). MPBs were subsequently observed attacking lightly injured lodgepole pine 2 years after wildfires in Oregon (Geiszler et al. 1984), fire-injured lodgepole pine 2–4 years after the 1988 Yellowstone fires (Rasmussen et al. 1996), and fire-injured ponderosa pine after wildfire in Arizona (McHugh et al. 2003). In all cases, MPB attacks made up a small percentage of total insect attacks and contributed little to postfire tree mortality (<5%). Two hypotheses were proposed to explain why the MPB was not a more prominent player in postfire tree mortality: MPB is ecologically separated from *Ips* species and other *Dendroctonus* in that it does not attack heavily stressed trees with poor phloem resources, and local MPB population levels were too low for response to the fire-injured trees after wildfire. Although the local population size was not recorded in most studies, MPB population levels were indeed reported to be low in the years before the 1988 Yellowstone fire (Amman and Ryan 1991) and the Arizona fire (McHugh et al. 2003). Over the past two decades, MPB population levels have been elevated across its range (Meddens et al. 2012), and MPBs have contributed significantly to ponderosa and lodgepole pine mortality after mixed-severity wildfire (Davis et al. 2012, Powell et al. 2012, Kulakowski and Jarvis 2013, Lerch 2013).

Mixed-severity wildfire provides a landscape mosaic of host trees with a range of crown and bole injuries that can increase susceptibility to MPB attack. In a study conducted in Colorado, fire injury did not influence lodgepole pine growth 1 and 5 years postfire, suggesting that a physiological response not associated with reduced tree vigor was responsible for the observed increase in the susceptibility of fire-injured trees to MPBs (Kulakowski and Jarvis 2013). Although resin flow (a measure of constitutive defense) is often higher in fire-injured than in uninjured trees (Perrakis et al. 2011,

Davis et al. 2012), fire injury reduces the manufacture of induced volatile monoterpenes important in tree defense against bark beetle attack (Powell and Raffa 2011). Fire injury also causes changes in the proportion of some individual compounds that could favor MPB attack success in lodgepole pine with higher injury levels (Powell and Raffa 2011). Pines attacked by MPBs had more bole and crown damage from wildfire than unattacked or strip-attacked trees (Davis et al. 2012, Lerch 2013), and the type of tree attacked was influenced by the local population size (Elkin and Reid 2004). At low population levels, lodgepole pine with low and moderate levels of fire-injury were attacked, and uninjured and severely burned trees were only attacked when population sizes were high (Powell et al. 2012). The level of fire injury in ponderosa pine that was suitable for attack by MPB differed from that in lodgepole pine (Davis et al. 2012, Powell et al. 2012, Lerch 2013), most likely due to the evolved characteristics of ponderosa pine that make it more resistant to fire injury. There was also an upper limit to the level of fire injury suitable for attack and reproduction in ponderosa pine (Davis et al. 2012). Large trees, which have more food resources than small trees, are most often attacked by MPBs (Cole and Amman 1969), and this trend was also seen after wildfire (McHugh et al. 2003, Kulakowski and Jarvis 2013).

Fire injury to the bole and crown increases the susceptibility of pines to attack by MPBs, and when populations are locally active, significant post-wildfire mortality can occur. The MPB response to fire injury, however, pulses and recedes within a few years postfire (Rust 1933, Davis et al. 2012, Lerch 2013). Fire-injured trees can initially provide an easily overcome reservoir for MPBs, although the progression to outbreak population levels is limited by the short temporal availability of suitable host trees and competition for the postfire phloem resource by other bark beetle and wood-boring species (Davis et al. 2012, Powell et al. 2012, Lerch 2013). The role of fire injury in sustaining already outbreak-level populations is unclear (Kulakowski and Jarvis 2013).

Bark Beetle Rotation as Related to Fuels and Fire Behavior

Of all bark beetle-host systems, the effects of bark beetle-caused tree mortality on fuels and fire behavior have been studied most extensively in MPB-attacked lodgepole pine forests of the Intermountain West (Jenkins et al. 2008, 2012, Hicke et al. 2012). Early work based on qualitative observations suggested that fuel accumulations caused by MPB activity led to increases in fire risk (i.e., probability of ignition) and hazard (i.e., ease of ignition, spread rate, and resistance to control) (Brown 1975, Gara et al. 1985, Amman 1991, Schmid and Amman 1992). However, little quantitative evidence was available to support the observations and hypotheses of fuel buildup, high-intensity fire, and cone serotiny often described (Brown 1975, Lotan 1976, Gara et al. 1985). Stand-level studies conducted more recently have detailed a much more complex relationship between MPB activity, fuels, and fire behavior in lodgepole pine forests (Page and Jenkins 2007a, Klutsch et al. 2009, 2011, Simard et al. 2011).

Jenkins et al. (2008) used the term “bark beetle rotation” to describe the period from the initiation of a bark beetle outbreak in susceptible stands to the death of the majority of large, old trees and the associated collapse of the bark beetle population to endemic levels. Jenkins et al. (2008, 2012) and Hicke et al. (2012) reviewed literature from studies conducted to determine relationships among bark beetle outbreaks, fuels, and fire behavior. The authors of these

articles used terminology familiar to forest health and other resource specialists to describe the changes in fuels as they relate to bark beetle epidemiology. The terms “endemic,” “epidemic,” and “postepidemic” are now widely accepted for describing phases in the bark beetle rotation as they relate to changes in the fuel profile (Klutsch et al. 2009).

Changes to Fuels During the Bark Beetle Rotation

Characteristic changes to the fuel profile within affected stands over the course of a bark beetle rotation have now been documented in a number of bark beetle/host systems including pinyon-juniper (*Pinus-Juniperus* spp.), woodlands (Clifford et al. 2008), ponderosa pine (Hoffman et al. 2012), lodgepole pine (Page and Jenkins 2007a, Klutsch et al. 2009, Simard et al. 2011, Schoennagel et al. 2012), Engelmann spruce (DeRose and Long 2009, Jorgensen and Jenkins 2011), and whitebark pine (Jenkins 2011). Bark beetle rotations follow similar trends across systems but differ due to variability in stand conditions (age, structure, and species composition), and site characteristics (Jenkins et al. 2008). During the endemic phase host tree mortality is typically limited to trees weakened by other insects, disease, or injury or small groups of trees concentrated around focal centers of bark beetle activity (Cunningham et al. 2005, Hood and Bentz 2007, Hebertson and Jenkins 2008) and generally has a limited affect on fuels beyond providing a low density of snags and down woody material. As the epidemic is initiated and levels of tree mortality increase, the resulting changes in fuels begin at the individual tree level (e.g., foliar moisture content and subsequent needle fall) and accumulate over time and space, eventually altering fuels at the stand and landscape scales. The majority of research to date has focused on changes at the stand level, and thus our discussion will be primarily directed to that scale. However, recent studies have also documented changes at the individual tree level, which will also be discussed.

Changes to Crown and Canopy Fuels

A common method of estimating time since tree death for lodgepole pine uses external indicators of needle color and retention simply referred to as the “green stage” (within 1 year of attack), “red stage” (1–3 years since death) and “gray stage” (>3 years since death) (Klutsch et al. 2009). Jenkins (2011) correlated changes in needle color with bark beetle population dynamics in whitebark pine to include green (G), green-infested (GI), yellow (Y), red (R), and gray (Gr) stages. Lodgepole pine follows a similar sequence of needle color changes with a shortened R stage that affects needle litter accumulations and the transition to Gr (Figure 2).

Early during an epidemic, at the individual tree scale important changes in needle retention, moisture content, and chemistry occur after bark beetle attack and subsequent tree death. Studies by Jolly et al. (2012a) in Colorado and Montana and by Page et al. (2012) in Idaho support the changes in needle moisture content, chemistry, and flammability in lodgepole pine hypothesized by Jenkins et al. (2008). Both Jolly et al. (2012a) and Page et al. (2012) reported substantial decreases in moisture content, the proportion of starches and sugars, and crude fats and increases in the proportions of lignin, cellulose, and hemicellulose in foliage of trees attacked by MPBs in the previous year (Y) or more than two years previously (R). Page et al. (2012) also found that several volatile monoterpenes were emitted at higher rates by Y foliage on MPB-attacked lodgepole pines, which were related to shortened time to ignition (*E*- β -ocimene and

tricyclene) and lowered temperature at ignition (*E*- β -ocimene). Moreover, seven of nine monoterpenes that were positively correlated with the maximum rate of mass loss (an indication of burning rate) were emitted at higher levels in Y versus G foliage (Page et al. 2012). Conifers produce large amounts of terpenoids, both within resins and emitted as volatiles, which play important roles in defense against herbivores and pathogens (Keeling and Bohlmann 2006, Zulaik and Bohlmann 2010, Ott et al. 2011). Amounts of terpenoids produced by conifers can increase dramatically in response to real or simulated insect feeding (Martin et al. 2002, McKay et al. 2003, Miller et al. 2005), including MPB attack (Boone et al. 2011, Ott et al. 2011). Terpenoids are highly flammable (Ormeño et al. 2009) and terpenoid “clouds” released from plants have been implicated in eruptive fire behavior (Barboni et al. 2011, Courty et al. 2012).

Hansen (2014) described the changes to stand structure and forest development after MPB outbreaks. From a fuels and fire behavior perspective, these changes are reflected in altered horizontal and vertical aerial fuel continuity. As canopy foliage dies and needles are shed, there is a reduction in horizontal canopy fuel continuity as the available canopy fuel load and resulting CBD decrease. The spatial arrangement and magnitude of the decrease are dependent on several site-specific factors such as the pre-epidemic stand condition (e.g., species composition and diameter distribution) and the rate and total amount of tree mortality. Where there are unevenly distributed patches of tree mortality across the landscape, corresponding to limits in tree size for MPB attack and host tree preferences (Cole and Amman 1969), the horizontal continuity of canopy fuels will be highly heterogeneous. Over time, as tree regeneration takes hold, vertical fuel continuity will increase as a continuous profile of crown fuels extends from the surface to the remaining canopy. This increase in the abundance of conifer tree regeneration has been observed in a number of studies (Page and Jenkins 2007a, Jenkins et al. 2008, Collins et al. 2012), although some have noted very poor regeneration after MPB outbreaks (McIntosh and Macdonald 2013). Regeneration will increase vertical fuel continuity at a rate dependent on the amount of regeneration, propagule availability, and seedling, sapling, and tree growth rates.

The opening of the main canopy as a result of needle fall has additional important implications to surface fuels and the physical environment within a stand. It is well known that continuous canopies provide both shade from the sun and sheltering from the wind, thereby altering surface fuel moisture and in-stand wind speed (Byram and Jemison 1943, Van Wagner 1969a, 1969b). Where canopy cover is decreased, increases in wind speed at the ground level are expected (Shaw et al. 1988, Meyer et al. 2001) as well as the total solar input to surface fuels, thereby affecting fuel temperature and moisture content (Byram and Jemison 1943, Countryman 1977, Whitehead et al. 2006). In relation to fire management, the importance of these two characteristics on the fire environment and potential fire behavior have been continually emphasized (Schroeder and Buck 1970, Rothermel 1983). Direct evidence of these changes in MPB-affected lodgepole pine stands is still limited, but Simard et al. (2011) reported that temperatures at the litter-duff interface in 25-year-old attacked stands of lodgepole pine were between 2.5 and 10° C warmer than the air temperature.

Changes in Litter and Fine Fuels

The most dramatic change to forest fuels at the onset of a MPB epidemic is the alteration of needles and their eventual loss from

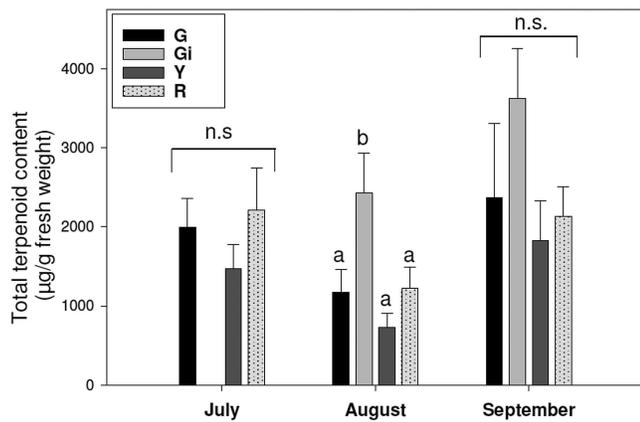


Figure 4. Total terpene content (mean + SE; $n = 6$) of litter underneath lodgepole pine trees of different mountain pine beetle crown condition classes (G, green uninfested; GI, green infested; Y, yellow; R, red) in July, August, and September of 2011. Different letters indicate significant differences among treatments ($P < 0.05$). n.s., no significance. Site information and tree selection are described in Page et al. (2012). Approximately 5 g of litter was collected 1 m from bole on the north, south, east, and west sides of trees and terpenoids were extracted following Ormeño et al. (2009) and analyzed as described for volatiles in Page et al. (2012), except that GC oven temperature was increased 5° C per minute to 200° C and then 25° C per minute to 250° C. Data were analyzed using one-way analysis of variance followed by pairwise multiple comparison (Holm-Sidak method).

dead and dying trees. At the individual tree, stand, and landscape scales, there is a net transfer of needles from the crown to the forest floor. This loss of needles leads to a reduction in CBD from maximum to minimum levels, increasing surface fuel accumulation while decreasing the shelter from wind and sun that tree crowns provide (Schroeder and Buck 1970, Albini and Baughman 1979). The time required for needle loss varies from tree to tree and among tree species ranging from as little as 1 year in Engelmann spruce (Massey and Wygant 1954) to 1–3 years in lodgepole pine (British Columbia Ministry of Forests 1995). The results of several studies have shown significant increases in needle litter load or litter depth during the early stages of an epidemic (Page and Jenkins 2007a, Klutsch et al. 2009, Jorgensen and Jenkins 2011, Simard et al. 2011, Schoennagel et al. 2012). There are also observable changes in other fine fuels (e.g., twigs), but statistical significance has been difficult to demonstrate, presumably because of the large variability associated with these measurements. Potentially rapid decomposition of accumulated litter and small twigs may limit the window in which these small fuels are above pre-epidemic levels (Keane 2008, Simard et al. 2012). Factors such as the decay rate, duration of the epidemic, and the total amount of tree mortality may affect both the amount and duration of impact (Hicke et al. 2012).

Preliminary data from field sampling also indicate that the chemical composition of litter may be affected by MPB outbreaks. In recent work, we found the total terpenoid contents of litter to be greater beneath GI lodgepole pine trees, but this was only significant for the month of August (Figure 4). Why this happens is unknown, but it could result from attacked trees dropping chemically altered foliage or the addition of boring dust, frass, and defensive resins (e.g., pitch tubes) that fall to the forest floor. This increase in the concentration of litter terpenoids, which has been shown to increase flammability in other tree species (Ormeño et al. 2009), corresponds

with peak wildfire activity in the western United States (Westerling et al. 2003).

Changes in Coarse Woody Material

Large quantities of coarse woody fuels can remain in the crown of standing trees (snags) for relatively long periods of time. The contribution to the surface fuel profile is gradual and balanced to some degree by decomposition. Ultimately, all of the woody fuel contained in bark beetle-killed trees is transferred to the forest floor after tree fall. This period varies considerably by physiography, soils, and tree species in the western United States. For example, Mitchell and Preisler (1998) followed the fall rates of >600 lodgepole pines killed by MPBs in central Oregon and reported half-lives (i.e., the period of time it takes for half of the population to fall) of 8 years in thinned stands and 9 years in unthinned stands. These results are in contrast with Harvey (1986), who reported that only 25% of trees fell 11 years after death in northeastern Oregon. In our research, we surveyed 25 0.081-ha plots each in Idaho and Utah and found the fall rate of lodgepole pines killed by MPB within the last 6 years (i.e., during the current epidemic) to be negligible (0 and 1.2% in Utah and Idaho, respectively) (C.J. Fettig, C.L. Jorgensen, and A.S. Munson, USDA Forest Service, unpublished data, January 20, 2013).

As the epidemic progresses, there is a gradual accumulation of medium and coarse woody fuels and increases in fuel bed depth. Page and Jenkins (2007a) found a 2.5- to 7.8-fold increase in coarse woody fuels in MPB-attacked lodgepole pine forests in Utah approximately 20 years after an epidemic. Similarly, Klutsch et al. (2009) and Collins et al. (2012) predicted 4.5- and 5.5-fold increases in large woody fuels, respectively, after MPB epidemics in Colorado. Late in the epidemic and into the postepidemic phase increases in live shrubs and forbs can also be quite pronounced (Jenkins et al. 2008, 2012, Hicke et al. 2012). This is due to increases in the amount of sunlight and moisture reaching the forest floor as needles are shed and CBD declines. Again, site-specific factors including the fall rate, decay rate, and timing of subsequent tree regeneration will affect the amount and length of changes to coarse woody and live surface fuels.

Changes to Fire Behavior During the Bark Beetle Rotation

The primary operational fire behavior prediction systems in the United States use the semiempirical surface fire spread model developed by Rothermel (1972), which relies on the use of fuel models to describe the specific characteristics of a fuelbed needed to satisfy model inputs (Albini 1976, Anderson 1982, Scott and Burgan 2005). To predict the onset of crowning and crown fire rate of spread, the most popular fire behavior modeling systems, Behave-Plus (Andrews et al. 2008) and NEXUS (Scott and Reinhardt 2001), link the output from the Rothermel (1972) model along with canopy fuel characteristics (canopy base height, foliar moisture content, and CBD) to Van Wagner's (1977) crown fire initiation and Rothermel's (1991) crown fire rate of spread models. Crown fire initiation is predicted to occur if the surface fireline intensity exceeds the critical surface fireline intensity needed for initial crown combustion following Van Wagner (1977). If the threshold intensity is met, either passive or active crowning is possible, depending on CBD and the rate of fire spread (Van Wagner 1977). Some fire behavior modeling systems such as NEXUS (Scott and Reinhardt 2001) also use a crown fraction burned function to produce intermediate rates of spread between the passive and active crown fire types.

Several attempts to predict fire behavior in MPB-affected stands have been made using the operational fire behavior models described above. Using BehavePlus, Page and Jenkins (2007b) created custom fuel models to represent lodgepole pine fuels affected by MPBs and determined that no existing fuel model accurately represented predicted surface fire behavior across a range of input variables. Predicted surface fire rates of spread and fireline intensities were higher in the epidemic and postepidemic cases due to the effects of increased fine fuel loading and reduced sheltering on mid-flame wind speed. Klutsch et al. (2011) used the Fire and Fuels Extension to the Forest Vegetation Simulator to model and compare potential fire behavior in plots unaffected by the MPBs, 7 years after outbreak initiation and where 10 and 80% of the affected trees were projected to fall. Uninfested plots were predicted to have more crown fire activity than MPB-attacked plots but less intensity than the attacked plots where only surface fires occurred because of high loadings of dead and down woody fuels. In addition, Simard et al. (2011) and Schoennagel et al. (2012) used NEXUS and BehavePlus, respectively, and custom fuel models to assess both surface and crown fire behavior in affected stands. Simard et al. (2011) concluded that active crown fire spread was less likely in MPB-affected stands both during the epidemic and postepidemic as a result of decreases in available CBD, whereas Schoennagel et al. (2012) concluded that active crown fire spread was higher in current epidemic stands but not qualitatively different under extreme burning conditions than in unaffected stands.

In addition to the application of operationally based models, recent research has attempted to use physics-based models in MPB-affected stands. Physics-based fire behavior prediction models such as the Wildland-Urban Interface Fire Dynamics Simulator (WFDS) (Mell et al. 2007) and FIRETEC (Linn et al. 2002) couple interactions between the fire and atmosphere in a three-dimensional grid by solving the fundamental equations of mass, momentum, and energy (Sullivan 2009). Hoffman et al. (2012) used WFDS to simulate crown fire hazard immediately after an epidemic, when the crowns of affected trees had all of their needles remaining. They found that as tree mortality increased there were increases in the amount of crown fuel consumption and intensity of crown fires. In addition, Hoffman et al. (2014) used WFDS to quantify the effect of recent MPB-caused tree mortality on crown fire behavior at varying surface fireline intensities. The largest effect of MPB-induced tree mortality on crown fire behavior was found using a moderate level of surface fireline intensity.

Challenges of Fire Behavior Prediction

To date the primary method of assessing fire behavior potential in MPB-affected stands has been with simulation studies using custom fuel models based on Rothermel's (1972) surface fire spread model and the associated linkages to crown fire initiation and spread models (Van Wagner 1977, Rothermel 1991). Cruz and Alexander (2010) have shown that the Rothermel (1972) model and the associated linkages display a clear underprediction bias when the onset of crowning and crown fire rate of spread is determined. The major sources of error include incompatible model linkages, the use of surface and crown fire models that have underlying underprediction biases, and the incorporation of unvalidated crown fraction burn functions (Cruz and Alexander 2010). These problems are compounded when the models are applied to MPB-affected stands with substantial amounts of canopy fuel in the R condition. As described previously, during the early stages of an epidemic, canopy fuels are

highly heterogeneous both spatially and in terms of moisture content, chemistry, and the resulting flammability. This heterogeneity violates the fundamental assumptions of homogeneity assumed in the application of fire behavior modeling systems and attempts to apply models that are clearly outside the conditions for which they were originally developed (i.e., live and healthy conifer stands) (Cruz and Alexander 2010, Jenkins et al. 2012). Jenkins et al. (2012) described in detail the fundamental underpinnings of fire behavior prediction based on the pioneering work of Byram (1959) and Van Wagner (1977) and the inherent limitations when it is applied to MPB-affected stands as described by Cruz and Alexander (2010).

The difficulties associated with accurate fire behavior prediction in MPB-affected stands have been exemplified by the controversy associated with Simard et al.'s (2011) methodology and interpretation of fire behavior in stands containing significant amounts of foliage in the R condition (Jolly et al. 2012b, Moran and Cochrane 2012). Despite previous evidence of the limitations of Rothermel's (1972) model and its link to crown fire initiation and spread models in US fire behavior prediction systems, Simard et al. (2011) concluded that active crown fire spread was less likely in MPB-affected stands than in unattacked stands. Jolly et al. (2012b) and Moran and Cochrane (2012) questioned the methodology of Simard et al. (2011) and the validity of the resulting conclusions. Inappropriate accounting of surface and crown fuels, the inappropriate application of operational fire behavior models, and unaccounted the potential for a foliar moisture effect (Van Wagner 1989) were cited as major flaws. Despite Simard et al.'s (2012) response, the fact remains that the models used were inappropriate for MPB-attacked stands, especially where significant amounts of foliage in the R condition are present.

The use of physics-based models has been suggested as a way to account for the inadequacies associated with operational fire behavior models (Mell et al. 2010, Hoffman et al. 2012). However, field validation to date has been limited, especially in conifer forests; thus, model results must be interpreted with caution (Alexander and Cruz 2013). These models are computationally demanding and, as a result, probably will not be used for real-time fire behavior prediction in the near future but do have valuable research applications in understanding the physics of fire spread in wildland fuels. In addition to the applications in MPB-affected stands by Hoffman et al. (2012, 2014), other applications of WFDS include the effectiveness of thinning treatments (Contreras et al. 2012) and the opening of serotinous cones (Michaletz et al. 2012). In addition, Linn et al. (2013) applied FIRETEC to bark beetle-attacked pinyon-juniper woodlands. Although some of the results from these studies have fit conceptually with expectations, until field validation of these models can be performed in conifer forests the results should be viewed with caution.

Implications for Fire and Forest Management

The dramatic changes imposed on the fuel complex over the course of the MPB rotation have important implications for fire management. Firefighter safety is dependent on recognition that unanticipated fire behavior and suppression challenges may be encountered in MPB-altered fuels and will vary with the stage of the infestation and the relative abundance of G, GI, Y, R, and Gr trees. Even forests with fully green canopies may be altered if GI trees are present (Page et al. 2012). Only by observing the presence of pitch tubes could suppression personnel know that the foliage has been

altered and fire behavior may be affected. Alexander and Stam (2003) and Jenkins et al. (2012) described some of the safety concerns firefighters may encounter in spruce beetle-affected forests of Engelmann spruce and MPB-affected forests of lodgepole pine, respectively.

Although recent research shows some disagreement over expected changes in fire behavior during the early portions of an epidemic, observations from recent wildfires suggest that recently attacked forests are capable of increased probabilities of torching and crowning and increased likelihood of spotting. An example is the 2012 Halstead Fire in southwestern Idaho for which fire planners issued safety advisories for dangerous fire behavior in MPB-affected fuels (National Interagency Fire Center 2012). Crews observed a rapid transition from surface to crown fires where mixtures of G and R needles existed in the canopy. Unusual fire behavior was observed including passive, active, and independent crown fire and spotting capable of igniting canopy fuels in the absence of surface fire. Such observations are consistent with predictions of increased fire behavior during the R phase by Jenkins et al. (2008, 2012) and summarized by Hicke et al. (2012). The basis for such fire behavior is the changes in fuel moisture and chemistry as described by Jolly et al. (2012a) and Page et al. (2012).

During the later stages of an epidemic, once snag fall has contributed to significant accumulations of dead and down woody fuels and produced “jack straw” conditions, suppression forces should expect increased difficulties in fireline construction, increased difficulties in establishment of access and egress, and trouble in establishing and using escape routes and safety zones. It is important to emphasize that these conditions are significant and not short-lived and that MPB-affected forests might exhibit some degree of altered fire behavior for up to a decade or more after a MPB outbreak. Creating forest structures that are more resilient to wildfire at the stand and landscape levels may decrease the concerns and costs associated with fire suppression activities and the susceptibility of forests to MPB outbreaks (Fettig et al., 2014).

Models that quantify fire-caused tree injuries most susceptible to bark beetle attacks (Sieg et al. 2006, Thies et al. 2006, Hood and Bentz 2007, Lerch 2013) provide land managers tools for developing prescribed fire plans and postfire management strategies when bark beetle populations are locally active (Hood et al. 2007a). When postfire management options such as salvage logging are considered, the important role of bark beetle-killed trees as a critical habitat for cavity-nesting species should be considered (Saab et al., 2014).

Given the significance and long-term implications of extensive levels of MPB-caused tree mortality on firefighter safety and suppression effectiveness surprisingly little has been done to quantify potential impacts. Practical applied research is urgently needed in these forests to address questions such as rates of deterioration and fall rates of MPB-killed trees, the impact of heavy accumulations of dead and down woody fuels on line construction and holding operations, fireline construction standards, and safety zone adequacy.

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